

DENTAL DEVELOPMENT AND ONTOGENETIC DIET SHIFTS OF *Roeboides paranensis* Pignalberi (OSTEICHTHYES, CHARACINAE) IN POOLS OF THE UPPER RIO PARANÁ FLOODPLAIN (STATE OF PARANÁ, BRAZIL)

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(With 5 figures)

ABSTRACT

Species of the characid genus *Roeboides* are known for their habit of tearing off and ingesting scales from other fishes. Specimens of *Roeboides paranensis* were taken monthly from March 1992 through February 1993 in five pools of the upper Rio Paraná floodplain and in one site in the Rio Paraná itself, with the aim of relating the dental development to ontogenetic diet shifts. Between 15-22 mm SL, fish had teeth with hypertrophied bases (mammiform) that moved to the outside of the mouth in both maxillas. During ontogeny, the diet shifted, with the smallest individuals eating more microcrustaceans and the larger ones eating more scales. Lepidophagy is non-obligatory, because the ingestion of insects and other invertebrates occurred at all sizes. Spatial variation in diet was large, however diet similarity was great for *Roeboides* from three floodplain pools that had similar proportions of the main diet categories.

Key words: *Roeboides paranensis*, dental development, diet shifts, Rio Paraná.

RESUMO

Desenvolvimento dentário e variações ontogenéticas na dieta de *Roeboides paranensis* Pignalberi (Osteichthyes, Characinae) em lagoas da planície de inundação do alto rio Paraná (Estado do Paraná, Brasil)

Espécies de caracídeos do gênero *Roeboides* são conhecidas por seu hábito de arrancar e ingerir escamas de outros peixes. Exemplares de *Roeboides paranensis* foram capturados mensalmente de março de 1992 a fevereiro de 1993 em cinco lagoas da bacia do alto rio Paraná e em um ponto na calha do rio Paraná, com o objetivo de relacionar o desenvolvimento dentário com alterações ontogenéticas na dieta. Entre 15-22 mm de comprimento-padrão, os peixes apresentam dentes com bases hipertrofiadas (mamiliformes), que migram para fora da boca em ambas as maxilas. Durante o desenvolvimento, a dieta altera-se, com os exemplares menores ingerindo mais microcrustáceos e os maiores alimentando-se mais de escamas. A lepidofagia nessa espécie é facultativa, pois a ingestão de insetos e outros invertebrados ocorre em exemplares de todos os tamanhos. Variações espaciais na dieta foram marcantes, entretanto os maiores valores de similaridade em três das lagoas estudadas devem-se à semelhança nas proporções do alimento principal.

Palavras-chave: *Roeboides paranensis*, desenvolvimento dentário, alterações na dieta, rio Paraná.

INTRODUCTION

Species of the genus *Roeboides* are widely distributed in the Neotropical region, and are known for their habit of tearing off and ingesting scales from other fishes, a behavior termed lepidophagy. This type of mutilating predation is also known in many species of the Characoidei (Géry, 1977), and is more frequent in tropical species (Sazima & Machado, 1982).

Feeding habits can be understood better by examining functional morphology. Intra-specific shifts in diet have been documented for many fishes, and shifts often are accompanied by changes in morphological characteristics. Roberts (1967) commented that in many species, the morphology of the functional dentition differs profoundly between juveniles and adults. Like other species of the genus, *Roeboides paranensis* Pignalberi, 1975, the “dentado”, has external teeth (Miquelarena, 1986) that are used to remove scales.

In the present work, we establish through examination of the diet and the extent to which this species makes use of its morphological attributes to obtain food (scales). We also evaluate possible ontogenetic and spatial changes in the composition of its food.

MATERIAL AND METHODS

The area studied is located on two islands in the upper Rio Paraná, in the region of Porto Rico in the northwestern part of the State of Paraná. In

this stretch, the river may be as much as 14 km wide, with an extensive floodplain on its right margin. Five pools were sampled in this investigation (Fig. 1): Pontal, Canal do Meio, Pau Velho, Porto Rico, and Três Amigos; and one station in the Rio Paraná. These pools vary in size, position and degree of connection with the main channel of the Rio Paraná according to its hydrological regime. Some of them remain in contact with the main channel throughout the year. The pools also differ in substrate, bank vegetation, exposure to light, aquatic vegetation, and cover (Okada, 1995).

Fish samples were taken monthly in the five pools from March 1992 through February 1993. In the Rio Paraná, a single sample was taken in November 1992, to obtain larger individuals in order to complement the analysis.

Specimens were captured using 20 m-long seine nets (10 mm meshes), measured and weighed, fixed in 10% formalin, and preserved in 70° GL alcohol. Ten specimens of each size class (19-34, 35-50, 51-66, and 67-82 mm SL) were used for dental descriptions.

The teeth were counted and a specimen of each size class was drawn using a drawing tube attached to a dissecting microscope, and another specimen cleared and stained according to the technique of Taylor (1967) and Dingerkus & Uhler (1977), modified by Potthoff (1984), to verify the presence or absence of tooth buds. The contents of 744 stomachs were analyzed by the frequency of occurrence method (Hynes, 1950), and the items identified to lowest possible taxonomic level.

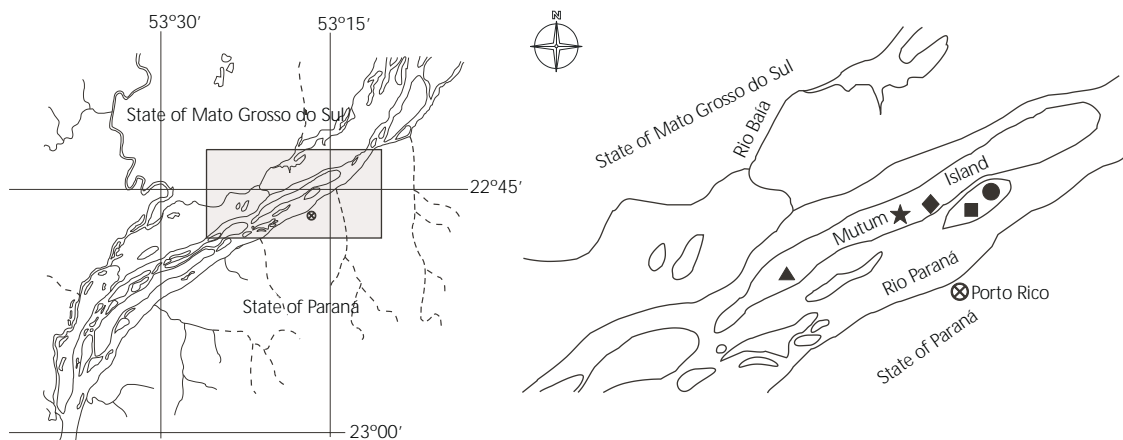


Fig. 1 — Sampling locations (▲: Três Amigos; ★: Porto Rico; ◆: Pau Velho; ■: Canal do Meio; ●: Pontal).

For comparison of tooth morphology with diet, the items were grouped as: microcrustaceans, insects, scales, and other.

The diet similarity in the different pools was obtained by applying a grouping analysis to a matrix of 22 (food categories) X 6 (sites) using Euclidean distance and UPGMA (unweighted pair-group average) as the linking method.

RESULTS

Dental development

The premaxillary, maxillary and dentary teeth in the four developmental stages considered, are shown in Fig. 2 and described as follows:

Premaxillary: In the smallest individuals (up to 22 mm), the anterior region, next to the symphysis has the normal aspect of other Characinae (e.g. *Charax* spp., Characidae), with the mouth terminal. Up to this length, individuals possess a series of conical teeth inside the mouth, one or two of these being larger and located next to the symphysis, and three to nine smaller, more lateral teeth. As the fish develops, gradually the anterior region of the bone begins to project forward, becoming more protuberant. Concomitantly, some of these teeth move outside the mouth. The process is initiated by one tooth of the middle region, followed by one nearer the articulation of this bone with the maxillary, and finally, by a tooth next to the symphysis.

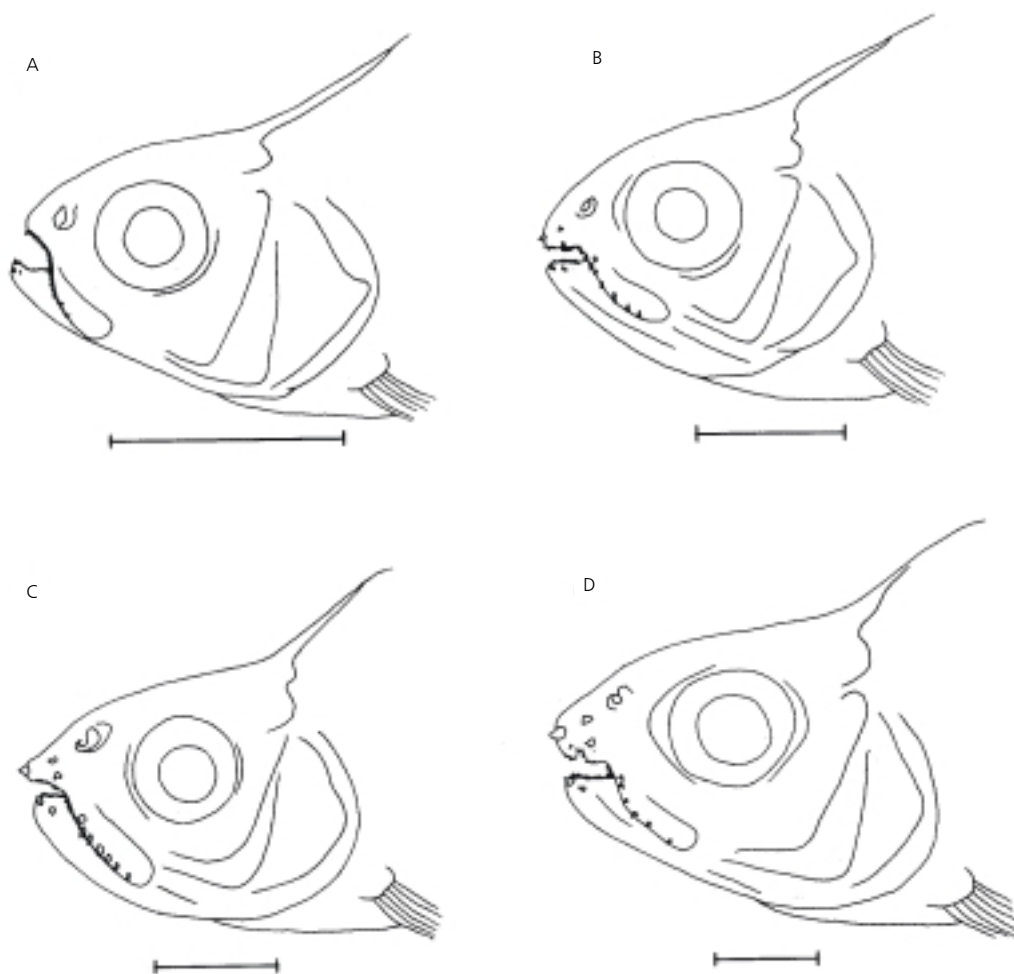


Fig. 2 — Dental morphology of *Roebooides paranensis* at different sizes: A = 31.6 mm; B = 45.0 mm; C = 57.0 mm; D = 73.8 mm. Scale bar: 50 mm.

These large teeth, with hypertrophied bases (mammiform), appear larger and more exterior as the individual fish grow.

Maxillary: In the smallest individuals, this bone bears from three to nine small conical teeth, arranged regularly on its anterior edge, in the region nearest its articulation with the premaxillary. Five to nine of the larger conical teeth are arranged, spaced farther apart, on the distal part of the anterior edge of this bone. In individuals longer than 40 mm, between these two types of teeth, one or two of the former type move slightly toward the outside, and these become larger and more mammiform as the individuals grow.

Dentary: On this bone, even in small individuals (up to 25 mm SL), there are already one or two teeth that have moved outside the mouth: a larger mammiform tooth near the symphysis, and another smaller tooth on the more lateral part. Only individuals shorter than 30 mm have these teeth in the normal position.

Within the mouth, in individuals of every size class, the teeth are arranged in the following manner: one or two large teeth next to the symphysis, followed laterally by three to five smaller teeth, another large tooth (somewhat mammiform), and latero-posteriorly by a regular row of up to 12 small conical teeth.

Ontogenetic diet shifts

The Fig. 3 illustrates the composition of food (main food groups) in the four size classes. The ingestion of scales increased considerably with size, varying in occurrence from 17.6% in the smallest individuals to 73.3% in the largest. Microcrustaceans were consumed more by small specimens and were less important in the diet as the fish grow, varying from 92.3% of the diet of the smallest fish to 36.7% for the largest specimens. Insects, on the other hand, were frequent in the diet of all size classes, except for individuals smaller than 34 mm.

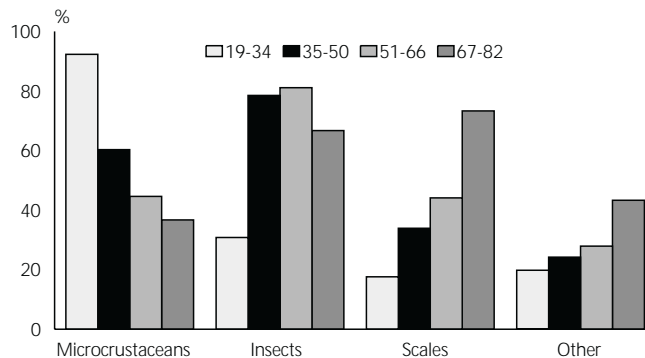


Fig. 3 — Frequency of occurrence of principal diet categories for *Roeboides paranensis* in four size classes (in mm).

Spatial variation in diet

Roeboides paranensis included different groups of aquatic organisms in its diet; however, microcrustaceans, insects, and scales dominated in the stomach contents (Fig. 4).

In the Rio Paraná, the food was less varied than in the pools, and the main item was microcrustaceans. Insects were prominent in the diet in the pools. In Pontal, insects represented 75.0% of the diet, in Canal do Meio 85.4%, in Pau Velho 89.2%, and in Porto Rico 83.0%. In Três Amigos, insects and microcrustaceans were con-

sumed in similar proportions, 68.2% and 64.2%, respectively. Hemiptera (Gerridae) followed by Diptera (mainly Chironomidae) were prominent constituents of the diet in all the pools.

Cladocerans were the most frequently consumed microcrustaceans, except in the Rio Paraná and Pool Três Amigos, where copepods attained the highest percentages. Scales were recorded in the stomachs in similar proportions in the six locations, however they were more frequent in stomachs of individuals from Canal do Meio (45.8%).

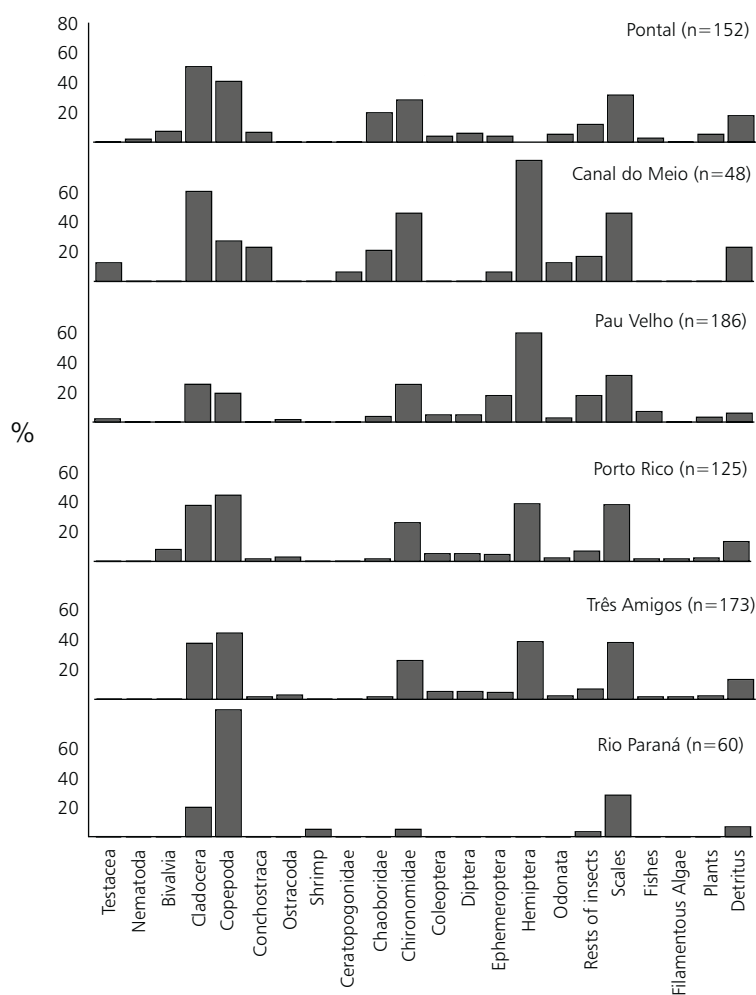


Fig. 4 — Frequency of occurrence of different diet categories for *Roebooides paranensis* at five pools and one site in the Rio Paraná.

Cluster analysis by locations (Fig. 5) showed the highest similarity values for the food of fish of pools Pontal and Porto Rico. These were followed by Três Amigos and a cluster of three sites, Pau Velho, Canal do Meio, and the Rio Paraná.

DISCUSSION

Ontogenetic morphological changes, such as form, number, and arrangement of the teeth of different characoids, were described by Roberts (1967). Morphological changes in accordance with the development of individuals were observed for the “dentado”, mainly regarding the mammiform teeth, which migrated outside of the mouth in

specimens larger than 22 mm. Analysis of cleared and stained specimens confirmed the absence of tooth buds where the mammiform teeth are found, so that dislocation of these teeth is the most probable hypothesis to explain their origin outside of the mouth. As the teeth become more exterior, larger, and therefore more functional, they accompany a gradual change in the feeding habits of this species. The “dentado” eats more scales as it grows, although it does not stop consuming other food items, thus indicating that lepidophagy is facultative in this species. Other investigators have found similar results for different species of *Roebooides* (Roberts, 1970; Sazima & Machado, 1982; Sazima, 1983; Peterson & Winemiller, 1997).

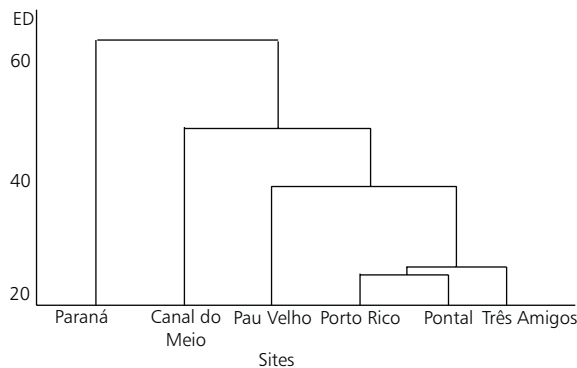


Fig. 5 — Dendrogram of Euclidian distances (ED) based on the diet of *Roeboides paranensis* specimens caught at five pools and one site in Rio Paraná.

Sazima & Machado (1982) commented that among the species of *Roeboides*, *R. prognathus* is the most specialized, with morphological and behavioral characteristics that are clearly adapted to this mode of life.

Although no quantitative data are available regarding the invertebrates found in the stomachs, consumption of invertebrates is probably related to the abundance of these items in the localities sampled. Of the microcrustaceans, cladocerans are most commonly consumed perhaps because of their low escape ability (Towsend & Winfield, 1985). Aquatic Hemiptera (Gerridae) because of their swimming movements on the surface film of the water, are easily detected.

The high similarity of different locations, regarding the food content, was not related to the proximity of the pools, since there are considerable distance (more than 1,000 m) from one another. It can not also be attributed to the physical structure of the environment, given that the pools differ considerably according to the amount of cover and abiotic conditions (Okada, 1995). Thus, we can conclude that this species use basically the same item independently of the site.

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