Ontogenetic shifts in the digestive tube and diet of *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae)

Mudanças ontogenéticas no tubo digestório e na dieta de *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae)

Suiberto, MR.[1], Galuch, AV.[2], Bialetzki, A.[3] and Nakatani, K.[3†]

[1]Programa de Pós-graduação em Zoologia, Instituto de Biociências, Universidade Estadual Paulista – UNESP, Campus de Botucatu, Distrito de Rubião Jr., s/n, CEP 18618-000, Botucatu, SP, Brazil
e-mail: mrs@ibb.unesp.br

[2]Programa de Pós-graduação em Biologia de Água Doce e Pesca Interior, Instituto Nacional de Pesquisas da Amazônia – INPA, Av. André Araújo, 2936, CEP 69083-000, Manaus, AM, Brazil
e-mail: galuch@gmail.com

[3]Programa de Pós-Graduação em Ecologia de Ambientes Aquáticos Continentais – PEA, Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura – Nupélia, Departamento de Biologia – DBI, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, bloco G-90, CEP 87020-900, Maringá, PR, Brazil
e-mail: bialetzki@nupelia.uem.br

Abstract: Aim: Studies on feeding of early life stages are very important to the understanding of the biology and trophic ecology of fish species. Therefore, the aim of this work is to describe the development of the digestive tube, and to characterize the diet of larvae and juveniles of *Bryconamericus stramineus* Eigenmann, 1908 of the upper Paraná River floodplain; **Methods:** Larvae were obtained from, monthly samples during nychthemeral cycles with four-hour interval between samplings from February/91 to February/92, utilizing a conical-cylindrical plankton net; **Results:** At the preflexion stage, larvae at approximately 4.00 mm SL, showed a morphologically undifferentiated straight tube, with the anterior region more dilated. At the flexion stage a differentiation in the anterior region of the digestive tube occurs, with the intestine wall getting thicker (8.30 mm SL). The formation of pyloric caeca occurs at 9.00 mm SL. At the postflexion stage the first loop is formed at 9.25 mm SL and the second loop at about 10.00 mm SL. *Bryconamericus stramineus* consumed mainly cladocerans, also ingesting copepods, rotifers, nematodes, algae, insects and inorganic particles. Along the development, there was an increase in the number of food items and a diversification in the number of consumed taxa; **Conclusions:** Changes in the diet of *B. stramineus* larvae were not observed, being them zooplanktivores during all the initial development. However, an increase of large preys, such as insects larvae, was observed at the end of the larval period and in juveniles, suggesting a tendency towards invertivory. Larvae and juveniles preferentially fed during the night.

Keywords: larvae, juveniles, feeding, *Bryconamericus stramineus*, floodplain.

Resumo: Objetivo: Estudos sobre a alimentação dos estágios iniciais de vida dos peixes são de grande importância para a compreensão da biologia e ecologia trófica das espécies. Assim, este trabalho tem como objetivo descrever o desenvolvimento do tubo digestório e caracterizar a dieta de larvas e juvenis de *Bryconamericus stramineus* Eigenmann, 1908 da planície alagável do alto rio Paraná; **Métodos:** Para a obtenção dos indivíduos foram realizadas coletas mensais ao longo de ciclos nictemerais com intervalo de quatro horas entre as amostragens no período de fevereiro/91 a fevereiro/92, utilizando-se rede de plâncton cônico-cilíndrica; **Resultados:** No estágio de pré-flexão, em larvas com aproximadamente 4,00 mm CP, o tubo digestório apresentou-se morfologicamente indiferenciado (retilíneo), com a região anterior mais dilatada. No estágio de flexão ocorre um espessamento da região anterior do tubo digestório, (8,30 mm CP) e a formação dos cecos pilóricos (9,00 mm CP). No estágio de pós-flexão ocorre a formação da primeira volta do intestino com 9,25 mm CP e da segunda volta com cerca de 10,00 mm CP. *Bryconamericus stramineus* consumiu principalmente cladóceros, sendo encontrados também copépodos, rotíferos, nematódeos, algas, insetos e partículas inorgânicas. Ao longo do desenvolvimento houve aumento no número de itens encontrados e uma diversificação no número de táxons consumidos; **Conclusões:** Não ocorreram mudanças na dieta das larvas, sendo estas zooplanctívoras durante todo o seu desenvolvimento inicial. No entanto, no final do período larval e nos juvenis, foi observado um acréscimo no número de presas maiores, como larvas de insetos, o que pode indicar uma mudança na dieta desta espécie para a invertivoria. O horário preferencial para a alimentação, tanto das larvas quanto dos juvenis, foi o período noturno.

Palavras-chave: larvas, juvenis, alimentação, *Bryconamericus stramineus*, planície de inundação.

† In memory of Prof. Dr. Keshiyu Nakatani.

1. Introduction

The study of resource exploitation among syntopic feeding guild members provides the most straightforward means of attaining a preliminary assessment of the relative importance of interactive processes within natural communities (Winemiller, 1989). These studies are fundamental to early life stages of fish considering that they provide support to understanding the mortality/survival process and recruitment.

In terms of feeding, fish larvae are essentially "separate species" when compared to their adult counterparts because they are so small and poorly developed and have a feeding pattern very differentiate (Gerking, 1994). Moreover, during the early development of fish important changes occur in the digestive tract, which is morphologically, hystologically and physiologically less elaborate than the alimentary canal of adult fishes (Govoni et al., 1986).

In the tropical region, most of the studies performed on fish feeding have been carried out for the adult phase. Among those about diet and morphology of the digestive tract of larvae, in South America, we can mention Rossi (1992) with *Prochilodus lineatus*; Cavicchioli and Leonhardt (1993) with *Prochilodus scrofa*; Santin et al. (2004) with *Apareiodon affinis*; Makrakis et al. (2005) with *Iheringichthys labrosus, Hypophthalmus edentatus* and *Plagioscion squamosissimus*; and Borges et al. (2006) with *Bryconamericus* aff. *iheringii*. All these studies associate the diet alterations with digestive system differentiation.

Bryconamericus stramineus Eigenmann, 1908, regionally known as "pequira", is distributed from the Prata Basin to the São Francisco River (Graça and Pavanelli, 2007), considering that in upper Paraná River, its occurrence can be considered moderated (Agostinho et al., 1997). *Bryconamericus stramineus* is a foraging species with no commercial interest due to its small size, reaching 76 mm length (Ringuelet et al., 1967). However, it has a great importance in the food web of the systems it lives on because it serves as food for piscivore fishes. For example, *P. squamosissimus* (curvina), a species of great importance for the professional fishery, had *B. stramineus* as one of the preferential preys (Almeida et al., 1997).

Feeding studies of *B. stramineus* were carried out only for adults by Casatti and Castro (1998) and by Casatti et al. (2003) that classified this species as omnivore and invertivore, respectively. Therefore, this work aimed to study the feeding of larvae and juveniles of *B. stramineus*, specially intending: (i) to describe the morphological development of the digestive tube; (ii) to characterize the diet through quantification and identification of food items; and (iii) to verify the preferential feeding time along the ontogenetic development of this species.

2. Material and Methods

The study site was located at Leopoldo´s Inlet (22° 45' S and 53° 16' W), right margin of Porto Rico Island, upper Paraná River floodplain (Paraná and Mato Grosso do Sul States) (Figure 1). Fish larvae and juveniles were caught monthly from February/91 to February/92. Samplings were carried out during nychthemeral cycles with four-hour interval between samplings. Samples were obtained using a conical-cylindrical plankton net (500 µm mesh), equipped with a flowmeter. Trawls were horizontal at approximately 20 cm depth, and lasted for 10 minutes.

The material obtained was immediately fixed in 4% formaline, buffered with $CaCO_3$. Larvae and juveniles were separated from the rest of the plankton under stereomicroscope and identified in accordance with the development sequence technique, proposed by Ahlstrom and Moser (1976) and adapted by Nakatani et al. (2001). Identified individuals were separated in accordance to their development stage, in larval period (preflexion, flexion and postflexion) and juveniles after Ahlstrom et al. (1976), modified by Nakatani et al. (2001).

To characterize the morphology of the digestive tube, individuals were grouped in five size classes. Size classes were established between the minimum (3.85 mm) and maximum (20.29 mm) standard length (SL) verified (precision of 0.01 mm), trying also separate according to development stages. Therefore, the following classes were obtained: class 1 - 3.85 to 6.35 mm (preflexion stage); class 2 - 6.36 to 8.86 mm (preflexion and flexion stage); class 3 - 8.87 to 11.37 mm (flexion and postflexion stage); class 4 - 11.38 to 13.88 mm (postflexion stage and juveniles); and class 5 - above 13.89 mm (juveniles). The development of the digestive tube for each size class was illustrated using a camera lucida.

To characterize the diet, whenever possible, 20 individuals of each size class were analyzed. The digestive tube was extracted through a longitudinal cut in the abdomen using a probe or scalpel when necessary. Digestive tubes were then opened on a 4 cm^2 squared slide containing 16 fields and covered with coverslip. Posteriorly, four fields were randomly chosen, and had the items counted, summed and multiplied to the others fields (Σ of item × in four field * 4), obtaining the total number of items in each digestive tube analyzed.

In individuals in preflexion and flexion stages all the digestive tube content was analyzed (classes 1, 2 and 3). Larvae in postflexion and juveniles (classes 4 and 5), that already showed a distinct differentiation of the digestive tube, had only the stomach contents and 2/3 of the intestine analyzed, due to a high degree of food item digestion in its final portion. The contents were quantified and the items identified to the lowest taxonomic level possible under stereomicroscope and optic microscope, according to

Needham and Needham (1982), Thorp and Covich (1991), Parra and Bicudo (1995) and Elmoor-Loureiro (1997). Copepods were separated according to their development in: nauplii, copepodits and adults.

Data were analyzed regarding the Frequency of Occurrence (%OF = percent of occurrence of each food item in relation to the total number of stomach with food) and the Numeric Frequency (%NF = percent of the total number

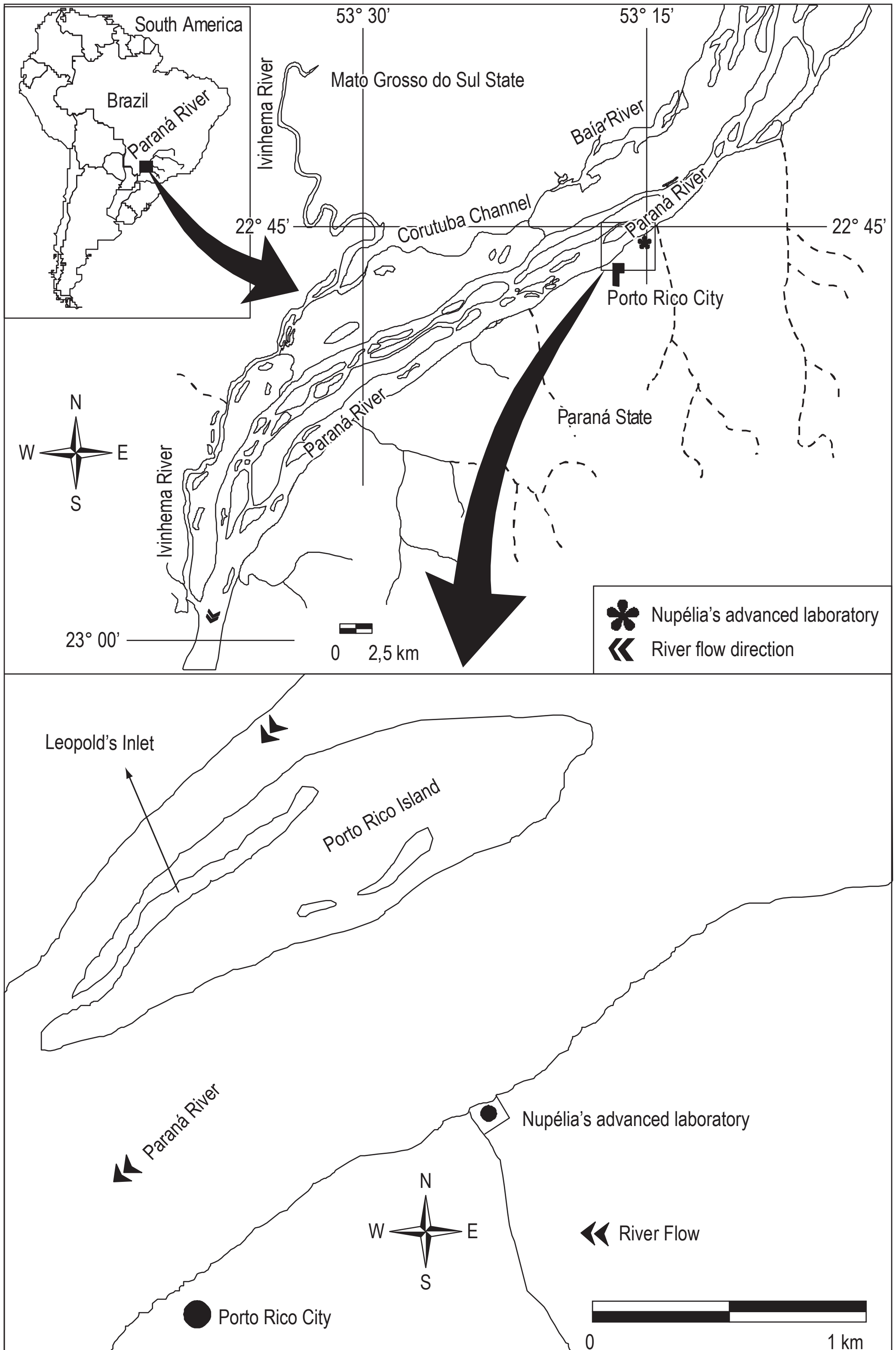

Figure 1. Location of the Leopoldo's Inlet in the upper Paraná River floodplain.

of components of each food category, in relation to the total number of items) (Laroche, 1982; Govoni et al., 1983).

For the study of preferential feeding time, the distribution of food items found in the contents was analyzed according to the size classes and sampling time.

3. Results

3.1. Morphological characterization of the digestive tube

The Figure 2a - f illustrates the morphological changes occurred in the digestive tube during the initial development of *B. stramineus*. The smallest individuals at the preflexion stage showed a morphologically undifferentiated straight tube with the anterior region more dilated (Figure 2a). At approximately 8.30 mm SL (flexion stage), a differentiation in the anterior region occurs, with the intestine wall getting thicker (Figure 2b). At about 8.80 mm SL, a pressure in the anterior region starts, dividing the straight tube into stomach and intestine. At 9.00 mm SL, the formation of pyloric caeca was observed, and at 9.25 mm SL (postflexion stage) the first loop is formed, separating stomach and intestine (Figure 2c). When larvae reached 10.00 mm SL, a second loop starts to form, which is totally formed at 10.12 mm SL. (Figure 2d). After the second loop is formed it is possible to see the division of the anterior and posterior intestines (Figure 2e). From this size on, there are no significant changes in morphology, but an increase in the size of the digestive tube (Figure 2f).

3.2. Diet characterization

During the initial development, *B. stramineus* consumed cladocerans, copepods, rotifers, nematodes, algae, insects and inorganic particles. Along the development there was an increase of number of items found and a diversification in the number of taxa (Table 1).

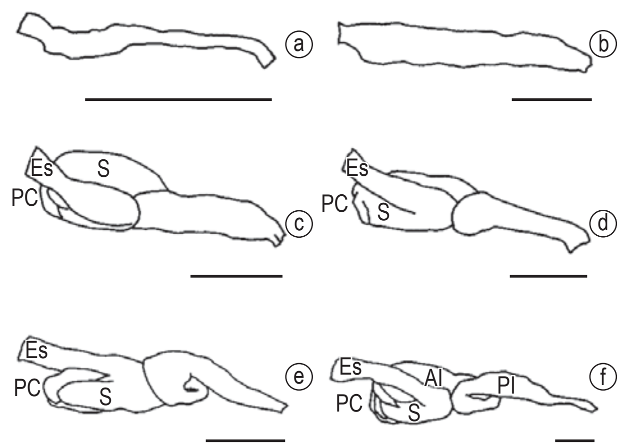

Figure 2. Morphological development of the digestive tube (view of left lateral face) of larvae and juveniles of *Bryconamericus stramineus*. a) SL = 4.10 mm; b) SL = 8.50 mm; c) SL = 9.25 mm; d) SL = 10.25 mm; e) SL = 11.43 mm; f) SL = 16.86 mm (Scale = 1.00 mm). Es = esophagus; S = stomach; PC = pyloric caeca; AI = anterior intestine; PI = posterior intestine.

Table 1. Frequency of Occurrence (%OF) and Numeric Frequency (%NF) of food items found in the digestive tube of larvae and juveniles of *Bryconamericus stramineus*.

Food Items	Size class (standard length)									
	3.85-6.35 mm PF (n = 20)		6.36-8.86 mm PF and FL (n = 20)		8.87-11.37 mm FL and FP (n = 20)		11.38-13.88 mm FP and J (n = 20)		>13.89 mm J (n = 20)	
	%OF	%NF	%OF	%NF	%OF	%NF	%OF	%NF	%OF	%NF
Microcrustaceans										
Bosmina hagmanni	100.00	82.46	95.00	87.56	100.00	76.14	93.75	72.38	72.22	37.91
Bosminopsis deitersi	25.00	10.53	35.00	4.89	47.37	6.25	43.75	14.64	22.22	3.61
Moina minuta			25.00	2.22	31.58	2.56			22.22	2.89
Diaphanosoma sp.					5.26	0.28	12.5	1.26	11.11	2.17
Cladocera (NI)	20.00	7.02	30.00	4.00	52.63	11.65	12.5	10.04	61.11	24.55
Calanoida			5.00	0.44	5.26	0.28			11.11	0.72
Copepodids					5.26	0.28	12.5	0.84		
Nauplii					5.26	0.28			5.56	0.72
Copepoda (NI)									16.67	1.08
Other invertebrates										
Rotifera									11.11	1.44
Nematoda									5.56	2.53
Insecta									27.78	3.61
Chironomidae (larvae)			5.00	0.89			6.25	0.42	27.78	3.25
Algae										
Bacillariophyceae									22.22	10.47
Chlorophyceae									11.11	3.97
Inorganic Particles					5.26	2.27				
Non identified							6.25	0.42	11.11	1.08

PF = preflexion; FL = flexion; FP = postflexion; J = juvenile; NI = non identified.

In all size classes there was a numeric and occurrence predominance of microcrustaceans, where *Bosmina hagmanni*, *Bosminopsis deitersi* and *Moina minuta* were the most frequent species. It was also verified the presence of copepods, which nauplii appeared in classes 3 and 5; copepodids appeared in classes 3 and 4; and adults, were found in classes 2, 3 and 5. The chironomids larvae appeared in classes 2, 4 and 5, while rotifers, nematodes and algae were only found in class 5. Inorganic particles were only found in class 3.

3.3. Feeding time

The nychthemeral distribution of larvae and juveniles of *B. stramineus* shows that the highest capture of larvae in preflexion stages (classes 1 and 2) and flexion (classes 2 and 3) occurred during the day (9:30 AM), while in postflexion (classes 3 and 4) and juvenile (class 5) occurred mainly at night (9:30 PM, 1:30 AM and 5:30 AM) (Figure 3).

The Figure 4 shows the frequency of the different food items found for each size class at the different sampling times. The main food item found in every size class was *B. hagmanni*, occurring almost exclusively during the night. The second most abundant item was *B. deitersi*, which appeared preferentially at the beginning of the night (Figure 4).

4. Discussion

The morphological changes occurred during the early life stages of *B. stramineus*, as the differentiation of the digestive tube into stomach and intestine, starting from a straight tube, follows a general pattern of development observed in larvae of other teleosts, like *A. affinis* (Santin et al., 2004), *I. labrosus*, *H. edentatus e P. squamosissimus* (Makrakis et al., 2005). According to Govoni et al. (1986), the straight tube shows three distinct areas: the foregut, which will originate the esophagus and the stomach; the

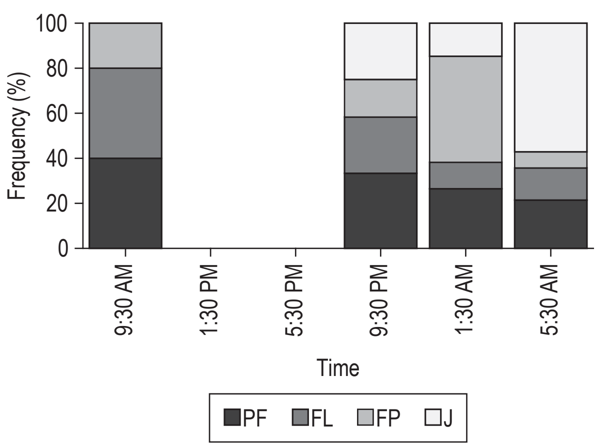

Figure 3. Frequency of capture of larvae and juveniles of *Bryconamericus stramineus* at different sampling times (PF = preflexion; FL = flexion; FP = postflexion; J = juvenile).

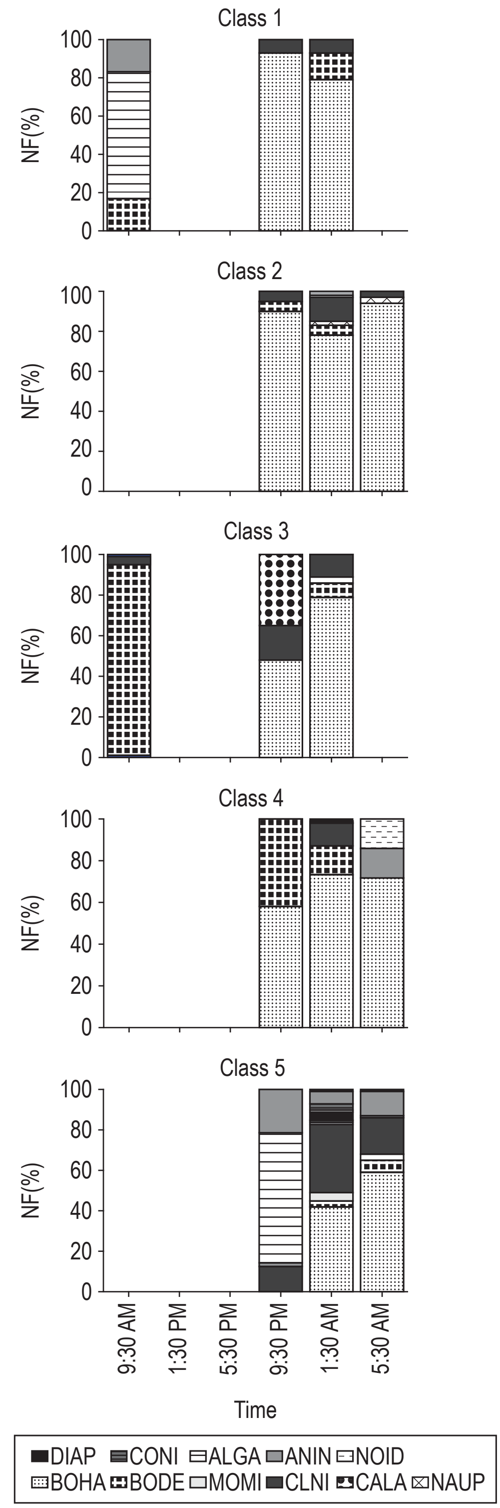

Figure 4. Numeric Frequency (%NF) of items found in the digestive tube of larvae and juveniles of *Bryconamericus stramineus* for each size class at different sampling times (CONI = Copepod non identified; ALGA = algae; ANIN = another invertebrate; INPA = inorganic particle; COPE = copepodids; NOID = non identified; BOHA = *Bosmina hagmanni*; BODE = *Bosminopsis deitersi*; MOMI = *Moina minuta*; CLNI = Cladocera non identified; CALA = Calanoida; NAUP = nauplii; DIAP = *Diaphanosoma* sp.).

midgut that will originate the anterior intestine, and the hindgut that will originate the posterior intestine. For the species herein studied, larvae in preflexion and flexion stages showed an undifferentiated straight tube, while those in postflexion showed differentiated esophagus, stomach, and anterior and posterior intestines.

The development of stomach and pyloric caeca constitutes the last major morphological change of the alimentary canal (Govoni et al., 1986). Pedersen and Falk-Petersen (1992) related that the stomach and pyloric caeca develop from the transition region between esophagus and intestine, which was also verified to *B. stramineus*. However, according to Drewe et al. (2004), the relationship between the diet and the structure and function of the pyloric caeca is also complex and still poorly understood.

Regarding the diet, the presence of algae in the stomach of more developed larvae, with high predation capability, could have been accidental and occurred with the capture of larger prey. Uieda (1983) also considered the ingestion of vegetal items, include algae, as accidental for some fish species.

According to Lansac-Tôha et al. (1997), *B. hagmanni* e *M. minuta* present highest densities in marginal and central areas of the different environments of the upper Paraná River floodplain. In a study conducted by Lansac-Tôha et al. (1995) in this environment, high densities of *B. hagmanni* were found in the middle of the water column during the day, migrating to the surface at the beginning of the night and returning to the middle of the water column during the night. Therefore, the high presence of *B. hagmanni* in the food contents of larvae caught during the night is probably the result of larvae feeding at the beginning of the night. In the same study, the authors also described the vertical migration of *B. deitersi*, which is distributed in the middle of the water column during the day, migrate to the surface at night and return again to the middle of the water column at the end of the night. Therefore, the presence of *B. deitersi* in food contents of larvae caught preferentially during the day can suggests that they consumed these organisms at night. Nevertheless, there are no studies about food digestion time in the literature.

The analyses of the nychthemeral distribution of larvae and juveniles of *B. stramineus* shows that during the day larvae in preflexion and flexion stages were more abundant. On the other hand, postflexion larvae and juveniles occurred mainly at night. This difference can be a result of avoidance the sampling gear by the great individuals during the day. The abundant daytime collections may be associated with larvae low visual acuity and swimming ability to avoid capture in the early life stages or even a mechanism to reduce intraspecific competition (Castro et al., 2002), considering that larvae food search is a behavior that is related to the development degree of motor and sensorial abilities (Santin et al., 2004).

The literature about feeding adults of *B. stramineus* indicates that they exhibit plasticity in relation to resources available and explored in the environment. In macrophyte banks in the Rosana Reservoir, this species was characterized as invertivore (Casatti et al., 2003), and in a stream of the upper Paraná River floodplain as insectivore (Abes and Agostinho, 2001). During the larval phase there were no changes in trophic category of this species, only an increase in the number of food items and species richness consumed as the larvae develop. It can be, therefore, considered initially as zooplanktivores. However, at the end of larval period and beginning of juvenile (classes 4 and 5), an increase in the number of prey occurred, and the presence of large preys as insect larvae can indicate changes in the diet of this species to invertivory.

Every item consumed by larvae and juveniles of *B. stramineus* are of autochthonous origin. In adults, Cassati et al. (2003) observed a predominance of animal items of autochthonous origin, represented mainly by Diptera (Chironomidae pupa and larvae). This similarity with the diet of larvae at the end of their development and of early juveniles, probably explain the partition of resources between the early life stages with the adults of the same species, however with different feeding times. Uieda (1984) observed that adults of *B. stramineus* distribute especially in the middle water and surface, and they feed during the day, while larvae and juveniles of Leopoldo's Inlet showed feeding activity at night.

According to Galuch et al. (2003), the increased larvae abundance at night was probably due to vertical migrational patterns. The large quantities of food provided by the vertical migration of zooplankton lead to greater larvae movement during the nocturnal period (Bialetzki et al., 2002). Also, the foraging hypothesis suggests that diel vertical movements occurs when larvae pursue and follow vertically migrating planktonic organisms so as to minimize prey-search time and maximize prey-capture rates (Clark and Levy, 1988).

Nevertheless, the present study is not to intend to investigate process influencing vertical migration, but is a pioneering work which has raised hypothesis to be worked in future studies.

Acknowledgements

The authors thank the Núcleo de Pesquisas em Limnologia, Ictiologia e Aqüicultura (Nupélia) of the Universidade Estadual de Maringá (UEM) for logistic support during the sampling period, Sebastião Rodrigues and Dr. Gilmar Baumgartner are acknowledged for their assistance with fieldwork and Drs. Ângela Maria Ambrósio and Rosemara Fugi for reading the manuscript.

References

AGOSTINHO, AA., JÚLIO Jr., HF., BINI, LM. and AGOSTINHO, CS. Composição, abundância e distribuição espaço-temporal da ictiofauna. In: Vazzoler, AEA., Agostinho, AA. and Hahn, NS. (eds.). *A planície de inundação do alto rio Paraná:* aspectos físicos, biológicos e socioeconômicos. Maringá: EDUEM - Nupélia, 1997. p. 179-208.

AHLSTROM, EH. and MOSER, HG. Eggs and larvae of fishes and their role in systematic investigations and in fisheries. *Rev. Trav. Inst. Peches Marit.*, 1976, vol. 40, no. 3, p. 379-398.

AHLSTROM, EH., BUTLER, JL. and SUMIDA, BY. Pelagic stromateoid fishes (Pisces, Perciformes) of the Eastern Pacific: kinds, distributions, and early life histories and observations of five of these from the Northwest Atlantic. *Bull. Mar. Sci.*, 1976, vol. 26, no. 3, p. 285-402.

ALMEIDA, VLL., HANH, NS. and VAZZOLER, AEA. Feeding patterns in five predatory fishes of the high Paraná River floodplain (PR, Brazil). *Ecol. Fresh. Fish.,* 1997, vol. 6, p. 123-133.

BIALETZKI, A., NAKATANI, K., SANCHES, PV., and BAUMGARTNER, G. Spatial and temporal distribution of larvae and juveniles of *Hoplias* aff. *malabaricus* (Characiformes, Erythrinidae) in the upper Paraná River floodplain, Brazil. *Braz. J. Biol.*, 2002, vol. 63, no. 2, p. 211-222.

BORGES, RZ., ASSAKAWA, LF., CUNHA, AB., BIALETZKI, A. and NAKATANI, K. Morfologia do trato digestório e dieta de larvas de *Bryconamericus* aff. *iheringii* (Boulenger, 1887) (Osteichthyes, Characidae). *Acta Sci. Biol. Sci.*, 2006, vol. 28, no. 1, p. 51-57.

CASATTI, L. and CASTRO, RMC. A fish community of the São Francisco River headwaters riffles, southeastern Brazil. *Ichthyol. Explor. Freshwaters*, 1998, vol. 9, no. 3, p. 229-242.

CASATTI, L., MENDES, HF. and FERREIRA, KM. Aquatic macrophytes as feeding site for small fishes in the Rosana Reservoir, Paranapanema River, Southeastern Brazil. *Braz. J. Biol.*, 2003, vol. 63, no. 2, p. 213-222.

CAVICCHIOLI, M. and LEONHARDT, JH. Estudo do desenvolvimento morfológico de larvas de Curimbatá, *Prochilodus scrofa* (STEINDACHNER, 1882), obtidas de reprodução induzida. *Rev. UNIMAR*, 1993, vol. 15, p. 109-124.

CLARK, CW. and LEVY, DA. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *Am. Nat.*, 1988, vol. 131, no. 2, p. 271-290.

DREWE, KE., HORN, MH., DICKSON, KA. and GAWLICKA, A. Insectivore to frugivore: ontogenetic changes in gut morphology and digestive enzyme activity in the characid fish *Brycon guatemalensis* from Costa Rican rain forest streams. *J. Fish Biol.*, 2004, vol. 64, no. 4, p. 890-902.

ELMOOR-LOUREIRO, LMA. *Manual de identificação de cladóceros límnicos do Brasil.* Brasília: Universa, UCB, 1997. 156 p.

GALUCH, AV., SUIBERTO, MR., NAKATANI, K., BIALETZKI, A. and BAUMGARTNER, G. Desenvolvimento inicial e distribuição temporal de larvas e juvenis de *Bryconamericus stramineus* Eigenmann, 1908 (Osteichthyes, Characidae) na planície alagável do alto rio Paraná, Brasil. *Acta Sci. Biol. Sci.*, 2003, vol. 25, no. 2, p. 335-343.

GERKING, SD. Larval feeding. In: Gerking, SD. (ed.) *Feeding ecology of fish.* California: Academic Press, 1994. p. 139-170.

GOVONI, JJ., HOSS, DE. and CHESTER, AJ. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico; *Brevoortia patronus, Leiostomus xanthurus* and *Micropogonias undulatus*. *Mar. Ecol. Prog. Ser.,* 1983, vol. 13, p. 189-199.

GOVONI, JJ., BOEHLERT, GW. and WATANABE, Y. The physiology of digestion in fish larvae. *Environ. Biol. Fishes,* 1986, vol. 16, p. 59-77.

LANSAC-TÔHA, FA., THOMAZ, SM., LIMA, AF., ROBERTO MC. and GARCIA, APP. Vertical distribution of some planktonic crustaceans in a "várzea" lake (lake Pousada das Garças) of the floodplain of high river Paraná, MS, Brazil. *Int. J. Ecol. Environ. Sci.*, 1995, vol. 21, p. 67-78.

LANSAC-TÔHA, FA., BONECKER, CC., VELHO, LFM. and LIMA, AF. Composição, distribuição e abundância da comunidade zooplanctônica. In: Vazzoler, AEA., Agostinho, AA. and Hahn, NS. (eds.). *A planície de inundação do alto rio Paraná: aspectos físicos, biológicos e socioeconômicos.* Maringá: EDUEM - Nupélia. 1997. p. 117-155.

LAROCHE, JL. Trophic patters among larvae of fish species of sculpins (Family: Cottidae) in a Maine estuary. *Fish. Bull.*, 1982, vol. 80, no. 4, p. 827-840.

MAKRAKIS, MC., NAKATANI, K., BIALETZKI, A., SANCHES, PV., BAUMGARTNER, G. and GOMES, LC. Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu Reservoir, Brazil. *Environ. Biol. Fishes*, 2005, vol. 72, p. 99-107.

NAKATANI, K., AGOSTINHO, AA., BAUMGARTNER, G., BIALETZKI, A., SANCHES, PV., MAKRAKIS, MC. and PAVANELI, CS. *Ovos e Larvas de peixes de água doce: desenvolvimento e manual de identificação.* Maringá: EDUEM, 2001. 378 p.

NEEDHAM, JG. and NEEDHAM, PR. *Guía para el estudio de los seres vivos de las aguas dulces.* Barcelona: Reverté S. A., 1982. 131 p.

PARRA, O. and BICUDO, CEM. *Introducción a la biología y sistemática de las algas de aguas continentales.* Santiago: Universidad de Concepción, 1995. 268 p.

PEDERSEN, T. and FALK-PETERSEN, IB. Morphological changes during metamorphosis in cod (*Gadus morhua* L.), with particular reference to the development of the stomach and pyloric caeca. *J. Fish Biol.*, 1992, vol. 41, p. 449-461.

RINGUELET, RA., ARÁMBURU, RA. and ARÁMBURU, AA. *Los Peces argentinos de agua dulce*. La Plata: Comisión de Investigación Científica, 1967. 602 p.

ROSSI, LM. Evolución morfológica del aparato digestivo de postlarvas y prejuveniles de *Prochilodus lineatus* (Val., 1847) (Pisces, Curimatidae) y su relación con la dieta. *Rev. Hydrobiol. Trop.*, 1992, vol. 25, no. 2, p. 159-167.

SANTIN, M., BIALETZKI, A. and NAKATANI, K. Mudanças ontogênicas no trato digestório e dieta de *Apareiodon affinis* (Steindachner, 1879) (Osteichthyes, Paradontidae). *Acta Sci. Biol. Sci.*, 2004, vol. 26, p. 291-298.

THORP, JH. and COVICH, AP. *Ecology and classification of North America freshwater invertebrates*. New York: Academic Press, 1991. 911 p.

UIEDA, VS. *Regime alimentar, distribuição espacial e temporal de peixes (Teleostei) em um riacho na região de Limeira, SP.* Campinas: UNICAMP, 1983. 151 p. (Master Thesis).

UIEDA, VS. Ocorrência e distribuição dos peixes em um riacho de água doce. *Rev. Bras. Biol.*, 1984, vol. 44, no. 2, p. 203-213.

WINEMILLER, KO. Ontogenetic diet shifts and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Environ. Biol. Fishes*. 1989, vol. 26, p. 177-199.

Received: 14 June 2007
Accepted: 22 December 2009