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Energy budgets of fish populations in two tributaries of the Paraná River, Paraná, Brazil

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ABSTRACT. The energy budget of all fish populations was estimated in two small tributaries of the Paraná River (Paraná, Brazil). Total energy consumed by fish in the Caracu and the Agua do Rancho Rivers was 4.1 and 1.8 MJ m^{-2} y^{-1}, and food items consumed were 2284 and 994.5 g wet weight m^{-2} y^{-1}, respectively. The gross (K_1) and net (K_2) ecological efficiency coefficients were very low, but 43.2 and 59.6% of the total fish diet in these two streams, respectively, consisted of plant detritus. In both fish communities, omnivorous (opportunist) species dominated and specialists were rare. Although the Caracu River was more affected by human activity than was the Agua do Rancho, ecological efficiency coefficients calculated for the dominant fish populations were not significantly different.

KEY WORDS: energy budget, ecological efficiency, fish populations, food consumption, Paraná River catchment, small tributaries

INTRODUCTION

There have been few bioenergetics investigations in tropical riverine ecosystems (Benke *et al.* 1988, Payne 1986), probably because of the difficult access to water temperature data throughout the year (Brandt & Hartman 1993). In many temperate countries, especially in North America and Europe, data on monthly water temperature are frequently available from governmental agencies or scientific institutes monitoring the quality of these environments; practically all fish energy budgets originate from these territories (Mann 1969, Ney 1993, Tytler & Calow 1985).

In a field study of the bioenergetics of fish in a small Venezuelan river, Penczak (1992) found that food was used relatively ineffectively for growth as compared with fish from the rivers of the temperate zone (Mann 1965, 1969, 1978; Mortensen 1985, Penczak 1995, Penczak *et al.* 1984).

The present study of tropical fish from two streams differing in morphology and water quality establishes the total amount of food consumed in mass units, its efficiency of transformation into growth and metabolism, and the energy budgets of the fishes.

STUDY AREA

Fish were sampled in two small east-bank tributaries of the Paraná River, in the north-west corner of Paraná State (Figure 1). The Caracu stream is 6.8 km and the Agua do Rancho 4 km long. The former flows directly into the Paraná, the latter into the Areia Branca, 7.8 km from its confluence with the Paraná. Data from six sampling sites in the Caracu stream over 5.5 km, and five in the

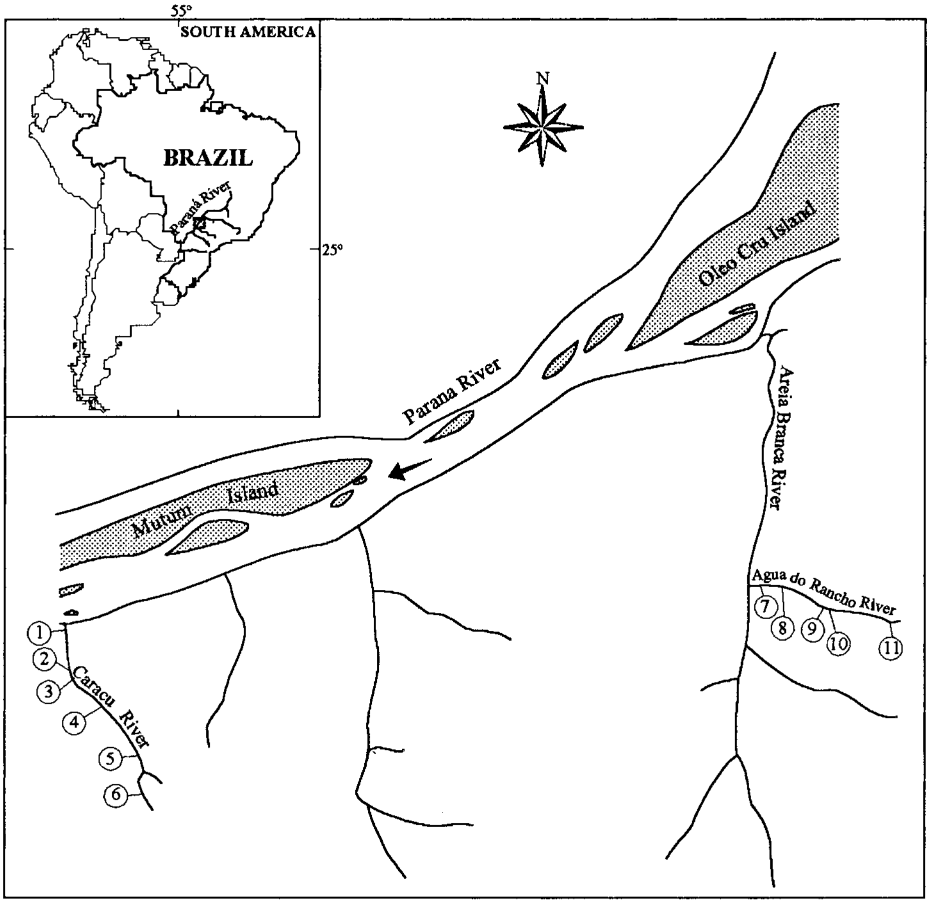

Figure 1. Map of the Caracu and Agua do Rancho Rivers in southwestern Brazil showing the locations of sites.

Table 1. Combined characteristics of the Caracu stream and the Agua do Rancho stream, Brazil.

	Caracu stream		Agua do Rancho stream	
Parameters	Mean	Range	Mean	Range
Site area (m^2)[1]	647		1034	
Width (m)	2.2	1.8–2.6	3	2.1–3.6
Depth (m)	0.3	0.2–0.5	0.2	0.1–0.4
Substratum[2]	s>>m,st		s>>st>m	
Macrophyte cover (%)	51	10–75	11	0–5
Hiding places (%)	17	2–30	10	5–2
Hiding type[3]	G		G,B,S	
Trees along banks (% of bank length)	4	0–12	68	3–100
Water velocity (m s^{-1})	1	0.4–2.1	1.8	0.5–3.1
pH	7.1	7–7.3	6.5	6.1–6.6
O_2 (ml l^{-1})	7.2	6.4–7.7	7.3	6.7–7.6
Conductivity (μS cm^{-1})	78.7	76–81	47.4	48–49
Total nitrogen (mg l^{-1})	0.5	0.4–0.6	0.3	0.2–0.6
Total phosphate (μg l^{-1})	59.2	38.8–73.8	42	25.1–63.4

Explanations: [1] – total area and number of sites, [2] – (s – sand, m – mud, st – stones), [3] – (G – overhanging grass), B – branches, S – snags (see text for further explanations)

Agua do Rancho over 3.5 km were combined to increase sample sizes (Watson & Balon 1985). Fish community and diversity data have been published previously (Penczak *et al.* 1994).

Morphology, physico-chemical parameters (Table 1) and mean monthly water temperature necessary for calculating standard metabolism were determined (Table 2). Data on the stream drainage basins and for each site separately were reported by Agostinho & Penczak (1995).

MATERIALS AND METHODS

The study was based on 1260 specimens belonging to 28 taxa representing 14 families (Table 3), but food consumption in energy and mass units was calculated for 27 taxa, because cichlids were represented by one individual only. Samples were collected during October 1992.

The electric fishing methods used, for a constant time at each site, were described by Penczak *et al.* (1994). The Zippin maximum-likelihood method was used for estimating population density (Zippin 1958), and the Mahon *et al.* (1979) equation for calculating standing crop.

The initial variables for estimating growth ratio and then production (density, mean body length and weight) were taken from histograms of length- and body weight-frequency, distinguishing classes of body size by polymodal frequency analysis (Agostinho & Penczak 1995). Where it was difficult

Table 2. Mean monthly water temperatures in the Caracu and Agua do Rancho streams.

Stream/Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Caracu	29.3	29.0	23.2	22.8	21.7	18.2	19.3	24.0	24.3	25.3	25.6	28.8
Agua do Rancho	28.7	28.4	22.6	22.2	21.1	17.6	18.7	23.4	23.7	24.7	25.0	28.2

Table 3. Taxonomic, ecological and dietary classification of the fish species in the Caracu and Agua do Rancho Streams.

Family	Species	Place in stream	Principal food	Number of guts examined
Characidae	*Astyanax scabripinis* (Eigenmann, 1927)	p	detritus, insects[1]	13
	Bryconamericus stramineus (Eigenmann, 1908)	p	insects[1]	16
	Astyanax bimaculatus (Linnaeus, 1758)	p	detritus, insects[1]	33
	Astyanax schubarti Britski, 1964	p	water plants, algae[3]	–
	Characidium fasciatum Reinhardt, 1866	b	algae, insects[3]	–
	Cheirodon notomelas (Eigenmann, 1915)	p-b	algae, detritus[2]	173
	Roeboides paranensis Pignalberi, 1975	p	insects, fish scales[3]	–
Pimelodidae	*Rhamdia quelen* (Quoy & Gaimard, 1824)	b	insects, detritus[1]	13
	Nannorhamdia schubarti Gomes, 1956	p-b	insecta[2]	22
	Cetopsorhamdia iheringi Schubart & Gomes, 1959	p-b	animal detritus, insects[2]	11
	Phenacorhamdia sp.	b	insects, animal detritus[2]	11
Loricariidae	*Hypostomus ancistroides* Ihering, 1911	b	plant detritus[1]	21
	Microlepidogaster sp.	b	plant detritrus[1]	11
	Loricariichthys platymetopon Isbrucker & Nijssem, 1979	b	detritus[2]	10
Anostomidae	*Leporinus silvestris* Boulanger, 1902	p-b	water plants, insects[3]	–
	Leporinus obtusidens (Valenciennes, 1847)	p-b	plant detritus[2]	1
	Leporinus friderici (Bloch, 1794)	p-b	water plants, insects[3]	–
Callichthyidae	*Corydoras aeneus* (Gill, 1864)	b	animal detritus, insects[2]	4
	Callichthys callichthys (Linnaeus, 1758)	b	insects, microcrustaceans[3]	–
Poecilliidae	*Phalocerus caudimaculatus* (Hensel, 1868)	b	algae, insects[3]	–
Synbranchidae	*Synbranchus marmoratus* (Bloch, 1795)	b	insects[3]	–
Sternopygidae	*Eigenmania trilineata* (Lopez & Castello, 1966)	p	insects, animal detritus[2]	7
Gymnotidae	*Gymnotus carapo* (Linnaeus, 1758)	p-b	detritus, insects[1]	33
Erythrinidae	*Hoplias malabaricus* (Bloch, 1794)	p-b	fish[3]	–
Auchenipteridae	*Parauchenipterus galeatus* (Linnaeus, 1766)	p	insects[3]	–
Curimatidae	*Steindachnerina insculpta* (Fernandes-Yepez, 1948)[4]	b	mud[3]	–
Prochilodontidae	*Prochilodus lineatus* Steindachner, 1882[4]	p-b	mud[3]	–
Cichlidae	*Cichlasoma paranaense* Haseman, 1911	b	one specimen, not investigated	–

p – pelagic, b – benthic, p-b – pelagic-benthic

[1] diet investigated in all size classes.

[2] diet investigated for all individuals together.

[3] data from literature or own data from other rivers.

[4] In former publications (Penczak *et al.*, 1994; Agostinho & Penczak 1995), *Steindachnerina insculpta* was named *Curimata insculpta*, and *Prochilodus lineatus* was named *Prochilodus scrofa*.

to distinguish body size classes, scattergrams of length-body weight were developed, which were congruent with groups of some fishes in temperate zone waters (Balon & Penczak 1980) as well as in tropical ones (Penczak & Lasso 1991). In the case of tropical fishes, whose biology is mostly not well known, the use of scales or opercular bones could entail serious error, or lead to erroneous results (Bagenal & Tesch 1978, Blake & Blake 1978, Casselman 1987). Hence, it was decided to use length-frequency histograms to distinguish body size class through polymodal frequency analysis. The reliability of these histograms, as in Watson & Balon (1985), is additionally increased by combining data from all sites ('big sample size').

The energy budget was derived from the model: $C = P + R + F + U$, where C is the energy content of food consumption, P is the production, R is the net loss of energy in respiration, U is the energy lost in nitrogen excretory products, and F is the energy lost in faeces (Winberg 1956). Consumption was calculated from Penczak's (1995) modified Winberg's (1956) equation: $C = p\,(P + S_aR_s)$, where p is the unsteady proportion of consumed food that is assimilated, S_a is the swimming activity factor and R_s is the standard metabolism.

P and R_s were calculated at the time of sampling and for more abundant species (Mann 1965):

$$P = \int_{d}^{d+1/12} N_t \, dw_t$$

$$R_s = \int_{d}^{d+1/12} N_t \, (Aw_t)^{0.81} dt,$$

where N_t is the number of individuals at time t, dw_t is growth increment at time t, 0.81 is a constant for mass-dependent metabolic rates, A is a constant ($A = 0.307\ q^{-1}$), determined by temperature according to Krogh's curve ($q = 1$ for 20 °C) (Winberg 1956), w_t is the mean body weight of an individual at time t; annual (d) growth and standard metabolism periods were divided into 1/12th parts of the year for calculations.

Population density (N_t) and mean body weight (w_t), for a given size-class were calculated from the exponential equations, as well as instantaneous growth (G) and mortality (Z) rates (Ricker 1975): $N_t = N_oe^{Zt}$, $w_t = w_oe^{Gt}$, $G = \ln(w_2/w_1)$, and $Z = -\ln(N_2/N_1)$, where N_1, N_2, w_1 and w_2 are numbers and mean body weights of fish in subsequent modes representing two size groups, respectively, distinguished by us. Initial parameters for calculating production are available in Agostinho & Penczak (1995).

Total metabolism (R) is the sum of three values: $R = R_s + R_d + R_a$, where R_d is the metabolic cost of synthetic processes required for growth (specific dynamic action), and R_a is the cost of swimming.

To convert energy lost (R_d) as heat for fish consuming carbohydrates we used 21.8 J ml^{-1} O_2, for those consuming fat—20.5 J ml^{-1}, those protein—19.7 J ml^{-1},

Table 4. Calorific content of fish species and swimming factor (S_a) used in multiplying R_s to calculate total respiration for the fish populations investigated in the Caracu and Agua do Rancho streams (see text for explanations).

Species	Calorific value kJ g^{-1} w.w. ± SD	S_a YOY	S_a > 1-y old
Hypostomus ancistroides	4.17 ± 0.12	1.5	1.2
Astyanax bimaculatus	8.26 ± 0.08	2.0	1.8
Gymnotus carapo	3.92 ± 0.07	1.7	1.5
Astyanax scabripinis	6.12 ± 0.18	2.0	1.8
Microlepidogaster sp.	7.05 ± 0.26	1.5	
Bryconamericus stramineus	4.95 ± 0.05	2.0	1.8
Rhamdia quelen	4.45 ± 0.03	1.5	1.2
Mean	5.56		

and for omnivorous fish an average of these values—20.15 J ml^{-1} O_2 (Solomon & Brafield 1972).

Because R_a is difficult to estimate under field conditions (Wootton 1990), R_s was multiplied by the swimming factor (S_a) to obtain total metabolism. S_a values were established using information on the position of fish in the water column (pelagic—swimming almost continuously, benthic—swimming slowly or resting on the bottom) (Table 3), as well as direct data on swimming ability of some species. Because mean monthly water temperatures were close to 20 °C or higher, S_a was differentiated according to body length only, i.e. separately for the first mode in the length-frequency histograms, which always correspond to the young-of-the year (YOY), and fish older than 1 y together, respectively (Table 4).

Waste products (F + U) were estimated using factor 1.25 (80% of energy is assimilated only) for insectivores and predators, 1.43 for omnivores and 1.69 for taxa consuming algae, plant detritus and mud (Brafield 1985). These values were adjusted for given species proportionally to the percentage of plant detritus, and sediment in their diet.

For non-dominant species, i.e. those for which the production and consumption were not investigated directly, C was estimated by dividing P taken from Agostinho & Penczak (1995), by the mean gross ecological efficiency $K_1 = 100\ C^{-1}$ calculated for directly studied species in a given stream and multiplying by 100 (Penczak 1992); P in this paper was calculated as mass transformed to energy units using mean calorific value, calculated for seven directly investigated taxa (Table 4).

Diet was established for 379 fish belonging to seven species. For 12 species general information on fish diet composition was taken from literature (Araujo-Lima *et al.* 1995, Esteves 1996, Fugi *et al.* 1996, Hahn *et al.* 1997), and for the other taxa unpublished data from other water bodies of Paraná State were available (Table 3).

Gut contents were analysed to estimate the total food consumed in wet weight (Penczak 1985, 1995). Small food items were separated in a Petri dish, then squashed on graph paper to a uniform depth of 1 mm to determine their area, volume and weight (Hellawell & Abel 1971), assuming that 1 mm^3 weighed 1 mg; large prey, such as whole fish, were weighed directly.

The percentage efficiency of energy transformation by fish populations (K_1 and $K_2 = P A^{-1}$, where A is assimilated energy ($A = C\text{-}FU$): Ivlev 1939, Grodzinski *et al.* 1975), and $R C^{-1}$ were calculated, as well as how much prey (kg wet weight) was used to produce 1 kg of fish tissue ($C P^{-1}$).

Calorific content of food items was taken from Cummins & Wuycheck (1971) and Penczak (1995). Calorific content of dominant fish species was calculated using the model of Hartman & Brandt (1995): energy density in $J g^{-1}$ wet weight = $45.29 W_D^{1.507}$, where W_D is the percent dry weight of the fish. W_D was calculated by drying five specimens of each dominant species to constant weight at 70 °C in an oven. Dispersion of measurements was very small (Table 4).

RESULTS

The Caracu River was more influenced by human impacts than was the Agua do Rancho (Table 1), particularly by bank deforestation, reduction of cover, scarcity of hiding places, and higher eutrophication. Despite these differences, directly estimated energy budget parameters (C, P, and R) and ecological efficiency coefficients (K_1, K_2, $R C^{-1}$, $C P^{-1}$) for both streams (Tables 5 and 6) were not significantly different ($P > 0.05$; Duncan's test).

Energy consumed by 3–4 interval of size group of *Hypostomus ancistroides* was calculated but we could not transform this value to wet weight of food items because no specimen of this size was dissected for diet analysis in the Caracu River (Table 5). The poor food conversion by *Microlepidogaster* sp. can be explained by the low calorific content of plant detritus eaten, but similar values of $C P^{-1}$ also for juveniles of *Bryconamericus stramineus*, which feed mainly on insects, are difficult to explain.

The wet weights and calorific content of the prey consumed by separate size-groups of dominants are listed in Tables 7–11. For some species diet was investigated as a total for all size groups (Table 12). In the Caracu River, plant and animal detritus predominated. In the Agua do Rancho, animal detritus and invertebrates dominated (Table 12), however the animal detritus was eaten mainly by *Cetopsorhamdia iheringi*, while the remaining three species ate mainly insects.

For twelve species from the Caracu River and four from the Agua do Rancho, the diet composition was available from the literature, and from fish collected in other rivers of the Paraná catchment (Table 13). Food eaten by *Hoplias malabaricus* could not be estimated, although the literature indicates that it is piscivorous. Its diet changes during ontogeny and juveniles consume large quantities of macroinvertebrates and algae (Hahn *et al.* 1997). Also, the volume of food consumed by *Roeboides paranensis*, which consumes fish scales and insects, was not estimated well (Hahn *et al.* 1997). Half of consumed energy was arbitrarily assigned the wet weight of insects, whereas energy of the scales was not, because we do not know their caloricity.

Table 5. Parameters of the energy budget (MJ ha^{-1} y^{-1}) and the coefficients of ecological efficiency (%) of dominant fish populations from the Caracu Stream. C P^{-1} is the consumption (kg wet weight kg^{-1} of fish production).

Size groups	P	R	C	K_1	K_2	R C^{-1}	C P^{-1}
Hypostomus ancistroides (detritivorous, benthic)							
0–1	43.1	390.8	899.9	4.8	9.3	43.4	77.8
1–2	38.8	525.2	956.7	4.1	6.9	54.9	100.9
2–3	63.9	1305.7	2331.9	2.7	4.7	56.0	148.6
3–4	44.1	1058.7	1879.7	2.4	4.0	56.3	†
4–5	12.1	413.6	728.0	1.7	2.8	56.8	230.8
Total or mean	202.0	3694.0	6796.2	3.1	5.5	53.5	139.5
Astyanax bimaculatus (omnivorous, pelagic)							
0–1	321.6	1076.5	2969.4	10.3	23.0	36.3	41.6
1–2	210.0	2029.2	4635.2	4.5	9.4	43.8	118.7
2–3	180.5	1704.0	3897.3	4.6	9.6	43.7	82.4
3–4	93.7	1034.1	2346.1	4.0	8.3	44.1	99.3
4–5	54.6	480.7	1104.0	5.0	10.2	43.5	80.2
Total or mean	860.4	6324.5	14952.0	5.7	12.1	42.3	84.4
Gymnotus carapo (omnivorous, bentho-pelagic)							
0–1	123.6	1540.0	3289.9	3.8	7.4	46.8	41.0
1–2	58.9	1696.5	3124.2	1.9	3.4	54.3	88.5
2–3	22.0	637.6	1174.1	1.9	3.3	54.3	105.6
Total or mean	204.5	3874.1	7588.2	2.5	4.7	51.8	78.4

†Missing value indicates that diet was not available.

Table 6. Parameters of the energy budget (MJ $ha^{-1}y^{-1}$) and the coefficients of ecological efficiency (%) of dominant fish populations from the Agua do Rancho stream (symbols as in previous table).

Size groups	P	R	C	K_1	K_2	$R\,C^{-1}$	$C\,P^{-1}$
Hypostomus ancistroides (detritivorous, benthic)							
0–1	99.6	934.4	2146.7	4.6	9.6	43.5	87.9
1–2	55.1	1016.2	1822.5	3.0	5.1	55.8	129.8
2–3	25.5	351.6	639.8	4.0	6.8	55.0	100.2
Total or mean	180.2	2302.2	4609.0	3.9	7.2	51.4	106.0
Astyanax scabripinis (omnivorous, pelagic)							
0–1	72.9	617.9	1570.4	4.6	10.6	39.4	39.3
1–2	69.1	688.5	1569.9	4.4	9.1	43.9	54.5
2–3	25.3	521.8	1157.5	2.2	4.6	45.1	144.5
Total or mean	167.3	1828.2	4297.8	4.0	8.1	42.8	79.4
Gymnotus carapo (omnivorous, bentho-pelagic)							
0–1	18.2	501.4	1044.7	1.7	3.5	48.0	119.7
1–2	3.4	124.7	228.6	1.5	2.7	54.6	103.9
Total or mean	21.6	626.1	1273.3	1.6	3.1	51.3	111.8
Microlepidogaster sp. (detritivorous, benthic)							
0–1	10.3	229.6	507.6	2.0	4.3	45.3	327.0
Bryconamericus stramineus (insectivorous, pelagic)							
0–1	15.6	278.7	687.6	2.3	5.3	40.5	74.6
1–2	2.5	245.5	533.4	0.5	1.0	46.0	310.4
2–3	8.4	136.8	305.7	2.8	5.8	44.8	52.8
Total or mean	26.5	661.0	1526.7	1.9	4.0	43.8	145.9
Rhamdia quelen (insectivorous, benthic)							
0–1	101.7	1221.7	2321.1	4.4	7.7	52.6	43.0
1–2	40.9	583.6	889.4	4.6	6.6	65.6	30.0
2–3	11.4	230.4	345.5	3.3	4.7	66.7	25.0
Total or mean	154.0	2035.7	3556.0	4.1	6.3	61.6	32.7

Table 7. Food items consumed (kg ha^{-1}y^{-1} wet weight (w.w.)) by *Gymnotus carapo* in the Caracu and Agua do Rancho streams.

	Prey calorific content	Caracu stream				Agua do Rancho stream		
Size groups Food items	kJ g^{-1}w.w.	0–1	1–2	2–3	Total	0–1	1–2	Total
Algae	2.558					7		7
Plant detritus	1.017	41	329	181	551	167	10	177
Animal detritus	2.020	837	659	260	1756	300	42	342
Odonata	5.151		203		203	3	5	7
Isoptera	8.793	3			3			
Plecoptera	3.177	34			34			
Hemiptera	3.581	135			135		1	1
Coleoptera	2.199	9			9	43	2	45
Trichoptera	3.759	211			211		5	5
Diptera, others	3.180	2			2	7		7
Simuliidae	3.001	4	137	91	233			
Chironomidae	4.606	6			6	16	2	18
Ceratopogonidae	3.596					12		12
Hymenoptera	7.666	11			11			
Insecta, others	3.178			60	60	2	24	26
Total		1293	1328	592	3214	557	91	647

Table 8. Food items consumed (kg ha^{-1} y^{-1} w.w.) by *Hypostomus ancistroides* in the Caracu and Agua do Rancho streams. Data for the size group 3–4 are not available.

Size groups Food items	0–1	1–2	2–3	4–5	Total
			Caracu stream		
Algae	53	2	5	2	62
Plant detritus	751	937	2271	709	4668
Protozoa[1]					1
Chironomidae				1	1
Total	804	939	2276	712	4732
			Agua do Rancho stream		
Algae	7	51	5		63
Plant detritus	2093	1663	603		4358
Diptera, others			4		4
Chironomidae			1		1
Total	2100	1714	613		4426

[1] *Protozoa* calorific content = 2.010 kJ g^{-1} w.w.

Ecological efficiency coefficients, K_1 and K_2, were higher for smaller size-groups of a given species; in contrast, R C^{-1} and C P^{-1} were lower ones, respectively. However, with one exception for *Hypostomus ancistroides* (the Caracu stream) correlations were not statistically significant ($P > 0.05$), probably because of a low number of the degree of freedom. Taking advantage of all data from Tables 5 and 6 ($n = 28$) a correlation matrix also did not reveal any statistically significant correlations among size-groups and K_1, K_2, R C^{-1} and C P^{-1}, due to considerable species-specificity related differences in the values of these coefficients. On the other hand, K_1 and K_2 were dependent on the form of swimming activity. For example, in the insectivorous benthic *Rhamdia quelen* K_1 and K_2 were higher than in the insectivorous pelagic *B. stramineus* (Table 6).

DISCUSSION

The reliability of changes introduced into the Winberg (1956) models was already discussed in previous studies (Penczak 1992, 1995). The locomotion activity (R_a) of given species is particularly important, because this may be a source of considerable error in estimating energy budgets (Boisclair & Sirois 1993, Facey & Grossman 1990, Hansen *et al.* 1993, Lucas *et al.* 1993, Ney 1993, Ware 1975). To compare the present results with those obtained for fish from a Venezuelan stream (Penczak 1992), the values of the intercept and the slope in the model for estimating standard metabolism of the Venezuelan fish were retained, although an age and species-specific differentiation of values might be expected (Post & Lee 1996). However, according to Ney (1993), it is more important whether the bioenergetics model “will remain better suited for making relative comparisons than for making precise quantitative predictions”.

In the 13.5-km Todasana River, draining to the Caribbean Sea, and having nine species of fish, some populations specialized with a narrow diet, and others were omnivorous with detritus constituting < 1% of their diet (Penczak 1992).

Table 9. Food items consumed (kg $ha^{-1}y^{-1}$ w.w.) by *Rhamdia quelen* and *Bryconamericus stramineus* in the Agua do Rancho stream.

	Rhamdia quelen				*Bryconamericus stramineus*			
Size groups Food items	0–1	1–2	2–3	Total	0–1	1–2	2–3	Total
Plant detritus	226	36	4	226	13		2	14
Animal detritus	201			201	38	15	7	60
Nematomorpha[1]			11	11				
Odonata		84		84		2		2
Ephemeroptera[2]	6			6				
Hemiptera					5	3	1	9
Coleoptera						18		18
Lepidoptera[3]	225	151		376	4		25	29
Diptera, others	85			85	10	7	6	24
Chironomidae					2			2
Hymenoptera	3		34	37	2	13	10	25
Insecta, others	238	4	15	257	161	100	40	300
Total	984	275	64	1283	235	158	91	483

[1] *Nematomorpha* calorific content = 5.569 kJ g^{-1} w.w.
[2] *Ephemeroptera* calorific content = 3.656 kJ g^{-1} w.w.
[3] *Lepidoptera* calorific content = 2.702 kJ g^{-1} w.w.

Table 10. Food items consumed (kg $ha^{-1}y^{-1}$ w.w.) by *Astyanax bimaculatus* in the Caracu stream.

Size groups Food items	0–1	1–2	2–3	3–4	4–5	Total
Plant detritus	777	2259	713	116	145	4010
Animal detritus	646	200	785	783	189	2603
Nematomorpha					95	95
Odonata		119				119
Orthoptera[1]			78			78
Homoptera[2]	8					8
Coleoptera				29		29
Diptera, others	5	19	24	4		52
Simuliidae	151	419	119	182		871
Chironomidae	19		8	7		34
Hymenoptera	7					7
Insecta, others					100	100
Aranea[3]	6					6
Fish			71			71
Total	1619	3016	1798	1121	529	8083

[1] *Orthoptera* calorific content = 9.407 kJ g^{-1} w.w.
[2] *Homoptera* calorific content = 3.178 kJ g^{-1} w.w.
[3] *Aranea* calorific content = 2.784 kJ g^{-1} w.w.

Table 11. Food items consumed (kg $ha^{-1}y^{-1}$ w.w.) by *Astyanax scabripinis* and *Microlepidogaster* sp. in the Agua do Rancho stream.

Size groups Food items	0–1	1–2	3–4	Total
Astyanax scabripinis				
Plant detritus	78	393	191	662
Animal detritus	126	74	293	492
Protozoa	42			42
Coleoptera			21	21
Trichoptera			56	56
Diptera, others	36			36
Hymenoptera	96	123		219
Insecta, others	91	25	36	152
Total	469	615	597	1680
Microlepidogaster sp.				
Algae	14			
Plant detritus	463			
Total	477			

In the Caracu and Agua do Rancho rivers, with 19 and 14 fish taxa respectively, plant detritus constituted 43.2 and 59.6%, and animal detritus 19.4 and 13.3% of the total diet, respectively. Narrow specialists ate organic detritus with the sediment (Fugi *et al.* 1996), but on average eight food types (range: 2–14) were eaten and these changed during their ontogeny. Hence, there were few specialists (*sensu* Gerking 1994), and a considerable percentage of generalists, while opportunists (i.e. omnivores switching between animal and plant diets, Gerking (1994), Araujo-Lima *et al.* (1995)) dominated.

The energy consumption of fish populations in the Caracu and the Agua do Rancho rivers was 4.1 and 1.8 MJ m^{-2} y^{-1}, respectively. In Venezuela's Todasana river's three sites (pool, riffle, raceway), it amounted to 7.9, 1.4 and 4.9

Table 12. Food items consumed (kg ha^{-1}y^{-1} w.w.) by fish populations from the Caracu and Agua do Rancho streams. Diet was investigated directly as an average for all individuals of a given species but then energy of consumption using production was converted to energy units and mean K_1 for species investigated directly was calculated at a given stream.

Stream	Caracu stream (K_1 = 3.77%)					Agua do Rancho stream (K_1 = 2.92%)				
Species	*N. schubarti*	*L. platymetopon*	*C. notomelas*	*C. aeneus*	Total	*N. schubarti*	*C. iheringi*	*Phenacorhamdia*	*E. trilineatus*	Total
Consumption (MJ ha^{-1}y^{-1})	250.7	185.8	20.6	10.3		32.4	894.9	338.9	771.2	
Food items										
Algae		2.2	5.2	0.0	7.4		44.8		2.7	47.5
Plant detritus	3.7	65.1	1.0	0.0	69.8	0.5	9.0		4.7	14.2
Animal detritus	5.7	48.8	2.1	2.5	59.1	0.7	164.9	23.9	86.1	275.6
Protozoa		0.3			0.3				13.3	13.3
Oligochaeta[1]								18.9		18.9
Nematomorpha		1.7			1.7				6.4	6.4
Microcrustacea[2]									2.5	2.5
Odonata	2.9				2.9	0.4				0.4
Ephemeroptera							14.3	16.8	4.2	35.3
Coleoptera	0.1				0.1	0.0		13.4		13.4
Trichoptera	45.0			1.1	46.1	5.8		22.7	75.1	103.6
Diptera others		1.0	0.1	0.1	1.2					
Simuliidae							34.1	1.7		35.8
Chironomidae	8.8	0.5	0.4	0.2	9.9	1.1	33.5	1.9	39.6	76.1
Insecta others	2.2				2.2	0.3	35.9	3.4	9.6	49.2
Aranea	0.9				0.9	0.1				0.1
Total	69.3	119.6	8.8	3.9	201.6	8.9	336.5	102.7	244.2	692.3

[1] *Oligochaeta* calorific content = 3.772 kJ g^{-1} w.w.

[2] *Microcrustacea* calorific content = 3.421 kJ g^{-1} w.w.

Table 13. Production (P), consumption (C) (MJ $ha^{-1}y^{-1}$) and food items consumed (kg $ha^{-1}y^{-1}$ w.w.) by populations not investigated directly. P in mass units was converted to P in energy units and C was calculated using a mean K_1 for a given stream. Plant det. is plant detritus, and *Microcrust.* is *Microcrustacea* (see Table 12 and text for explanation).

			Food items					
Species	P	C	Sediment	Algae	Plant det.	*Microcrust.*	Insects	Total
Caracu stream (K_1 = 3.77%)								
Hoplias malabaricus	132.8	3523.3						[1]
Callichthys callichthys	98.0	2600.1				304.0	490.9	794.9
Leporinus silvestris	41.4	1098.7			1080.0		138.3	1218.3
Phalocerus caudimaculatus	6.2	165.2		38.7			20.8	59.5
Characidium fasciatum	5.7	151.9		35.6			19.1	54.7
Synbranchus marmoratus	36.3	961.6					302.6	302.6
Roeboides paranensis	1.5	39.8					6.3	6.3[2]
Prochilodus lineatus	109.7	2909.8	4156.8					4156.8
Leporinus obtusidens	22.0	584.0			574.1			574.1
Leporinus friderici	2.6	69.3			68.1		8.7	76.8
Steindachnerina insculpta	2.3	61.9	88.5					88.5
Parauchenipterus galeatus	1.4	36.9					11.6	11.6
Total food items			4245.3	74.3	1722.2	304.0	998.3	7344.1
Agua do Rancho stream (K_1 = 2.92%)								
Synbranchus marmoratus	13.5	460.8					145.0	145.0
Phalocerus caudimaculatus	4.8	165.7		38.9			20.9	59.8
Characidium fasciatum	0.4	13.3		3.1			1.7	4.8
Astyanax schubarti	0.2	7.6		1.2	2.7			3.9
Total of food items				43.2	2.7		167.6	213.5

[1] not calculated

[2] without scales

MJ m^{-2} y^{-1}, respectively (Penczak 1992). The highest reported value was 8.13 MJ m^{-2} y^{-1} for *Cyprinodon nevadensis* in the outflow of a thermal artesian well (28–34 °C) in the California desert, where its algal food was not limited (Naiman 1976). These values are one order of magnitude higher than those calculated for fish populations living in small temperate lowland streams: 0.17–0.30 (one result: 1.05) MJ m^{-2} y^{-1} (Penczak *et al.* 1982, 1984) as well as in large rivers: 0.09–0.35 MJ m^{-2} y^{-1} (Penczak 1995), except for fish in the very productive temperate River Thames, at 4.45 MJ m^{-2} y^{-1} (Mann 1975).

The mean R C^{-1} of the dominant species was 49.0 ± 6.7% (mean ± S.D.). For four species from the Todasana River mean total respiration was 31.3 ± 19.7%, but this mean value is not significantly lower.

Mean gross ecological efficiencies (K_1) for fish in the Todasana and the Caracu rivers were similar. The mean K_1 of fish from the Agua do Rancho was a little lower than these, but not significantly so ($P > 0.05$). The mean K_2 value for fish in the Todasana River was 21.6% and 42% higher than those for fish in the Caracu and Agua do Rancho rivers. These differences are explained partially by the high percentage of detritus and higher ranges in upper water temperature in the tributaries of the Paraná River. This and earlier research (Penczak 1992) supports the observations of Naiman (1976) that fish living in warm water expend large amounts of energy on metabolism and the suggestion of Kinne (1960) that at maximal temperatures for tropical regions food is weakly affected by digestive processes.

Previous literature has provided data on the frequency of occurrence of food items in Paraná fishes (Araujo-Lima *et al.* 1995, Esteves 1996, Fugi *et al.* 1996, Hahn *et al.* 1997), but not on quantities consumed or on consumption efficiencies. These qualitative investigations are influenced by differences in habitat as much as differences between species. For example, *A. bimaculatus* in a floodplain lake of the Paraná catchment consumed many Chironomidae but no Simuliidae (Esteves 1996), whereas in our streams it ate very few Chironomidae and many Simuliidae. Fish constituted 14% of its diet in the lake, but < 1% in our streams, whereas detritus was marginally important in the floodplain lake and dominant in our streams.

During a year, fish ate large amounts of food in the sites located in the Caracu and Agua do Rancho rivers, respectively. More than half of this was detritus, but invertebrates accounted for hundreds of kilograms per site area (Table 13). Quantities of insects consumed were questionable: in the Caracu they constituted 326.6, and in the Agua do Rancho 244.7 g w.w. m^{-2} y^{-1}. Even if terrestrial insects constituted 25–41% in the diet of fishes as in the neighbouring river belonging to the same catchment (Esteves 1996), then much more than 100 g m^{-2} y^{-1} is of aquatic origin and one can presume that their production must be still higher. However, "predator consumption by itself is not recommended as a method to measure prey production" (Benke 1984). We believe that such indirect estimates may serve to calibrate direct production measurements, hence it would be worthwhile to investigate whether the major discrepancies recorded between invertebrate production and fish food consumption, known as the Allen Paradox, occur in tropical rivers also (Benke *et al*. 1988, Gerking 1962, Hynes 1970, Penczak *et al*. 1996, Waters 1993).

We calculated that average wet weight of food consumed for the production of 1 kg fish tissue of dominants in the Caracu River was 100 kg, and in the Agua do Rancho 57 kg. The latter was close to 47.3 kg per kg production consumed by fish populations in the Todasana River (Penczak 1992). Nevertheless, all three results diverged from $C P^{-1}$ values for fish from temperate rivers, where most estimates were < 10 kg per 1 kg fish production (Penczak *et al*. 1984, 1986, Penczak 1995). In our present study high variation in food consumption efficiency for growth was observed. Hewett & Kraft (1993) noted that the allometric effect of body size on metabolism can alter the direct effect of consumption rate on growth rate.

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