Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu Reservoir, Brazil

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Synopsis

We analyzed the ontogenetic shifts in digestive tract morphology and diets of the young of *Iheringichthys labrosus*, *Hypophthalmus edentatus* and *Plagioscion squamosissimus*, sampled in the Itaipu Reservoir, Brazil-Paraguay. We described the dental structures, the gill rakers and the digestive tract, and analyzed the diet of the young fish. We observed teeth in the jaws and pharynx in young of the three species. In *H. edentatus*, the gill rakers developed more rapidly, and were longer and more numerous on the first arch, related to their planktivorous feeding habit. *I. labrosus* and *P. squamosissimus* had long gill rakers only on the first arch, they were short and thick on the rest. The stomach was defined only in *P. squamosissimus*, with pyloric caeca. Their diets were mainly zooplankton. *I. labrosus* fed particularly on cladocerans and rotifers; *H. edentatus* consumed essentially cladocerans; and *P. squamosissimus* fed basically on copepods. We observed greater similarity in diet between the young of *I. labrosus* and *H. edentatus*, especially for the first length classes. The diet of *I. labrosus* became more diversified at the end of the larval period, indicating a transition in the feeding habit and habitat for this species. *P. squamosissimus* showed a very different diet from the others species. The differences in oral anatomy, allied to the morphology of the digestive tract, visual acuity, swimming hability, way of foraging, and especially mouth position, form and size, were determining factors in the diets of these species.

Introduction

The initial ontogeny of fishes can be considered as a series of vulnerable periods, of which the most important is the transition between endogenous and exogenous feeding (Kamler 1992). It is a period in which the survival of the young depends on the quantity of endogenous food supply and the availability of adequate food at the first feed-ing. Survival also depends on the development of organs necessary for feeding (Porter & Theilacker 1999) among others factors. During the initial of exogenous feeding, many morphological changes occur; those of the digestive tract are the most important.

Information about feeding of young freshwater fishes in Brazil, both in rivers and reservoirs, is scarce. Trophic ecology is known for adults of

some species (Lansac-Tôha et al. 1991, Hahn et al. 1997, Abes et al. 2001) in the Itaipu Reservoir (Paraná River). Nevertheless, no study has been carried out for their early life stages. There are only descriptions of the morphological development of the young of some species (Nakatani et al. 1997, Nakatani et al. 1998, Nakatani et al. 2001).

Fishes such as 'mandi', *Iheringichthys labrosus* (Kroeyer 1874), 'mapará' , *Hypophthalmus edentatus* (Spix 1829) and 'curvina', *Plagioscion squamosissimus* (Heckel 1840) have been of great importance to the fishing productivity of the Itaipu Reservoir. The adults of these species have different feeding behavior (mapará is planktivorous; curvina is piscivorous and mandi is benthivorous) and habitats (mapará and curvina are pelagic; mandi is benthic). However, it is known that their young are pelagic and they overlap seasonally (November to April). Thus, this paper analyzes the changes that occur in the digestive tract morphology and the diet of the young of these species of the Itaipu Reservoir, to answer these questions: (1) is the development of mouth, teeth, gill rakers and digestive system determined by the future feeding habitat of the species; and (2) do the adaptations for future feeding affect the feeding capability of the young.

Material and methods

We undertook monthly sampling between October 1996 and March 1997 in the Itaipu Reservoir, Brazil-Paraguay. We used a conical-cylindrical net (500 μm mesh) equipped with a flowmeter for surface collections. The trawl-nets were horizontal (depth 20 cm), with a duration of 10 min, always in the nocturnal period between 19:00 and 23:00 h. We fixed samples with 4% formaldehyde buffered with $CaCO_3$.

We counted and identified all young fishes to the level specific of species based on descriptions in Nakatani et al. (2001). We described dental structures, gill rakers-gills on the left side, and the digestive tract in specimens of different sizes. We measured the standard length (SL) of young fishes with an ocular micrometer in a stereoscopic microscope, and dissected and analyzed the specimens morphologically. We used a camera lucida coupled to the same microscope to make the illustrations.

To describe the diet, we analyzed 30 individuals by standard length classes, when possible. We identified the food items in the intestinal contents of each species and counted them under a stereoscopic microscope and an compound microscope. We used both the numeric and occurrence methods (Hynes 1950, Hyslop 1980) to calculate the numeric (NF%) (with the exception of algae and plant remains) and occurrence (OF%) frequencies of each food item by standard length class of the young fishes.

We analyzed similarity in diets through species ordination in different standard length classes. We analyzed four standard length classes per species (*I. labrosus*: I1 = 3–5 mm SL (25 specimens); I2 = 5.1–7 (25 specimens); I3 = 7.1–9 (30 specimens), and I4 = 9.1–12 (30 specimens); *H. edentatus*: H1 = 4–7 mm SL (30 specimens); H2 = 7.1–10 (30 specimens); H3 = 10.1–13 (30 specimens), and H4 = 13.1–20 (05 specimens); *P. squamosissimus*: P1 = 3–5 mm SL (30 specimens), P2 = 5.1–7 (30 specimens); P3 = 7.1–9 (30 specimens), and P4 = 9.1–11 (24 specimens)). We used the Detrended Correspondence Analysis (DCA) (Graham & Vrijenhoek 1988) for the occurrence frequency data for each food item (42 food items).

Results

Dental structures

We observed oral teeth in young *Iheringichthys labrosus*. Young at a 3.57 mm SL had a sub-terminal mouth, with small conical teeth in the upper and lower jaws (Figure 1A; a). Later, in addition to teeth in the jaws, structures appear which are extensions of the upper and lower lips (Figures 1A; b, and c). At the end of the larval period, the lips are well-defined and the teeth persist in the jaws (Figure 1A; d). The pharyngeal teeth are located in the upper and lower parts of the posterior pharynx, visualized in the young at 5.29 mm SL (Figure 1A; b1, and b2). After that, the pharyngeal teeth are more developed and greater in number (Figure 1A; c1, c2, d1, and d2).

Hypophthalmus edentatus has a terminal mouth early in development, with small conical teeth in
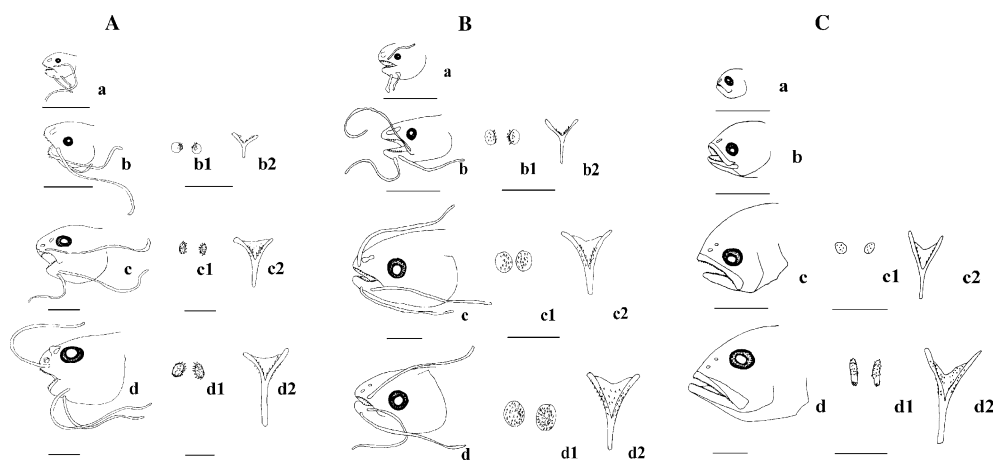
Figure 1. Development of the oral (a–d) and pharyngeal (b1 to d1-upper, b2 to d2-lower) teeth in A: *I. labrosus* (a = 3.57 mm SL; b = 5.29; c = 8.71, and d = 11.71); B: *H. edentatus* (a = 5.00 mm SL; b = 6.86; c = 10.29, and d = 16.29); C: *P. squamosissimus* (a = 2.86 mm SL; b = 4.00; c = 4.86, and d = 8.71). Scale = 1 mm.

the upper and lower jaws (Figure 1B; a). With increasing development, the young have a terminal mouth with several teeth in the jaws (Figure 1B; b, c, and d). The pharyngeal teeth develop in the upper and lower parts of the posterior pharynx (Figure 1B; b1, and b2). Later, these teeth are well-defined and numerous (Figure 1B; c1, c2, d1, and d2).

P. squamosissimus young possess a terminal, protractile mouth with some conical teeth in the upper and lower jaws (Figure 1C; a, and b). The teeth become more numerous and pointed (Figure 1C; c), and later there is a progressive increase in the number of teeth and a decrease in their size until the end of the larval period (Figure 1C; d). Pharyngeal teeth can be observed in the young (Figure 1C; c1, and c2), in the upper and lower parts of the posterior pharynx. These teeth become more numerous and larger with development (Figure 1C; d1, and d2).

Gill rakers

The branchial arches are poorly developed in *Iheringichthys labrosus* larvae at the beginning of exogenous feeding, and the rakers are visible only in the second and third arches, which appear as small bumps (Figure 2A; a). At 5.29 mm SL, the larva have rakers on every arch, where their number decreases in the direction of the fourth branchial arch (Figure 2A; b). During growth, the rakers develop, some appearing longer and finer on the first and second arches, in the larva at 8.71 mm SL (Figure 2A; c). At the end of the larval period, the rakers on the first branchial arch are well-developed as long, thin structures (Figure 2A; d). On the second arch, there are only a few long rakers and another row of rakers begins forming. On the third and fourth branchial arches, two rows of rakers, which appear as bumps, are also observed.

Gill rakers appear in *Hypophthalmus edentatus* young (Figure 2B; a) as small, bumpy structures along the extension of all the branchial arches. The rakers stay short and thick and are more numerous on the first and fourth arches (Figure 2B; b). At 10.29 mm SL, the rakers are finer and longer on the second and third arches (Figure 2B; c). On the fourth branchial arch, some long rakers appear among the conical and short ones; the first arch, however, has only short, conical rakers. Later, an accentuated development of rakers occurs; on the first arch the rakers are longer and more numerous (Figure 2B; d).

P. squamosissimus young initially have gill rakers as small bumps on the first and fourth branchial arches (Figure 2C; a). They are absent from the second and third arches (Figure 2C; b). Later, we observed rakers on all the arches (Figure 2C; c). At the end of the larval period (Figure 2C; d),
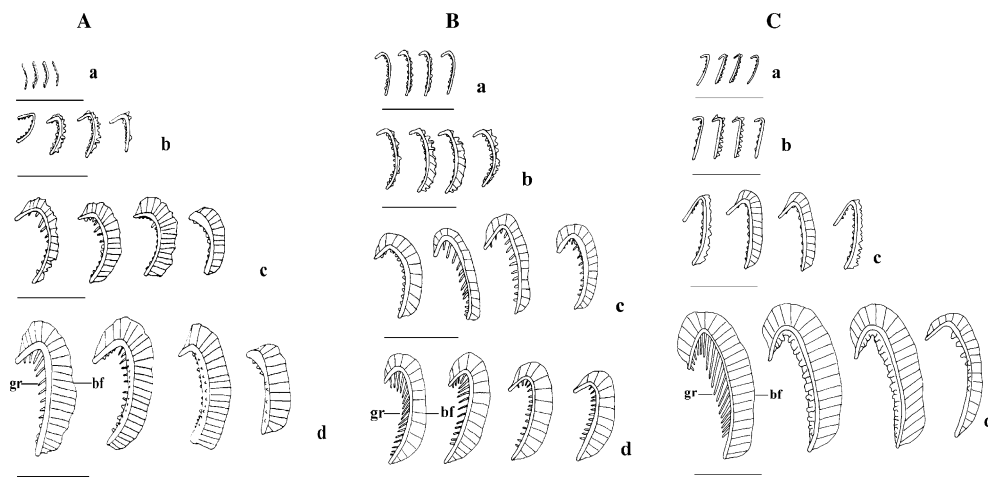
Figure 2. Development of gill rakers in A: *I. labrosus* (a = 3.57 mm SL; b = 5.29; c = 8.71, and d = 11.71); B: *H. edentatus* (a = 5.00 mm SL; b = 6.86; c = 10.29, and d = 16.29); C: *P. squamosissimus* (a = 2.86 mm SL; b = 4.00; c = 4.86, and d = 8.71). gr = gill-raker, bf = branchial filaments. Scale = 1 mm.

all the rakers on the first arch are more elongated and numerous. On the second and third arches, the rakers are shorter and thicker, and more numerous compared to the fourth arch.

Digestive tract

Iheringichthys labrosus young initially have a digestive tract with a dilated anterior region, an elongated posterior, and two intestinal folds (Figure 3A; a). The intestine increases relatively little in length during development (Figure 3A; b, and c). At the end of the larval period, the stomach is only slightly differentiated and the intestine is thicker, with three intestinal folds (Figure 3A; d).

At the beginning of exogenous feeding, *Hypophthalmus edentatus* larvae (5.0 mm SL) possess a relatively elongated digestive tract (Figure 3B; a). Later, the anterior region of the digestive tract appears more dilated, verifying two intestinal folds (Figure 3B; b). With larval development, the anterior region begins to differentiate into a stomach and the intestine becomes longer, with three intestinal folds (Figure 3B; c, and d).

P. squamosissimus young in the initial stage of development, with remains of the yolk sac, have a saclike anterior region of the digestive tract, followed by an intestinal fold and a rectum (Figure 3C; a). During growth, the posterior region of the digestive tract increases relative to length

(Figure 3C; b). The stomach is differentiated in young at a SL of 4.86 mm (Figure 3C; c) and the pyloric caeca also appear. They are well-developed at the end of the larval period (Figure 3C; d).

Diet

The diet of the *I. labrosus* larvae was composed mainly of cladocerans and rotifers, in addition to copepods, insects, fish larvae, algae, and plant remains; however, at low frequencies (Table 1). Among the cladocerans, *Bosminopsis deitersi* and *Bosmina hagmanni* were the species that occurred most frequently. *Brachionus calyciflorus* and rotifer eggs predominated among the rotifers. The food items changed little among the different standard length classes, with the above-cited cladocerans and rotifers standing out. However, for copepods, insects, fish larvae and algae, there was an increase with larval development.

H. edentatus larvae fed on cladocerans, copepods, rotifers, insects, fish eggs and algae (Table 1). The cladocerans were the most frequent during the entire larval period, with some variations in the species in accordance with growth. Those that stood out and their SLs: *Ceriodaphnia cornuta* and *Bosmina hagmanni* (H1), *C. cornuta* (H2), *Diaphanosoma spinulosum* and *C. cornuta* (H3), *D. spinulosum* (H4). Copepods and algae were more frequent in the H3 and H4 classes. On
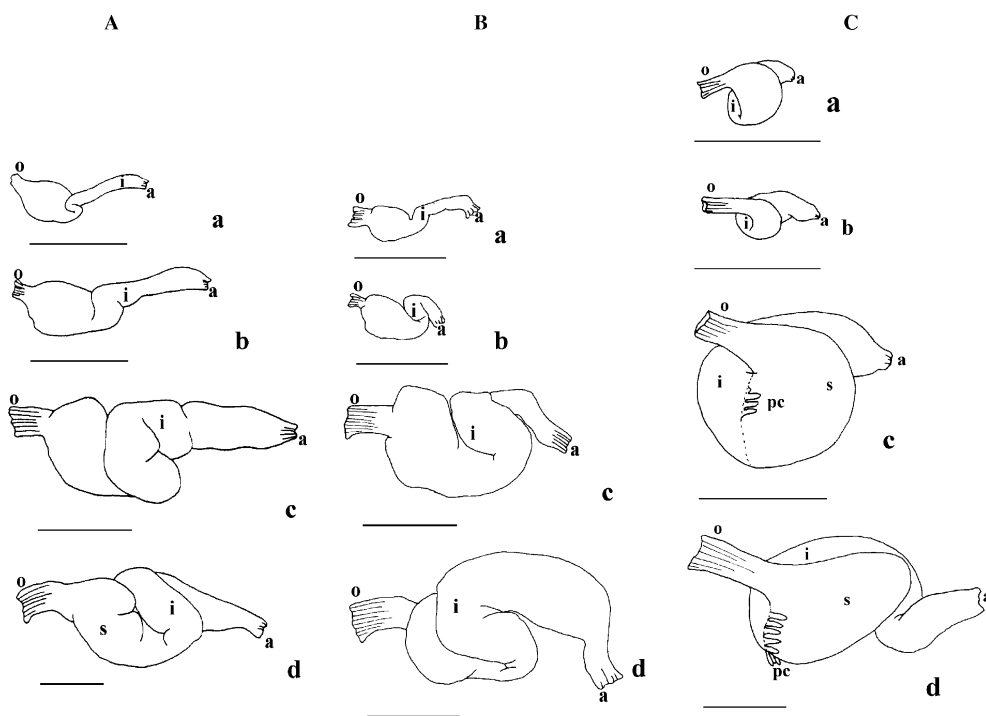
Figure 3. Development of the digestive tract in A: *I. labrosus* (a = 3.57 mm SL; b = 5.29; c = 8.71, and d = 11.71); B: *H. edentatus* (a = 5.00 mm SL; b = 6.86; c = 10.29, and d = 16.29); C: *P. squamosissimus* (a = 2.86 mm SL; b = 4.00; c = 4.86, and d = 8.71). o = oesopagus, s = stomach, pc = pyloric caeca, i = intestine, a = anus. Scale = 1 mm.

the other hand, rotifers were more frequent initially in the H1 class. Insects, however, appeared in the diet in the H3 class, increasing in frequency with larval growth.

The diet of *P. squamosissimus* larvae was constituted basically of cladocerans, copepods, rotifers, fish larvae and algae (Table 1); however copepods were the most frequent, followed by cladocerans. Among the copepods, the species *Notodiaptomus* sp. stood out in all the standard length classes. *Argyrodiaptomus* sp., in second place, appeared in the diet of larvae having a SL of at least 5.1 mm (P2). Some variation in the cladocerans as regards larval development was verified: *Bosmina hagmanni* and *Diaphanosoma spinulosum* were more frequent in the P1 class; *D. spinulosum* in the P2 class, and *D. gessneri* and *D. spinulosum* for the P3, and P4 classes. Among the algae, the species *Oscillatoria* sp. occurred during the entire larval period, with greater frequencies for P3, and P4 classes. The rotifers and the fish larvae were found at low frequencies.

The species ordination on the DCA axes showed five different groups: (1) P2, P3, and P4; (2) I2, I3, H1, H2, H3, and P1; (3) I1; (4) H4, and (5) I4 (Figure 4). Axis 1 (Eigenvalue = 0.52) separated the *P. squamosissimus* larvae from those of *I. labrosus* and *H. edentatus*, whereas axis 2 (Eigenvalue = 0.10) separated the larvae of *I. labrosus* and *H. edentatus* into the standard length classes I4 and H4, respectively.

Discussion

We observed morphological changes during ontogeny of the species which then resulted in changes in the feeding structure that allowed the capture of larger or more energy-rich food particles. The larvae of *I. labrosus* consume mainly cladocerans and rotifers, as well as some copepods, fish larvae, insects, algae and plant remains. The adults of this species are characterized by Fugi et al. (1996) and Abes et al. (2001) as

Table 1. Numeric and occurrence (algae and plant remains) frequencies of the food items registered in the intestinal contents of *I. labrosus, H. edentatus, P. squamosissimus.*

| Food items | Standard length classes | | | | | | | | | | | |
| | *I. labrosus* | | | | *H. edentatus* | | | | *P. squamosissimus* | | | |
	I1	I2	I3	I4	H1	H2	H3	H4	P1	P2	P3	P4
Cladocera												
Bosmina hagmanni-BHA	21.4	14.9	3.3	4.2	17.7	8.8	5.1	3.4	12.2	2.1	0.5	0.9
B. huauriensis-BHU	2.6	3.1	1.2	1.2	4.8	1.8	0.7	1.0	0.8	–	–	–
Bosminopsis deitersi-BDE	25.6	33.7	15.0	7.5	8.2	3.3	3.2	1.4	3.3	2.1	0.2	–
Ceriodaphnia cornuta-CCO	0.9	4.2	4.1	6.6	34.6	51.0	24.8	9.7	3.3	2.5	5.5	3.9
Daphnia gessneri-DGE	–	0.3	1.2	4.4	0.4	2.2	6.8	10.6	–	5.5	15.9	10.8
Diaphanosoma spinulosum-DIA	–	–	–	0.5	0.4	8.3	43.0	55.1	13.0	6.4	6.7	19.7
Moina minuta-MOI	0.9	4.5	1.0	2.7	5.6	8.3	3.9	1.9	8.1	2.5	0.5	0.4
Efípio-EFI	–	–	–	–	–	0.4	–	–	–	–	–	–
Copepoda												
Copepodit (Cyclopoida)-CCY	–	–	0.3	0.1	–	0.2	0.4	–	–	–	–	–
Copepod (rest of Cyclopoida)-CYD	–	0.3	–	0.1	–	–	0.2	–	–	–	–	–
Thermocyclops decipiens-TDE	–	0.7	–	0.1	0.4	–	0.1	0.5	2.4	0.8	1.0	0.4
T. minutus-TMI	0.9	–	–	0.6	0.4	0.4	0.4	1.0	0.8	0.4	0.5	0.4
Copepodit (Calanoida)-CCA	–	–	–	0.2	–	–	0.1	–	–	–	–	–
Copepod (rest of Calanoida)-CAD	–	–	0.1	0.0	–	–	–	–	–	–	–	–
Notodiaptomus sp.-NOT	–	–	0.1	0.1	–	–	–	–	56.1	70.3	40.7	58.4
Argyrodiaptomus sp.-ARG	–	–	–	0.3	–	–	–	–	–	5.9	3.6	5.0
Rotifera												
Brachionus calyciflorus-BCA	23.1	19.4	47.9	45.8	16.9	10.1	6.7	–	–	0.4	–	–
Keratella americana-KER	2.6	0.3	–	–	–	–	–	–	–	–	–	–
Lecane ludwigi-LLU	0.9	0.3	–	–	–	–	–	–	–	–	–	–
Trichocerca capucina-TCA	0.9	–	–	–	–	–	–	–	–	–	–	–
T. cilíndrica-TCI	0.9	0.3	–	–	–	–	–	–	–	–	–	–
T. bicristata-TBI	–	–	–	0.1	–	–	–	–	–	–	–	–
Eggs-ORO	17.9	14.2	24.6	24.4	10.4	4.8	4.3	13.0	–	–	–	–
Insecta												
Chironomidae (larvae)-CLA	1.7	1.7	0.6	0.8	–	–	–	1.0	–	–	–	–
Chironomidae (pupa)-CPU	–	–	0.1	–	–	–	0.1	1.0	–	–	–	–
Chaoboridae-CHA	–	–	–	0.1	–	–	–	–	–	–	–	–
Diptera (pupa)-DIP	–	–	–	0.1	–	–	–	–	–	–	–	–
Pisces												
Larvae (*P. Squamosissimus*)-LPS	–	–	–	–	–	–	–	–	–	0.4	0.2	–
Larvae (*H. Edentatus*)-LHE	–	–	–	–	–	–	–	–	–	0.4	0.2	–
Larvae-LNI	–	1.7	0.4	0.2	–	–	–	–	–	–	0.2	–
Larvae (Siluriforme)-LSI	–	–	–	0.1	–	–	–	–	–	–	–	–
Eggs-OPE	–	–	–	–	–	0.2	–	–	–	–	–	–
Algae												
Aulacoseira sp.-ALA	4.0	–	–	–	–	–	–	–	–	–	–	–
Anabaena sp.-ANA	8.0	4.0	10.0	30.0	–	–	–	–	–	–	–	–
Botriococcus protuberans-BPR	1.0	8.0	3.3	6.7	–	3.3	6.7	–	–	–	–	–
B. braunii-BRA	–	4.0	3.3	–	–	–	–	–	–	–	–	–
Microcystis aeruginosa-MAE	20.0	4.0	13.3	30.0	3.3	10.0	16.7	20.0	3.3	3.3		
Oscillatoria sp.-OSC	–	–	–	–	–	6.7	10.0	–	3.3	23.3	63.3	79.2
Asphanoteceae-ASP	–	–	–	–	–	6.7	10.0	20.0	–	–		4.2
Chlorophyceae-CHL	–	–	–	3.3	–	3.3	3.3	–	–	–		4.2
Chlorococcaceae-CHC	–	–	3.3	–	–	–	–	–	–	–	–	–
Plant remains-VEG	–	–	–	6.7	–	–	–	–	–	–	–	–

benthophagous, feeding mainly on aquatic insects and molluscs. The different foods of larvae and adults result from differences in foraging behavior, habitat, mouth position and digestive tract morphology, and teeth. The gill rakers, long only on the first arch, help to retain small organisms. In addition, the stomach is not completely defined in the larvae. The change in feeding habit and habitat in this species, from plankton to benthos, seems to begin at the end of the larval period. Pedersen & Falk-Petersen (1992) established that the change in habitat from a pelagic area to a demersal life in juveniles of *Gadus morhua* is accompanied by a change in diet and mouth position as an adaptation to the change to benthonic prey.

For *H. edentatus*, the food resources exploited did not change much during ontogeny. The juveniles and adults of this species were classified by Carvalho (1980) as zooplanktophagus, due to the consumption mainly of cladocerans, copepods and ostracods. Lansac-Tôha et al. (1991) classified them as planktivorous, with the consumption of cladocerans and Cyanophyceae. Carvalho (1980) showed that juveniles and adults filter water through numerous long gill rakers, which increase in number with growth. In our study, the larvae of the species consumed essentially cladocerans. Copepods were infrequent in the diet. The presence of teeth in the jaws and pharynx reveal that the *H. edentatus* larvae are, initially, essentially predators. By the end of the larval period the morphology of the gill rakers (relatively more numerous and not very long in relation to the juveniles and adults) seems to indicate an intermediate stage where the larvae use both feeding methods; particulate and

filtration. Possibly, the change of foraging behavior in the species occurs in the juvenile period, at a standard length above 20 mm.

The young of *P. squamosissimus* in the Itaipu Reservoir and on the floodplain upstream feed essentially on insects, changing gradually to fishes in as much as the species is considered a piscivore by Hahn et al. (1997). On the other hand, the larvae had a diet comprised mainly of copepods. Cladocerans were more frequent initially, insects were absent and fish larvae were present with low numeric and occurrence frequency with SL between 5.1 and 9 mm coincided with the development of the stomach and pyloric caeca. Differences in the diet during the ontogeny of *P. squamosissimus* must be associated with the morphological development of the mouth and digestive tract. Its functional, and especially physiological characteristics seem to gradually define what restricts its abilities to ingest larger or more energy-rich prey.

The larvae of our study species showed intra- and interspecific differences in their diet composition, in different phases of larval development. The *P. squamosissimus* larvae constituted an isolated group (group 1) from the rest of the species by having a diet represented mainly by calanoids, fish larvae (*P. squamosissimus* – LPS; *H. edentatus* – LHE), algae (*Oscilattoria* sp. – OSC) and also by not consuming insects during the larval period. However, the P1 class was next with initial classes of *H. edentatus* (group 2) in function of the consumption, especially of cladocerans, and also cyclopoids. Hahn et al. (1999) commented that curvina is a visual predator, and the same seems to be true for their larvae. The visual orientation in
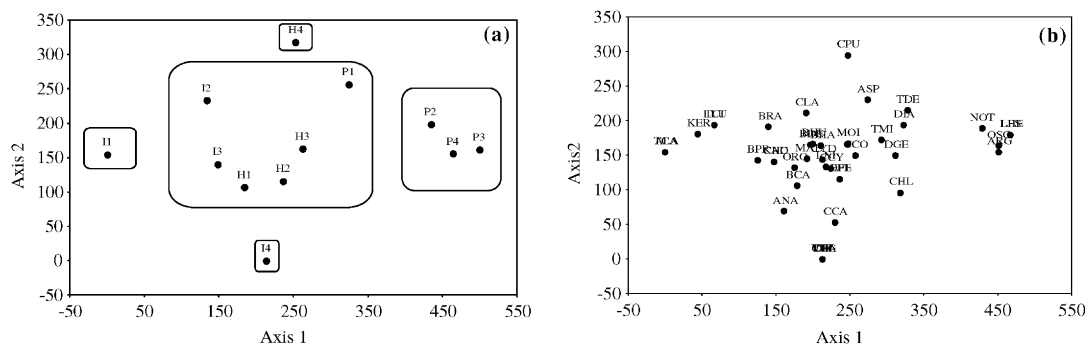

Figure 4. Ordenation of the standard length classes of the species (a), and the occurrence frequency of each prey item (b) along the DCA axes.

the search for food, allied to the rapid development of its fins at hatching, especially the caudal fin, which gives it greater propulsion (Webb & Weihs 1986) and better swimming ability, as well as the large mouth size and jaw protrusion, permits the larvae of this species to capture copepods, despite their being larger and faster in relation to the rest of the zooplanktonic organisms.

On the other hand, the larvae of *I. labrosus* and *H. edentatus* had a more similar diet in the standard length classes 2 and 3 (group 2), characterized mainly by cladocerans and rotifers. The similarity in their use of food resources probably is a reflection of similarities in mouth size. In comparison to *P. squamosissimus*, the larvae of these two species possess less mobility as a consequence of the slower development of the rest of their bodies. However, the standard length class I1 (group 3) was separated because the larvae ate algae (ALA), and rotifers (TCA, TCI, LLU). The classes I4 and H4 of these species, which covers the end of the larval period, larvae of *I. labrosus* (I4-group 5; fish larvae – LSI, rotifers – TBI, insects – CHA and DIP, plants – VEG) presented a more diversified diet than that of *H. edentatus* (H4-group 4; insects – CPU). This reveals a transition period for the *I. labrosus* larvae, between the planktonic and benthic regions, which is defined in the juvenile period. According to Wanzenböck & Schiemer (1989), many fish species are zooplanktivorous during their initial phases of life, later exhibiting a distinct differentiation in their foraging biology. Such a change in the way of feeding could be related to different optical necessities.

Differences in oral anatomy may determine the fundamental trophic niche of fish species (Luczkovich et al. 1995). Thus, for the larvae of the three species analyzed, the formation of the teeth and the gill rakers, coupled with digestive tract morphology, visual acuity, swimming ability, foraging mode, and especially mouth size, form and position were determinant factors of the diet of the species.

Acknowledgements

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