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FOOD HABITS AND MORPHOLOGICAL CHANGES DURING ONTOGENY IN THREE SERRASALMIN FISH SPECIES OF THE VENEZUELAN FLOODPLAINS.—

Since Eigenmann (1915), Gosline (1951) and Myers (1972), three genera of serrasalmin fishes, *Pristobrycon, Pygocentrus* and *Serrasalmus,* have been considered as "obligatory carnivores." The evidence used to support such a hypothesis was associated with the jaw structure, tooth formation and anatomy of the branchial apparatus. However, detailed studies on the adult food habits of those serrasalmin groups (Goulding, 1980; Machado, 1982, 1984b) rejected that hypothesis and indicated a more expanded diet related principally to seasonal changes and food availability. The purpose of this study was to describe changes in diet and morphology that occur during ontogeny.

Materials and methods.—During the rainy season of 1982, 1983 and 1984 collections from the "Esteros de Camaguán" and the Apure and Portuguesa rivers (Guarico State, Venezuela) (Fig. 1) were made that included specimens of *Pygocentrus notatus, Pristobrycon* (cf) *striolatus* and *Serrasalmus rhombeus.* All three species share a common habitat, the near shore area protected by floating plants and grasses.

The collections were made using beach seines (10.0 mm mesh) and hand nets. Specimens were preserved in formalin (10%) and neutralized with sodium borate to prevent decalcification. Some specimens selected for osteological studies were cleared and counterstained for bone and cartilage following the method of Dingerkus and Uhler (1977) to observe patterns of cartilage and bone growth.

Drawings of jaw structure were made using a Wild (M5) stereoscopic microscope with a camera lucida attachment.

Analyses of food items were performed after dissecting the digestive tract. Items identified were assigned to 11 categories: cladocerans (CLAD), copepods (COP), dipterans (DIP), ostracods (OST), hemipterans (HEM), hydracarina (HYD), ephemeropterans (EPH), fish scales (SCAL), fish fins (FINS), seeds (SEED) and fish flesh (FLESH). Empty stomachs and foreguts were discarded. In those specimens in which the stomachs had food, the frequency of occurence method (Windell, 1971) was applied and the results were expressed as percentage of the total number analyzed of specimens containing food.

Results.—A summary of the percentages of food items and relationships with size (SL) in juveniles of *Pygocentrus notatus, Pristobrycon striolatus* and *Serrasalmus rhombeus* is given in Table 1.

These three species live sympatrically in the flooded areas of the low plains of Venezuela. The early stages of their development (10–25 mm SL) are characterized by a planktivorous diet consisting of copepods, cladocerans, diptera larvae and fish scales. Remains of ostracodans, hemipterans, hydracharina and ephemeropterans also appear in the stomach contents but less frequently. This diet is more or less shared by the early stages of development of other sympatric characid species, particularly with respect to the planktivorous categories. Analyses performed in other characid groups such as: *Colossoma macropomum, Ctenobrycon spilurus, Markiana* (cf) *nigripinnis, Moenkhausia di-*

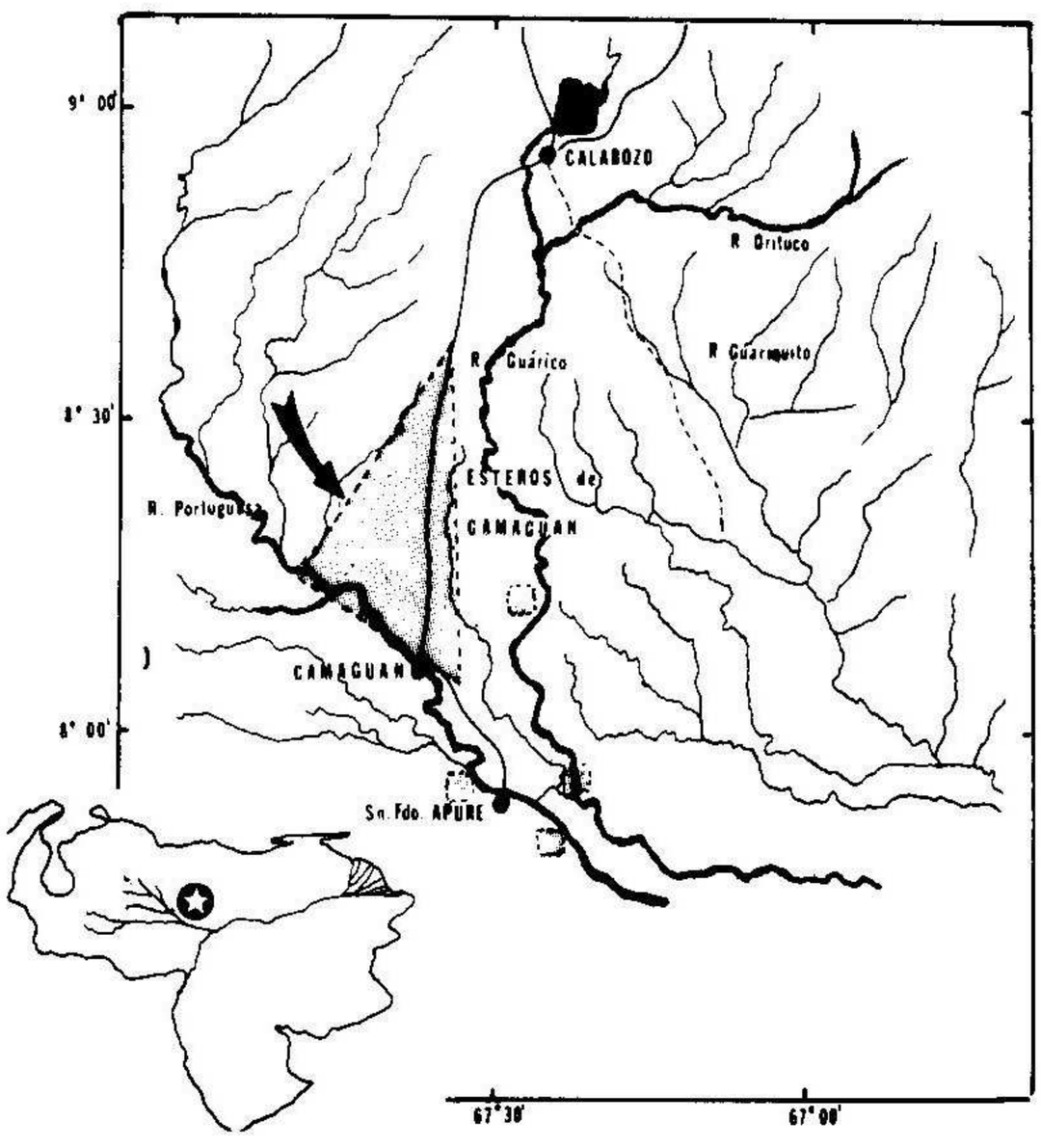

Fig. 1. Map of the studied area (shaded) and relative position in Venezuela (star).

TABLE 1. PERCENTAGE AND FOOD ITEM RELATIONSHIP WITH SIZE IN THREE SPECIES OF SERRASALMIN FISHES FROM THE VENEZUELAN FLOODED PLAINS.

Species	N	Size (SL) (mm)	CLAD %	COP %	DIP %	OST %	HEM %	HYD %	EPH %	SCAL %	FINS %	SEED %	FLESH %
Pygocentrus	10	10–25	80	90	90	20	20	20	20	40	—	—	—
notatus	10	25–40	80	80	50	10	—	10	—	80	20	50	—
(N = 44)	10	40–70	—	—	20	—	—	—	20	50	80	20	—
	14	70–	—	—	—	—	—	—	—	20	85	—	92
Pristobrycon	10	10–25	80	80	90	20	10	—	—	—	20	20	—
striolatus	10	25–40	60	20	50	80	—	—	—	50	60	20	—
(N = 40)	9	40–70	—	—	—	—	—	—	10	—	88	60	—
	11	70–	—	—	—	—	—	—	—	—	91	54	10
Serrasalmus	20	10–25	90	—	85	—	—	10	—	80	25	—	—
rhombeus	10	25–40	—	—	—	—	20	—	—	20	80	40	—
(N = 50)	10	40–70	—	—	—	—	—	—	20	—	80	50	—
	10	70–	—	—	—	—	—	—	20	—	90	20	20

chroura, Mylossoma duriventris, Piaractus brachypomus, Triportheus angulatus, T. elongatus and *T. rotundatus,* sampled during the same period of time indicate a great availability of these food items in these flooded areas during the rainy season. The presence of fish scales in the stomach contents of the serrasalmin species studied here corroborates earlier hypotheses (Sazima, 1984).

Specimens of about 40–70 mm SL showed a mixed diet that included fish fins and cyperacean seeds. There were also remains of diptera larvae, ephemeropterans and fish scales. All three species at this stage attack the fins of other fishes. This habit was observed in aquaria where some specimens of these species were kept. Also, samples of fishes in the same area showed a particular semicircular wound caused by this activity.

Juveniles, more than 70 mm SL showed interspecific differences. Specimens of *Pygocentrus notatus* had stomachs filled with fin remains, pieces of fish flesh and scales. In the other two species (*Pristobrycon striolatus* and *Serrasalmus rhombeus*), juveniles had the stomach contents composed principally of fins and cyperacean seeds, which suggests a diet characteristic of the adult.

Morphological changes observed during ontogeny are illustrated in Fig. 2. These changes include:

A) Jaws and teeth: Early juveniles (10–25 mm SL) of these species shared a monocuspid tooth (Fig. 2A) on both jaws. These teeth are replaced by modified tricuspid teeth of irregular shape (Fig. 2B) in specimens of about 30 mm SL. As Roberts (1967), Berkovitz (1975) and Shellis and Berkovitz (1976) discussed, there occurs a simultaneous replacement of all the teeth on one side of the jaw, due to an interlocking system that holds the teeth together. Each tooth has a strong cusp that fits snugly inside a recess in the base of the adjacent tooth so that all the teeth in each half jaw are mutually locked into place (Roberts, 1967; Machado, 1984b). This interlocking system is apparently a synapomorphy shared by all the genera of the Serrasalminae (Machado, 1984a).

On the other hand, there is a difference in jaw structure that distinguishes *Pygocentrus, Pristobrycon* and *Serrasalmus* from all other serra-

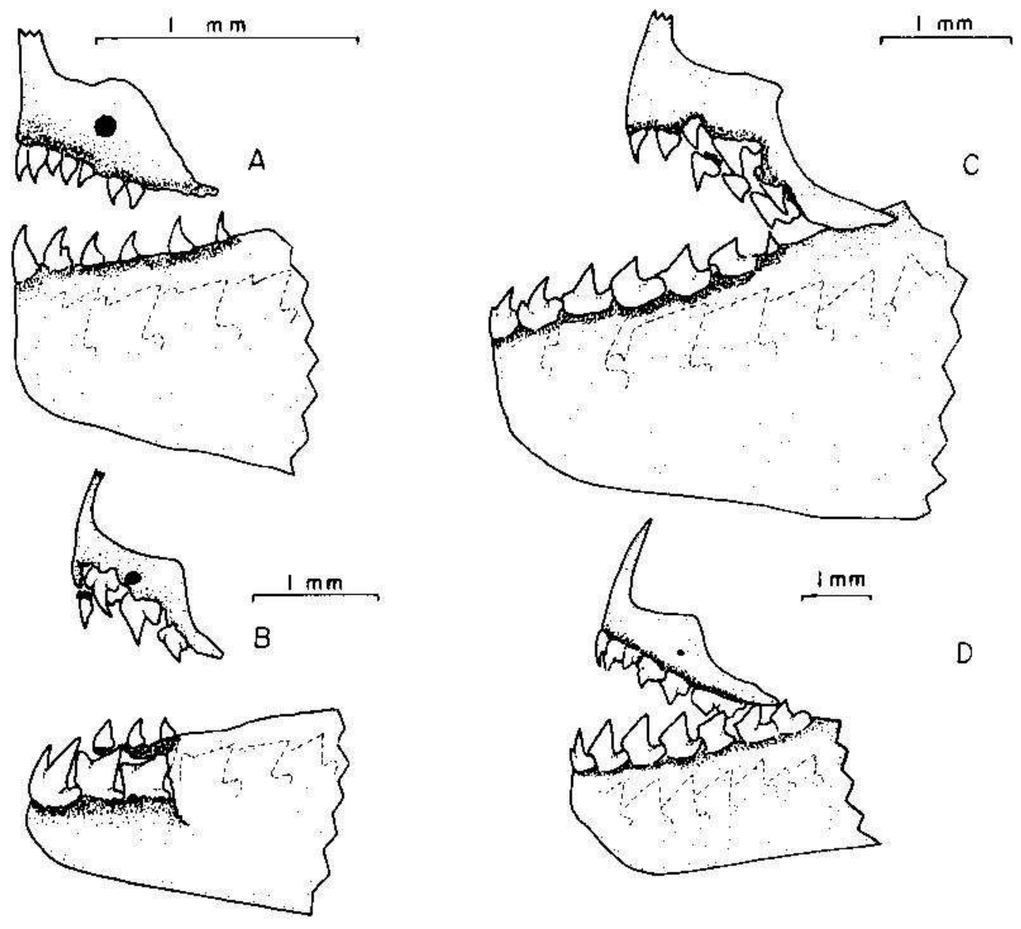

Fig. 2. Morphological changes in early juveniles of *Pygocentrus notatus.* A. 20.0 mm SL; B. 25.0 mm SL; C. 30.0 mm SL; D. 35.0 mm SL.

salmin groups in particular and from all other characoids in general. The replacement tooth trenches on the lower jaw are shielded by a plate of cancellous bone. This plate of bone is reabsorbed during the replacement process and reossified posteriorly when all teeth series are locked into place. This structure was observed in early juveniles of about 30 mm SL.

In juveniles greater than 50 mm SL (Fig. 2C, D) there are several tooth replacements. Each one is characterized by the substitution of a sharper and bigger tooth series than the preceding ones. The dental anatomy observed in these three species agrees with that discussed by Shellis and Berkovitz (1976).

B) Ectopterygoid teeth: Early juveniles of several characid genera, including serrasalmins, have a series of single cusp teeth on the ectopterygoid bones. These teeth dissapear ontogenetically in the majority of genera. In species of *Pristobrycon* and *Serrasalmus* the monocuspid teeth are replaced by strong and sharply modified tricuspid teeth similar to those of the jaws. In *Pristobrycon striolatus* and *Serrasalmus rhombeus* this replacement occurs in specimens of about 30 mm SL. There is osteological and myological evidence that support the hypothesis that this structure functions as an accessory upper jaw in these groups of fishes, such as the development of a strong socket-like cavity on the vomer and lateral ethmoid region to articulate the dorsal portion of the palatine bone and the increase in size of the anterior section of the adductor arcus palatini muscle (Machado, 1982, 1984b).

C) Gill rakers: Early juveniles (10–25 mm SL) show a gill structure characterized by reduced rakers compared to other characid or serrasalmin genera. The raker is a short and conical structure with the ossified basal area covered by small denticles. As the fishes increase in size, the rakers become progressively reduced until they are represented by triangular spinous plates. *Pygocentrus notatus* is characterized by having well developed dermal tooth plates covering the hypobranchial bones in adults (Machado, 1982, 1984b).

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