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Gut evacuation in barbel (*Barbus sclateri* G., 1868) and nase (*Chondrostoma willkommi* S., 1866)

Encina L, Granado-Lorencio C. Gut evacuation in barbel (*Barbus sclateri* G., 1868) and nase (*Chondrostoma willkommi* S., 1866).
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Abstract – In this study we estimated the rates of summer gut evacuation for two cyprinids with detritivorous-omnivorous feeding habits, *Barbus sclateri,* Günther 1868 (barbel) and *Chondrostoma willkommi,* Steindachner 1866 (nase). This study was performed at two sampling stations in the upper Guadalete River (south Spain). A previous study reported differences in the natural diet of both species. The gut evacuation rate was estimated from the regression of gut contents weight against time. Linear and exponential models best described the pattern of gut emptying in the two species. There was no significant difference in the gut evacuation rate between both sampling stations for barbel. However there was a discrepancy related to the model that provided the best fit to empirical data. In contrast, the same model provided the best fit to the empirical data for nase in both sampling stations, but the gut evacuation rate was significantly different in both sampling stations. The results of these study provide the first data of evacuation rates for Iberian freshwater fish species directly measured in the field.

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Key words: feeding habits; diet energy content; gut evacuation

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Gut evacuation studies play an important role in estimating the feeding rates of fish populations, which is essential for research on trophic dynamics, fish production, fish management, aquaculture, etc. The processes of digestion and gut evacuation of teleost fish have been described using a variety of models (Kapoor et al. 1975; Jobling 1980; Bromley 1987; Elliot 1991; Karjalainen et al. 1991; Rogers & Burley 1991). Linear, exponential, square root, logistic, surface area and sigmoid models have all been used to describe the pattern of gut emptying in fish. In practice, the preference for one model over another is usually determined by choosing the mathematical expression that give the best fit to empirical data.

During the 1980s, there was considerable discussion over which of these models best describes gut evacuation in fish. Gut evacuation studies have usually been carried out in the laboratory, where the multiple biotic and abiotic factors affecting the evacuation processes are experimentally controlled. It is now generally accepted that the wide variety of evacuation patterns observed may be a consequence of the great plasticity of gut emptying in response to environmental and endogenous factors, as well as experimental design and methods (Hunt & Stubbs 1975; Cho et al. 1976; Flowerdew & Grove 1979; Jobling & Davies 1979; Persson 1979; Bromley 1980; Dos Santos & Jobling 1991a,b). The factors include species, water temperature, body size, quantity and quality of food ingested, digestibility of food items, biochemical composition of food, energy content of diet, feeding habits, ect. The natural environment and feeding habits of fish populations are usually reproduced with difficulty in laboratory conditions, so estimates of evacuation rates derived from experiments in laboratory may have limited application to studies of food consumption in the field.

Barbel and nase are two of the most common fish species in the freshwater fish fauna of Iberian Peninsula (Doadrio et al. 1991). Their natural feeding habits are well described (Guillén 1982; Granado-Lorencio 1983; Encina 1986, 1991, Bellido et al 1989), but little is known about the rates of food intake and gut evacuation of natural populations. Therefore, the aim of this study was to determine the gut evacuation rates for these fish species in the field. Also, to detect whether changes in their natural diet (an event common for both species, both in time and in space) affect the pattern and/or the rate of gut evacuation.

Material and methods

The study was performed during summer at two sampling stations (E-1 and E-2 locations) in the upper Guadalete River (southern Spain). Both barbel and nase had shown changes in their natural diet composition at both sampling sites in a previous study; these changes were mainly related to variations in the proportion of inert solids in the diet of both species, further details may be seen in Encina (1991) and Encina & Granado-Lorencio (1991).

Samples were taken with electrofishing. Fish were captured every 3 h throughout a 24-h period. Each fish was measured (total length, TL) and weighed (BW) *in situ*. For each species, individuals covering as broad a size range as possible were selected from each collection. For each capture five fish were placed alive into a food free cage at the same river water temperature (control group), and other fish were immediately killed (t=n). Fish from the control group were killed after 3 h in the food free cage (t=n+3). Water temperature was measured at each location and sampling hour. Since these two species do not have a differentiated

Table 1. Mean values ($\bar{X}$) and standard deviation (SD) of total length (TL), body weight (BW), gut content weight (GCW) and diet energy content (EC) at each sampling time for barbel. *n* is the total number of fish examined. R is the number of pills burned (see text).

		TL (mm)		BW (g)		GCW (g)		EC (J/g)				
									GCFW		GCDW	
Sampling time	*n*	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	R	$\bar{X}$	SD	$\bar{X}$	SD
E-1 sampling location												
t-0	17	172.4	14.6	54.4	12.5	1.21	0.10	5	3496.1	491.2	12901.4	0860.6
t-3	22	168.6	15.8	45.2	07.9	0.56	0.12	5	3444.7	643.1	12532.3	1089.9
t-6	24	177.0	11.6	54.8	10.7	0.17	0.05	5	3445.1	397.5	12888.8	1028.0
t-9	16	169.0	14.2	51.0	14.1	0.09	0.04	2	3757.2	084.5	12690.1	0655.2
E-2 sampling location												
t-0	27	178.5	12.2	52.43	08.83	4.32	0.63	5	2474.8	225.9	5305.7	362.3
t-3	22	168.1	14.3	44.00	09.11	3.14	0.63	5	2515.0	248.9	5347.9	796.6
t-6	22	170.0	14.2	46.90	11.26	2.32	0.37	5	2647.6	279.1	5094.8	894.5
t-9	16	164.7	12.1	41.62	07.63	1.34	0.24	5	2678.2	217.9	5015.7	560.2
t-12	12	160.0	09.2	36.48	04.79	0.19	0.14	4	2707.9	261.1	4813.3	888.3

Table 2. Mean ($\bar{X}$ and SD) of total length (TL), body weight (BW), gut content weight (GCW) and diet energy content (EC) at each sampling time for nase. *n* is the total number of fish examined and R, the number of pills burned (see text).

		TL (mm)		BW (g)		GCW (g)		EC (J/g)				
									GCFW		GCDW	
Sampling time	*n*	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD	R	$\bar{X}$	SD	$\bar{X}$	SD
E-1 sampling location												
t-0	18	157.2	13.5	24.4	9.31	0.97	0.08	5	2531.7	055.2	3463.1	180.2
t-3	19	146.1	13.7	21.3	7.39	0.58	0.09	5	2463.9	192.5	3396.6	124.3
t-6	8	141.5	07.3	18.5	4.29	0.04	0.02	1	2478.2		3630.8	
E-2 sampling location												
t-0	14	180.7	14.2	47.1	11.46	2.84	0.19	5	2213.7	353.9	3186.5	417.9
t-3	21	156.7	17.9	31.3	09.58	2.00	0.23	5	2148.9	201.2	3002.0	215.1
t-6	18	143.9	17.9	24.9	08.03	1.19	0.21	5	2134.2	193.3	3002.0	165.2
t-9	14	149.7	12.6	24.6	07.37	0.21	0.09	5	2152.2	170.7	2994.5	269.8

stomach, the whole intestinal tract (gut) was excised and the contents extracted, weighed to the nearest 0.01 g (GCW) and deep frozen.

In the laboratory, all guts extracted from specimens collected at the same sampling hour and sampling location were pooled, liophilized and burned in a Parr calorimeter for dietary energy contents determination. Analysis was carried out using pills of 0.5 g of dry weight. Except in 3 cases (Tables 1, 2), 5 pills from each sampling hour, sampling location and fish species were burned. The caloric content of samples is given in joules per gram of fresh weight (J/g GCFW) and joules per gram of dry weight (J/g GCDW). Two-factor ANOVA without replication was used to test differences in the caloric content of the diet.

Barbel is mainly a detritivore-omnivore feeder, with a diet composed of a wide variety of aquatic invertebrates, periphyton algae and organic debris; some inert solids (i.e., sand and gravel) are ingested as a result of detritus consumption. The main food item in the diet of nase is sedimented detritus, with a high proportion of sand and gravel (Encina 1991). Both barbel and nase displayed a cyclical 24-h feeding pattern closely related to the light-dark cycle; feeding activity starts chiefly at dawn, a peak of fullness is reached around the evening, with a gradual decline from evening to night (Encina & Granado-Lorencio 1991).

According to Lane et al. (1979), we assumed that fish did not feed from evening to night, so that the drop in weight of intestinal contents during this period reflected only the evacuation of the digestive tract. The hour at which the highest mean

Table 3. Mean values ($\bar{X}$) and standard deviation (SD) of intestinal content weight (GCW) at each sampling time for barbel examined immediately after captured (OG) and those examined after 3 h in a food-free cage (CG) (see text), and results of the ANOVA with multiple-contrast analysis.

E-1 Sampling location

OG				CG			
		CGW (g)				GCW (g)	
sampling time	n	$\bar{X}$	SD	sampling time	n	$\bar{X}$	SD
t 3	22	0.56	0.12	t 0+3	5	0.59	0.12
t 6	24	0.17	0.05	t 3+3	4	0.20	0.07
t 9	16	0.09	0.04	t 6+3	7	0.07	0.03

Analysis of variance

Source of variation	F	P
Main effects		
A: sampling time	176.98	0.000
B: fish group (OG/CG)	000.19	0.669
Interaction AB	000.72	0.492

E-2 Sampling location

OG				CG			
		CGW (g)				GCW (g)	
sampling time	n	$\bar{X}$	SD	sampling time	n	$\bar{X}$	SD
t 3	22	3.14	0.63	t 0+3	4	3.03	0.44
t 6	22	2.32	0.37	t 3+3	5	1.89	0.49
t 9	16	1.34	0.24	t 6+3	5	1.19	0.20
t 12	12	0.19	0.14	t 9+3	5	0.32	0.14

Analysis of variance

Source of variation	F	P
Main effects		
A: sampling time	118.00	0.000
B: fish group (OG/CG)	001.61	0.207
Interaction AB	001.22	0.308

Table 4. Mean values ($\bar{X}$) and standard deviation (SD) of intestinal content weight (GCW) at each sampling time for nase examined immediately after captured (OG) and those examined after 3 h in a food-free cage (CG) (see text). ANOVA with multiple-contrast analysis.

E-1 Sampling location

OG				CG			
		CGW (g)				GCW (g)	
sampling time	n	$\bar{X}$	SD	sampling time	n	$\bar{X}$	SD
t 3	19	0.58	0.09	t 0+3	5	0.53	0.13
t 6	8	0.04	0.02	t 3+3	5	0.02	0.01

Analysis of variance

Source of variation	F	P
Main effects		
A: sampling time	279.87	0.000
B: fish group (OG/CG)	000.95	0.347
Interaction AB	000.18	0.679

E-2 Sampling location

OG				CG			
		CGW (g)				GCW (g)	
sampling time	n	$\bar{X}$	SD	sampling time	n	$\bar{X}$	SD
t 3	21	2.00	0.23	t 0+3	5	1.82	0.25
t 6	18	1.19	0.21	t 3+3	5	1.07	0.28
t 9	14	0.21	0.09	t 6+3	5	0.18	0.10

Analysis of variance

Source of variation	F	P
Main effects		
A: sampling time	261.82	0.000
B: fish group (OG/CG)	001.79	0.106
Interaction AB	000.37	0.689

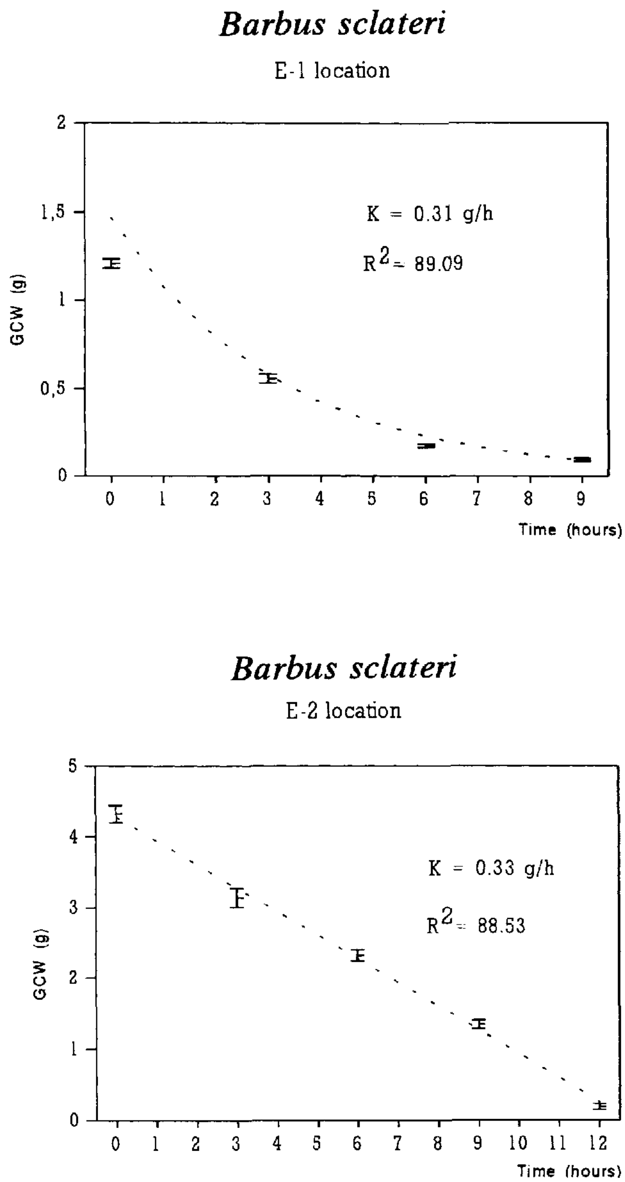

Fig. 1. Mean gut content weight and 95% CL (bars) at each campling time and fitted best decay curve in *Barbus sclateri*. *K*: estimated gastric evacuation rate; R^2: coefficient of determination of the regression analyses. E-1 location: exponential model; E-2 location: linear model.

weight for the intestinal contents was measured was taken as initial time (t_0). To confirm the assumption that the observed pattern of decline of intestinal content solely reflects evacuation and not a balance between evacuation and consumption, we used ANOVA with multiple contrasts analysis to test for significant differences in the gastrointestinal content weight between fish killed immediately after capture and those from the corresponding control group.

Gut evacuation rate (K) was estimated from the regression of weight of intestinal contents against time. Empty guts were omited during data analysis because the time they became empty could not be determined (Olson & Boggs 1986, Olson & Mullen 1986). Linear, exponential, square root, logistic and sigmoid models were tested. Elliott's exponential model (Elliott 1972) and the Thorpe's linear model (Thorpe 1977) were selected. ANCOVA (analysis of covariance) was used to test for differences in the gut evacuation rates between sampling sites.

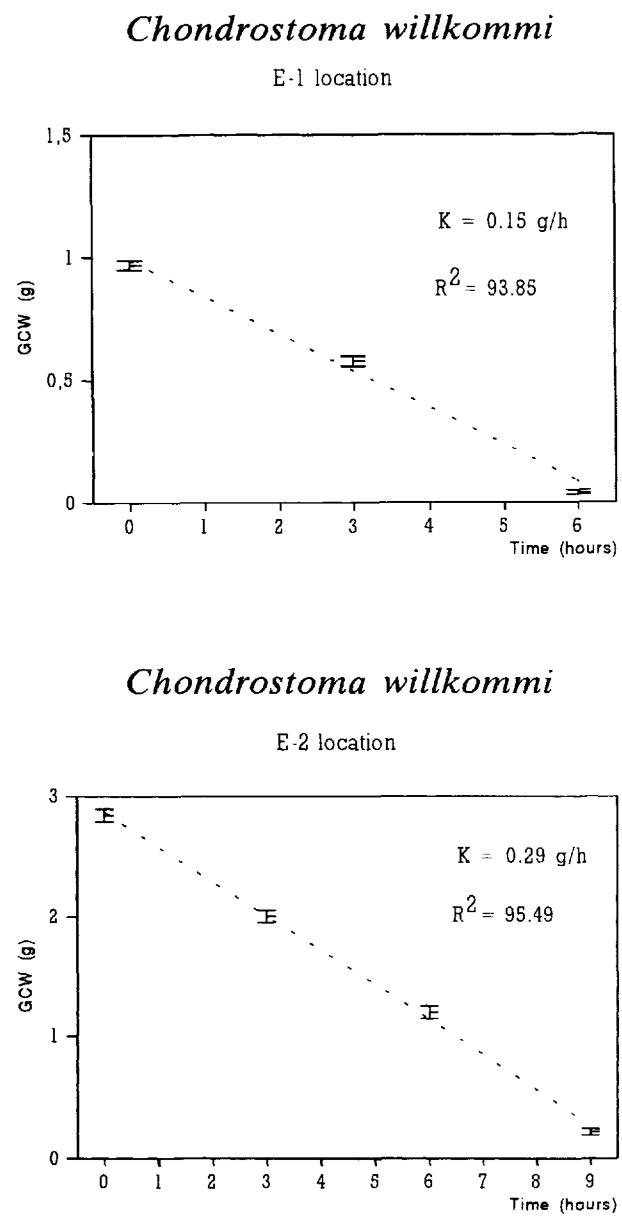

Fig. 2. Mean gut content weight and 95% CL (bars) at each sampling time and fitted best decay curve in *Chondrostoma willkommi*. *K*: estimated gastric evacuation rate; R^2: coefficient of determination of the regression analyses. Both E-1 and E-2 locations linear model.

Table 5. Estimates to the rates of gut evacuation (K) from linear and exponential models, including the coefficient of determination (R^2) for intestinal content weight against time. Mean water temperature (°C) and standard deviation at each sampling location. K is expressed both as g/h and as percentage of the mean fish body weight (in parenthesis). Best set of estimates for K values from the comparison of R^2 are shown in bold.

		Barbus sclateri		*Chondrostoma*	*Willkommi*
		E-1	E-2	E-1	E-2
Linear model	K	0.13	**0.33**	**0.15**	**0.29**
		(0.24)	**(0.73)**	**(0.79)**	**(0.92)**
	R^2	85.32	**88.53**	**93.85**	**95.49**
Exponential model	K	**0.31**	0.23	0.48	0.29
		(0.61)	(0.51)	(1.91)	(0.91)
	R^2	**89.90**	67.74	76.36	77.44
Water temperature	$\bar{X}$	22.68	23.35	22.68	23.35
	SD	1.26	0.63	1.26	0.63

Results

Tables 1 and 2 show the mean values and standard deviation for length, weight, intestinal content weight and diet energy content for fish immediately killed at each time and sampling location. No differences were found in the gastrointestinal content weight between the above-mentioned fish samples and their corresponding control groups for both species (Tables 3 and 4), so we can argue that the observed pattern of decline of intestinal content weight can be assumed to solely reflect the gut evacuation.

The decrease in the intestinal content weight against time for both species and sampling locations, as well as the best fit curve, are given in Fig. 1 and 2. Estimates of the instantaneous evacuation rates are given in Table 5, together with the coefficient of determination (R^2) of the regression analysis for each model and the mean water temperature during the sample period.

The comparison between the coefficients of determination of the regressions of the intestinal contents weight against time shows a discrepancy related to the model that provides the best fit to the empirical data both between and within species. Whereas the results obtained gave good fits to the exponential model in the case of barbel from E-1, in barbel from E-2 and nase from both E-1 and E-2 the linear model proviced the best fit to the empirical data.

Concerning the values estimated for the instantaneous evacuation rate, no differences were found between both sampling locations (after linear transformation of E-1 data) in barbel (ANCOVA, F=1.51, NS). However, evacuation rate estimated in nase from E-2 was higher than that from E-1 (ANCOVA, F=115.94, P<0.01).

In those cases in which the lineal model provided the best fit (barbel from E-2 and nase from E-1 and E-2), evacuation rate values obtained by the regression analyses were comparable with independent estimates of the rate of gut evacuation obtained by comparing the gut contents of the fish killed immediately with those of fish kept in food-free enclosures (K', Table 6). In barbel from E-1, independent estimates of the rate of gut evacuation are in agreement with an exponential model.

The results obtained for the dietary energy were similar for both species (Table 7): no differences were found between sampling hours, but there was a significant difference between the two sampling locations. Both in barbel and nase the dietary energy content (both in J/g GCFW and J/g GCDW) was significantly lower at E-2 than at E-1. The

Table 6. Independent estimates of the rate of gut evacuaion (K', g/h) obtained by comparing the gut contents of the fish examined immediately after captured (OG) with those of fish kept in food-free enclosures (CG).

	E-1					E-2				
	OG		CG		K'	OG		CG		K'
	Sampling time	GCW (g)	Sampling time	GCW (g)	(g/h)	Sampling time	GCW (g)	Sampling time	GCW (g)	(g/h)
Barbus sclateri										
	t 0	1.21	t o+3	0.59	0.21	t 0	4.32	t 0+3	3.03	0.43
	t 3	0.56	t 3+3	0.20	0.12	t 3	3.14	t 3+3	1.89	0.42
	t 6	0.17	t 6+3	0.07	0.03	t 6	2.32	t 6+3	1.19	0.37
						t 9	1.34	t 9+3	0.32	0.34
				mean:	–				*mean:*	0.39
Chondrostoma willkommi										
	t 0	0.97	t 0+3	0.53	0.15	t 0	2.84	t 0+3	1.82	0.34
	t 3	0.58	t 3+3	0.02	0.19	t 3	2.00	t 3+3	1.07	0.31
						t 6	1.19	t 6+3	0.18	0.34
				mean:	0.17				*mean:*	0.33

Table 7. Two-factor ANOVA without replication analysis carried out for the energy content comparisons of the diet of barbel and nase.

Barbus sclateri

	GCFW (J/g)		GCDW (J/g)	
Source of variation	*F*	*P*	*F*	*P*
Main effects				
A: sampling time	002.89	0.205	0001.28	0.436
B: sampling location	242.89	0.001	3265.03	0.000
Contrast E-1–E-2	$\bar{X}$	SD	$\bar{X}$	SD
E-1	3496.61	462.50	12764.25	895.17
E-2	2600.48	243.34	04866.58	736.47

Chondrostoma willkommi

	GCFW (J/g)		GCDW (J/g)	
Source of variation	*F*	*P*	*F*	*P*
Main effects				
A: sampling time	0015.76	0.102	00.48	0.728
B: sampling location	1251.02	0.001	27.53	0.025
Contrast E-1–E-2	$\bar{X}$	SD	$\bar{X}$	SD
E-1	2496.13	131.17	3448.12	154.89
E-2	2162.25	223.30	3046.37	272.92

highest dietary energy content was recorded for barbel from E-1.

Discussion

A significant relationship between gut evacuation rate and quality and quantity of food consumed by the fish has been established by several authors (Pandian 1967; Jobling 1981, 1986a, 1987; Dos Santos & Jobling 1988, 1991a,b; and others). Differences in dietary energy content and the physical form of food items or degree of prey integrity influence patterns of gut emptying in fish, so changes in emptying patterns occur when different food items are eaten. It is generally accepted that an exponential function best describes the evacuation of small, relatively easily digested, low energy prey items (microphagous/zooplanktivorous feeding habits) and evacuation in fish feeding on invertebrates (Elliott 1972). Otherwise, a linear regression better fit data for the evacuation of high energy, large-sized food items, as for piscivorous feeding habits fish.

However, many fish do not fit neatly into either of these two feeding modes. Their digestive tracts may contain food items of varying energy content, different digestibility or different sizes. Little is known about the rates and patterns of gut evacuation for herbivorous, detritivorous or omnivorous fish, among which barbel and nase are included.

Jobling (1981, 1986b, 1987), Bromley (1987) and Dos Santos & Jobling (1988) reported great influence of the physical form in which the diet is fed has on gastric evacuation rates. However, in the case of the barbel, the physical form in which the diet is eaten is not a factor related to the observed discrepancy in the gut evacuation pattern between the sampling locations, since there are no differences in the physical form of diet amont them (Encina 1991). The results obtained by this author (Encina, 1991) belonging to the same summer period from a year after and a year before this study, are in agreement with our results, and they seem to reflect a relation between the evacuation pattern and the differences in the dietary energy content registered between both sampling sites.

Nevertheless it is uncertain whether the factor influencing the pattern of gut evacuation is the energy content of the diet *per se,* or other variables, such the content of inert solid. Several authors have suggested that inert solids and indigestible food may be emptied from the digestive tract as relatively large particles, that is, according to a linear function (Molnar et al. 1967; Pandian 1967; Kelly 1980; Meyer 1980; Mojaverian et al. 1985; Jobling 1987). Encina (1991) noted that proportions of sand and gravel were significantly lower in the diet of barbel from E-1 than in barbel from E-2 and nase from both E-1 and E-2. In barbel at E-1 proportions of these components were always <10% (range 1–9%, mean value 5.06%), whereas they were >20% in barbel at E-2 (range 21–36%, mean value 28.5%), nase at E-1 (range 28–36%, mean value 31.91%) and nase at E-2 (range 36–45%, mean value 40.55%). These indigestible inert components affect directly the dietary energy content, so this is lower per unit of intestinal content weight. This could have an important effect on gut evacuation, both in terms of the goodness-of-fit of different models and in the rates of evacuation.

Several workers have reported that fish, when fed a variety of diets, regulate their food consumption to maintain a relatively constant energy intake (Cowey et al. 1972; Lee & Putnam 1973; Page & Andrews 1973; Cho et al. 1976; Jobling 1980). Two ways in which this could be achieved would be 1) by increasing the digestion and evacuation rate of low energy diets and 2) by increasing the absorption efficiency of low energy content or more difficult digested diets (as high energy-large sized food items). Concerning the first point, several studies demonstrate that low energy diets are evacuated from the stomach more rapidly than those with a higher energy content, so an increase in the energy content of the diet leads to an increase in the time required to empty the stomach (Windell et al. 1969; Grove et al. 1978; Flowerdrew & Grove 1979; Jobling 1986a, 1987). The results for nase may be in agreement with this strategy.

Concerning the second point, several studies note that the pattern of gut evacuation is closely related to the composition, nutritive density and energy content of the diet. A linear pattern of gut emptying, in which the amount of food evacuated from the digestive tract is constant over time, may be the most appropriate for 1) diets composed by high energy-large sized food items, and 2) diets with high proportions of inert solids and indigestible food remains (Molnar et al. 1967; Pandian 1967; Jobling 1981; Olson & Boggs 1986). The stragegy consists not in a decrease in time required to empty the full stomach but in an increase of food amount that remains in the digestive tract (Jobling 1986a, Bromley 1987). The results for barbel seem to be in agreement with this strategy.

Resumen

1. El principal objetivo de este estudio fué determinar la tasa de evacuación intestinal en condiciones naturales para el periodo estival en *Barbus sclateri,* Günther 1868 (barbo) y *Chondrostoma willkommi,* Steindachner 1866 (boga), ambos ciprínidos, con hábitos alimenticios de tipo detritívoro-omnívoro. El trabajo se llevó a cabo en dos estaciones de muestreo situadas en el tramo alto del Río Guadalete (sur de España), en las que previamente había sido verificada la existencia de diferencias en la dieta natural para ambas especies.
2. La tasa de evacuación fué estimada a partir de análisis de regresión de los contenidos intestinales frente al tiempo. Los modelos que mejor se ajustaron a la descripción del patrón de vaciado intestinal fueron lineal y exponencial.
3. En el caso del barbo no se registraron diferencias significativas para la tasa de evacuación gástrica entre las dos estaciones de muestreo, pero sí una diferencia en el modelo de vaciado que mejor se ajustó a los datos empíricos. Sin embargo, en el caso de la boga, no aparecieron cambios en el modelo de evacuación intestinal. Por el contrario la tasa de evacuación intestinal para esta especie fué significativamente diferente en ambas estaciones de muestreo.
4. Los resultados de este trabajo representan los primeros datos que se obtienen sobre tasas de evacuación gástrica en condiciones naturales en especies de peces de agua dulce de la península Ibérica.

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