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VARIATION IN ENERGY CONTENT OF SOMATIC AND REPRODUCTIVE, TISSUES RELATED TO THE REPRODUCTIVE CYCLE AND FEEDING OF FEMALE *Pimelodus maculatus* Lacépède, 1803 (Siluriformes, Pimelodidae) AND *Schizodon borellii* Boulenger, 1895 (Characiformes, Anostomidae)

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ABSTRACT. The aim of this paper is to test a hypothesis that the variation trends in the energy content of the somatic and reproductive tissues and feeding activity are a function of the reproductive cycle in female *S. borellii* and *P. maculatus* under natural conditions and elucidated aspects of the energetic equilibrium of these species. Specimens were caught in the upper Paraná River floodplain (22º40' - 22º50'S and 53º10' - 53º40'W) from March 1992 to February 1994. Eighteen female *S. borellii* and twenty-one *P. maculatus* in the immature, resting, maturing and mature stages of the reproductive cycle were sampled for muscle, liver and gonad calorimetry. Means of the condition factor, stomach repletion index and visceral-somatic relation were obtained for the same stages from biometric data. Results reveal the patterns in the allocation equilibrium of female *S. borellii* and *P. maculatus* during the reproductive period. Since significant variations in the energy content of reproductive components related to vitellogenesis occur even with a decrease in feeding activity in adult and without any detriment to somatic reserves (skeletal muscle and liver) and to the somatic growth, we propose the hypothesis that in this phase of the reproductive process, visceral fat functions as an accessory source of energy which guarantees gonadal development and the maintenance of other components.

Key words: bioenergetics, fish reproduction, fish feeding, fish physiology.

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VARIAÇÃO DO CONTEÚDO ENERGÉTICO DE COMPONENTES SOMÁTICOS E REPRODUTIVOS RELACIONADA À ATIVIDADE ALIMENTAR EM FUNÇÃO DO CICLO REPRODUTIVO EM FÊMEAS DE *S. borellii* E *P. maculatus*

RESUMO. Este trabalho tem como objetivo verificar a tendência de variação do conteúdo energético de componentes somáticos e reprodutivos e a atividade alimentar em função do ciclo reprodutivo em fêmeas de *S.borellii* e *P.maculatus*, na natureza, com o propósito de elucidar aspectos do balanço energético destas espécies. Os exemplares estudados foram capturados na planície de inundação do alto Rio Paraná durante o período de março de 1992 a fevereiro de 1994. Para o estudo do valor calorimérico dos componentes fígado, músculo e gonadas foram amostradas 18 fêmeas de *S.borellii* e 21 *P. maculatus* nos seguintes estágios de maturação do ciclo reprodutivo: imaturo, repouso, maturação e maduro. Para os mesmos estágios, foram obtidas as médias do valor médio do fator de condição, do índice de repleção estomacal e da relação víscero-somática a partir dos dados biométricos. Os resultados revelaram equilíbrio na alocação de energia durante o período reprodutivo em fêmeas de *S.borellii* e *P.maculatus.* As variações significativas verificadas no conteúdo energético de componentes reprodutivos foram relacionadas ao processo de vitelogênese, que ocorreram com a diminuição da atividade alimentar nos indivíduos adultos e sem a diminuição das reservas somáticas (músculo esquelético e fígado) e da taxa de crescimento somático (fator de condição), sugerindo que, nesta fase do processo reprodutivo, a gordura visceral atue como fonte de reserva acessória, garantindo o desenvolvimento gonadal e a manutenção dos outros componentes.

Palavras-chave: bioenergia, reprodução, alimentação, fisiologia de peixes.

INTRODUCTION

All living things, ecosystems and the whole biosphere have the ability of creating and maintaining a certain degree of internal order through a continuous and efficient exchange of energy and matter (Odum, 1985). Knowledge of patterns of transference and energy transformation of a species may help one understand its physiology and autoecology.

The equilibrium in the allocation of assimilated energy to metabolism or to somatic and reproductive growth has important implications for the survival and reproductive success of fish (Winberg, 1970; Tytler and Calow, 1985; Wootton, 1990). Allocation may be influenced by changes in the reproductive cycle, food consumption and environmental conditions (Webb, 1978; Pandian and Wivekanandam, 1985).

The energy content of somatic and reproductive components may be good indicators of the physiological condition of a fish since they reflect environmental, physiological and nutritional factors (Cui and Wootton, 1988).

A variety of direct and indirect methods may be used to measure the energetic content of organic matter. Calorimetry measures directly the quantity of heat liberated in the process of the combustion of matter with the help of a calorimeter and oxygen as an oxidation agent.

The pattern of energy allocation may differ according to the degree of the individual's maturity, since maturation of gonads and/or reproductive activity imply the utilization of materials obtained from ingested food and energy reserves deposited in different parts of the body. This factor may lead to a decrease in somatic production and/or in metabolism (Tytler and Calow, 1985).

Food supply also influences the relative growth rate of somatic and reproductive components (Tytler and Calow, 1985), justifying the importance of studies on food activity so that one may understand the bioenergetic patterns of a species. Temporal changes in feeding may be measured by fluctuations in the relative weight of the stomach. These fluctuations essentially reflect differences in the quantity of food present (Hyslop, 1980).

Studies related to fish bioenergetics are rare, especially freshwater species in their natural environment. In Brazil, such research has been undertaken on marine fish. Soares (1992) investigated the daily consumption of demersal species of the Ubatuba region through field data and evacuation rates taken from literature. Ngan *et al*. (1993) began their pioneer studies of consumption estimates from bioenergetic models based on experimentally obtained data on oxygen consumption. Reyna-Kurtz (1993) evaluated stomach evacuation rates of *Paralonchurus brasiliensis* in laboratory conditions.

The species collected for the present analysis belong to the dominant ichthyofauna at the upper stretch of the Paraná River floodplain, between March 1992 and February 1994 (FUEM-PADCT/CIAMB, 1993).

The mandi, *Pimelodus maculatus* (Lacépede, 1803) (Osteichthyes: Siluriformes, Pimelodidae), is a middle-sized species (averaging between 8.00 cm and 35.5 cm in medium length) which undertakes lateral migrations in the floodplain, especially in lentic and semi-lotic environments. The *mandi* presents a maturing period from October to March and does not have any parental care. With regard to its feeding habits it is classified as omnivorous (Basile-Martins *et al*., 1986; FUEM-PADCT/CIAMB, 1993; Lolis and Andrian, 1996).

The piava, *Schizodon borellii* (Boulenger, 1895) (Osteichthyes: Characiformes, Anostomidae), a middle-sized species (averaging between 6.00 cm and 32.00 cm in medium length), is classified as herbivorous and may be found principally in lotic environments. It does not show parental care and its maturing period takes place between November and February (FUEM-PADCT/CIAMB 1993; Andrian *et al*. 1994).

The present paper describes the variation trends in the energy contents of body components, in the visceral-somatic relationship and in feeding activity as a function of the reproductive cycle in female *S. borellii* and *P. maculatus*, under natural conditions, so that aspects of the energy budget of these species may be elucidated.

MATERIALS AND METHODS

Specimens were caught in the rivers Paraná, Ivinheima and Baía, and lakes Patos and Guaraná environments, all components of the floodplain of the upper Paraná River in the states of Paraná and Mato Grosso do Sul (22º40’- 22º50’S and 53º10’- 53º40’W). The region has a subtropical and tropical climate and is subjected to seasonal modifications because of the hydrological regime. In most places, riparian vegetation is altered by anthropogenic action, and macrophytes banks are overgrown by (*Eichhornia azurea*, *Eichhornia crassipes*, *Pistia* sp and *Salvinia* sp) and *Polygonum* sp in the littoral zone (FUEM-PADCT/CIAMB, 1992; FUEM-PADCT/CIAMB 1993).

Monthly collections were taken between March 1992 and February 1993 with gillnets set over 24 hours and with landings at every 4 hours, giving a total of 449 female *P. maculatus* and 542 *S. borellii*.

Standard length (Ls), total weight (Wt), stomach weight (We) and visceral weight (Wv) were taken by a millimeter scale ichthyometer and electronic weighting-machine (precision of 0.01g), respectively. Each reproductive stage was classified according to Vazzoler (1981).

During the period from March 1993 to February 1994 samples of liver, muscle (dorsal skeleton) and gonads of *S. borellii* (N=21) and *P.*

maculatus (N=18) females were taken at the following stages of gonadal development: immature, resting, maturing and mature. The samples were transported to the Nupélia labs (Maringá, Paraná, Brazil) in liquid nitrogen at - 180ºC. They were then dehydrated for one or two days in a drying oven at a temperature of 60ºC and stored in a vacuum desiccator (Winberg, 1970).

The calorimetric value (cal/g dry weight) of the organs was obtained by the direct physical method, evaluating the liberated heat by the combustion of organic matter using Parr's calorimeter at the Ecophysiology lab of the Oceanographic Institute of the Universidade de São Paulo, São Paulo, Brazil (Prus, 1975). Calories (cal) were used as units of energy (Prus, 1975; Wootton 1990). Using STATISTICA program, Tukey's multiple comparison test was applied and the reliability interval was obtained for each stage.

The physiological state of the females was evaluated by the condition factor (K) (Le Cren, 1951) calculated by the expression:

$$K = \frac{Wt}{Ls^b}.100 \text{, where}$$

Wt = total weight of individual,
Ls = standard length of individual,
b = angular coefficient of weight/length relationship ($Wt = a.Ls^b$).

Exponents of 3.08395 and 3.09079 were adopted for *P. maculatus* and *S. borellii* respectivily. These values were obtained from biometric data of the studied females.

Temporal variation of feeding activity for each reproductive stage was evaluated by the trend of the Repletion Index (IR) (Hyslop 1980):

$$IR = \frac{We}{Wt - Wv} \text{, where}$$

We = stomach weight,
Wt = individual weight,
Wv = viscera weight.

As an indicator of the variation in visceral fat accumulation, visceral-somatic relationship, the ratio between the weight of viscera and the total weight of the individual was obtained by: (Vazzoler, 1981)

$$RVS = \frac{Wv}{Wt}.100 \text{, where}$$

Wt = weight of individual,
Wv = weight of viscera.

Analysis variance method (ANOVA) and Tukey's multiple comparison test were used to test the differences (at a 5% level) of values RVS, IR and K in individuals at different stages of gonadal development (Sokal and Rohlf, 1981). For calculations the program STATISTICA was used.

RESULTS AND DISCUSSION

Many investigations have shown seasonal differences in the caloric content of biological matter (Golley, 1961; Tyler, 1973). In animals these variations may be associated to food supply (Allen and Wootton, 1982), reproductive condition (Craig *et al.*, 1989; Wootton, 1990) and accumulation of energy reserves (Dawson and Grimm, 1980). Differences have also been measured in different parts of the body which increase or decrease in weight and/or energy during certain periods of the year (Dalberg, 1985).

The comparison test between averages of calorific contents of somatic and reproductive components of *S. borellii* and *P. maculatus* females at different stages of gonadal development differed significantly only between values obtained for gonads and this was due to low values for the resting stage of the ovaries. However, it was observed from graphs of averages and of samplings' reliability intervals that the caloric content of the liver does not show any significant difference between stages, even when the average value verified for the immature stage does not reach the smallest values of the other stages (Table 1 and Figure 1).

Nevertheless, the necessity of grouping muscle samples of immature individuals in a single pellet (because of their small size) for calorimetry may have probably influenced the result of the analysis, even though four immature females of both species were examined. The same was done to the liver samples of the imature female.

Average caloric values for samples of skeletal muscles did not vary significantly between stages, suggest that the muscle does not function as an accessory source of energy reserves either for gonadal development or for metabolism in both species. This is contrary to what was verified for some species (Eliassen and Vahl 1982; Dalberg, 1985) (Table 1 and Figure 1). This fact does not seem to be affected by the reproductive process, probably because of favourable environmental conditions (with regard to food availability) in which individuals occurred during the period under analysis (Lolis and Andrian, 1996; Andrian *et al*., 1994).

The difference verified in the graph (Figure 1) between mean caloric values of liver of individual adults (resting, maturing and mature) and immature ones suggests that the precursor process of vitellogenic production at the level of hepatocytes (liver) and, probably, the concentration of energy reserves (lipids and protein) begins in adults at the resting stage. As suggested by Allen and Wootton (1982) these reserves would be spent on gonadal development and/or mobilized by other reproductive events, such as migration. In the meantime, the contribution of the liver to the total energy reserves spent or reproduction is questioned by some authors. They report seasonal variations in this organ to a reduction in food supply verified in the winter or in the pre-reproductive period which causes changes in weight and in the lipid and protein composition of the liver (Dawson and Grimm, 1980).

The participation of other reserve sources in the organic maintenance of the species during the reproductive cycle (e.g. visceral fat) may be followed by the variation in the relative weight of these structures. With regard to the species under analysis, the mean visceral-somatic relationship observed in the different stages (Figure 2) showed, at the beginning of the reproductive activity, greater reserves of visceral fat. It seems that this fat is metabolized for gonadal maturation and/or development of other sexual characteristics. This fact is evidenced by the lower value of RVS for mature individuals and in the statistically significant difference of the other stages (Table 2).

Variations during the process of gonadal development in accumulated reserves in structures such as visceral fat were also observed in *Schizodon nasutus* and *S. platae* (Benemann, 1985), *S. intermedius* (Yabe and Bennemann, in press) and in the liver of *Pseudoplatystoma corruscans*

(Pimelodidae) (Marques, 1993) and *Sebastis flavidus* (MacFarlane *et al*., 1992). Variations were inversely proportional to gain in gonadal weight, suggesting that they were the possible sources of energy. However, in the case of *S. borellii* and *P. maculatus*, statistical analysis of data shows that the utilization of visceral fat as an energy reserve during the reproductive period seems to be more evident.

Studies on ovary microscopic anatomy (Chaves and Vazzoler, 1984), suggest that the increase in the gonadal caloric content of maturing individuals may be related to the process of lipid vitellogenesis at the oocyte level. Through ovarian development and, consequently, vitelline accumulation in ovaries, there is an increase in the values of gonadosomatic indices (GSI). Variation tendency in GSI described during the reproductive cycle for the species under analysis by Vazzoler and Agostinho (1991), follows the trend in caloric values of gonads (Figure 3).

Table 1. Calorimetric means (cal/g dry weight) of gonads, muscle and liver in the maturation stages. The Tukey's multiple comparison test (at a 5% level). The means with different letter (a or b) are significant.

	Muscle (cal/g)	Gonada(cal/g)	Liver (cal/g)
S. borellii			
immature	4946.30		4938.32
resting	5305.96 (a)	4850.26 (a)	5716.84 (a)
maturing	5235.25 (a)	6128.14(ab)	5686.70 (a)
mature	5344.16 (a)	6391.69 (b)	
P. maculatus			
immature	5168.72		5081.52 (a)
resting	5305.96 (a)	4909.53 (a)	5592.25 (a)
maturing	5235.25 (a)	5585.40 (a)	5569.70 (a)
mature	5276.48 (a)	6047.04 (a)	5500.29 (a)

Fluctuations in the energy reserves of some organs related to biological events such as the reproductive process and feeding activity, which influence the individual's physiology, may be indicated by variations in the values of the condition factor (K)(Le Cren 1951; Isaac-Nahum and Vazzoler 1983).Only IR for the immature stage was significantly different from that of the others. Juveniles consume relatively more food and transform all their availably useful energy into somatic tissues. In adults, energy is also diverted for the production of gonadal tissues (Tytler and Calow, 1985). This increases the total weight of the organism and is reflected in the K value.

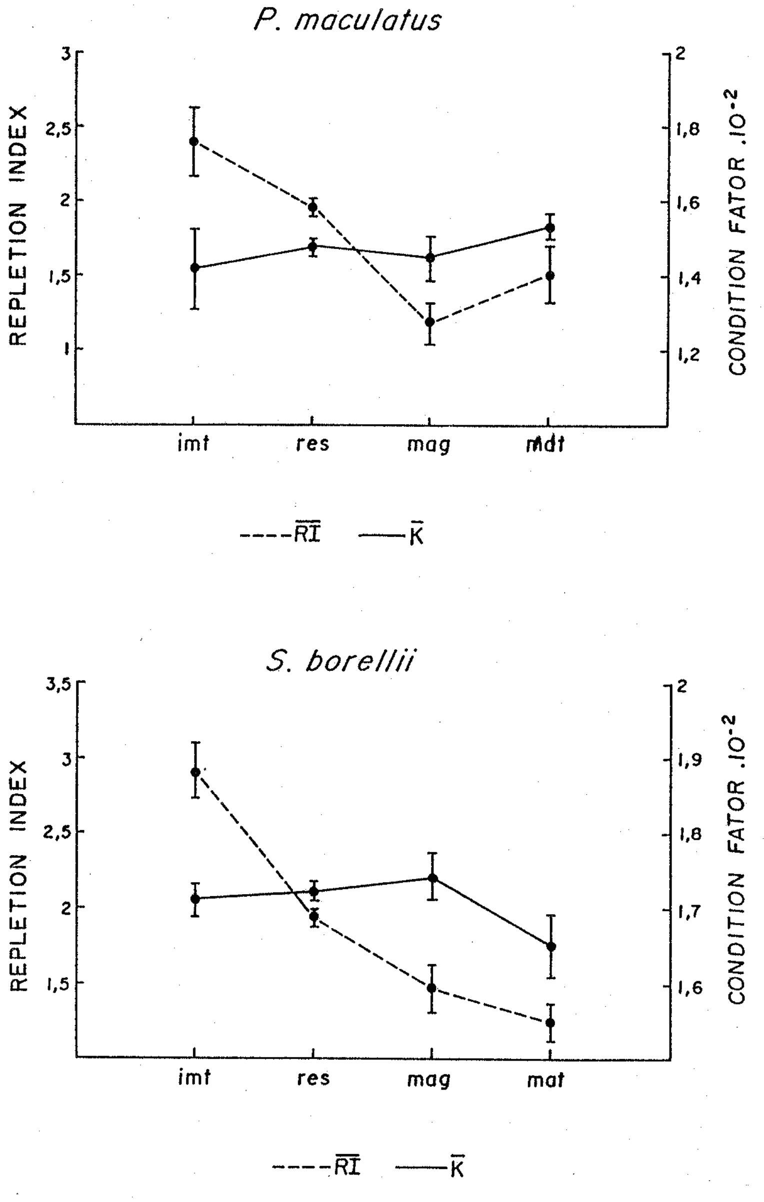

Figure 1. Average calorimetric values of the liver and muscle (cal/g dry weight) of females at immature (imt), resting (res), maturing (mag) and mature (mat) stages. Vertical bars show the standard error .

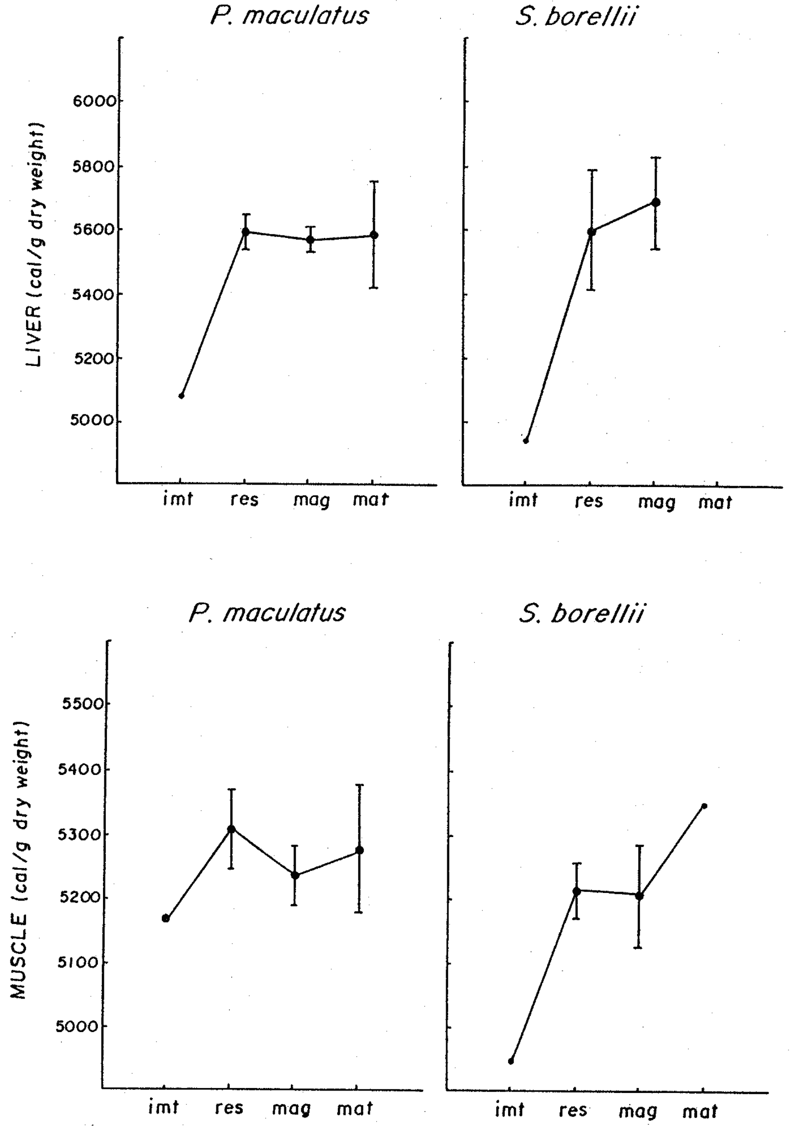

Figure 2. Average calorimetric values (cal/g dry weight) of gonads; gonadal-somatic relationship (%) (Source: Vazzoler and Agostinho, 1991) and visceral-somatic relationship (%) of females at immature (imt), resting (res), maturing (mag) and mature (mat) stages. Vertical bars on gonads calorimetric values show the standard error.

The K and RI values of resting individuals seem to be influenced by the fact that this stage includes individuals that are maturing for the first time (*P. maculatus* L50 = 14.4 cm and *S. borellii* L50= 14.6 cm according to Vazzoler and Agostinho 1991. L50 = first maturing mean length) and also those that are recovering for a new reproductive cycle and thus have different characteristics. According to Braga (1986), K values for juveniles which will integrate the adult population are justified because of the metabolically advantageous feeding of individuals in this phase. These values may also be the result of rapid growth, noted in individuals at the phase preceding maturity. According to Lowe-McConnell (1987) it is an adaptation that helps fish escape from their predators, since smaller fishes are more easily captured.

Analysing the reproductive cycle of the above-mentioned species by means of the graph in Table 2 and Figure 3, a decrease in IR values and insignificant variations in K values in during the process of maturation were noted in both species. These facts suggest that feeding activity decreases in adults but it does not seem to affect negatively the somatic growth.

A decrease in feeding activity in relation to an increase in body size follows the general pattern observed in fish. In adults, a great portion of assimilated energy is chiefly shared between metabolic and reproductive processes, with a reduction in the allocation for somatic growth and metabolism. In the case of juveniles, energy is allocated for metabolic expenditure and somatic production (Webb, 1978; Tytler and Calow,1985). Soares (1992) and Ngan *et al.* (1993) noted the same trend for species of demersal fish at the Ubatuba littoral. It seems that bigger-sized fish need a lesser quantity of feeding energy because of a decrease in their metabolic rates.

Some authors relate this phenomenon to variations in the feeding sources, principally with regard to temperate regions where an increase in feeding activity occurs in summer, with an increase in nutrient availability and during the reproductive peak (Tyler and Dunn, 1976). However, when the principal alimentary items found in the diet of *S. borellii* (leaves and stalks of riparian vegetation such as Poaceae and periphytic algae) and in that of *P. maculatus* (fish, animal remains, Chironomidae, Bivalvia and Odonata) are considered together with the fact that these same items are available independently of fluctuations in the fluviometric level, it must be admitted that food for these species is probably not a limiting factor for their bioenergetic equilibrium (Lolis and Andrian, 1996; Andrian *et al*., 1994).

Table 2. Mean RI, K and RGS for the maturation stages. The Tukey's multiple comparison test (at a 5% level). The means with diferent letter (a, b or c) are significant.

	RI (mean)	K (mean)	RGS (mean)
P. maculatus			
immature	2.39 (a)	1.41 (a)	3.58 (a)
resting	1.96 (b)	1.47 (a)	3.79 (a)
maturing	1.90 (b)	1.52 (a)	9.19 (b)
mature	1.52 (b)	1.44 (a)	44.2 (c)
S. Borellii			
immature	2.92 (a)	1.71 (a)	2.28 (a)
resting	1.93 (a)	1.72 (a)	4.47 (a)
maturing	1.47 (b)	1.74 (a)	23.37 (b)
mature	1.24 (b)	1.65 (a)	37.91 (c)

The maturation period of gonads in *S. borellii* and *P. maculatus*, noted in the high water period (October/November 1992) and with the flood peak (December 1992 and January/February 1993), indicates a closer relationship between fluctuations of the fluviometric level and the reproductive cycle than with changes in the feeding activity (Lowe-McConnell 1987; FUEM-PADCT/CIAMB 1993).

Changes in weight, chemical composition and energetic value of body parts during the reproductive cycle are highly efficient reproductive strategies verified in species of fish subjected to seasonal climatological conditions. These strategies aim at maximizing the adaptability of the species (Junk, 1985).

Some considerations may be proposed with regard to the influence the type of life of the species under analysis has on feeding activity and metabolism. Since *P. maculatus* is a short-distance migratory species (lateral migration) (Vazzoler, personal communication), principally found in lentic environments, with omnivorous habits and feeding on prey that impose greater energetic expenditure in capture and seizure, it may be suggested that this species needs a greater energy consumption. However, in *S. borellii*, its essentially herbivorous diet may be a determinant consumption rate reflecting a pattern of low efficient assimilation verified for herbivorous fish (Pandian and Wivekanandam, 1985). This also suggests a greater consumption rate, although vegetal feeding items do not need elaborate mechanisms of capture.

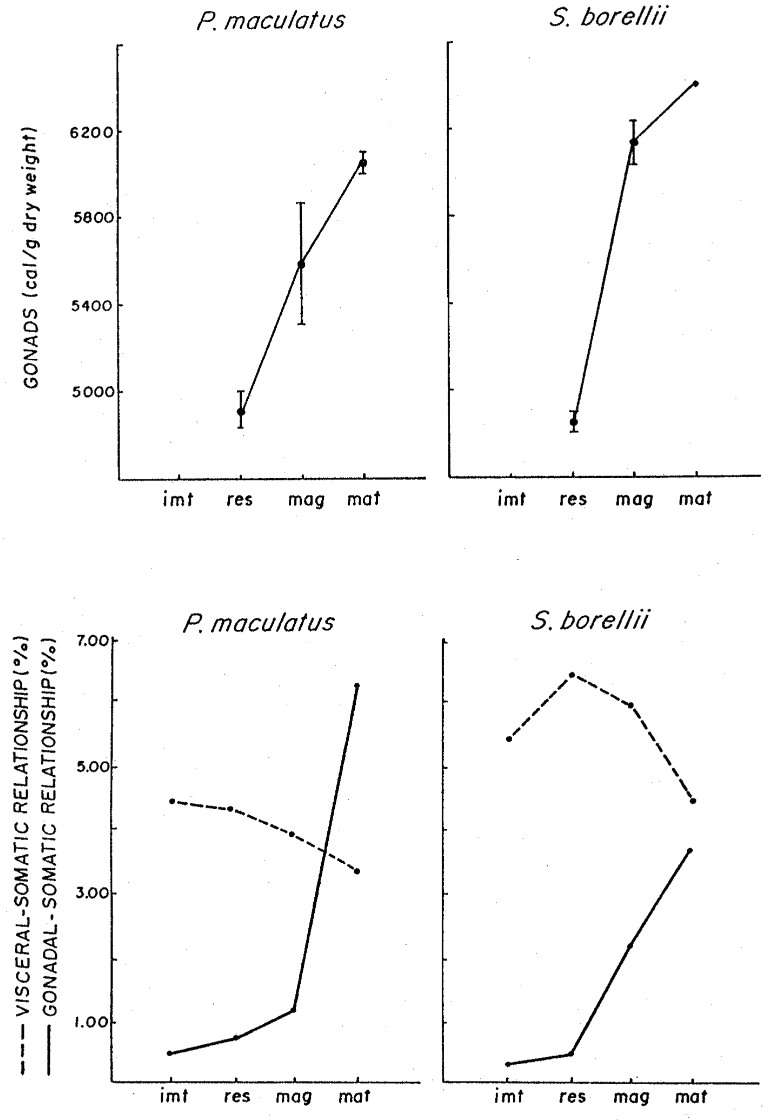

Figure 3. Average values of the condition factor (- $\overline{K}$) and repletion index (- -$\overline{IR}$) of females in immature (imt), resting (res), maturing (mag) and mature (mat) stages. Vertical bars indicate the standard error of the sample.

In this context, the effect of food supply on the relative growth rate of somatic and reproductive components of the body is extremely interesting. This is due to its relevance for the understanding of strategies in energy and material sharing among body components (Tytler and Calow, 1985). Generally these strategies are related to patterns of the life cycle. The species *Brevoortia tyrannus*, studied by Dalberg (1985) because of its migratory habits, shows a depletion in its reserves of visceral and body fats accumulated during the period of greater feeding intensity and at the beginning of the maturing process.

Tyler and Dunn (1976) found that in situations of scanty food supply, females of *Pseudopleuronectis americanus* maintain the somatic content of the body, probably at the expenses of the ovaries wich do not enter the process of vitellogenesis and of the liver that diminishes in size. In the case of females of *Gasterosteus aculeatus* the pattern weight change of ovaries seems to be independent of food supply (Allen and Wootton, 1982). Ovary growth is maintained during the reproductive cycle even under unfavourable feeding conditions, while the somatic and liver components stabilize themselves or decrease. These authors suggest that during the reproductive period, the quantity of food is crucial in the determination of events. If the energy demand associated with reproduction is higher than the energy supply produced from available food, the use of accumulated reserves will be necessary (Eliassen and Vahl, 1982).

CONCLUSIONS

Results revealed well-defined patterns in the bioenergetic allocation of females of *S. borellii* and *P. maculatus* during the reproductive period. Since significant variations in the energetic content of reproductive components related to the process of vitellogenesis occur even in the face of a decrease in feeding activity of adults and without any detriment to somatic reserves (skeletal muscle and liver) or to the somatic growth rate, we suggest that in this phase of the reproductive process the visceral fat functions as an accessory reserve source which guarantees the gonadal development and the maintenance of the other components.

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