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Life history traits of a small-sized characid fish (*Diapoma alburnum*) in a subtropical river of Brazil

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Abstract. Small-sized characid fishes are diverse and abundant in streams and upper sections of rivers in the Neotropics. However, knowledge of their life history is still insufficient. This study describes the reproductive biology of the small-sized characid fish *Diapoma alburnum*, in the upper section of a least impacted river stretch (Sinos River) located in the subtropical region of South Brazil. The sex ratio of the population was male-biased. Reproductive period occurred during spring and summer, from September to March. Mean total fecundity was 1,535 (593 SD) oocytes and mean relative fecundity was 0.35 (0.10 SD) oocytes/mg total weight. Oocyte size analysis revealed that *D. alburnum* reproduces continuously during each breeding season. The size at first maturity was 43.01 mm for males and 37.34 mm for females, suggesting that females reach gonadal maturity earlier than males. Bony hooks (a structure of sexual dimorphism) were more developed in adult males with larger and more developed gonads, mainly in the reproductive period. In the studied subtropical drainage, *D. alburnum* seems to adopt a mixed life history strategy between that expected for small and opportunistic characids and that expected for large-sized characids with seasonal and short-time breeding.

Key words: *Cyanocharax alburnus*; Characidae; breeding; Sinos River; Neotropical.

Resumo: Características de história de vida de um peixe caracídeo de pequeno porte (*Diapoma alburnum*) em um rio subtropical do Brasil. Peixes caracídeos de pequeno porte são diversos e abundantes em riachos e em trechos superiores de rios na região Neotropical. Contudo, o conhecimento de suas histórias de vida ainda é insuficiente. Esse estudo descreve a biologia reprodutiva de *Diapoma alburnum* em um trecho pouco impactado do rio dos Sinos, na região subtropical do sul do Brasil. A proporção sexual da população foi maior para machos. O período reprodutivo ocorreu entre a primavera e o verão, de setembro a março. A fecundidade média foi de 1.535 (593 DP) oócitos e a fecundidade relativa foi de 0,35 (0,10 DP) ovócitos/mg de peso total. A análise do tamanho ovocitário revelou que *D. alburnum* se reproduz continuamente durante a estação reprodutiva. O tamanho de primeira maturação foi 43,01 e 37,34 mm para machos e fêmeas, respectivamente, sugerindo que fêmeas atingem a maturação antes que os machos. Ganchos ósseos (uma estrutura de dimorfismo sexual) foram mais desenvolvidos em machos com gônadas mais desenvolvidas, principalmente no período reprodutivo. Na drenagem subtropical estudada, *D. alburnum* parece adotar uma estratégia de história de vida mista entre aquela esperada para caracídeos pequenos e oportunistas e aquela esperada para caracídeos de grande porte com reprodução sazonal em um curto período.

Palavras-chave: *Cyanocharax alburnus*; Characidae; reprodução; Rio dos Sinos; Neotropical.

Introduction

The Neotropical region harbors the most diverse freshwater fish fauna of the world, but the real number of species is still unknown (Vari & Malabarba 1998, Bertaco *et al*. 2016). The number of fish species in Neotropics may reach a total of 8,000, as estimated by Schaefer (1998). Equally remarkable is the diversity of morphologies, behaviours and life history strategies observed in the Neotropical fishes (Vari & Malabarba 1998). Because of this high diversity, studying Neotropical fish is a difficult task and several species are still seldom studied regarding their life history traits and behaviour (Lowe-McConnell 1987).

Understanding life history, population dynamic and the function of fish species on ecosystems largely rely on studies revealing the reproductive strategy of species and variation in its reproductive traits. In freshwater environments of the Neotropics, fish species adopt very distinct life history strategies (Azevedo 2010). These strategies result from a large number of morphological, physiological and behavioural adaptations related to a variety of environments (Breder & Rosen 1966, Vazzoler 1996). For example, Characidae family is a highly diverse group, with 1203 valid species (Fricke *et al*. 2020), that inhabits most of the freshwater environments in Neotropics. Around 200 species of characid were described in the last ten years, which significantly increased the number of species within the group (Fricke *et al*. 2020). Reproductive tactics of characids range from complex matting behaviour, internal insemination and spawning of a few eggs in submerged leafs (as observed in Glandulocaudinae) to pelagic spawning of thousands of eggs in one or a few specific events seasonally (Nelson 1964, Burns *et al*. 1995, Azevedo 2010).

Small-sized characid fishes are diverse and abundant in streams and upper sections of rivers in the Neotropics. Despite the importance of characids for such riverine ecosystems, the reproductive biology of most species is still unknown, mainly considering headwaters and upper river sections, where human alterations are incipient. *Diapoma alburnum* (Hensel 1870) is a small-sized characid typically found in subtropical freshwaters of Brazil [previously known as *Cyanocharax alburnus* (Hensel 1870) and changed to the genus *Diapoma* after Thomaz *et al*. (2015)]. The species has a wide distribution ranging from Uruguay and Lagunas dos Patos basins to coastal rivers of South Brazil (Malabarba *et al*. 2013). This characid is frequently and commonly captured in several water bodies, including both lowland and upland rivers, and feeds mainly on insects and plankton (Hartz *et al*. 1996, Vilella *et al*. 2002, Artioli *et al*. 2003). Despite its wide distribution and high abundance, there are still few studies that investigated the aspects of life history of *D. alburnum* (e.g. Fontoura *et al*. 1993, Artioli *et al*. 2003). Most life history traits of *D. alburnum* have yet to be investigated, mainly considering riverine habitats.

This study describes the reproductive biology of a population of *D. alburnum* from the upper section of a least impacted subtropical river of South Brazil. Specifically, the reproductive traits described herein include sex ratio, gonadal development, reproductive period and its relation to abiotic and biotic factors, fecundity, spawning mode and size at first maturity. In addition, we tested whether the development of secondary sexual dimorphism (bony hooks) in males is related to the reproduction. This study contributes to better understand what is the life history strategy adopted by small and abundant characids in headwaters and in upper river sections of subtropical zones in the Neotropics.

Materials and Methods

The study was carried out in the upper Sinos River, in the municipality of Caraá, state of Rio Grande do Sul, South Brazil. The Sinos River watershed drains an area of 3,746 km² in the Northeast Rio Grande do Sul. The river extension is about 190 km long. Its springs are located approximately 20 km upstream from the studied site and its mouth about 170 km downstream, in the Lake Guaíba. The Sinos River is one of the main rivers of the Patos Lagoon system, the largest Atlantic coastal hydrographic system of South Brazil (Secretaria Estadual do Meio Ambiente 2016).

Specimens of *D. alburnum* were collected monthly, between January and December 2007, in a 150 m long stretch of the Sinos River (29°45'50" S, 50°25'37" W) (Fig. 1). This site is located at 80 m elevation, corresponding to a 4th order river segment. Riffle habitats of moderated flow velocity, followed by deep pools, are predominant in this site. Water turbidity is commonly low, channel wetted width varies from 10 to 17 m and the substrate grain size is mainly composed by boulder, cobble and gravel. In the pools, maximum depth can reach 2 m (Dala-Corte & Azevedo 2010).

In each month, sampling effort included 20 benthic samples with dipnet (mesh 2.0 mm) and three water column samples with seine net (mesh 2.5 mm).

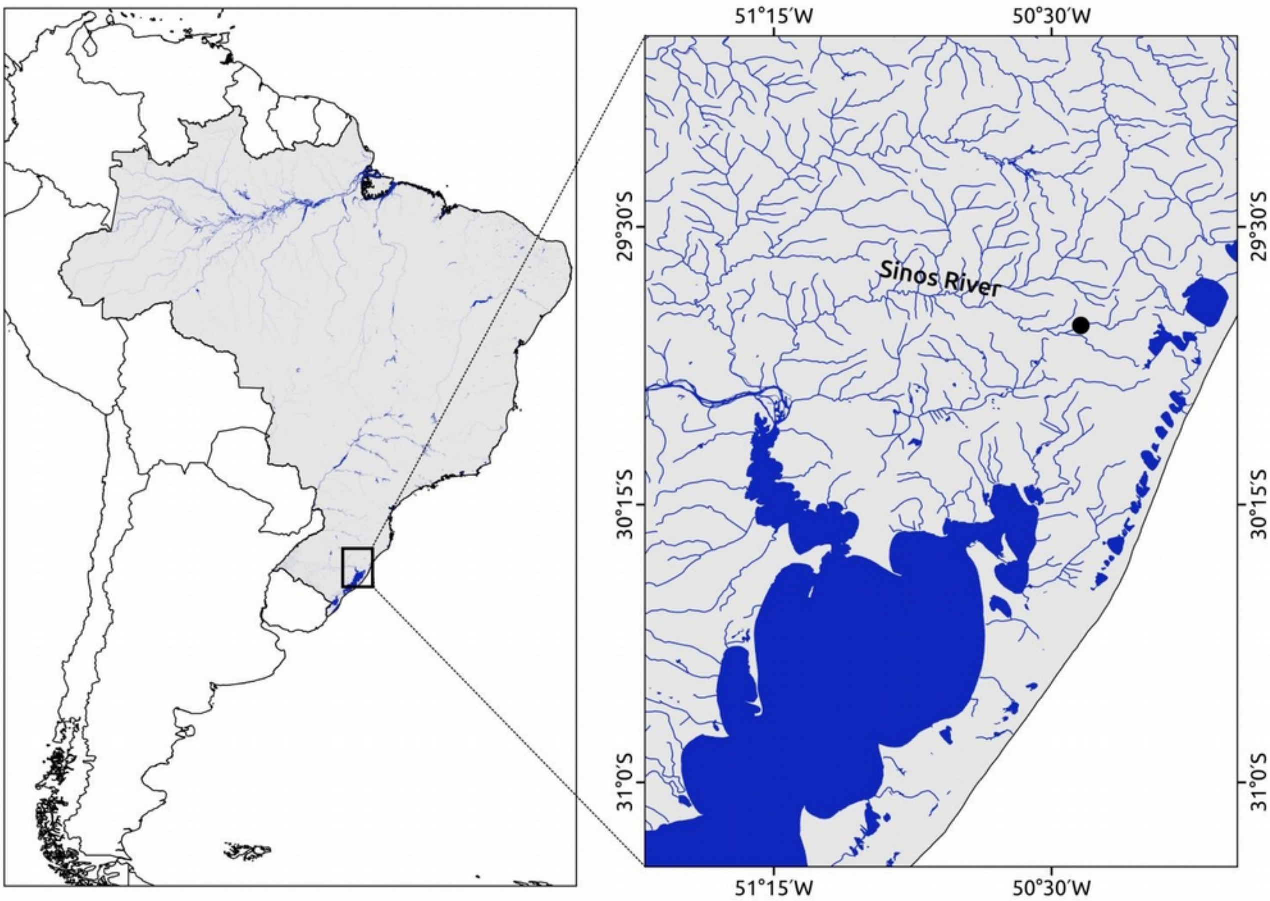

Figure 1. Location of the sampling site in the upper Sinos River, Rio Grande do Sul, Brazil, where individuals of *Diapoma alburnum* were sampled monthly, between January and December of 2007.

Individuals collected were preserved in formaldehyde 10% and, posteriorly, transferred to ethanol 70%. For each individual, we recorded standard length (SL, mm), total weigh (WT, g), stomach weight (WS), liver weight (WL) and gonads weight (WG). These weights were used to calculate the gonadosomatic index (GSI), repletion index (RI) and hepatosomatic index (HSI), following the equations: GSI = (WG/WT) x 100; RI = (WS/WT) x 100 (Santos 1978); and HSI = (WL/WT) x 100 (Vazzoler 1996).

Sex identification was performed initially by checking the presence of bony hooks on anal fin, a trait typically exclusive to males (Malabarba & Weitzman 2003). Posteriorly, we performed macroscopic analysis of gonads using a stereomicroscope to confirm sex identification. Differences in sex ratio of males and females in the population was tested with the chi-square test (χ^2), including evaluations of month, body size (SL) classes and total individuals.

The macroscopic classification of gonads followed Brown-Peterson *et al*. (2011). Accordingly, we considered the following gonad maturing phases: immature, developing, spawning capable, regression and regenerating. The reproductive period was inferred based on the interpretation of mean GSI variation and frequency of maturing phases across the months.

In order to evaluate the relationship between gonadal maturation and environmental factors that vary seasonally we tested the correlation between the indices GSI, RI and HSI with water temperature (°C), rainfall (mm) and photoperiod length (minutes), using the Pearson correlation (*r*). Water temperature was measured immediately after the fish sampling with a mercury-filled thermometer. Rainfall data was obtained in the 8º Distrito of the Instituto Nacional de Meteorologia (INMET). Day length (photoperiod) was calculated with the software Skymap Pro 9.0.

The size at first gonadal maturation (L_{50}), considered as the size at which 50% of the population is adult, was determined by analysing the frequency of adult individuals in the population according to body size (Santos 1978). To estimate

L_{50}, we fitted a logistic regression using body size (SL) as predictor variable of adult frequency in the population, computed as juvenile (0) and adult (1).

The total fecundity of *D. alburnum* was estimated by counting the total number of vitellogenic oocytes in 10 females in the spawning capable gonadal maturing phase. Afterwards, the relative fecundity was calculated as the number of oocytes per female weight (mg). Then, the type of oocyte development was inferred by analysing the distribution frequency of oocyte sizes (Vazzoler 1996). The size of oocytes in each spawning capable female was measured as the maximum diameter of oocytes using a stereomicroscope.

Lastly, we quantified the number of bony hooks in the anal fin rays of males by counting the number of rays with bony hooks and the number of bony hooks in the first branched ray. Also, we visually estimated the development degree of these hooks on anal fin by size classes and maturing phases of fishes. All the statistical analyses were performed using R environment (R Core Team 2018).

Results

A total of 358 individuals of *Diapoma alburnum* were analysed: 205 males (35.7 to 68.9 mm SL) and 153 females (45.7 to 70.8 mm SL). The sex ratio regarding number of individuals was male biased considering the total samples and for some months and size classes. Specifically, the number of males was significantly larger in January, April, June and September, as well as for the following size classes: 41├46 mm, 56├61 mm and 61├66 mm (Table I).

A higher frequency of spawning capable females, as well as a higher mean GSI values for females, were observed between September and March (Figs. 2 and 3a). No spawning capable males were collected. Males with gonads in developing phase were mainly found in the months of January, March, September and December, agreeing with higher GSI values (Figs. 2 and 3b).

Although GSI peak occurred in months when temperature was high for females, there was no correlation of GSI values with RI (r = 0.57; p = 0.14) or HSI (r = 0.70; p = 0.05), as well as with water temperature (r = 0.14; p = 0.76), day length (r = 0.64; p = 0.12) and rainfall (r = 0.44; p = 0.32) (Table II). The size at fist maturity (L_{50}) was estimated as 37.34 mm for females and 43.01 mm for males (Figs. 4a, b). Mean total fecundity was 1,535 (593 SD) oocytes and the mean relative fecundity was 0.35 (0.10 SD) oocytes/mg. The oocyte size class frequency distribution showed no clear modes besides the first one, composed by immature oocytes of small diameters (0.05 - 0.15 mm) (Fig. 5). Therefore, the oocyte development was inferred as a tendency to be asynchronous. The presence of small reserve oocytes indicates an iteroparous strategy.

Bony hooks on anal fin were rarely found in immature individuals. A higher frequency of bony hooks on anal fin was observed in males with developing gonads. No spawning capable males were recorded. Post-reproduction males (regression and regeneration testes) in general showed smaller and fewer bony hooks (Fig. 6a). Females did not show bony hooks on anal fin. Small individuals (< 36 mm SL) also had no bony hooks. These structures were common on males larger than 41 mm SL (Fig. 6b). For males, there was a positive correlation between the mean number of bony hooks on the first anal fin branched ray with SL (r = 0.39; p < 0.001) and GSI (r = 0.40; p < 0.001). Also, there was a positive correlation between the number of anal fin rays with bony hooks and SL (r = 0.41; p < 0.001) and GSI (r = 69; p < 0.001).

Discussion

Among the reproductive characteristics of fish, sex ratio indicates important factors that affect the population dynamics. Most fish species shows a 1:1 sex ratio, *i.e.* a balanced number of males and females in the population (Nikolsky 1969, Vazzoler 1996). However, as we found for *D. alburnum*, there are some population for which sex ratio differs from the 1:1 expectation (Mazzoni *et al.* 2002, Artioli *et al.* 2003, Ferriz *et al.* 2007). Several factors can interfere differently on males or females and drive bias in the individual number for one sex (Vazzoler 1996). Such factors commonly include differences in growing (Munro 1976, Vicentini & Araujo 2003), mortality and population segregation (Orsi *et al.* 2004), as well as food availability (Nikolsky 1969) or sampling method selectivity (Gurgel 2004).

One plausible explanation for the male biased sex ratio observed in *D. alburnum* is related to energetic allocation for growth and reproductive tissues (McBride *et al.* 2015, Ozga & Castiglioni 2017). Size at first maturing (L_{50}) for species of *Diapoma* has been reported to be smaller for females than males (Fontoura *et al.* 1993, Azevedo 2010). Our results for *D. alburnum* agree with this information, as the size at fist maturity for females (37 mm) was smaller than for males (43 mm).

Table I. Sex ratio by size class (standard length - SL) and months of *Diapoma alburnum* in the upper Sinos River, Rio Grande do Sul, January to December 2007. *indicates significant differences ($p < 0.05$) by Chi-square test (χ^2). Blank cells are absence of individuals in the samples.

	Males	Females	χ^2		Males	Females	χ^2
21 ├26	8	10	0.22	**Jan**	48	30	4.15*
26 ├31	12	20	2.00	**Feb**	2	6	2.0
31 ├36	17	17	0.00	**Mar**	55	43	1.46
36 ├41		1		**Apr**	33	17	5.12*
41 ├46	12	1	9.31*	**May**	9	12	0.42
46 ├51	23	23	0.00	**Jun**	6	14	3.2*
51 ├56	31	36	0.37	**Jul**	4	2	0.66
56 ├61	47	20	10.88*	**Aug**			
61 ├66	50	18	15.06*	**Sep**	34	18	4.92*
66 ├71	5	5	0.00	**Oct**			
71 ├76		1		**Nov**			
				Dec	14	10	0.66
Total	205	152	7.87*				

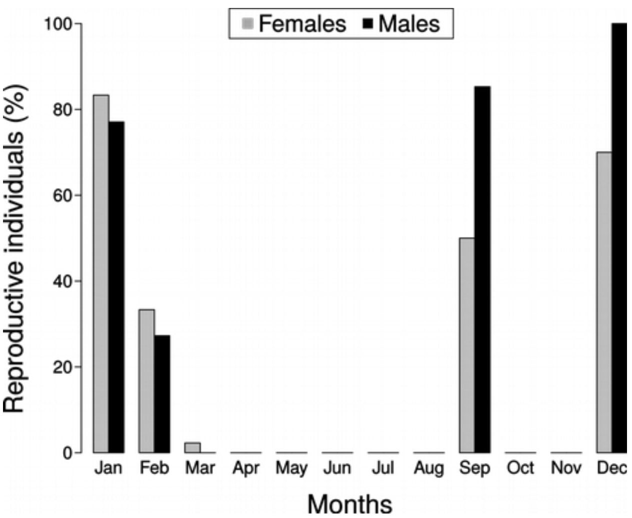

Figure 2. Monthly frequency of spawning capable females and developing males of *Diapoma alburnum*, sampled in the upper Sinos River, Rio Grande do Sul, Brazil, between January and December of 2007.

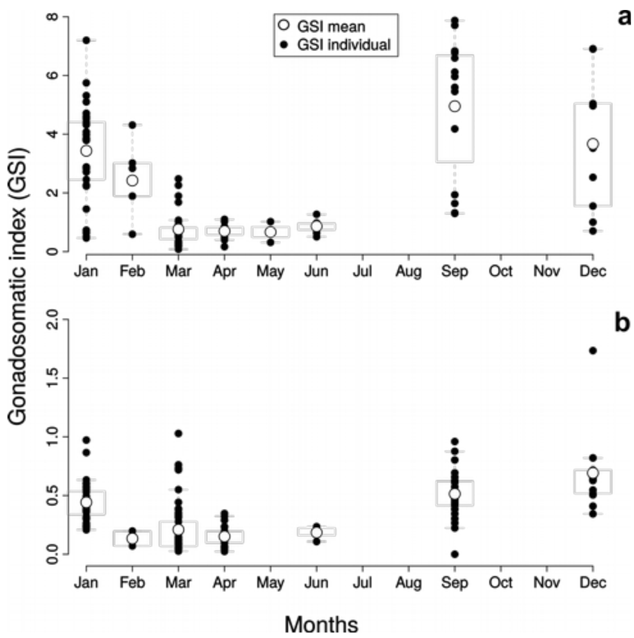

Figure 3. Monthly variation in gonadosomatic index (GSI) of *Diapoma alburnum* females (a) and males (b) of upper Sinos River, Rio Grande do Sul, Brazil, between January and December 2007. Immature individuals were not included. Missing values in some months represent months when no individuals were captured.

Hence, it seems that females invest more energy in reproduction than growing, compared to males, which may cause a larger mortality of females due to their smaller body sizes, which may be more susceptible to predation. In addition, results from L_{50} reported here are smaller than found by Fontoura *et al*. (1993) for females of *D. alburnum* in the lagoa Fortaleza, RS (45-50 mm). Thus, local environment characteristics of upstream Sinos River may be selecting early maturation in *D. alburnum* compared to more stable environment such as lakes, but this hypothesis needs to be tested.

Most characifoms possess seasonal reproduction occurring between the spring and summer in South hemisphere, which is synchronized with raises in temperature, day length or rainfall, but the specific period can vary accordingly to region and species (Vazzoler & Menezes 1992). In subtropical region of the Neotropics, seasonal differences in temperature are more pronounced, so small characids tend to breed during late spring and summer (Azevedo *et al*. 2000, Azevedo 2010, Dala-Corte & Fialho 2014). The results found here for *D. alburnum* agree with this seasonal pattern for subtropical zones of Brazil. A seasonal reproduction during the spring and summer was also reported for other species of the genus *Diapoma* (Menni & Almirón 1994, Azevedo *et al.* 2000, Azevedo 2010), and for two other populations of *D. alburnum* in very different environments (Fontoura *et al*. 1993, Artioli *et al*. 2003).

Comparative studies have shown that fecundity of small-sized characids (< 120 mm) range from 100 to 10,000 oocytes (Gonçalves *et al*. 2005, Azevedo 2010). But almost 60% of the species produces less than 1,000 oocytes (Azevedo 2010). The mean fecundity of *D. alburnum* (1,535 oocytes) was three-fold the mean number of oocytes reported for other two species of the genus *Diapoma*: *D. terofali* (322 oocytes, Azevedo 2010) and *D. speculiferum* (491 oocytes, Azevedo *et al*. 2000). This result may be explained by the larger size of *D. alburnum* (70.76 mm SL) compared to *D. terofali* (52.6 mm SL) and *D. speculiferum* (48.7 mm SL). In addition, differing from *D. alburnum, D. terofali* and *D. speculiferum* are inseminating species, which may increase success of offspring production in relation to oocyte number. Conversely, the relative

Table II. Monthly mean gonadosomatic index (GSI), stomach repletion index (RI), hepatosomatic index (HSI), water temperature (T), photoperiod (minutes) and rainfall (mm) for females and males of *Diapoma alburnum* sampled in the upper Sinos River, Rio Grande do Sul, January to December 2007. Blank cells are missing data (absence of individuals in the sample).

	T (ºC)	Photoperiod	Rainfall	Sex	GSI	RI	HSI
January	23.7	837	80.6	Females	3.43	2.27	0.73
				Males	0.43	1.79	0.48
February	23.6	805	185.7	Females	2.42	2.55	1.04
				Males	0.13	1.64	0.73
March	23.8	739	172	Females	0.76	2.05	0.55
				Males	0.19	1.97	0.56
April	21.5	670	74.1	Females	0.57	2.14	0.66
				Males	0.11	2.15	0.76
May				Females	0.45	1.53	0.69
				Males			
June	12.7	615	124.5	Females	0.86	1.72	0.97
				Males	0.18	1.63	0.81
July				Females			
				Males			
August				Females			
				Males			
September	18	742	222.9	Females	4.95	2.09	1.16
				Males	0.45	1.83	1.01
October				Females			
				Males			
November				Females			
				Males			
December	24	844	142.5	Females	3.66	2.75	1.04
				Males	0.69	2.07	0.86

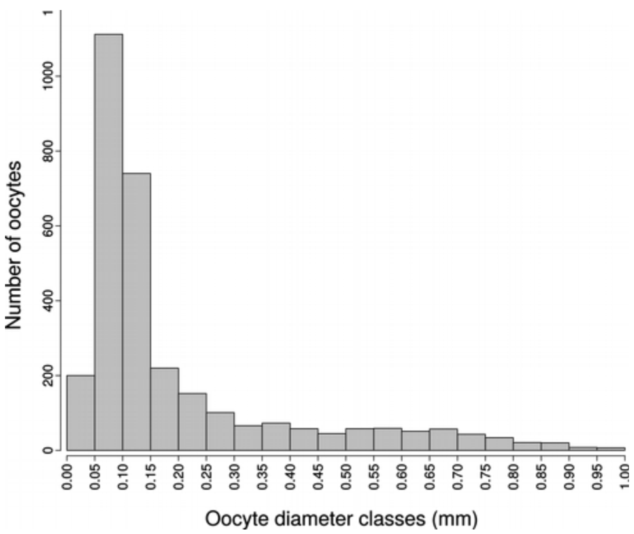

Figure 5. Mean number of oocytes by size of oocytes (diameter classes) for *Diapoma alburnum* females, sampled in upper Sinos River, Rio Grande do Sul, Brazil.

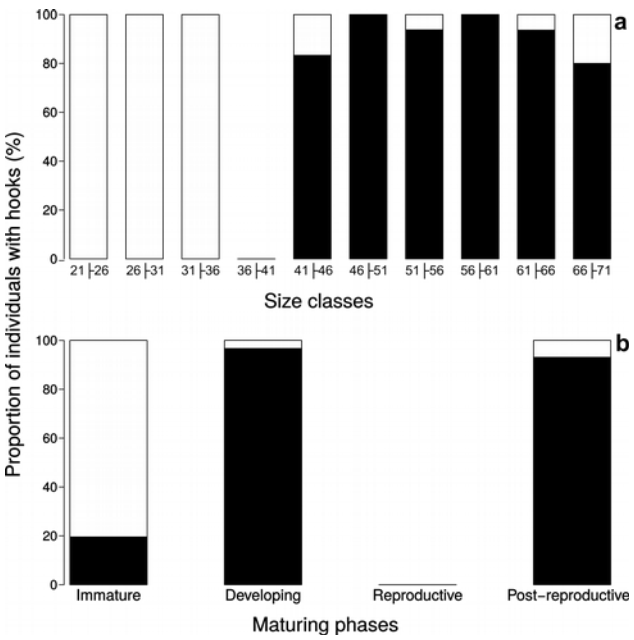

Figure 6. Percentage of *Diapoma alburnum* males with and without bony hooks on the anal fin by gonadal maturing phase (A) and size classes of standard length (mm) (B). Missing bars represent missing individuals.

fecundity of *D. alburnum* (0.35 oocytes/mg) was lower that of *D. terofali* (0.56 oocytes/mg) and *D. speculiferum* (0.41 oocytes/mg), suggesting a lower relative energetic allocation in oocyte production.

A tendency to asynchronous oocyte development, as observed in *D. alburnum*, is uncommon to characid species with seasonal spawning (Azevedo 2010). In subtropical regions, small characids usually exhibit synchronous oocyte development, and females spawn a batch of mature oocytes in one or a few events during a short time span (e.g. Dala-Corte & Azevedo 2010, Dala-Corte & Fialho 2014). Total spawning is mainly common in larger-sized and migratory Characiformes in the neotropics (Vazzoler & Menezes 1992, Vazzoler 1996, Azevedo 2010). On the other hand, asynchronous development is more often observed in species with continuous reproduction living in unpredictable or stochastic environments without clear seasonal variations (Winemiller 1989, Dala-Corte & Fialho 2014). Therefore, the evidence of seasonal reproduction along with the possibility of continuous spawning indicate that *D. alburnum* adopt a mixed life history strategy in the upper stretches of the studied subtropical river. However, further evidences are needed, including histological analysis, to confirm whether the species really possesses asynchronous oocyte development.

Our results indicate that bony hooks on anal fin develop along with the growing of *D. alburnum* males, coupled with the sexual maturation. In addition, these hooks seem to regress after the seasonal breeding, when testes undergo regression. These results are similar to the findings of Dala-Corte & Fialho (2014) for another species of small characid. This indicates that the development of bony hooks in characid males may be subjected to hormonal control. Fins with bony hooks of males enter in contact to the body of females during the spawning moment. The function of these hooks may be tactile, allowing males to know the exact location of females (Foster 1967, Collette 1977). In this sense, bony hooks would not be useful for males during non-reproductive months. This structure may be fundamental for species that exhibit complex mating behavior, such as that described for inseminating species of *Diapoma* and *Mimagoniates* (Nelson 1964). However, the real function of bony hooks in Characidae and whether there are variations among species and hormonal control still need to be further investigated.

The absence of spawning capable males observed in *D. alburnum* may have four probable explanation: 1) males and females may have distinct behavior throughout the breeding season, such as habitat segregation and dispersion; 2) the sample site is not a preferential site for the species to conclude the reproduction; 3) sampling missed to capture spawning capable males; 4) males are able to reproduce even with gonads in developing phase. All these explanations exemplify how far we are from understanding the life history strategies of small-sized characids in the Neotropics.

In summary, in the studied subtropical river, we found evidence that *D. alburnum* adopt a mixed life history strategy. This mixed strategy includes traits expected for small and opportunistic characids of stochastic environments (e.g. early maturation and asynchronous spawning) and that expected for large-sized characids with seasonal and short-time breeding (e.g. seasonal breeding and high fecundity of small oocytes).

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