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Ontogenetic dietary shifts in the summer feeding intensity of brown trout in relation to fish condition

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Abstract. We examined condition factor, hepatosomatic index and stomach fullness in brown trout to study if feeding intensity can be related to fish condition. Trout were collected at three locations during the summer in temperate rivers (Galicia, NW Spain). Our findings suggest that the feeding intensity is inversely related with the fish condition because the stomach fullness decreases with fish age and size and the condition factor is the lowest in young-of-the-year (YOY). In general, no significant differences among age classes were found in the hepatosomatic index, except in one river (the River Lengüelle) in which YOY shows the highest value. The high feeding intensity of YOY during summer could be related with the increases in fish condition and survival in the later autumn and winter.

Key words: *Salmo trutta*, feeding activity, condition factor, hepatosomatic index, ontogeny

Introduction

The intake of food by fishes has a great importance to the fish development, and when the daily intake is above the maintenance level, the total energy content of the fish increases and growth occurs (Elliott 1994). Hence, several studies emphasize the importance of the feeding intensity in the acquisition of energetic reserves (e.g., Rikardsen et al. 2006), feature that is especially important in juveniles because the corporal reserve is higher in older fishes (e.g., Nomura et al. 2001).

Studies of the feeding ecology of *S. trutta* are frequent across the world (e.g., Jensen et al. 2004, Fochetti et al. 2008, Sánchez-Hernández et al. 2011), and the fullness index have been widely used to study the feeding intensity in salmonids (Kara & Alp 2005, Shustov et al. 2012, Cobo et al. 2013). Although the shifts in the feeding behaviour of brown trout during the ontogeny are well documented (e.g., Fochetti et al. 2008, Sánchez-Hernández & Cobo 2012, Sánchez-Hernández et al. 2013), other aspects of its feeding behaviour such as the ontogenetic shifts in the feeding intensity remain unclear. In this context, Kara & Alp (2005) found that the brown trout between 5.7 cm and 32 cm fed most intensively, whilst the intensity declined above 32 cm length. So, the aims of the present study were (1) to study if the feeding intensity of brown trout varies with age during the summer and (2) to verify whether this difference in the feeding intensity among age classes could be related to fish condition.

Material and Methods

Individuals were collected using pulsed D.C. backpack electrofishing equipment (Hans Grassl GmbH, ELT60II) following the standardised electric fishing procedures described in the European CEN directive Water analysis – Fishing with electricity (EN 14011; CEN 2003) for wadable rivers. Brown trout were collected in three wadeable riffle sections in oligotrophic rivers draining granitic catchments in Galicia (NW Spain) (Martínez-Ansemil & Membiela 1992) during three consecutive days of September 2007: the River Anllóns (43°13′ N and 8°53′ W), the River Furelos (42°52′ N and 8°01′ W) and the River Lengüelle (42°58′ N and 8°27′ W).

A total of 139 individuals were captured (Table 1), measured to the nearest 1 mm and weighed to the nearest 1 g. Age of each individual was determined by scale reading. In the laboratory, individuals were dissected in order to extract the stomach and the liver. The condition factor (*CF*) was calculated using the formula $CF = 100\ W/L^3$, where W is the wet weight (g) before evisceration and L is the fork length (cm).

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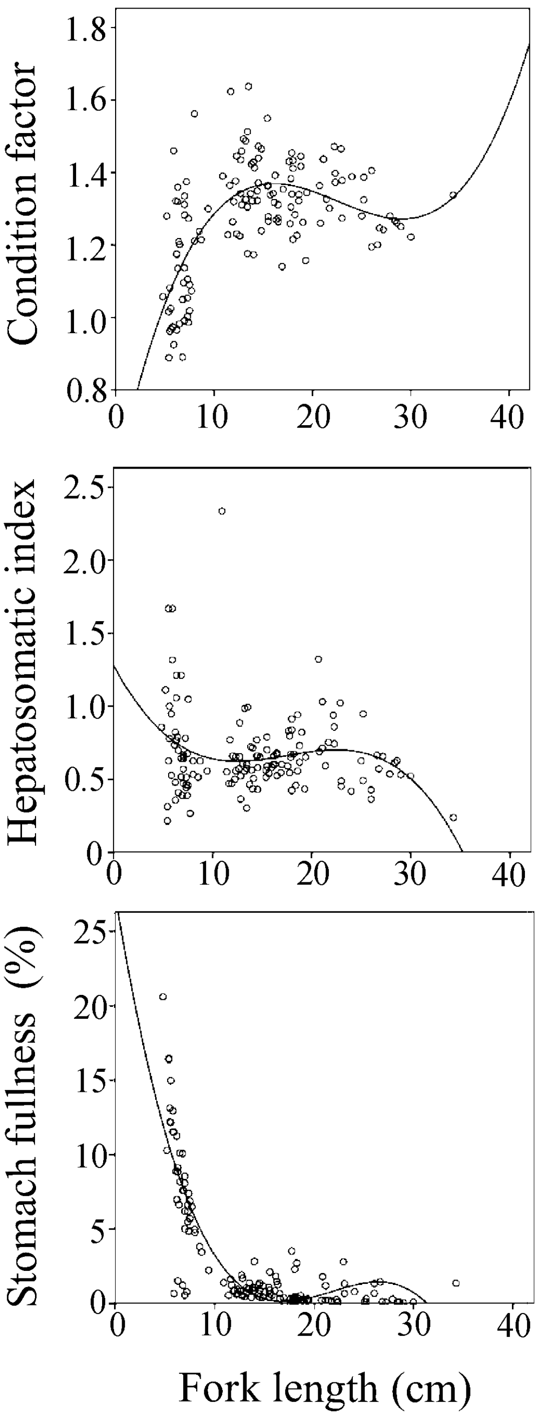

Fig. 1. Plots of curve estimation procedure between variables (condition factor, hepatosomatic index and stomach fullness index) and fork length in total using pooled data for brown trout. Observed (dots) and cubic regression model (lines).

Hepatosomatic index (*HSI*) was calculated as: $HSI = (W_l/W_b) \times 100$, where W_l is the wet liver weight and W_b is the wet body weight. The stomach fullness index (*f*) was calculated as $f = (W_s/W) \times 100$, where W_s is the total stomach content mass (g) and *W* is the fish mass (g).

The non-parametric Kruskal-Wallis tests for non-normal data were used for detecting differences in the *CF*, *HSI* and *f* among age classes in each studied river and in total using pooled data. In order to explore the possibility of a nonlinear relationship between variables (*CF*, *HSI* and *f*) and fork length the curve estimation procedure was used, which compared 11 different models (linear, quadratic, cubic, exponential…). The model with the highest adjusted R^2 was chosen. All tests were considered statistically significant at *p* level < 0.05. Statistical analyses were conducted using the programme IBM SPSS Statistics 20.

Results

Regarding morphological indices, in spite of *CF* was lower in young-of-the-year (YOY) than the other age classes in the three studied rivers, the significant differences were found only in the River Furelos (Table 2). Opposite, only significant differences in the *HSI* were found in the River Lengüelle in which the age-0+ shows the highest value (Table 2). With pooled data (total), differences among age classes were significant for *CF* and *HSI* (Table 2).

In the three studied rivers, results of the stomach fullness index showed high variations among age classes, being higher in age-0+ than the other age classes (Table 2). According to the curve estimation procedure the relationship between variables (*CF*, *HSI* and *f*) and fork length was best described by a cubic regression model (Fig. 1). As expected, the relation between the stomach fullness and fish size was negative in all cases. However, only in the River Furelos the relationship between *CF* and *HSI* and fish length was significant, being the correlation positive for *CF* and negative for *HSI* (Table 3).

Discussion

The energetic reserves in the body of the fish changes depending on the age and season (e.g., Nomura et al. 2001, Rikardsen et al. 2006). Several researchers have demonstrated that the condition factor and the hepatosomatic index serve to assess the overall fish condition, providing information on energy reserves (Herbinger & Friars 1991, Van der Oost et al. 2003, Cobo et al. 2013). In spite that statistical differences between rivers and age-class might be due to the differences in sample size; in our case, only in the River Lengüelle the *HSI* decreases with fish age. Results that may reflect the storage of glycogen in the liver in YOY as a result of the higher food intake, and similar than studies about starvation and refeeding under laboratory conditions (e.g., Machado et al.

Table 1. Size and the number of brown trout used in the present study. Mean ± standard error (SE). Data are presented for each age class and in total.

	Age-0+	Age-1+	Age-2+	Age-3+	Age-4+	Total
the River Anllóns						
Mean size (cm)	7.9 ± 1.45	14.7 ± 0.48	19.2 ± 0.52	28.5 ± 0.39	-	17.8 ± 0.99
Maximum size (cm)	9.4	17.9	22.3	30	-	30
Minimum size (cm)	6.5	10.9	17.7	27	-	6.5
Number of trout (*n*)	2	18	9	6	0	35
the River Furelos						
Mean size (cm)	6.6 ± 0.16	14.5 ± 0.32	21.7 ± 1.07	26.2 ± 0.20	34.6	11.5 ± 0.81
Maximum size (cm)	8.7	17	24	26.6	-	34.6
Minimum size (cm)	4.8	12	18	26	-	4.8
Number of trout (*n*)	37	20	5	3	1	66
the River Lengüelle						
Mean size (cm)	6.6 ± 0.19	12.7 ± 0.19	19.7 ± 0.49	25.5 ± 0.42	-	16.1 ± 0.96
Maximum size (cm)	7.2	13.9	22.9	26.8	-	26.8
Minimum size (cm)	5.9	11.7	16.5	25	-	5.9
Number of trout (*n*)	6	12	16	4	0	38
Total number of trout (*n*)	45	50	30	13	1	

Table 2. Condition factor (*CF*), hepatosomatic index (*HSI*) and stomach fullness index (*f*). Mean ± standard error (SE). Data are presented for each age class. Kruskal-Wallis test for comparisons between age classes within rivers and rivers within age classes. Significant differences are marked in bold.

	Age-0+	Age-1+	Age-2+	Age-3+	Age-4+	Kruskal-Wallis test
Condition factor						
the River Anllóns	1.24 ± 0.049	1.35 ± 0.025	1.32 ± 0.032	1.25 ± 0.008	-	$H = 6.48$; $p = 0.090$
the River Furelos	1.10 ± 0.025	1.33 ± 0.172	1.34 ± 0.031	1.26 ± 0.069	1.34	$H = 30.92$; **$p < 0.001$**
the River Lengüelle	1.29 ± 0.058	1.43 ± 0.037	1.36 ± 0.018	1.31 ± 0.030	-	$H = 5.68$; $p = 0.128$
Total (pooled data)	1.13 ± 0.023	1.36 ± 0.015	1.34 ± 0.014	1.27 ± 0.018	1.34	$H = 46.90$; **$p < 0.001$**
Kruskal-Wallis test	$H = 8.09$; **$p = 0.017$**	$H = 4.96$; $p = 0.084$	$H = 0.58$; $p = 0.746$	$H = 2.06$; $p = 0.357$	-	-
Hepatosomatic index						
the River Anllóns	0.63 ± 0.070	0.66 ± 0.100	0.67 ± 0.050	0.58 ± 0.200	-	$H = 3.49$; $p = 0.322$
the River Furelos	0.66 ± 0.05	0.64 ± 0.028	0.59 ± 0.092	0.48 ± 0.091	0.24	$H = 4.97$; $p = 0.290$
the River Lengüelle	1.05 ± 0.156	0.61 ± 0.054	0.78 ± 0.057	0.66 ± 0.099	-	$H = 9.49$; **$p = 0.023$**
Total (pooled data)	0.71 ± 0.049	0.64 ± 0.039	0.72 ± 0.038	0.58 ± 0.039	0.24	$H = 24.04$; **$p < 0.001$**
Kruskal-Wallis test	$H = 7.10$; **$p = 0.029$**	$H = 4.27$; $p = 0.118$	$H = 3.47$; $p = 0.176$	$H = 1.09$; $p = 0.577$	-	-
Stomach fullness						
the River Anllóns	5.20 ± 2.979	0.72 ± 0.092	0.85 ± 0.433	0.11 ± 0.034	-	$H = 19.67$; **$p < 0.001$**
the River Furelos	9.02 ± 0.643	1.09 ± 0.139	1.00 ± 0.246	1.15 ± 0.24	1.36	$H = 48.29$; **$p < 0.001$**
the River Lengüelle	1.81 ± 0.958	1.02 ± 0.129	0.57 ± 0.204	0.16 ± 0.050	-	$H = 19.51$; **$p = 0.001$**
Total (pooled data)	7.9 ± 0.665	0.94 ± 0.074	0.73 ± 0.171	0.36 ± 0.135	1.36	$H = 125.5$; **$p < 0.001$**
Kruskal-Wallis test	$H = 13.32$; **$p = 0.01$**	$H = 6.79$; **$p = 0.033$**	$H = 4.63$; $p = 0.099$	$H = 8.65$; **$p = 0.013$**	-	-

Table 3. Spearman's rank correlation (R^2) according to the curve estimation procedure between variables (condition factor, hepatosomatic index and stomach fullness index) and fish length. Data are presented for each river and in total (pooled data). Significant differences are marked in bold.

	R^2	*p*-value	Type of regression model	Regression model equation
Condition factor				
the River Anllóns	0.15	0.177	Cubic	$y = 0.069x^3 – 0.003x^2 + 0.001x + 0.907$
the River Furelos	0.52	**< 0.001**	Cubic	$y = 0.001x^3 – 0.005x^2 + 0.166x + 0.553$
the River Lengüelle	0.11	0.274	Cubic	$y = 0.001x^3 – 0.005x^2 + 0.085x + 0.928$
Total (pooled data)	0.40	**< 0.001**	Cubic	$y = 0.001x^3 – 0.006x^2 + 0.124x + 0.554$
Hepatosomatic index				
the River Anllóns	0.04	0.698	Cubic	$y = –0.001x^3 + 0.005x^2 – 0.109x + 1.453$
the River Furelos	0.06	**0.039**	Linear	$y = –0.010x + 0.746$
the River Lengüelle	0.41	**< 0.001**	Cubic	$y = –0.001x^3 + 0.036x^2 – 0.575x + 3.507$
Total (pooled data)	0.07	**0.026**	Cubic	$y = –0.001x^3 + 0.008x^2 – 0.130x + 1.282$
Stomach fullness				
the River Anllóns	0.70	**< 0.001**	Cubic	$y = –0.003x^3 + 0.189x^2 – 3.692x + 23.838$
the River Furelos	0.86	**< 0.001**	Cubic	$y = –0.004x^3 + 0.238x^2 – 4.899x + 32.214$
the River Lengüelle	0.38	**< 0.001**	Exponential	$y = –0.121^x + 3.330$
Total (pooled data)	0.76	**< 0.001**	Cubic	$y = –0.003x^3 + 0.199x^2 – 4.116x + 27.521$

1988). As expected, the correlation between *CF* and fish length was positive in the River Furelos and in total (pooled data), and also *CF* changes depending on the age as it can be seen in Table 2. These findings are in agreement with previous studies, and in salmonids, as in many other fish species; there is normally a shift in the condition factor and energetic reserves during the ontogeny, being lower in young fishes (e.g., Nomura et al. 2001).

Our results demonstrate that the feeding intensity decreases with the fish age and length. However, as proved by the results obtained by several authors, for brown trout, as in many other salmonids species, the stomach fullness may vary considerably during the year (e.g., Lagarrigue et al. 2002, Kara & Alp 2005). So, under natural conditions, stomach fullness index was the lowest in autumn, then increased from winter to summer (Lagarrigue et al. 2002). In our case, surveys was carried out at the end of the summer season (September) coinciding with the low water level of the studied rivers, and the interpretation of the results of this study should take into account the phenology of feeding intensity. Indeed, although the data of the present study is limited to a September, the end of the summer is the most interesting moment to survey because energetic reserves at this moment will be determinant for the survival on the coming winter.

The acquisition of energetic reserves in fishes is extremely linked with the feeding intensity (e.g., Rikardsen et al. 2006). Studies developed in brown trout have demonstrated that fishes between 5.7 cm and 32 cm fed most intensively, whilst the intensity declined above 32 cm length (Kara & Alp 2005). In contrast with the findings found by Kara & Alp (2005), in our case the feeding intensity was the highest in YOY (with sizes between 4.8 and 9.4 cm) and declined drastically in the age-1+ (with sizes between 10.9 and 17.9 cm). Additionally, the present study demonstrated that the relation between the stomach fullness and fish size was negative.

In brown trout, the peak feeding periods also corresponded with an increase in both condition factor and lipid content (Rikardsen et al. 2006). Hence, the negative relation between the stomach fullness and fish size and the positive relation between the condition factor and fish length found in this study could indicate that the feeding intensity is related with the fish condition, as other researchers have found in previous studies (e.g., Rikardsen et al. 2006). In this context, it is important to note that the high feeding intensity of YOY during the end of the summer could be related with the increases in fish condition and survival in the later autumn and winter.

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