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ORIGINAL RESEARCH

Geographic and seasonal variation analysis of digestive morphology in the catfish *Iheringichthys labrosus* along lower Río Uruguay

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Abstract: The study of geographic variation of individual traits is an important component of evolutionary research, in that individual morphological features can be subjected to multiple selective pressures. The present work is aimed to analyze the geographic and seasonal variation in several digestive traits in *Iheringichthys labrosus* along three localities in the lower Río Uruguay. Statistically significant differences among locations and between seasons were found for all the variables assessed, the most noticeable of differences being observed were intestinal length, intestine weight, and liver weight. In part, these differences could be an adaptive response to changes in food availability and/or in the energetic costs of reproduction. Results obtained herein also suggest that individuals of this species spend enough time in each locality as to show a consistent response to local conditions in their digestive traits morphology.
Keywords: *Iheringichthys labrosus*, physiological flexibility, Río Uruguay

Introduction

Geographic analysis of variation in individual traits is an important component of evolutionary research since individual morphological features can be subjected to multiple selection pressures, often leading to tradeoffs in the optimization of their form–function relationship.[1] Because the gut represents the functional link between energy intake and metabolizable energy, it could be expected that gut size would be under strong selection pressures.[2] In this sense, reversible adjustments in the size of the digestive organs, ie, digestive flexibility, is a widespread phenomenon among vertebrates, and the congruence between empirical data and optimal digestion models strongly supports the idea that it has evolved by natural selection.[3,4–8]

However, studies comparing digestive morphology among individuals belonging to different geographical sites, and having different trophic habits, are by far scarcer than studies analyzing digestive flexibility within populations. In any event, existing studies indicate (1) there is an important amount of variation in digestive features among populations and (2) there is agreement with digestion theory,[2] in the sense of there is a positive correlation between the size of the digestive organs and the amount of refractory material in the diet.[9–14] Nevertheless, current information regarding the link between individual resource use and digestive trait morphology comes mainly from tetrapods, and only limited attention has been paid to fish populations,[1,15–18] despite implications that fish represent an excellent model organism to study adaptive phenotypic plasticity.[19]

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Within this context, the present work is aimed at analyzing the geographic and seasonal variation in several digestive traits in *Iheringichthys labrosus* (Lütken 1874) along three localities in the lower Río Uruguay. Our focal species is one of the most abundant and widely distributed siluriform fish along Río Paraná and Río Uruguay basins,[20] and it has been recently proposed as a sentinel species for environmental impact assessments.[21] Nevertheless, only a few studies considering this fish species were carried out in the Río Uruguay,[22–24] an area where important agricultural (eg, soybeans monocultures), forest (eg, eucalyptus monocultures), and industrial (eg, pulp mill industries) activities have been increasing during the last decade.

Materials and methods

Study area and sample collection

The study area comprises three localities along the lower Rio Uruguay (Figure 1): Fray Bentos, an area with putative anthropogenic impact; Nuevo Berlín, northwards to Fray Bentos; and Las Cañas, southwards to Fray Bentos locality, all situated within a Ramsar zone and the protected area of Parque Nacional Esteros de Farrapos e Islas del Río Uruguay. Surveys of these sites indicate that water physicochemical parameters such as temperature, dissolved oxygen, turbidity, conductivity, and pH did not differ among localities (Table 1). Individuals of the *I. labrosus* species were collected during November 2009 in Las Cañas (n = 17), and then during April 2010 in Las Cañas (n = 26), Nuevo Berlín (n = 21), and Fray Bentos (n = 29). For the purpose of collection we used eight standard Nordic gill nets (5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm knot-to-knot, each of them 2.5 m long); four of them were set parallel to the littoral zone and the remaining four were set parallel to each other in the pelagic area, from sunset to sunrise, (approximately 12 hours).

Morphological determinations and statistical analysis

Standard length of each fish was measured with a plastic rule (±0.1 cm), and then stomach, intestine, liver, and gonads were removed. Stomach and intestine lengths were measured with a plastic rule (±0.1 cm), then they were washed with running water, dried with paper towels, and weighed with an electronic balance (±0.001 g). Total weight of liver and eviscerated body weight were also measured as described above.

Comparisons among collection sites were carried out with reference to samples obtained during April 2010, while comparisons among collection periods were conducted using individuals sampled in Las Cañas locality. In both cases, differences in length and weight of internal organs were separately studied by means of analyses of covariance, using standard length (for organ lengths) or eviscerated body weight (for organ masses) as covariate in order to remove the size-effect over the variables analyzed. Prior to all analysis of covariance (ANCOVA) analyses, we evaluated the interaction between the categorical and continuous predictors in order to choose the appropriate model. Post hoc comparisons were evaluated by means of Unequal N HSD tests. In order to obtain a proxy of the reproductive status of individuals between different times of sampling, we also analyzed the temporal variation in the gonadosomatic index ([gonad weight/total body weight] × 100) for females from Las Cañas using an

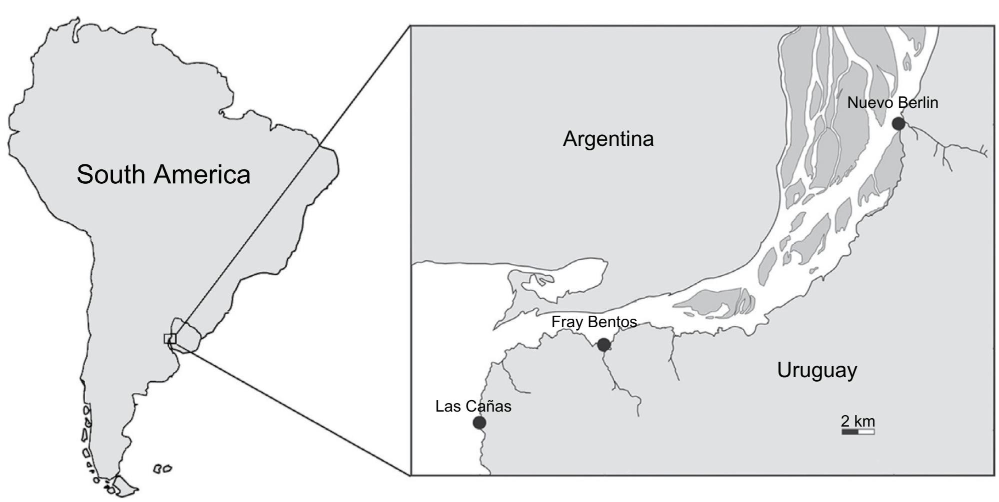

Figure 1 Sampling localities of *Iheringichthys labrosus* analyzed in this work.
Notes: Approximate geographic coordinates: Nuevo Berlín 32°58′52″S, 58°04′06″W; Fray Bentos 33°06′35″S, 58°16′39″W; Las Cañas 33°09′48″S, 58°21′43″W.

Table 1 Descriptive values of water physicochemical parameters for each locality, measured monthly from July to December of 2009 and compared with Kruskal–Wallis test

	Nuevo Berlín		Fray Bentos		Las Cañas		$H_{(2, 18)}$	*P*-value
	Median	Range	Median	Range	Median	Range		
Oxygen (mg/L)	8.97	4.10	9.04	4.66	8.96	5.08	0.056	0.973
Conductivity (µS/cm)	50.65	45.30	55.65	50.00	56.25	48.10	1.338	0.512
pH	7.53	1.22	7.35	0.79	7.40	1.24	0.667	0.716
Temperature (°C)	18.70	12.80	18.15	12.50	17.60	12.60	1.004	0.605

Notes: The parameter, [$H_{(2,18)}$] is related to the Kruskall–Wallis test, and is commonly associated with this analysis. The H subindices represents: 2 = degrees of freedom of the analysis and 18 = sample size used.

analysis of variance (ANOVA) test. All data analyzed were examined for assumptions of normality and homoscedasticity using Kolmogorov–Smirnov and Levene tests ($P < 0.05$), respectively. In all cases, data were log-transformed to meet the assumptions of the analyses.

Results

Statistically significant differences among localities were found for all the variables assessed, with the most noticeable differences observed for intestinal length, intestine weight, and liver weight (Table 2). In almost all variables, individuals from Nuevo Berlín showed the greatest values, followed by individuals from Las Cañas, and then by individuals from Fray Bentos (Table 2). Temporal analysis also revealed significant differences for intestinal length and liver weight, with individuals collected in November 2009 showing lower values than those collected in April 2010 (Table 3). Finally, gonadosomatic index also showed statistically significant differences between sampling periods, but in this case, individuals collected in November 2009 showed greater gonadosomatic index values than those sampled during April 2010 (Table 3).

Discussion

Fish have been known to exhibit developmental plasticity in response to prey type, and the consequences of this plasticity have been highlighted in several studies.[19,25–29] For instance, it is accepted that this developmental plasticity would allow species to become morphologically specialized in response to local environmental conditions.[19] In addition, more recent work demonstrates that reversible, flexible changes in digestive traits during adult life of individuals could be achieved over a period of few days in response to nutritional changes.[16,30–32] In line with this idea, results obtained here showed a clear differentiation in the morphology of the digestive traits among collection sites as well as between collection periods, particularly considering the intestinal length and liver weight.

Regarding the spatial analysis, variation in digestive traits among sites agreed with previous studies that considered *I. labrosus* as a generalist feeder, with a wide feeding spectrum,[33,34] which would enable the species to adapt its digestive system to the most abundant, or available, prey items in each locality. However, the recorded pattern of variation for digestive traits did not clearly match existing data on *I. labrosus* diet for the same three sampled localities. In this sense, Masdeu,[33] based on a correspondence analysis, proposed that adult individuals from Las Cañas were mainly associated with the consumption of Bivalvia, while individuals from the other two localities were mainly associated with the consumption of Diptera and Ostracoda. By contrast, the digestive features recorded here indicate that individuals from all the three sites differ among them to a similar extent.

Table 2 Descriptive statistics of the traits analyzed in different localities

Variable	Nuevo Berlín			Fray Bentos			Las Cañas		
	Mean	SD	N	Mean	SD	N	Mean	SD	N
SL (cm)	15.8[a]	3.7	21	12.6[b]	2.3	29	15.4[a]	3.7	26
EWB (g)	59.866[a]	39.084	21	27.975[b]	14.796	29	51.054[a]	26.622	26
ESTL (cm)	1.2[a]	0.2	21	1.3[b]	0.2	29	1.2[a]	0.2	26
IL (cm)	18.1[a]	2.8	21	17.7[b]	3.4	29	17.8[c]	2.7	26
SW (g)	0.242[a]	0.051	21	0.234[b]	0.077	29	0.240[c]	0.048	26
IW (g)	0.309[a]	0.087	21	0.271[b]	0.131	29	0.262[c]	0.083	26
LW (g)	0.310[a]	0.054	21	0.327[b]	0.082	29	0.293[c]	0.052	26

Notes: [a–c]indicate statistically significant differences among groups ($P < 0.05$ after a Tukey HSD test).
Abbreviations: Mean, absolute mean (for SL and EWB) or least squares-adjusted means (for remaining variables); N, sample size; SD, standard deviation; SL, standard length; EWB, eviscerated body weight; ESTL, stomach length; IL, intestinal length; SW, stomach weight; IW, intestinal weight; LW, liver weight.

Table 3 Descriptive statistics of the temporal analyses of traits

Variable	2009			2010			*P*-value
	Mean	SD	N	Mean	SD	N	
SL (cm)	13.5	4.3	17	15.4	3.7	26	0.288
EWB (g)	1.265	0.457	17	51.054	26.622	26	0.127
ESTL (cm)	1.3	0.2	17	1.2	0.2	26	0.284
IL (cm)	19.4	2.5	17	17.5	2.5	26	**0.026**
SW (g)	0.264	0.056	17	0.240	0.056	26	0.106
IW (g)	0.394	0.092	17	0.262	0.092	26	0.103
LW (g)	0.302	0.061	17	0.294	0.062	26	**0.022**
GSI	0.473	0.095	8	0.333	0.095	21	**0.002**

Notes: Values in bold indicate statistically significant differences among groups ($P < 0.05$ after a Tukey HSD test).
Abbreviations: Mean, absolute mean (for SL, EWB and GSI) or SL-adjusted means (for remaining variables); SD, standard deviation; N, sample size; SL, standard length; EWB, eviscerated body weight; ESTL, stomach length; IL, intestinal length; SW, stomach weight; IW, intestinal weight; LW, liver weight; GSI, gonadosomatic index.

Moreover, individuals from Las Cañas occupied an intermediate position – in the morphological space – in relation to individuals from the other two collection sites. Given that the study of Masdeu[33] was not conducted at the same time as our study, temporal change in food availability and consumption among sites cannot be disregarded.

On the other hand, temporal analysis showed that there is a clear seasonal variation in digestive traits and also in the gonadosomatic index. Previous work analyzing the reproduction period of this species in Brazil had shown a peak of maturity from October to January.[35,36] If this is also the case for *I. labrosus* of lower Río Uruguay, the sampling scheme of this work would correspond with the beginning and the end of the spawning season of this species. The clear reduction in the gonadal size between November 2009 and April 2010 is also in line with this idea (see Table 3). Thus, it is possible that the increase in gut length and liver weight that occurred during April 2010 was associated with the major energy demands linked to reproductive efforts in this species, as is the case of other fish[37] and other ectothermic vertebrates[38].

In summary, *I. labrosus* showed geographical and temporal variation in digestive trait morphology, which could be, in part, an adaptive response to changes in food availability and/or in the energetic costs of reproduction. The results obtained here also suggest that individuals of this species spend enough time in each locality to show a consistent response to local conditions in the morphology of their digestive trait. Such a finding is remarkable, taking into account the limited geographic area covered in this study. Finally, further analyses are needed in order to elucidate the factors driving the trophic and morphological differences exhibited by *I. labrosus* sampled in these localities.

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Disclosure

The authors report no conflicts of interest in this work.

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