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Ontogenetic variations and feeding habits of a Neotropical annual fish from southern Brazil

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ABSTRACT. Knowing the feeding biology of a population and its ontogenetic aspects can help in understanding the functioning of fish assemblages, essential to the conservation of the habitat biodiversity in which these species are found. Annual fishes complete their life cycle in temporary aquatic environments, existing in adult stage only for brief annual periods. Changes in the feeding habits between different size classes could indicate that a species belongs to different feeding groups in different growth phases. The aim of this work was to characterize the diet of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of southern Brazil, taking into consideration possible alterations in feeding habits in different body size classes caused by ontogenetic changes, to explain the coexistence of these individuals in a short space of time. The diet analysis indicated that *C. fulgens* is a generalist, consuming small crustaceans and autochthonous insects. Intraspecific differences in diet were determined when compared between nine classes of standard length. Adults fed mainly on autochthonous insects, and juveniles ingested mostly crustaceans, with the population being separated into two trophic groups: invertivores and invertivores with a tendency towards zooplanktivory. It is possible to conclude that the ontogenetic changes in the diet of *C. fulgens* are related to morphological restrictions due to the size of the individuals, since feeding competitive relations are probably not so evident.

KEYWORDS. *Cynopoecilus fulgens*, invertivory, intraspecific feeding overlap, generalist feeding strategy.

RESUMO. Variações ontogenéticas e hábitos alimentares de um peixe anual Neotropical do sul do Brasil. Conhecer a biologia alimentar de uma população e seus aspectos ontogenéticos podem auxiliar na compreensão do funcionamento de assembleias de peixes, fundamental para a conservação da biodiversidade do habitat no qual estas espécies são encontradas. Peixes anuais completam seu ciclo de vida em ambientes aquáticos temporários, sendo encontrados no estágio adulto somente em breves períodos anuais. Mudanças nos hábitos alimentares entre diferentes classes de tamanho podem indicar que uma espécie pertence a distintos grupos alimentares nas diferentes fases do crescimento. Este trabalho teve como objetivo caracterizar a dieta de *Cynopoecilus fulgens* Costa, 2002 em uma área temporariamente alagada na planície costeira sul-riograndense, levando em consideração possíveis alterações nos hábitos alimentares nas diferentes classes de tamanho corporal causadas por mudanças ontogenéticas, visando explicar a coexistência destes indivíduos em um curto espaço de tempo. A análise da dieta indica que *C. fulgens* é uma espécie generalista, ingerindo pequenos crustáceos e insetos autóctones. Diferenças intraespecíficas na composição da dieta foram verificadas quando comparadas entre as nove classes de comprimento padrão estabelecidas. Adultos se alimentaram principalmente de insetos autóctones, enquanto os juvenis ingeriram principalmente crustáceos, sendo a população separada em dois grupos tróficos: invertívoros e invertívoros com tendência à zooplanctivoria. É possível concluir que as mudanças ontogenéticas na dieta de *C. fulgens* estejam relacionadas a restrições morfológicas decorrentes do tamanho dos indivíduos, já que as relações competitivas, em termos alimentares, não são aparentemente tão evidentes.

PALAVRAS-CHAVE. *Cynopoecilus fulgens*, invertivoria, sobreposição alimentar intraespecífica, estratégia alimentar generalista.

Annual fishes belong to a diversified group of Cyprinodontiformes, represented in the Americas by the Cynolebiidae family (previously Rivulidae), which are small-sized and generally sexually dimorphic and dichromatic (Costa, 2008). The so-called annual fishes complete their entire life cycle in temporary aquatic environments, found in the adult stage only during short annual periods, rapidly reaching sexual maturity and spawn (Myers, 1952; Costa, 1995, 1998, 2003; Keppeler *et al.*, 2013). As the temporary ponds dry out and these individuals slowly die, their eggs deposited in the sediment remain in diapause (Vaz-Ferreira *et al.*, 1966; Wourms, 1972). When the rains return after a few months, those eggs hatch, and the fishes show a rapid developmental rate and reach sexual maturity in a few months (Loureiro & de Sá, 1996).

Annual fishes are the most remarkable and abundant top predators in temporary habitats, presenting a generalist diet composed mainly of aquatic organisms, constituting a very important component of this type of ecosystem (Laufer *et al.*, 2009; Polačik & Reichard, 2010). The same biological characteristics that allow annual fishes to live in temporary habitats, make them highly vulnerable to anthropic impacts, such as drainage of wet areas for agriculture purposes and urbanization (Reis *et al.*, 2003; Rosa & Lima, 2008; Lanés & Maltchik, 2010). The majority of annual fish species deserves particular attention with respect to their conservation status due to their high degree of endemism, which increases their vulnerability (Gonçalves *et al.*, 2011). Considering the rapid environmental degradation and the little scientific knowledge of annual fishes, there is an urge of ecological studies that provide scientific support for the development of conservation programs for these temporary environments (Maltchik *et al.*, 2010).

Despite the large diversity of the Cynolebiidae family (Costa, 2008) and the vulnerability of some species (Reis *et al.*, 2003; Rosa & Lima, 2008), ecological characteristics such as feeding, reproduction, behavior patterns, growth, species richness and abundance of annual fishes in temporary environments are poorly known (Arenzon *et al.*, 1999, 2001, 2002; Errea & Danulat, 2001; Shibatta & Rocha, 2001; Shibatta, 2005, 2006; García *et al.*, 2008; Laufer *et al.*, 2009; Arim *et al.*, 2010; Gonçalves *et al.*, 2011; Volcan *et al.*, 2011; Canavero *et al.*, 2013; Lanés *et al.*, 2013, 2014a, b, 2016; Keppeler *et al.*, 2013, 2015; Ortiz & Arim, 2016).

Cynopoecilus fulgens Costa, 2002 (a senior synonym of *C. multipapillatus* according to Costa (2016) and Costa *et al.* (2016)), is distributed in the northern coastal plain of State of Rio Grande do Sul (RS) and southern of State of Santa Catarina (SC) (Costa, 2002b). This species inhabit temporary ponds, including semipermanent wetlands, associated to rivers and lakes, where they are extremely abundant in mid-water (Costa, 2002b; Volcan *et al.*, 2015). Studies on *C. fulgens* covering aspects of life history, embryonic development and toxicity have been conducted in a temporary water body in Tramandaí (RS) (Arenzon *et al.*, 1999, 2001, 2002, 2003) and in temporary ponds in Parque Nacional da Lagoa do Peixe (RS) (Lanés *et al.*, 2014b, 2016). However, to our knowledge, there is only a few information on the trophic ecology of this species (Keppeler *et al.*, 2013, 2015)..

The feeding abilities frequently change during the fish ontogeny, mainly due to modifications in body characteristics that could determine physical restrictions on the prey size and consequent feeding selectivity (Wainwrigth & Richard, 1995; Arim *et al.*, 2010; Keppeler *et al.*, 2013, 2015). Changes in feeding resources choices could indicate that a species belongs to different trophic niches in specific phases of its ontogeny (Rezsu & Specziár, 2006). Therefore, individuals of a population with similar body sizes probably might have similar levels of capture and preferences for prey, will be capable of utilizing the same range of resources, and will interact more competitively than those with different body sizes (Santos-Filho, 1997). There is special interest in knowing which size classes show greater propensity for competition, since the partition of intraspecific resources has been generally neglected in ecological and population studies (Werner & Gilliam, 1984; Persson, 1987).

Assuming that biological characteristics (e.g. feeding habits) interfere directly with population dynamics and represent basic information of the bionomics of a species (Hughes, 1993), knowing the feeding biology of a fish population and its ontogenetic aspects can help in understanding the functioning of an assemblage, essential for the conservation of the biodiversity of their habitat. Considering the biological characteristics of annual fishes, their vulnerability to habitat loss and the scarcity of ecological information for the majority of these species, the aim of this study was to characterize the diet of *C. fulgens* in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, taking into consideration possible changes in feeding habits in different body size classes caused by ontogenetic changes, explaining the coexistence of these individuals in a short space of time, since it is an annual species.

MATERIAL AND METHODS

Study area. The coastal plain of State of Rio Grande do Sul is inserted in the Pampa Biome, characterized by subtropical grasslands, with floristic components of the southern Atlantic Forest, composed by largely pioneer species and restinga forests fragments (Instituto Brasileiro de Geografia e Estatística, 2004). This region is considered of extreme biological importance and one of the prioritized areas for conservation in Brazil due to its heterogeneous and productive environments, with high biological diversity and endemism of ichthyic species (Ministério do Meio Ambiente, 2000; Ministério do Meio Ambiente/Secretaria de Biodiversidade e Florestas, 2006; Volcan *et al.*, 2010).

The Lagoa dos Barros, also known as Lagoa Bacopari, is located in the municipality of Mostardas, along the southern border of the Rio Tramandaí basin (Fig. 1). The sampling site (30°31'48.07"S, 50°25'29.58"W) is situated in the southeast bank of Lagoa dos Barros, temporarily flooded in periods of heavy rains. The sampled area is shallow with muddy substrate, occupied by abundant submersed aquatic vegetation and surrounded by grasses around the margins (Fig. 2). The hydroperiod of the temporary flooded area varied over the

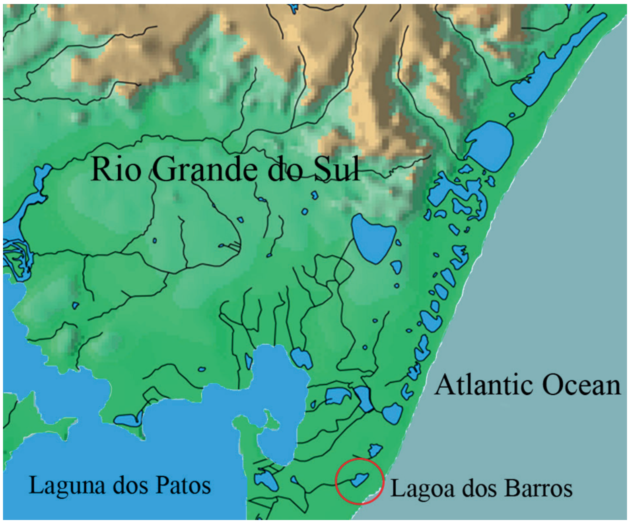

Fig. 1. Map of the study area, showing Lagoa dos Barros, municipality of Mostardas, State of Rio Grande do Sul, Brazil.

year, with the largest volume of rain occurring between July and November of 2010 (during winter and spring seasons), when the rain volume superceded losses from evaporation. During spring, as the air temperature increased, the volume of water began to decrease until the temporary flooded area dried up completely.

Sampling. *Cynopoecilus fulgens* specimens were collected monthly, between July and November of 2010. No samplings were conducted in other months due to the lack of surface water in this temporary flooded area. Samplings were carried out during daylight, at a depth of approximately 40 cm, with seine nets measuring 10 m in length and 2.5 m in height, with a mesh of 0.5 cm. Specimens were euthanized with Eugenol (clove oil, 70 mg/L) and fixed in 10% formalin solution at the sampling site. In the laboratory, specimens were transferred to 70% alcohol, and the standard length (SL) and the intestine length (IL) (both in millimeters) were recorded for each individual. Voucher specimens were deposited in the ichthyological collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul (UFRGS 16220).

Data analysis. The stomach contents of *C. fulgens* were analyzed using a stereomicroscope, and food items identified up to the lowest taxonomic level possible with the help of specific literature (Needham & Needham, 1978; McCafferty, 1981; Mugnai *et al*., 2009).

The food items were grouped into taxonomic and/or ecological categories, as follows: Mollusca, Annelida, Crustacea, Arachnida, autochthonous insects (larvae of Coleoptera, larvae and pupae of Diptera, larvae of Ephemeroptera, adults of Heteroptera, larvae of Odonata, larvae of Trichoptera, larvae of Plecoptera and parts of autochthonous insects), allochthonous insects (adults of Diptera and Plecoptera and parts of allochthonous insects), fish and scales, and material of plant origin (plant matter, seeds and filamentous algae) according to Dias & Fialho (2009, 2011).

The stomach content analysis was based on the frequency of occurrence (Fo, calculated considering the number of stomachs containing a particular food category in relation to the total number of stomachs) (Hynes, 1950) and volumetric frequency (Vo, estimated taking into consideration the quantitative contribution of each item, determined by the number of checkered squares occupied by each item millimeter on ruled paper, in relation to the total number of squares occupied by all items) (Hyslop, 1980). The relative importance of each food category was established according to the feeding index (IAi) (Kawakami & Vazzoler, 1980), calculated according to the formula: $IAi = [(Fo_i \times Vo_i)/\Sigma(Fo_i \times Vo_i)] \times 100$, where i = food item; Fo = frequency of occurrence; and Vo = volumetric frequency.

The diets of males and females of *C. fulgens* were compared by the Spearman correlation test utilizing the Vo values. A positive and significant Spearman coefficient value was expected if the items occurred in the same order of importance for males and females.

A comparative analysis of *C. fulgens* diet, according according to SL class, was carried out to determine the putative influence of body size on feeding habits. The SL classes were defined by the Sturges' method (Vieira, 1991), with the specimens being divided into nine SL classes, as follows: SL1 (n = 19), less than 15.99 mm; SL2 (n = 39), between 16 and 18.85 mm; SL3 (n = 38), between 18.86 and 21.71 mm; SL4 (n = 81), between 21.72 and 24.57 mm; SL5 (n = 61), between 24.58 and 27.43 mm; SL6 (n = 34), between 27.44 and 30.29 mm; SL7 (n = 47), between 30.3 and 33.15 mm; SL8 (n = 35), between 33.16 and 36.01; and SL9 (n = 12), over 36.02 mm (Tab. I). Through observation of gonadal development and/or secondary sexual characteristics, and according to Arenzon *et al*. (1999), the individuals here classified among the classes SL1 and SL3 represent the juveniles in initial and intermediate developmental phases, while the individuals belonging to the SL4 and SL9 classes are the mature adults in advanced developmental phases.

Fig. 2. General view of the sampling points of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

The diet food items proportions in the different SL classes of *C. fulgens* was evaluated on the basis of Fo and Vo values combined in the graphic method proposed by Costello (1990), modified by Amundsen *et al*. (1996). This method consists in a bi-dimensional representation of Vo (abundance) values on the y-axis, and Fo (frequency) values on the x-axis.

To test for ontogenetic differences in the diet of *C. fulgens* between the SL classes, a similarity matrix was generated on the basis of the Bray-Curtis coefficient for the food items using the Vo values. This matrix was used on a non-metric multidimensional scaling analysis (nMDS) with overlap of complete linkage clustering. The data were evaluated by the method of analysis of similarity (ANOSIM), with the food items as samples and the SL classes as factors. ANOSIM compares the similarity between two or more groups or sampling units (factors, in the case of SL classes) and generates a statistic R, which varies between -1 and +1 (Clarke & Gorley, 2006). An R value of zero represents the null hypothesis (there are no differences between the set of samples), meaning that similarities within and between samples were the same, and an R value of 1 indicates that the set of samples (the contribution of the items) between the size classes (factors) were more similar between them than between the levels of each factor. The similarity of percentage (SIMPER) was also determined, using the food items as samples and SL classes as factors. SIMPER analysis was utilized to identify which food item contributed on the differences between the size classes. All analyses were performed with Primer v6 software (Clarke & Gorley, 2006).

The intestinal quotient (IQ) was calculated for each size class of *C. fulgens* to identify the ontogenetic variations in response to feeding behavior (Zavala-Camin, 1996). This quotient is the result of the IL divided by the SL of the fish (Knöppel, 1970; Zavala-Camin, 1996). The IQ values of the different length classes were evaluated by analysis of variance (ANOVA), assuming the prerequisites of normality and homogeneity of variances, using the Primer v6 software (Clarke & Gorley, 2006).

The feeding specialization degree in each size class of *C. fulgens* was determined by calculating the trophic niche breadth by Levins' index measure (Krebs, 1989) utilizing the Vo values. The formula of Hurlbert (1978) was applied to standardize the measure of trophic niche, that can vary from 0 to 1, according to the formula: $Ba_i = \{[1/(n-1)] / [(1-S_j p_{ij}^2)-1]\}$, where: Ba_i = Levins' standardized index for predator i; p_{ij} = proportion of the diet of predator i that consists of prey j; and n = total number of food items. Trophic niche breadth can vary as follows: high (> 0.61), intermediate (0.41 to 0.6) and low (< 0.4) (Novakowski *et al*., 2008).

Food overlap was determined by paired comparisons between the length classes of *C. fulgens* using the simplified Morisita index (Krebs, 1989). Food overlap index varied from 0, when the diets are completely different, to 1, when they showed the same importance of items. According to Zaret & Rand (1971) and Amundsen *et al*. (2003), a value equal to or greater than 0.6 indicates a significant overlap in diets.

RESULTS

A total of 366 specimens of *C. fulgens* were collected, including 218 males (SL between 13.57 and 39.54 mm) and 148 females (SL between 13.14 and 35.19 mm). The monthly distribution of different size classes is shown in table I. The abundance of juveniles (SL1, SL2 and SL3) tends to decrease from July to September, while the adults (SL4 to SL9) increase in abundance from September (Fig. 3).

Cynopoecilus fulgens showed a wide spectrum of consumed food items. Its diet was composed by 25 different items, of which 23 and 18 were found in the stomach contents of males and females, respectively (Tab. II). The Spearman correlation test indicated that the diets of males and females were similar in volume ($r_s = 0.8667$, $p < 0.01$), indicating that there were no significant differences in feeding habits between sexes.

In general, *C. fulgens* fed mainly on crustaceans (for the most part Cladocera, Copepoda and Amphipoda) and on autochthonous insects (especially larvae of Diptera and Odonata), complemented by molluscs (Gastropoda), allochthonous insects (adults of Heteroptera) and plant material (plant matter, seeds and filamentous algae). Subtle differences in diet composition were found between the nine established SL classes (Tab. III), especially between juveniles (SL1 to SL3) and adults (SL4 to SL9). The most abundant food items in the stomach of the first length classes (SL1 to SL3) were crustaceans (67.63%, 60.82% and 53.93%, respectively), followed by autochthonous insects (30.1%, 37.44% and 41.54%, respectively). The same pattern was observed with respect to food importance: crustaceans were the most important food item in the first length classes (SL1 to SL3) (81.58%, 71.1% and 60.45%, respectivelly), followed by autochthonous insects (18.15%, 28.79% e 38.58%, respectivelly), characterizing an invertivory feeding habit with a tendency towards zooplanktivory. The fourth SL

Tab. I. Sampled individuals of *Cynopoecilus fulgens* Costa, 2002 separated by sex and size classes (SL) in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

Standard Lenght	sex	July	August	September	October	November
SL1	F	7	9	1	0	0
	M	2	0	0	0	0
SL2	F	7	22	3	0	0
	M	7	0	0	0	0
SL3	F	2	11	3	5	2
	M	12	2	1	0	0
SL4	F	2	15	6	19	7
	M	20	10	0	2	0
SL5	F	0	5	2	11	5
	M	9	13	2	11	4
SL6	F	1	0	0	2	0
	M	2	9	5	12	3
SL7	F	0	0	0	0	0
	M	0	22	4	19	2
SL8	F	0	0	0	1	0
	M	0	6	2	24	2
SL9	F	0	0	0	0	0
	M	0	2	0	9	1

class (SL4) showed intermediate values of abundance and importance between crustaceans (46.95% and 49.58%) and autochthonous insects (47.49% and 49.52%). Starting with the fifth SL class (SL5) a gradual transition was observed in values of abundance and importance. Autochthonous insects were the food consumed in greatest amount and showed the highest values of food importance (SL5: 52.93% and 54.26%; SL6: 57.3% and 59.69%; SL7: 53.5% and 53.55%; SL8: 57.78% and 59.07%; SL9: 55.15% and 58.91%), followed by crustaceans (SL5: 42.45% and 45.1%; SL6: 32.06% and 38.01%; SL7: 40.47% and 45.57%; SL8: 33.15% and 38.27%; SL9: 37.09% and 39.62%), characterizing an invertivorous diet.

These ontogenetic changes in diet could also be observed with the comparison between the Fo and Vo values, as seen in the Costello graphs (shown in figure 4). Through this graphic representation, we note that juveniles (SL1 to SL3) showed a high preference for crustaceans, and that in the course of ontogenetic development, as observed in the next size classes (SL4 to SL9), starts to consume greater amounts of autochthonous insects and less crustaceans. This supports the categorization of a generalist feeding strategy for *C. fulgens*, regardless of the size class of the individuals.

Similarity analysis by non-metric multidimensional scaling (nMDS) with cluster overlap demonstrated the difference between the diet of juveniles and adults (Fig. 5). The similarity between the first length classes (SL1 and SL2) was of 88-89%, and the grouping of these classes with SL3, with 78% similarity, was due to the high preference for crustaceans in juveniles (Fig. 6). The grouping of the classes SL5 and SL7 with SL4, and SL6 and SL8 with SL9, both with 95 to 98% similarity was due to the great importance of autochthonous insects in the diet. The highest similarities were found between the length classes SL6-SL8

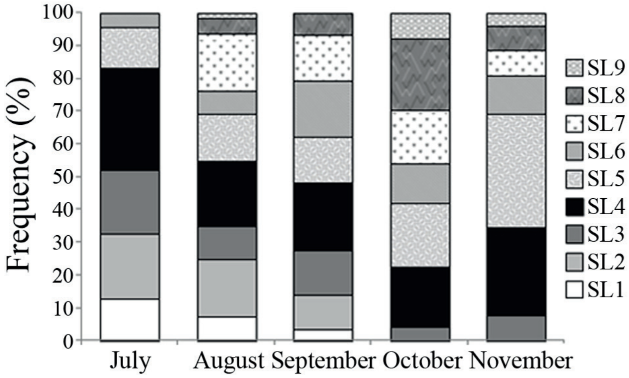

Fig. 3. Frequency (abundance) of *Cynopoecilus fulgens* Costa, 2002 individuals collected in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil, separated in size classes for each month.

Tab. II. Frequency of occurrence (Fo%), volumetric frequency (Vo%) and feeding index (IAi%) for the food items found in the diet of males and females of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil. Standard length (SL, mm) (number of stomachs analyzed): males = 13.57-39.54 mm (218); females = 13.14-35.19 mm (148). * = allochthonous food items.

Alimentary Items	Females			Males		
	Fo	Vo	IAi	Fo	Vo	IAi
Mollusca						
Bivalvia	0.68	0.06	<0.01	0	0	0
Gastropoda	10.14	1.95	0.30	13.31	4.31	1.06
Annelida						
Hirudinea	1.35	0.31	<0.01	0.46	0.07	<0.01
Crustacea						
Amphipoda	10.14	2.88	0.44	16.97	8.72	2.74
Cladocera	87.84	28.46	37.66	74.77	19.82	27.42
Copepoda	77.03	15.72	18.24	75.23	11.07	15.41
Ostracoda	8.78	0.71	0.09	8.26	0.59	0.09
Arachnida						
Hydracarina	18.92	0.45	0.13	14.22	0.38	0.10
Insecta						
Coleoptera larvae	0.68	0.12	<0.01	0	0	0
Diptera larvae	70.95	38.58	41.24	70.18	36.86	47.87
Diptera pupae	0.68	0.06	<0.01	2.75	0.60	0.03
Diptera adult*	0	0	0	0.92	0.12	<0.01
Ephemeroptera nymph	5.41	1.30	0.11	7.80	1.49	0.22
Heteroptera adult	3.38	0.59	0.03	12.39	2.36	0.54
Odonata larvae	14.87	5.69	1.27	21.10	8.24	3.22
Trichoptera larvae	8.11	1.05	0.13	17.89	2.96	0.98
Plecoptera nymph	1.35	0.14	<0.01	1.38	0.21	<0.01
Plecoptera adult*	0	0	0	0.46	0.07	<0.01
Autochthonous insects parts	0	0	0	0.46	0.07	<0.01
Allochthonous insects parts*	0	0	0	0.46	0.10	<0.01
Fish	0	0	0	0.46	0.03	<0.01
Fish scales	0	0	0	6.88	0.53	0.07
Plant material						
Vegetal matter	13.51	1.62	0.33	11.01	0.99	0.20
Seeds	4.73	0.31	0.02	6.42	0.25	0.03
Chlorophyta	0	0	0	4.13	0.16	0.01

Tab. III. Frequency of occurrence (Fo%), volumetric frequency (Vo%) and feeding index (IAi%) of the food items found in the diet of nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil. Classes of standard length (SL, mm) (number of stomachs analyzed). SL1 = less than 15.99 mm (19); SL2 = 16-18.85 mm (39); SL3 = 18.86-21.71 mm (38); SL4 = 21.72-24.57 mm (81); SL5 = 24.58-27.43 mm (61); SL6 = 27.44-30.29 mm (34); SL7 = 30.3-33.15 mm (47); SL8 = 33.16-36.01 mm (35); and SL9 = over 36.02 mm (12). * = allochthonous food items.

Alimentary Items	SL1			SL2			SL3			SL4			SL5			SL6			SL7			SL8			SL9		
	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi	Fo	Vo	IAi
Mollusca																											
Bivalvia	0	0	0	0	0	0	0	0	0	1.23	0.10	<0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	5.26	0.55	0.05	2.56	0.45	0.02	7.89	1.37	0.16	12.35	2.68	0.49	13.11	2.57	0.56	17.65	7.94	2.55	10.64	2.58	0.42	25.71	6.53	3.06	8.33	3.91	0.71
Annelida																											
Hirudinea	0	0	0	0	0	0	0	0	0	1.23	0.10	<0.01	1.64	0.44	0.01	2.94	0.43	0.02	0	0	0	0	0	0	0	0	0
Crustacea																											
Amphipoda	5.26	1.11	0.09	0	0	0	2.63	0.91	0.04	9.88	1.68	0.25	19.67	7.38	2.43	17.65	7.40	2.38	19.15	8.29	2.44	37.14	10.79	7.32	16.67	27.33	9.90
Cladocera	89.47	35.97	52.12	82.05	37.22	45.98	86.84	35.15	46.59	86.42	29.79	38.16	78.69	22.54	29.68	67.65	14.58	17.97	85.11	20.78	27.19	65.71	12.62	15.14	58.33	4.59	5.82
Copepoda	78.95	28.56	36.52	87.18	23.15	30.39	68.42	17.35	18.12	75.31	14.61	16.31	75.41	12.14	15.32	70.59	10.08	12.95	82.98	10.95	13.97	77.14	8.35	11.76	50.00	4.88	5.30
Ostracoda	15.79	1.99	0.51	2.56	0.45	0.02	7.89	0.52	0.06	11.11	0.87	0.14	6.56	0.38	0.04	0	0	0	8.51	0.45	0.06	17.14	1.39	0.43	8.33	0.29	0.05
Arachnida																											
Hydracarina	10.53	0.89	0.15	7.69	0.27	0.03	23.68	0.85	0.31	19.75	0.54	0.16	16.39	0.25	0.07	11.76	0.46	0.10	6.38	0.18	0.02	28.57	0.47	0.25	16.67	0.20	0.07
Insecta																											
Coleoptera larvae	0	0	0	2.56	0.89	0.03	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera larvae	26.32	23.24	9.91	51.28	29.87	23.06	68.42	31.35	32.74	80.25	34.75	41.33	75.41	36.65	46.25	70.59	44.29	56.92	78.72	43.31	52.42	74.29	36.37	49.32	75.00	45.88	74.77
Diptera pupae	0	0	0	0	0	0	0	0	0	0	0	0	6.56	1.26	0.14	2.94	0.22	0.01	2.13	0.27	0.01	0	0	0	8.33	1.95	0.35
Diptera adult*	0	0	0	0	0	0	0	0	0	0	0	0	1.64	0.22	0.01	0	0	0	0	0	0	0	0	0	8.33	0.73	0.13
Ephemeroptera nymph	5.26	1.66	0.14	5.13	2.22	0.17	13.16	4.56	0.92	11.11	2.38	0.39	6.56	0.88	0.10	5.88	1.52	0.16	2.13	0.13	<0.01	0	0	0	8.33	1.46	0.26
Heteroptera adult	5.26	1.11	0.09	2.56	1.78	0.07	10.53	2.13	0.34	11.11	2.43	0.40	11.48	2.24	0.43	8.82	0.65	0.10	4.26	0.95	0.06	14.29	1.91	0.50	8.33	0.49	0.09
Odonata larvae	5.26	3.32	0.28	2.56	0.45	0.02	2.63	1.53	0.06	14.81	5.30	1.16	26.23	7.55	3.31	35.29	9.68	6.22	23.40	7.75	2.79	37.14	15.49	10.50	8.33	5.37	0.97
Trichoptera larvae	5.26	0.55	0.05	5.13	1.34	0.10	13.16	1.67	0.34	17.28	2.53	0.65	21.31	4.14	1.48	11.76	0.94	0.20	8.51	1.09	0.14	22.86	3.31	1.38	0	0	0
Plecoptera nymph	5.26	0.22	0.02	2.56	0.89	0.03	2.63	0.30	0.02	1.23	0.10	<0.01	0	0	0	0	0	0	0	0	0	2.86	0.70	0.04	0	0	0
Plecoptera adult*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.13	0.27	0.01	0	0	0	0	0	0
Autochthonous insects parts	0	0	0	0	0	0	0	0	0	0	0	0	1.64	0.22	0.01	0	0	0	0	0	0	0	0	0	0	0	0
Allochthonous insects parts*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.13	0.41	0.01	0	0	0	0	0	0
Fish	0	0	0	0	0	0	0	0	0	1.23	0.10	<0.01	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fish scales	0	0	0	0	0	0	0	0	0	0	0	0	8.20	0.38	0.05	5.88	0.33	0.04	8.51	0.82	0.11	2.86	0.17	0.01	25.00	1.46	0.79
Plant material																											
Vegetal matter	0	0	0	0	0	0	7.89	1.37	0.16	18.52	1.99	0.55	9.84	0.49	0.08	17.65	1.04	0.33	17.02	1.22	0.33	8.57	1.60	0.25	25.00	1.46	0.79
Seeds	5.26	0.28	0.02	5.13	1.02	0.08	10.53	0.85	0.14	2.47	0.05	<0.01	6.56	0.16	0.02	8.82	0.22	0.04	2.13	0.41	0.01	11.43	0.16	0.03	0	0	0
Chlorophyta	5.26	0.55	0.05	0	0	0	2.63	0.09	<0.01	0	0	0	3.28	0.11	0.01	2.94	0.22	0.01	4.26	0.14	0.01	5.71	0.14	0.01	0	0	0

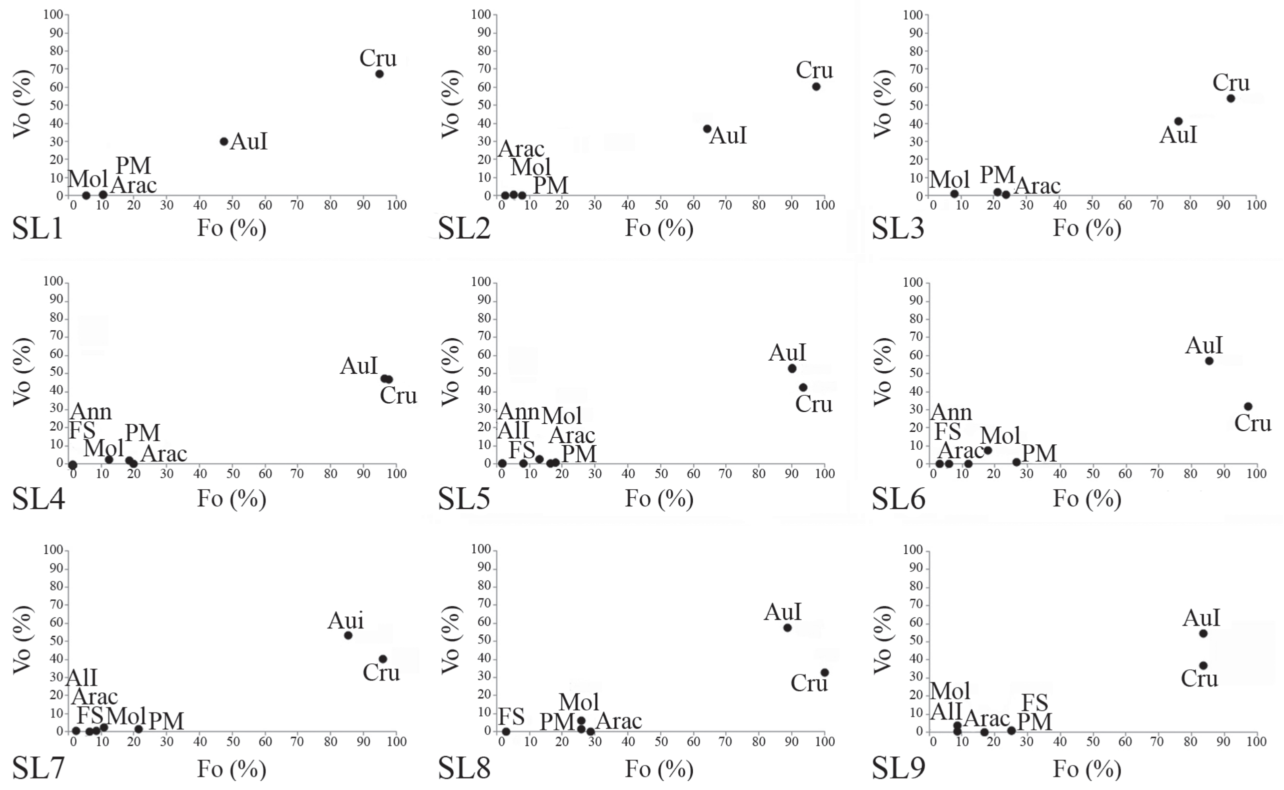

Fig. 4. Costello graphics showing the proportion of food items found in the diet of nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

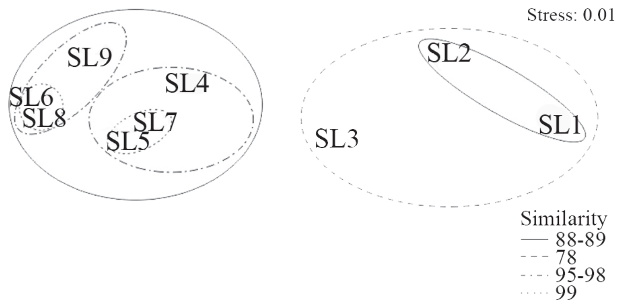

Fig. 5. Ordering according to non-metric multidimensional scaling analysis (nMDS) with cluster overlap (traces), utilizing the Bray-Curtis similarity coefficient, comparing the diets of the different standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

and SL5-SL7 (99% similarity). The similarity between these classes, besides the preference for autochthonous insects in classes SL6 and SL8, occurred due to the representativity of Mollusca and Arachnida, while the similarity between SL5 and SL7 was because of the allochthonous insects and fish and scales. Multivariate analyses of the data also revealed a clear ontogenetic pattern of separation of diet composition and contribution estimated according to size class as indicated by one-way ANOSIM (global $R = 0.067$, $p < 0.01$) (Tab. IV).

SIMPER results (Tab. V) also showed dissimilarity between the diets of the different size classes of *C. fulgens* (42.82%), mainly due to crustaceans and autochthonous insects food items. The highest representativity of crustaceans was observed in the length classes SL1 (77.6%), SL2 (66%) and SL3 (58.6%); crustaceans and autochthonous insects showed similar representativity in the diet of SL4 (49.2% and 45.5%, respectivelly), while the greatest contribution of autochthonous insects was in the diet of SL5 (49.6%), SL6 (50.8%), SL7 (50.8%), SL8 (47.1%) and SL9 (51.1%).

During growth, *C. fulgens* showed morphological alteration in the intestine length/standard length ratio, as seen in the variation in the mean IQ values (Fig. 7). The intestine exhibited negative allometric growth, where it was significantly shorter in the adults ($F = 7.685$, $df = 8$, $p < 0.01$).

The values of the intraspecific trophic niche breadth (Ba) are presented in figure 8. Low niche breadth was shown by the length classes SL1 to SL5 (SL1 Ba = 0.279; SL2 Ba = 0.243; SL3 Ba = 0.352; SL4 Ba = 0.347; SL5 Ba = 0.366), while the length classes SL6 to SL9 displayed intermediate values of niche breadth (SL6 Ba = 0.431; SL7 Ba = 0.404; SL8 Ba = 0.553; SL9 Ba = 0.511), demonstrating a generalist feeding strategy for *C. fulgens*.

The intraspecific food overlap between the size classes of *C. fulgens* was high between all classes (> 0.6). However, smaller values (but still representing food overlap) were observed between the smallest size class (SL1) and the largest ones (SL5 to SL9) (Tab. VI).

DISCUSSION

Despite ther higher incidence of *C. fulgens* juveniles at the beginning of the annual hydrologic cycle and the

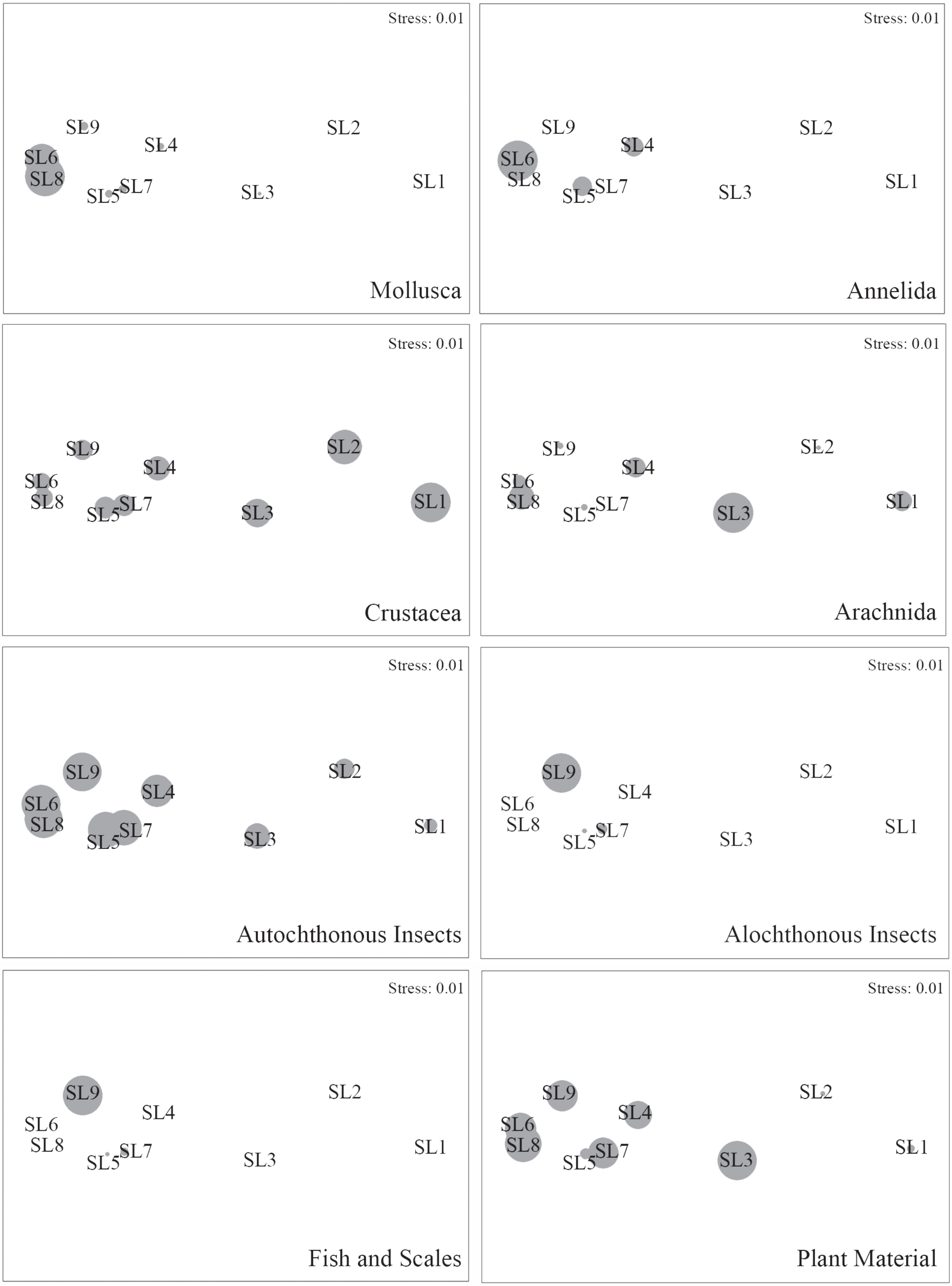

Fig. 6. Contribution of Mollusca, Annelida, Crustacea, Arachnida, autochthonous insects, allochthonous insects, fish and scales and plant material to the diet of nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil, according to the ordering from non-metric multidimensional scaling analysis (nMDS) with cluster overlap. The larger the gray circle, the higher volumetric frequency values of the items.

Tab. IV. Results of analysis of similarity (one-way ANOSIM) between the nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil, showing R and p values. Global R = 0.067, p < 0.01. * = significant values.

ANOSIM one-way		SL1	SL2	SL3	SL4	SL5	SL6	SL7	SL8	SL9
SL1	R value	0								
	p value	0								
SL2	R value	0.394	0							
	p value	<0.001*	0							
SL3	R value	0.017	-0.008	0						
	p value	0.253	0.578	0						
SL4	R value	0.208	0.063	0.052	0					
	p value	<0.001*	<0.001*	<0.001*	0					
SL5	R value	0.141	0.043	0.018	0.021	0				
	p value	<0.001*	<0.001*	0.157	0.075	0				
SL6	R value	0.171	0.108	0.048	0.106	0.020	0			
	p value	<0.001*	<0.001*	<0.001*	<0.001*	0.185	0			
SL7	R value	0.199	0.081	0.038	0.041	-0.007	0.001	0		
	p value	<0.001*	<0.001*	<0.001*	<0.001*	0.614	0.398	0		
SL8	R value	0.256	0.118	0.059	0.061	0.013	-0.005	-0.003	0	
	p value	<0.001*	<0.001*	<0.001*	0.052	0.271	0.492	0.480	0	
SL9	R value	0.260	0.251	0.162	0.241	0.124	0.043	0.102	0.123	0
	p value	<0.001*	<0.001*	<0.001*	<0.001*	<0.001*	0.234	0.087	0.061	0

Tab. V. Results of similarity percentage analysis (SIMPER), showing mean abundance values of each food item in the nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

	Mollusca	Annelida	Crustacea	Arachnida	Autochthonous insects	Allochthonous insects	Fish/ Fish scales	Plant material
SL1	0.47	0	77.60	0.53	20.90	0	0	0.50
SL2	0.62	0	66.00	0.17	31.50	0	0	1.71
SL3	0.93	0	58.60	0.74	38.00	0	0	1.73
SL4	2.74	0.05	49.20	0.64	45.50	0	0.07	1.80
SL5	2.34	0.33	46.10	0.27	49.60	0.24	0.42	0.70
SL6	6.19	0.25	40.40	0.53	50.80	0	0.27	1.56
SL7	2.82	0	41.90	0.15	50.80	0.91	1.22	2.20
SL8	8.78	0	40.40	1.12	47.14	0	0.18	2.38
SL9	8.31	0	35.50	0.16	51.10	0.28	2.67	1.98

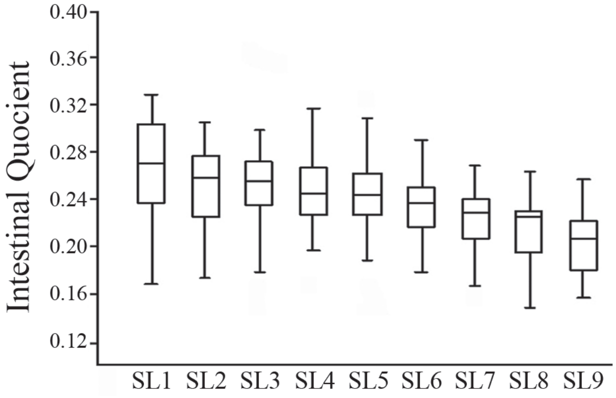

Fig. 7. Intestinal quotient values determined for nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

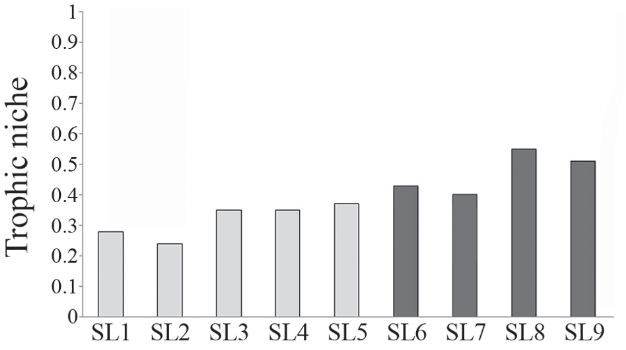

Fig. 8. Trophic niche breadth values calculated by Levins index (Ba) for the diet of nine classes of standard length of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil (SL1 Ba = 0.279; SL2 Ba = 0.243; SL3 Ba = 0.352; SL4 Ba = 0.347; SL5 Ba = 0.366; SL6 Ba = 0.431; SL7 Ba = 0.404; SL8 Ba = 0.553; and SL9 Ba = 0.511). Gray bars indicate a small niche breadth, while the black bars indicate an intermediate niche breadth.

majority of adults at the end of this period, individuals of all size classes were sampled in almost every month, suggesting an asynchrony in hatching times resulting in multiple cohorts per year (Ward *et al*., 2006). As pointed by Arenzon *et al*. (1999), *C. fulgens* does not present a specific reproductive period, spawning continuously over a prolonged time, that is, the recruitment is continuous. Thus, rapid gonadal development, prolonged reproductive period, continuous egg production and spawning, and the diapause process of *C. fulgens* are strategies that result in a "stock"

Tab. VI. Values of food overlap index calculated from paired comparison of the nine standard length classes of *Cynopoecilus fulgens* Costa, 2002 in a temporary flooded area in the coastal plain of State of Rio Grande do Sul, Brazil.

	SL1	SL2	SL3	SL4	SL5	SL6	SL7	SL8	SL9
SL1	1								
SL2	0.983	1							
SL3	0.929	0.981	1						
SL4	0.831	0.917	0.976	1					
SL5	0.779	0.878	0.952	0.996	1				
SL6	0.698	0.812	0.906	0.976	0.992	1			
SL7	0.786	0.883	0.956	0.997	0.999	0.990	1		
SL8	0.702	0.816	0.909	0.978	0.993	0.999	0.991	1	
SL9	0.715	0.826	0.917	0.981	0.995	0.999	0.994	0.999	1

of eggs at different stages of embryonic development in the substrate. These eggs will give rise to embryo hatching flows when abiotic conditions become favorable again, producing different cohorts (Arenzon *et al*., 1999), causing the occurrence of individuals of all length classes in the same sampling, as observed in our study. Such asynchrony in hatching dates could be attributed to a progressive flooding of the pond, with eggs that are deposited on the deeper parts of the substrate hatching first, or as a result of the union of adjacent ponds by accumulating water at different rates and uniting in a larger pond, as seen by Polačik *et al.* (2011), for *Nothobranchius* Peters, 1868 species. This strategy protects the species from a single massive hatching during a short rainy season, which would not allow the fish to mature and reproduce (Arenzon *et al*., 1999). In addition, factors such as intra and interspecific competition and predation could also play important roles on the observed decreased abundance in juveniles of *C. fulgens* over time (Nico & Thomerson, 1989; Winemiller & Jepsen, 1998; Lanés *et al*., 2014b), as detected in our study.

On the other hand, recent studies with members of the Cynolebiidae family demonstrated that there is generally an increase in individual's average size over time, without necessarily the co-occurrence of juveniles and adults in the same period, wich could indicate a hatching synchrony in these populations. Lanés *et al*. (2014b, 2016) observed that the abundances of *Austrolebias minuano* Costa & Cheffe, 2001 and *C. fulgens* in southern Brazil tended to decrease from fall to spring, while the juveniles of both species occur only in the fall and no adult was observed during this season, suggesting a single cohort. Likewise, Lanés *et al*. (2012) found that the average size of *Atlantirivulus riograndensis* (Costa & Lanés, 2009) in Parque Nacional da Lagoa do Peixe (RS) increased over the year, explaining that the variation in body size was related to individual growth through the year.

As a result of the sexual dimorphism in size observed in *C. fulgens* (also observed by Arenzon *et al*., 2001) and of the behavioral patterns of some species (males are territorial in some cynolebiids, according to Shibatta (2006)), feeding was first contrasted between males and females to determine putative differences in this character (Tab. II). Feeding differences between males and females are more evident in species with marked sexual dimorphism in size and are a widely observed phenomenon in animals (Shine, 1989). Also, sexual morphological differences could cause a lower feeding overlap and lower intraespecific competition in some species (Rueffer *et al*., 2006; Cooper *et al*., 2011). However, in our study, the intersexual size differences was not sufficient to result in diet differenciation, as observed by Shibatta & Rocha (2001) for *Simpsonichthys boitonei* Carvalho, 1959 (by frequency and volume), Contente & Stefanoni (2010) for *Atlantirivulus santensis* (Köhler, 1906) (by volume and abundance), and Gonçalves *et al*. (2011) for *Cynopoecilus melanotaenia* (Regan, 1912) (by frequency). These studies and our results reinforce that morphological differences in size between males and females probably did not evolve as a response to minimize intraspecific competition for food. Also, this may be occuring due to a spatial overlap between males and females, resulting in a similar prey capture situation and ability (Contente & Stefanoni, 2010). On the other hand, Laufer *et al*. (2009) for two *Austrolebias* species, Keppeler *et al*. (2013) for *C. fulgens*, and Cavalheiro & Fialho (2016) for *A. riograndensis*, found differences in prey selectivity among males, females and juveniles, attributed to morphological characteristics that could predispose intersexual dissimilarities in diet.

The analysis of diet indicates that *C. fulgens* is a generalist species with an invertivorous diet. This annual fish shows a wide feeding spectrum (25 food items), consuming mostly small crustaceans (mainly Cladocera and Copepoda), and autochthonous insects (mainly larvae of Diptera). A generalist diet, consisting of small autochthonous invertebrates, was also found by Keppeler *et al*. (2013) to *C. fulgens* (52 food items) and by Gonçalves *et al*. (2011) and Laufer *et al*. (2009) to *C. melanotaenia* (26 and 23 food items, respectively), suggesting that this characteristic can be standard in the family (Harrington & Rivas, 1958; Huehner *et al*., 1985; Costa, 1987, 1998, 2009; Davis *et al*., 1990; Taylor, 1992; Shibatta & Rocha, 2001; Shibatta & Bennemann, 2003; Arim *et al*., 2010; Abilhoa *et al*., 2010a, b; Contente & Stefanoni, 2010; Polačik & Reichard, 2010; Cavalheiro & Fialho, 2016; Loureiro & de Sá, 2016; Ortiz & Arim, 2016). The generalist feeding strategy is an expected characteristic for the life history of *C. fulgens* and other annual fishes, since they live in temporary habitats with varied environmental conditions, conferring high resistance to changes in food resources (Costa, 1995, 2002a; Laufer *et al*., 2009; Polačik & Reichard, 2010; Gonçalves *et al*., 2011; Keppeler *et al*., 2013). Moreover, there are few opportunities for feeding specialization in freshwater fishes

(Larkin, 1956), and generalization is especially favored when the preferred food type is available. Thereby, diet specialization would demand significant costs due to the large variation in availability of prey in these environments (Gonçalves *et al*., 2011).

Ontogenetic feeding changes are well known in fishes (Wootton, 1999; Amundsen *et al*., 2003) and have been recorded in some Cynolebiidae species (Santos-Filho, 1997; Laufer *et al*., 2009; Abilhoa *et al*., 2010b; Canavero *et al*., 2013; Keppeler *et al*., 2013, 2015; Cavalheiro & Fialho, 2016; Ortiz & Arim, 2016). These ontogenetic changes in annual fish populations may reduce a potential intraspecific competition for prey items through diet segregation or by reducing direct interactions through spatial and/or temporal segregation (Laufer *et al*., 2009; Canavero *et al*., 2013; Ortiz & Arim, 2016), since is known that competitive interactions are stronger among individuals of similar body sizes (Santos-Filho, 1997; Canavero *et al*., 2013; Ortiz & Arim, 2016). The ontogenetic changes in diet between size classes of *C. fulgens* might occur as a consequence of the increase in body size (Arim *et al*., 2010), and not as a response for minimize intraspecific competition in this studied population. We believe that the most important morphological changes during *C. fulgens* ontogeny are the increase of the mouth gape limitation (Keenleyside, 1979; Magnan & FitzGerald, 1984), handling efficiency of prey items (Xue *et al*., 2005) and swimming ability (Wootton, 1999; Ward *et al*., 2006; Keppeler *et al*., 2015), allowing the consumption of a variety of food items, larger prey items and with a higher caloric content (Abelha *et al*., 2001; Arim *et al*., 2010). This can be interpreted in light of the theory of optimal foraging, which predicts that foragers should select prey items for optimizing their energy intake in relation to the costs of catching, ingesting and digesting these preys (Pyke *et al*., 1977; Werner & Gilliam, 1984; Gerking, 1994; Wainwright & Richard, 1995). However, the abundance of prey items in the environment would not be the only factor that would explain food selection by fishes, since the ontogenetic morphological characteristics related to capture and ingestion could explain the absence of some food items in the diet, despite their abundance in the environment (Sánchez-Hernández *et al*., 2011, 2012; Sánchez-Hernández & Cobo, 2012).

The greater consumption of crustaceans by juveniles was probably the main ontogenetic variation in C. *fulgens* diet. Juvenile fish should maximize growth and survival due to their vulnerability in the early stages of life (Pilatti & Vanni, 2007), consuming abundant prey itens with important sources of protein and keratin, such as crustaceans (Canto-Maza & Vega-Cendejas, 2007). Various studies have demonstrated the preference of juvenile cynolebiids for crustaceans (Gonçalves *et al*., 2011; Keppeler *et al*., 2013; Cavalheiro & Fialho, 2016), probably due to the high availability of this resource, the small size of this prey and the limited agility of juvenile fish. Finally, adults of *C. fulgens* had a tendency to ingest, in addition to crustaceans, a greater amount of autochtonous insects, such as Diptera and Odonata larvae. Probably this behavior reflects the great success of the larger size classes in catching these prey items, being this efficiency in capture increased through ontogeny in response to a higher nutritional demand in adults (Wainwright & Richard, 1995; Adriaens *et al*., 2001; Ortiz & Arim, 2016). Thus, being known that the differentiation of trophic niches within a single population can occur through ontogeny (Werner & Gilliam, 1984; Ward *et al*., 2006), juveniles and adults of C. *fulgens* was separated into two trophic groups according to body size: invertivores with a tendency towards zooplanktivory and invertivores, respectively. It is important to observe that these groups are not truly independent from each other (Woodward & Hildrew, 2002; Arim *et al*., 2010), since they overlap significantly in food preferences. Some studies suggest that with the increase in size of the fish, larger prey items are progressively added to the diet (e.g. insects), while small items are substituted or ingested in smaller amounts (e.g. crustaceans) (Keast & Webb, 1966; Popova, 1967, 1978; Laufer *et al*., 2009; Arim *et al*., 2010; Keppeler *et al*., 2013, 2015; Ortiz & Arim, 2016). As a result, a large-sized adult fish feeds on all prey consumed by the juveniles, along with larger prey items that are available in the environment (Werner & Gilliam, 1984; Woodward & Hildrew, 2002; Ramos-Jiliberto *et al*., 2011; Ortiz & Arim, 2016), as seen in our study.

The invertivorous diet exhibited by *C. fulgens* is consistent with the low IQ values found on the different size classes, and is in agreement with the IQ values found for other cynolebiids (Shibatta & Rocha, 2001; Gonçalves *et al*., 2011). It is well known that the diet influences the intestine length, with carnivorous fishes presenting a shorter intestine than herbivorous, while an intermediate length is typical of omnivorous species (Al-Hussaini, 1949; Kapoor *et al*., 1975; Kramer & Bryant, 1995). Intestine length can be a very useful parameter to evaluate ontogenetic changes that reflect feeding behavior (Knöppel, 1970; Zavala-Camim, 1996). In *C. fulgens*, the intestine presented negative allometry, with lower IQ values shown by the adults (invertivorous diet) and the higher values found in juveniles (invertivorous with a tendency towards zooplanktivory) (Fig. 7). The significance of this allometry might be related to the effect of the increase on the intestine absorption capacities and be a reflection of the dietary habits and needs expressed during development (Kramer & Bryant, 1995; Teixeira de Melo *et al*., 2006). Also, the intestine negative allometric growth in *C. fulgens* might be a result of either: the preadaptation to the invertivorous diet regardless of its stage of ontogenetic development, and/or the negative allometry observed in juveniles agrees with a general behavioral strategy, allowing to grow more in body size during a short period of time (Munch & Conover, 2003; Teixeira de Melo *et al*., 2006). Also, changes in the intestine length could ensure that food will be retained longer in the digestive tract and more nutrients will be absorbed (Karachle & Stergiou, 2012). This would lead to the allocation of more energy for growth in size than in weight to reach adult stages (with a strictly invertivorous diet), since survival (Sogard, 1997) and reproductive success increases with body size (Roff, 1992).

Data on trophic niche breadth are extensively utilized to complement the study of diet composition of fish, where they are useful in the interpretation of the degree of feeding specialization or generalization of a species. The trophic niche breadth of *C. fulgens* increased during ontogeny (Fig. 8). In other words, as the fishes increased in size, they showed preference for a greater diversity of prey items becoming more generalist in relation to the type of food they selected (Winemiller, 1989; Schafer *et al.*, 2002; Woodward & Hildrew, 2002; Winemiller & Kelso-Winemiller, 2003; Ramos-Jiliberto *et al.*, 2011; Sánchez-Hernández & Cobo, 2012; Sánchez-Hernández *et al.*, 2012; Keppeler *et al.*, 2015). This increase in prey richness consumed by adults may be associated with the need of larger fishes to diversify their diets to support higher energy demands (Arim *et al.*, 2010). Also, the increase in trophic niche breadth through ontogeny probably occurred due to the increased in mouth gape limitation, better food handling and swimming capacity, characteristics directly correlated to the larger body size in adults, mentioned before.

The food resources partitioning means the division of prey items by ages or body size classes in a single species through spatial and/or temporal segregation, for the purpose of exploiting food resources to their maximum (Schoener, 1974; Hurlbert, 1978; Violle *et al.*, 2012). We believe that the high feeding overlap observed among the different body size classes in C. *fulgens* does not necessarily imply that the intraspecific competition exists. The juveniles and adults cynolebiids with similar morphology may present segregated diets, occuping different trophic niches, or may reduce intraspecific interferences by feeding at different times and/or microhabitats, reinforcing the role of interactions influenced by body size as an important determinant in the interactions between species and the structure of the food chain in this temporary system (Laufer *et al.*, 2009). Arim *et al.* (2010), Canavero *et al.* (2013) and Ortiz & Arim (2016) observed a clear spatial segregation in annual fishes of different body size classes in temporary ponds in Uruguay, where the main determinants of the assembly structure appear to be the differences in the trophic niche and the opposing interactions between size classes. Thus, spatial segregation by body size classes could allow coexistence by reducing intraspecific interactions (Canavero *et al.*, 2013), and we believe that it may be happening in the population studied here. In addition, we also believe that the available food items were sufficiently abundant (Gerking, 1994; Dias & Fialho, 2009, 2011), not being the cause of competition, allowing the feeding patterns observed in *C. fulgens* in this temporary flooded area, although the availability of food resources was not evaluated in the present study.

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