



Effects of light-dark cycle on the spatial distribution and feeding activity of fish larvae of two co-occurring species (Pisces: Hypophthalmidae and Sciaenidae) in a Neotropical floodplain lake

P. H. S. Picapedra^{a}, P. V. Sanches^a and F. A. Lansac-Tôha^b*

^aGrupo de Pesquisas em Recursos Pesqueiros e Limnologia, Universidade Estadual do Oeste do Paraná – UNIOESTE, Rua da Faculdade, 645, CEP 85903-000, Toledo, PR, Brazil

^bNúcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá – UEM, Av. Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil

*e-mail: pablo_picapedra@hotmail.com

Received: April 25, 2017 – Accepted: July 12, 2017 – Distributed: November 30, 2018
(With 4 figures)

Abstract

Most studies on mechanisms regulating fish larvae processes have focused on assessing the isolated effects of food distribution and feeding behavior. However, in natural ecosystems, fish larvae may strongly interact with zooplankton organisms in an array of complex, direct and indirect interdependencies. This study analyzed the spatial distribution, diet and feeding behavior of early stages of *Hypophthalmus edentatus* and *Plagioscion squamosissimus*, two fish species co-occurring in an isolated floodplain lake, during the light-dark cycle. Larvae fed more actively during dark periods (dusk and night) when they migrated toward the surface of the lake, and remained on the bottom and fed less during light periods (day and dawn). Cladocerans represented the most frequent prey in the diet of *H. edentatus* larvae. In turn, *P. squamosissimus* larvae initially preferred cladocerans and, as they developed, included calanoid copepods in the diet. Significant differences were detected in the frequencies of food items consumed during larval development, which could be related to a better ability of the most developed stages to explore the environment in search of other prey.

Keywords: diet, predation, feeding preference, trophic strategy, zooplankton.

Efeitos do ciclo claro-escuro na distribuição espacial e na atividade alimentar de larvas de peixes de duas espécies coexistentes (Pisces: Hypophthalmidae e Sciaenidae) em uma lagoa de planície de inundação Neotropical

Resumo

A maioria dos estudos de mecanismos que regulam os processos de larvas de peixes se concentra na avaliação dos efeitos isolados da distribuição do alimento e do comportamento alimentar. No entanto, em ecossistemas naturais, as larvas de peixes podem interagir fortemente com os organismos do zooplâncton em uma série de interdependências complexas, diretas e indiretas. Este estudo analisou a distribuição espacial, dieta e comportamento alimentar dos estágios iniciais de vida de *Hypophthalmus edentatus* e *Plagioscion squamosissimus*, duas espécies de peixes coexistentes em uma lagoa isolada de planície de inundação, durante o ciclo claro-escuro. As larvas se alimentaram mais ativamente durante os períodos escuros (crepúsculo e noite) quando ascenderam em direção à superfície da lagoa, enquanto durante os períodos luminosos (dia e amanhecer) permaneceram no fundo e pouco se alimentaram. Os cladóceros foram as presas mais frequentes na dieta de larvas de *H. edentatus*. Por sua vez, larvas de *P. squamosissimus* inicialmente preferiram cladóceros, e a medida que se desenvolveram incluíram copépodes calanóides na dieta. Diferenças significativas foram detectadas nas frequências dos itens alimentares consumidos durante o desenvolvimento larval, o que poderia estar relacionado a uma melhor capacidade dos estágios mais desenvolvidos em explorar o ambiente na busca por outras presas.

Palavras-chave: dieta, predação, preferência alimentar, estratégia trófica, zooplâncton.

1. Introduction

The combined investigation of feeding behavior and spatial distribution of food resources allows the elucidation of ecological relationships between fish species (Temming et al., 2002; Neves et al., 2015). Feeding strategies of fish larvae are complex. Factors such as composition and availability of food (Sánchez-Velasco, 1998), development of the digestive tract, visual acuity and swimming performance of larvae (Makrakis et al., 2008), and the lighting cycle (Probst and Eckmann, 2009) are important to understand these relationships.

Studies have shown that the lighting cycle is the main driving factor in the distribution of fish larvae in the water column. This includes light-dark or day-night cycles, which are bright or dark periods separated by brief crepuscular periods (dusk, dawn) when light changes rapidly, and the decrease of light during the nightfall that stimulates the migration of larvae toward surface layers, while the increase of illumination in the morning induces the movement to deeper layers (Donner and Eckmann, 2011; Mehner, 2012; Picapedra et al., 2015). During crepuscular periods, light levels minimize the risk of predation and allow the visualization of food in the surface layers (Scheuerell and Schindler, 2003). This behavior is seen as a multi-adaptive strategy, conferring advantages in avoiding predators, bioenergetics efficiency and foraging on zooplankton (Scheuerell and Schindler, 2003; Donner and Eckmann, 2011; Mehner, 2014).

The species *Hypophthalmus edentatus* (Spix, 1829) (Hypophthalmidae, Siluriformes) and *Plagioscion squamosissimus* (Heckel, 1840) (Sciaenidae, Perciformes) have a prominent position in the region studied in the present work, especially because of their economic importance and ecological aspects. *H. edentatus* is a planktivorous filter-feeding fish (specializations of gill rakers) (Lansac-Tôha et al., 1991) and has had great significance for commercial fishing, especially after the damming of the Itaipu Reservoir, when a sudden increase in its stock took place (Ambrósio et al., 2003). *P. squamosissimus* is a piscivore that was introduced in 1967 into the Pardo River by the Companhia de Energia de São Paulo (CESP). Consequently, it spread throughout the Paraná River basin (Torloni et al., 1993). These two species have become successful and are among the dominant species in many environments of the Upper Paraná River floodplain (Langeani et al., 2007), including in areas of environmental protection, such as the Parque Nacional de Ilha Grande (Daga et al., 2009; Baumgartner et al., 2010; Mendonça et al., 2015) and the Parque Estadual das Várzeas do Rio Ivinhema (Reynalte-Tataje et al., 2011).

In the Upper Paraná River floodplain, the distribution of fish larvae abundance has been studied mainly in relation to hydrological factors (e.g. Baumgartner et al., 2008; Silva et al., 2011; Gogola et al., 2013). However, studies on how trophic processes affect the survival of fish larvae are missing. Studies combining diet ontogeny of fish larvae with the distribution of the food resource are still scarce (e.g. Santin et al., 2005; Makrakis et al., 2008).

Avoiding predators and ensuring food are influent factors on the spatial distribution patterns of species (Pearre-Junior, 2003). Based on this assumption, this study tested the hypothesis that fish larvae are distributed differently in the water column during the light-dark cycle in the Xambrê Lake, causing important changes in predation on zooplankton, given the visual foraging nature of fish larvae. We intended to answer the following questions: (i) Does the abundance of larval stages (pre-flexion, flexion and post-flexion) differ between sampled depths (surface and bottom) in the different periods of the light-dark cycle?; (ii) Is there any relationship between the distribution of larval density and selected zooplankton groups?; (iii) Is there any preference period for larvae feeding?; (iv) What are the frequent and dominant food items of larval stages?

2. Material and Methods

2.1. Study site

The studied environment is an isolated marginal lake, Xambrê Lake, approximately 5km long, 1km wide and 3m deep. The Xambrê Lake is located on the left bank of the Paraná River, within the limits of the Parque Nacional de Ilha Grande. It has an extensive floodplain area on its right margin that separates it from the Paraná River (Figure 1). Currently, it is maintained by groundwater and a small stream. Its connection with the Paraná River was sporadic in years with very high floods; the last record was in 1996. However, after the construction of the Porto Primavera Reservoir, there have been no such floods to connect the lake with the Paraná River (Daga et al., 2009; Mendonça et al., 2015).

2.2. Sampling

Monthly samplings were taken from October 2012 to September 2013. Fish larvae were collected in two horizontal transects at two water layers in the Xambrê Lake - surface (0.3 m) and bottom (3 m) - at four different times - day (16:00), dusk (20:00), night (04:00) and dawn (08:00). For fish larvae sampling on the water surface, we used a conical-cylindrical plankton net (500 µm mesh size), which was trawled by boat for 10 min at low speed ($\pm 5 \text{ km h}^{-1}$). For bottom collections, a plankton net of the same mesh size was attached to an iron sled frame and dragged for the same time. Both nets had a mechanical flowmeter (Flowmeter General Oceanics™) attached to the net frame for obtaining the filtered water volume. The captured fish larvae were anaesthetized with benzocaine hydrochloride, in compliance with resolution #714 of 20 June 2002 of the Conselho Federal de Medicina Veterinária, which regulates euthanasia procedures and methods for animals used in research. After this procedure, the material was fixed and stored in plastic flasks (500 ml), filled with 4% formalin, buffered with calcium carbonate.

Zooplankton samples were concomitantly collected with fish larvae. Zooplankton samples were taken using a motorized pump to filter 200 L of water per sample through a conical-cylindrical plankton net (60 µm mesh size). Samples were fixed and stored in plastic flasks (500 ml), filled with 4% formalin, buffered with calcium carbonate.

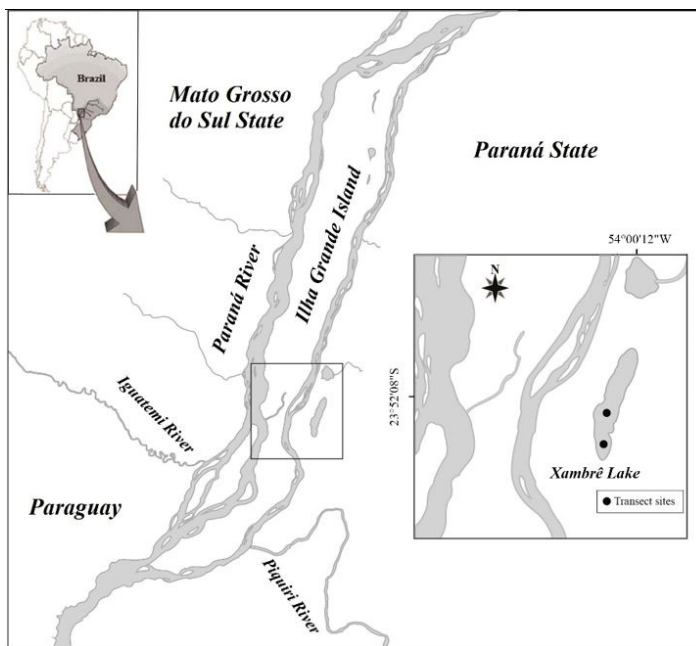


Figure 1. Location of transect sites in the Xambrê Lake, Upper Paraná River floodplain, Brazil.

2.3. Laboratory analysis

Fish larvae were sorted from the rest of the material in a Bogorov acrylic plate under a stereo-microscope (10× magnification). Larvae were classified according to the degree of notochord flexion and development of the caudal fin supporting elements, as proposed by Nakatani et al. (2001), into the stages: (i) pre-flexion: from the beginning of the exogenous feeding to the beginning of the notochord flexion with the emergence of the caudal fin supporting elements; (ii) flexion: from the notochord flexion through the formation of the caudal fin supporting elements to the beginning of pelvic fin formation; and (iii) post-flexion: from the beginning of pelvic fin formation to the segmentation of ray fins, embryonic fin absorption and the emergence of scales. Then, the data on larval abundance were standardized to a volume of 10 m⁻³ of water filtered, according to Nakatani et al. (2001).

Zooplankton abundance was determined by counting the individuals using a Sedgewick-Rafter chamber under an optical microscope (10× to 100× magnification range). This counting was performed in sets of three sequential sub-samples obtained by a Hensen-Stempel pipette, evaluating 7.5 ml from each sample in total. Zooplankton was classified into four functional groups: microfilterers (rotifers and nauplii), cladocerans, calanoids and cyclopoids. Specific bibliography for each study group was used for identification of the organisms. The total abundance was expressed in individuals per m⁻³.

To investigate the diet of fish larvae, we analyzed 348 individuals of *H. edentatus* and 659 of *P. squamosissimus*. Digestive tubes were removed and placed on slides and examined under optical-microscope (40× magnification). In pre-flexion and flexion larvae, the entire digestive tract

was analyzed, and in post-flexion larvae, the stomach and only the anterior two thirds of the intestine was analyzed because of the high degree of digestion of food items in the final portion. The contents were quantified and the items identified at the group level and, whenever possible, at lower taxonomic levels. To identify the preferred period of the day in which feeding occurs, we analyzed the degree of digestion of food items consumed by fish larvae, according to the following criteria: (i) low: when the item was found largely intact; (ii) medium: when only the carapace, or part of it, was found sufficiently preserved; (iii) high: when the item had lost its original shape and had a highly digested carapace (Sánchez-Velasco, 1998).

2.4. Statistical analysis

To test differences in the abundance of different ontogenetic stages (pre-flexion, flexion and post-flexion) of fish species (*H. edentatus* and *P. squamosissimus*) and zooplankton groups (microfilterers, cladocerans, calanoids and cyclopoids) between the surface and the bottom of the lake, we applied a one-way analysis of variance (one-way ANOVA) to each period of the light-dark cycle, with $p < 0.05$ considered significant. We tested for data normality with the Shapiro-Wilk test, and for homoscedasticity, with the Levene test. When the assumptions of ANOVA were not met, we used a nonparametric analysis of variance (Kruskal-Wallis test) to test for differences between medians.

Multiple linear regressions were applied to test the influence of zooplankton in determining the vertical position of fish larvae during the light-dark cycle, with $p < 0.05$ considered significant. For this analysis, we used the weighted mean depth values (WMD) of fish species and zooplankton groups. The average depth during the

different hours of the day for each zooplankton group and fish species was calculated according to the equation of Frost and Bollens (1992): $WMD = (\sum ni \times di) / (\sum ni)$, where ni is the density (individuals per m^{-3}) of the population i and di is the depth of the sample i , which is considered as the midpoint of each depth layer.

To analyze the feeding ontogeny of the larvae, we used the frequency of occurrence (FO) method, whereby the number of stomachs in which a particular item is found is expressed as the percentage of the total number of examined stomachs containing food. We also used the dominance (D) method, analyzing the percentage of the number of times that a particular item is numerically dominant (occurs more often) in a stomach, according to the total of the stomachs (Hyslop, 1980). A permutational multivariate analysis of variance (PERMANOVA) was used to determine whether the composition of food items in the diet differed between ontogenetic stages of the larvae. For this, we used the matrix of frequency of occurrence. Jaccard distance was used as a dissimilarity measure and 9,999 permutations were run to evaluate the significance of the pseudo- F of PERMANOVA ($p < 0.05$).

We calculated ANOVAs and multiple linear regressions in Statistic 7.1 (Statsoft, 2005), and PERMANOVA in PAST 1.68 (Hammer et al., 2001). Before analysis, all data were log-transformed [$(\log x+1)$] to homogenize variances.

3. Results

Early stages of development of *H. edentatus* and *P. squamosissimus* exhibited a clear preference (one-way ANOVA, $p < 0.05$) for the bottom during light periods (day and dawn), and were distributed throughout the two layers at dark periods (dusk and night). Pre-flexion *H. edentatus* larvae showed differences during day and dawn; flexion larvae, during day, dusk and dawn; and post-flexion larvae, during day and dawn. In turn, pre-flexion *P. squamosissimus* larvae showed differences during day and dawn; flexion larvae, during day, dusk and dawn; and post-flexion larvae, during day (Figure 2).

Among zooplankton groups, the abundance of microfilterers at the surface and the bottom were not significantly different, indicating that organisms were

distributed along the water column without preference for any layer during the light-dark cycle. However, differences (one-way ANOVA, $p < 0.05$) were observed in the distribution of microcrustaceans, which had a clear preference for the bottom during light periods (day and dawn) and for the surface during dark periods (dusk and night). Cladocerans, calanoids and cyclopoids copepods showed differences during day, dusk, night and dawn (Figure 3).

Multiple linear regressions pointed out significant correlations ($p < 0.05$) between the WMDs of fish larvae and zooplankton, except between fish larvae and microfilterers. The distribution of *H. edentatus* larvae was correlated with that of cladocerans, calanoids and cyclopoids; and the distribution of *P. squamosissimus* larvae was correlated with that of cladocerans, calanoids and cyclopoids (Table 1).

The degree of digestion of prey consumed by *H. edentatus* larvae revealed that over 58% of the prey had a low degree of digestion during dusk, night and dawn periods, unlike individuals caught during the day, in which 79% of the prey consumed were found in a more advanced degree of digestion (medium and high level) (Figure 4a). As for *P. squamosissimus* larvae, the degree of digestion revealed that more than 60% of the prey consumed had a low level of digestion during dusk and night periods, while during day and dawn periods, over 69% of the prey were already in more advanced degrees of digestion (medium and high) (Figure 4b).

The diet of *H. edentatus* larvae was mainly composed of cladocerans, but there were also copepods, rotifers, algae and insect larvae. Cladocerans were the most frequent prey throughout the larval period, and *Bosmina hagamni* Stingelin, 1904 and *Ceriodaphnia cornuta* Sars, 1886 were the dominant items in the diet, while rotifers and young and adult copepods were the least frequent. The diet of *P. squamosissimus* larvae was basically composed of cladocerans, copepods, rotifers, insect larvae and aquatic mites. Cladocerans, especially *B. hagamni*, were the most frequent and dominant item in the diet of pre-flexion larvae, while calanoid copepods, especially *Argyrodiaptomus furcatus* (Sars, 1901), were the most frequent and dominant for the flexion and post-flexion

Table 1. Multiple linear regressions summary for fish larvae (*Hypophthalmus edentatus* and *Plagioscion squamosissimus*) weighted mean depth (WMD) versus the zooplankton (microfilterers, cladocerans, calanoids and cyclopoids) at that WMD.

Dependent variable	Independent variable	slope	intercept	r^2	p
<i>Hypophthalmus edentatus</i>	microfilterers	-0.361	2.529	0.01	0.376
	cladocerans	1.372	-0.261	0.43	<0.001
	calanoids	1.394	-0.300	0.44	<0.001
	cyclopoids	1.272	-0.052	0.33	<0.001
<i>Plagioscion squamosissimus</i>	microfilterers	-0.108	2.229	0.00	0.722
	cladocerans	0.952	0.539	0.32	<0.001
	calanoids	1.035	0.393	0.29	<0.001
	cyclopoids	0.932	0.590	0.26	<0.001

r^2 = coefficient of determination; $p < 0.05$ indicate significant correlations.

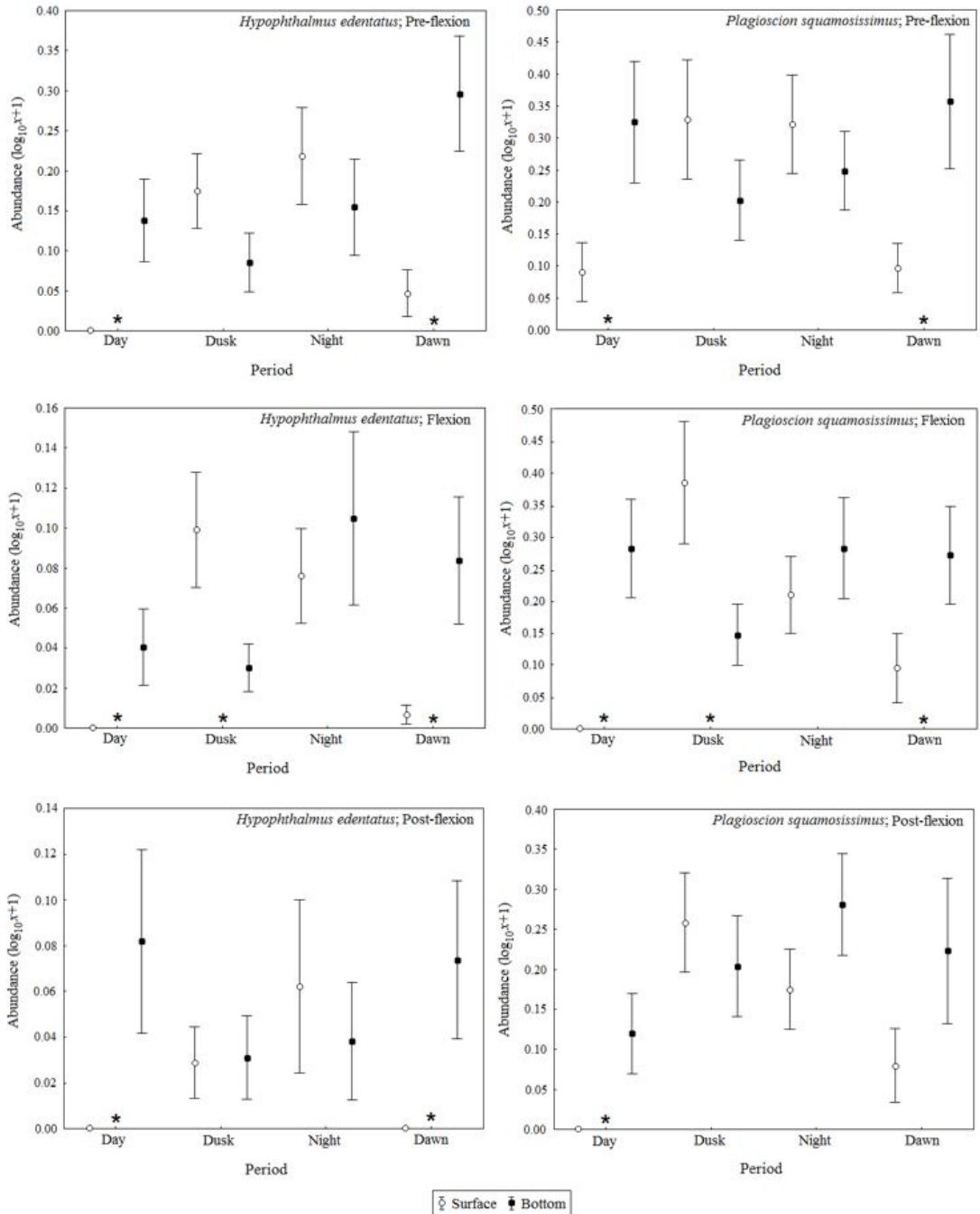


Figure 2. Spatial variation in the mean density of larval stages of *Hypophthalmus edentatus* and *Plagioscion squamosissimus* during light-dark periods in the Xambrê Lake. Symbol: mean value of density; bar: standard error. Asterisks values indicate significant differences ($p < 0.05$) between the depths.

larvae. Rotifers, young stages of copepods (nauplii and copepodids) and cyclopoid copepods were the least frequent in the diet (Table 2). Significant differences in the frequency of occurrence of food items were evidenced by PERMANOVA for the ontogenetic stages of *H. edentatus* (pseudo- $F=14.92$, $p < 0.001$) and *P. squamosissimus* (pseudo- $F=16.95$, $p < 0.001$).

4. Discussion

Data on the spatial distribution patterns of larval abundance of *H. edentatus* and *P. squamosissimus* in the Xambrê Lake demonstrated that even larvae with lower swimming performance (pre-flexion) performed migrations in the water column during the light-dark cycle. After the

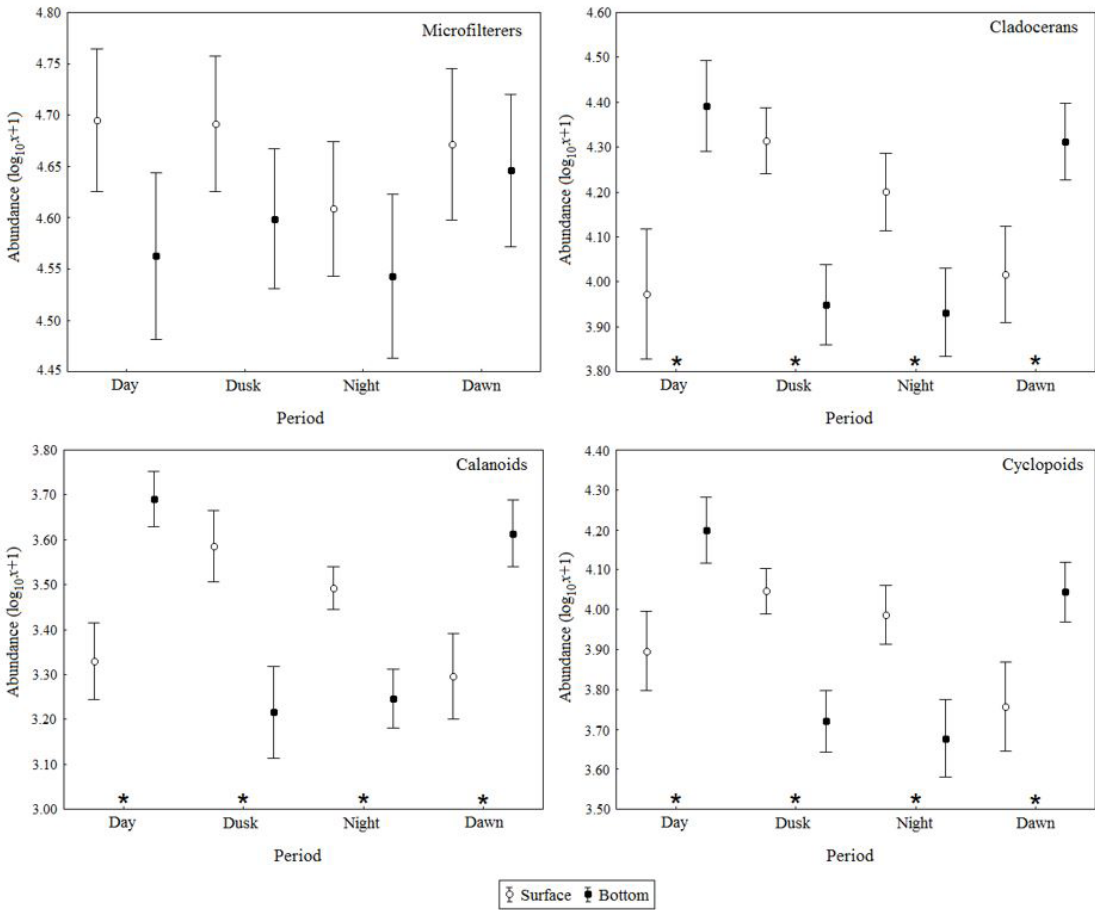


Figure 3. Spatial variation in the mean density of zooplankton (microfilterers, cladocerans, calanoids and cyclopoids) during light-dark periods in the Xambrê Lake. Symbol: mean value of density, bar: standard error. Asterisks values indicate significant differences ($p < 0.05$) between the depths.

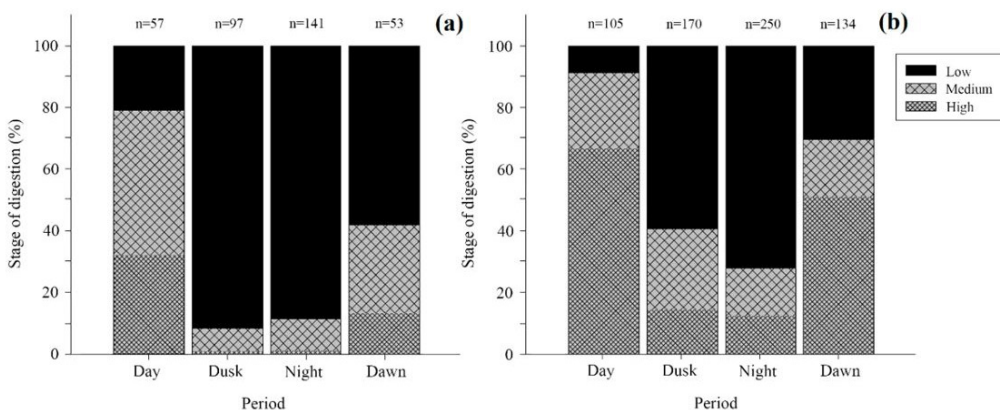


Figure 4. Accumulated percentage to degree of digestion of prey consumed by *Hypophthalmus edentatus* (a) and *Plagioscion squamosissimus* (b) larvae during light-dark periods in the Xambrê Lake. n = number of analyzed stomachs.

flexion of the notochord (flexion and post-flexion stages), larvae are able to control passive drift, and become able to move toward deeper environments in search for shelter and food, while pre-flexion larvae usually presented

difficulty to move and often depended almost entirely on the movement of water to displace, until flexion of the notochord (Grioche et al., 2000). However, the lentic characteristic of the environment combined with the development of

Table 2. Frequency of occurrence (FO) and dominance (D) of food items in the diet of larval stages (PF = pre-flexion, FL = flexion and FP = post-flexion) of *Hypophthalmus edentatus* and *Plagioscion squamosissimus*. n = number of analyzed stomachs.

Food items	<i>Hypophthalmus edentatus</i>						<i>Plagioscion squamosissimus</i>					
	Pre-flexion		Flexion		Post-flexion		Pre-flexion		Flexion		Post-flexion	
	n=157		n=135		n=56		n=171		n=220		n=268	
	FO	D	FO	D	FO	D	FO	D	FO	D	FO	D
Rotifera												
<i>Brachionus calyciflorus</i>	3.7	-	9.7	2.9	2	-	-	-	-	-	0.5	0.6
<i>Filinia opoliensis</i>	-	-	-	-	2	-	-	-	-	-	-	-
<i>Filinia terminalis</i>	0.9	-	-	-	-	-	-	-	-	-	-	-
<i>Keratella americana</i>	-	-	-	-	2	-	-	-	-	-	-	-
Cladocera												
<i>Bosmina hagmanni</i>	80.1	86.6	95.8	87.1	100	75.5	26.9	39.1	42	39.2	44.7	30.3
<i>Ceriodaphnia cornuta</i>	30.1	7.4	66.6	8.6	95.9	14.3	7	5.4	9.1	0.9	14.3	3.3
<i>Ceriodaphnia silvestrii</i>	2.8	-	22.2	-	20.4	-	0.5	-	0.6	-	2.7	0.6
<i>Daphnia gessneri</i>	-	-	1.3	-	4	-	-	-	1.8	-	17.1	3.3
<i>Diaphanosoma spinulosum</i>	-	-	-	-	2	-	2.3	1.2	0.6	-	3.8	-
<i>Moina minuta</i>	5.6	1.2	11.1	1.4	28.5	2	9.3	7.6	1.2	0.9	7.1	-
Unidentified	9.4	4.8	1.3	-	16.3	8.2	16.3	19.5	8.5	3.6	16	5.8
Copepoda												
Cyclopoida nauplii	-	-	-	-	-	-	0.5	-	-	-	-	-
Calanoida	-	-	-	-	-	-	9.3	10.8	7.3	2.7	12.1	1.9
copepodites												
Cyclopoida copepodites	0.9	-	-	-	2	-	2.3	1.2	-	-	4.9	-
<i>Argyrodiaptomus furcatus</i>	-	-	-	-	2	-	11.7	7.6	42.6	42.8	71.8	49
<i>Mesocyclops</i> sp.	-	-	-	-	-	-	-	-	-	-	0.5	-
<i>Thermocyclops minutus</i>	-	-	-	-	-	-	-	-	-	-	0.5	-
Unidentified	-	-	-	-	-	-	6.4	7.6	9.1	9.9	5.5	3.3
Others												
Algae	-	-	1.3	-	-	-	-	-	-	-	-	-
<i>Chaoborus</i> sp.	-	-	-	-	10.2	-	-	-	0.6	-	10.5	1.3
Hydracarina	-	-	-	-	-	-	-	-	-	-	0.5	0.6

swim-bladder at pre-flexion stage (Partridge et al., 2011) allows the vertical displacement of larvae at this stage in the water column.

For most organisms, avoiding the surface layers during light periods is commonly considered as an antipredator behavior (Williamson et al., 2011; Mehner, 2012). The migratory behavior exhibited by fish larvae is probably a defense against visual predation by piscivorous fish. The stay in the bottom during light periods is an effective strategy for survival in the early stages of life, as help them avoid predators in the pelagic zone. The migratory behavior of larvae may be further induced by the isolation of the Xambrê Lake, as this implies an extremely high risk of predation due to the abundance of piscivorous fish (mainly adult *P. squamosissimus*) that cannot disperse to other environments of the floodplain.

The linear regressions between the WMDs of fish larvae and of microcrustaceans revealed significant correlations ($p < 0.05$) and suggest that fish larvae simultaneously follow the migration of microcrustaceans through the water column. According to Donner and Eckmann (2011), some fish species adapt their migration to coincide with the ascent of zooplankton that may also occur in such a way as to synchronize it to the light-dark cycle. This way, diel migration in the early stages of fish life would play an important role in their survival and maximize food intake. However, the higher digestibility of prey consumed during the light periods (day and dawn) suggest that larvae do not actively feed in these periods. Instead, we suggest that larvae feed most actively at dusk and night, when they migrate along with their prey toward the surface, where the lower degrees of digestion of prey were observed.

It is likely that the permanence of larvae at the bottom of the lake during the day and dawn poses a limitation on the feeding activity, as the reduced light penetration at the bottom may hinder the visibility of prey. According to Werner (2002), most fish larvae are visual predators and need adequate light to locate their prey. However, the reduction of light at the bottom is beneficial for the larvae, as this environment limits the success of visual predators to locate them.

Diurnal and nocturnal feeding activity must be related to different light intensity, leading to the alternation in the period of time of light and dark phases of the day (Carvalho and Soares, 2006). Probst and Eckmann (2009) found evidence of “crepuscular windows”, noting that, especially at dusk, fish larvae seem to use this light window to search for prey. Hunter (1968) suggested that with adequate light, as when there is a full moon, some fish are able to feed at the surface at night. When migration toward the surface occurs, fish larvae are probably able to see their prey against the illuminated surface of the environment, which increases the contrast between the prey and the bottom (Cech and Kubecka, 2002). Crepuscular feeding has been also observed during the diel migration of juvenile salmon (*Oncorhynchus nerka*, Walbaum, 1792) (Scheuerell and Schindler, 2003) and may be related to the greater feed efficiency during light windows in crepuscular hours, where fish and zooplankton would be equally abundant. The intensity and duration of feeding during crepuscular and nocturnal periods are decisive for food uptake of planktivorous fish, because the abundance of zooplankton available for fish is usually higher at night, thus potentially facilitating higher crepuscular and nocturnal feeding rates than those rates during the day (Mehner, 2012).

The interaction between fish and zooplankton plays an important role in structuring communities, acting directly on the density, biomass, diversity, and behavior of organisms (Brooks and Dodson, 1965; Zaret, 1980). The consumption of zooplankton prey is usually linked to the size, shape, pigmentation and escape ability of these organisms as well as to the vision, preference, hunger and feeding behavior of predators (Zaret, 1980; Makrakis et al., 2008).

H. edentatus larvae consumed mainly the cladocerans *B. hagmanni* and *C. cornuta* at all stages of development. The preference of *H. edentatus* for cladocerans may be related to the opportunistic characteristic of these larvae (Makrakis et al., 2008), which feed on the most abundant prey in the environment. This is endorsed by traits of the cladocerans, namely, the slow movement, the contrasting eyes and pigmentation that increase their visibility and make them more vulnerable to predation (Zaret, 1980; Rezende et al., 2011). Rotifers and copepods were less frequent in the diet. The lower consumption rate of rotifers may be related to their smaller size and lower pigmentation in relation to cladocerans. Copepods, in turn, are larger and more visible than cladocerans, but are better swimmers, what hinders capture (Zaret, 1980).

P. squamosissimus larvae basically consumed cladocerans and calanoid copepods (mainly *A. furcatus*),

and more predominantly copepods at the flexion and post-flexion stages. Makrakis et al. (2005) and Neves et al. (2015) associated the preference for calanoid copepods in *P. squamosissimus* diet during the larval period with increased visual acuity, swimming ability and protrusion of the jawbone. These characteristics facilitate the capture of copepods by these fish larvae despite the larger size and greater agility of copepods in relation to rotifers and cladocerans. Young stages of copepods (nauplii and copepodids) were less frequent in the diet of larvae, possibly due to lower visibility compared to adults.

The PERMANOVA detected significant differences ($p < 0.05$) in the frequency of occurrence of items consumed between ontogenetic stages of *H. edentatus* and *P. squamosissimus* larvae. The ontogenetic change in the diet could be related to a better capacity of the most developed stages (flexion and post-flexion) to explore the environment in search of larger prey (Mayer and Wahl, 1997). The consumption of larger prey such as calanoid copepods, chironomid larvae (*Chaoborus* sp.) and water mites, found mainly among post-flexion larvae, can support the idea that they try to maximize the gain of energy available in order to compensate for energy expenses with attacks, capture and ingestion of food (Nunn et al., 2012).

In summary, our results provide strong evidence that fish larvae feed preferably during the migration toward the surface in dark periods, as a strategy of larvae to detect their prey close to the illuminated surface, besides the benefit of reduced risk of being predated. On the other hand, the permanence of fish larvae in the darker layer (bottom) of the lake during light periods represents a strategy against visual predators; however, this behaviors seems to hinder their predation on zooplankton. We are able to assert that there are clear evidences of temporal organization in the feeding activity of *H. edentatus* and *P. squamosissimus* during the light-dark cycle. Based on the nocturnal activity, we can suggest the hypothesis of a circadian rhythm for this species, synchronized by the light-dark cycle and/or by the cycle of availability of food. Our findings also showed that the diets of *H. edentatus* and *P. squamosissimus* were mainly made up of microcrustaceans. *H. edentatus* consumed mainly cladocerans, but presented a more diverse diet in the final stage (post-flexion); and *P. squamosissimus* initially preferred cladocerans but expanded its preference to larger prey, such as copepods as the development stage of larvae advanced.

Acknowledgements

We thank Dr. Andréa Białetzki, Dr. Gilmar Baumgartner, Dr. Luiz Felipe Machado Velho and Dr. Paulina Maria Maia Barbosa for suggestions, criticisms and contributions. The authors also acknowledge the Grupo de Pesquisas em Recursos Pesqueiros e Limnologia of the Universidade Estadual do Oeste do Paraná (GERPEL/UNIOESTE), Universidade Estadual de Maringá (UEM), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the logistic and financial support.

References

- AMBRÓSIO, A.M., GOMES, L.C. and AGOSTINHO, A.A., 2003. Age and growth of *Hypophthalmus edentatus* (Spix), (Siluriformes, Hypophthalmidae) in the Itaipu Reservoir, Paraná, Brazil. *Revista Brasileira de Zoologia*, vol. 20, no. 2, pp. 183-190. <http://dx.doi.org/10.1590/S0101-81752003000200002>.
- BAUMGARTNER, G., GUBIANI, É.A., DELARIVA, R.L. and SANCHES, P.V., 2010. Spatial patterns in fish assemblages of Ilha Grande National Park, Brazil. *Wetlands*, vol. 30, no. 2, pp. 309-320. <http://dx.doi.org/10.1007/s13157-010-0031-0>.
- BAUMGARTNER, G., NAKATANI, K., GOMES, L.C., BIALETZKI, A., SANCHES, P.V. and MAKRAKIS, M.C., 2008. Fish larvae from the Upper Paraná River: do abiotic factors affect larval density? *Neotropical Ichthyology*, vol. 6, no. 4, pp. 551-558. <http://dx.doi.org/10.1590/S1679-62252008000400002>.
- BROOKS, J.L. and DODSON, S.I., 1965. Predation, body size and composition of the plankton. *Science*, vol. 150, no. 3692, pp. 28-35. PMID:17829740. <http://dx.doi.org/10.1126/science.150.3692.28>.
- CARVALHO, M.R. and SOARES, L.S.H., 2006. Diel feeding pattern and diet of rough scad *Trachurus lathami* Nichols, 1920 (Carangidae) from the Southwestern Atlantic. *Neotropical Ichthyology*, vol. 4, no. 4, pp. 419-426. <http://dx.doi.org/10.1590/S1679-62252006000400005>.
- CECH, M. and KUBECKA, J., 2002. Sinusoidal cycling swimming pattern of reservoir fishes. *Journal of Fish Biology*, vol. 61, no. 2, pp. 465-471.
- DAGA, V.S., GOGOLA, T.M., SANCHES, P.V., BAUMGARTNER, G., BAUMGARTNER, D., PIANA, P.A., GUBIANI, É.A. and DELARIVA, R.L., 2009. Fish larvae assemblages in two floodplain lakes with different degrees of connection to the Paraná River, Brazil. *Neotropical Ichthyology*, vol. 7, no. 3, pp. 429-438. <http://dx.doi.org/10.1590/S1679-62252009000300010>.
- DONNER, M.T. and ECKMANN, R., 2011. Diel vertical migration of larval and early-juvenile burbot optimizes survival and growth in a deep, pre-alpine lake. *Freshwater Biology*, vol. 56, no. 5, pp. 916-925. <http://dx.doi.org/10.1111/j.1365-2427.2010.02536.x>.
- FROST, B.W. and BOLLENS, S.M., 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 49, no. 6, pp. 1137-1141. <http://dx.doi.org/10.1139/f92-126>.
- GOGOLA, T.M., SANCHES, P.V., GUBIANI, É.A. and SILVA, P.R.L., 2013. Spatial and temporal variations in fish larvae assemblages of Ilha Grande National Park, Brazil. *Ecology Freshwater Fish*, vol. 22, no. 1, pp. 95-105. <http://dx.doi.org/10.1111/eff.12007>.
- GRIOCHE, A., HARLAY, A., KOUUBI, P. and FRAGA-LAGO, L., 2000. Vertical migrations of fish larvae: Eulerian and Lagrangian observations in the Eastern English Channel. *Journal of Plankton Research*, vol. 22, no. 10, pp. 1813-1828. <http://dx.doi.org/10.1093/plankt/22.10.1813>.
- HAMMER, D.A., HARPER, T. and RYAN, P.D. 2001 [viewed 5 September 2015]. PAST: Paleontological Statistics Software package for education and data analysis. *Paleontologia Electronica* [online], vol. 4, no. 1, pp. 1-9. Available from: <http://paleo-electronica.org/>
- HUNTER, J.R., 1968. Effects of light on schooling and feeding of jack mackerel *Trachurus symmetricus*. *Journal of the Fisheries Research Board of Canada*, vol. 25, no. 2, pp. 393-407. <http://dx.doi.org/10.1139/f68-031>.
- HYSLOP, E.J., 1980. Stomach contents analysis, a review of methods and their application. *Journal of Fish Biology*, vol. 17, no. 4, pp. 411-429. <http://dx.doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- LANGEANI, F., CASTRO, R.M.C., OYAKAWA, O.T., SHIBATTA, O.A., PAVANELLI, C.S. and CASATTI, L., 2007. Diversidade da ictiofauna do Alto Rio Paraná: composição atual e perspectivas futuras. *Biota Neotropica*, vol. 7, no. 3, pp. 1-17. <http://dx.doi.org/10.1590/S1676-06032007000300020>.
- LANSAC-TÔHA, F.A., LIMA, A.F., HAHN, N.S. and ANDRIAN, I.F., 1991. Composição alimentar de *Hypophthalmus edentatus* (Spix, 1829) (Pisces, Hypophthalmidae) no reservatório de Itaipu e em um de seus tributários. *Revista Unimar*, vol. 13, pp. 147-162.
- MAKRAKIS, M.C., NAKATANI, K., BIALETZKI, A., GOMES, L.C., SANCHES, P.V. and BAUMGARTNER, G., 2008. Relationship between gape size and feeding selectivity of fish larvae from a Neotropical reservoir. *Journal of Fish Biology*, vol. 72, no. 7, pp. 1690-1707. <http://dx.doi.org/10.1111/j.1095-8649.2008.01845.x>.
- MAKRAKIS, M.C., NAKATANI, K., BIALETZKI, A., SANCHES, P.V., BAUMGARTNER, G. and GOMES, L.C., 2005. Ontogenetic shifts in digestive tract morphology and diet of fish larvae of the Itaipu Reservoir, Brazil. *Environmental Biology of Fishes*, vol. 72, no. 1, pp. 99-107. <http://dx.doi.org/10.1007/s10641-004-6596-9>.
- MAYER, M. and WAHL, D.H., 1997. The relationship between prey selectivity and growth and survival in a larval fish. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 54, no. 7, pp. 1504-1512. <http://dx.doi.org/10.1139/f97-056>.
- MEHNER, T., 2012. Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives. *Freshwater Biology*, vol. 57, no. 7, pp. 1342-1359. <http://dx.doi.org/10.1111/j.1365-2427.2012.02811.x>.
- MEHNER, T., 2014. Partial diel vertical migration of sympatric vendace (*Coregonus albula*) and fontane cisco (*Coregonus fontanae*) is driven by density dependence. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 72, no. 1, pp. 116-124. <http://dx.doi.org/10.1139/cjfas-2014-0009>.
- MENDONÇA, M.M., PICAPEDRA, P.H.S., FERRONATO, M.C. and SANCHES, P.V., 2015. Diel vertical migration of predators (planktivorous fish larvae) and prey (zooplankton) in a tropical lagoon. *Iheringia. Série Zoologia*, vol. 105, no. 2, pp. 174-183. <http://dx.doi.org/10.1590/1678-476620151052174183>.
- NAKATANI, K., AGOSTINHO, A.A., BAUMGARTNER, G., BIALETZKI, A., SANCHES, P.V., MAKRAKIS, M.C. and PAVANELLI, C.S., 2001. *Ovos e larvas de peixes de água doce: desenvolvimento e manual de identificação*. Maringá: Eduem, 378 p.
- NEVES, M.P., DELARIVA, R.L., GUIMARÃES, A.T.B. and SANCHES, P.V., 2015. Carnivory during ontogeny of the *Plagioscion squamosissimus*: a successful non-native fish in a lentic environment of the Upper Paraná River basin. *PLoS One*, vol. 10, no. 11, pp. e0141651. PMID:26524336. <http://dx.doi.org/10.1371/journal.pone.0141651>.
- NUNN, A.D., TEWSON, L.H. and COWX, I.G., 2012. The foraging ecology of larval and juvenile fishes. *Reviews in Fish Biology and Fisheries*, vol. 22, no. 2, pp. 377-408. <http://dx.doi.org/10.1007/s11160-011-9240-8>.
- PARTRIDGE, G.J., BENETTI, D.D., STIEGLITZ, J.D., HUTAPEA, J., MCINTYRE, A., CHEN, B., HUTCHINSON, W. and SCHOLEY, V.P., 2011. The effect of a 24-hour photoperiod on the survival, growth and swim bladder inflation of pre-flexion yellowfin tuna

- (*Thunnus albacares*) larvae. *Aquaculture*, vol. 318, no. 3-4, pp. 471-474. <http://dx.doi.org/10.1016/j.aquaculture.2011.05.039>.
- PEARRE-JUNIOR, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews of the Cambridge Philosophical Society*, vol. 78, no. 1, pp. 1-79. PMID:12620061. <http://dx.doi.org/10.1017/S146479310200595X>.
- PICAPEDRA, P.H.S., LANSAC-TÔHA, F.A. and BIALETZKI, A., 2015. Diel vertical migration and spatial overlap between fish larvae and zooplankton in two tropical lakes, Brazil. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, vol. 75, no. 2, pp. 352-361. PMID:26132018. <http://dx.doi.org/10.1590/1519-6984.13213>.
- PROBST, W.N. and ECKMANN, R., 2009. The influence of light on the diel vertical migration of young-of-the-year burbot *Lota lota* in Lake Constance. *Journal of Fish Biology*, vol. 74, no. 1, pp. 150-166. PMID:20735530. <http://dx.doi.org/10.1111/j.1095-8649.2008.02120.x>.
- REYNALTE-TATAJE, D.A., NAKATANI, K., FERNANDES, R., AGOSTINHO, A.A. and BIALETZKI, A., 2011. Temporal distribution of ichthyoplankton in the Ivinhema river (Mato Grosso do Sul State/Brazil: influence of environmental variables. *Neotropical Ichthyology*, vol. 9, no. 2, pp. 427-436. <http://dx.doi.org/10.1590/S1679-62252011005000017>.
- REZENDE, C.F., MAZZONI, R., CARAMASCHI, E.P., RODRIGUES, D. and MORAES, M., 2011. Prey selection by two benthic fish species in a Mato Grosso stream, Rio de Janeiro, Brazil. *Revista de Biología Tropical*, vol. 59, no. 4, pp. 1697-1706. PMID:22208086.
- SÁNCHEZ-VELASCO, L., 1998. Diet composition and feeding habits of fish larvae of two co-occurring species (Pisces: Callionymidae and Bothidae) in the North-western Mediterranean. *ICES Journal of Marine Science*, vol. 55, pp. 299-308.
- SANTIN, M., DI-BENEDETTO, M., BIALETZKI, A., NAKATANI, K. and SUIBERTO, M.R., 2005. Aspects of the diet of *Astyanax janeiroensis* (Eigenmann, 1908) (Osteichthyes, Characidae) larvae, in the Guaricana Reservoir, Arraial River, Paraná State. *Boletim do Instituto de Pesca*, vol. 31, no. 1, pp. 73-80.
- SCHEUERELL, M.D. and SCHINDLER, D.E., 2003. Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology*, vol. 84, no. 7, pp. 1713-1720. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[1713:DVMBJS\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[1713:DVMBJS]2.0.CO;2).
- SILVA, E.B., PICAPEDRA, P.H.S., SANCHES, P.V., REZENDE, R.E.O., GAVIÃO, A.M., MENDONÇA, M.M., GONÇALVES, E.D.V. and CONTE, R.B., 2011. Larvae occurrences of *Rhamdia quelen* (Quoy & Gaimard, 1824) (Siluriformes: Heptapteridae) in an area under dam influence in the Upper Paraná River region, Brazil. *Neotropical Ichthyology*, vol. 9, no. 2, pp. 419-426. <http://dx.doi.org/10.1590/S1679-62252011005000019>.
- STATSOFT, 2005 [viewed 5 September 2015]. *Statistica (data analysis software system), version 7.0* [online]. Tulsa: Statsoft Inc. Available from: <http://www.statsoft.com/>
- TEMMING, A., BØHLE, B., SKAGEN, D.W. and KNUDSEN, F.R., 2002. Gastric evacuation in mackerel: the effects of meal size, prey type and temperature. *Journal of Fish Biology*, vol. 61, no. 1, pp. 50-70. <http://dx.doi.org/10.1111/j.1095-8649.2002.tb01736.x>.
- TORLONI, C.E.C., CORRÊA, A.R.A., CARVALHO JUNIOR, A.A.C., SANTOS, J.J., GONÇALVES, J.L., GERETO, E.J., CRUZ, J.A., MOREIRA, J.A., SILVA, D.C., DEUS, E.F. and FERREIRA, A.S., 1993. *Produção pesqueira e composição das capturas em reservatórios sob concessão da CESP nos rios Tietê, Paraná e Grande, no período de 1986 a 1991*. São Paulo: CESP, 73 p.
- WERNER, R.G., 2002. Habitat requirement. In: L.A. FUIMAN and R.G. WERNER, ed. *Fishery science: the unique contributions of early life stages*. Oxford: Blackwell Science, pp. 161-182.
- WILLIAMSON, C.E., FISCHER, J.M., BOLLENS, S.M., OVERHOLT, E.P. and BRECKENRIDGE, J.K., 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: integrating ultraviolet radiation and water transparency into the biotic paradigm. *Limnology and Oceanography*, vol. 56, no. 5, pp. 1603-1623. <http://dx.doi.org/10.4319/lo.2011.56.5.1603>.
- ZARET, T.M., 1980. *Predation and freshwater communities*. New Haven: Yale University Press, 187 p.