

## Quantitative analysis of published data on the growth, metabolism, food consumption, and related features of the red-bellied piranha, *Serrasalmus nattereri* (Characidae)

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### Synopsis

A tentative set of growth parameters of the von Bertalanffy growth equation were estimated for the red-bellied piranha, *Serrasalmus nattereri*, a common characid of the Amazonas and adjacent floodplains, based on length-frequency data collected by R.H. Lowe-McConnell in Guyana. These parameters and related statistics are then used, along with published data from metabolic, field and feeding experiment data to estimate the relative food consumption of a population of *S. nattereri*. This is complemented with biological data assembled from the scattered literature on *S. nattereri* to provide a 'snapshot' of this species.

### Introduction

This contribution is to consolidate and interpret some published data on the red-bellied piranha, *Serrasalmus nattereri* (Kner, 1860), an abundant species of South American floodplains (Fig. 1, Table 1).

The author has no personal experience with this fish – except for having seen it in various public and private aquaria. However, this is a species for which a large, albeit very scattered literature exists. Thus, this contribution may illustrate how small bits of information distributed throughout the literature can be consolidated into a synoptic 'snapshot' to provide a basis for more comprehensive studies (Rosa

1965) or for entry into FishBase, the computerized encyclopedia on fish.<sup>1</sup>

### Nomenclature

*Serrasalmus nattereri* (family Characidae) was originally described by Kner (1860) as *Pygocentrus nattereri*, and is named after Johann Natterer (1787–1843), an Austrian naturalist who sampled Brazilian animals for nearly 18 years.<sup>2</sup> Synonyms include *P. altus*, *P. stigmaterythraeus*, *Rooseveltiella natteri* and *Serrasalmo piranha* (Riehl & Baensch 1991).

<sup>1</sup> Froese, R. 1990. FISHBASE: an information system to support fisheries and aquaculture research. *Fishbyte* 8: 21–24, and Pauly, D. & R. Froese. 1991. *FishBase: assembling information on fish*. Naga, ICLARM Q. 14: 10–11.

<sup>2</sup> Anon. 1845. Johann Natterer. *Neuer Nekrolog der Deutschen* 21: 1843.



Fig. 1. Distribution of the red-bellied piranha *Serrasalmus nattereri* in South America (modified from Braga 1975 and Schulte 1988). Note question mark for the Orinoco basin, where *S. nattereri* is replaced by *S. notatus*, a close relative or synonym.

The taxonomic status and hence the distribution of this and related piranhas are not well-established and some closely related species, such as *S. notatus*, the 'caribe colorao' of the Orinoco River Basin, may be synonyms (Géry 1977, Schulte 1988).

Alternatively, what is now considered a single widespread species ('*S. nattereri*') may end up being split into several species with narrower ranges (Schulte 1988, Riehl & Baensch 1991), and again bearing Kner's original generic name (Machado 1985).

Given its broad natural range, and its use as aquarium fish, *S. nattereri* has a number of common names, notably 'palometa' (Argentina, Bolivia), 'pañá' (Peru), 'palometa de río' (Uruguay), 'caribe boca de locha' (Venezuela); 'red pirai' (Guyana);

'Natterers Sägesalmler' (German). In the Cuiabá rivers and the Pantanal, *S. nattereri* is called 'piranha-queixcudá', i.e. 'big jawed' (I. Sazima personal communication), but in most of Brazil, the common name is 'piranha caju', or cashew-fruit piranha, because of the color similarity between cashew fruit and the fish when both are ripe (Goulding 1981).

#### Growth and natural mortality

Formal studies on the growth of *S. nattereri*, or of other piranhas for that matter, do not appear to have been conducted. However, Lowe-McConnell (1964) presented various information which when re-expressed as in Table 2 allows estimation of the

parameters of the von Bertalanffy growth function (VBGF, von Bertalanffy 1938), which has the form

$$L_t = L_\infty (1 - e^{-K(t-t_0)}) \quad (1)$$

where  $L_t$  is the length at age  $t$ ,  $L_\infty$  the mean size the fish would reach if they were to grow indefinitely,  $K$  a growth coefficient of dimension  $\text{time}^{-1}$  and  $t_0$  is (theoretical) age at which  $L = 0$ . Estimation of these parameters was done with the program of Gaschütz

et al.,<sup>3</sup> with very high weighting factors for the extreme lengths (1 and 26 cm in Table 2); this resulted in the following estimates:  $SL_\infty = 26$  (in cm),  $K = 0.893 \text{ year}^{-1}$  and  $t_0 = -0.05 \text{ year}$ .

The corresponding growth curve and data points

<sup>3</sup> Gaschütz, G., D. Pauly & N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length-frequency data. Int. Coun. Explor. Mer, Coun. Meet. 1980/D:6, Stat. Cttee. 14 pp.

Table 1. Selected occurrence records of and biological information on red-bellied piranha *Serrasalmus nattereri* and its close relative *S. notatus* (Venezuela only).

Occurrence	Maximum reported length (cm) <sup>a</sup>	Remarks	Source
<i>Brazil</i>			
Cuiabá River, Matto Grosso	–	Origin of type specimens	Kner (1860)
Pantanal, Matto Grosso	24 (SL)	Common in creeks and interconnected ponds, where it influences distribution and feeding of other fish.	Sazima & Machado (1990)
Tocantin River	25 (SL)	Common in lakes adjacent to and slow-flowing segments of this river and similar rivers, where it functions as a 'grand prédateur'.	Dos Santos et al. (1984); De Merona et al. (1987)
Rio Machado & Rio Negro		Rare, occurring predominantly in areas of high primary production; replaced by <i>S. rhombeus</i> in nutrient-poor areas	Goulding (1980)
Rio Madeira		Most abundant predator; caught from February to May with pole and line; tears gillnets	Goulding (1981)
<i>Peru</i>			
Amazon Basin		Details in Géry (1964b, not seen)	Ortega & Vari (1986)
<i>Bolivia</i>			
Rio Mamoré	26 (SL)	Largest specimen caught (= 1.05 kg)	Lauzanne & Loubens (1985)
<i>Venezuela</i>			
Orinoco Delta	31.5 (TL)	Largest specimen caught (= 1.0 kg)	Novoa et al. (1982); Novoa & Ramos (1978)
Orinoco, Apure State	30 (SL)	Most abundant piranha in the Llano 'where common [ <i>S. notatus</i> ] may have a pervasive effect on the spatial structuring of fish communities'	same as above Winnemiller (1989)
Orinoco, Middle course	48 (TL)	Such large specimens do not appear to occur in <i>S. nattereri</i> (except in neighboring 'Guyane'?)	same as above
<i>Guiana/Guyane</i>			
Rupununi River System	30 (TL)	Peak migration at dawn and early morning; locked in savanna ponds during dry season	Lowe-McConnell (1964, 1975)
'Guyane'	43 (?)	A large, aggressive 'form'	Géry (1964a)
<i>Various countries</i>			
Aquaria	30 (TL?)	optimum: 25–27° C; water hardness up to 10° H, pH 6.8	Paysan (1975); Franke (1978); Axelrod et al. (1987)

<sup>a</sup> SL = Standard Length, i.e., from the tip of the snout to the end of the caudal peduncle; TL = Total length, i.e., from the tip of the snout to the end of the (longest) caudal fin lobe.

Table 2. Summary of information on the growth of *S. nattereri* in Guyana (extracted from Lowe-McConnell 1964).

Age (month)	Standard length (cm)	Remarks
		Approximate length at hatching, at the onset of the rains, in mid-May
4		Modal length of fish caught at Karenambo, in mid-September 1957 (range 4–9 cm)
7	12	Mean length of fish caught in January 1960, and resulting from late rains (June 1959), hence assumed one month younger than 'May' fishes
12	16	Length at first maturity in May (i.e., at 1 year of age)
	26	Maximum size of <i>S. nattereri</i> , converted from TL $\approx$ 30 cm (Table 1)

are shown in Figure 2 together with rainfall data (adapted from Fig. 2 in Lowe-McConnell 1964) showing the relationship between spawning/hatching, growth and the seasonal cycle of rains in the Rupununi savanna district, Guyana.

Nico & Taphorn (1986) wrote that '... the Orinoco red-bellied piranha reaches 5 to 8 inches SL by their second rainy season'. This statement (which refers to *S. notatus*) implies a (mid-range) length of 16.5 cm SL at an age of about 1 year, very close to the values in Table 2 and Figure 2. The growth curve in Figure 2 is also confirmed by Schulte (1988) who reports that in aquaria, *S. nattereri* reaches 4.5 cm after 2 months and that 'when aged eight months, the largest fish were 120 mm (5 inches) long'.

Table 3 presents data for establishing a length-weight relationship in red-bellied piranha; given its broad range, no attempt was made to derive a precise allometric relationship. Rather, isometry shall be assumed (i.e., an exponent = 3), leading to

$$W = 0.028 (\text{TL})^3 = 0.043 (\text{SL})^3, \quad (2)$$

where  $W$  is in g live weight and length in cm, and where  $\text{TL} \approx 0.87 * \text{SL}$ .

Thus, the growth in weight of *S. nattereri* (and of *S. notatus* in locations such as the Orinoco Delta,

where a length of 30 cm TL is not usually exceeded) can be described from

$$W_t = 756 (1 - e^{-0.893(t + 0.05)})^3, \quad (3)$$

The estimates of asymptotic sizes ( $\text{SL}_\infty = 26$ ,  $\text{TL} = 30$  cm,  $W_\infty = 756$  g) do not preclude that larger and heavier red-bellied piranha do occur. Rather, these values are in line with the definition of  $L_\infty$  (and  $W_\infty$ ) as *means* (see above and Pauly 1984).

The estimate of asymptotic length (TL) and of  $K$ , and a mean annual temperature of 28° C, entered into the empirical equation of Pauly (1980), leads to an estimate of  $M = 1.66 \text{ year}^{-1}$ , implying that about 81% of a stock of juvenile and/or adult *S. nattereri* will die annually of natural causes (Fig. 2). Here again, no account is taken of seasonal changes, and hence this natural mortality estimate must be seen as referring mainly to between-, and less to within-year changes.

### Metabolic rate

Experiments on the oxygen consumption of piranha appear to have been conducted only by Braga (1975), and a summary of his results may be found in Table 4; note that various experimental details are lacking, notably on the activity of the fish. Nevertheless, these data were analyzed using a multiple (log) linear regression which yielded, for prediction of the metabolic rate ( $C$ , in  $\text{mgO}_2 \cdot \text{h}^{-1}$ ) in small *S. nattereri*, the model

$$C = 0.387 * W^{0.539} * O_2^{1.13}, \quad (4)$$

where  $W$  is the live weight of the fish in g, and  $O_2$  is the oxygen content of the water, in  $\text{mg l}^{-1}$ . The overall fit is good ( $R = 0.950$  and see Fig. 3a); the standard errors of the exponents are 0.163 and 0.205, respectively, for 4 degrees of freedom. Given the small range of weights considered here, the relatively large standard errors about the estimates, and the low number of degrees of freedom, it would not be appropriate to assume that the slope linking  $O_2$  consumption and body weight is, in *S. nattereri*, significantly different from that proposed by Winberg

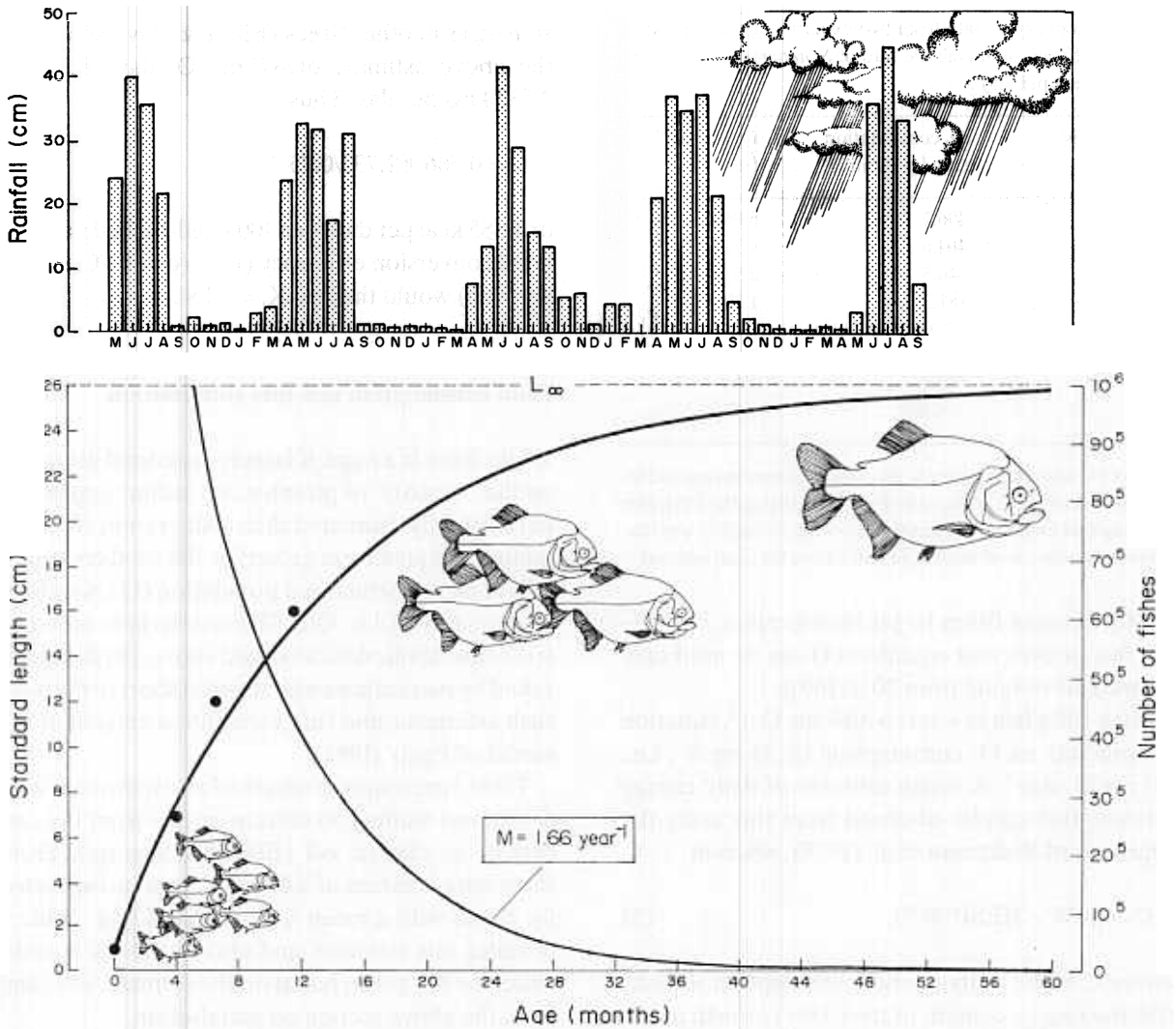


Fig. 2. Growth and (natural) mortality of red-bellied piranha *S. nattereri*, as inferred from data in Table 2. Note that both growth and natural mortality are probably subjected to seasonal oscillations, linked with rainfall, a process not investigated here.

Table 3. Data for establishing a length-weight relationship in red-bellied piranha (*S. nattereri* and *S. notatus*; data referring to the latter are marked with an \*).

SL	Length (cm) TL	Weight (live, g)	Condition factor <sup>a</sup> (SL/W)	(TL/W)	Source of L, W data <sup>b</sup>
	31.5*	1000*	–	3.12*	Novoa et al. (1982)
	25.0	400	–	2.56	Dos Santos et al. (1984)
			4.44 <sup>c</sup>	–	De Merona et al. (1987)
–	9.0	19.0	–	2.61	Bellamy (1968)
6.8*		13.3*	4.23*	2.8*	Nico (1990)
Mean condition factors:			4.3	2.8	This study

<sup>a</sup> c.f. = a·100, where a is the multiplicative factor in a length-weight relationship of the form W = a·L<sup>3</sup>.

<sup>b</sup> To ensure that a broadly-based L/W relationship emerges, only one L/W data pair were taken from each site.

<sup>c</sup> Average of 4 values for different months and sites.

Table 4. Summary of data from two experiments conducted by Braga (1975) on the metabolic rate of *S. nattereri* (mean temp. 28.4° C, mean pH 7.5)<sup>a</sup>.

Weight of fish (g)	O <sub>2</sub> consumption (mg kg <sup>-1</sup> ·hour <sup>-1</sup> )	O <sub>2</sub> content <sup>b</sup> (mg l <sup>-1</sup> )
20.8	496.2	6.05
20.8	464.6	4.24
20.8	346.5	2.53
20.8	181.3	1.30
20.8	56.06	0.71
158	203.2	3.23
158	27.22	1.04
158	4.386	0.63

<sup>a</sup> Free CO<sub>2</sub> was about 1 ppm at the onset of experiments and increased to 16.5 mg l<sup>-1</sup> at the end of series involving the 158 g fish; the weighted mean CO<sub>2</sub> content was = 7 mg l<sup>-1</sup>; salinity was 0‰.

<sup>b</sup> Geometric means of initial and end values for each interval.

(1960) for most fishes larger than guppies, i.e., 0.7–0.8; this implies that equation (4) can be used only for weights ranging from 20 to 160 g.

For a 100 g fish in water with 6 mg O<sub>2</sub> l<sup>-1</sup>, equation (4) predicts an O<sub>2</sub> consumption of 35 mg h<sup>-1</sup>, i.e., 841 mg O<sub>2</sub> day<sup>-1</sup>. A rough estimate of daily energy consumption can be obtained from this using the approach of Wakeman et al. (1979), wherein

$$C = (\Delta W + \text{RESP})/0.75, \quad (5)$$

where C is the daily energy consumption in kcal, ΔW the energy content of the (daily) growth increment, and RESP is the oxygen consumption.

The first derivative (i.e., growth rate) of the von Bertalanffy equation in terms of wet weight is

$$dw/dt = 3KW((W_{\infty}/W)^{1/b} - 1). \quad (6)$$

This, solved for  $W_{\infty} = 756$  g,  $K = 0.893/365 = 0.00245$  day<sup>-1</sup>, and  $b = 3$ , gives for a 100 g fish a daily growth increment of 0.706 g, corresponding to 0.706 kcal if the calorific value of fish wet weight is set equal to unity (Brett & Blackburn 1978). The available information on body composition of 'piranha caju' flesh (Junk 1976, in Smith 1979) is 8.2% fat, 15.0% protein, and 4.4% ash, not very different from values reported from other fishes (Bykov 1983). If an oxy-caloric equivalent of 0.00325 kcal mg<sup>-1</sup> O<sub>2</sub> is as-

sumed, as in other fishes (Elliot & Davidson 1975), the above estimate of 841 mg O<sub>2</sub> day<sup>-1</sup> becomes 2.733 kcal per day. Thus

$$C = 0.706 + 2.733/0.75 \quad (7)$$

or 4.585 kcal per day for a 100 g red-bellied piranha. Food conversion efficiency ( $K_1 = (dw/dt)/C$ , see Ivlev 1966) would then be  $K_1 = 0.154$ .

### Food consumption and diet composition

While there is a huge, if largely anecdotal literature on the 'voracity' of piranhas, no author appears to have actually estimated their daily ration ( $R_d$ , pertaining to a given size group) or the food consumption of an age-structured population (Q), weighted by biomass (B), i.e., Q/B. This is done here based on (i) the metabolic data analyzed above, (ii) data published by two authors who stopped short of deriving such estimates, and (iii) a simplified version of the model of Pauly (1986).

Table 5 presents the results of an experiment with *S. nattereri* feeding ad libitum on bits from the carcass of an electric eel (*Electrophorus* sp.). From these data, a ration of 2.46 g day<sup>-1</sup> can be estimated for fishes with a mean live weight of 19 g. Table 6 includes this estimate, and also recalls an  $R_d$  estimate, for 100 g fish, based on the estimate of C and  $K_1$  in the above section on metabolism.

Figure 4 presents a diurnal feeding cycle in young *S. notatus*, based on stomach content data in Nico (1990), fitted with Model I of Sainsbury (1986), as modified in Jarre et al. (1991) and implemented by Jarre et al.<sup>4</sup> The fit is excellent, and leads to the following estimates: beginning of feeding period ≈ 02:00 h; end of feeding period ≈ 14:00 h; feeding rate ≈ 1% of body weight per hour; instantaneous stomach evacuation rate = 9.65% of stomach content per hour.

<sup>4</sup> Jarre, A., M.L. Palomares, F.C. Gayanilo, Jr. & D. Pauly. 1992. A user's manual for MAXIMS, a computer program for estimating the food consumption of fishes from diel stomach contents data and population parameters. Vers. 1.0. ICLARM Software 4. 27 pp.

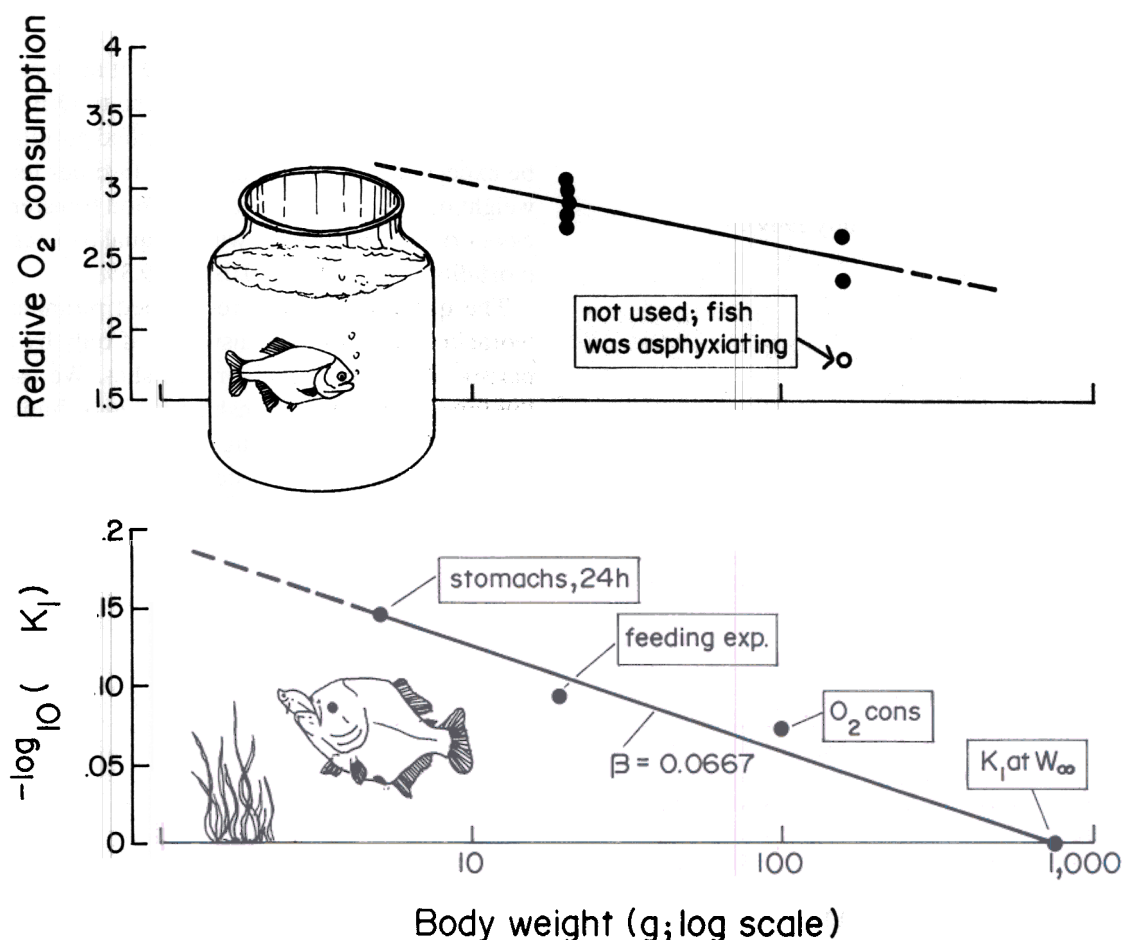


Fig. 3. Weight dependence of two physiological processes in red-bellied piranha: a – Relationship between oxygen consumption and body weight (after account has been taken of different ambient O<sub>2</sub> levels, see equation 7. b – Relationship between a log-transformation of gross food conversion efficiency ( $K_1$ ) and body weight (based on data in Table 6).

The feeding rate, multiplied by the feeding period leads to a ration estimate of 12.14% BWD for *S. notatus* with a mean length of 4.9 cm SL, i.e., a mean weight of 5 g (Table 6).

Table 6 presents the  $K_1$  and  $W$  data used here to estimate the parameter  $\beta$  of a general relationship linking fishes, food conversion efficiency ( $K_1$ ) and body weight ( $W$ ) in the form

$$K_1 = 1 - (W/W_\infty)^\beta \quad (8)$$

where  $K_1$  = growth increment/food consumed, for any body weight between hatching and asymptotic size (Pauly 1986, Silvert & Pauly 1987). Estimation of  $\beta$  was done here as shown in Figure 3b, i.e., via a

plot of  $-\log_{10}(1 - K_1)$  vs.  $\log_{10} W$ , with the X intercept of the abscissa forced through  $\log_{10}(W_\infty)$ , and whose slope, with sign changed, provides an estimate of  $\beta = 0.067$ .

As might be seen, this plot shows that the three available estimates of  $R_d$  and the 4 estimates of  $K_1$  are mutually compatible, despite the widely different type of data and models used for their estimation. The relative food consumption ( $Q/B$ ) of an age-structured population of red-bellied piranhas can thus be estimated using

$$Q/B = \int_{t=0}^{t=\infty} [(dw/dt) \exp(-M(t-t_0))]^\beta dt \quad (9)$$

$$\int [W_t \cdot \exp(-M(t-t_r))] dt.$$

for which all parameters are as estimated above (Pauly 1986, Palomares & Pauly 1989).

Table 5. Data for the estimation of ration in *S. nattereri* of 18–20 g, feeding ad libitum with bits from the carcass of an electric eel, with additional data on blood glucose contents (as read off Fig. 1 in Bellamy 1968).

Time (hours)	Day one food intake (g per 100 g)		Day two food intake (g per 100 g)		Mean	Blood glucose (mg%) Means
	Low	High	Low	High		
0800	3.49	3.94	2.19	3.58	3.30	56.75 <sup>a</sup>
0900	0.93	1.34	1.33	1.75	1.34	
1000	0.22	0.47	0.88	1.12	0.67	
1100	0.07	0.19	0.19	0.38	0.21	
1200	0.38	0.42	0.22	0.29	0.33	
1300	0.08	0.14	0.05	0.18	0.11	
1400	0.11	0.28	0.12	0.22	0.18	
1500	0.08	0.19	0.02	0.25	0.14	
1600	1.32	1.67	1.49	2.00	1.62	
1700	0.78	0.94	0.92	1.03	0.92	
1800	1.43	1.79	1.06	1.34	1.41	90.50
1900	1.02	1.16	0.28	0.57	0.76	
2000	0.78	0.82	0.31	0.42	0.58	87.50
2100	0.08	0.27	0.09	0.26	0.18	
2200	0.17	0.28	0.11	0.17	0.18	77.00
2300	0.08	0.13	0.17	0.17	0.14	
2400	0.17	0.22	0.11	0.11	0.15	69.00 <sup>b</sup>
0100	0.19	0.31	—	—	0.25	
0200	0.12	0.22	—	—	0.18	61.00
0300	0.04	0.11	—	—	0.08	
0400	0.04	0.04	—	—	0.04	66.00
0500	0.02	0.02	—	—	0.02	
0600	0.05	0.05	—	—	0.05	56.00
0700	0.58	1.27	—	—	0.93	
Average food intake (per hour)					0.57	

<sup>a</sup> Based on means (58.5 & 55.0) for 08:00 h, at beginning and end of 24-hour cycle.

<sup>b</sup> Value interpolated linearly.

The MAXIMS program of Jarre et al.<sup>4</sup> was used to integrate equation (9) and this led to  $Q/B = 17.8 \text{ year}^{-1}$ . Thus, a population of red-bellied piranha can be expected to eat approximately 18 times its own weight per year, while the overall food transfer efficiency of that population will be equal to: (natural) mortality \*  $1/(Q/B)$ , i.e., 0.093, or 9.3%.

The question whether red-bellied piranhas are 'voracious' can now be answered, if only by comparison with other carnivorous fishes. We use for this four empirical relationships, based on hundreds of different species, linking  $Q/B$  with various predictor variables, and adjusted to account for carnivory, i.e., those of Palomares & Pauly (1989):

Table 6. Data for estimating the growth conversion efficiency ( $K_1$ ) and related statistics of red-bellied piranha in nature.

Weight <sup>a</sup>	dw/dt <sup>b</sup>	Ration (g day <sup>-1</sup> ) observed/ predicted	$K_1$	Source
5	0.159	0.558/0.588	0.285	Fig. 1
19	0.473	2.46/1.54	0.192	Table 4
100	0.706	4.58/5.59	0.154	Equation (6)
756	0 <sup>d</sup>	-/127.7 <sup>e</sup>	0 <sup>d</sup>	See text and <sup>e</sup>

<sup>a</sup> Live weight in g; the largest value is  $W_\infty$ .

<sup>b</sup> First derivative of equation (2).

<sup>c</sup> Conventional definition;  $K_1$  = growth increment/food ingested (Ivlev 1966); here  $K_1 = (dw/dt)/Rd$ .

<sup>d</sup> By definition, since fish at  $W_\infty$  do not grow.

<sup>e</sup> Estimated by solving Equation 5 for a value of  $W$  slightly smaller than  $W_\infty$ , and dividing by the corresponding value of  $dw/dt$ .

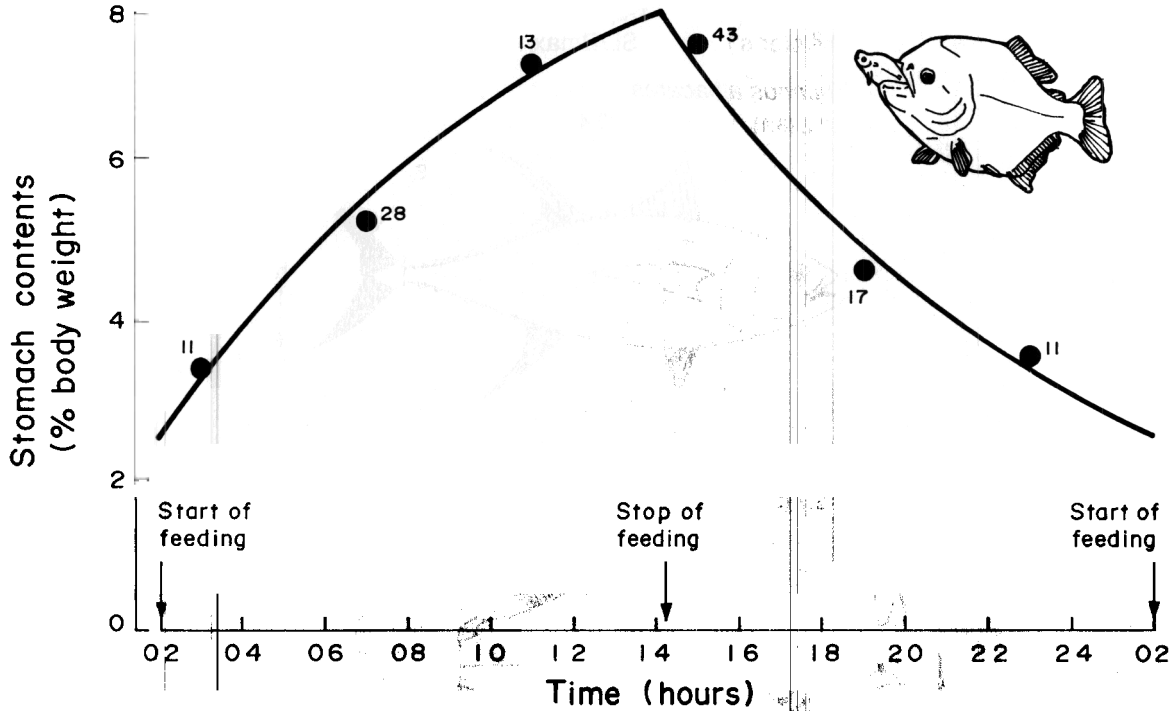


Fig. 4. Diurnal feeding cycle of 5 g red-bellied piranha (*S. notatus*), with data points from Figure 1 in Nico (1990) [fitted with model and software of Jarre et al. (1991,<sup>4</sup>), respectively.] The representation of *S. notatus* grasping its prey after a chase (a characin, *Astyanax bimaculatus*) is adapted from Sazima & Machado (1990).

$$Q/B = 3.06 * T^{0.612} * W_{\infty}^{-0.202} * A^{0.516}, \quad (10)$$

Pauly (1989):

$$Q/B = 0.790 * T^{0.444} * W_{\infty}^{-0.115} * A^{0.427} * D^{0.577} * P^{-0.464}, \quad (11)$$

Palomares (1991):

$$Q/B = 1.82 * T^{0.759} * W_{\infty}^{-0.165} * A^{0.405}, \quad (12)$$

and Christensen & Pauly<sup>5</sup>:

$$Q/B = 10^{6.4} * 0.0313^{T_k} * W_{\infty}^{-0.168}, \quad (13)$$

where T = mean annual water temperature (here 28° C); T<sub>k</sub> = temperature transformed, i.e. T<sub>k</sub> = 1,000/(T/T+273.1); W (or W<sub>∞</sub>) = (asymptotic) live weight, in g (here 756); A or A' = aspect ratio of the

caudal fin (here A = 3.7 and A' = 2.8, see Fig. 5); D = standard length over maximum body depth (here see Fig. 5); P = depth of caudal peduncle over maximum body depth (here 0.19, see Fig. 5).

Palomares (1991) demonstrated, based on a large number of cases from both types of environments, that the Q/B values of marine and freshwater fishes are not significantly different when account is taken of food type, temperature and of morphological variables, and hence all four equations presented above can be applied to red-bellied piranhas.

The four equations above predict values of Q/B = 12.1, 7.6, 11.6 and 8.3 year<sup>-1</sup>, with a mean of 9.9 year<sup>-1</sup>. With an estimated Q/B of 17.8 year<sup>-1</sup>, red-bellied piranhas consume about twice as much as would be expected based on their size and shape and the temperature of their habitat. Thus *S. nattereri* may indeed be described as 'voracious'.

All studies so far conducted on *S. notatus* (e.g., Nico & Taphorn 1988, Winemiller 1989) and on *S. nattereri* (e.g., Bonetto et al. 1967, Braga 1975) confirm the strong tendency of red-bellied piranhas to

<sup>5</sup> Christensen, V. & D. Pauly. 1992. A guide to the ECOPATH II software system (version 2.1). ICLARM Software 6. 72 pp.

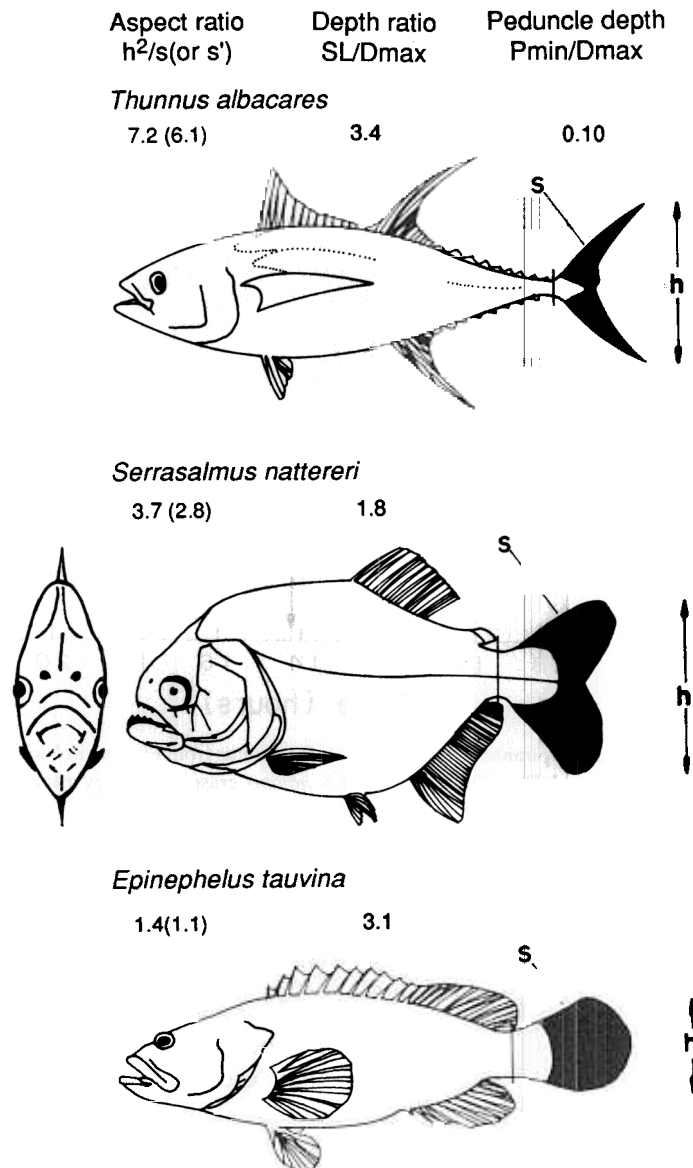


Fig. 5. Comparison of shape between three types of piscivorous fishes, with emphasis on three indices that can be used to identify these types: (i) Aspect ratio, defined by  $h^2/s$  (or  $h^2/s'$ , in brackets, with  $s'$  including the surface area up to the thinnest section of the caudal peduncle or  $P_{min}$ ); (ii) standard length over maximum depth ( $SL/D_{max}$ ); and (iii)  $P_{min}/D_{max}$ . Note intermediate position of *S. nattereri* in two of these indices and high value of  $SL/D_{max}$ . The frontal view of *S. nattereri* is from Figure 1 in Sazima & Machado (1990), the lateral view is adapted from Kner (1860).

feed on whole fishes and/or pieces thereof (Table 7). Other foods are taken, however, and these include arthropods (insects, crustaceans), molluscs and small vertebrates or parts thereof, as well as small amounts of plant materials (and see the Discussion for mammals as food items of piranhas).

### Reproduction

Schulte (1988) discusses the reproduction of red-bellied piranhas in some details; the following account of reproduction in *S. nattereri* in aquaria was adapted, however, because of its conciseness from Riehl & Baensch (1991):

Table 7. Some reported morphological and behavioral adaptations for carnivory by red-bellied piranha *S. nattereri* [author's comments in square brackets].

Item	Source
Relatively short intestine, Length of intestine/SL $\approx$ 1.1	Luengo (1965); Jégu & Dos Santos (1988)
Highly evolved auditory capacity	Stabentheiner (1988); Nico (1990)
Adults feed mainly at dusk and dawn [as is common among piscivores]	Sazima & Machado (1990); Bellamy (1968); Hobson (1972)
(Daytime) 'lurking', then 'dashing' [as also implied by relatively low caudal fin aspect ratio and high caudal peduncle]	Sazima & Machado (1990) [see Fig. 5 and text]
Teeth replacement on alternating sides of jaw, allowing continuous feeding	Sazima & Machado (1990)
Hierarchies within 'packs' (i.e., small schools) [as also occurs, e.g., in wolves]	Zbinden (1973)

'Reproduction generally occurs after "new" water with a neutral pH and a hardness of 6° H has been added; the males, dig plate-sized pits in gravel, into which the eggs are deposited. Spawning occurs from 4–5 AM. The male defends the spawn; for 24 h, he is supported in this by the female, after which he drives her away (if the eggs are removed, the male spawns with another female of the same school 2–3 days later). The 500–1000 eggs are transparent-golden, and stick to the gravel. The larvae hatch after 8 days, and start feeding after 4–5 days, i.e. once their yolk sac is consumed. The juveniles have black spots and their only red coloration is on a spot near and on the lower part of the operculum, and on the anal fin.'

Unfortunately, this description is too concise to unequivocally assign *S. nattereri* to one of the ethological-ecological groups proposed by Balon

(1990), i.e., future research will have to determine whether they are indeed 'phytophil clutch tenders', the most likely category (see also Table 8).

Other information on the reproduction of red-bellied piranha is compiled in Table 8; note that the available size at first maturity (in Table 2), divided by the asymptotic size (Table 1 and equation 1) leads to  $L_m/L_\infty = 0.67$ , i.e., to an estimate of 'reproductive load' that is compatible with values reported from other fishes (Cushing 1981, Pauly 1984).

### Thermal tolerance

Braga (1975) conducted a set of experiments on the cold and heat tolerance of *S. nattereri*, of unknown weight, summarized in Figure 6.

As might be seen, the temperature range be-

Table 8. Selected information on the reproduction of red-bellied piranha (*Serrasalmus nattereri* and *S. notatus*).

Item	Source
No visible differences between ♀ and ♂ in the specimens sent by J. Natterer from Brazil	Kner (1860)
No reliable external sex difference in <i>S. nattereri</i>	Paysan (1975)
In ' <i>Serrasalmus</i> sp. aff. <i>nattereri</i> ', reported to occur in the Orinoco Basin (Venezuela, Guyana), the males have heads that are more 'bull-like', but are more slender than the females	Riehl & Baensch (1991)
Mature specimens are found from March to June (esp. in April) in the Orinoco River ( <i>S. notatus</i> )	Novoa et al. (1982)
In <i>S. nattereri</i> , spawning generally occurs in May, at the onset of the rains; eggs are laid on tree roots trailing in the waters, and are guarded; reproductive success (i.e. recruitment) may strongly vary from year to year depending on how the savanna was flooded	Lowe-McConnell (1964, 1975)
'A single spawning may produce 4 000–5 000 large eggs which adhere to the plants and are not attacked by the parent fishes. They hatch in 9 to 10 days'	Mills & Vevers (1989)
Reproductive load, i.e., $L_m/L_\infty = 0.65$	See Table 2 and text
Detailed account of reproduction in the aquarium	Schulte (1988)

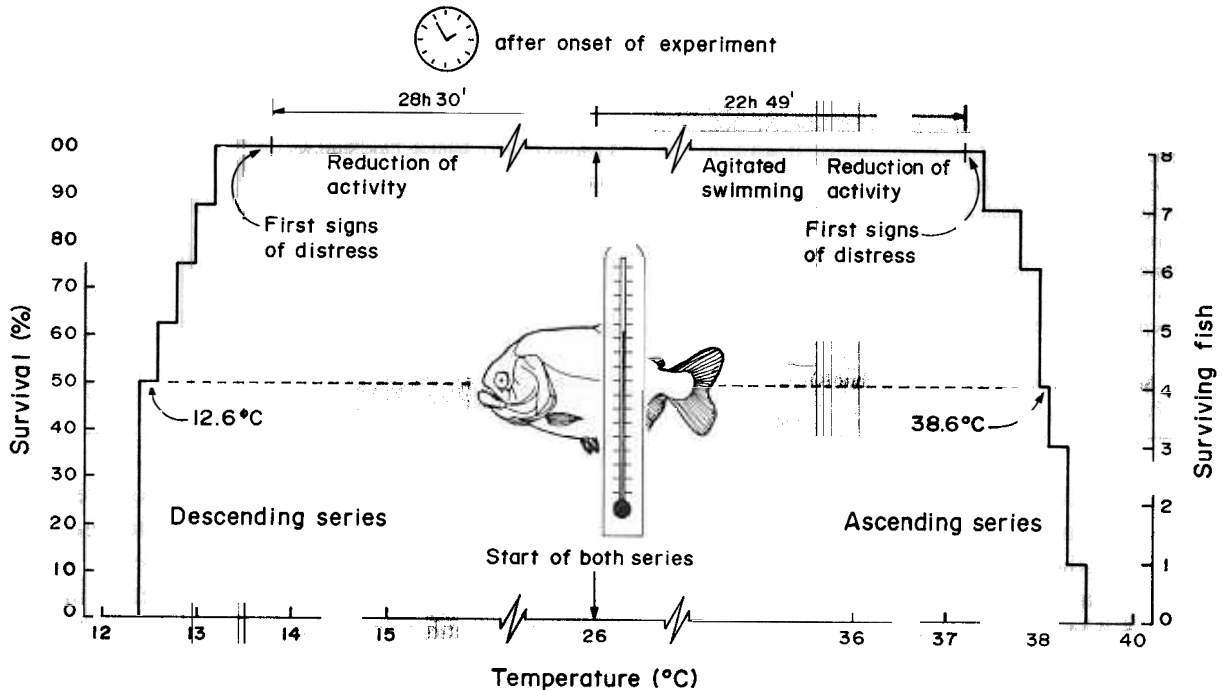


Fig. 6. Graphical summary of experiments by Braga (1975) on the thermal tolerance of *S. nattereri*.

tween the two lethal limits was 24° C. The upper limit (38.6° C) does not have obvious ecological implications, as extremely high temperatures probably occur only under conditions where other factors (notably O<sub>2</sub> and food) are likely to be limiting as well. On the other hand, the lower limit of 12.6° C is ecologically interesting because it clearly impacts on the southward expansion of *S. nattereri*. Indeed, Bonetto et al. (1967) show that winter mortalities are the main limiting factor for *S. nattereri* (and some other piranhas) in the middle and particularly in the lower Parana River, where winter temperatures drop well below 10° C.

### Parasites

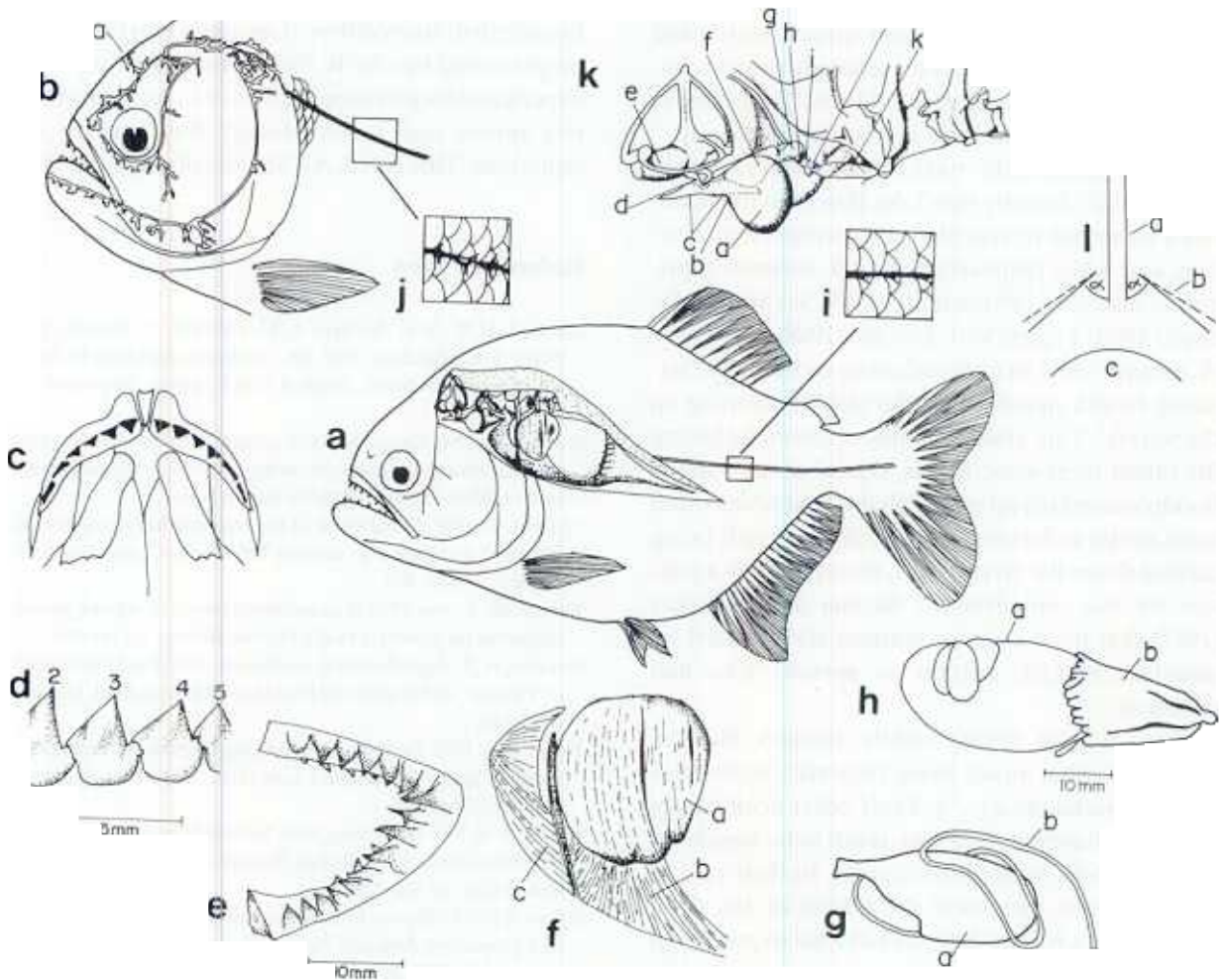
Thatcher (1991) reported the following parasites from *S. nattereri*— Monogeneoidea: *Amphithecium brachycirrum*; *A. calycinum*; *A. camelum*; *A. cataloensis*; *A. falcatum*; *A. junki*; *Anacanthorus anacanthorus*; *A. brazilensis*; *A. maltae*; *A. neotropicalis*; *A. reginae*; *A. rondonensis*; *A. thatcheri*; *Cleidiscus amazonensis*; *C. piranhus*; *C. serrasalmus*;

*Notothecium aegidatum*; *N. mizellei*; *Notozothecium penetrarum*; *N. minor*; *Urocleidus crescentis*; *U. orthus*. Nematoda: *Spirocamallanus inopinatus*. Copepoda: *Rhinergasilus piranhus*. Branchiura: *Argulus multicolor*; *Argulus* sp.; *Dolops bidentata*; *D. carvalhoi*; and *D. longicauda*.

### Discussion

Figure 7 is an attempt to illustrate, for the anatomy of *S. nattereri*, what the text has attempted with regard to its biology and ecology: a 'reconstruction' of the red-bellied piranha from various elements scattered in the literature. Such reconstruction, synthetic as it might be, appears to require a second-order synthesis, presenting the species as a whole, i.e., an attempt to answer the question: 'What is a red-bellied piranha?'

The Fisheries Administrative Order 'prohibiting the importation and/or possession of any live pira-



**Fig. 7.** Aspects of the functional anatomy of red-bellied piranha *Serrasalmus nattereri*: a – adult specimen, with ribs, vertebral processes and head bones partly removed, to show auditory and drumming apparatus (adapted from Kner 1860 and Stabentheiner 1988); b – head, showing lateral line canals; a = junction canal between the left and right sides of the head (adapted from Stabentheiner 1988); c – upper premaxillary, showing position of teeth (adapted from Géry 1964a); d – teeth on side of lower jaw, numbered from median tooth (from Jégu & Dos Santos 1988); e – external lateral view of gill rakers on first branchial arch (source: as in d-); f – drumming apparatus; a = gas bladder; b = tendon of drumming muscle; c = *tunica externa*, to which *tripus* is attached (see K) (source: as in b-); g – alimentary tract; a = stomach, b = intestine (source: as in d-); h – left lateral view of gall bladder; a = cranial sac; b = caudal sac (sources: as in b- and d-); i and j – magnified details of the trunk canal of the lateral line (source: as in b-); k – details of the auditory apparatus; a = *legana*; b = *foramen socculo-lagenaris*; c = *sacculus*; d = *canalis transversus*; e = *utricle*; f = *sinus imper*; g = *scaphium*; h = *claustrum*; i = *ligamenti*; j = *intercalarium*; k = *tripus*; l – dorsal view (schematic); a = *saccular macula*; b = *lagenar macula*; c = gas bladder. The angle ( $\alpha$ ) ranges from 50 to 55° (source: as in b-).

nha' in the Philippines<sup>6</sup> defines piranha as 'fishes with lacerating teeth and strong set of well-developed mandibles with which to take bites out of the flesh of its victims, usually found in northern South America. They are found in northern South America. They are strictly freshwater species, sturdy and could adapt easily to new environment, even in confinement under aquarium conditions.' [Needless to say, piranhas are available in Manila pet shops.]

Clearly, this and the many similar restatements of the piranha's ferocity won't do. Based on the material I reviewed to complete the present contribution, and while emphasizing that *S. nattereri* is primarily piscivore (Winnemiller 1989, Sazima & Machado 1990) I agree with Schulte (1988) who views '*S. nattereri* and its close relatives as the only fast-acting health squad [with] the task of cleaning up the waters'. This 'task' is mainly required following the rather large-scale floods, typical of the various floodplains which piranhas inhabit, and which often leads to the cadavers of terrestrial mammals being carried down the rivers. This, then provides a context for the contention of Sazima & Guimaraes (1987) that most cases of humans skeletonized by piranhas, in fact, pertain to persons who had drowned.

Thus Schulte (1988) rightly stresses that 'of course, piranhas attack living creatures, sometimes sick or injured ones [. . .]. Their other ecologically important function, however, tends to be largely ignored in these sensational reports. In their role as carrion-eaters, they clear the waters of any dead creature long before they get a chance to putrefy in the warm water. It is this extremely important role played by piranhas in the ecosystems of the South American rivers and streams that has so far hardly been brought to the general public's attention with the necessary emphasis'.

And to scientists, as well.

<sup>6</sup> Anon. 1982. Updated Index to Presidential Decrees on Fisheries. Bureau of Fisheries and Aquatic Resources, Quezon City. 124 pp.

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