

THE FOOD HABITS OF THREE ALLOCHTHONOUS FEEDING CHARACOIDS IN FRENCH GUIANA

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Some life history traits of certain native freshwater fishes of French Guiana, as well as their local market values, make them potential candidates for aquaculture (Boujard *et al.*, 1988). Such is the case, for instance, for *Leporinus friderici* (Bloch, 1794) (Characoïdei, Anostomidae) and *Myleus rhomboidalis* (Cuvier, 1817) (Characoïdei, Serrasalminidae). Therefore, the breeding-cycle and growth characteristics of both species were studied and the results published (Le Bail *et al.*, 1986 ; Lecomte *et al.*, 1985, 1986 ; Meunier *et al.*, 1985 ; Rojas-Beltran, 1986). The present paper deals with the food habits of *L. friderici*, *M. rhomboidalis* and *Myleus ternetzi* (Norman, 1929) in their natural environment. The last two species are very close to each other from a phylogenetic point of view, and are sympatric.

So far, most studies of the food habits of South American Characoids were carried out in Brazil. Such was the case for *Brycon* spp. (Menezes, 1969), some scale-eating fishes (Roberts, 1970), *Colossoma bidens* (Honda, 1974), *Leporinus copelandii* (Nomura, 1976), *Tripopterus* spp. (Almeida, 1980), a few Anostomidae (Santos, 1981), *Astyanax bimaculatus* (Souza & Andrade, 1982) and *Hemiodus* spp. (Holanda, 1982). Other investigations dealt with fish guilds in specific environments, such as the Rupununi savanna in Guyana (Lowe-McConnell, 1964), the Redondo lake (Marlier, 1968), some small rivers near Manaus (Knöppel, 1970), the Arpuana area (Soares, 1970) and the Madeira river (Goulding, 1980).

Unfortunately, very little is known on the diet of the three species previously mentioned, though they are widespread in the neotropical region. Twenty one stomach contents of *L. friderici* were studied by Goulding (1980) and 68 by Santos (1982), while Ferreira (1984) was only able to examine 5 stomachs of *M. ternetzy*.

From a more general point of view the trophic relationships of primary consumer fishes in the neotropical region were discussed by Lowe-McConnell (1979, 1987), Goulding (1980) and Prejs & Prejs (1987). These authors emphasized the fact that most of the vegetarian species fed on allochthonous materials : fruits, leaves and arthropods fallen from the forest canopy. Their dentition is indeed

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often adapted to such food items (Géry, 1977). According to Gottsberger (1978), and Goulding (1980), these vegetarian fishes might also act as seed dispersers.

MATERIALS AND METHODS

Fishes were collected at two distinct sites in French Guiana, i.e. in the Approuague river between Saint-Esprit and the Athanase rapids (52° 20' W ; 4° 05' N), and the Sinnamary river at Petit-Saut (53° 05' W ; 5° 10' N). Both rivers are somewhat brackish because of their low pH and conductivity (Sioli, 1967).

A total of 236 fishes were caught between August 1981 and June 1983, and from June 1986 to May 1987, during 29 sampling sessions of four days each. Trammel nets 25 to 50 m long, with a mesh size ranging from 10 to 60 mm (between knots) were used, as described previously (Boujard et Rojas-Beltran, 1988a). The nets were set during the whole diel cycle. At first, fishes were removed from the nets twice a day (at 07.00-09.00 and 17.00-19.00 hours). As it was later observed that nearly all fishes were caught during the night whatever the season, nets were examined only in the morning during the last year of our study.

In order to allow comparisons, some of our data were pooled. Thus the stomach contents of the few *L. friderici* collected in the Approuague river (n = 14) were combined with those from the Sinnamary river. All available information was allocated to the following major time periods :

— the « dry season » (DS), from July through November, when the river stays in its channel ;

— the « short rains » (SR), which last from December through February. During this period, the level of the river is higher than during the dry season, the river often leaving its bed for short periods ;

— the « rainy season » (RS), which lasts from April through June. At that time of the year, floods last for several consecutive days, and fishes can then be able to enter the « flooded forests » (Goulding, 1980).

Between-season comparisons of the fish diets is justified in our case, as our fish catches were carried out throughout the year at the same sites, mostly during the night and close to the banks, where most of the available food was to be found (Boujard et Rojas-Beltran, 1988b).

The data collected during the « short dry season », in March, were not analysed for three reasons : i) this season is usually very short, ii) its beginning is unpredictable, and iii) few fishes were collected.

The stomach contents were weighed and the volume of each food item recorded. Hence, the study of the food habits of our fishes were based on 3 criteria : stomach fullness, frequency of occurrence of a given item, and the proportion of each food item :

— stomach fullness is defined as : $r_i/r_{i_{max}}$; r_i being the fresh weight of the stomach contents of the « i » th individual divided by its somatic fresh weight. This index ranges from 0 to 1. This fullness value is compared statistically for each season using the Kruskal-Wallis one-way analysis of variance by ranks (Dagnelie, 1975) ;

— the frequency of occurrence (in %) is defined as the percentage of stomachs in which each food item is found :

— the proportion of each item (in %) is defined as the total fresh weight of an item divided by the total fresh weight of all the stomach contents.

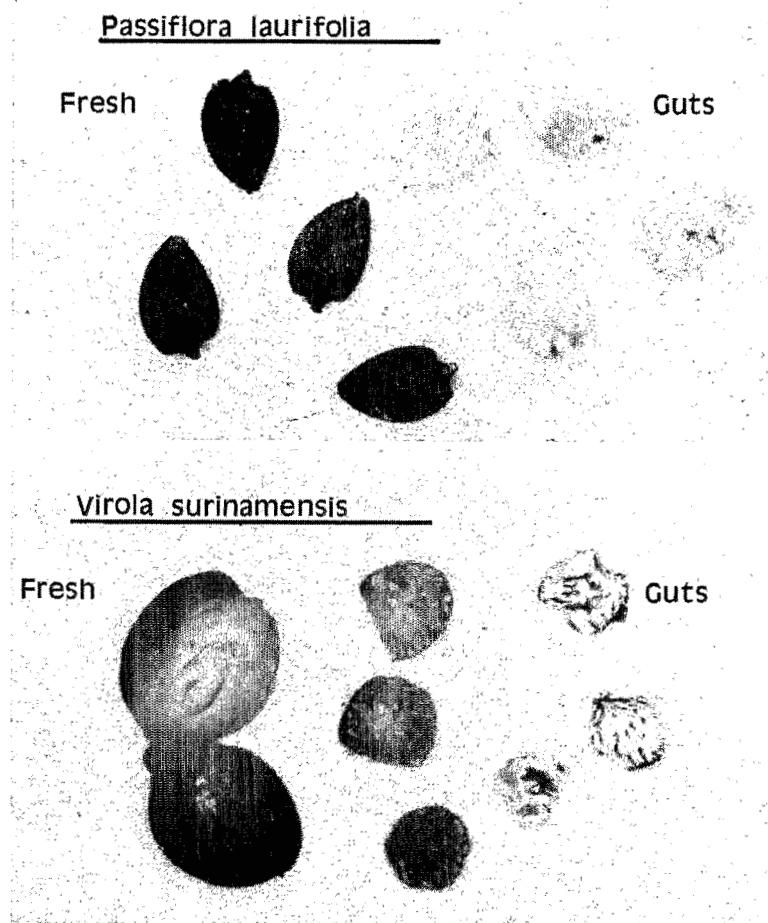


Figure 1. — Comparison between some seeds found in the gut contents and fresh seeds.

Whole or masticated seeds collected were compared with specimens in the ORSTOM herbarium (Cayenne) for identification (Fig. 1).

RESULTS

M. ternetzi stomachs had a mean fullness of 37 %, without any significant seasonal variation. The ingested food was made exclusively of allochthonous plant material. The proportion and frequency of occurrence of the leaf fragments accounted for the main variations in the stomach contents (Table I, Fig. 2).

TABLE I

Frequency of occurrence of the various food items for each fish species, according to the season.

RS. = Rainy Season ; DS = Dry Season ; SR = Short Rains ;
N = number of fish stomachs examined.

Species Season	<i>M. ternetzi</i>			<i>M. rhomboidalis</i>			<i>L. friderici</i>					
	Sinnamary			Sinnamary			Approuague			Sinn. + Appr.		
	DS.	RS.	SR	DS.	RS.	SR	DS.	RS.	SR	DS.	RS.	SR
Seeds	14	37	56	37	73	22	80	100	73	.	48	27
Flowers	14	.	19	19	6	.	5	.	13	10	3	20
Fruits	.	.	37	.	6	.	.	.	7	.	21	.
Leaves	100	100	75	31	6	22	17	9	27	5	21	27
Fragments	.	.	.	6	3	11	10	14	13	5	24	20
Podostemonaceae	.	.	.	56	15	33	5	.	20	.	.	.
Animal material	.	.	.	25	39	22	17	54	27	5	45	27
Occurrence of plants	100	100	100	100	79	89	82	100	93	15	70	66
N	7	8	10	16	33	7	40	22	13	20	33	10

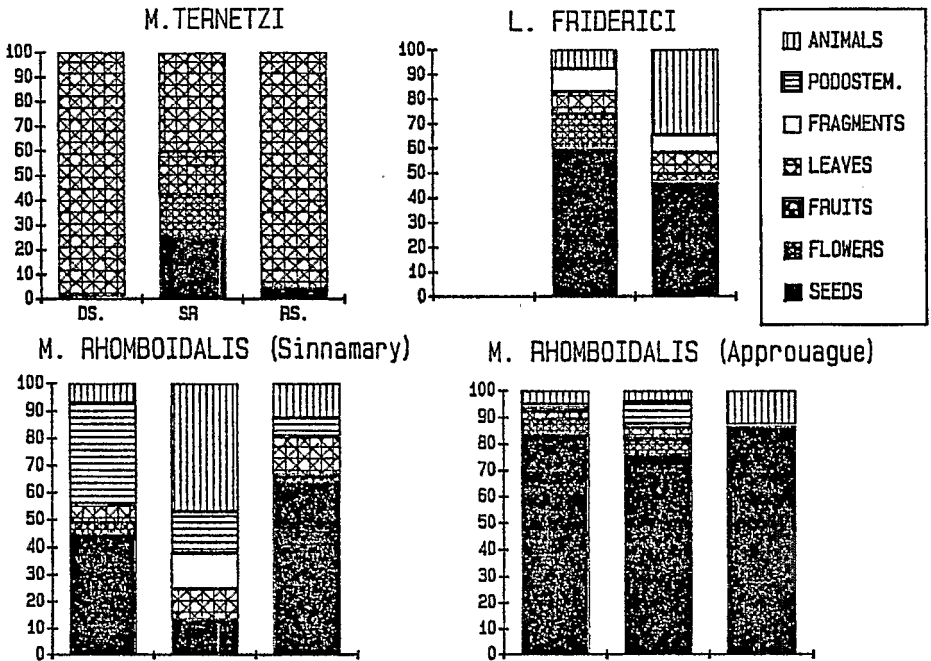


Figure 2. — Total percentage of each item per season (DS = dry season ; SR = short rainy season ; RS = rainy season).

However, some differences between the leaves ingested during the rainy and the dry season were noticed. During the dry season fishes could only reach drifting leaves, but during the rainy season, *M. ternetzi* browsed on the leaves of the flooded riverine vegetation, particularly those of *Inga meissneriana* which is widespread at the sampling sites, and *Cydista aequinoctialis* (Fig. 3). *M. ternetzi* also often ate seeds, which represented only a small part of their stomach contents, except during the short rainy season when their diet was more varied.

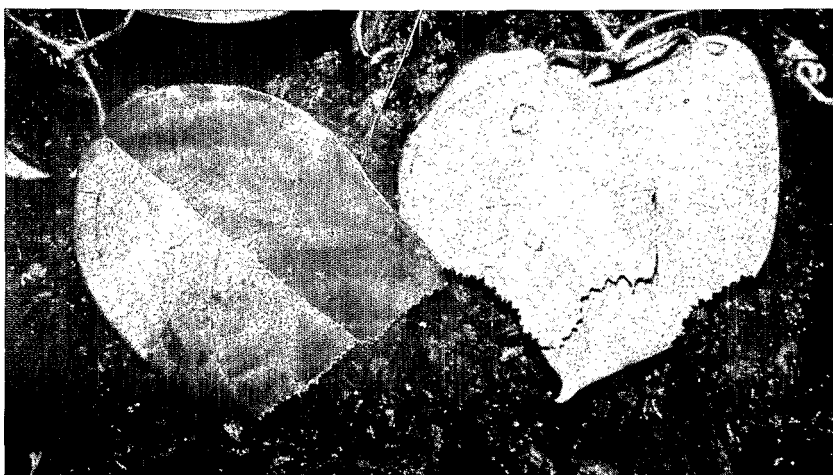


Figure 3. — Leaves of *Cydista aequinoctialis* (L.) Miers, a BIGNONIACEAE « grazed » by *Myleus ternetzy* (M.F. Prévost phot.).

No significant statistical differences in stomach fullness were noted between the *M. rhomboidalis* of the two rivers sampled. However, their mean fullness was significantly higher during the rains (20 %, n = 55) than during the dry season (13 %, n = 56) (χ^2 , P < 0.05). Seeds were the major item of the diet, both in frequency of occurrence and in proportion. The animal items were less common and the Podostemonaceae even scarcer. Flowers, fruits, leaves and fragments of plant material represented only a minor part of the stomach contents. No seasonal variation in the stomach contents of fishes from the Approuague river was noted. However, seeds accounted for the major part of the diet in the Sinnamary river during the rainy season, to be replaced by Podostemonaceae during the dry season. It is interesting to note that the local name of the Podostemonaceae *Mourea fluviatilis* is « Salade Coumarou » and that « Coumarou » is also the vernacular name of *M. rhomboidalis*. During the short rains, animal items were the most abundant.

No difference was noted between the two rivers in the proportion of animal material eaten. Throughout the year 60 % of this material was made of allochthonous species (beetles, caterpillars, termites, locusts, unidentified arthropods and mammalian excrement) and 40 % were made of autochthonous prey (shrimps, crabs, copepods, fish scales).

Forty-five different kinds of seeds were found in the stomach contents of *M. rhomboidalis*, and 16 of them were identified (Table II). During the dry season, most of the seeds eaten were those of the palm *Euterpe oleracea*, and in the rainy season those of *Macrobium* sp. and cf. *Taralea oppositifolia*, both in terms of frequency and proportion. The ingested seeds were more varied during the rains than during the dry season, and the number of unidentified seeds was correspondingly greater.

TABLE II

Proportion (and frequency of occurrence) of the various seed species found in the stomach contents of M. rhomboidalis.

DS. = Dry Season ; SR = Short Rains ; RS. = Rainy Season ;
App. = Approuague river ; Sinn. = Sinnamary river.

Species and FAMILY	DS.		SR		RS.	
	App.	Sinn.	App.	Sinn.	App.	Sinn.
<i>Euterpe oleracea</i> Mart. ARECACEAE	49(25)	69(2)	2(2)			
<i>Strychnos</i> sp. LOGANIACEAE	7(3)					
<i>Diospyros guianensis</i> Guerke EBENACEAE	2(1)					
<i>Carapa</i> cf. <i>guianensis</i> Aubl. MELIACEAE	2(1)		6(1)			
<i>Inga</i> spp. MIMOSACEAE		2(1)		(1)		
<i>Coccoloba</i> sp. POLYGONACEAE	4(2)		1(1)			1(1)
<i>Posoqueria longiflora</i> Aubl. RUBIACEAE	1(1)	1(1)	3(1)			2(1)
cf. <i>Taralea oppositifolia</i> Aubl. PAPILIONACEAE	1(2)		27(5)		9(3)	
Poaceae indet. POACEAE	1(1)					5(2)
<i>Oenocarpus bacaba</i> Mart. ARECACEAE			2(2)			
<i>Passiflora laurifolia</i> L. PASSIFLORACEAE			1(1)			
<i>Crudlia oblonga</i> Benth. CAESALPINIACEAE			6(1)		3(1)	
Cyperaceae indet. CYPERACEAE						7(2)
<i>Virola surinamensis</i> (Rol.) Warb. MYRISTICACEAE		1(1)	14(2)	(1)	2(1)	5(5)
<i>Macrobium</i> cf. <i>bifolium</i> (Aubl.) CAESALPINIACEAE	1(1)	4(1)	24(2)		23(7)	8(4)
Unidentified seeds						
Proportion (and frequency of occurrence)	33(10)	25(4)	15(5)	(2)	63(13)	71(17)
Number of seed species encountered	17	9	14	3	22	20
Total number of fishes studied	40	16	13	7	22	33

The fullness values of *L. friderici* stomachs were very low in the dry season (2 %, n = 20), significantly lower than during the rains (χ^2 , P < 0.01), and the number of empty stomachs was very high (13/20 = 65 %) at that time of the year.

L. friderici mostly feed during the rainy season (stomach fullness = 21 %, n = 33), mainly on seeds and, to a lesser extent, on animal material, leaves and plant fragments. All the plant material ingested was allochthonous. Few seeds

were identified (*Gustavia augusta*, *Carapa* sp, *Virola surinamensis*). The low frequency of occurrence of these seeds in the stomachs did not allow a detailed comparison with *M. rhomboidalis*. However, *G. augusta* was not found in the stomach contents of the latter species.

The animal material consumed by *L. friderici* was made of ants, termites and unidentified arthropods. Freshwater animals were found on only three occasions : one small fish during the dry season, one shrimp during the short rains, and one crab during the rainy season. The volume was negligible in each case.

DISCUSSION

Between-species comparison

M. ternetzi is strictly folivorous, and eats exclusively allochthonous food. Both *L. friderici* and *M. rhomboidalis* are omnivorous with a preference for plant material, more particularly seeds. *L. friderici* feeds nearly exclusively on allochthonous food. This is not the case with *M. rhomboidalis* which also grazes freshwater plants and eats a variety of freshwater animals. Goulding (1980), among others, has pointed out that this preference for allochthonous food (fruits, seeds, leaves, terrestrial arthropods) is common among Characoids living in poor, plankton free, neotropical waters.

According to Ferreira (1984), *M. ternetzi* fed only on plant material in a dam-lake (Para, Brazil). However, this author did not distinguish between different kinds of plants, though he mentions algae in some stomach contents.

Santos (1982) studied the food habits of four species of Anostomidae, including *L. friderici*, in Lake Janauaca (Amazonas, Brazil). He observed omnivorous food habits in this species whose diet included, in decreasing order of importance, plant fragments, Ephemeroptera larvae, Diptera and other Arthropods, various plant materials, fruits, seeds, fish scales, Bryozoa and Mollusca. These results, somewhat different from ours, demonstrate the plasticity of the food habits of *L. friderici*. The results of the study carried out by Goulding (1980) in the Rio Machado (Brazil) did not differ much from our own : this author examined 21 specimens of *L. friderici*, among which 11 had ingested fruits, 3 whole fishes and 2 scales.

The comparison of our results with those of the other authors shows that there is a certain flexibility of the food habits of the species concerned, as already mentioned in connection with the seasonal variations of the diet. This flexibility, however, concerns only the proportion of the various food items. No major difference of food categories was observed.

The importance of seeds

Seeds are of major importance in the diet of *M. rhomboidalis* and *L. friderici*. The occurrence of those of *Euterpe oleracea* in the diet of *M. rhomboidalis* is particularly interesting. Seeds or fragments of seeds of this palm are easy to identify and cannot be confused with others : the albumen presents a radial fibrous structure, and the invaginated tegument only allows a characteristic

fractioning into little claviform elements. The frequency of occurrence of these seed fragments is very high and quasi-exclusive during the dry season, despite the fact that the main period of production of *Euterpe oleracea* seeds is during the short rains (Grenand, 1980). This situation can only be explained by an active selection of this kind of seed by *M. rhomboidalis* at that time of the year, the seeds of *E. oleracea* not being consumed during the rainy season, even if they are more numerous (Sabatier, 1985).

Goulding (1980) considers that some Amazonian plants are dispersed by fish (ichtyochoy). However, among the seeds found in the stomachs we studied, some of them were clearly adapted to be dispersed by floating. Those of *Crudia oblonga*, for example, keep some air between their two cotyledons. In this case, fishes cannot be considered as the sole « seed dispersers ». Others are short-lived and germinate quickly (e.g. *Inga* spp., *Carapa* spp. and *Virola* spp., unpublished) and are killed by flooding. Only the seeds of *Passiflora laurifolia* were found intact in the stomachs studied, and this plant might therefore be potentially dispersed by fish. However, we know nothing about the germination potential of these seeds after their transit through the fish digestive tract, or a long stay in the water. Hence, our limited observations do not allow us to entirely support Goulding's conclusions.

Seasonal variations

The food habits of *M. ternetzi* are most varied during the short rains, when this fish enriches its usual leaf diet with many seeds, flowers and fruits. At the same time *M. rhomboidalis* consumes less seeds (in the two rivers studied) and more animal material (Sinnamary) or Podostemonaceae (Approuague). It is also at that time of the year that breeding reaches its peak (Le Bail *et al.*, 1986) and the catches per unit effort of *M. ternetzi* their maximum (Boujard et Rojas-Beltran, 1988b). Moreover, it is also during the short rains that many woody species produce the most fruits (Sabatier, 1985).

The food habits of the three species studied vary seasonally. During the dry months *M. ternetzi* feeds mainly on leaves, while *M. rhomboidalis* mostly consumes seeds, and *L. friderici* feeds on both seeds and allochthonous animals. It is also at this time of the year that stomach fullness reaches maximal values, whereas large fat deposits are noticeable only at the end of the rainy season. During the dry season there is no longer any overlap between the diets of the three species, since *M. ternetzi* feeds on dead leaves, *M. rhomboidalis* on seeds and Podostemonaceae and *L. friderici* eats less or may even go without food.

Feeding strategies

There is still some disagreement between authors on the meaning of the seasonal dietary changes of neotropical fishes. In their study of the food habits of 9 sympatric species of fish in Costa Rica, Zaret and Rand (1971) showed that there was no interspecific competition during the dry season (when food was scarce), and concluded that their findings entirely agreed with the competitive exclusion principle. On the other hand, Lowe-McConnell (1964, 1979), Goulding (1980) and Prejs and Prejs (1987) conclude that it is during the rainy season, when there is an abundance of food, that food specializations are the most marked.

The three species we studied clearly show some seasonal differences between their food habits. These differences are easy to explain. During the rainy season the food resources are abundant and varied, and the observed dietary differences can be explained by the competitive exclusion principle, each species selecting different kinds of food. The abundance of food at that time of the year also allows some overlap between the various dietary spectra. The situation is very different during the dry season, when food is scarce. Then the fishes have to rely on a survival strategy, and eat what is left available. *M. ternetzi* has to make do with foods of low nutritive value, and the high proportion of empty stomachs among *L. friderici* testifies that a number of individuals are starving.

CONCLUSION

Few studies are available on the food habits of non-carnivorous neotropical fishes living in seasonal freshwater environments. Nevertheless, some of their general characteristics have been emphasized by Lowe-McConnell (1987) and Prejs and Prejs (1987).

The food of these species is often mainly allochthonous. Access to such food resources is often made possible by special morphological adaptations of the fish species concerned. Moreover, such specialized diets are possible only when the resources are particularly abundant. In this case the food spectrum widens, and some overlap becomes possible between coexisting species (Blondel, 1987). The season of food abundance alternates with a dry season when food resources may decrease drastically, causing the fish to live on the fat deposits stored during the rainy season, or to feed on plant fragments of little nutritive value. In this case, the animals may eat more food of low caloric value in the dry than in the rainy season (Prejs and Prejs, 1987). Therefore the dry season corresponds to the « limiting » period of the year from a demographic point of view, because of restricted access to food resources due, at least in part, to the spatial reduction of the habitat. This season is rightly called the « physiological winter » by Lowe-McConnell (1967).

Recent skeletochronological studies have shown that the fish we studied in French Guiana (*L. friderici* among others) present two annual growth cycles (Lecomte *et al.*, 1985, 1986; Meunier *et al.*, 1985), like some African tropical freshwater fish (Garrod, 1959; Okedi, 1969; Bruton and Allanson, 1974; Blake and Blake, 1978, Robben and Van den Audenaerde, 1984). Each year, two periods of fast growth alternate with two periods of slower growth and these periods can be correlated respectively to the wet and dry seasons.

The strong seasonality of the environment of our fishes also seems to determine their reproductive cycle. Lowe-McConnell (1979) distinguishes between two main categories of riverine fish communities, the « total spawners » which spawn just prior to or during the floods, and the « partial spawners » which spawn several times during the rainy seasons.

Junk (1985) demonstrated that all spawners he studied in Amazonia were accumulating fat stores during flooding, and ceased feeding, or fed less during the dry periods. He also noticed that the gonads develop during the dry seasons and that the energy used for their development probably comes from the mobilisation of the fat stores.

For at least a few of the fish species we studied in French Guiana, a strong seasonality of feeding, growth, and spawning was observed. We know nothing of

the endogenous or exogenous character of these rhythms, or of their « synchronizer(s) ». In temperate zones, seasonality is commonly linked with variations in temperature or photoperiod. In tropical latitudes climatic seasonality is less marked and other factors like flooding and food availability may be involved, at least for primary consumers.

SUMMARY

The food habits of two distinct populations of *Leporinus friderici*, *Myleus rhomboidalis* and *Myleus ternetzi* were studied in French Guiana. Stomach contents were collected during three of the four seasons characteristic of this neotropical area, i.e. the rainy season, the dry season, and the short rains.

M. ternetzi is strictly vegetarian and feeds nearly exclusively on drifting leaves during the dry season, and attached leaves during the floods.

M. rhomboidalis feeds mainly on seeds of *Euterpe oleracea* during the dry season, and eats various kinds of seeds and arthropods during the rainy season.

L. friderici appears to be the most omnivorous of the 3 species, and feeds mainly on seeds and arthropods in the rainy season, whereas it seems to fast during the dry season.

These results also show that these fishes exhibit specific food preferences during the rainy season, whereas survival strategies become preponderant during the dry season.

RÉSUMÉ

Une analyse des contenus stomacaux de *Leporinus friderici*, *Myleus rhomboidalis* et *M. ternetzi* a été réalisée à partir d'échantillons provenant de deux peuplements distincts de Guyane Française, prélevés aux différentes saisons caractéristiques de cette région néotropicale : la grande saison des pluies, la grande saison sèche et la petite saison des pluies, l'étude du régime alimentaire en petite saison sèche ayant été volontairement omise.

M. ternetzi est un herbivore strict, qui consomme quasi-exclusivement des feuilles prélevées sur les arbres pendant les inondations de la saison des pluies, et des feuilles flottant à la dérive en saison sèche.

M. rhomboidalis se nourrit surtout de graines d'*Euterpe oleracea* en saison sèche. Cette espèce diversifie son régime alimentaire en saison des pluies en consommant plusieurs espèces de graines et des arthropodes.

Le régime de *L. friderici* présente un caractère omnivore marqué. Ce poisson se nourrit essentiellement en saison des pluies et consomme alors des graines et des arthropodes tombés des feuillages.

Ces résultats sont interprétés comme exprimant les préférences alimentaires de ces espèces en saison des pluies, alors qu'en saison sèche se développent des stratégies de survie.

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