

Populations and production of fish in two small tributaries of the Paraná River, Paraná, Brazil

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Abstract

Mean biomass (\bar{B}) and production (P) of fish in two small tributaries of the Paraná River (Paraná, Brazil) were 61 kg ha⁻¹ and 48 kg ha⁻¹ yr⁻¹ in the Caracu River and 29 kg ha⁻¹ and 26 kg ha⁻¹ yr⁻¹ in the Agua do Rancho River, respectively. Matrix correlation analysis revealed high positive correlations of both \bar{B} and P to maximum depth and hiding places and, at a lower level of significance, to mean depth, pH and oxygen level. Lower \bar{B} and P values were found in the Agua do Rancho River, whose valley has retained a more natural character, rich canopy and scarcity of macrophytes, but also lower conductivity and nitrogen and phosphate levels than those in the Caracu River.

Introduction

Studies by Watson & Balon (1984) in Borneo and Penczak & Lasso (1991) in Venezuela indicate that the opinion that tropical aquatic ecosystems are more productive than temperate ones is not universally applicable. In large tropical rivers (Kafue, Amazon) very high values of fish production occur (Kapetsky, 1974; Bayley, 1983), but this is not the case in small rivers. Moreover, data for small tropical rivers suggest that they may be less productive than large rivers (Watson, 1982; Watson & Balon, 1984), which is the reverse of the situation in the temperate zone.

However, two sets of data on fish production in only two small tropical rivers are scarcely enough to make any firm conclusions on this problem, particularly as the geographical locality, in addition to climate, also strongly affects population parameters (Krebs, 1985; Lowe-McConnell, 1987).

Hence the aim of this study is to present a third attempt to investigate fish production in very small tropical rivers, because very high production was deter-

mined in rivers of similar size in the temperate zone (Mann, 1971; Penczak, 1981).

Study area

Eleven sites were selected in two small left-side tributaries of the Paraná River, in the north-western corner of the Paraná State, Brazil (Fig. 1). The Caracu River is 6.8 km long and flows directly into the Paraná, and the Agua do Rancho River, 4 km long, flows into the Areia Branca River, 7.8 km from the mouth of the latter to the Paraná River.

Drainage basins of both streams are located over the eolithic cretaceous sandstone from the Caiua Formation covered in the deepest parts of the valleys by alluvial sand (Stevaux, 1991; Penczak *et al.*, 1994).

Site morphology is based on bathymetric maps. Water depth was measured at 5–10 cm intervals (depending on river depth) along transects (10 m apart) across the rivers, and used to construct isobaths. Bot-

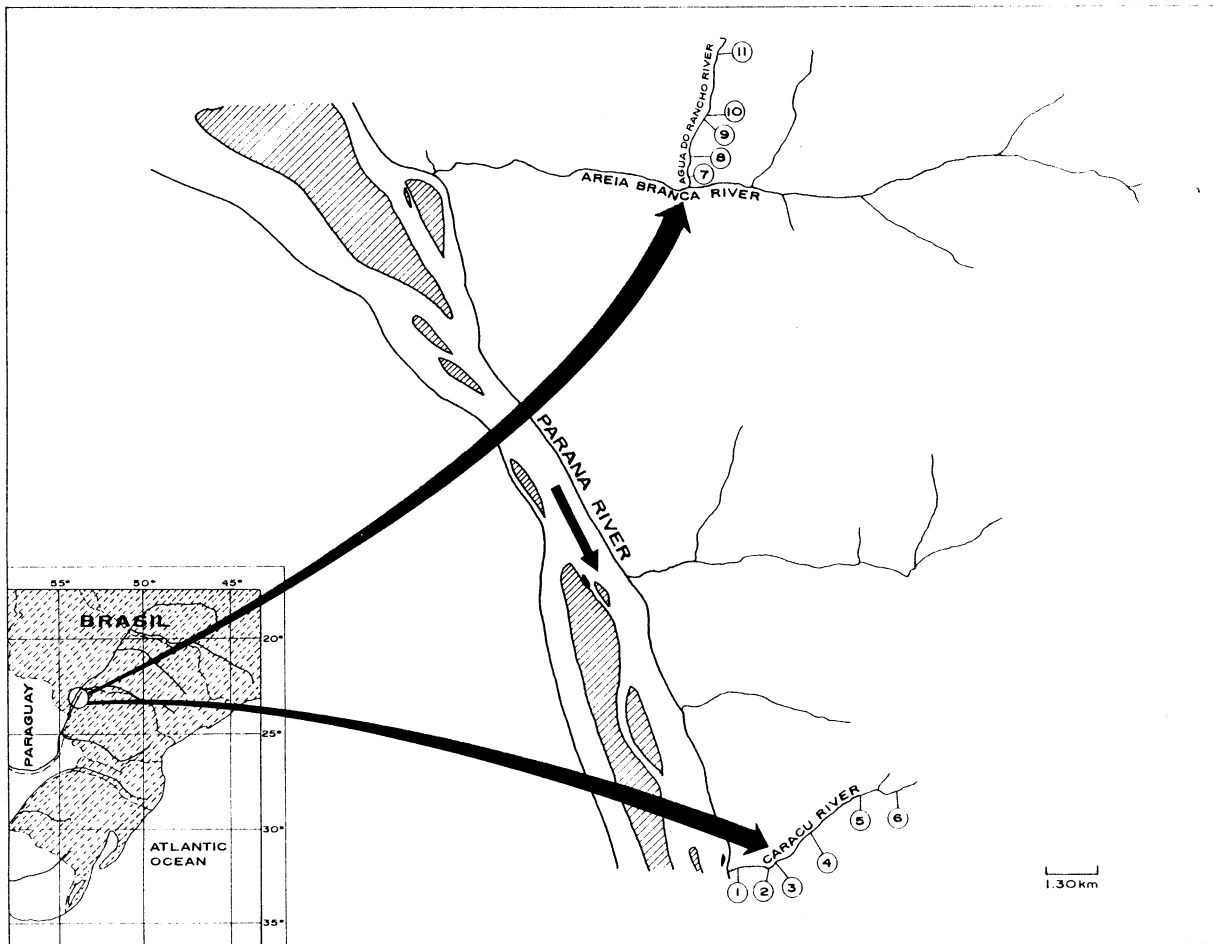


Fig. 1. Map of the Caracu and Agua do Rancho Rivers showing location of sites.

tom structure, vegetation, and hiding places were also recorded along these transects.

The sites' morphology and physico-chemical water parameters are included in Table 1. At sites 6 and 8, macrophytes covering the bottom were not recorded in detail, and only the range for this characteristic is included, not its mean. Extensive deforestation has altered the hydrology of these river systems, although the riparian ecotones with poor remnants of jungle have been retained in the middle and source areas of the Agua do Rancho (A. A. Agostinho, personal communication).

Material and methods

A total of 1260 fish identified to 27 taxa and representing 14 families were collected: family Characi-

dae: *Astyanax scabripinnis* (Eigenmann, 1927), *Bryconamericus stramineus* (Eigenmann, 1908), *Astyanax bimaculatus* (Linnaeus, 1758), *Astyanax schubarti* Britski, 1964, *Characidium fasciatum* Reinhardt, 1866, *Cheirodon notomelas* (Eigenmann, 1915), *Roeboides paranensis* Pignalberi, 1975, family Pimelodidae: *Rhamdia quelen* (Quoy & Gaimard, 1824), *Nannorhamdia schubarti* Gomes, 1956, *Cetopsorhamdia iheringi* Schubart & Gomes, 1959, *Phenacorhamdia* sp, family Loricariidae: *Hypostomus ancistroides* Ihering, 1911, *Microlepidogaster* sp, *Loricariichthys platymetopon* Isbrucker & Nijssen, 1979, family Anostomidae: *Leporinus silvestris* Boulanger, 1902, *Leporinus obtusidens* (Valenciennes, 1847), *Leporinus friderici* (Bloch, 1794), family Callichthyidae: *Corydoras aeneus* (Gill, 1864), *Callichthys callichthys* (Linnaeus, 1758), family Poeciliidae: *Phalocerus caudimaculatus* (Hensel, 1868), fam-

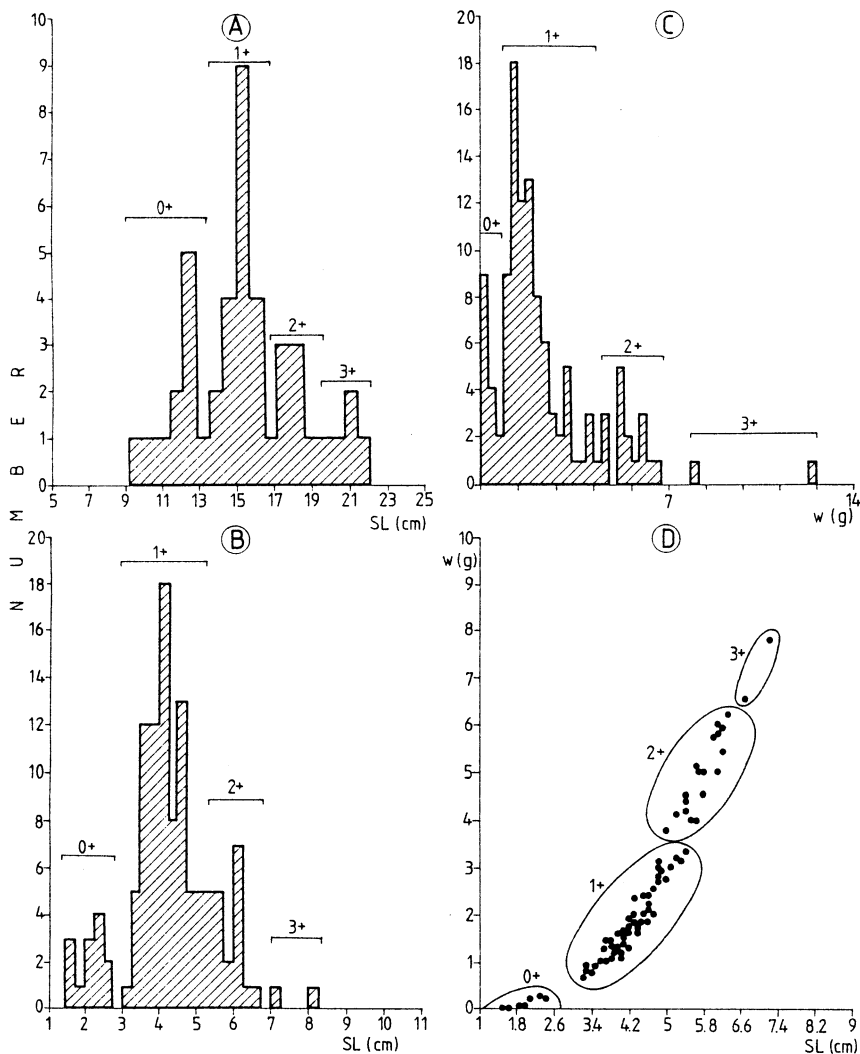


Fig. 2. Length-frequency histograms for *G. carapo* from the Caracu River (A), and *H. ancistroides* from Agua do Rancho River (B). Body weight-frequency histogram for *H. ancistroides* (C). Length-body weight scattergram for *H. ancistroides* (D). SL is standard length; w is body weight. The size classes distinguished represent age groups 0+–3+.

ily Synbranchidae: *Synbranchus marmoratus* (Bloch, 1795), family Sternopygidae: *Eigenmannia trilineata* (Lopez & Castello, 1966), family Gymnotidae: *Gymnotus carapo* (Linnaeus, 1758), family Erythrinidae: *Hoplias malabaricus* (Bloch, 1794), family Auchenipteridae: *Parauchenipterus galeatus* (Linnaeus, 1766), family Curimatidae: *Curimata insculpta* (Fernandes-Yepey, 1948), family Prochilodontidae: *Prochilodus scrofa* Steindachner, 1882, family Cichlidae: *Cichlasoma paranaense* Haseman, 1911. *Phenacorhamdia* sp. and *Microlepidogaster* sp. are

still investigated by taxonomists and thus a description of respective new species is not yet included.

Samples were taken on 28–31 October 1992. A stop net (2 mm diam. mesh) was placed at the downstream limit of each site. The catch per unit of effort (CPUE) method was used. Two people waded upstream and electrofished with anode-dipnets for a constant time at each site (Mahon *et al.*, 1979; Penczak, 1981; Penczak *et al.*, 1981; Penczak & Moliński 1984). Full-wave rectified current was taken from a 3 kW generator with an output of 220 V, and 1.5–2.5 A at the dipnets. In the Aqua do Rancho River, whose water displayed a

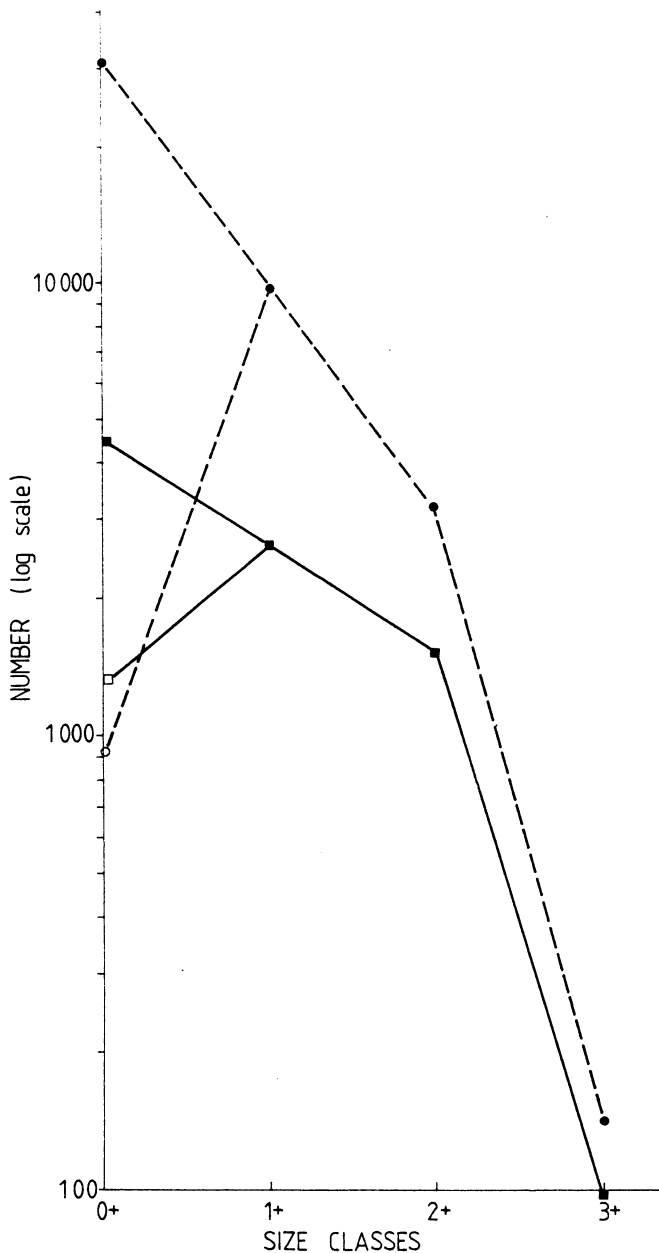


Fig. 3. Graphical estimate of initial population number of first (0+) size class (regression line fitted to second (1+) and third (2+) size classes). Squares = *G. carapo* (The Caracu River), circles = *H. ancistroides* (the Agua do Rancho River). White field, square or circular = real number of first size class (not an approximation).

lower conductivity (Table 1), several plastic, punched sacks filled up with salt were sunk. They were enough to eliminate the problems obstacles otherwise caused by low conductivity (Penczak & Lasso 1991). Stunned

fish were fixed in 4% formalin, because their identification in the field was rarely possible. In the laboratory, fish from each catch were separately identified, counted and weighed. Fish caught in the downstream net were added proportionally to the successive catches, but if only one specimen was caught it was added to the last catch.

The Zippin maximum-likelihood method for three catches (Zippin, 1956, 1958) was used for estimating population density (N). If the Zippin method was not applicable, density was calculated by multiplying the total number of fish caught (C_s) by a N/C_s ratio, estimated for species with the lowest catch efficiency (\hat{p}) at a given site. Absolute estimates (= total catch) were used for a population in which the total number of fish captured in a given site did not exceed three individuals in three catches. The equation for calculating the standing crop (B) is: $B = B_s N/C_s$, where B_s is the total weight of fish caught, and C_s is the total number of fish caught.

The initial variable values for estimating production (biomass and decrease in density) were taken from histograms of length- and body weight-frequency, distinguishing classes of body size by polymodal frequency analysis (Fig. 2). 'Big sample size' (Watson & Balon, 1985) for drawing these histograms was obtained by combining sites for each river. The distance between sites 1 and 6 in the Caracu River was 5.5 km, and between sites 7 and 11 of the Agua do Rancho River only 3.5 km. Hence, it was arbitrarily assumed that there were no significant differences in growth between their respective populations. Where it was difficult to distinguish body size classes, scattergrams of length-body weight (Fig. 2) were developed, which were congruent with groups of some fishes in temperate zone water bodies (Balon & Penczak, 1980), as well as in tropical ones (Penczak & Lasso, 1991).

Average biomass (\bar{B}) and yearly production calculated for the time of sampling (P) were estimated by Ricker's (1975) algebraic method: $P = G\bar{B}$, where G is the instantaneous growth between successive peaks of the polymodal weight-frequency distribution. For *G. carapo* from the Caracu River and *H. ancistroides* from the Agua do Rancho River, Allen's (1951) production graph was employed additionally to compare the results from the Ricker method. It is assumed (T. Penczak) that Allen's graph is parallel to a weight-frequency histogram, which also compares the lifetime of a population at a given site (smallest (t_o) and largest (t_n) specimens).

Table 1. Physical and chemical characteristics of sites in the Caracu River (1-6) and the Agua do Rancho River (7-11). Explanations: m - mud, s - sand, st - stones, G - overhanging grass, T - trunks, B - branches, p - pasture, al - arable land, ^a - as a percentage of bottom surface, ^b proportions - between types in brackets (see text for explanation)

Parameters	Sites										
	1	2	3	4	5	6	7	8	9	10	11
Mean width (m)	2.18	2.44	1.86	2.62	2.43	1.77	2.10	3.62	3.57	3.27	2.35
Mean depth (m)	0.43	0.34	0.41	0.35	0.18	0.24	0.36	0.21	0.20	0.19	0.12
Maximum depth (m)	0.52	0.45	0.54	0.47	0.26	0.31	0.43	0.36	0.27	0.28	0.18
Site length (m)	70	37	50	38	50	50	68	70	75	50	80
Area (m ²)	152.3	91.0	92.9	100.5	121.5	88.3	143.2	253.4	286.0	163.5	187.8
Volume (m ³)	65.55	31.06	38.15	35.64	21.67	21.30	51.24	52.58	50.12	31.52	21.70
Substratum	s	s>m	s>st	s	s	s	s	s>m	s>st	s>st	s
Macrophyte cover (%)	75	75	75	25	50	5-10	50	5-10	0	0	0
Hiding places (%) ^a	25	25	30	15	2	2	20	8	10	5	5
Hiding type ^b	G	G	G	G:B (7:3)	G	G	G:B (9:1)	G:B (8:2)	B:T:S (4:4:2)	B:T:S (2:7:1)	B:T (7:3)
Trees along banks (%)	0	0	12	10	0	0	3	50	100	95	90
Adjacent area	p	p	p	p	p	p	p	p	p,al	p	p
Water velocity (m s ⁻¹)	0.54		0.42	0.87	2.14	0.88	1.46	1.35	2.46	3.12	0.50
Air temperature (°C)	26.0	16.5	16.5	16.5	23.0	23.0	27.0	21.5	24.1	23.0	25.0
Water temperature (°C)	25.5	19.5	19.5	19.5	21.0	21.0	24.0	21.5	21.5	22.5	21.0
pH	7.10	7.26	7.26	7.26	6.96	6.96	6.63	6.59	6.51	6.49	6.08
O ₂ (ml l ⁻¹)	6.42	7.65	7.65	7.65	6.79	6.79	7.23	7.55	7.63	7.55	6.65
Conductivity (μS cm ⁻¹)	76	78	78	78	81	81	47	48	47	46	49
Total nitrogen (mg l ⁻¹)	0.57		0.57				0.39	0.28	0.26	0.24	0.59
Total phosphate (μg l ⁻¹)	73.80		65.10				38.80	46.40	47.80	25.10	26.80

As the curve displaying changes in animal standing crop over the annual cycle has a parabolic shape (Winberg *et al.*, 1971), the mean biomass equals standing crop only at one point of the rising curve and at one point of the falling curve. Hence, where we do not know the biology of a particular species, it is necessary to estimate how much the standing crop on a given day diverges from the mean biomass. This correction is essential because, for each site production of each species was estimated by multiplying mean biomass by the mean turnover ratio.

The conversion from the mean standard body length for a given peak to the mean body weight was achieved from the linear logarithmic regression of the body weight on fish standard length. This was estimated using data from all sites; all correlation coefficients were highly significant ($p < 0.0000$).

The number of fish of each species represented by the first peak in the polymodal size distribution was obtained from back-extrapolation of a catch curve

using data for each subsequent peak (Fig. 3). This method assumes that the mortality rate between successive peaks is constant, although it is likely to be higher during the first few months of life (Mann, 1971). Hence, the initial population size is likely to be an underestimate. The distinguished size classes for numbering their sequence (peaks) are marked in this paper by symbols used commonly for age groups.

Results

Estimated density and standing crop

Data related to density estimates in the Caracu River are summarized in Tables 2–7, and those for the Agua do Rancho in Tables 8–12. Of the 98 estimates of density, the Zippin method was used in 49% and absolute counts in 37%. The Zippin was not applicable in a further 9% of occasions, and in 5% new species were

Table 2. Number (numerator) and standing crop (g) (denominator) obtained from site 1 on the Caracu River by the successive removal electrofishing method (C_n). C_s and B_s (g) are total number and standing crop. N is estimated density with 95% CL, and B (g) is estimated standing crop. * indicates Zippin method not applicable ($p < 0.05$), a is an absolute estimate. n are fish caught by net only. R is statistics of the Zippin model. p is catch efficiency (see text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>	5/ 25.1	2/ 15.5	1/ 0.2	8	40.8	9	3	45.9	0.50	0.57	591	3.01
<i>H. ancistroides</i>	13/ 8.4	9/ 54.2	5/ 18.4	27	81.0	36	16	108.0	0.70	0.37	2364	7.09
<i>G. carapo</i>	7/ 70.1	3/ 40.9	1/ 6.2	11	117.2	12	3	127.9	0.45	0.61	788	8.40
<i>C. fasciatum</i>	5/ 3.6	3/ 2.0	4/ 2.9	12	8.5	16*		11.3			1051	0.74
<i>C. callichthys</i>			1/ 19.5	1	19.5	1 ^a		19.5			66	1.28
<i>N. schubarti</i>			2/ 0.7	2	0.7	2 ^a		0.7			131	0.46
<i>H. malabaricus</i>	1/ 0.1		1/ 79.5	2	79.6	2 ^a		79.6			131	5.23
<i>C. notomelas</i>	1/ 0.3			1	0.3	1 ^a		0.3			66	0.02
<i>C. insculpta</i>			3/ 8.5	3	8.5	3 ⁿ		8.5			197	0.56
<i>R. paranensis</i>			1/ 1.5	1	1.5	1 ⁿ		1.5			66	0.10
<i>L. platymetropon</i>			1/ 5.2	1	5.2	1 ⁿ		5.2			66	0.34
<i>L. obtusidens</i>		1/ 80.3		1	80.3	1 ^a		80.3			66	5.27
<i>C. aeneus</i>	1/ 1.3			1	1.3	1 ^a		1.3			66	0.09
<i>P. galeatus</i>			1/ 5.0	1	5.0	1 ^a		5.0			66	0.33
Total	33/108.9	18/192.9	21/147.6	72	449.4	87		495.0			5715	32.92

Table 3. Number (numerator) and standing crop (g) (denominator) obtained from site 2 on the Caracu River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>	6/ 28.4		3/ 23.6	9	52.0	11	8	63.6	0.67	0.40	1209	6.99
<i>H. ancistroides</i>	8/ 73.9	8/ 76.1	9/ 96.9	25	246.9	38*		370.4			4175	40.70
<i>G. carapo</i>	6/ 63.1	2/ 17.3	3/ 26.6	11	107.0	15	15	145.9	0.73	0.34	1648	16.03
<i>C. fasciatum</i>	2/ 1.3	1/ 0.7	1/ 0.6	4	2.6	6	13	3.9	0.75	0.32	659	0.43
<i>C. callichthys</i>		2/ 72.0		2	72.0	2 ^a		72.0			220	7.91
<i>N. schubarti</i>	1/ 1.0	2/ 2.3	4/ 7.6	7	10.9	11*		16.4			1209	1.80
<i>L. silvestris</i>	1/ 6.1		1/ 0.3	2	6.4	2 ^a		6.4			220	0.70
<i>H. malabaricus</i>		2/ 88.5		2	88.5	2 ^a		88.5			220	9.72
<i>C. notomelas</i>	3/ 1.1			3	1.1	3 ^a		1.1			330	0.12
<i>C. paranaense</i>		1/ 2.3		1	2.3	1 ^a		2.3			110	0.25
Total	27/174.9	18/259.2	21/155.6	66	589.7	91		770.5			10000	84.65

recorded only in the blocking net. The latter was only in the Caracu River, where dense macrophyte growth concealed many stunned fish and made dipnetting difficult.

Matrix correlation analysis was used to determine which site characteristics (Table 1) influence fishing efficiency (\hat{p}). At a statistically significant level, \hat{p} was

negatively correlated with mean width ($p = 0.018$) and positively with water temperature ($p = 0.048$) only.

Taking into account the variables included in Table 1, the two rivers differed significantly (2-sample T-test) in the following parameters: width ($p < 0.04$), macrophytes ($p < 0.05$), trees along banks ($p < 0.004$), pH ($p < 0.0002$) and conductivity ($p < 0.0000$). For sev-

Table 4. Number (numerator) and standing crop (g) (denominator) obtained from site 3 on the Caracu River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>	34/187.7	24/118.4	32/202.9	90	509.0	144*		814.4			15497	87.65
<i>N. ancistroides</i>	12/ 52.1	8/ 23.9	1/ 3.9	21	79.9	23	4	87.5	0.48	0.59	2475	9.42
<i>G. carapo</i>	2/ 29.5	2/ 22.1	1/ 27.1	5	78.7	8	125	125.9	0.80	0.27	861	13.55
<i>C. fasciatum</i>	2/ 1.9			2	1.9	2 ^a		1.9			215	0.20
<i>L. silvestris</i>	3/ 25.3	1/ 19.0	1/ 10.1	5	54.4	6	4	65.3	0.60	0.47	646	7.03
<i>H. malabaricus</i>	1/ 56.7		1/ 17.0	2	73.7	2 ^a		73.7			215	7.93
<i>S. marmoratus</i>			1/ 4.6	1	4.6	1 ^a		4.6			108	0.50
<i>P. scrofa</i>	2/ 79.8	1/ 45.6	1/ 37.2	4	162.6	6	13	243.9	0.75	0.32	646	26.25
<i>L. friderici</i>		1/ 5.8		1	5.8	1 ^a		5.8			108	0.62
Total	56/433.0	37/234.8	38/302.8	131	970.6	193		1423.0			20771	153.1

Table 5. Number (numerator) and standing crop (g) (denominator) obtained from site 4 on the Caracu River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>	9/119.9	4/48.7	2/ 19.8	15	188.4	17	6	213.5	0.53	0.54	1692	21.24
<i>H. ancistroides</i>	4/ 32.2	4/ 36.3	1/ 17.8	9	87.3	11	8	106.7	0.67	0.40	1095	10.62
<i>G. carapo</i>	6/ 66.0	3/35.8	3/ 70.8	12	172.6	18	23	258.9	0.75	0.32	1791	25.76
<i>P. caudimaculatus</i>	2/ 0.4	4/ 1.4	1/ 0.3	7	2.1	11*		3.2			1095	0.32
<i>C. callichthys</i>	7/136.0	1/ 7.5		8	143.5	8	0	143.5	0.13	0.88	796	14.28
<i>L. silvestris</i>		1/21.9		1	21.9	1 ^a		21.9			100	2.18
<i>H. malabaricus</i>			1/ 89.6	1	89.6	1 ^a		89.6			100	8.92
Total	28/355.5	17/151.6	8/198.3	53	705.4	67		837.3			6669	83.32

eral other parameters the differences were close to a significant level.

Production of dominant populations

Information required to calculate the production of dominant species is given in Table 13 (Caracu River) and Table 14 (Agua do Rancho River). Only in two cases were the catchabilities of the first size class considered reliable (and thus density was not then approximated), viz. *H. ancistroides* in the Caracu River and for *Microlepidogaster* sp. in the Agua do Rancho River. The method of approximation is illustrated in Fig. 3, using two species as examples.

The mean body weight for species whose production values were estimated directly was calculated from mean standard length using equations included in Table 15.

The data of mean biomass (\bar{B} kg ha⁻¹), production (P kg ha⁻¹ yr⁻¹), turnover ratio (P/\bar{B}), and of the percentage of standing crop that constitute the mean biomass of dominant populations are all included in Tables 16 and 17. Mean biomass of the other species was calculated using the above mean ratio ($\bar{B}\%$ as standing crop) calculated for the dominant species in each river. Their production was calculated by multiplying the mean biomass by the average P/\bar{B} of directly investigated species in a given river. Average biomass and production were 60.97 kg ha⁻¹ and 48.34 kg ha⁻¹ yr⁻¹ in the Caracu River (6 sites) and 28.98 kg ha⁻¹ and 26.27 kg ha⁻¹ yr⁻¹ in the Agua do Rancho River (5 sites), respectively.

Table 6. Number (numerator) and standing crop (g) (denominator) obtained from site 5 on the Caracu River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>		2/15.3	1/3.4	3	18.7	3 ^a		18.7			247	1.54
<i>H. ancistroides</i>	2/16.8	1/18.5		3	35.3	3	1	35.3	0.33	0.70	247	2.91
<i>G. carapo</i>			1/35.7	1	35.7	1 ⁿ		35.7			82	2.94
<i>P. caudimaculatus</i>		1/0.3		1	0.3	1 ^a		0.3			82	0.02
<i>C. notomelas</i>	2/0.5			2	0.5	2 ^a		0.5			165	0.04
Total	4/17.3	4/34.1	2/39.1	10	90.5	10		90.5			823	7.45

Table 7. Number (numerator) and standing crop (g) (denominator) obtained from site 6 on the Caracu River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	\hat{p}	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>A. bimaculatus</i>			2/24.0	2	24.0	2 ^a		24.0			226	2.72
<i>H. ancistroides</i>	3/12.6			3	12.6	3 ^a		12.6			340	1.43
<i>G. carapo</i>	2/31.6		1/17.2	3	48.8	4	4	65.1	0.67	0.40	453	7.37
<i>P. caudimaculatus</i>	21/5.7	7/3.7	2/0.4	30	9.8	31	3	10.1	0.37	0.68	3510	1.14
<i>S. marmoratus</i>	3/61.3		1/10.9	4	72.2	4	2	72.2	0.50	0.57	453	8.17
Total	29/111.2	7/3.7	6/52.5	42	167.4	44		184.0			4982	20.83

Discussion

Without knowledge of the time and duration of spawning, longevity, possible sexual dimorphism and without repeat sampling on other occasions, aging fish from the temperate zone is difficult even when calcified tissues are used (Casselman, 1987). 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 completely erroneous results (De Bont, 1967; Tesch, 1968; Bagenal & Tesch, 1978; Blake & Blake, 1978; Casselman, 1987). Hence, it was decided to apply length-frequency histograms to distinguish body size classes through polymodal frequency analysis, utilizing body weight-frequency histograms in similar situations or even with length-weight scattergrams (Balon & Penczak, 1980; Penczak & Lasso, 1991). The reliability of these histograms, according to suggestions by Watson & Balon (1985), is increased by combining data from all sites.

Two items of information favour the decision to rely on size classes while estimating production in these tropical studies. Le Cren (1974) stated that the accuracy of production calculation depends more on precise

estimates of biomass and density of a given population than on the accuracy of aging. In addition, Watson & Balon (1985) claimed that 'age classes could be identified from the length-frequency histograms, with sufficient accuracy for production to be calculated.'

While analysing Allen's (1951) production graph, one can see two pieces of information that are collected in it on time scale: (1) increase in body growth and (2) decrease in numbers. These two important values for estimating production may be read from the length-frequency and body weight-frequency histograms, first analysing the first histogram, and then the second, because the first has more clear peaks. Because production is calculated here on the time of sampling and not at the time of annulus formation or spawning, credible aging is not necessary (Penczak & Lasso, 1991). The P/\bar{B} ratio calculated from Allen's graph for *G. carapo* was the same as by Ricker method ($P/\bar{B}=0.66$), and for *H. ancistroides* it differed at the second decimal place below zero. Difference in mean biomass and production values for both the species calculated by the methods did not exceed 5%.

Before discussing the results, we wish to lend support to the opinion that electrofishing in tropical rivers

Table 8. Number (numerator) and standing crop (g) (denominator) obtained from site 7 on the Agua do Rancho Rive (see Table 2 and text for explanation).

Species	C ₁	C ₂	C ₃	C _s	B _s	N	95% CL	B	R	\hat{p}	N ha ⁻¹	B (kg) ha ⁻¹
<i>Microlepidogaster</i> sp.	101/38.8	46/18.0	22/8.7	169	65.5	189	18	73.3	0.53	0.54	13203	5.12
<i>H. ancistroides</i>	27/43.9	17/34.9	6/7.3	50	86.1	58	13	99.9	0.58	0.49	4052	6.98
<i>A. scabripinnis</i>	2/7.2	1/2.8	2/1.5	5	11.5	6*		13.8			419	0.96
<i>B. stramineus</i>	6/5.6	8/10.2		14	15.8	16	7	18.1	0.57	0.50	1118	1.26
<i>R. quelen</i>	4/38.0	2/9.7		6	47.7	6	1	47.7	0.33	0.70	419	3.33
<i>G. carapo</i>	2/8.7	3/24.7		5	33.4	6	4	40.1	0.60	0.47	419	2.80
<i>C. iheringi</i>	7/18.6	2/5.6		9	24.2	9	1	24.2	0.22	0.80	629	1.69
<i>Phenacorhamdia</i> sp.	6/9.6	5/9.2		11	18.8	12	3	20.5	0.45	0.61	838	1.43
<i>S. marmoratus</i>	1/7.5			1	7.5	1 ^a		7.5		7	0	0.52
<i>E. trilineata</i>	7/64.2	1/5.9		8	70.1	8	0	70.1	0.13	0.88	559	4.90
Total	163/242.1	85/121.0	30/17.5	278	380.6	311		415.2			21726	28.99

Table 9. Number (numerator) and standing crop (g) (denominator) obtained from site 8 on the Agua do Rancho River (see Table 2 and text for explanation).

Species	C ₁	C ₂	C ₃	C _s	B _s	N	95% CL	B	R	\hat{p}	N ha ⁻¹	B (kg) ha ⁻¹
<i>Microlepidogaster</i> sp.	22/10.9	21/10.8	5/3.0	48	24.7	59	16	30.4	0.65	0.42	2328	1.20
<i>H. ancistroides</i>	23/58.9	12/30.2	13/28.7	48	117.8	78	165	191.4	0.79	0.28	3078	7.55
<i>A. scabripinnis</i>	15/62.8	4/30.2	6/29.4	25	122.4	31	11	151.8	0.64	0.43	1223	5.99
<i>B. stramineus</i>	4/7.6	8/19.3	6/11.7	18	38.6	29*		62.7			1144	2.47
<i>P. caudimaculatus</i>	12/4.4	16/6.2	4/1.8	32	12.4	47	37	18.2	0.75	0.32	1855	0.72
<i>R. quelen</i>	8/82.2	8/143.6	5/92.8	21	318.6	34*		517.7			1342	20.43
<i>G. carapo</i>	11/66.6	4/23.8	4/16.1	19	106.5	23	10	128.9	0.63	0.44	908	5.09
<i>C. iheringi</i>	4/11.2	2/4.3	2/7.7	8	23.2	12	19	34.8	0.75	0.32	474	1.37
<i>S. marmoratus</i>	1/7.4			1	7.4	1 ^a		7.4			39	0.29
<i>E. trilineata</i>	1/17.2			1	17.2	1 ^a		17.2			39	0.68
<i>A. schubarti</i>		1/1.2		1	1.2	1 ^a		1.2			39	0.05
<i>C. fasciatum</i>	1/2.8		1/2.5	1	2.5	1 ^a		2.5			39	0.10
<i>N. schubarti</i>				1	2.8	1 ^a		2.8			39	0.11
Total	102/332.0	76/269.6	46/193.7	224	795.3	318		1167.0			12547	46.05

is not very efficient owing to low water conductivity. Watson & Balon (1984), while electrofishing in the Baram River (Borneo), do not refer to conductivity-related sampling difficulties in that river although its conductivity was as low as 40 $\mu\text{S cm}^{-1}$.

\bar{B} and P values in both investigated rivers were similar to a small stream in northern Venezuela (Penczak & Lasso, 1991). \bar{B} values in the two streams of the Paraná River were also similar to that in the catchment of the Baram River (Borneo) except 'Kejin River 1' (173 kg ha⁻¹). In contrast, production was there about

half, but lower also was the P/\bar{B} value. Out of the 9 direct estimates of P/\bar{B} in this study (Tables 16 and 17) only once was its value higher than 1.0. An 'unexpectedly low' turnover ratio was recorded also in Brazil for the assemblage-dominant pike-cichlid, *Crenicichla lepidota* Heckel, in the two tributaries of the Uruquay River (Lobón-Cerviá *et al.*, 1993). Averages for pike-cichlid populations, containing three first age groups at 5 sites, ranged from 0.19 to 0.39. We support the view of Lobón-Cerviá *et al.* (1993) that poor growth influenced this parameter.

Table 10. Number (numerator) and standing crop (g) (denominator) obtained from site 9 on the Agua do Rancho River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	$\hat{\rho}$	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>Microlepidogaster</i> sp.	1/0.8	1/0.3		2	1.1	2 ^a		1.1			70	0.04
<i>H. ancistroides</i>	31/97.8	10/30.3	19/35.7	60	163.8	100	432	273.0	0.80	0.27	3497	9.55
<i>A. scabripinnis</i>	9/60.8	5/33.1	2/13.8	16	107.7	18	7	121.2	0.56	0.51	629	4.24
<i>B. stramineus</i>	16/45.7	11/31.1	5/13.3	32	90.1	40	14	112.6	0.66	0.41	1399	3.94
<i>R. guelen</i>			1/15.2	1	15.2	1 ^a		15.2			35	0.53
<i>G. carapo</i>	2/13.2			1	13.2	2 ^a		13.2			70	0.46
<i>C. iheringi</i>	5/16.7	4/11.9	1/3.0	10	31.6	12	6	37.9	0.60	0.47	420	1.32
<i>Phenacorhamdia</i> sp.	2/1.1	2/2.2	1/1.4	5	4.7	8	125	7.5	0.80	0.27	280	0.26
<i>S. marmoratus</i>	1/10.8			1	10.8	1 ^a		10.8			35	0.38
<i>N. schubarti</i>	1/3.3			1	3.3	1 ^a		3.3			35	0.12
Total	68/250.2	33/108.9	28/82.4	129	441.5	185		595.8			6470	20.84

Table 11. Number (numerator) and standing crop (g) (denominator) obtained from site 10 on the Agua do Rancho River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	$\hat{\rho}$	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>Microlepidogaster</i> sp.	3/1.7		4/1.8	7	3.5	11*		5.4			673	0.33
<i>H. ancistroides</i>	31/112.2	12/42.8	5/17.3	48	172.3	51	6	183.1	0.46	0.60	3119	11.20
<i>A. scabripinnis</i>	9/59.0	4/39.4	5/17.8	18	116.2	28	55	180.8	0.78	0.29	1713	11.06
<i>B. stramineus</i>	8/18.2	3/11.7	2/6.0	13	35.9	15	5	41.4	0.54	0.53	917	2.53
<i>G. carapo</i>	2/7.2	2/13.1		4	20.3	4	2	20.3	0.50	0.57	245	1.24
<i>C. iheringi</i>	4/8.7	3/8.0	2/5.1	9	21.9	14	39	34.1	0.78	0.29	856	2.09
<i>Phenacorhamdia</i> sp.	9/8.7	1/0.9	2/1.8	12	11.4	13	3	12.4	0.42	0.64	795	0.76
<i>S. marmoratus</i>		1/14.0	1/3.5	2	17.5	2 ^a		17.5			122	1.07
Total	66/215.8	26/129.9	21/53.3	113	399.0	138		495.0			8440	30.28

Table 12. Number (numerator) and standing crop (g) (denominator) obtained from site 11 on the Agua do Rancho River (see Table 2 and text for explanation).

Species	C_1	C_2	C_3	C_s	B_s	N	95% CL	B	R	$\hat{\rho}$	$N \text{ ha}^{-1}$	$B \text{ (kg) ha}^{-1}$
<i>Microlepidogaster</i> sp.	1/0.9			1	0.9	1 ^a		0.9			53	0.05
<i>H. ancistroides</i>	1/6.0	1/12.7		2	18.7	2 ^a		18.7			106	1.00
<i>A. scabripinnis</i>	52/136.0	33/69.3	8/11.8	93	217.1	104	13	242.8	0.53	0.54	5537	12.93
<i>P. caudimaculatus</i>	8/3.2	7/1.5	4/0.8	19	5.5	31	92	9.0	0.79	0.28	1651	0.48
<i>B. guelen</i>	12/42.0		1/7.3	13	49.3	13	1	49.3	0.15	0.86	692	2.62
<i>G. carapo</i>	8/41.7	2/12.1		10	53.8	10	1	53.8	0.20	0.82	532	2.86
<i>S. marmoratus</i>	3/13.4		1/6.6	4	20.0	4	2	20.0	0.50	0.57	213	1.06
Total	85/243.2	43/95.6	14/26.5	142	365.3	165		394.5			8784	21.00

Table 13. Mean values (\bar{x}) of standard length (\bar{l} , cm), and body weight (\bar{w} , g), sample size (n), estimated density at sites (N), estimated density per hectare ($N \text{ ha}^{-1}$) for distinguished size classes (0+ - 5+) of *H. ancistroides* (H.a.), *A. bimaculatus* (A.b.), and *G. carapo* (G.a.) (on the time of sampling in the Caracu River). The initial population size estimated from a semilog plot is given in parantheses, a - see Fig. 2 (see text for further explanations).

Size class	0+		1+		2+		3+		4+		5+		
	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	
Species	\bar{x}	1.82	0.16	4.46	2.44	6.25	6.85	7.71	13.04	9.08	21.49	10.25	31.10
	n	27		7		25		14		6		1	
	N	38		10		36		20		9		1	
	$N \text{ ha}^{-1}$	3565		938		3378		1877		844		94	
H.a.	\bar{x}	2.00	0.21	4.82	3.09	6.19	6.61	7.75	13.09	9.25	22.41	10.90	40.75
	n	4		69		33		15		4		1	
	N	6		102		49		22		6		2	
	$N \text{ ha}^{-1}$	628(22218)		10673		5127		2302		628		209	
A.b.	\bar{x}	11.90	5.00	16.5	14.60	18.70	22.10	21.70	33.80				
	n	10		20		12		1					
	N	14		27		16		1					
	$N \text{ ha}^{-1}$	1357(4419)		2618		1551		97					
G.a. ^a	\bar{x}	2.17	0.21	4.23	1.78	5.55	4.28	7.75	12.59				
	n	13		145		45		2					
	N	19		204		63		3					
	$N \text{ ha}^{-1}$	910(31659)		9778		3020		144					
M.	\bar{x}	2.85	0.39	3.55	0.75								
	n	206		9									
	N	251		11									
	$N \text{ ha}^{-1}$	15668		658									
A.s.	\bar{x}	3.27	0.74	4.84	2.85	6.37	7.31	7.18	11.02				
	n	51		65		28		12					
	N	61		78		34		14					
	$N \text{ ha}^{-1}$	3106(9110)		3971		1731		713					
B.s.	\bar{x}	3.73	0.80	4.82	1.83	5.64	2.11	6.40	4.70				
	n	9		40		23		5					
	N	12		52		30		7					
	$N \text{ ha}^{-1}$	549(4129)		2381		1373		320					
G.c.	\bar{x}	10.47	4.26	13.07	7.37	15.30	10.76						
	n	27		11		2							
	N	30		12		2							
	$N \text{ ha}^{-1}$	1449(3468)		580		97							
R.q.	\bar{x}	6.32	4.39	8.83	11.69	11.25	23.75	12.60	37.30				
	n	7		22		5		1					
	N	11		34		8		2					
	$N \text{ ha}^{-1}$	507(6654)		1567		369		92					

Table 14. Population characteristics of *H. ancistroides* (H.a.), *Microlepidogaster* sp. (M.), *A. scabripinis* (A.s.), *B. stramineus* (B.s.), *G. carapo* (G.c.), and *R. quelen* (R.q.) at the time of sampling in the Agua do Rancho River (symbols as in Table 13).

Size classes	0+		1+		2+		3+		
	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	\bar{l}	\bar{w}	
Species	\bar{x}	2.17	0.21	4.23	1.78	5.55	4.28	7.75	12.59
	n	13		145		45		2	
	N	19		204		63		3	
	$N \text{ ha}^{-1}$	910(31659)		9778		3020		144	
H.a. ^a	\bar{x}	2.85	0.39	3.55	0.75				
	n	206		9					
	N	251		11					
	$N \text{ ha}^{-1}$	15668		658					
M.	\bar{x}	3.27	0.74	4.84	2.85	6.37	7.31	7.18	11.02
	n	51		65		28		12	
	N	61		78		34		14	
	$N \text{ ha}^{-1}$	3106(9110)		3971		1731		713	
A.s.	\bar{x}	3.73	0.80	4.82	1.83	5.64	2.11	6.40	4.70
	n	9		40		23		5	
	N	12		52		30		7	
	$N \text{ ha}^{-1}$	549(4129)		2381		1373		320	
B.s.	\bar{x}	10.47	4.26	13.07	7.37	15.30	10.76		
	n	27		11		2			
	N	30		12		2			
	$N \text{ ha}^{-1}$	1449(3468)		580		97			
G.c.	\bar{x}	6.32	4.39	8.83	11.69	11.25	23.75	12.60	37.30
	n	7		22		5		1	
	N	11		34		8		2	
	$N \text{ ha}^{-1}$	507(6654)		1567		369		92	
R.q.	\bar{x}	11.90	5.00	16.5	14.60	18.70	22.10	21.70	33.80
	n	10		20		12		1	
	N	14		27		16		1	
	$N \text{ ha}^{-1}$	1357(4419)		2618		1551		97	

Table 15. Standard length (1 cm) and body weight (w,g) relationships of dominant species from the Caracu (C) and Agua do Rancho (AR) Rivers. The correlation coefficients (r) for these relationships were significant (minimum at $p < 0.0000$)

River	Species	$\log w = b \log l - \log a r$		
		b	$\log a$	r
C	<i>H. ancistroides</i>	3.062	-1.601	0.996
	<i>A. bimaculatus</i>	3.041	-1.587	0.995
	<i>G. carapo</i>	3.291	-2.837	0.910
AR	<i>H. ancistroides</i>	3.226	-1.769	0.992
	<i>Microlepidogaster</i> sp.	2.998	-1.773	0.949
	<i>A. scabripinis</i>	3.425	-1.892	0.997
	<i>B. stramineus</i>	3.241	-1.948	0.960
	<i>G. carapo</i>	2.473	-1.888	0.880
	<i>R. quelen</i>	2.926	-1.700	0.987

The most important factor influencing production in Borneo's rivers was organic benthic material, but in the current studies both \bar{B} and P were positively correlated at high probability levels ($p = 0.01$) with maximum depth (pools) and abundance of hiding places for fish. Positive correlations, but at the minimum probability levels ($p = 0.05$), were calculated also for mean depth, pH and O_2 , macrophytes, canopy, conductivity, but nitrogen and phosphates did not display any statistically significant relationships with mean biomass and production.

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Table 16. Mean biomass (\bar{B} kg ha⁻¹) and production (P kg ha⁻¹ yr⁻¹) and turnover ratio (P/\bar{B}) of fish at six sites the Caracu River. B - standing crop, ^a - species investigated directly, ^b - mean \pm 95CL for directly investigated species.

Species/Site	1		2		3		4		5		6		$P\bar{B}$	\bar{B} as % of \bar{B}
	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}	P		
<i>H. ancistroides</i> ^a	6.49	4.80	37.27	27.58	8.63	6.39	9.73	7.20	2.66	1.97	1.31	0.97	0.74	91.58
<i>A. bimaculatus</i> ^a	2.74	2.55	6.36	5.91	79.74	74.16	19.32	17.97	1.40	1.30	2.47	2.30	0.93	90.98
<i>G. carapo</i> ^a	8.94	5.90	17.07	11.27	14.43	9.52	27.43	18.10	3.13	2.07	7.85	5.18	0.66	106.48
<i>H. malabaricus</i>	5.04	3.93	9.37	7.30	7.64	5.96	8.59	6.70						
<i>C. callichthys</i>	1.23	0.96	7.62	5.94			13.76	10.73						
<i>L. silvestris</i>			0.67	0.53	6.77	5.28	2.10	1.64						
<i>P. caudimaculatus</i>							0.31	0.24	0.02	0.02	1.10	0.86		
<i>C. fasciatum</i>	0.71	0.56	0.41	0.32	0.19	0.15								
<i>C. notomelas</i>	0.02	0.02	0.12	0.09					0.04	0.03				
<i>S. marmoratus</i>					0.48	0.38					7.87	6.14		
<i>N. schubarti</i>	0.44	0.35	1.73	1.35										
<i>R. paranensis</i>	0.10	0.08	0.24	0.19										
<i>P. scrofa</i>					25.29	19.73								
<i>L. obtusidens</i>	5.08	3.96											0.78 ^b	96.35 ^b
<i>L. friderici</i>					0.60	0.47							± 0.34	± 21.81
<i>C. insculpta</i>	0.54	0.42												
<i>L. platymetropon</i>	0.33	0.26												
<i>P. galeatus</i>	0.32	0.25												
<i>C. aeneus</i>	0.09	0.07												
Total	32.07	24.11	80.86	60.48	143.77	122.04	81.24	62.58	7.25	5.39	20.60	15.45		

Table 17. Mean biomass (\bar{B} kg ha⁻¹), production (P kg ha⁻¹ yr⁻¹) and turnover ratio (P/\bar{B}) of fish populations at five sites in the Agua do Rancho River (see Tab. 16 for symbols explanation).

Species/Site	7		8		9		10		11		\bar{B}	B as % of B
	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}	P	\bar{B}	P		
<i>H. ancistroidesa</i> ^a	6.14	8.29	6.64	8.96	8.40	11.34	9.85	13.30	0.88	1.19	1.35	87.93
<i>A. scabripinis</i> ^a	0.84	0.75	5.26	4.68	3.72	3.31	9.71	8.64	11.35	10.10	0.89	87.75
<i>G. carapo</i> ^a	2.42	1.23	4.40	2.24	0.40	0.20	1.07	0.55	2.47	1.26	0.51	86.43
<i>Microlepidogaster</i> sp. ^a	1.69	1.10	0.40	0.26	0.01	0.01	0.11	0.07	0.02	0.01	0.65	33.09
<i>B. stramineus</i> ^a	1.18	0.66	2.30	1.29	3.68	2.06	2.36	1.32			0.56	93.30
<i>R. quelen</i> ^a	5.20	4.26	31.88	26.14	0.83	0.68			4.09	3.35	0.82	156.04
<i>S. marmoratus</i>	0.47	0.38	0.26	0.21	0.34	0.28	0.97	0.78	0.96	0.77		
<i>C. iheringi</i>	1.53	1.23	1.24	0.99	1.20	0.96	1.90	1.52				
<i>Phenacorhamdia</i> sp.	1.30	1.04			0.24	0.19	0.69	0.55				
<i>E. trilineata</i>	4.45	3.56	0.62	0.49							0.80	90.76
<i>P. caudimaculatus</i>			0.65	0.52					0.44	0.35	± 0.32	± 41.00
<i>N. schubarti</i>			0.10	0.08	0.11	0.09						
<i>C. fasciatum</i>			0.09	0.07								
<i>A. schubarti</i>			0.05	0.04								
Total	25.22	22.50	53.89	45.97	18.93	19.12	26.66	26.73	20.21	17.03		

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