POLSKIE ARCHIWUM HYDROBIOLOGII (Pol. Arch. Hydrobiol.)	35	3–4	341–359	1988

JOSE LUIS SUAREZ, LUIS REIRIZ, RICARDO ANADON

FEEDING RELATIONSHIPS BETWEEN TWO SALMONID SPECIES AND THE BENTHIC COMMUNITY

Departamento de Biologia de Organismos y Sistemas, Area de Ecologia, Universidad de Oviedo, 35005 Oviedo, Spain

ABSTRACT

Stomach contents of brown trout (*Salmo trutta* L) and Atlantic salmon (*Salmo salar* L) were studied in relation to the benthic community in the Pigueña River in four months of 1986. Diptera, Ephemeroptera and Trichoptera were the numerically most important items in stomach contents. Structural parameters (diversity, density, number of taxa) of stomach contens and benthos were compared. Only diversity variations were similar between benthos and fish prey. Differences in diet were analyzed according to four size classes of fish, larger fish had wider trophic niche. Intraspecific differences between the four monthly sample were found, while significant interspecific differences were demonstrated only in May and November.

1 INTRODUCTION

In spite of the large bibliography on salmonid feeding (Wankowski, Thorpe 1979; Wankowski 1981; Lopez-Alvarez 1984; Papageorgiou et al. 1984; Gårnas, Hvidsten 1985; Vøllestad, Andersen 1985) there is no agreement about the trophic interrelations between salmonid food supply and benthos. This work attemps to determine the qualitative and quantitative relationships between both communities by sampling fishes and benthos in the same area at the same time. We made samples in different seasons and considered different size classes of fishes to determine the changes in the diet for different life phases.

2. MATERIAL AND METHODS

The River Pigueña is situated in the Middle-West of Asturias (Northern Spain) (Fig. 1). Its basin has 40 km^2 and is 54 km long. In the studied area (Fig. 1) the aquatic vegetation is composed of periphytion, moss and several species of *Ranunculus*, the canopy is well developed and the mean slope is 0.84%.

The benthos and fishes were sampled in April, May, July and November 1986. Fish sampling were laken at stations 1, 2 and 3, while those of benthos were taken at station 1 (no differences between the benthos of the stations were find). Station 1 is situated in a low slope zone, with uniform bed of pebbles and some boulders. Station 2 has a steeper slope and the substratum is composed of boulders over a bed of pebbles. Station 3 has intermediate characteristics.

Benthic samples were taken with a Surber net (500μm of mesh size), with a sampling area of 1600 cm^2 (minimal structural area, Lopez 1981). Samples were stored in 4% formalin solution until they were determinated and counted. Only one replicate was taken at each date. Substrate was disturbed until the sand appeared with no organic matter The general type of habitat sampled was riffle, with a substrate of small stone and pebbles over sand. There was not significative differences between samples of the three stations in the first month, so we have used only station 1 benthic samples in this work.

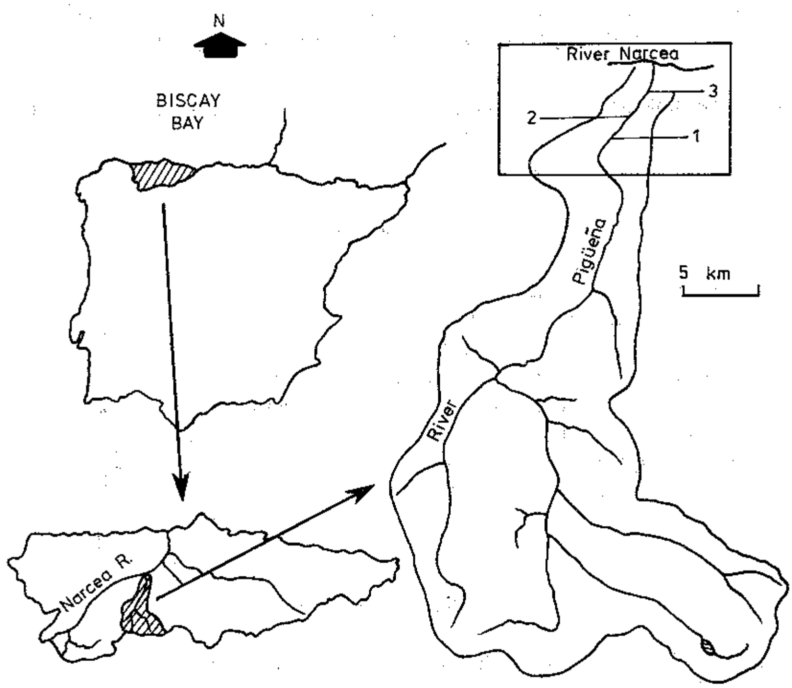

Fig. 1. Location of the Pigueña River showing the sampling sites

We sampled stations 1 and 2 in April, May and July and stations 1 and 3 in November. We selected stations 2 or 3 according to water conditions; these stations were used for obtain fishes of size classes with low captures in station 1. Each station was always sampled in the same sector.

Fish were caught by electrofishing (alternate current 0.2–0.6 A, 120–140 V). Captured fishes were kept cool by storing on ice. Stomach contents were taken out in the laboratory and stored individually (4% formalin) for identification and enumeration a month later.

A total of 104 stomachs of *Salmo trutta* L. and 74 of parr of *Salmo salar* L. were analyzed (Tab. II). For each month's sample, the number of prey in each stomach were counted and the data summarized as: total number of individuals, number and relative abundance of taxa, taxa frequency, sample diversity (Shannon-Weaver index).

A discriminant analysis was used (Dixon 1983) to examine differences in the feeding of *Salmo trutta* L. and *S. salar* L. and between different size classes (fork length) in each species (1: $\leq$10 cm, 2: 10.1–15 cm, 3: 15.1-20 cm, 4: $\geq$20.1 cm).

3. RESULTS

COMPOSITION OF BENTHOS

In the benthic community we found 49 taxa belonging to 34 families (Tab. I). During the sampling period the densities fluctuated between 7369 individuals per m^2 in April and 4075 in November (Tab. I). Ephemeroptera and Diptera were the most abundant, comprising from 79% in April to 32% in July of total density. Genera *Baetis*, *Ephemerella ignita* and Chironomidae Tanytarsini are the dominant taxa, reaching 31% (2284 individuals per m^2) in April.

Table I. Composition of benthos samples (ind./m^2)

	April	May	July	Nov.
EPHEMEROPTERA				
Baetis rhodani	1144	1125	—	—
Baetis spp.	656	150	444	1569
Caenis moesta	144	156	37	137
Ecdyonurus venosus	100	169	87	12
Epeorus silvicola	12	69	256	19
Ephemerella ignita	637	1200	362	6
Rhithrogena semicolorata	—	6	—	—
PLECOPTERA				
Amphinemura sulcicollis	6	—	—	—
Leuctra inermis	—	—	587	6
Leuctra geniculata	262	644	494	—
Protonemura meyeri	6	—	6	—
TRICHOPTERA				
Agapetus sp.	75	6	394	—
Glossosoma boltoni	—	12	62	—
Hydropsyche spp.	212	94	594	137
Holocentropus stagnalis	6	—	—	—
Hydroptila sp.	75	69	—	12
Lype phaeopa	—	6	—	—
Metalype fragilis	6	—	—	—
Lepidostoma sp.	112	12	—	—
Micrasema longulum	94	19	31	125
Neureclipsis bimaculata	—	25	—	—
Philopotamus montanus	—	—	—	19
Polycentropus kingi	44	—	44	12
Rhyacophila dorsalis	37	69	125	31
Sericostoma pedemontanum	—	—	37	94
Tinodes waeneri	56	6	312	6
COLEOPTERA				
Dytiscidae	6	—	—	6
Elmis aenea	119	100	537	131
Esolus parallelepipedus	137	506	419	144
Hydraena sp.	—	—	25	—
Hydrocyphon sp.	—	6	—	—
Limnius volckmari	106	194	169	6
Oulimnius troglodytes	12	56	112	31

Tab. I cont.

DIPTERA				
Atherix sp.	6	6	81	106
Chironomini	400	69	225	—
Tanytarsini	494	950	219	69
Orthocladiinae	1187	75	281'	537
Tanypodinae	31	25	31	—
Ceratopogonidae	6	19	—	—
Empididae	12	6	12	—
Limoniinae	12	—	62	—
Liponeura sp.	75	119	—	—
Simulium sp.	894	106	81	450
AMPHIPODA				
Echinogammarus berilloni	6	25	—	75
ACARI				
Hydracarina	162	550	650	56
GASTROPODA				
Ancylus fluviatilis	—	—	12	56
Lymnaea peregra	—	—	—	25
Potamopyrgus jenkinsi	6	—	19	125
OLIGOCHAETA				
Eiseniella sp.	6	6	19	69
TOTAL	7369	6656	6831	4075

Table II. Number of stomachs analized in each month for different fish size classes

Fish	Brown trout				Atlantic salmon			
Month	April	May	July	Nov.	April	May	July	Nov.
Size class (cm)								
≤10	0	2	19	2	0	5	17	13
10.1-15	7	7	2	4	1	13	5	13
15.1-20	12	10	10	9	2	0	3	2
≥20.1	6	4	4	6	–	–	–	–
TOTAL	25	23	35	21	3	18	25	28

SEASONAL VARIATION IN DIET

The most abundant taxa in the stomach (Tab. III) were Diptera, Ephemeroptera and Trichoptera. The most frequent groups in the two species were Diptera, Ephemeroptera and Trichoptera, while the Coleoptera, Gastropoda, terrestrial prey and Gammaridae were most frequent in brown trout (Tab. IV) and define differences with salmon.

A one-way variance analysis applied to data shows significative numerical, differences between months for trout ($p<0.01$). In salmon, however, only the sample of July is different of the rest. The average number of preys by stomach (Fig. 2) shows a similar seasonal variation in the trout and salmon

Table III. Relative abundance (%) of preys types (N = nymphs, L = larvae, P = pupae, A = adults, E = emergents) in brown trout and Atlantic salmon, for months, from stations 1-3, Pigueña river, 1986

Fish	Brown trout				Atlantic salmon			
Number of stomachs	25	23	35	21	3	18	25	28
Month	April	May	July	Nov.	April	May	July	Nov.
EPHEMEROPTERA								
Baetis sp. (N, E)	9.9	19	11.4	11.5	8.08	36.47	13.83	26.33
Eperous sp. (N)	0.3	0.8	0.8	0	0.85	0.54	2.08	0.17
Ephemerella sp. (N)	0	2.1	2.3	0	0	2.88	0.52	0
Ecdyonurus sp. (N)	0.1	0.1	1.7	0.1	0.45	0.15	1.56	0
Caenis sp. (N)	0	0.4	0.2	0	0	0.93	0	0
Rhithrogenia sp. (N)	0.4	0	4.8	0	0.45	0.07	0	0
Unidentified	1.2	2.8	4.8	0.4	0	1.17	1.56	0.35
DIPTERA								
Simulium sp. (L)	13.6	26.1	8.3	19	57.02	31.02	13.83	24.02
(P,E)	0.6	13.6	0.8	3.3	0.42	6.39	0.26	0.06
Chironomidae (L)	27.5	1.4	16.6	24.1	16.59	1.09	36.55	43.22
(P)	23.2	1.5	1.7	9.2	4.25	1.09	0	0.83
(A)	12.7	1	0	2.6	6.8	0	0	0
Blephariceridae (L)	1.1	5.4	0.2	0	1.7	3.27	0	0
Empididae (L)	0.1	0.1	0.6	0	0	0.23	0.78	0
Limoniinae (L)	0	0	0	0	0	0.07	0	0.11
Stratyomidae (L)	0	0	0	0.1	0	0	0	0
Unidentified (L)	0.1	0.1	1	0.3	0.85	0.15	0.52	0.18
TRICHOPTERA								
Hydropsyche sp. (L)	1.5	1.1	3.3	1	0.85	1.01	1.3	0.41
Brachycentridae (L)	2.8	11	0.2	0.5	0	6.54	0.26	0.06
Rhyacophila sp. (L)	0.4	2.1	8	2.2	0.85	1.17	5.22	2.49
Hydroptila sp. (L)	0.8	1	0.6	0.4	0	0.54	0.26	0.23
Psychomyiidae (L)	0	0.6	1.4	0.1	0	0.39	3.65	0.17
Glossosomatidae (L)	0.4	0.9	0.6	0.4	0	0	0.78	0,23
Beraeidae (L)	0	0	1	0	0	0	0	0
Unidentified (L)	1.8	1.4	10.3	0.9	0.42	0.78	10.7	0.41
Emergent pupae	0	6.3	0.4	0.1	0	2.33	0	0
PLECOPTERA (N)	0	0	0.8	0.2	0	0.46	2.86	0.12
COLEOPTERA								
Elmis sp. (L)	0.03	0	0.2	0	0	0.07	0	0
(A)	0	0.3	0	0	0	0	0	0
Esolus sp. (A)	0	0	0.2	0	0	0.07	0	0
Limnius sp. (L)	0	0	0.2	0	0	0	0	0
(A)	0	0	0	0.1	0	0	0	0
Unidentified (L)	0	0	1.6	0	0	0	0.26	0
(A)	0.2	0.2	0.2	0	0	0	0	0
GASTROPODA								
Potamopyrgus jenkinsi	0.1	0	0	11.3	0	0	0	0.17
Lymnaea sp.	0	0	0.2	6.7	0	0	0	0.12
Ancylus fluviatilis	0	0	0	0.8	0	0	0	0
Unidentified	0.03	0.1	2.7	2.8	0	0.07	0	0.23

Tab. II cont.

AMPHIPODA *E. berilloni*	0.1	0.1	1.2	0.4	0	0	0.26	0
FISHES	0.03	0	0.6	0.1	0	0	0	0
UNIDENTIFIED PREY (L)	0.5	0.1	1	1	0	0.15	0.52	0
TERRESTRIAL PREY	0.5	1.5	11.6	0.6	0.45	0.78	2.35	0.06
No. OF INDIVIDUALS	3174	1556	482	1082	235	1283	383	1682

Table IV. Occurrence frequency (%) of taxonomic groups of prey in brown trout and atlantic salmon from stations 1-3, Pigueña river, 1986. Comparison between months

Fish	Brown trout				Atlantic salmon			
Number of stomachs	25	23	35	21	3	18	25	28
Month	April	May	July	Nov.	April	May	July	Nov.
EPHEMEROPTERA	96	100	74.3	80.9	100	88.9	84	96.4
DIPTERA	92	95.6	82.8	85.7	100	94.4	76	100
TRICHOPTERA	92	91.3	71.4	76.2	66.7	88.9	84	78.6
PLECOPTERA	0	0	31.4	9.5	0	16.7	24	7.1
COLEOPTERA	24	21.7	20	4.8	0	5.6	4	0
GASTROPODA	8	8.7	20	71.4	0	5.6	0	10.7
GAMMARIDAE	8	4.3	11.4	19	0	0	4	0
FISH	4	0	2.8	4.8	0	0	0	0
TERRESTRIAL PREY	36	39.1	45.7	19	33.4	22.2	12	3.6

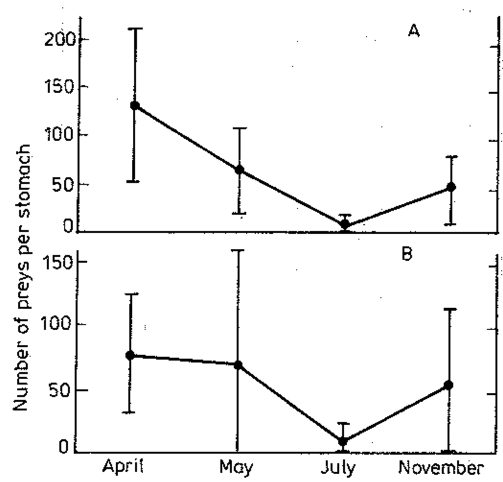

Fig. 2. Average number of prey per stomach in brown trout (A) and Atlantic salmon (B) in the four study months. Vertical lines give standard deviation

Table V. Discriminant analysis: A) grouping of prey for the discriminant analysis; B) Grouping of size classes of brown trout; C) grouping of species of fishes and months (T1, T2, T3 and T4 are the size classes of brown trout. ⩽ 10. 10.1-15, 15.1-20 and ⩾ 20 cm, respectively; T = brown trout S = atlantic salmon)

A)

VARIABLE	TAXA	VARIABLE	TAXA
G1	*Baetis* sp., Ecdyonuridae	G6	emergent Trichoptera emergent *Baetis* sp.
G2	*Ephemerella* sp., *Caenis* sp.	G7	Plecoptera
G3	*Simulium* sp., Blephariceridae, Limoniinae, Empididae, Chironomidae, unidentified Diptera larvae	G8	Coleoptera (adults)
		G9	Coleoptera (larvae)
		G10	Gastropoda
G4	*Hydropsyche* sp., *Rhyacophila* sp	G11	Fish
G5	Brachycentridae, *Hydroptila* sp., Glossosomatidae, Beraeidae	G12	Surface prey
		G13	*Echinogammarus berilloni*

B)
- VARIABLES REMOVED BY THE PROGRAM
  G12 G3
- EIGENVALUES.
  0.17654 0.08447
- CUMULATIVE PROPORTION OF TOTAL DISPERSION.
  0.68 1.00
- F-MATRIX, DEGREES OF FREEDOM = 2.95

C)
- VARIABLES REMOVED BY THE PROGRAM
  G10 G3 G2 G5 G1
- EIGENVALUES.
  0.83754 0.70645 0.31320 0.22208 0.04144
- CUMULATIVE PROPORTION OF TOTAL DISPERSION.
  0.39 0.73 0.88 0.98 1.00
- F-MATRIX, DEGREES OF FREEDOM = 5.162

	T1	T2	T3
T2	5.11		
T3	6.76	2.31**	
T4	6.54	4.32*	0.85**

* REJECTED FOR $p<0.01$
** " " $p<0.05$

	TAPR	TMAY	TJUL	TNOV	SAPR	SMAY	SJUL
T MAY	10.95						
T JUL	22.1	5.73					
T NOV	23.58	17.86	16.36				
S APR	1.08**	1.64**	1.57**	3.73			
S MAY	17.06	3.42	5.04	16.7	2.05**		
S JULY	16.46	4.99	0.53**	14.73	1.2 **	5.79	
S NOV	14.44	9.75	8.32	16.06	0.89**	6.82	5.5

The maximum occurred in April (132.3 preys per stomach in trout and 78.3 in salmon), and the minimum in July (14.5 and 15.3, respectively).

In order to establish the seasonal variation in the diet of both species, a discriminant analysis was made with all the information of the stomach contents (Tab. III). For this analysis, we grouped stomach contents data into thirteen groups of prey whose morphological similarity and/or way of life require a similar strategy in their capture (Tab. VA). Taxonomical groups Diptera (G3), Plecoptera (G7), Gastropoda (G10), Amphipoda (G13) and fish (G11) were included each in a group. Coleoptera was divided in two morphological groups, larvae (G9) and adults (G8). Ephemeroptera was divided in two behaviour groups, swimming and high current speed adapted larve (G1) and walking and climbing larvae (G2). Trichoptera was divided in two size groups, large larvae (G4) and small larvae (G5). Two very different groups are emergent Ephemeroptera and Trichoptera (G6) and surface preys (G12).

This analysis shows (Fig. 3 and Tab. V C) intraspecific differences between the four monthly sample for both species of fish (the sample of salmon in April was not considered because only three individuals were caught). Significant

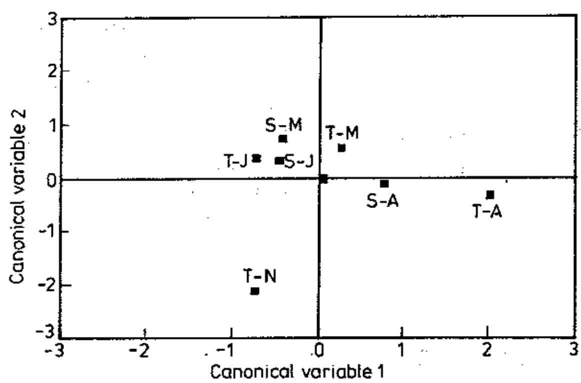

Fig. 3. Relative position of stomach content data on the plane defined by the two principal variables removed by the discriminant analysis, for salmon (S) and trout (T) by months. (A-April, M-May, J-July, N-November)

interspecific differences were also found between May and November, but not in the other months. The variables that explain this variation are, in order of extraction G10, G3, G2, G5 and G1 (see Tab. VA).

COMPARISON BETWEEN FISH DIET AND THE MACROINVERTEBRATE COMMUNITY

A similar seasonal variation is observed in the number of taxa in the diet and benthos (less evident in the latter) (Fig. 4). In both cases, diet and benthos, the values of these parameters in the brown trout are larger than those in the salmon. However, there apparently are any parallel trends in the case of density. Due to prey damage in the fish digestive tract, the taxonomic precision has been less than that in the benthic samples. Therefore the differences in diversity and number of taxa between fish and benthos cannot be analyzed statistically, although the data are useful for general comparison.

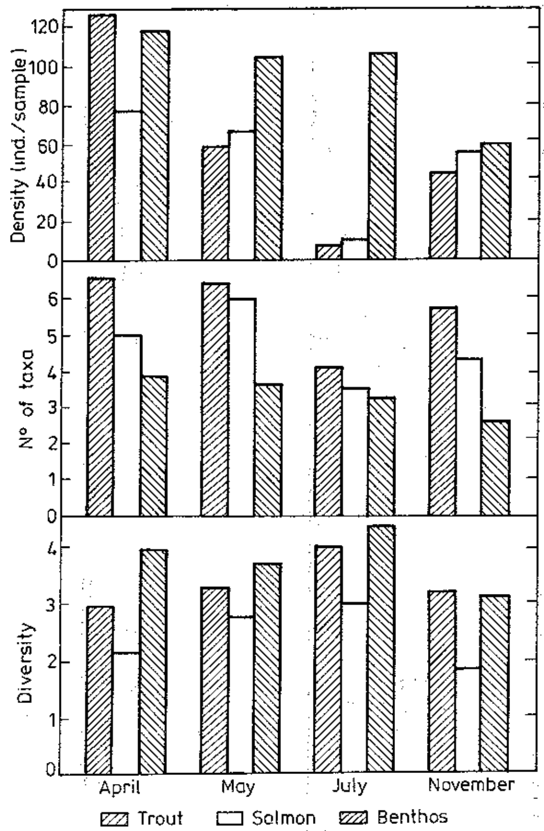

Fig. 4. Temporal variation of density, number of taxa and diversity in fish and benthos. Values of density and number of taxa for benthos are expressed in tens

The most abundant groups in the fish (Fig. 5) are Diptera (range 79–29% in trout and 42–9% in salmon) and Trichoptera (27–5% in the trout and 22–2% in the salmon), apart from the trout in November where the Gastropoda are in the second place (21.5%). The relative importance of prey taken from the surface, mainly terrestrial origin (Formicidae), some adults of species with an aquatic larval life, mainly Diptera and Ephemeroptera, should be noted. This kind of prey is more important in the trout (11.6–0.5%) than in the salmon (2.3–0.1%). The composition of benthos (Fig. 5) is more variable over the months, although Diptera (42–14%) and Ephemeroptera (43–17%) are generally the most abundant, and Trichoptera make only a medium or low contribution (23–4%).

A chi-square test of homogeneity by means of two way contingency tables (Sokal, Rohlf 1969) was made in order to establish if the differences observed

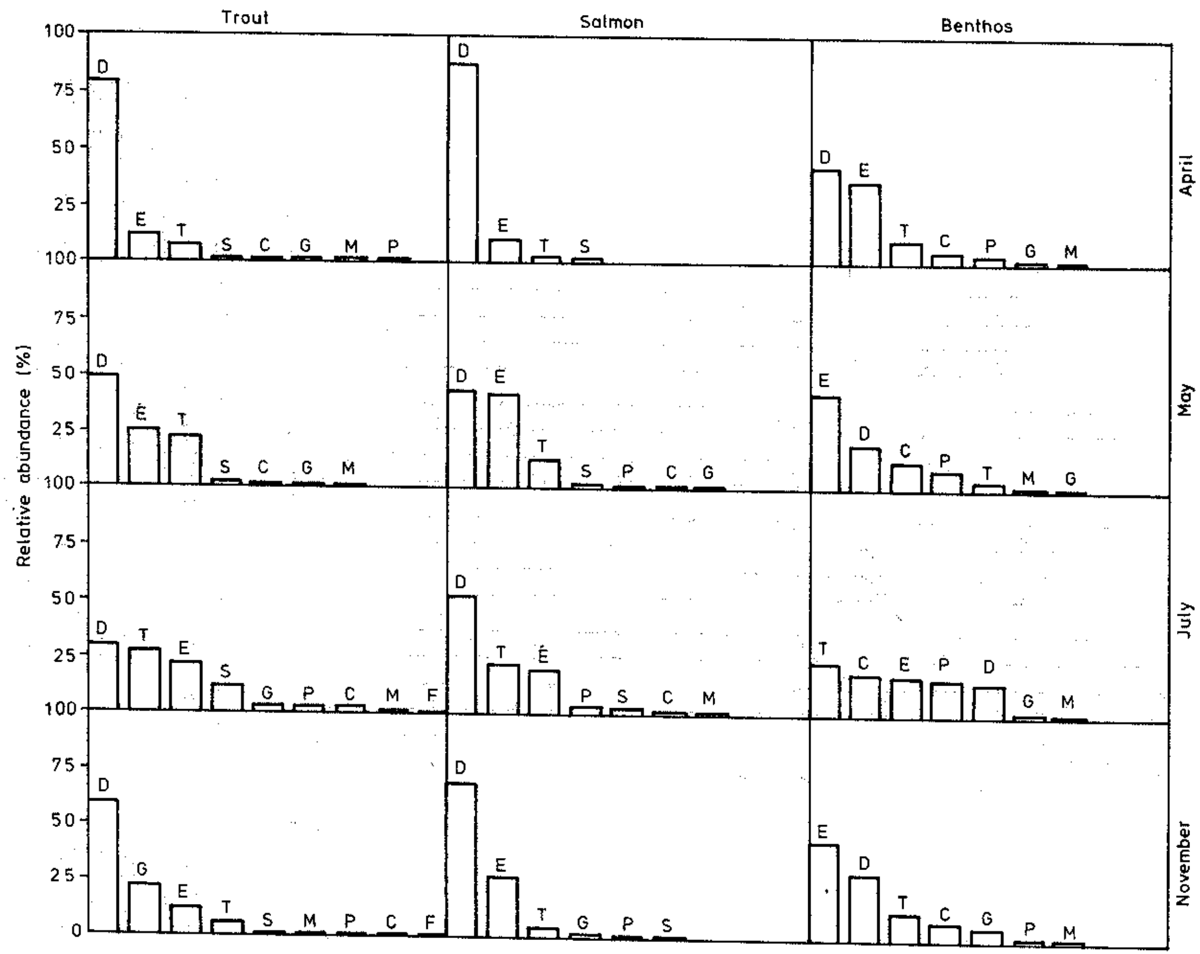

Fig. 5. Relative abundance of the main prey groups in fish and benthos in the four months of study (D: Diptera; E: Ephemeroptera; T: Trichoptera; S: surface prey; C: Coleoptera; G: Gastropoda; M: Gammaridae; P: Plecoptera; F: Fish)

in the absolute abundances in the stomachs and in the benthos of the three groups most eaten by the fishes (Trichoptera, Ephemeroptera and Diptera) were significant. The null hypothesis (H_0) is that fish eat at random, in which case that is so the abundances should be distributed equally in benthos and stomachs. Te result is that H_0 must be rejected at a significance level lower than 0.001, so the populations of stomach contens and benthos are non-homogeneous.

The relative abundances in stomachs and benthos of selected taxa, that represent different habitats or different ways of larval life (Fig. 6 and 7), show

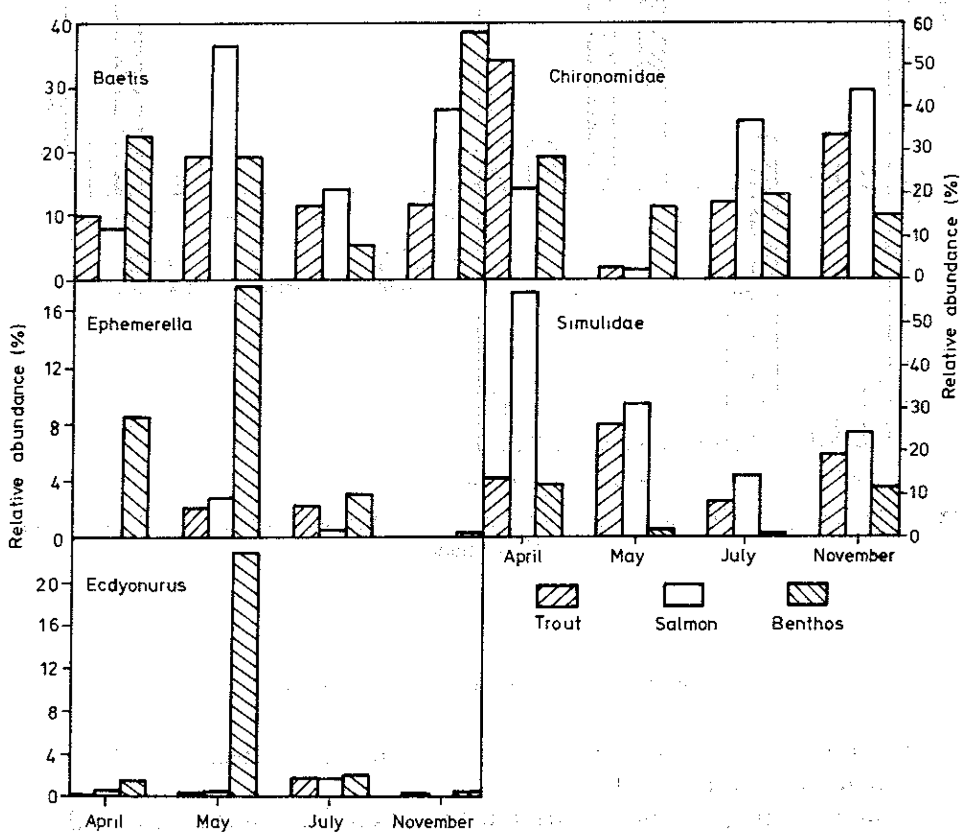

Fig. 6. Relative abundance of groups of prey in fishes and benthos: Ephemeroptera and Diptera

a fish consumption proportionally to their abundance in the benthos in some cases (genera *Baetis*, *Rhyacophila* and *Potamopyrgus*) while in others the response is not clear (Chironomidae, genera *Hydropsyche* and *Simulium*) or apparently does not exist (Plecoptera, Brachycentridae, genera *Ephemerella* and *Ecdyonurus*).

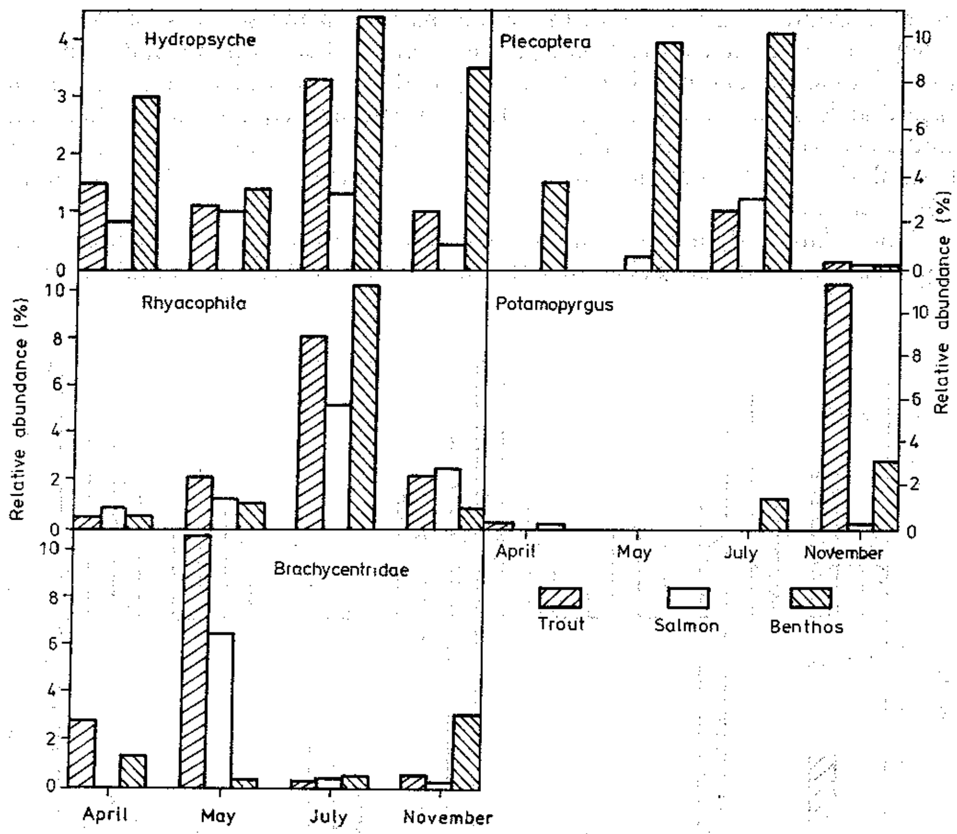

Fig. 7. Relative abundance of groups of prey in fish and benthos: Trichoptera, Plecoptera and Gastropoda

DIFFERENCES IN DIET BETWEEN SIZE CLASSES

For a statistical analysis we have rejected the three specimens of Atlantic salmon in the third size class.

Number of preys groups contributing an appreciable amount to the diet of brown trout increases with increasing size classes in November (Fig. 8). The situation in the rest of the months is similar. Diptera are always the most abundant (82-40% in the trout and 73-61% in salmon). Prey of terrestrial origin became more frequent as the size of the fish increased, both for trout and salmon. Small fish occur as prey only in trout larger than 20 cm (Tab. VII). Also for trout, there is a decrease of the contribution of the most eaten groups, resulting in a more diverse diet. This fact has not been proved in the salmon, because our sample were only adequate for the two first size classes.

The discriminant analysis for the different size classes in trout (Fig. 9 and Tab. V B) shows significant differences between the diet of class 1 and the rest

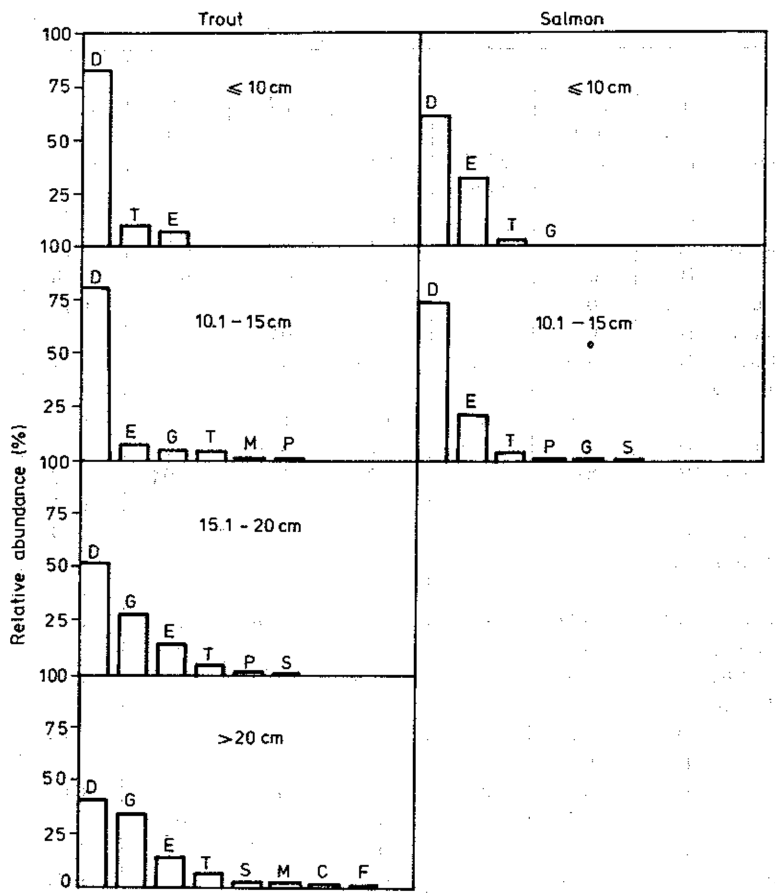

Fig. 8. Relative abundance (percentages) of the main prey groups for fish by size classes in November Codes as in Fig. 4

Table VI. Relative abundance (%) of prey (N = nymphs, L = larvae, P = pupae, A = adults, E = emergents) in four size classes of brown trout and atlantic salmon

Fish	Brown trout				Atlantic salmon		
Number of stomachs	23	20	41	20	35	32	7
Size class (cm)	≤ 10	10.1-15	15.1-20	≥ 20.1	≤ 10	10.1-15	15.1-20
EPHEMEROPTERA							
Baetis sp. (N,E)	16.71	9.83	12.03	16.32	25.31	29.37	18.83
Epeorus sp. (N)	1.15	0.12	0.16	0.46	0.73	0.47	0.68
Ephemerella sp. (N)	1.44	0.84	0.69	0.39	0.63	1.41	0
Ecdyonurus sp. (N)	2.3	0.06	0.13	0.07	0.31	0.12	1.02
Caenis sp. (N)	0.28	0.18	0.13	0	0	0.51	0
Rhithrogenia sp. (N)	0	0.3	0.13	0.23	0	0.04	0.34
Unidentified	1.15	0.84	2.42	1.48	1.15	0.68	0

Tab. VI cont

DIPTERA								
Simulium sp.	(L)	13.25	20.93	18.04	11.71	17.85	29.02	47.94
	(P,E)	0.57	2.11	5.81	4.53	0.42	3.46	0
Chironomidae	(L)	30.83	30.88	15.38	12.03	40.23	20.52	19.52
	(P)	3.17	14.53	12.49	18.75	0.63	1.11	2.05
	(A)	0	4.16	10.8	4.06	0	0.55	1.02
Blephariceridae	(L)	0.28	2.59	1.36	2.73	0.1	1.75	1.37
Empididae	(L)	0.28	0	0.16	0	0.42	0.08	0
Limoniinae	(L)	0	0	0	0	0	0.12	0
Stratyomidae	(L)	0	0	0	0.07	0	0	0
Unidentified	(L)	0.86	0.18	0.19	0.07	0.1	0.17	1.02
TRICHOPTERA								
Hydropsyche sp.	(L)	2.3	0.6	1.89	1.32	0.73	0.72	1.02
Brachycentridae	(L)	0	3.98	4.68	4.76	0.1	3.59	0.34
Rhyacophila sp.	(L)	8.07	0.54	1.79	1.32	2.94	1.92	2.05
Hydroptila sp.	(L)	1.15	1.02	0.59	0.62	0.1	0.42	0.34
Psychomyiidae	(L)	2.02	0.36	0.13	0	1.26	0.42	0
Glossosomatidae	(L)	0.86	0.24	0.23	0.54	0.21	0.21	0
Beraeidae	(L)	0	0	0.16	0	0	0	0
Unidentified	(L)	6.34	1.81	2.02	2.18	4.41	0.55	1.37
Emeregent pupae		0	1.51	1.26	2.96	0	1.28	0
PLECOPTERA	(N)	2.01	0.12	0.13	0.07	1.36	0.25	0
COLEOPTERA								
Elmis sp.	(L)	0.28	0.06	0	0	0	0.04	0
	(A)	0	0.06	0.09	0	0	0	0
Esolus sp.	(A)	0.28	0	0	0	0	0.04	0
Limnius sp.	(L)	0.28	0	0	0	0	0	0
	(A)	0	0	0	0.07	0	0	0
Unidentified	(L)	0.86	0	0.16	0	0	0.04	0
	(A)	0	0.12	0.19	0.31	0	0	0
GASTROPODA								
Potamopyrgus jenkinsi		0	0.06	2.09	4.76	0.31	0	0
Lymnaea sp.		0	0.48	1.46	1.71	0	0.08	0
Ancylus fluviatilis		0	0.06	0.09	0.39	0	0	0
Unidentified		0	0.24	0.66	1.71	0.42	0.04	0
AMPHIPODA								
E. berilloni		1.44	0.18	0.06	0.23	0	0.04	0
FISH		0	0	0	0.39	0	0	0
UNIDENTIFIED PREY	(L)	0	0.66	0.43	0.78	0.1	0.12	0
TERRESTRIAL PREY		1.73	0.3	1.79	2.8	0.1	0.72	1.02
Nº OF INDIVIDUALS		347	1658	3009	1280	952	2339	292

($p < 0.01$) and between class 2 and 4 ($p < 0.05$). The variables that explain the differences are, in order of extraction, G12 and G3 (see Tab. V A). The same analysis showed no significant differences between size classes in the Atlantic salmon.

Table. VII. Occurrence frequency (%) of taxonomic prey groups in four size classes of brown trout and atlantic salmon

Fish	Brown trout				Atlantic salmon		
Number of stomachs	23	20	41	20	35	32	7
Size class (cm)	⩽ 10	10.1-15	15.1-20	⩾ 20.1	⩽ 10	10.1-15	15.1-20
EPHEMEROPTERA	82.6	95	87.8	80	88.6	93.7	85.7
DIPTERA	86.9	95	92.7	75	91.4	93.7	71.4
TRICHOPTERA	69.6	95	87.8	70	77.1	87.5	85.7
PLECOPTERA	26.1	10	9.7	5	20	12.5	0
COLEOPTERA	17.4	15	19.5	20	0	6.2	0
GASTROPODA	0	15	31.7	50	2.9	9.4	0
GAMMARIDAE	13	15	4.9	15	0	3.1	0
FISH	0	0	0	15	0	0	0
TERRESTRIAL PREY	17.4	15	41.5	70	2.9	18.7	28.6
NO. OF PREY GROUPS CONTRIBUTING 5% OR MORE	7	8	7	9	4	7	4

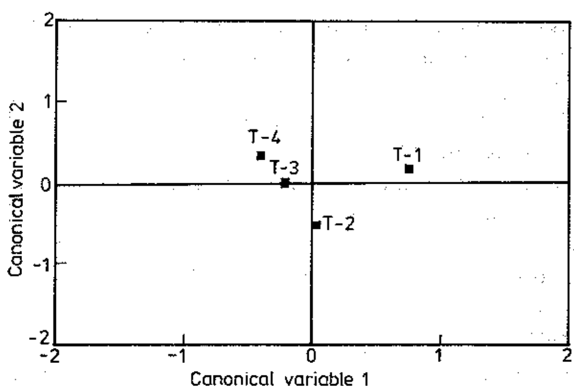

Fig. 9. Relative position of trout stomach contens data on the plane defined by the two principal variables removed by the discriminant analysis, by size classes. (1. ⩽ 10 cm, 2. 10.1-15 cm, 15.1-20 cm, ⩾ 20.1 cm.

4. DISCUSSION

Salmonids obtain their prey visually (Ringler 1985; Wankowski 1979; Jonsson, Gravem 1985), selecting them as a result of the integration of their visual accuracy with morphometric and physiological factors in the fishes, as well as accessibility and availability of the prey (Wankowski 1979). Also there are important visual factors such the colour contrast between prey and the bottom (Healey 1984). According to these considerations and studies on stomach contents, the diet of salmonids consists of nymphs and larvae of large benthic animals, as well as drifting larvae and terrestrial insects which fall into the water accidentaly (Gårnas, Hvidsten 1985). The two latter groups should be independent of the local productivity of the benthos (Wankowski 1981).

Our results confirm this opinion. The animals most abundant in the diet are: 1) the main component in the river drift in Asturias (*Baetis* sp., Chironomidae and Simulidae) (López 1981), and 2) the bigger nymphs in the benthos of the river Pigueña (*Hydropsyche* sp., and *Rhyacophila* sp.). Terrestrial preys, mostly winged adults Formicidae, were abundant in the stomach in summer. These results coincides with the found by Jonsson and Gravem (1985). Although Plecoptera were recognized as an important component of salmonid food (Jonsson, Sandlund 1979; Papageorgiou et al. 1984; Gárnas, Hvidsten 1985) especially *Perla* genus (Papageorgiou et al. 1984), which is absent from the benthos in Pigueña River. Gastropoda of genus *Potamopyrgus* which are eaten in a great quantity by the trout in November, are associated with aquatic plants, a favourite habitat of the larger size classes of trouts in the Pigueña River. The high consumption of Brachycentridae family in May remains unexplained since they are small animals, and rare in the drift.

The density of the most important prey group taken by the fish is not proportional to its abundance in the benthos. But it is reasonable to expect that the density of prey in drift and in fish stomachs would be related, a fact demostrated by Ringler (1979) in studies with artificial streams.

The temporal variations in diet do not depend only on the variations in abundance of the macroinvertebrate community. The relationship between temperature as well as perhaps the photoperiod and the feeding activity of salmonids is well documented, so the quantity of eaten food is directly proportional to the water temperature (Papageorgiou et al. 1984). In addition, the feeding activity of fish depends on the physiological state, intensity of growth and gonad development (Wankowski, Thorpe 1979; Wankowski 1981).

The importance of prey availability as a factor causing seasonal variations in diet quality is due to species with great density variations over the whole time of the study, not only in the benthos but also in the drift (Gastropoda and Driptera larve), and not to species whose density is more or less regular over that time.

The largest temporary variation is found in the quantity of prey eaten. That the lowest density in stomachs was observed in July does not correspond to the idea of temperature being an important influence, for if this were so, the minimal should have been found in November. However, the minimum in July corresponds to the beginning of the gonadal development of the trout (Garcia, Braña, in print), a phenomenon capable of changing the relationship between temperature and feeding greatly, as has been observed by Papageorgiou et al. (1984). This explanation does not hold for young salmon, since these do not reach their sexual maturity in the river. We must consider other factors, such as a more rapid digestive rate in the warm months (Windell 1978), wich would result in the prey staying a shorter time in the stomach.

The differences observed in diet suggest that the size classes were segregated in the space. Spatial segregation or the prey selection are mechanisms often cited for reducing interspecific competition (Jonsson, Gravem 1985; Voøllestad, Andersen 1985). The existence of spatial segregation, and the presence of young salmons only, explain partly the differences in diet of both species month by month, since different areas in the river have a different composition in their benthonic fauna and possibly in the drift.

Differential prey selection according to fish size is well documented (Wankowski 1979; Jonsson, Gravem 1985; Voøllestad, Andersen 1985). The influence of this factor and of spatial segregation result in a diet which is more diverse with increasing fish size, as larger fish eat more prey. In our study, this was obvious in the diversity values and taxa number, being higher in brown trout than in young Atlantic salmon because the former have more size classes and a much greater range in length. We suppose that the space segregation between age and size classes explains the results shown in Figure 9 and Table V B in which the difference between size classes becomes apparent, i.e. the bigger the size classes become the more separated they are. These results contrast with those of Papageorgiou et al. (1984), who didn't record any such differences. The presence of a small number of size classes of Atlantic salmon in the river is reflected in the above mentioned parameter values, being smaller than those in trout, and the existence of no significant differences between the size classes.

5. SUMMARY

The stomach contens of 104 brown trout (*Salmo trutta*) and 74 of young Atlantic salmon (*Salmo salar*) caught in April, May, July and November 1986 were analized and compared with the benthos composition in the same periods. The diet composition is what might be expected in animals that hunt visually. Drift components (*Baetis* sp., Chironomidae, Simulidae), big benthic prey (*Hydropsyche* sp., *Rhyacophila* sp.) and terrestial prey form a bulk of diet. Due to the importance of drift in the diet, the proportions of prey in the stomachs and benthos are different. Minimum prey density in the stomachs in July is related to physiology of fish (gonadal development starts then, among other things) and effects of water temperature. Interspecific differences in diet suggest the existence of spatial segregation between both species. Their diet becomes more diverse with increasing fish size, larger fish eat a wider range of prey.

6. SUMARIO

Se analizaron los contenidos de 104 estómagos de trucha común (*Salmo trutta*) y 74 de juveniles de salmón atlántico (*Salmo salar*) capturados en Abril, Mayo, Julio y Noviembre de 1986, comparándose con la composición del bentos en el mismo periodo. La composición de la dieta

responde a lo esperado en animales que cazan visualmente. Elementos del arrastre (*Baetis* sp., Chironomidae, Simulidae), grandes presas del bentos (*Hydropsyche* sp., *Rhyacophila* sp.) y presas terrestres forman mayoritariamente la dieta. Debido a la importancia del arrastre en la dieta las proporciones de las presas en los estómagos y el bentos son diferentes. La mínima densidad de presas en los estómagos en Julio se relaciona con la fisiología de los peces (se inicia el desarrollo gonadal, entre otros) y a la temperatura del agua. Las diferencias interespecífias de la dieta sugieren la existencia de segregación espacial entre ambas especies. La dieta se hace más diversa con la talla del pez, consumiendo los peces mayores un rango más amplio de presas.

ACKNOWLEDGEMENTS

The present study has been performed thanks to a research scholarship promoted by Asociación Asturiana de Pesca, and financially supported by Consejería de Agricultura y Pesca del Principado de Asturias.

We wish to thank to Dr. Florentino Braña for his suggestions, Dr Angeles Gil for her help with statistical analysis, and Maria Jesús Rodriguez for the translation of the manuscript to the English language. Our acknowledgements to Dr. Ewa Kamler, Dr T. G Northcote and one anonimous reviewer for their critical revisions of this paper.

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Received 8 December, 1987
Accepted 28 March, 1988