

First feeding diet of young brown trout fry in a temperate area: disentangling constraints and food selection

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Abstract Diet composition of newly emerged brown trout fry in natural areas remains poorly known, and foraging abilities at this early stage, although presumably reduced, are still under discussion. We have studied gut content composition of brown trout fry in a temperate area (Galicia, NW Spain) and compared it to the benthic macroinvertebrate community. Small prey such as chironomid larvae and baetid nymphs were the most important food items for newborns, some of them still presenting yolk remnants. However, the positive selection observed for *Polycentropodidae* and *Simuliidae* and the rejection of *Elmidae* and *Leuctricidae* suggest that other factors apart from size, such as locomotor abilities of fish or accessibility and antipredator

behaviour of prey play an important role in feeding behaviour. Additionally, analysis of diet changes on the studied fry suggests a dramatic shift in niche breadth at the moment of complete yolk absorption, which might be related to the improvement of swimming and handling ability of fry for capturing and ingesting prey. The presence of aerial imagoes only in the stomachs of fry with no yolk provides further support to this hypothesis. Planning of restoration works on spawning grounds should then allow enough time for complete recolonization by benthic macroinvertebrates, including first instars, as searching for food in newborns is limited to the nest area due to mobility constraints.

Keywords Brown trout · Fry · First feeding · Diet · Yolk resorption · Foraging abilities

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Introduction

First feeding is the major critical period for fish fry survival. It is the phase where the deepest physiological and ecological changes occur and, both in natural populations and fish cultures, this period constitutes a primary focus of interest. In salmonids, many of the factors that determine first feeding of newly emerged fry are linked to maternal traits. Thus, for example, female decision on nest choice will condition the first diet of the newly emerged

juveniles, since their poor swimming ability obliges them to feed in the surrounding area (Elliott, 1986; García de Leániz et al., 2000). As well, the amount of yolk available for embryos will determine the time nestlings emerge from the gravel nest to open water for feeding, as the exhaustion of yolk remnants forces them to find food resources (Armstrong & Nislow, 2006). However, feeding can occur even prior to emergence in brown trout (Zimmerman & Mosegaard, 1992; Skoglund & Barlaup, 2006). Beside these, there are also individual traits, such as the ability to acquire a feeding territory, that play an important role in the success of first feeding (Titus, 1990), and the observed aggressive behaviour of newly emerged fry is known to contribute to the dispersal of emerging batches and to the establishment of a social hierarchy (Elliott, 1990). Among the abiotic factors that influence feeding, water temperature plays a major role, as it influences emergence, food intake and activity (Crisp, 1988; Elliott & Hurley, 1998; Ojanguren et al., 2001).

Brown trout is a species of Eurasian origin, but at present it is naturalized in many other areas all over the world. It has an outstanding socio-economic importance, both in commercial and sport fisheries, and it is frequently used as tourist attraction (Aas et al., 2000; Butler et al., 2009). A consequence of this importance is the enormous amount of literature on the species, with published monographs on different aspects, including feeding (e.g. Baglinière & Maise, 1991; Elliott, 1994). However, even though first feeding is a critical period, diet composition of newly emerged fry in natural areas remains poorly known, and the limited information available on the food of brown trout fry comes mainly from studies in boreal areas (see Skoglund & Barlaup, 2006). Better knowledge on this subject would, however, provide important information on the larval feeding behaviour and food quality in this period, thus helping understand the trophic requirements of fry. Moreover, a better understanding on the use of food resources during this critical phase would help stakeholders to take decisions on the management of natural spawning areas (Armstrong & Nislow, 2006). Thus, the objective of this paper was to analyse the diet and foraging abilities of young brown trout fry in four natural spawning streams in a temperate area, where brown trout is the most important angling species.

Materials and methods

Fry were collected in four streams located in Galicia (NW Spain). Two of them, Castromaioir (STR1, UTM: 29T 618591 4800096) and Xemil (STR2, UTM: 29T 646561 4754400) are first-order streams tributaries on the watershed of River Miño (308 km total length), while Iso (STR3, UTM: 29T 569408 4751246) is a first-order tributary of River Ulla (132 km total length). The River Eo flows into the Cantabrian Sea, and it is 79 km in length, but fry were collected at its source area (STR4, UTM: 29T 646023 4779958). All sampling streams are oligotrophic courses draining granitic catchments, and sampling sites were located on sections of an average width of 2–3 m. Medium water temperature of the four locations varies between 10°C in winter and 14°C in summer, with a summer flow of 0.6 m³/s that raises to ca. 1.2 m³/s during winter (Río-Barja & Rodríguez-Lestegás, 1992). Substrate of nursery areas consisted mainly of coarse gravel (10–30 mm diameter).

Fry were collected throughout the months of March and April 1996 in various parts of nursery areas during routine fish sampling using pulsed D.C. backpack electrofishing equipment (Hans Grassl GmbH, ELT60II). The number of captured fry was 19 at STR1, 25 at STR2, 29 at STR3 and 26 at STR4. All individuals were captured in open water over the gravel bed, at short distances of nests. Fry 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.

Prior to electrofishing in STR3, benthic invertebrate samples ($n = 9$) were collected from riffles using a 0.1 m² Surber sampler. After collection, we preserved samples in 70% ethanol and stored them for later processing. In order to study prey selection, we quantified the abundance and composition of aquatic invertebrates. Maximum prey length (± 0.01 mm) was measured for each prey item. Prey was grouped into 0.5-mm length classes.

Laboratory procedures were performed following Skoglund & Barlaup (2006), except for the estimation of stomach fullness and yolk remnants. Thus, fry were defrosted and the total length (L_T) was recorded to the nearest 0.5 mm and weighed (W) to the nearest 0.1 mg, despite the fact that freezing induces a loss in length and weight of fishes (Ogle, 2009). Before

dissection, fry were stored in formaldehyde to completely extract yolk under a binocular microscope (Nikon Eclipse 80i). If yolk was present, remnants were registered as percentage with respect to the wet weight of the fry.

Mouth gape was measured to determine morphological feeding limitations of fry from STR3. We used a digital micrometer, inserting the tip of a conical wood device into the mouth cavity of fry until the jaws were well separated (Ward & McCulloch, 1991).

The degree of stomach fullness (f) was calculated for each fry as $f = (W_s/W) \times 100$, where W_s is the total stomach content wet weight (mg) and W is the fry wet weight (mg). Prey items were identified to the family level when possible. 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. Preys were grouped into 0.5-mm classes.

For the description of the diet, data are offered on frequency of occurrence of preys ($F_i = (N_i/N) \times 100$, where N_i is the number of fry with prey i in their stomach and N is the total number of fry with stomach contents of any kind) and relative abundance of preys ($A_i = (\sum S_i/\sum S_t) \times 100$, where S_i is the stomach content (number) composed of prey i , and S_t the total stomach content of all stomachs in the entire sample) (Amundsen et al., 1996). Moreover, the niche width of the individuals was estimated using the Shannon diversity index ($H' = -\sum P_i \log_{10} P_i$, where P_i is the proportion of the prey item i among the total number of preys), and the specialization in the diet evaluated using the Pielou's evenness index ($J = H'/H'_{\max}$), considering that values close to zero mean a stenophagous diet and those closer to one more of a euryphagous diet (Ruginis, 2008).

Each prey item was converted into energy and chemical composition using dry weight-energy

equations (Cummins & Wuycheck, 1971; Cobo et al., 1999, 2000), and the total energy in the stomach was summarized for each fish.

The feeding selectivity of fry was measured using Ivlev's selectivity index (Ivlev, 1961), $E = (r_i - p_i)/(r_i + p_i)$, where r_i is the relative abundance of food category i in the stomach (as a proportion or percentage of all stomach contents) and p_i is the relative abundance of this prey in the environment. Values of this index range from -1 to $+1$, with negative values indicating rejection or inaccessibility of the prey, zero indicating random feeding, and positive values indicating active selection.

Statistical analyses were conducted using the programme SPSS 16.0. All tests were considered statistically significant at P level < 0.05 . Kruskal–Wallis tests for non-normal data were used for detecting differences among rivers. Differences in the number of taxa and number of prey between STR2 and STR3, the only places with enough individuals that had started feeding, were tested using a Mann–Whitney U test. Student t test was used to compare the mouth gape among individuals in STR3. The Spearman correlation was used to examine correlations between variables.

Results

Biometric data of fry (mean L_T and W) in the four streams are shown in Table 1. Total length (L_T) of fry ranged from 19 to 44 mm, with fry from STR3 being the longest ($28 \text{ mm} \pm 1.12$). Significant differences were observed in length and weight among streams (Kruskal–Wallis test: $H = 38.47$, $P < 0.05$; Kruskal–Wallis test: $H = 39.39$, $P < 0.05$).

Mean mouth gape of individuals in STR3 was $2.27 \text{ mm} \pm 0.103$ (range: 1.65–3.51 mm), being different among individuals (Student t test: $t = 21.88$, $P < 0.05$).

Table 1 Biometric data of the fry (mean values \pm S.E.)

	Castromaior (STR1)	Xemil (STR2)	Iso (STR3)	Eo (STR4)
Total length (mm)	24 \pm 0.22	22.9 \pm 0.29	28 \pm 1.19	25 \pm 0.21
Weight (g)	0.13 \pm 0.003	0.10 \pm 0.003	0.27 \pm 0.043	0.14 \pm 0.003
Yolk (%)	12.51 \pm 0.873	5.17 \pm 1.929	0	3.16 \pm 0.702
Number of fry	19	25	29	26

Concerning yolk, 48.48% of the total fry presented still remnants of the yolk sac, ranging from 0.6 to 25.97% with respect to the fry total wet weight. When yolk was fully consumed, fry L_T ranged from a minimum of 22 mm in STR3 to a maximum of 44 mm in STR4.

Of the total captured fry, 49.5% had initiated feeding (49 individuals), while the rest (50.5%) did not present any food particle in the stomach or intestines. Of the total fry that had initiated feeding, only 7 (21.21%) presented yolk remnants and, as expected, mean stomach fullness was lower for fry with yolk (3.20% stomach fullness) than for fry without yolk (5.47%). Figure 1 shows the proportion of fry which had initiated feeding in relation to the amount of yolk, being 21% for fry with 0–10% wet weight of yolk and 82.35% for fry with no yolk. No food particles were found in the stomachs or intestines of fry having >10% of the yolk sac remaining.

As the amount of remaining yolk decreased, the number of preys in stomachs increased (Fig. 2).

The composition of benthic invertebrates in STR3 included 36 taxa (density = 4559 ind/m² and biomass = 33.81 g/m²). The beetle *Elmidae* was the most abundant taxa and represented 30.14% of the total number of individuals. *Leuctricidae* and *Ephemerelellidae* contributed 16.86 and 15.5%, respectively, to the total abundance. Less numerous in the benthos, but very important in trout diet in other studies, were families such as *Chironomidae* (8.98%) and *Baetidae* (7.68%) (Table 2). Invertebrates presented a wide size range (range: 0.5–26 mm), with prey ≥ 4 mm being the most abundant ones (29.3%) (Table 3).

A total of 398 preys were identified in the stomach contents of fry, and the diet composition includes 14

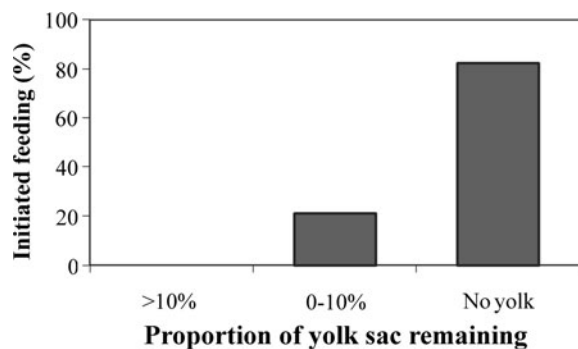


Fig. 1 Percentages of brown trout fry which had initiated feeding in relation to the amount of yolk remaining

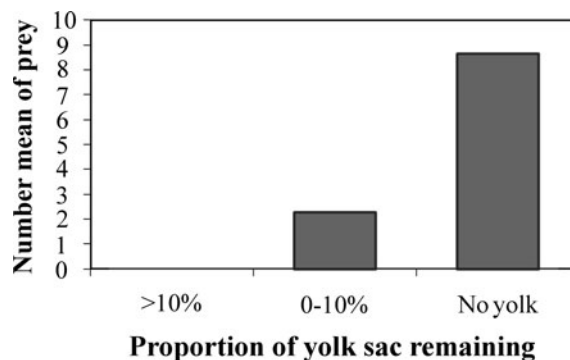


Fig. 2 Number of prey in the stomach of fry in relation to the amount of yolk remaining

types of prey (Table 4). Thirteen of the 14 categories were benthic prey, and only one category corresponded to aerial prey (chironomid imagoes), which were only found in stomachs of fry with no yolk, and were probably eaten on the water surface. The number of prey taxa consumed by fry showed significant differences between STR2 and STR3 (Mann–Whitney U test: $U = 130.5$, $P < 0.05$), being higher in STR3 (2.59 ± 0.208) than in STR2 (1.80 ± 0.262). The most abundant taxa in the diet were chironomid larvae and baetid nymphs (Table 4). Chironomid larvae constituted 59.05% of the total number of identified items, and were identified in the 79.59% of the stomachs with food. Copepods were also present in the diet of fry collected at STR2 and STR3, while mites (Hydracharina) were found only at STR3. The rest of the taxa present were aquatic insects: Ephemeroptera, Trichoptera, Plecoptera, and other Diptera families (*Simuliidae* and *Ceratopogonidae*).

The trophic diversity of fry was relatively low ($H' = 0\text{--}0.28$; Table 4). As for the evenness index ($J = 0.13\text{--}0.47$), it indicates that fry tend to be stenophagous. The trophic diversity consumed by fry increases with fry size (Fig. 3), results were obtained using pooled data ($r = 0.56$; $P < 0.05$) but also separately in STR2 and STR3 ($r = 0.57$, $P < 0.05$; $r = 0.58$, $P < 0.05$, respectively). The trophic diversity and the number of prey were significantly higher in STR3 than in STR2 (Mann–Whitney U test: $U = 137$, $P < 0.05$; Mann–Whitney U test: $U = 123$, $P < 0.05$, respectively) (Table 4).

The biochemical composition of the diet showed a high stability, although significant differences in energy intake were found between sites STR2 and STR3, being STR3 > STR2 (Table 5). Some prey

Table 2 Benthos composition and Ivlev's index in STR3

	Developmental stage	Number of prey (<i>N</i>)	Abundance (A_i)	Ivlev's index
<i>Planariidae</i>	Adult	60	0.44	-1
Oligochaeta ^a	Adult	840	6.15	-1
<i>Sphaeriidae</i>	Adult	15	0.11	-1
Hydracharina	Adult	96	0.7	-0.36
<i>Gammaridae</i>	Adult	90	0.66	-1
Ostracoda ^a	Adult	3	0.02	-1
Copepoda ^a	Adult	-	-	-1
<i>Baetidae</i>	Nymph	1050	7.68	-0.61
<i>Ephemerellidae</i>	Nymph	2118	15.5	-0.88
<i>Ephemeridae</i>	Nymph	33	0.24	-1
<i>Heptageniidae</i>	Nymph	147	1.08	-0.24
<i>Leptophlebiidae</i>	Nymph	564	4.13	-0.85
<i>Chloroperlidae</i>	Nymph	75	0.55	-1
<i>Leuctridae</i>	Nymph	2304	16.86	-1
<i>Nemouridae</i>	Nymph	27	0.2	-1
<i>Cordulegasteridae</i>	Nymph	3	0.02	-1
<i>Sialidae</i>	Larvae	3	0.02	-1
<i>Elmidae</i>	Larvae/Adult	4119	30.14	-0.97
<i>Gyrinidae</i>	Larvae	24	0.18	-1
<i>Hydraenidae</i>	Adult	21	0.15	-1
<i>Glossosomatidae</i>	Larvae	6	0.04	-1
<i>Goeridae</i>	Larvae	42	0.31	-1
<i>Hydropsychidae</i>	Larvae	93	0.68	-1
<i>Lepidostomatidae</i>	Larvae	3	0.02	-1
<i>Limnephilidae</i>	Larvae	33	0.24	-1
<i>Polycentropodidae</i>	Larvae	3	0.02	0.87
<i>Psychomyiidae</i>	Larvae	3	0.02	-1
<i>Rhyacophilidae</i>	Larvae	15	0.11	-1
<i>Sericostomatidae</i>	Larvae	144	1.05	-1
<i>Thremmatidae</i>	Larvae	12	0.09	-1
<i>Athericidae</i>	Larvae	102	0.75	-1
<i>Ceratopogonidae</i>	Larvae	51	0.37	-0.067
<i>Chironomidae</i>	Larvae	1227	8.98	0.73
<i>Empididae</i>	Larvae	21	0.15	-1
<i>Limoniidae</i>	Larvae	81	0.59	-1
<i>Psychodidae</i>	Larvae	78	0.57	-1
<i>Simuliidae</i>	Larvae	162	1.19	0.31

^a Not identified

organisms were of obvious importance, such as chironomid larvae and baetid nymphs, which represented >80% of the energetic input (STR1 = 100%, STR2 = 81.2% ± 6.82, STR3 = 90.3% ± 2.64, STR4 = 45.4% ± 26.47) (Fig. 4).

Fry fed mainly on prey within the 0.05–9.2 mm size range, with prey of 3–4 mm being the most commonly

consumed (87.18% of total). There were differences in the average prey size consumption between sites STR2 and STR3 (Mann–Whitney *U* test: $U = 85$, $P < 0.05$), prey being longer in STR3 (3.51 mm ± 0.077) than in STR2 (3.04 mm ± 0.226), but no correlation between average prey size and the total length of fry was found (STR2: $r = 0.25$, $P = 0.321$; STR3: $r = -0.16$,

Table 3 Diet of fry and benthos according to prey size in STR3

Prey size categories	1	2	3	4	5	6	7	8	9
Size (mm)	0–0.5	0.5–1	1–1.5	1.5–2	2–2.5	2.5–3	3–3.5	3.5–4	≥4
Stomach occurrence	1	0	0	21	0	10	181	107	3
Benthos occurrence	0	64	142	2113	1159	3646	1752	786	4006

Prey were grouped into nine prey size categories, each of them of 0.5 mm-interval

Table 4 Diet composition

	Castromaior (STR1)			Xemil (STR2)			Iso (STR3)			Eo (STR4)		
	<i>N</i>	<i>A_i</i> (%)	<i>F_i</i> (%)	<i>N</i>	<i>A_i</i> (%)	<i>F_i</i> (%)	<i>N</i>	<i>A_i</i> (%)	<i>F_i</i> (%)	<i>N</i>	<i>A_i</i> (%)	<i>F_i</i> (%)
Aquatic invertebrates												
Hydracharina	–	–	–	–	–	–	1	0.31	3.45	–	–	–
Copepoda	–	–	–	3	4.92	20	17	5.26	3.45	–	–	–
<i>Baetidae</i>	1	100	100	7	11.48	40	99	30.65	96.55	–	–	–
<i>Ephemere</i> llidae	–	–	–	–	–	–	3	0.93	10.34	–	–	–
<i>Heptageni</i> idae	–	–	–	1	1.64	6.67	2	0.62	3.45	–	–	–
<i>Leptophlebi</i> idae	–	–	–	–	–	–	1	0.31	3.45	1	7.69	25
<i>Leuctri</i> dae	–	–	–	–	–	–	2	0.62	6.90	–	–	–
<i>Elmi</i> dae	–	–	–	–	–	–	1	0.31	3.45	–	–	–
<i>Hydropsy</i> chidae	–	–	–	–	–	–	–	–	–	1	7.69	25
<i>Polycentrop</i> odidae	–	–	–	–	–	–	1	0.31	3.45	–	–	–
<i>Ceratopogon</i> idae	–	–	–	–	–	–	1	0.31	3.45	–	–	–
<i>Chironomi</i> dae	–	–	–	44	72.13	88.67	181	56.04	82.76	10	76.92	50
<i>Simuli</i> idae	–	–	–	4	6.56	20	7	2.17	20.69	1	7.69	25
Aerial invertebrates												
<i>Chironomi</i> dae	–	–	–	2	3.28	13.33	7	2.17	20.69	–	–	–
Other preys												
Vegetal rests	–	–	–	–	–	–	–	–	3.45	–	–	–
Nematoda	–	–	–	–	–	–	–	–	13.79	–	–	–
No. total prey	1			4.07 ± 0.796			10.48 ± 2.374			3.25 ± 2.250		
No. prey taxa	1			1.8 ± 0.262			2.59 ± 0.208			1.25 ± 0.25		
Aerial invertebrates (%)	0			1.94 ± 1.340			2.78 ± 1.172			0		
Shannon diversity index	0			0.154 ± 0.049			0.28 ± 0.033			0.035 ± 0.035		
Evenness index	0			0.13 ± 0.043			0.47 ± 0.055			0.25 ± 0.25		
Fullness index (%)	4.13			4.43 ± 0.781			5.59 ± 1.065			4.87 ± 1.39		
Fry with food	1			15			29			4		
Total fry	19			25			29			26		

Number of prey (*N*), abundance (*A_i*), frequency of occurrence (*F_i*) (mean ± S.E.). Due to the low occurrence of Nematoda and vegetal rests, their abundance was not quantified, and only the number of stomachs in which it appeared was noted

$P = 0.403$). The size distributions of prey ingested by fry differed from those present in the benthos. Thus, in STR3 the most abundant prey size categories in the benthos were different from those in the stomachs (Fig. 5), and no correlation between average prey size

consumption and mouth gape was found ($r = -0.20$; $P > 0.05$).

A comparison of benthic macroinvertebrate availability and prey selectivity using the Ivlev's selectivity index shows that fry selected positively for

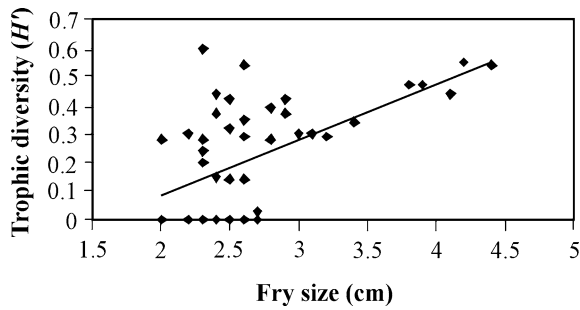


Fig. 3 Trophic diversity-size relationship in brown trout fry. Linear regression equation $y = 0.1926x - 0.2983$ ($r^2 = 0.309$)

Polycentropodidae, *Chironomidae* and *Simuliidae*, but negatively for Hydracarina, Copepoda, *Baetidae*, *Ephemeroptera*, *Heptageniidae*, *Leptophlebiidae*, *Leuctricidae*, *Elmidae* and *Ceratopogonidae* (Table 2; Fig. 6). Nonetheless, *Baetidae* remained a large component of the diet for all fry.

Discussion

Feeding of brown trout fry has been studied before, both in lab conditions and in natural spawning areas. Results of those studies show that feeding in recently emerged fry can be initiated before complete yolk exhaustion, as found in our study, even while alevins are still in the gravel nest. However, comparisons among studies on the amount of yolk still present on the onset of exogenous feeding in salmonids are difficult to establish because of differences in the methodologies used. Thus, Thorpe et al. (1984) indicate that Atlantic salmon fry initiate feeding when yolk constitutes around 3% wet weight of the total wet weight of the alevin, and Kane (1988) refers to Thorpe et al. (1984) and considers alevins of Atlantic salmon to be ready for exogenous feeding

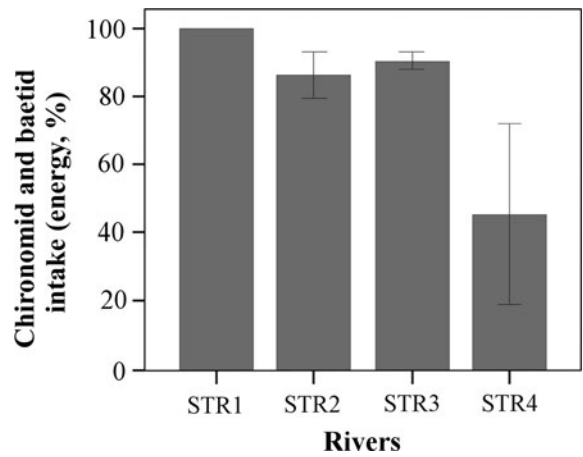


Fig. 4 Contributed energy by chironomid larvae and baetid nymphs (%)

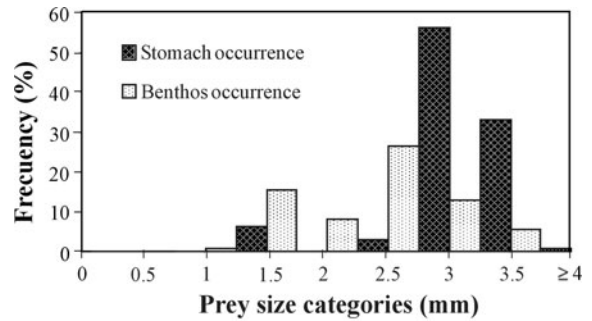


Fig. 5 Benthos and stomach size-frequency distributions in STR3

when yolk constitutes 5% of the total wet weight. Zimmerman & Mosegaard (1992) observed that alevins of brown trout began feeding in experimental conditions when yolk constituted approximately 40% of the total alevin dry weight, while Skoglund & Barlaup (2006) indicate that brown trout fry under natural conditions start feeding when having almost 30% of yolk sac remaining compared to the presumed original size of the yolk sac at hatching.

Table 5 Biochemical composition of the diet and results of comparisons between fry diet in STR2 and STR3 (mean ± S.E.)

	Xemil (STR2)	Iso (STR3)	Mann–Whitney <i>U</i> test
Energy (kJ/g)	0.99 ± 0.205	2.31 ± 0.672	$P < 0.05$
Protein (%)	59.83 ± 0.207	59.97 ± 0.048	$P > 0.05$
Lipid (%)	10.03 ± 0.912	11.64 ± 0.542	$P > 0.05$
Fibre (%)	5.41 ± 0.672	5.92 ± 0.258	$P > 0.05$
Free nitrogen extract (%)	24.71 ± 1.397	22.45 ± 0.783	$P > 0.05$

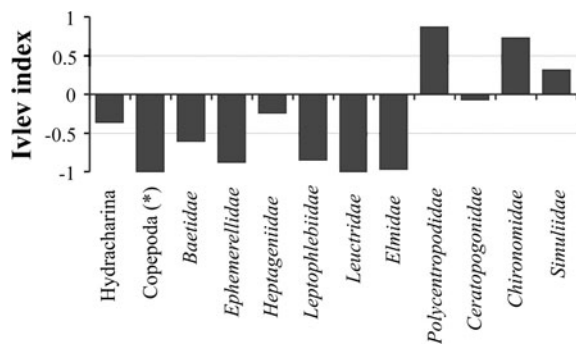


Fig. 6 Ivlev's selectivity index of fry diet in STR3 (*not identified)

Values of yolk remnants at first feeding obtained in our study are clearly greater than those obtained by Thorpe et al. (1984) or Kane (1988) for Atlantic salmon, but using the visual estimation method of Skoglund & Barlaup (2006) we have obtained values close to 30% of yolk sac remaining for brown trout, as indicated by those authors. However, while they analyzed feeding of both pre-emergent and post-emergent individuals in a boreal area, we studied only post-emergent fry, so the possibility of an onset of feeding with higher amounts of yolk remnants while in the nest in our study area might be possible. Indeed, Hendry et al. (1998) observed that the proportion of yolk remnants at emergence in sockeye salmon (*Onchorhynchus nerka*) significantly increased with increasing incubation temperature, and Ojanguren & Braña (2003) showed that not only is the development of brown trout embryos at higher temperatures faster, but exogenous feeding also starts earlier. Further studies using pre-emergent fry need to be done for clarifying this hypothesis. Interestingly, exogenous feeding has been found to decrease yolk absorption rates in brown trout fry (Raciborski, 1987), and Zimmerman & Mosegaard (1992) suggested that exogenous feeding while yolk is still being absorbed may increase the survival potential of alevins, thus saving yolk reserves for periods when external food is limited. However, the real influence of "precocious feeding" on fish size, growth rate or survival is still under discussion (Skoglund & Barlaup, 2006).

Concerning diet composition, our results are in good agreement with those obtained in other studies in salmonids. Chironomid larvae and baetid nymphs

seem to be the most important food items for newborns, as found by many researchers in different geographical areas (McCormack, 1962; Fahy, 1980; Hubert et al., 1993; Keeley & Grant, 1997; Nikcevic et al., 1998; Degerman et al., 2000; Skoglund & Barlaup, 2006), since those are probably the most accessible invertebrates living in the gravel interstices on nesting grounds at the moment of emergence. In our case they provided over 80% of the energetic input.

However, it is not clear whether fry are selective or not at the moment of first feeding, and authors suggest that selection might be based on the size of food items (Fahy, 1980; Keeley & Grant, 1997; Skoglund & Barlaup, 2006). Prey size may affect the prey ingestion in early fish larvae, and much literature concentrates on the relationship between prey size and mouth size as the primary determinant of prey selection (Shirota, 1970; Cunha & Planas, 1999). In general, positive selection for *Polycentropodidae* and *Simuliidae* was greater than would be expected from their body size (>4 mm), suggesting that other factors apart from size, such as locomotor abilities of fish or accessibility of prey are important. Contrastingly, *Leucitricidae* and *Elmidae* were negatively selected compared with other prey of similar body size. Indeed, the availability to the predator and specific prey characteristics such as swimming ability, colour and antipredator behaviour have been found to affect prey selection by larval fishes (O'Brien, 1979; Houde & Schekter, 1980; Reiriz et al., 1998). Thus, the rejection of elmids, as observed by Oscoz et al. (2005), may be due to their lower energetic value because of their intense sclerotization (Power, 1992; Oscoz et al., 2000) or due to their bad taste (Ochs, 1969). All these hypotheses may explain the absence of some items in the stomachs in spite of their abundance in the benthos.

Studies on diet changes that occur during summer growth show a dietary niche shift as fry size increases, with an increase in the diversity, size and number of preys in few months (Hubert et al., 1993; King, 2005; Tonkin et al., 2006). However, when comparing results obtained in our study for fry collected in the four sites, a difference is clear for individuals of STR3, where fry analyzed are slightly longer and heavier than those collected in the other three sites and, more importantly, none of them presented yolk remnants, due to a probable earlier emergence at that site. Interestingly, analysis of their

diet shows the presence of food in all the individuals, as well as a wider feeding niche and a higher average prey size.

There could be several reasons for these differences. First, as already discussed, morphological constraints such as mouth gape certainly impose limitations on feeding behaviour of small fry (Hunter, 1981; Schael et al., 1991; Wainwright & Richard, 1995). However, in our case it seems there is a marked shift in prey capture that occurs in a short phase of fry development, as size differences among the four sites we studied are small. Second, perceptive constraints of newly hatched fry due to the incomplete development of visual system would impede also the capture of diverse preys, although the presence of various taxa in the first diet of fry in all the sites suggest that at least capture seems possible at a very early phase (Novales-Flamarique & Hawryshyn, 1996). Third, locomotor abilities of fry peak only at the end of yolk sac absorption, and at this time velocity and acceleration are at their highest levels with respect to body length (Hale, 1999). Our results seem to be in accordance with this hypothesis, as they suggest a dramatic shift in niche breadth just at the moment of complete yolk absorption, which might be due to the improvement of swimming and handling ability of fry for capturing and ingesting prey. The presence of aerial imagoes only in the stomachs of fry with no yolk provides further support to this hypothesis.

The important constraints in feeding imposed by reduced mobility of fry with yolk remnants have been highlighted before (Thomas et al., 1969; Greenland & Thomas, 1972; Jensen et al., 1991). However, although the influence of early feeding on fry growth and survival is still not clear (Skoglund & Barlaup, 2006), other authors highlight the importance of diet composition during first feeding, as this may have important consequences on physiological functions in later life (Geurden et al., 2007 and references therein). Thus, at the moment of hatching a certain density of small preys is required to be present in the gravel, as searching for food is limited to the nest area and fry forage on available prey. Restoration works on spawning grounds should then allow enough time for complete recolonization by benthic macroinvertebrates, including first instars, in order to assure the presence of the required amount of prey for the feeding of young fry.

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