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Biochemical composition of a dominant detritivorous fish *Prochilodus lineatus* along pollution gradients in the Paraná-Río de la Plata Basin

E. D. Speranza and J. C. Colombo*

Laboratorio de Quimica Ambiental y Biogeoquimica, Av. Calchaqui Km. 23.5, Florencio Varela (1888), Buenos Aires, Argentina Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina and Comision de Investigaciones Científicas de la Provincia de Buenos Aires (CIC), La Plata, Buenos Aires, Argentina

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The biochemical composition of muscle, liver and stomach contents of a detritivorous fish *Prochilodus lineatus* was analysed and compared to settling particles and sediments along pollution gradients over 1500 km of the Río de la Plata Basin to evaluate the effects of anthropogenic discharges in a detritus food chain. The stomach contents of *P. lineatus* collected in the polluted Metropolitan Buenos Aires coast were enriched in proteins, carbohydrates and lipids, similar to settling particulates collected in the sewer area, and two to five times higher than underlying sediments, supporting the interpretation that *P. lineatus* feeds on unconsolidated organic flocs freshly decanted from mixed industrial and sewage outfalls. Fish from Buenos Aires had consistently higher standard length (L_S) and mass (M_T) slopes ($b = 3{\cdot}5$), condition indexes ($K = 3{\cdot}01 \pm 0{\cdot}47$, mean ± s.d.) and muscle fat content (fat = $23{\cdot}8 \pm 13{\cdot}8\%$ wet mass, mean ± s.d.) relative to northern fish ($b = 2{\cdot}7$, $K = 2{\cdot}22 \pm 0{\cdot}39$, fat = $3{\cdot}4 \pm 3{\cdot}2\%$ wet mass, respectively), suggesting that sewage-derived organic matter was an enriched diet, which allowed an enhanced body mass gain and fat accumulation compared to organic-poor vegetal detritus in the north Paraná area. Buenos Aires fish also showed higher hepato-somatic indices (mean ± s.d. I_H $1{\cdot}41 \pm 0{\cdot}49$ *v.* $0{\cdot}70 \pm 0{\cdot}32$, respectively), which correlated with their two to three orders of magnitude higher hydrocarbon and polychlorinated biphenyl (PCB) loads, suggesting an enhanced detoxifying metabolism. The northward migration of fatty *P. lineatus* was evidenced by the presence of clear outliers in the L_S and M_T relationship, *K* and fat content along the Paraná River.

Key words: detritivory; lipids; mass–length relationships; settling particles; sewage.

INTRODUCTION

Detritivory is an important route of energy flux and material cycling in aquatic ecosystems, especially in turbid, subtropical ecosystems (Bowen, 1983). Although only a relatively small percentage of fishes are detritivorous, they may represent

*Author to whom correspondence should be addressed. Tel. and fax: +54 011 4275 8266; email: laqab@intervar.com.ar

a large part of the total biomass. This is especially true in large South American rivers, such as the Río de la Plata Basin which cover >3 million km^2 in tropical and temperate areas of Brazil, Argentina, Paraguay, Bolivia and Uruguay. The Paraná (3780 km) and Uruguay rivers (1790 km) carry 500–880 km^3 fresh water to the Río de la Plata and *c.* 90×10^6 and 8×10^6 t of suspended solids and total organic carbon per year, respectively (Degens *et al.*, 1991). Due to this massive contribution of material, waters are turbid with a prevailing input of allochthonous organic matter and a high sedimentary charge, which feed a vast delta in front of Buenos Aires city. This area supports one-third of the total Argentinean population and most of its industrial capacity resulting in a heavy impact in the coastal zone, which receives crude effluent discharges containing persistent organic pollutants (POP), hydrocarbons and heavy metals (Colombo *et al.*, 2005*a*, *b*, *c*). Massive vertical fluxes of total particles (mean $\pm$ S.D. 361 $\pm$ 124 g m^{-2} day^{-1}), organic carbon (29 $\pm$ 26 g m^{-2} day^{-1}), aliphatic hydrocarbons (350 mg m^{-2} day^{-1}) and polychlorinated biphenyls (PCBs) (26 $\pm$ 19 μg m^{-2} day^{-1}) have been measured in this area, which constitutes the feeding ground of several specialized detritivores.

Sewage-derived organic matter has been previously recognized as an important energy source for aquatic food webs, basically through assimilation by benthic organisms, which can lead to a fish production increase and a trophic structure alteration (deBruyn & Rasmussen, 2002; deBruyn *et al.*, 2003). These effects could be further amplified when highly specialized detritivorous fishes feed directly on anthropogenic organic matter. In the Río de la Plata Basin, this niche is occupied by *Prochilodus lineatus* (Valenciennes), locally known as 'sábalo' (Prochilodontidae, Characiform), which dominates the fish community constituting >60% of the ichthyomass (Bonetto *et al.*, 1969). *Prochilodus lineatus* is a strict detritivore with several anatomical and physiological adaptations for the efficient collection and digestion of detritus (Bowen, 1983). It has a sucker-like mouth with oral ridges to separate coarse inorganic particles from flocculant organic matter, followed by a three-dimensional gill-raker filtering structure. The highly muscularized pyloric stomach grinds the food, and numerous pyloric caeca serve in post-gastric assimilation, whereas the intestinal absorptive surface is increased by an extensive development of mucosal folds.

The Río de la Plata receives large inputs of untreated effluents discharged from port facilities and sewage outfalls (*i.e.* Berazategui sewer: *c.* 2 million m^3 day^{-1}) that provides food for the detritivores. *Prochilodus lineatus* from this area biomagnify organic pollutants from anthropogenic detritus and become a critical contamination pathway for humans (Colombo *et al.*, 2000, 2007*a*, *b*). Several thousand tonnes of *P. lineatus* are captured every year and are destined to local markets, export and manufacture of by-products (Sverlij *et al.*, 1993). In addition, *P. lineatus* is the main food item of major predators such as the shovelnose catfish *Pseudoplatystoma* sp. and the dorado *Salminus maxillosus* Valenciennes. *Prochilodus lineatus* also migrates in large schools upstream in autumn from the Rio de La Plata migrate northward hundreds of kilometres to the Parana River to reproduce (Agostinho *et al.*, 2004), returning in spring following the breading season (Sverlij *et al.*, 1993). Due to these migratory movements, *P. lineatus* acts as a biological carrier of pollutants throughout the basin.

The degree of bioaccumulation and toxicity of hydrophobic organic contaminants is strongly influenced by the fat content of the fishes (Gobas & Mackay, 1987; Van Veld, 1990; Geyer *et al.*, 1997). According to the hypothesis of 'survival of the fattest', high-lipid fishes may have an increased tolerance to toxicants (Lassitier & Hallam, 1990). Thus, lipid content may have an adaptative value for detritivorous fishes inhabiting heavily polluted environments with increased availability of easily assimilable organic matter. Furthermore, organic pollutants may interfere with lipid metabolism, increasing fat accumulation (Addison, 1982), which might in turn lead to the development of a positive feedback between the fat contents and the accumulation of persistent organic pollutants. In this paper, the biochemical composition of *P. lineatus* muscle, liver and stomach contents compared to sediments and settling particles collected along pollution gradients in the Paraná-Rio de la Plata Basin was studied to evaluate the effects of anthropogenic organic matter in a detritivorous fish.

MATERIALS AND METHODS

SAMPLING

Fish were collected every 3 months between 2002 and 2007 at the main sewer outfall of Buenos Aires (Berazategui, BZ; Fig. 1). In addition, between 2003 and 2007, *P. lineatus* were also collected once a year at southern stations in the Río de La Plata (sRLP) in autumn and spring, and at 16 sites along the Paraná and Paraguay rivers extending 1500 km north (PAR) in winter. Fish were caught with gillnets by local fisherman. A total of 602 fish were collected (163 in BZ, 128 in s RLP and 311 in PAR). The fish were weighed (M_T), measured (standard length, L_S), opened along the ventral line and the sex was determined by visual inspection of the gonads. The liver was weighed (M_L) and collected in plastic flasks as well as the cardiac stomach contents when available. A portion of dorsal muscle was excised and wrapped in aluminium foil. Samples were immediately frozen in dry ice, transported to the laboratory and stored at $-20°$ C until analysis.

Superficial sediments and settling particles were collected at selected locations (Fig. 1) using a Van Veen grab and fixed sediment traps deployed at 1·5 m from the surface during 12–36 h. Sediments and trap material were refrigerated and transported to the laboratory.

BIOCHEMICAL ANALYSIS

Biochemical analyses were performed on 276 muscle samples, 165 liver samples, 16 stomach contents samples, 32 settling particles samples and 17 sediment samples. Water and ash content were determined gravimetrically after drying (120° C, 24 h) and calcination (500° C, 24 h) of 0·5–1·0 g of homogenized tissue. Proteins and carbohydrates were determined spectrophotometrically with Folin reagent (Lowry *et al.*, 1951) and phenol–sulphuric acid (Dubois *et al.*, 1956) after homogenization of *c.* 0·5 g of fish tissue with an Elvejheim Potter with 0·05 M Tris–HCl buffer (Sigma-Aldrich; www.sigmaaldrich.com) at pH 7. Bovine serum albumin (Merck; www.merck.com) and dextrose (J. T. Baker, Phillipsburg; www.mallbaker.com) were used as standards. For sediments, settling particles and stomach contents, a modified phenol–sulphuric acid method was used (Liu *et al.*, 1973). Glycogen was determined in selected samples according to Montgomery (1957).

Total lipids were determined gravimetrically after extraction with chloroform:methanol (2:1v/v; Folch *et al.*, 1957) for fish liver and muscles and ultrasonically with petroleum ether:dichloromethane (2:1) for sediments, trap material and stomach contents. Reproducibility of water, ash, lipid, protein and carbohydrate analyses was assessed

FIG. 1. Sampling stations of fish (F), sediments (S) and settling particles (T) in the Río de la Plata Basin. South Río de la Plata (sRLP), Berazategui (BZ), Paraná (PAR) and extreme north sites (N) are indicated.

by quintuplicate analyses of randomly selected samples; the relative standard deviation (R.S.D.) for these analyses ranged between 2 and 7%.

STATISTICAL ANALYSIS

Statistical analysis was carried out using XLSTAT (Addinsoft SARL; www.hoovers.com). Data are expressed as mean ± S.D. A *t*-test was performed to compare two means as well as to evaluate the correlation coefficients significance. To compare differences between regression slopes, ANCOVA was employed. For comparisons between multiple samples, ANOVA and the Tukey test were used. A significance level of $P < 0{\cdot}05$ was employed, except where otherwise indicated.

RESULTS

BASIC MORPHOMETRIC CHARACTERISTICS

Prochilodus lineatus collected in the Paraná–Río de la Plata Basin had a sex ratio of 0·61:1 (males:females), and a L_S ranging from 280 to 600 mm (mean ± S.D.: 422 ± 56 mm) and a M_T of 500–5900 g (mean ± S.D. 2000 ± 1000 g). The L_S and M_T relationship ($M_T = a L_S^b$) expressed in its logarithmic form [$\log_{10} M_T = \log_{10} a + b \text{ Log}_{10} L_S$, where a is relative or allometric condition factor (intercept) and b the allometry coefficient (slope)] was calculated for all *P. lineatus* (Fig. 2). The slope, b, of the relationship (3·4; $r^2 = 0{\cdot}82$) is significantly higher than 3·0 ($P < 0{\cdot}05$). Where the fish collected at Berazategui were considered separately, the relationship improved ($r^2 = 0{\cdot}89$) and the slope increased to 3·5, being significantly steeper than those from PAR (3·2; $P < 0{\cdot}05$) and sRLP (3·0; $P < 0{\cdot}05$) (Fig. 2).

The L_S and M_T of *P. lineatus* collected in the extreme north reaches covered by the study, from Corrientes to Paso de la Patria and Pilcomayo (1000–1400 km north from Berazategui; Fig. 1) was significantly lower than that of Berazategui and Paraná *P. lineatus* (2·7 *v.* 3·5 and 3·2, respectively; $P < 0{\cdot}01$). The slope of fish collected along the Paraná River was reduced when 22 Paraná outliers plotted very close to Berazategui fish were excluded (Fig. 2). This depurated Paraná slope (2·9) was comparable to that of *P. lineatus*

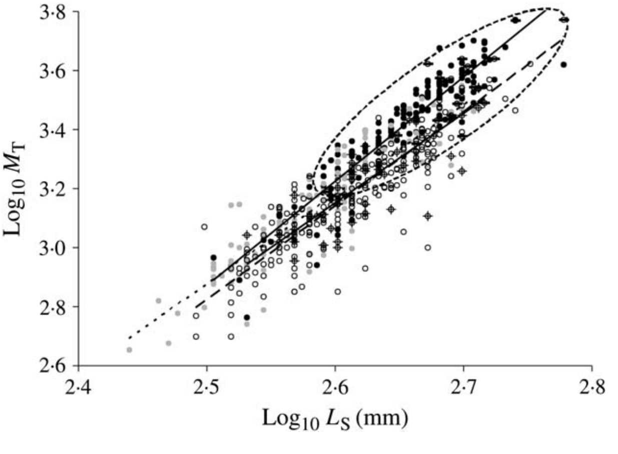

FIG. 2. Logarithmic standard length (L_S) and total mass (M_T) relationships of *Prochilodus lineatus* collected in south Río de la Plata (sRLP; ●), Berazategui (BZ; ●) and Paraná (PAR; ○) with extreme north fish indicated (N; ⊕) (see Fig. 1). Paraná outliers plotted close to BZ are encircled by a dashed ellipse. The curves were fitted by: BZ (upper ——): $y = 3{\cdot}53\,x - 2{\cdot}43$ ($r^2 = 0{\cdot}89$), sRLP (· · ·): $y = 3{\cdot}03\,x - 1{\cdot}67$ ($r^2 = 0{\cdot}83$), PAR (----): $y = 3{\cdot}16\,x - 1{\cdot}92$ ($r^2 = 0{\cdot}80$) and N (lower ——): $y = 2{\cdot}71\,x - 1{\cdot}18$ ($r^2 = 0{\cdot}70$).

TABLE I. Biochemical composition of *Prochilodus lineatus* muscle (values are mean ± S.D.)

Sampling station (see Fig. 1)	n	M_T (g)	L_S (mm)	K	Water (%)	Ash (% wet mass)	Protein (% wet mass)	Carbohydrate (% wet mass)	Lipid (% wet mass)
sRLP	128	1522 ± 682[a]	389 ± 53[a]	2·44 ± 0·35[b]	72·5 ± 5·6[b]	1·48 ± 0·30[b]	17·7 ± 2·6[b]	0·32 ± 0·11[c]	8·1 ± 6·7[a]
BZ	163	2745 ± 1015[b]	450 ± 49[b]	3·01 ± 0·47[c]	61·0 ± 12·1[a]	1·13 ± 0·32[a]	14·9 ± 3·2[a]	0·30 ± 0·08[b]	23·8 ± 13·8[b]
PAR	311	1775 ± 857[a]	420 ± 53a	2·26 ± 0·46[a]	72·3 ± 8·9[b]	1·39 ± 0·20[b]	17·3 ± 2·8[b]	0·16 ± 0·12[a]	8·0 ± 10·2[a]
N	62	1690 ± 603[a]	419 ± 47[a]	2·22 ± 0·39[a]	77·1 ± 3·2[c]	1·44 ± 0·11[b]	17·4 ± 2·6[b]	0·11 ± 0·12[a]	3·4 ± 3·2[a]
ALL	602	1990 ± 992[ab]	422 ± 56[a]	2·46 ± 0·52[a]	68·2 ± 11·2[ab]	1·30 ± 0·29[ab]	16·1 ± 3·8[b]	0·21 ± 0·12[a]	13·7 ± 13·5[a]

Values with different superscript lowercase letters within each column indicate significant differences ($P < 0·05$).
K, condition index; L_S, standard length and M_T, total mass.

collected in the extreme north (2·7) and in the southern area of the Río de la Plata, 45–100 km south from Berazategui (3·0; sRLP; Fig. 1). The segregation of these outliers was supported by their very high loads of aliphatic hydrocarbons (106 ± 75 μg g^{-1} wet mass) and PCBs (8·9 ± 5·1 μg g^{-1} wet mass), similar to Berazategui *P. lineatus* (82 ± 53 and 5·3 ± 3·6 μg g^{-1} wet mass, respectively), and two to three orders of magnitude higher than those of extreme north fish (5·3 ± 4·8 and 0·01 ± 0·02 μg g^{-1} wet mass, respectively; J. C. Colombo, E. Speranza, A. Barreda, N. Cappelletti & M. C. Migoya, unpublished data).

In addition to the geographical variations of the L_S and M_T relationship, clear sexual differences were observed. In south Rio de La Plata *P. lineatus*, the slope of this relationship is significantly steeper in females than in males (3·3 *v.* 2·7; $P < 0{\cdot}01$), whereas the opposite trend was observed in Parana (2·9 *v.* 3·3; $P < 0{\cdot}05$). No differences between males and female were observed in Berazategui *P. lineatus* (3·3 *v.* 3·3).

As well as the L_S and M_T relationships, different morphometric indexes were evaluated in the fish. The condition index (*K*), closely related to the L_S and M_T relationship, was calculated each individual ($K = M_T L_T^{-3}$). The value of *K* ranged from 1·5 to 4·3 (mean ± S.D. 2·5 ± 0·5) and increased from 2·0 ± 0·4 in *P. lineatus* weighing <1000 g to 3·3 ± 0·5 in fish >4000 g. Comparing individuals of similar M_T, the *K* of *P. lineatus* from Berazategui was significantly higher ($P < 0{\cdot}05$) than those from Parana, except for individuals of >4000 g, whose *K* do not differ significantly (3·3 ± 0·4 *v.* 3·2 ± 0·6). Differences between *K* values of Berazategui and sRLP fish were less pronounced, with *K* values significantly higher ($P < 0{\cdot}05$) in Berazategui fish only in individuals >2000 g.

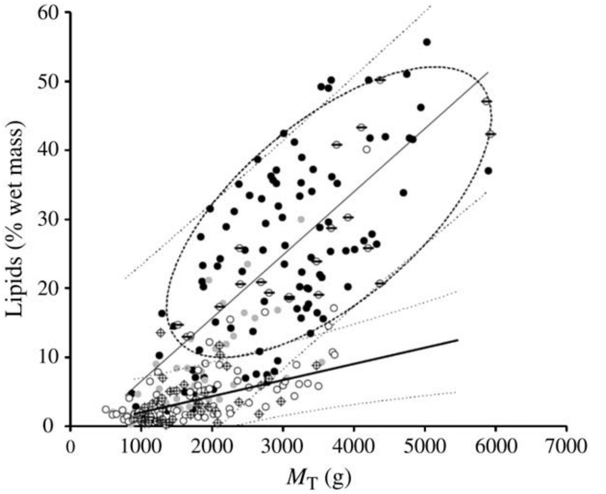

FIG. 3. Relationship of muscular lipid content with total body mass (M_T) of *Prochilodus lineatus* collected in south Río de la Plata (sRLP; ●), Berazategui (BZ; ●), Paraná (PAR; ○) with extreme north fish (N; ⊕) and Paraná outliers (⊖ encoded by a dashed ellipse). The curves were fitted by: BZ (upper —): $y = 0{\cdot}009\,x - 2{\cdot}700$ ($r = 0{\cdot}70$), N (lower —): $y = 0{\cdot}002\,x - 0{\cdot}396$ ($r = 0{\cdot}44$). The 95% CL for the regression of BZ and N fish are indicated (· · ·).

TABLE II. Biochemical composition of liver *Prochilodus lineatus* (values are means ± S.D.)

Sampling station (see Fig. 1)	n	M_T (g)	L_S (mm)	I_H	Water %	Ash (% wet mass)	Protein (%wet mass)	Carbohydrate (%wet mass)	Lipids (%wet mass)
sRLP	44	1826 ± 717[a]	407 ± 55[a]	1·11 ± 0·28[b]	76·9 ± 2·4[a]	1·66 ± 0·43[a]	13·8 ± 2·0[a]	1·8 ± 1·7[a]	5·5 ± 1·7[a]
BZ	83	2902 ± 1088[b]	456 ± 50[b]	1·41 ± 0·49[c]	75·7 ± 3·5[a]	1·91 ± 0·75[a]	13·5 ± 3·0[a]	2·3 ± 1·7[a]	6·5 ± 2·3[a]
PAR	38	1683 ± 754[a]	421 ± 49[a]	0·70 ± 0·32[a]	75·8 ± 2·7[a]	1·89 ± 0·34[a]	12·7 ± 2·1[a]	2·4 ± 2·2[a]	5·9 ± 1·9[a]
N	19	1611 ± 518[a]	403 ± 36[a]	0·60 ± 0·20[a]	76·2 ± 3·0[a]	1·96 ± 0·30[a]	11·6 ± 1·9[a]	1·9 ± 2·0[a]	6·4 ± 2·0[a]
ALL	165	2334 ± 1089[ab]	432 ± 56[ab]	1·17 ± 0·49[b]	76·0 ± 3·1[a]	1·84 ± 0·61[a]	13·4 ± 2·6[a]	2·2 ± 1·8[a]	6·0 ± 2·1[a]

Values with different superscript lowercase letters within each column indicate significant differences ($P < 0·05$).
I_H, hepato-somatic index; L_S, standard length and M_T, total mass.

TABLE III. Biochemical composition of the stomach contents of *Prochilodus lineatus* settling particles and sediments (values are means ± S.D.)

Sampling station (see Fig. 1)	*n*	NC	Water	Proteins (% wet mass)	Carbohydrates (% wet mass)	Lipids (% wet mass)
	Stomach contents					
PAR	9	37·4 ± 13·2	59·3 ± 11·1	1·20 ± 0·40	1·74 ± 0·47	0·333 ± 0·202
BZ	7	45·9 ± 18·6	49·9 ± 11·2	0·86 ± 0·55	2·42 ± 1·44	0·946 ± 0·899
Mean	16	41·1 ± 14·7	55·2 ± 11·8	1·03 ± 0·49	2·08 ± 0·92	0·602 ± 0·666
	Settling particles					
PAR	6	66·8 ± 8·1	32·7 ± 12·5	0·30 ± 0·25	0·16 ± 0·15	0·026 ± 0·025
BZ	26	35·5 ± 8·9	60·2 ± 7·8	1·57 ± 0·78*	1·80 ± 0·87*	0·986 ± 0·644*
Mean	32	41·3 ± 8·4	55·0 ± 14·0	1·38 ± 0·86	1·55 ± 1·01	0·821 ± 0·683
	Sediments					
PAR	11	75·1 ± 6·7	24·7 ± 6·6	0·09 ± 0·08	0·09 ± 0·09	0·017 ± 0·017
BZ	6	56·3 ± 17·2	42·0 ± 16·5	0·76 ± 0·48*	0·71 ± 0·58*	0·226 ± 0·139*
Mean	17	68·5 ± 14·4	30·8 ± 13·6	0·33 ± 0·43	0·31 ± 0·45	0·084 ± 0·133

Significant differences ($P < 0{\cdot}05$) between PAR and BZ, within each column are indicated (*).
NC, non-characterized material.

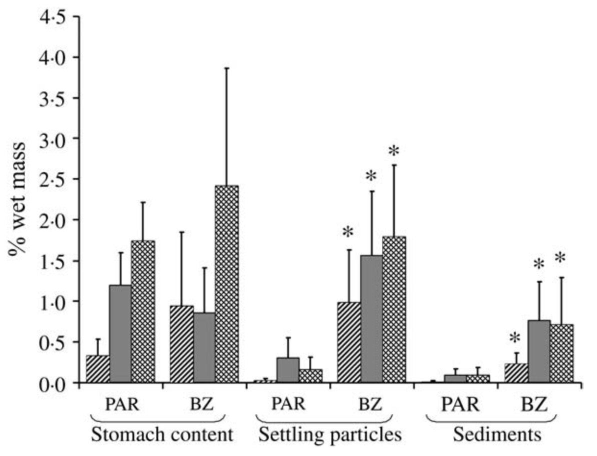

FIG. 4. Biochemical composition [lipids (▨), proteins (■) and carbohydrates (⊠)] of sediments, trap material and stomach contents of *Prochilodus lineatus* in the Paraná River (PAR) and Berazategui (BZ) in the Río de la Plata; values are means ± S.D. Significant differences ($P < 0·05$) between PAR and BZ, within each compartment are indicated (*).

The hepato-somatic index (I_H) was derived from $I_H = 100 M_L M_T^{-1}$. The I_H values for *P. lineatus* showed a wide range of variation (0·3–3·0) with a general mean ± S.D. of 1·17 ± 0·49. Fish from Berazategui had consistently higher I_H values (1·41 ± 0·49) compared with Paraná (0·70 ± 0·32, $P < 0·001$) and sRLP fish (1·11 ± 0·28; $P < 0·001$).

BIOCHEMICAL COMPOSITION

Muscle

Table I summarizes the muscle biochemical composition. In general, muscles contained a mean ± S.D. of 68·2 ± 11·2% water followed by a very homogeneous protein content (16·1 ± 3·8%), highly variable lipid values (13·7 ± 13·5%), low ash (1·30 ± 0·29) and almost negligible carbohydrates (0·21 ± 0·12) composed of 29 ± 20% glycogen ($n = 60$). Carbohydrates did not show any significant correlation with other variables in Río Paraná-Río de la Plata *P. lineatus*. The ash content was only significantly correlated with water and lipids ($r = 0·65$ and $r = -0·63$; $P < 0·01$). The protein contents were relatively homogeneous (7–25%, R.S.D. = 24%) and were inversely correlated to lipid contents ($r = -0·66$).

The most significant pattern of the biochemical composition of *P. lineatus* muscles was the inverse co-variation of % water (W) and % lipids (L_i) ($r = -0·95$) as M_T increased. Thus, both variables had opposite and significant general regressions with M_T ($L_i = 0·009\ M_T - 8·2$, $r = 0·77$ and $W = -0·008\ M_T + 86·5$, $r = -0·77$) and were significantly correlated ($L_i = -1·2\ W + 94$, $r = -0·97$). As M_T increased from <1000 to >4000 g, the mean ± S.D. water content of muscles decreased from 78·1 ± 1·4 to 48·7 ± 8·4% with a parallel increase of lipid content from 1·9 ± 1·2 to 38·2 ± 10·1%.

The most important geographical variations of muscle biochemical composition were associated with lipid content. The muscular lipid content of Berazategui *P. lineatus* was very high (23·8 ± 13·8% wet mass), reaching >50% fresh mass in some individuals of 4000–5000 g M_T (Table I and Fig. 3). Lipid contents of *P. lineatus* from Paraná and south Río de la Plata were significantly lower (8·0 ± 10·2 and 8·1 ± 6·7%, respectively; $P < 0·0001$) and this difference was even more pronounced when compared to extreme north fish (3·4 ± 3·2%; $P < 0·001$).

In order to compare the rate of lipid increase with body mass, the lipid and mass relationship was analysed (Fig. 3). As observed for the L_S and M_T relationship, the regressions differed significantly ($P < 0·01$) between *P. lineatus* from Berazategui and extreme north fish (Fig. 3). The regression for *P. lineatus* collected in sRLP was intermediate ($L_i = 0·006\ M_T - 2·8$; $r = 0·64$) and its slope differed both from Berazategui and extreme North ($P < 0·05$). The Paraná regression ($L_i = 0·0076\ M_T - 7·3$; $r = 0·77$) did not differs significantly from that of Berazategui but was strongly influenced by the heaviest individuals who had very high fat contents, in the range of Berazategui values. Excluding these 22 Paraná outliers (common in the L_S and M_T and L_i and M_T relationships) (Fig. 3), the slope of this regression decreased significantly ($L_i = 0·0029\ M_T - 0·48$, $r = 0·58$; $P < 0·001$) resembling that of north *P. lineatus*. As can be seen in Fig. 3, these outliers were within the 95% CL ($P < 0·05$) of the Berazategui relationship and outside these of the of extreme north relationship.

Liver

The biochemical composition of the liver was rather conservative and had no significant relationship with morphometric variables (Table II). Overall, water represented 76·0 ± 3·1% of the liver wet mass with a much lower variability (R.S.D. = 4·1%) compared to muscle, whereas proteins were 13·4 ± 2·6% wet mass and were significantly higher than the lipid contents (6·0 ± 2·1% wet mass; $P < 0·001$). Liver carbohydrates were more abundant than in muscle (2·2 ± 1·8% wet mass; $P < 0·01$), as well as the proportion of glycogen, which represented 77 ± 22% of total carbohydrates. As in muscle, the ash contents of the liver was low (1·84 ± 0·61% wet mass) and was weakly correlated with other biochemical variables.

The basic inverse relationship between water and lipids observed in muscles also held for liver ($r = -0·63$) with a lower relationship between water and proteins ($r = -0·49$). There were no clear geographical differences in liver biochemical composition. Although liver lipid content of Berazategui *P. lineatus* (6·5 ± 2·3% wet mass) was significantly higher than that of south Rio de La Plata *P. lineatus* (5·5 ± 1·7%; $P < 0·05$), it did not differ from that of Parana (5·9 ± 1·9%).

Stomach contents, settling particles and sediments

The biochemical composition of stomach contents of *P. lineatus* compared to settling particles and sediments is shown in Table III and Fig. 4. Settling particles from Berazategui showed a consistent average 10 times enrichment in organic carbon (8·0 ± 6·0 *v.* 0·6 ± 0·5%, respectively), and a two to five times increase in lipid, protein and carbohydrate contents (0·99 ± 0·64, 1·57 ± 0·78 and 1·80 ± 0·87% *v.* 0·23 ± 0·14, 0·76 ± 0·48 and 0·71 ± 0·58% wet mass, respectively; $P < 0.05$) compared to underlying sediments. The biochemical composition of the stomach contents of *P. lineatus* from Berazategui was similar to the trap material, in terms of lipids (0·95 ± 0·90%), proteins (0·86 ± 0·55%) and carbohydrates (2·4 ± 1·4% wet mass; Fig. 4). The concentrations of lipids, proteins and carbohydrates in trap material (0·026 ± 0·025, 0·30 ± 0·25 and 0·16 ± 0·15% wet mass) and sediments (0·017 ± 0·017, 0·09 ± 0·8%, 0·09 ± 0·09% wet mass) collected along the Paraná gave a more comparable composition and were four to 20 times lower relative to Berazategui ($P < 0.01$). The biochemical composition of the stomach contents of Paraná fish (lipids: 0·333 ± 0·202, proteins: 1·20 ± 0·40 and carbohydrates: 1·74 ± 0·47) was not significantly different from Berazategui.

DISCUSSION

BASIC MORPHOMETRIC CHARACTERISTICS

The slope of the general L_S and M_T relationship (3·4; r^2: 0·82) was significantly higher than 3·0 ($P < 0.05$), and it increased to 3·5 for the fish collected at Berazategui (Fig. 2). A review of the length and mass relationships from the FishBase database (http://www.fishbase.org) ($n = 2565$) indicated that the slopes for marine and freshwater fishes usually range from 2·8 to 3·2 with a general mean ± S.D. of 3·0 ± 0·3 (Froese & Pauly, 2005), which reflects the cubic relationship between length and mass typical of an isometric or proportional growth (Ecoutin & Albaret, 2003). Slopes >3·5 are rather unusual; only 1·7% of the whole database ($n = 43$) are higher than this value. The atypical character of the high slope values of Berazategui *P. lineatus* was confirmed by results from previous studies of >6500 *P. lineatus* from the upper reaches of the Paraná Basin which reported L_S and M_T slopes ranging from 2·1 to 3·3 with a general mean ± S.D. of 2·7 ± 0·4 (Cordiviola de Yuan, 1971; Bonetto, 1980; Carozza & Cordiviola de Yuan, 1991; Benedito-Cecilio *et al.*, 1997; Bechara *et al.*, 1999). Similarly, the slopes reported for *P. lineatus* from the Pilcomayo and Bermejo rivers, north affluents of the Paraná, ranged between 2·5 and 2·9, with a general mean ± S.D. of 2·8 ± 0·2 (Kasyanov & Izyumov, 2000; Escobar, 2004). The high slope values of *P. lineatus* collected at Berazategui indicate a positive allometry with a disproportional mass increase compared with fish from the upper Basin. This suggests that anthropogenic effluents discharged in Metropolitan Buenos Aires area constitute a favourable food resource for this fish.

Due to the migratory habits of this species, *P. lineatus* from Parana River constitute a heterogeneous group made up of individuals with contrasting morphometric characteristics. By contrast, the L_S and M_T relationship of *P. lineatus* collected in the extreme north reaches is not influenced by migratory individuals from the Rio de La Plata because migration distances longer >1000 km are uncommon (Sverlij *et al.*, 1993). This fish has a low L_S and M_T slope, comparable to previous reports from the upper Paraná reaches, suggesting that northern fish present a reduced mass compared to Berazategui. Exclusion of the outliers identified by their high pollutant concentrations and their strong positive allometry, significantly reduced the L_S and M_T slope of Parana fish, reinforcing the interpretation of mixing of different *P. lineatus* stocks in the Parana mainstream.

The differences observed between sexes in the L_S and M_T slopes might be associated with the reproductive cycle. In the Rio de La Plata, which serves as a feeding ground for *P. lineatus* before northward reproductive migration, the ovaries mature, reaching up to 30% of body mass (Sverlij *et al.*, 1993), explaining the steeper L_S and M_T relationship in sRLP females. In the Parana, were reproduction takes place, the lower slope of females is probably related to the significant body mass loss due to the oviposition. The lack of differences between males and females in Berazategui *P. lineatus* is probably due to the abnormal lipid contents of these fish which mask any difference associated with sex.

The high K values of Berazategui *P. lineatus* is consistent with the K increase observed by other authors in fishes exposed to sewage pollution (Porter & Janz, 2003; Alberto *et al.*, 2005). Overall, the evaluation of L_S and M_T relationships in *P. lineatus* from the Río de la Plata basin indicate a significant positive allometry in *P. lineatus* from Berazategui compared to other locations, suggesting that the metropolitan area of the Rio de La Plata, heavily polluted with urban and industrial effluents, offers abundant nutritional resources.

The I_H may be affected by fish metabolism and exposure to xenobiotics (Van der Oost *et al.*, 2003). The I_H values for *P. lineatus* show a wide range of variation (0·3–3·0) with a general mean ± S.D. of 1·17 ± 0·49. Interestingly, *P. lineatus* from Berazategui, heavily polluted with a complex xenobiotic mixture including aliphatic hydrocarbons, PCBs, linear alkyl benzenes and polybrominated diphenyl ethers (Colombo *et al.*, 2000; Cappelletti *et al.*, 2005), present consistently higher I_H values (1·41 ± 0·49), compared with Paraná fish (0·70 ± 0·32, $P < 0{\cdot}001$) and sRLP fish (1·11 ± 0·28; $P < 0{\cdot}001$). This liver enlargement has been observed in *P. lineatus* exposed to sediments polluted with urban effluents (Almeida *et al.*, 2005) and is probably related to the enhancement of the detoxifying metabolism in the liver (Van der Oost *et al.*, 2003). This interpretation is supported by the observation of more degraded aliphatic hydrocarbon traces as indicated by a consistent reduction of C17/pristane and C18/phytane ratios in livers (0·58 ± 0·37 and 0·45 ± 0·33) relative to muscles (1·0 ± 0·55 and 0·81 ± 0·41, respectively) in Berazategui *P. lineatus* (unpublished data).

BIOCHEMICAL COMPOSITION

In muscle, protein contents are relatively homogeneous (7–25%, R.S.D. = 24%), probably reflecting the prevailing structural role of proteins in fishes (Huss, 1995). Lipids, by contrast, are highly variable because they are correlated with body mass. The general inverse relationship between lipids and water of *P. lineatus* (Fig. 3) reflects the replacement of water by lipids as fishes grow (Lagler *et al.*, 1977), and is similar to those obtained for fatty fishes such as scombrids ($L_i = -1{\cdot}3 \pm 0{\cdot}28\ W + 87 \pm 13$; $r = -0{\cdot}96 \pm 0{\cdot}02$; Vlieg, 1988;

Wheeler & Morrisey, 2003; Morrisey *et al.*, 2004), whereas lean fishes usually show lower slopes (*e.g. Merluccius hubbsi* Marini: $L_i = -0.43\ W + 37$; $r = 0.83$; Méndez and González, 1997). The low carbohydrate concentration reflects the prevailing protein and lipid-based energy storage of fishes (Henderson, 1996).

Prochilodus lineatus has a high muscle lipid content (24 ± 14% wet mass). Fish lipid contents usually range between 0·2 and 25% and rarely attain 67% as extreme values (Huss, 1995). In the FishBase proximate analysis database (>709 data from 528 species), only 8% have a mean lipid content >10% (Froese & Pauly, 2005). In addition to the muscle fat, *P. lineatus* also store high quantities of lipids in visceral deposits, which led to its past industrial utilization (Brenner, 1952). In contrast, lipid contents of *P. lineatus* from Paraná and south Río de la Plata are significantly lower (8·0 ± 10 and 8·1 ± 6·7% respectively; $P < 0.001$) and this difference was even more pronounced when compared to extreme north *P. lineatus* (3·4 ± 3·2%; $P < 0.001$).

Prochilodus lineatus from Berazategui stand out by their high lipid content (22 ± 15%), which is among the highest reported even compared with fatty fishes such as tunas or herrings (Jacquot, 1961). This high muscle fat content is in sharp contrast to those of fish collected in northern locations, and to values previously reported for *P. lineatus* from the upper Paraná (3·7%; Matsuhita & de Souza, 1994), middle Paraná (5·6–14%; Bayo & Maitre, 1983), Uruguay River (0·2–7·1%; Angelini & Seigneur, 1992) and southern Río de la Plata (7·1–11% with one value of 34% considered as exceptionally high; Brenner, 1953). *Prochilodus lineatus* from extreme north sites Corrientes, Formosa, Pilcomayo and Paso de La Patria have similarly low fat percentages (3·4 ± 3·2%), comparable to lipid contents of Brazilian *Prochilodus*: 2·5 ± 1·7% in *Prochilodus scrofa* Steindachner (Maia *et al.*, 1983), 3·8 ± 1·5% in *Prochilodus brevis* Steindachner (Maia *et al.*, 1999) and 6·7–9·0% in *Prochilodus* sp. (Luzia *et al.*, 2003). The slope of the relationship between muscular lipid content and body mass was significantly steeper in Berazategui than in extreme north fish. In Paraná fish, this relationship was clearly influenced by the outliers, supporting the interpretation of mixing during upstream migration indicated for the L_S and M_T relationship. This difference in lipid content is related to a feeding strategy based on consumption of anthropogenic organic matter at Berazategui. The possible interaction of organic pollutants on lipid metabolism cannot be ruled out since previous reports suggest that these contaminants may produce an increase in lipid contents related to a reduced catabolism and interference with thyroid hormones (Dillon & Engler, 1988; Geyer *et al.*, 1994).

The interpretation that the fattiest *P. lineatus* collected along the Paraná River are in fact migrating fish from Berazategui implies little consumption of lipid reserves during the upstream movement of the fish. This observation is consistent with the interpretation that visceral fat, which can constitute up to 7% of *P. lineatus* body mass (Brenner, 1953), is the main energy source for migration (Bayley, 1973). Considering the typical calorific content of lipids (38 kJ g^{-1}) and a 7% visceral fat content, a 3000 g *P. lineatus* could store *c.* 7917 kJ in these deposits, enough for a >500 km journey assuming the consumption of 0·016–0·017 kJ m^{-1} for an upstream migration as reported for *Prochilodus mariae* Eigenmann in Venezuela (Saldaña & Venables, 1983).

The liver, by contrast, has a homogeneous biochemical composition, not significantly correlated with morphometric variables (Table II). The higher carbohydrate content of the liver reflects the accumulation of dietary carbohydrates in hepatic glycogen deposits.

The enrichment in organic carbon of settling particles from Berazategui relative to underlying sediments reflects the fresher nature of the material collected by the traps in a coastal area affected by crude effluent discharges (Colombo *et al.*, 2005*a*, 2007*c*). The extensive organic matter degradation at or near the sediment–water interface is also evidenced by the reduction in lipid, protein and carbohydrate contents between settling particles and consolidated sediments. The similarity, in terms of biochemical composition, between the stomach contents of *P. lineatus* and the settling particles suggest that *P. lineatus* feeds directly on the organic-rich, flocculent layer deposited at the sediment–water interface. This interpretation is supported by the similarity, in terms of hydrocarbons, PCBs and linear alkylbenzenes, between settling particles and *P. lineatus* muscle (Colombo *et al.*, 2007*a*, *b*, *c*). The lower lipid, protein and carbohydrate contents in settling particles and sediments collected along the Paraná relative to Berazategui reflects a lower contribution of organic matter, basically terrestrial detritus and phytoplanctonic inputs. The rather homogeneous composition of stomach contents from Paraná and Berazategui fish is probably related to the partial alteration of the food by digestive processes. Nevertheless, higher organic matter concentrations in stomach contents of Río de la Plata *P. lineatus* relative to Paraná fish have been previously interpreted as indicative of selective feeding on organic-rich anthropogenic discharges (Villar *et al.*, 2001). The present results reinforce previous interpretations relating the spatial variability of *P. lineatus* along the Río de la Plata Basin with organic matter abundance in the water column (Quirós & Baigún, 1985), emphasizing the importance of settling material as the best proxy to characterize feeding grounds and organic matter sources.

In summary, the discharge of untreated urban-industrial effluents in the Metropolitan Buenos Aires coast introduce a significant amount of easily degradable organic matter, which is efficiently absorbed by a specialized detritivorous fish. This energy subsidy permits a rapid mass increase and lipid accumulation with a parallel contaminant absorption in Buenos Aires *P. lineatus* relative to leaner northern fish whose diet is based on 'natural' organic-poor vegetal detritus. Thus, the feeding strategy based on sewage-derived organic matter appears beneficial for *P. lineatus* which present better condition indices in polluted areas at the expense of a higher exposure to multiple contaminants. Within the context of equilibrium partitioning, the increased fat accumulation of these fish would favour the bioaccumulation of hydrophobic (lipophilic) pollutants, which in turn may interfere on lipid metabolism reinforcing a positive lipid-contaminant feedback. The large muscle lipid reserves of *P. lineatus*, apparently immobilized even after >800 km long migrations indicate that they act as a long-term storage compartment, reducing the pollutant circulation and potential adverse effects due to their lower turnover. Nevertheless, the consistently higher I_H of fatty *P. lineatus* suggest an enhanced detoxifying metabolism, which is supported by their degraded contaminant pattern pointing to some metabolic cost of detritus feeding in polluted environments.

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