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Adaptive flexibility in the feeding behaviour of brown trout: optimal prey size

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Abstract

Background: Brown trout, *Salmo trutta* Linnaeus, 1758, is a species of significant conservation and socio-economic importance. A consequence of this importance is the enormous amount of literature that has been published on the species in the last few decades. In general terms, brown trout has been considered as a size-selective predator, even though it is able to feed on a wide range of prey sizes. Nevertheless, there are still some gaps in our knowledge, for example the theoretical relationship between prey numbers and prey sizes eaten by the fish need to be addressed. This research aimed to study optimal prey size in the environment (benthos and drift) as well as the potential relationship between prey size and two other feeding variables (prey numbers and stomach fullness). Additionally, ontogenetic shifts in these variables were addressed.

Results: Brown trout showed a clear preference for 4- to 6-mm-length prey, although the use of prey larger than 10-mm length may be feasible. The similarity of the prey size frequency distribution between the environment (benthos and drift) and the diet in some cases was considerable (from 57.7% to 95.9%). Moreover, the results revealed that the feeding strategy can be related to prey size and the numbers of prey eaten by the brown trout; as food size decreased, prey numbers increased. On the contrary, the correlation between the average prey size and fish length was positive but statistically nonsignificant. A significant ontogenetic shift, in terms of prey size sorted by age classes, was found in only two of eight studied populations. No clear relationship between prey size and stomach fullness was found.

Conclusions: The feeding strategy of this species is flexible and clearly influenced by the size frequency distribution of potential prey: trout fed on either small numbers of large prey or large numbers of small, and theoretically low energy, prey. Our approach covers a general subject in trophic ecology and animal behaviour that may be applicable to other fish species to improve our understanding of predator feeding behaviour.

Keywords: Trophic ecology; Foraging behaviour; Flexible behaviour; *Salmo trutta*; Prey size; Available prey; Benthos; Drift

Background

Ecologists have considered the prey size hypothesis, the relationships between prey size and handling efficiency by predators, as one of the main factors involved in feeding behaviour (e.g. Mock 1985; Török 1993; Denoël and Joly 2001). With regard to fish species, much research has focused on the relationship between prey size and handling efficiency (e.g. Mittelbach 1981; Reimchen 1991), and some fishes may be gape-limited predators, especially when they are young (e.g. Schmitt and Holbrook 1984; Schael et al. 1991; Sánchez-Hernández et al. 2011a). Indeed, prey size is a key variable in the feeding behaviour of fishes (see Keeley and Grant 2001 and references therein), which is usually considered to be size selective (e.g. O'Brien et al. 1976; Bannon and Ringler 1986). For example, studies under controlled laboratory conditions have demonstrated that fishes show a clear preference for large prey items (Ringler 1979; Wetterer 1989), which are normally the most profitable in energetic terms, even though handling costs increase with increasing prey size (e.g. Gill 2003). However, it is important to note that prey energy content may exhibit substantial variations depending on seasonal development, life history strategies or taxonomic group (e.g. Gupta and Pant 1983; Cobo et al. 1999; 2000). Factors other than prey size and handling efficiency, such as

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some fish characteristics (e.g. prior experience, locomotor abilities, stomach fullness and sensory capabilities) and physical habitat characteristics (e.g. flow patterns and structural complexity of habitat) may also play an important role in the feeding behaviour of fishes (e.g. Gill and Hart 1994; Gerking 1994; Sánchez-Hernández et al. 2013). Although the feeding behaviour of fish species has received considerable attention from the scientific community (see above literature), to the best of our knowledge, the theoretical relationship between prey numbers and prey sizes eaten by fish has not been addressed so far.

Brown trout *Salmo trutta* Linnaeus, 1758 (henceforth simply trout), is a species of Eurasian origin but, at present, is naturalized in many other areas all over the world (Klemetsen et al. 2003). Fortunately, the feeding behaviour of trout has been well studied (e.g. Fochetti et al. 2003; Oscoz et al. 2008; Evangelista et al. 2014), and during their life history, trout undergo ontogenetic dietary shifts (Sánchez-Hernández et al. 2013 and references therein). With regard to changes in prey size during ontogeny, mean prey size usually increases with both trout size and age (e.g. Steingrímsson and Gíslason 2002; Montori et al. 2006; Jensen et al. 2008; Sánchez-Hernández and Cobo 2012; Sánchez-Hernández et al. 2013). In spite of this ontogenetic shift, several researchers have demonstrated that the influence of gape-limited prey ingestion in this species is insignificant (Newman 1987; Rincón and Lobón-Cerviá 1999). Notwithstanding, trout may be used as a model species in studies of feeding behaviour, regardless of the apparent lack of a relationship between mouth dimensions and prey size. Here, we studied optimal prey size in the environment (benthos and drift) as well as the potential relationship between prey size and other variables (prey numbers, stomach fullness, fish size and fish age). We hypothesized that prey numbers should be low when the predator feeds on large prey items, and *vice versa*. We further hypothesized that prey size may be highly dependent on fish size, fish age and stomach fullness.

Methods

For the purpose of the study, and in order to avoid possible differences in feeding behaviour among populations due to differences in physical habitat characteristics, samples were collected in wadeable riffle sections with similar environmental characteristics. In total, eight neighbouring rivers of Galicia (NW Spain) were sampled (Figure 1) during June 2003 (Rois, Santa Lucía, Sar and Traba rivers) and September 2007 (Anllóns, Furelos, Lengüelle and Tambre rivers). Prior to electrofishing, samples of potential prey items (benthic and drifting invertebrates) were collected to study prey availability in the environment. Benthic invertebrates were collected from riffles using a 0.1-m^2 Surber sampler ($n = 3$), and a Brundin net (250-μm mesh size, 1 m long, 30-cm mouth diameter) was used to collect drifting invertebrates. Drift nets were set at sunrise (8:00 a.m.) and retrieved after at least 2.5 h (ranging between 179 and 200 min). After collection, we fixed samples using 4% formalin and stored them for later processing. Information on prey availability is only provided for rivers surveyed in 2007.

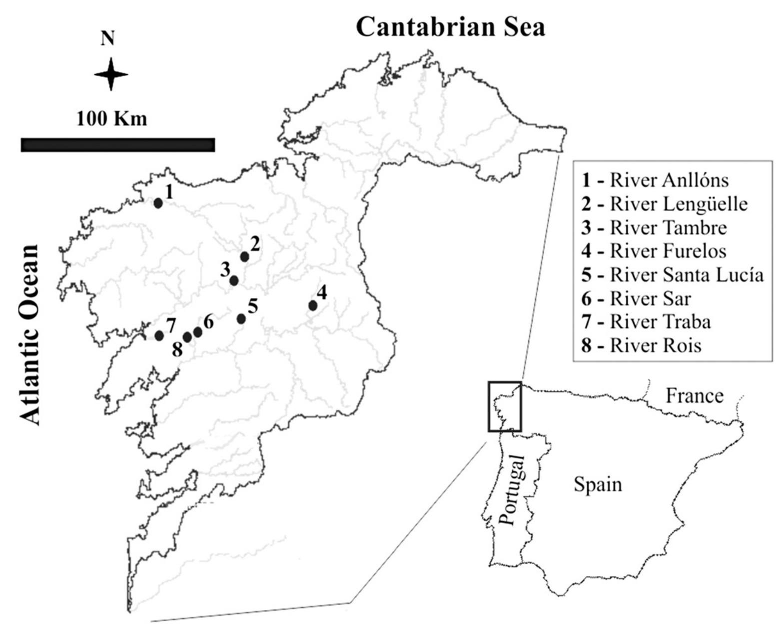

Figure 1 Maps of the Iberian Peninsula and north-western Spain showing the sampling sites.

Table 1 Size frequency (%) of the prey consumed by trout

	Size class (mm)										
	0 to 2	**2 to 4**	**4 to 6**	**6 to 8**	**8 to 10**	**10 to 12**	**12 to 14**	**14 to 16**	**16 to 18**	**18 to 20**	**>20**
Anllóns											
0+ (*n* = 2)	0	10.8	27.0	2.7	13.5	45.9	0	0	0	0	0
1+ (*n* = 18)	1.3	18.4	23.7	3.0	27.3	24.7	0	0.3	0	0.7	0.7
2+ (*n* = 9)	0.4	18.9	56.9	1.3	4.7	17.0	0	0.2	0	0	0.6
3+ (*n* = 6)	0	15.1	52.8	15.1	1.9	11.3	1.9	1.9	0	0	0
Pooled data	0.7	18.2	43.7	2.8	12.8	20.6	0.1	0.3	0	0.2	0.6
Furelos											
0+ (*n* = 37)	2.1	3.2	33.5	0	1.9	51.0	0	6.5	0	0	1.8
1+ (*n* = 19)	1.4	4.8	81.0	0.1	0.2	6.0	0	3.9	0	0	2.6
2+ (*n* = 5)	0.5	2.8	54.1	0	8.7	4.1	0	8.7	0	0	21.1
3+ (*n* = 3)	3.2	18.5	15.3	0.8	0	33.1	0	0	0	0	29.0
Pooled data	1.6	4.8	60.7	0.1	1.5	20.9	0	4.9	0	0	5.4
Lengüelle											
0+ (*n* = 6)	0	2.4	62.9	0	13.7	19.4	0	0.8	0	0	0.8
1+ (*n* = 13)	0	18.3	37.7	0.4	16.5	20.4	0	0	0	0	6.7
2+ (*n* = 16)	0.8	7.9	53.1	0.8	4.3	24.1	0	0.2	0	0	8.7
3+ (*n* = 4)	5.8	1.9	32.7	0	9.6	38.5	0	0	0	0	11.5
Pooled data	0.7	10.0	48.7	0.5	9.4	23.2	0	0.2	0	0	7.2
Tambre											
1+ (*n* = 24)	1.6	12.6	59.6	0.7	6.7	17.0	0	0.9	0	0	0.8
2+ (*n* = 6)	0.3	5.2	56.0	0.9	4.0	28.4	0	2.4	0	0	2.8
Pooled data	1.4	11.2	58.9	0.8	6.2	19.2	0	1.2	0	0	1.2
Rois											
1+ (*n* = 31)	2.7	7.7	33.8	3.2	14.3	33.9	0	2.7	0	0.2	1.4
2+ (*n* = 2)	2.0	6.0	28.0	6.0	4.0	46.0	0	2.0	0	0	6.0
Pooled data	2.7	7.6	33.6	3.4	13.8	34.5	0	2.7	0	0.2	1.6
Santa Lucía											
1+ (*n* = 24)	2.2	29.4	34.7	7.0	5.0	7.9	0	8.0	0.3	2.3	3.4
2+ (*n* = 5)	3.2	20.6	40.2	10.6	4.2	15.3	0	4.8	0	0.5	0.5
Pooled data	2.4	27.7	35.8	7.7	4.8	9.3	0	7.4	0.2	1.9	2.9
Sar											
1+ (*n* = 25)	0.6	33.8	4.0	0.9	1.1	57.8	0	0.2	0	0.1	1.6
2+ (*n* = 4)	1.0	17.7	3.0	0.5	3.4	70.4	0	1.5	0	0	2.5
Pooled data	0.6	32.2	3.9	0.9	1.3	59.0	0	0.3	0	0.05	1.7
Traba											
1+ (*n* = 15)	0.3	4.8	45.5	0.4	14.8	33.8	0	0.2	0	0	0.1
2+ (*n* = 14)	0.5	7.6	51.5	1.0	10.7	28.1	0	0.2	0	0	0.2
Pooled data	0.4	5.7	47.6	0.6	13.4	31.8	0	0.2	0	0	0.2
Total (*n* = 288)	3.44	5.00	44.44	3.42	8.27	31.97	0.01	1.30	0.03	0.17	1.97

Data are displayed for each sampling site, each age class and in total using pooled data. Prey were grouped into 2-mm-length classes. The sample size (*n*) of each age class is shown in brackets.

Trout were collected using pulsed D.C. backpack electrofishing equipment (ELT60II, Hans Grassl GmbH, Schönau am Königssee, Germany). Fishes were killed immediately with an overdose of anaesthetic (benzocaine) and transported in cool boxes (approximately 4°C) to the laboratory, where they were frozen at −30°C until processing. In the laboratory, fishes were measured for fork length (FL; nearest 1 mm) and weighed (nearest 0.01 g), and the stomachs were removed. Estimates of fish age were made by scale examination and by using Petersen's length-frequency method (Bagenal and Tesch 1978). Age-4+ individuals were not included in the diet analysis because only one specimen was captured in the River Furelos. No empty stomachs were found, and the stomach fullness index (f) was calculated as $f = (Ws/W) \times 100$, where Ws is the total stomach content mass (g) and W is the fish mass (g).

Potential (benthic and drifting invertebrates) and actual prey items were counted and measured (total length) with a digital micrometer (0.01-mm resolution, Mitutoyo Absolute, Mitutoyo Corporation, Takatsu-ku, Japan). The number of fragmented or partially digested invertebrates 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 and Lobón-Cerviá 1999), which was normally the best-preserved part.

The similarity between the size distributions of potential prey in the environment (benthos and drift) and those consumed by trout was assessed using the Bray-Curtis similarity index. The data were first transformed by $Y = \log(x + 1)$, and the similarity index was calculated using the PRIMER statistical package version 5.0 (Clarke and Gorley 2001). In the present study, in order to assess whether prey size selection is dependent upon the size frequency distribution of available prey, we clustered all trout regardless of age at each sampling site. Additionally, to explore ontogenetic shifts, the similarity matrix was calculated separately for each age class.

Finally, with the aim of exploring the possibility of a nonlinear relationship between prey size and the other analysed variables (prey numbers, stomach fullness and fish size), the curve estimation procedure was used using pooled data, which compared eight different models (linear, logarithmic, inverse, quadratic, exponential, power, compound and S-curve). The model with the highest adjusted Pearson's rank correlations coefficient (R) was chosen. The data were not normally distributed, so in order to analyse differences among age classes in the studied variables (prey size, prey numbers and stomach fullness), nonparametric analyses (Mann-Whitney and Kruskal-Wallis tests) were used. The Mann-Whitney U-test was used to compare differences between two independent groups because in some rivers (Rois, Santa Lucía, Sar, Traba and Tambre rivers) only two age classes were analysed (1+ and 2+). Kruskal-Wallis test was used to detect differences among four groups (0+, 1+, 2+ and 3+) in the other rivers (Anllóns, Furelos and Lengüelle). Statistical analyses were conducted using the programme IBM SPSS Statistics 20 software (IBM Corporation, Armonk, NY, USA). All of these tests were considered statistically significant at P level < 0.05.

Results

A total of 288 trout (range = 48 to 300 mm) was examined in the present study, with 15,131 prey items (range = 1.1

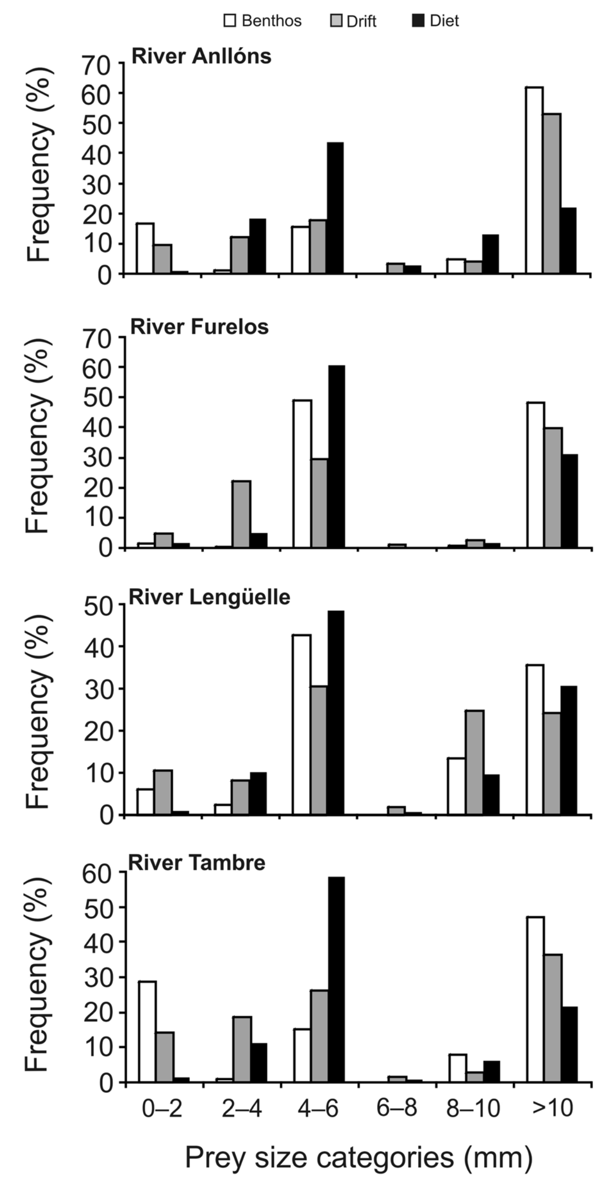

Figure 2 Size frequency of the benthos, drift and trout diet. Size frequency of the benthos, drift and trout diet from Anllóns, Furelos, Lengüelle and Tambre rivers surveyed in September 2007. Diet data were pooled regardless fish age for each sampling site.

Table 2 Values of the Bray-Curtis index of size frequency distribution similarity between the environment (benthos and drift) and diet

	Diet *versus* benthos				Diet *versus* drift			
	Anllóns	Furelos	Lengüelle	Tambre	Anllóns	Furelos	Lengüelle	Tambre
0+	70.6	89.1	88.0	-	85.3	84.8	78.2	-
1+	69.2	81.4	82.4	75.5	84.5	74.1	84.0	83.7
2+	68.3	82.7	83.5	71.8	80.7	77.8	83.3	81.6
3+	57.7	74.6	95.9	-	76.2	88.4	84.8	-
Pooled data	67.2	88.4	86.2	72.6	82.6	83.4	85.2	83.7

Similarities are shown as percentages. Data are only displayed for rivers surveyed in 2007.

to 60 mm), 3,855 benthic macroinvertebrates (range = 2 to 60 mm) and 980 drifting invertebrates (range = 0.5 to 30 mm) measured. Trout fed mainly on prey within the 2- to 6-mm size range, with prey of 4 to 6 mm being the most commonly consumed, except at two sampling sites (Rois and Sar) where it was 10 to 12 mm (Table 1). The observed prey size frequency distribution in the stomachs was not identical to the potential prey in the environment (benthos and drift) and varied among sampling sites (Figure 2). However, the Bray-Curtis similarity index (Table 2) showed that the similarity of the size frequency distribution between the environment (benthos and drift) and the diet in some cases was considerable and accounted for >55% in all cases, ranging from 57.7% to 95.9% (Table 2). In general, 4- to 6- and 6- to 8-mm size categories were more frequently encountered in the diet than in the environment, whereas invertebrates larger than 10 mm were more frequently found in the environment than in the diet (Figure 2).

With regard to ontogenetic shifts, the 4- to 6-mm size category was generally dominant in all age groups (Table 1), as previously observed from pooled data. There were only differences in the average prey size among age classes in two rivers (Table 3), where prey size increased with increasing fish age (Figure 3). Prey numbers were only statistically different among age classes in two rivers (Table 3), achieving the highest value in 2+ fish in both populations (Table 4). In most cases, stomach fullness varied among age classes (statistical analysis shown in Table 3), with young-of-the-year (YOY) fish having the highest values and fullness decreasing with age (Table 5).

The relationship between average prey size and stomach fullness was positive but only statistically significant for the exponential model ($R = 0.138$, $P = 0.019$). The correlation between mean prey size and fish length was positive but statistically nonsignificant ($P > 0.05$ in all cases). A noteworthy result of this study is the negative relationship between prey numbers and mean size ($P < 0.01$ in all cases); as prey numbers increased, prey size decreased (Figure 4; logarithmic regression model $R = -0.293$, $P = 0.001$).

Discussion

This study demonstrated that trout have a clear preference for certain prey size categories according to prey availability in the environment, corroborating the theoretical considerations predicted by Bannon and Ringler (1986) and field observations reported by several researchers (Newman and Waters 1984; Newman 1987; Rincón and Lobón-Cerviá 1999). In addition, the study exemplifies the feeding behaviour flexibility of this fish species with respect to the relationship between prey sizes and numbers eaten.

The size frequency distribution of potential prey can have a strong influence on prey size selection. Although

Table 3 Statistical comparisons of the mean prey size, prey numbers and stomach fullness index (*f*) among age classes

	Mean prey size		Prey numbers		Stomach fullness index	
	Test	*P* value	Test	*P* value	Test	*P* value
Anllóns	$H = 3.1$	0.373	$H = 12.3$	*0.006*	$H = 19.7$	*<0.001*
Furelos	$H = 8.7$	*0.033*	$H = 3.6$	0.303	$H = 46.2$	*<0.001*
Lengüelle	$H = 4.3$	0.226	$H = 1.5$	0.672	$H = 19.5$	*0.001*
Tambre	$U = 41.0$	0.108	$U = 69.5$	0.897	$U = 24.0$	*0.013*
Rois	$U = 18.0$	0.327	$U = 25.0$	0.650	$U = 4.0$	*0.042*
Santa Lucía	$U = 43.0$	0.326	$U = 24.5$	*0.040*	$U = 52$	0.644
Sar	$U = 12.0$	*0.016*	$U = 38.0$	0.448	$U = 46$	0.800
Traba	$U = 71.0$	0.138	$U = 63.0$	0.067	$U = 33.0$	*0.002*

Kruskal-Wallis (*H*) and Mann-Whitney (*U*) tests. Data are displayed for each sampling site. Statistically significant results are marked in italics.

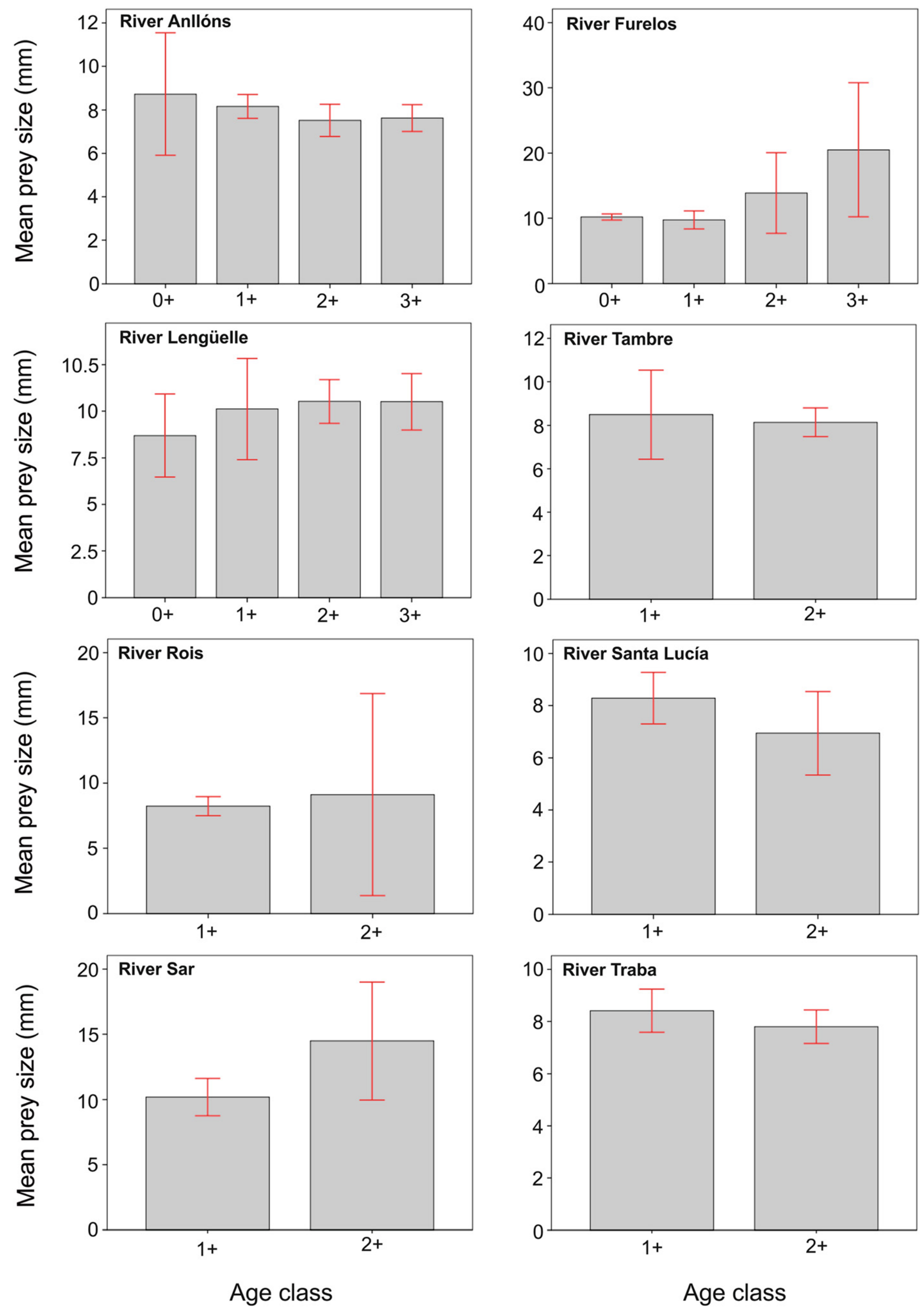

Figure 3 Mean prey size (mm) consumed by trout. Error bars represent the 95% confidence intervals.

the size frequency distribution of prey in the diet was not identical to that of potential prey in the environment, as anticipated, prey size selection was highly dependent upon the size frequency distribution of available prey (Rincón and Lobón-Cerviá 1999). Predictive models have estimated an optimal prey size of between 2.8 and 97 mm for trout (Bannon and Ringler 1986); however, a great variety of results, with respect to prey size, have been observed in the wild (e.g. McLennan and MacMillan 1984; Rincón and Lobón-Cerviá 1999; Montori et al. 2006; Sánchez-Hernández et al. 2011a; 2011b). In fact, studies have demonstrated that newly emerged trout fry mainly consume prey of 3 to 4 mm (Sánchez-Hernández et al. 2011a), whereas older age-0 individuals feed on prey of 5.5 mm mean size (Sánchez-Hernández et al. 2011b). McLennan and MacMillan (1984) found that trout preyed upon prey items varying in length between 6 and 10 mm. Rincón and Lobón-Cerviá (1999) demonstrated that organisms of 1 to 2 mm long were generally the most numerous in trout diets, while Montori et al. (2006) stated that 2 to 3 mm prey

Table 4 Mean prey numbers among age classes

	0+	1+	2+	3+	Total (pooled data)
Anllóns	18.5 (18 to 19)	16.9 (2 to 38)	52.3 (13 to 224)	8.3 (2 to 19)	24.7 (2 to 224)
Furelos	19.6 (4 to 82)	69.6 (3 to 363)	43.6 (7 to 139)	41.3 (3 to 100)	37.3 (3 to 363)
Lengüelle	20.7 (8 to 55)	22.4 (7 to 38)	30.9 (4 to 173)	13.0 (8 to 17)	24.6 (4 to 173)
Tambre	-	55.7 (1 to 214)	54.5 (6 to 117)	-	55.5 (1 to 214)
Rois	-	32.8 (7 to 85)	25.0 (24 to 26)	-	32.3 (7 to 85)
Santa Lucía	-	32.8 (7 to 62)	58.4 (32 to 103)	-	37.2 (7 to 103)
Sar	-	76.6 (12 to 309)	50.7 (33 to 88)	-	73.0 (12 to 309)
Traba	-	189.2 (8 to 388)	119.9 (11 to 235)	-	155.7 (8 to 388)

Data are displayed for each sampling site. Minimum and maximum are shown in brackets.

are commonly consumed. Steingrímsson and Gíslason (2002) found that the size of some prey items eaten by trout varied between 2.5 and 6.5 mm and between 1.5 and 12.5 mm for *Simulium vittatum* Zetterstedt, 1838, and *Radix* (=*Lymnaea*) *peregra* (Müller, 1774), respectively. However, the optimal prey size may vary ontogenetically, with mean sizes between 4.2 and 8.4 mm in 0+ and 2+ fish, respectively (Sánchez-Hernández and Cobo 2012). In addition, studies have demonstrated that optimal prey size is higher in lakes than rivers due to the piscivorous behaviour of trout in still waters (Keeley and Grant 2001 and references therein); generally, prey items range from 25 to 87 mm in lakes (e.g. L'Abée-Lund et al. 1992; Sánchez-Hernández and Amundsen 2015). Hence, based on the reviewed literature and the present study, the optimal prey size for trout appears to be 2 to 10 mm, although prey longer than 10 mm can be consumed.

Trout often undergo ontogenetic dietary shifts, and it has been demonstrated that mean prey size usually increases throughout ontogeny (e.g. Steingrímsson and Gíslason 2002; Montori et al. 2006; Sánchez-Hernández and Cobo 2012; Sánchez-Hernández et al. 2013). On the contrary, our study did not reveal consistent, significant increases in prey size with increasing fish length (no significant relationships) or age (statistically significant positive relationships were found for two of eight populations). The lack of allometric scaling in this study could partly be an artefact of our fish samples, which lacked large (>300 mm) individuals. Alternatively, the results may corroborate the suggestions of previous studies (Newman 1987; Rincón and Lobón-Cerviá 1999) that, in the absence of very small specimens, such as young larvae in which prey size may affect prey ingestion (Sánchez-Hernández et al. 2011a), gape-limited prey ingestion may not occur.

The sizes of prey consumed may affect the numbers of prey eaten by trout. A notable result of this study was that the relationship between mean prey size and prey numbers was significant and negative. A range of factors can influence whether large or small food items are consumed, but in the current study, it appeared that trout fed on either small numbers of large prey or large numbers of small, and theoretically low energy, prey. Stomach fullness, i.e. limitations of stomach volume, might therefore be a key variable in prey size selection. Within the limits imposed by gape size, fishes with big stomachs should be able to feed on a wider range of prey sizes than fishes with small stomachs (e.g. Gosch et al. 2009), but when the stomach is partially full, fish might choose small rather than large food items (Truemper and Lauer 2005). In this study, the relationship between average prey size and stomach fullness was positive, but was only statistically significant for the exponential model, suggesting that trout may be able to use relatively large food items regardless of their stomach fullness. This result could be because feeding intensity was low in the

Table 5 Mean feeding intensity (%), measured as stomach fullness index (*f*), among age classes

	0+	1+	2+	3+	Total (pooled data)
Anllóns	5.2 (2.2 to 8.2)	0.7 (0.3 to 1.6)	0.8 (0.1 to 3.5)	0.1 (0.1 to 0.3)	0.9 (0.1 to 8.2)
Furelos	9.0 (3.4 to 20.6)	1.0 (0.1 to 2.1)	1.0 (0.4 to 1.8)	1.2 (0.7 to 1.4)	5.6 (0.1 to 20.6)
Lengüelle	1.9 (0.5 to 6.6)	1.0 (0.3 to 1.9)	0.6 (0.1 to 2.8)	0.2 (0.1 to 0.3)	0.9 (0.1 to 6.6)
Tambre	-	0.8 (0.1 to 1.9)	0.3 (0.1 to 0.6)	-	0.7 (0.1 to 1.9)
Rois	-	4.8 (1.5 to 15.8)	1.9 (1.8 to 1.9)	-	4.6 (1.5 to 15.8)
Santa Lucía	-	5.1 (0.9 to 12.9)	4.3 (3.1 to 7.3)	-	5.0 (0.9 to 12.9)
Sar	-	10.5 (1.7 to 26.9)	7.7 (5.2 to 9.9)	-	10.1 (1.7 to 26.9)
Traba	-	16.6 (1.3 to 28.2)	7.3 (0.5 to 14.2)	-	12.1 (0.5 to 28.2)

Data are displayed for each sampling site. Minimum and maximum are shown in brackets.

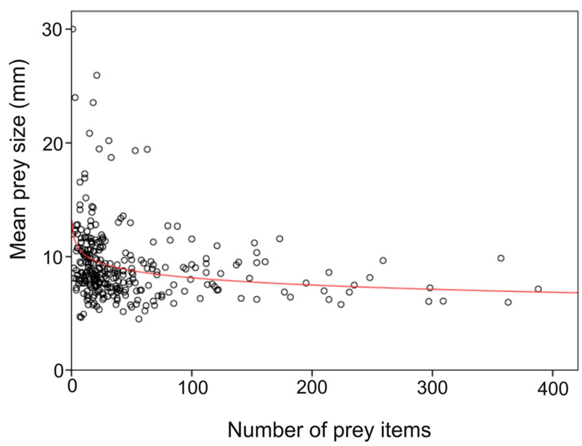

Figure 4 Relationship between mean prey size (mm) and numbers of prey eaten by trout using pooled data. Logarithmic regression equation is shown in red.

majority of the fishes; 85.1% of the fish had values of stomach fullness below 10%. Furthermore, the study confirmed a previous observation (Sánchez-Hernández and Cobo 2013) that summer feeding intensity of trout may decrease with fish age, being considerably higher in juveniles than in older age groups.

Conclusions

The feeding strategy of trout is flexible and clearly influenced by the size frequency distribution of potential prey: trout fed on either small numbers of large prey or large numbers of small, and theoretically low energy, prey. This study covers a general subject in trophic ecology and animal behaviour that may be applicable toward other fish species, especially other salmonids, to improve our understanding of feeding behaviour.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

FC participated in the design and coordination of the study, and JSH participated in field sampling and conducted the laboratory work. FC helped to draft the manuscript and JSH finalized the manuscript. Both authors read and approved the final manuscript.

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