Neotropical Ichthyology, 14(2): e150178, 2016
DOI: 10.1590/1982-0224-20150178

Journal homepage: www.scielo.br/ni

Diet-morphology relationship in the stream-dwelling characid *Deuterodon stigmaturus* (Gomes, 1947) (Characiformes: Characidae) is partially conditioned by ontogenetic development

Renato Bolson Dala-Corte[1], Eliane Regina da Silva[2] and Clarice Bernhardt Fialho[3]

We tested whether interindividual variations in diet composition within a population of *Deuterodon stigmaturus* can be explained by morphological differences between individuals, and whether diet-morphology relationships are dependent on the ontogenetic development. We analyzed diet of 75 specimens sampled in a coastal stream of Southern Brazil. Variation in stomach content was summarized with a Principal Coordinate Analysis (PCoA). The retained PCoA axes were tested as response to standard length (SL), and to values of intestine length (IL) and mouth length (ML) independent of body size, using linear mixed-effects models (LMM). The most consumed food items by *D. stigmaturus* were filamentous algae (41%), terrestrial plants (20.3%), detritus (12%), and aquatic invertebrates (8.8%). The LMMs showed that SL was positively related to consumption of terrestrial plants, whereas IL independent of SL was negatively related to aquatic invertebrates and positively related to filamentous algae. When body sized was held constant, ML was not related to diet variation. Interindividual diet differences conditioned to body size suggest that individuals shift their trophic niche and function in the ecosystem along the ontogenetic development. Relationships between intestine length and diet composition suggest interindividual differences in foraging ability and digestibility of distinct food items.

Nós testamos se variações na composição da dieta de uma população de *Deuterodon stigmaturus* podem ser explicadas por diferenças morfológicas entre indivíduos, e se as relações entre morfologia e dieta são dependentes do desenvolvimento ontogenético. A dieta de 75 indivíduos amostrados em um riacho costeiro do sul do Brasil foi analisada. Uma Análise de Coordenadas Principais (PCoA) foi utilizada para sumarizar variações individuais no conteúdo estomacal. Os eixos retidos da PCoA foram testados como resposta ao comprimento padrão (CP) e ao comprimentos do intestino (CI) e da boca (CB), independentes do tamanho corporal, usando modelos lineares mistos (LMMs). Os itens macroscópicos mais consumidos por *D. stigmaturus* foram algas filamentosas (41%), plantas terrestres (20,3%), detritos (12%), e invertebrados terrestres (8,8%). Os LMMs mostraram que o CP foi positivamente relacionado ao consumo de plantas terrestres, enquanto que valores de CI independentes de CP foram negativamente relacionados ao consumo de invertebrados aquáticos e positivamente relacionados ao consumo de algas filamentosas. Quando o CP foi mantido constante, CB não foi relacionado a composição da dieta. As diferenças na dieta condicionadas ao tamanho corporal sugerem que os indivíduos mudam seu nicho trófico e função no ecossistema ao longo do desenvolvimento ontogenético. As relações entre o tamanho do intestino e composição da dieta sugerem diferenças individuais na habilidade de forragear e digerir itens alimentares distintos.

Keywords: Characin, Coastal drainage, Feeding, Freshwater fish, Intraspecific variation.

Introduction

Freshwater fishes can exhibit a high degree of intraspecific plasticity in their feeding habits (Winemiller, 1989; Horppila *et al*., 2000; Hegrenes, 2001; Svanbäck & Bolnick, 2007). Several factors can influence variation in food items consumed by conspecific fish individuals, such as spatial and temporal availability of food items (Amundsen *et al*., 2001; Vitule *et al*., 2008; Scharnweber *et al*., 2011), morphological and physiological differences within or between populations (Turingan *et al*., 1995; Bouton *et al*., 1999; Pfaender *et al*., 2010) and changes along the ontogenetic development (García-Berthou & Moreno-Amich, 2000; Drewe *et al*., 2004; Ward-Campbell

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[1] Programa de Pós-Graduação em Biologia Animal, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil. renatocorte@gmail.com (corresponding author)

[2] Programa de Pós-Graduação em Botânica, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil. anesilva.bio@gmail.com

[3] Departamento de Zoologia, Universidade Federal do Rio Grande do Sul. Av. Bento Gonçalves, 9500, 91501-970 Porto Alegre, RS, Brazil. cbfialho@pro.via-rs.com.br

& Beamish, 2005). On the other hand, some fish species specialize in foraging on one or few food items, and become limited to exploit alternative resource types (*e.g.* Collar *et al*., 2009; López-Fernández *et al*., 2012; Brooker *et al*., 2014) hence, low interindividual variation in diet composition can be expected.

A number of studies have documented that several characid species can alter their diets according to food availability (*e.g.* Kramer & Bryant, 1995b; Bojsen, 2005; Casatti & Castro, 2006; Uieda & Pinto, 2011), suggesting that characins may comprise one of the groups with highest feeding plasticity among freshwater fishes. For example, characids may present intraspecific variation in the ingestion of food items according to longitudinal location within a given stream (Manna *et al*., 2012). Also, characins can alter their diets in response to riparian deforestation (Bojsen, 2005). In addition to diet variation between populations, great differences were evidenced in stomach content of characid individuals within a given population, such as those owing to seasonal availability of food (Vitule *et al*., 2008; Uieda & Pinto, 2011), or from ontogenetic shifts (Drewe *et al*., 2004; Vitule *et al*., 2008; Manna *et al*., 2012).

Among the mechanisms that can lead to interindividual differences in diet of a species, some studies have suggested that morphological divergences between individuals that occur along the ontogenetic development play a relevant role (Kramer & Bryant, 1995a; Novakowski *et al*., 2004; Ward-Campbell & Beamish, 2005 ; Zhao *et al*., 2014). For example, Novakowski *et al*. (2004) demonstrated that three species of characins of the *Roeboides* Günther shift their feeding behavior and diet composition by increasing the amount of scale-eating along the ontogenetic development, and these changes match the migration of teeth to the exterior of the mouth. Drewe *et al*. (2004) found that *Brycon guatemalensis* Regan, 1908 shifts its diet from insectivorous to frugivorous, concomitant with an increase in intestine length, along the ontogenetic development.

Intestine length is an important trait associated with diet composition of fish species (Kramer & Bryant, 1995a, b). Species that ingest low nutritional and more difficult to digest food items usually have longer digestive tracts (Kramer & Bryant, 1995b). Therefore, detritivorous are expected to have longer intestines than herbivorous, which in turn are expected to have longer intestines than omnivorous and insectivorous species (Kramer & Bryant, 1995b; Davis *et al*., 2013). In addition, interindividual differences in intestine length within a population have been suggested to be related to the type of ingested food (German & Horn, 2006; Wagner *et al*., 2009; Scharnweber *et al*., 2011). Longer intestines are expected to more efficiently digest vegetal matter, detritus and less nutritional food resources (Kramer & Bryant, 1995b), which may potentially have an effect on individual fitness. Furthermore, size of intestine can be constrained by body size and thus larger individuals are expected to have longer intestines, which may also influence detection of changes in dietary composition along the ontogenetic development (Kramer & Bryant, 1995a; Drewe *et al*., 2004; Vitule *et al*., 2008). Despite the several well known potential sources of variation in feeding composition of fish individuals, it is still not fully understood how small-scale interindividual variations in morphological characteristics constrain feeding behavior and dietary composition of fishes.

Deuterodon Eigenmann is a genus of small-sized characins that inhabit stream ecosystems in southern and southeastern Brazil (Lucena & Lucena, 2002). *Deuterodon* species are known by the atrophy of their upper lip on the sides of the head leading to exposed teeth in the maxilla and premaxilla (Lucena & Lucena, 2002). These exposed teeth are used by *Deuterodon* species to graze the periphyton layer of streambeds and to browse leaves and submerged plant fragments (Sabino & Castro, 1990), though other items as aquatic insects can be commonly found in their diets (Vitule *et al*., 2008). Therefore, although the mouth of *Deuterodon* species suggests a specialized diet, studies evidence that species can present omnivorous and opportunistic behavior, depending on food availability (Sabino & Castro, 1990; Vitule *et al*., 2008), which is an expected characteristic for characin species without an apparent specialization in mouth morphology. Also, Vitule *et al*. (2008) indicated that diet of *Deuterodon* shifts along the ontogenetic development concomitant with an increase in the intestine length.

Regarding interindividual variation in diet and in morphology of characins, we aimed to investigate the feeding strategy of *Deuterodon stigmaturus* (Gomes, 1947), testing whether variations in stomach content is explained by interindividual differences in morphology, and whether morphology-diet relationships are related to ontogenetic development. We specifically aimed to answer the following questions: 1) Does diet composition of individuals with longer intestines include a higher proportion of low-protein and indigestible food items, such as detritus, vascular plants and algae? 2) Is mouth length (measured as length of maxilla and premaxilla bones with exposed teeth) - hypothesized to be a *Deuterodon* feeding specialization - positively related to the ingestion of specific food such as periphyton? 3) Are shifts in diet composition and morphology conditioned to ontogenetic development (measured as standard length)?

Material and Methods

Study area and fish sampling. The study was carried out in the Paraíso stream, a second order tributary of the Mampituba River in the Southern Brazil coastal region (29°23’55”S 49°55’01”W, 16 m a.s.l.; Fig. 1). Mampituba is a mountain river that lies at the Atlantic forest region. Regional climate has well-defined seasons with a mean annual precipitation of 1,409 mm and mean monthly temperature of 18.3°C (Maluf, 2000). The sampled site comprised a 120-m long stream segment, which includes riffle-pool sequences with rocky bed and low turbidity. The channel of the sample site has about 10-m width, with 20-30 cm depth in the riffles and 80-100 cm depth in the pools. Local canopy shading is reduced due to sparse riparian vegetation. Sampling site was chosen because previous investigation has shown that the sampled site holds a great abundance of *D. stigmaturus* (Dala-Corte, personal observation).

We collected specimens of *D. stigmaturus* during five different months using a combination of sampling methods, which were both applied for riffle and pool habitats. Total number of individuals caught was 75; with a mean of 15, minimum of 10 and maximum of 18 individuals per month: August (n = 18) and September (n = 10) of 2010, and March (n = 16), May (n = 17) and July (n = 14) of 2011. The sampling methods included seine (5 mm mesh), gillnets (15 mm mesh) and cast nets (12 mm mesh). All captured fishes were anesthetized with eugenol (clove oil) before fixation with 10% formalin. In addition, in the same site where we sampled fishes, we also performed underwater observations of the feeding behavior of *D. stigmaturus* using method *ad libitum* (Sabino, 1999), in order to interpret the results in the light of the species' behavior. We carried out these observations in five additional field expeditions during the summer (December 2010 to February 2011).

Morphological traits. We used intestine length, mouth length and body size as morphological traits to predict diet variation because of previous information indicating importance of these variables to diet of *Deuterodon* and other fish species. Intestine length may constrain digestion of different food items (Kramer & Bryant, 1995b); mouth length may be important because of previous underwater observation of the feeding behavior of *Deuterodon* species (Sabino & Castro, 1990); body size is widely recognized by its importance to determine prey size and also to influence morphology and size of other morphological traits (Gatz, 1979).

To answer the questions about the effects of intraspecific variation in morphology on the dietary composition of *D. stigmaturus*, we first measured standard length, intestine length, and mouth length of 75 individuals. Standard length (SL) - used to infer ontogenetic development - was measured from the tip of the snout to the posterior end of the last vertebra, *i.e.*, excluding the caudal fin. Intestine length (IL) was measured from the joint with stomach to the most distal part of the intestine (ending at urogenital opening), with the intestine fully extended. Mouth length (ML) was the length of maxillary and premaxillary bones with exposed teeth on the right side of mouth. All measurements were taken using a digital calliper with precision of 0.01 mm.

Standard length was highly correlated to IL ($r = 0.95$) and to ML ($r = 0.99$). Hence, in order to obtain values of IL and ML that are independent of SL (*i.e.* independent of ontogenetic development), we regressed IL and ML against SL and recorded their residuals. In other words, we calculated values of IL ($IL_{residuals}$) and ML ($ML_{residuals}$) that are not explained by body size, reducing their correlations with SL. The correlations of SL values with $IL_{residuals}$ ($r < 0.001$), and with $ML_{residuals}$ ($r < 0.001$) were almost zero, allowing us to interpret their independent effects on diet. We carried out these analyses using R (R Development Core Team, 2015).

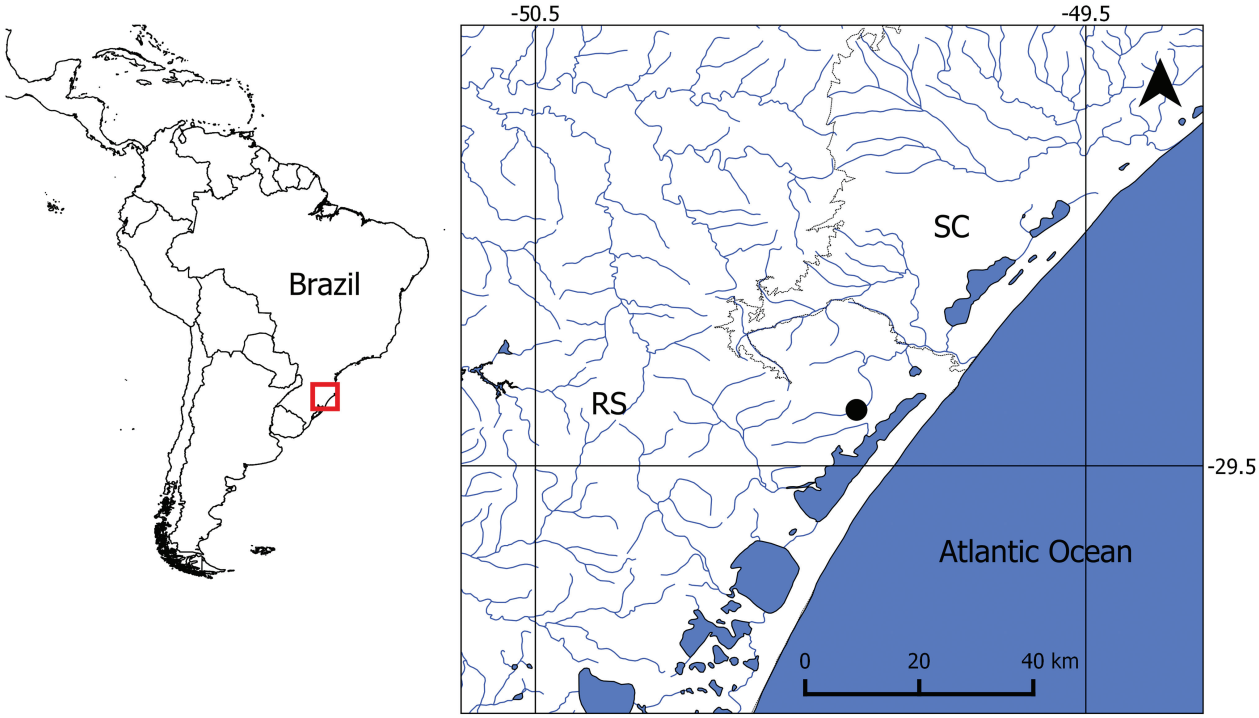

Fig. 1. Location of the sampling site of *Deuterodon stigmaturus* (black dot) in the Paraíso stream, a tributary of the Mampituba River in Southern Brazil coastal region, between Rio Grande do Sul (RS) and Santa Catarina (SC) states.

Stomach content. We analyzed a total of 75 individuals of *D. stigmaturus*, ranging from 29.11 to 101.35 mm SL (Table S1, supplementary material). This size range included individuals within the full range of sexual maturity according to the size at first maturity (L_{50} = 63 mm SL) and also to the size at which 100% of individuals are mature (L_{100} = 80 mm SL), provided by Dala-Corte & Fialho (2014). Macroscopic items found in the stomachs were quantified using an adaptation of the point method (Hynes, 1950; Hyslop, 1980). This adaptation consisted in quantifying the volume of each food item in a stereomicroscope using a graph paper under a Petri dish. Stomach contents were compressed to 1 mm height in order to allow calculating the volume in each cell of the graph paper (mm^3). This method allowed us to calculate the relative volume of each food item in the stomachs.

A large volume of items in the stomachs was too small to identify macroscopically. Then, we used a microscopic analysis to more accurately identify the items that compose the ingested detritus (*i.e.* particulate matter). Sub-samples of detritus found in each stomach were taken and 10 randomly selected fields in a transparent graph paper of 1-mm^2 were analyzed using a 100-fold microscopic increase. The number of times in which each microscopic food item was found was recorded in detritus analysis to calculate frequency of occurrence.

Data analysis. To visualize possible patterns regarding the food items ingested by *D. stigmaturus* individuals, a matrix with Hellinger-transformed (Legendre & Gallagher, 2001) food items volume (*i.e.* dietary composition) was submitted to a Principal Coordinate Analysis (PCoA), using Bray-Curtis dissimilarity. We used the package *BiodiversityR* to test which axes explained significant percentage of variance based on the broken-stick criterion (Kindt & Coe, 2005). We thus retained the four first Principal Coordinate (PCo) axes because each one summarized a significant proportion of diet variation based on broken-stick criterion. Subsequently, to test whether intraspecific variation in stomach content differs due to changes in mouth morphology and intestine length, as well as standard length, we fitted liner mixed-effects models using the scores of the retained PCo as response variables and SL, $IL_{residuals}$ and $ML_{residuals}$ as fixed effect predictors, in a total of nine different models. Liner mixed-effects modeling allows model fitting using random effects as blocking variable to control for their effects on response variables (Bates, 2010). Thus, in each one of our fitted models, we used the five sampling months as random effect variable to control for this source of variation on individual's diet. Response variables (PCo) were submitted to logarithmic transformation to meet assumptions of normality and homogeneity of variance of model residuals. We interpreted the validity of models based on five criteria for model evaluation: (i) standardized beta coefficient (Std-beta), which is standardized mean slope value of the fixed effect; (ii) Z-value; which is the standard score or the number of standard deviations that the observation is above the mean; (iii) R^2 (fixed-effect), which consisted in the variation explained exclusively by the fixed effect variable; (iv) R^2 (full model), which is the summed variation explained by both fixed and random effects; and (v) P-value, which is the fixed effect significance. Calculation of the R^2 for the linear mixed-effects models were based on Nakagawa & Schielzeth (2013) and was carried out with the package *MuMIn* (Bartoń, 2015) for R environment (R Development Core Team, 2015). The PCoA and the linear mixed-effects models were carried out using the packages *vegan* (Oksanen *et al*., 2013) and *lme4* (Bates *et al*., 2015), respectively, for R environment (R Development Core Team, 2015).

Results

The most consumed macroscopic food items by *D. stigmaturus* were filamentous algae (41%), terrestrial plants (20.3%), detritus (12%) and terrestrial invertebrates (8.8%), which represented 82.1% of the total volume (Table 1). In the microscopic analysis of detritus content, the most frequently found food items were diatomaceous algae (100%), particulate organic matter (82.8%), microscopic filamentous algae (73.3%), sediment (65%), and desmids algae (20%) (Table 2).

First four axes of the Principal Coordinate Analyses (PCoA) summarized significant proportion of variation in diet composition based on the broken-stick criterion: 35.9% (PCo1); 12% (PCo2); 9.5% (PCo3) and 7.5% (PCo4). The PCo1 summarized a gradient from individuals that ingested mainly filamentous algae (negative PCo1 scores) to those that ingested relatively more terrestrial plants (positive PCo1 scores) (Fig. 2). The PCo2 segregated those individuals that differed regarding consumption of organic matter (positive PCo2 scores) and detritus (negative PCo2 scores) (Fig. 2). The PCo3 distinguished individuals regarding the volume of aquatic invertebrates (positive PCo3 scores); whereas PCo4 axis was related mainly to ingestion of sediment (positive PCo4 scores) (Fig. 3; Table 1).

Linear mixed models to predict diet variation summarized in PCo1, PCo2, PCo3 and PCo4 indicated that SL and $IL_{residuals}$ were the only morphological traits that affected feeding composition of *D. sigmaturus* individuals (Table 3). The PCo1 was positively related to SL (Std-beta = 0.46; R^2 = 0.22; $P < 0.001$; Fig. 4) and negatively related to $IL_{residuals}$ (Std-beta = -0.25; R^2 = 0.09; P = 0.03; Fig. 5). A negative relationship was also observed between PCo3 and $IL_{residuals}$ (Std-beta = -0.34; R^2 = 0.11; P = 0.005; Fig. 6). Both PCo2 and PCo4 were not related to morphological traits (Table 3). Also, $ML_{residuals}$ was not significantly related to any Principal Coordinates ($P > 0.05$). In summary, larger individuals (higher SL) ingested more terrestrial plants and less filamentous algae, whereas individuals with longer intestines ingested proportionally less aquatic invertebrates and more filamentous algae.

Table 1. Mean relative volume and correlation coefficients between food items and the Principal Coordinates (PCo) of a PCoA based on diet composition of the stream-dwelling characid fish *Deuterodon stigmaturus*. Boldface highlights the highest correlations.

Macroscopic food items	Name abbreviation	Mean relative volume (%)	PCo1	PCo2	PCo3	PCo4
Aquatic Chironomidae larvae	Aquachir	0.6	-0.10	0.18	0.16	-0.07
Aquatic Coleoptera larvae	Aquacolel	0.3	0.07	-0.03	0.12	0.27
Aquatic Coleoptera adult	Aquacoleoad	0.7	0.15	0.05	-0.03	-0.02
Aquatic Diptera larvae or pupae	Aquadipt	0.8	0.00	0.05	0.17	-0.16
Aquatic Ephemeroptera nymph	Aquaephe	0.8	0.22	0.09	0.15	0.02
Aquatic Invertebrates (remains)	Aquainve	8.8	0.37	-0.28	**0.74**	0.34
Aquatic Lepidoptera larvae	Aqualepi	1.4	0.27	0.12	-0.05	-0.05
Aquatic Odonata nymph	Aquaodon	0.1	-0.07	-0.06	0.05	-0.01
Aquatic Plecoptera nymph	Aquaplec	1.1	0.15	-0.02	0.24	0.22
Aquatic Trichoptera larvae	Aquatric	0.6	-0.02	-0.07	0.08	0.09
Bryophyta	Bryophy	< 0.1	0.06	0.01	0.01	0.08
Detritus	Detritus	12.0	-0.59	**-0.63**	-0.12	0.21
Filamentous algae	Filalgae	41.0	**-0.91**	0.05	0.08	-0.14
Fish remains	Fishfrag	0.9	0.41	0.22	-0.08	0.35
Invertebrates eggs	Inverteggs	< 0.1	0.12	-0.02	0.08	0.04
Not identified items	NotId	0.9	0.14	0.04	0.06	0.20
Organic matter	Orgmatter	2.8	-0.04	**0.76**	0.26	0.00
Sediment	Sediment	4.7	-0.06	0.31	-0.52	**0.70**
Terrestrial Acari	Terracari	< 0.1	0.11	0.11	0.31	0.12
Terrestrial Coleoptera adult	Terrcoleo	0.5	0.26	-0.09	0.16	0.03
Terrestrial Collembola adult	Terrcollem	< 0.1	-0.11	0.25	0.05	-0.18
Terrestrial Diptera adult	Terrdipt	< 0.1	0.06	0.21	-0.03	0.26
Terrestrial Formicidae adult	Terrformi	< 0.1	0.26	0.21	-0.06	-0.10
Terrestrial Hemiptera adult	Terrhemi	< 0.1	0.15	0.05	-0.03	-0.02
Terrestrial Hymenoptera adult	Terrhyme	0.3	-0.07	-0.15	0.02	0.06
Terrestrial Invertebrates (fragments)	Terrinve	1.2	0.37	0.01	0.35	0.23
Terrestrial Lepidoptera larvae	Terrlepi	< 0.1	0.03	0.19	-0.08	0.20
Terrestrial Orthoptera adult	Terrorth	< 0.1	-0.06	-0.11	-0.01	-0.03
Terrestrial plants	Terrplant	20.3	**0.92**	-0.12	-0.18	-0.20
Terrestrial Tardigrada	Terrtardi	< 0.1	-0.06	0.05	-0.01	0.08

Table 2. Mean relative volume of microscopic food items found in the stream-dwelling characid fish *Deuterodon stigmaturus*. Microscopic items were analyzed from the macroscopic food items previously classified as detritus.

Microscopic food items	Volume (%)
Diatomaceous algae	100
Organic matter (not identified)	82.8
Microscopic filamentous algae	73.3
Sediment (inorganic fragments)	65.0
Desmids (algae)	20.0
Aquatic invertebrates reamains	9.2
Protozoa	5.0
Unicellular or colonial Chlorophyta	1.9
Plant fragments	1.7
Microcrustaceans	0.3

Table 3. Twelve models fitted with linear mixed-effects modeling to predict diet variation (PCo1, PCo2, PCo3 and PCo4) of *Deuterodon stigmaturus* individuals based on morphological traits (fixed effect variables). Sampling months were used as random effect variable to control for temporal effects on diet variation. N = number of individuals; Df = degrees of freedom; Std-beta = Standardized beta coefficient (effect size); SE = Standard Error; Z-value = standard score or number of standard deviations the observation is above the mean; R^2 (fixed-effect) = variation explained exclusively by fixed effect variable; R^2 (full model) = variation explained by both fixed and random effect variables; P-value = model significance. Boldface highlights models with significant fixed-effect.

Models	N	Df	Std-beta	SE	Z-value	P-value	R^2 (fixed-effect)	R^2 (full model)
PCo1~SL	**75**	**1, 5**	**0.46**	**0.13**	**3.49**	**<0.001**	**0.22**	**0.34**
PCo1~IL$_{residuals}$	**75**	**1, 5**	**-0.25**	**0.11**	**-2.17**	**0.030**	**0.09**	**0.12**
PCo1~ML$_{residuals}$	75	1, 5	0.09	0.13	0.68	0.498	0.00	0.12
PCo2~SL	75	1, 5	-0.12	0.11	-1.10	0.272	0.01	0.23
PCo2~IL$_{residuals}$	75	1, 5	-0.04	0.12	-0.35	0.728	0.00	0.23
PCo2~ML$_{residuals}$	75	1, 5	-0.26	0.17	-1.49	0.136	0.07	0.40
PCo3~SL	75	1, 5	-0.09	0.17	-0.51	0.609	0.01	0.13
PCo3~IL$_{residuals}$	**75**	**1, 5**	**-0.34**	**0.12**	**-2.82**	**0.005**	**0.11**	**0.12**
PCo3~ML$_{residuals}$	75	1, 5	0.02	0.12	0.12	0.902	0.00	0.05
PCo4~SL	75	1, 5	0.11	0.07	1.67	0.095	0.09	0.36
PCo4~IL$_{residuals}$	75	1, 5	-0.03	0.04	-0.64	0.522	0.01	0.20
PCo4~ML$_{residuals}$	75	1, 5	-0.07	0.04	-1.89	0.059	0.04	0.23

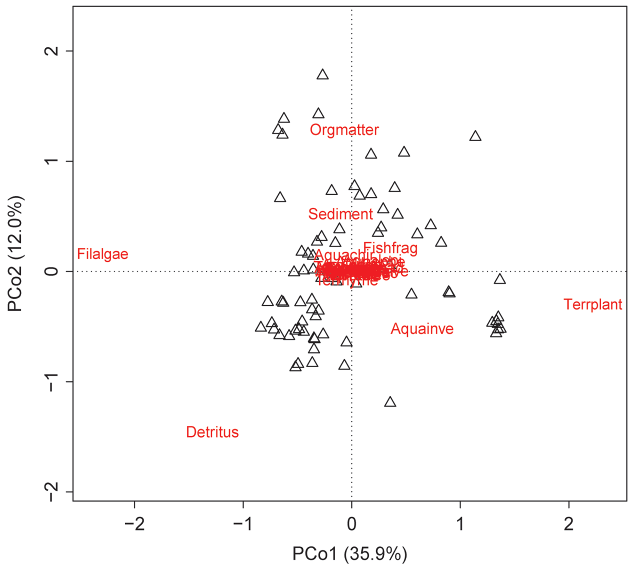

Fig. 2. Principal Coordinate Analysis (PCoA) showing PCo1 and PCo2 based on Bray-Curtis dissimilarities of diet composition of 75 individuals of the stream-dwelling characid *Deuterodon stigmaturus*. Food items name abbreviations are listed in Table 3.

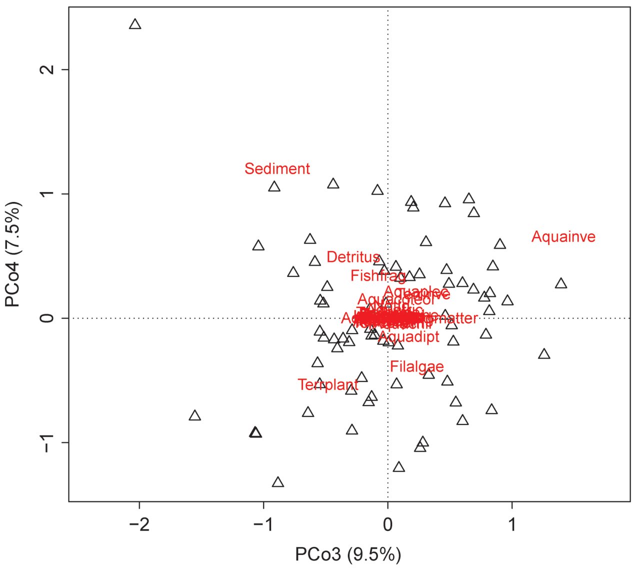

Fig. 3. Principal Coordinate Analysis (PCoA) showing PCo3 and PCo4 based on Bray-Curtis dissimilarities of diet composition of 75 individuals of the stream-dwelling characid *Deuterodon stigmaturus*. Food items name abbreviations are listed in Table 3.

Discussion

We asked three questions in order to better understand the drivers of interindividual variation in diet composition of *D. stigmaturus*. Regarding the first question, when controlling for body size differences, we found that individuals with longer intestines ingested less aquatic invertebrates and a higher proportion of filamentous algae. However, diet of individuals with longer intestine did not shift completely to low-protein and indigestible food items. Regarding the second question, we did not find evidence that the length of maxilla and premaxilla bones with exposed teeth influence diet specialization of individuals, such as feeding on periphyton. We observe, however, allometric growth in mouth length in relation to standard length. This finding relates to the third question, as we found that standard length (used to infer ontogenetic development) also influenced diet composition, but standard length by itself did not completely explain diet-morphology relationships.

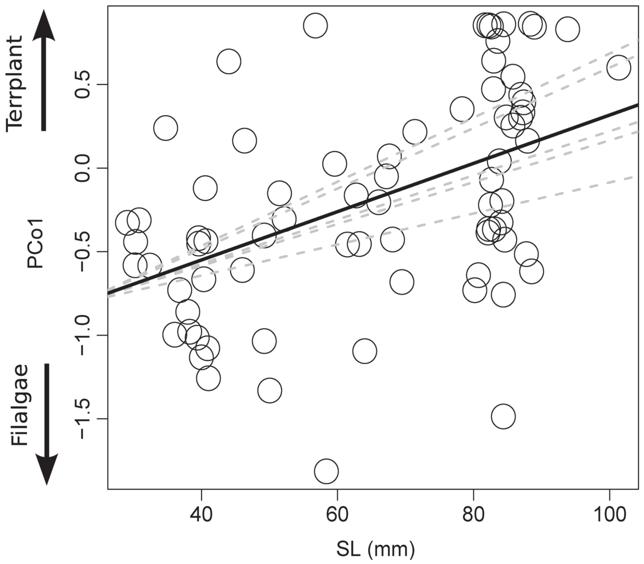

Fig. 4. Relationships between diet composition of *Deuterodon stigmaturus* summarized by the PCo1 of a Principal Coordinate Analysis (PCoA) and the standard length (SL) of individuals. Higher values of PCo1 indicate a greater proportion of terrestrial plants (Terrplant) and lower values indicate a greater proportion of filamentous algae (Filalgae) ingested by individuals. Sampling months (dashed lines) were used as random effect variable and SL was used as a fixed effect (solid line) variable to fit a linear mixed-effects model.

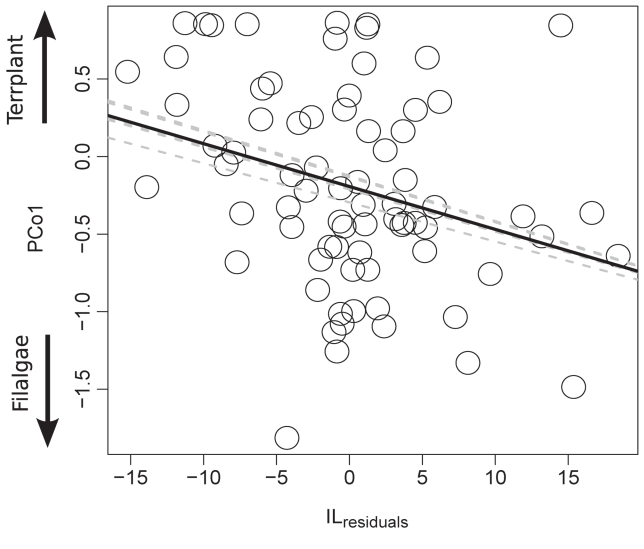

Fig. 5. Relationships between diet composition of *Deuterodon stigmaturus* summarized by the PCo1 of a Principal Coordinate Analysis (PCoA) and intestine length independent of standard length ($IL_{residuals}$). Higher PCo1 values indicate a greater proportion of terrestrial plants (Terrplant) and lower values indicate a greater proportion of filamentous algae (Filalgae). Sampling months (dashed lines) were used as random effect variable and $IL_{residuals}$ was used as a fixed effect (solid line) variable to fit a linear mixed-effects model.

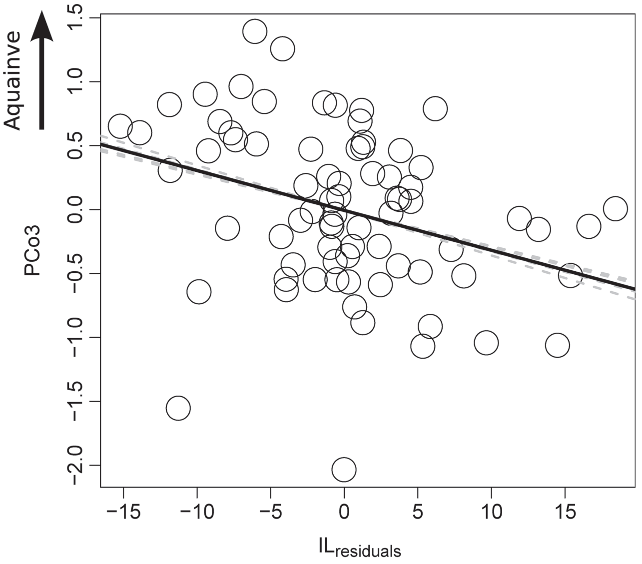

Fig. 6. Relationships between diet composition of *Deuterodon stigmaturus* summarized by the PCo3 of a Principal Coordinate Analysis (PCoA) and intestine length independent of standard length ($IL_{residuals}$). Higher PCo3 values indicate a greater proportion of aquatic invertebrates ingested by individuals. Sampling months (dashed lines) were used as random effect variable and $IL_{residuals}$ was used as a fixed effect (solid line) variable to fit a linear mixed-effects model.

When controlling for body size, our results revealed that variation in the intestine length between individuals led to two distinct trends: i) individuals with shorter intestines ingested more aquatic invertebrates in detriment of the other food items; and ii) individuals with longer intestines consumed more algae and detritus, but less terrestrial plants. We discuss these two trends in the next two paragraphs, respectively.

Studies have documented that some characid species may exhibit shifts in the intestine length coupled with reduction in the consumption of animal origin items along the ontogenetic development (*e.g.* Kramer & Bryant, 1995a,b; Drewe *et al*., 2004; Vitule *et al*., 2008). Differing from these studies, however, we did not find evidence that ingestion of animal origin items increases along the ontogenetic development. Rather, we found that these items were related to intestine length independent of ontogenetic development. The probable explanation for this difference is that intestine length did not show a pronounced allometric growth for *D. stigmaturus* along ontogenetic development, as it is expected to occur for several fish species (Kramer & Bryant, 1995a). We noted that in the linear regression between standard length (SL) and intestine length (IL), which we used to obtain residuals of intestine length, the relationship between IL and SL was almost linear, *i.e.* isometric growth. We therefore speculate that the extent of shifts that occur in diet composition along individual growth of a given species or a given population will be directly related to the degree of allometry between intestine and body size, *i.e.* when intestine grows disproportionally longer than the body does along the ontogenetic development.

The finding that *D. stigmaturus* individuals with longer intestines consumed more algae and less terrestrial plants when body size was held constant is counterintuitive, because we found the opposite relationship in the models with body size (SL). Even though we have controlled for body size in the intestine length values, raw intestine length values were highly correlated to body size (r = 0. 95), showing that in fact larger individuals are expected to have longer intestines. We did not find information in literature on differences in digestibility between algae and terrestrial plants for fishes. In addition, digestion efficiency may depend on taxonomic group, *e.g.* characids may be highly different from loricariids. Experimental manipulations of these food items and studies on digestion efficiency will greatly contribute to understand relationships between intestine length and diet variation for different species.

The opposite trend regarding algae ingestion between body size and intestine length independent of body size may be explained by other factors than intestine size by itself. For example, larger body size allows exploration of different habitats. Also, other morphological traits that shift concomitant with body growing, such as mouth morphology, might influence the ability of *D. stigmaturus* individuals to feed on different types of food items. In this sense, the combination of morphological characteristics that yields higher fitness for fish individuals can be conditioned by body size and thus may shift along the ontogenetic development.

We asked whether mouth length (ML, measured as the exposed teeth area at mouth sides) could explain diet variation between individuals. We expected this would be an important trait for the species feeding because of previous information about *Deuterodon* feeding behavior (Sabino & Castro, 1990), and also based on our underwater observations on foraging behavior of this species. However, when body size was held constant, our results did not provide support that small inter-individual difference in ML lead to variation in diet composition. However, ML by itself (raw values) was highly correlated to body size (r = 0.99). Hence, we cannot rule out that mouth morphology conditioned by ontogenetic development has influence on individuals feeding. For example, it is possible that a longer area with exposed teeth in large-sized adults confers an advantage to browse terrestrial plants or pick up plant fragments in the flowing water in relation to juveniles with small body size, which may explain the changes in diet composition along the ontogenetic development.

We observed that a great proportion of variation in diet composition of *D. stigmaturus* individuals was not explained by the morphological measures used by us, even though models included sample months as variable to control for temporal variation in food availability. This indicates that other sources of variability, such as feeding plasticity independent of the measured traits, are important factors influencing feeding of this species. This result is not surprising given previous studies that demonstrated the great feeding plasticity of fishes in relation to resource availability, mainly for characid species (Amundsen *et al*., 2001; Abelha *et al*., 2006; Uieda & Pinto, 2011; Manna *et al*., 2012). For *Deuterodon*, Vitule *et al*. (2008) also found a great variability in the diet of *D. langei* individuals. Additionally, our results are based on only a picture of the individual's stomach content and we did not evaluate past selective pressures for intestine size, such as those that are expected to occur in the early phases of the ontogenetic development. Regardless these other sources of variation, we found evidences supporting that small interindividual morphological variations play an important role constraining at least part of the diet and feeding behavior within a fish population.

In conclusion, our findings suggest that part of interindividual variations in diet composition within a given stream fish population may be constrained by morphological changes that occur along the ontogenetic development and also by morphological variations between individuals that are independent of ontogenetic development. These results corroborate previous suggestion that fishes may shift their functional and trophic niches along the ontogenetic development (Zhao *et al*., 2014). Furthermore, results indicate that a fish population can exhibit small-scale interindividual feeding variation due to divergences in the individual's morphology independent of ontogenetic development, which will influence the capacity of individuals to ingest and assimilate specific food items. These findings shed new light on the understanding of small-scale interindividual feeding variation within fish populations in stream ecosystems.

Acknowledgements

The authors are very grateful to the people who helped during the field works, including Vinicius R. Lampert, Juliano Ferrer, Luiz G. Artioli, João Paulo M. Santos, Marley B. Dala Corte, Domingos Dala Corte, Fernando R. Carvalho, Renata Maia, Ismael Franz, Bárbara Calegari, and Antônio Q. Lezama. The authors also thank to the two anonymous reviewers that provided valuable contributions to the manuscript. The first and the second authors received scholarship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (process 132140/2010-1 for the first author). All fish samplings were previously authorized by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis - IBAMA (SISBIO #25144-1).

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Submitted November 02, 2015
Accepted April 18, 2016 by Norma Hahn

Table S1. Stomach content of 75 individuals of *Deuterodon stigmaturus*, ranging from 29.1 to 101.3 mm SL. (continua)

Months	SL	IL	ML	Allochthonous plants	Filamentous algae	Detritus	Sediment	Organic matter	Autochthonous invertebrates	Aquatic Chironomidae larvae	Aquatic Diptera larvae or pupae	Aquatic Coleoptera larvae	Aquatic Coleoptera adult	Aquatic Ephemeroptera nimph	Aquatic Plecoptera nimph	Aquatic Trichoptera larvae	Aquatic Odonata nimph	Tardigrada	Aquatic Lepidoptera larvae	Invertebrates eggs	Fish fragments	Bryophyta	Allochthonous invertebrates	Terrestrial Collembola adult	Terrestrial Hymenoptera adult	Terrestrial Formicidae adult	Terrestrial Orthoptera adult	Terrestrial Coleoptera adult	Terrestrial Hemiptera adult	Terrestrial Lepidoptera larvae	Terrestrial Diptera adult	Terrestrial Acari	Not identified
August	82,12	90,16999999	7,22	2	175	95	15	80	8	0	5	1	0	0	0	0	0	1	0	0	8	0	4	0	0	0	0	0	0	0	0	0	0
August	82,64	76,52000001	6,72	12	67	60	1	0	39	0	5	0,75	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0
August	80,18	76,56000001	6,64	2	420	150	9	0	13	0	15	0	0	0	0	0	3	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
August	82,21	94,98	7,48	15	200	75	5	5	12	0	8	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0
August	67,18	54,89999998	5,42	4	40	16	0	0	14	0,5	6	1,5	0	4	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	1
August	80,72	95,30000003	6,75	12	295	135	0	10	4	6	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	68,08	68,75999999	5,74	2	113	75	2	0	12	1	0	0	0	0	0	0	0	0	0	0	0	0	25	0	0	0	0	0	0	0	0	0	0
August	52,15	51,39999998	4,03	1	53	22	1	0	7	3	0	0	0	6	8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0,5
August	32,4	27,72000001	2,21	0,5	24	7	0,5	0	2	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	39,59	35,41999999	2,93	1	41	24	0,5	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	0	0	0	0	0	0	0	0,5
August	36,07	32,55999999	2,75	0,5	39	10	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	30,31	30,11000001	2,28	0,5	24	0	0	0	0,5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	61,45	62,83999998	5,36	1	215	9	0,5	0	15	0	0,5	0	0	1	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
August	50,03	54,34	3,9	0	87	72	3	0	0,5	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	49,22	48,58000002	3,54	1	75	16	4	0	10	1	0	0	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
August	49,23	52,68	3,74	0	129	19	4	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	46	47,35	3,53	1	36	12	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
August	40,33	34,54999998	2,97	2	51	20	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	84,8	80,59999999	7,44	25	7	42	3	0	50	2	0	0	0	0	4	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	82,93	73,64999998	7	26	25	0	1	5	68	1	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0,25	0
September	85,78	66,71000004	7,04	25	12	0	5	5	40	0	0	0	0	0	25	0	0	0	0	0	6	0	2	0	0	0	0	0	0	0	0	0,25	0
September	82,96	67,23000003	7,21	35	4	0	0	0	35	2	25	0	0	0	45	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
September	71,37	64,05999998	5,95	22	75	0	8	0	0,5	3	1	0	0	4	0	0	0	0	0	0	4	0	5	0	0	0	0	0	0	0	0	0	0
September	66,05	61,60999998	5,35	0	75	0	2	25	17	1	0	1	0	2	9	2,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	63,2	55,41999999	5,43	4	100	28	7	0	3	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
September	51,47	51,48	4,09	6	80	20	1	9	25	5	2	0	0	3	0	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	46,33	43,82999998	3,49	7	27	0	2	20	9	2	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
September	39,56	35,12000002	3,18	1	43	13	0,5	0	4	0	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
March	88,53	85,37999999	7,46	4	125	30	27	2	0	1,5	0	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	87,93	87,74999999	7,14	19	100	0	110	10	0	0	0	2	0	13	0	2	0	0	0	0	0	0	17	0	0	0	0	0	0	4	1	0	45
March	87,24	71,55999999	7,23	25	50	0	20	20	26	3	0	0	0	6	0	2	0	0	0	0	4	0	2	0	0	0	0	0	0	0	0	0	0
March	84,37	90,17000004	7,28	5	150	30	55	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	82,48	75,65999999	7,03	4	60	20	28	5	15	1	0	25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	85,78	79,31999998	6,66	13	55	0	18	5	25	3	0	0	0	6	5	4	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0,5	0	0
March	87,37	83,50000002	7,27	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0	0	0
March	86,94	77,11999998	7,39	50	45	0	2	0	50	0	0	0	0	4	0	4,5	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
March	86,91	87,57999997	7,48	15	40	0	3	0	10	0	0	0	0	6	2	0	0	0	0	1	10	3	0	0	0	0	0	0	0	0	0	0	0

Table S1. (conclusão).

Months	SL	IL	ML	Allochthonous plants	Filamentous algae	Detritus	Sediment	Organic matter	Autochthonous invertebrates	Aquatic Chironomidae larvae	Aquatic Diptera larvae or pupae	Aquatic Coleoptera larvae	Aquatic Coleoptera adult	Aquatic Ephemeroptera nimph	Aquatic Plecoptera nimph	Aquatic Trichoptera larvae	Aquatic Odonata nimph	Tardigrada	Aquatic Lepidoptera larvae	Invertebrates eggs	Fish fragments	Bryophyta	Allochthonous invertebrates	Terrestrial Collembola adult	Terrestrial Hymenoptera adult	Terrestrial Formicidae adult	Terrestrial Orthoptera adult	Terrestrial Coleoptera adult	Terrestrial Hemiptera adult	Terrestrial Lepidoptera larvae	Terrestrial Diptera adult	Terrestrial Acari	Not identified
March	84,03	86,01999997	6,74	11	60	50	55	10	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	59,58	47,81999998	4,7	4	20	0	5	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	78,31	80,64999998	6,37	50	100	0	0	25	50	0	0	0	0	10	0	4	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0
March	40,65	37,91999998	3,06	0	21	10	2	5	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	39,98	35,12000002	3,13	0	40	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
March	38,26	36,38999999	3,13	0	15	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0
March	41,02	36,36000002	3,01	0	25	5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	87,76	97,1	7,18	15	240	35	0	10	0	6	1	0	0	0	0	4	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	88,93	99,55999997	7,92	700	0	0	3	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	84,58	84,47999997	7,2	5	125	25	1	0	15	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	84,38	95,9	7,16	0	235	65	5	0	0	5	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	81,7	67,97999996	6,92	25	0	0	0	0	1	0,5	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
May	83,06	71,82000002	6,63	0	1	0	0	0,5	0	0,5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	84,43	69,29999996	7,32	70	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	58,36	50,24999997	4,91	0	40	20	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	69,46	57,91999999	5,69	0	21	20	0	0	6	0	0	0	0	0	0	1,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	56,75	54,19000001	4,44	200	0	0	0	0	2	0	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	64	62,54	5,09	0	56	25	1	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	67,62	54,55999999	5,4	1	15	0	10	3	9	0	1	0	0	0	0	0	0	0	0	0	0	0	0,5	0	0	0	0	0	0	0	0	0	0
May	44,02	45,55000001	3,19	25	2	0	0,5	0	0,25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	62,75	59,47999999	5,15	2,5	65	0	0,5	0	0,5	1	1	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
May	36,79	34,25000001	2,85	0	40	60	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	30,83	27,98000001	2,26	0	2	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
May	30,23	25,08999999	2,33	0	15	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	101,35	98,47999999	8,7	200	25	0	15	10	25	1	4	0	75	0	0	0	0	0	20	0	0	0	10	0	0	2	0	0	4	0	0	0	0
July	93,83	91,14999995	8,23	300	0	0	0	0	180	0	0	0	0	0	0	0	0	0	50	0	0	0	40	0	0	0	0	50	0	0	0	0	50
July	88,34	83,63999998	7,58	100	0	0	0	0	10	0	3	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
July	83,57	78,73999998	6,98	100	2	0	0	27	0	1	0	0	0	2	0	0	0	0	35	0	7	0	2	0	0	2	0	0	0	0	0	0	0
July	82,61	69,30999999	7,15	35	0	0	0	0	50	0	0	5	0	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0	0
July	84,16	66,40999997	7,16	0,5	30	0	0	0	4	0	1	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	83,78	82,38000001	6,57	50	160	20	70	0	15	6	0	0	0	0	0	0	0	0	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	82,26	71,4	7,07	35	0	0	0	0	25	0	0	0	0	4	0	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0
July	40,9	36,60000001	3,17	0	23	0	1	0	0	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	40,55	32,81000002	3,32	1	13	0	12	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	39,37	34,94999998	2,96	0	15	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	37,98	32,00000001	2,83	0	19	10	0,5	0	2	0,5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July	34,73	24,86	2,39	1	6	0	0	1	9	1,5	0	0	0	0	0	0,5	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0,5	0
July	29,11	21,13000001	2,08	0	4	0	0	0	2	0,2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0