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Population dynamics of a freshwater amphipod from South America (Crustacea, Amphipoda, Hyalellidae)

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ABSTRACT

This study aimed to characterize the population dynamics of Hyalella bonariensis Bond-Buckup, Araujo & Santos, 2008 from headwater spring in a rural area of state of Rio Grande do Sul, Brazil. Four samples were collected in August (winter) and October (spring) of 2012 and January (summer) and April (autumn) of 2013. Ovigerous females and precopula pairs were separated from other individual in the field. A total of 5,266 specimens were sampled, being 1,878 males, 2,073 females (including 240 ovigerous females) and 1,315 juveniles. The frequency distribution of size classes (measured as cephalothorax length, CL) was polymodal and bimodal in males and females, respectively. Males reach larger size than females. Sexual maturity of males and females was estimated at 0.40 and 0.38 mm for CL, respectively. Total sex ratio favored females, and these were more frequent in intermediate size classes, while males were more frequent in larger size classes. Ovigerous females and couples were found in four seasons, but both were more abundant in winter. Juveniles were also found in all seasons, being more frequent in winter and spring. These results showed that this H. bonariensis population has similar dynamics to other species of Hyalella Smith, 1874 from Brazil, but present variations when compared to other freshwater amphipods.

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KEY WORDS

Body size, *Hyalella*, reproductive period, sex ratio, sexual maturity.

INTRODUCTION

The conservation of an ecosystem depends on knowledge of ecological aspects of its populations. The study of the abundance and size of a population, its stability, productivity, role in the food chain, reproductive period, recruitment, average lifetime, emigration and immigration rates, among other aspects, are crucial for long-term conservation plans (Cooper, 1965; Hutchinson, 1981; Muskó, 1992). All the information about population dynamics of a species support and guide the creation of conservation programs, the evaluation of its extinction risk and sustainable use, as well as its potential use in bioindication and ecotoxicological studies (Brawn and Robinson, 1996).

The crustaceans of the genus *Hyalella* Smith, 1874 have a great ecological importance, as they provide energy transfer between different trophic levels, convert detritus into fine particulate organic matter and serve as food for many waterfowl, fish and invertebrates (Swanson, 1984; Wen, 1992; Wellborn, 2002; Wellborn and Cothran, 2007). Besides, *Hyalella* are organisms most commonly used in environmental quality tests in temperate climates mainly due to their high sensitivity to contaminants and environmental impacts (Duan *et al.*, 1997; Rinderhagen *et al.*, 2000; Neuparth *et al.*, 2002; Morris *et al.*, 2003; Wilcoxen *et al.*, 2003; Gust, 2006; Ding *et al.*, 2011).

The genus Hyalella comprises species of amphipod crustaceans that occur in freshwater ecosystems and have distribution restricted to Americas (Bento and Buckup, 1999). Among the 66 described species, 23 are found in Brazil and of these, nine species occur in the southernmost state, Rio Grande do Sul, region with the highest diversity of the genus in the country (Bueno et al., 2014; Marrón-Becerra et al., 2014; Rodrigues et al., 2014; Colla and César, 2015). Among the species that occur in Brazil, Hyalella bonariensis Bond-Buckup, Araujo & Santos, 2008 has a wide geographical distribution, occurring in Argentina and also in 13 wetlands in the state of Rio Grande do Sul (Bueno et al., 2014). However, its biology and ecology are still unknown. Regarding the biology of native species of Hyalella from Brazil, studies have been conducted about ecology and reproduction of two sympatric species, Hyalella pleoacuta González, Bond-Buckup and Araujo, 2006 and Hyalella castroi González, Bond-Buckup and

Araujo, 2006 (Castiglioni and Bond-Buckup, 2007; 2008a; 2008b; 2009; Castiglioni *et al.*, 2007).

Thus, this study aimed to characterize the population dynamics of the freshwater amphipod *H. bonariensis* from southern Brazil, and for this the frequency distribution, body size, sexual maturity, sex ratio, reproductive period and recruitment were analyzed. These biological aspects can be used to create conservation and ecotoxicology programs for freshwater aquatic environments in Brazil.

MATERIAL AND METHODS

Specimens of the *H. bonariensis* population were sampled in August (winter) and October (spring) of 2012 and January (summer) and April (autumn) of 2013, from a headwater spring in a rural area called Portal do Roio (29°39'25.14"S 53°37'33.53"W), in Silveira Martins municipality, central region of state of Rio Grande do Sul, southern Brazil. The samples were performed by only one person, with the aid of a hand net (mesh of 250 µm) for 20 minutes.

Ovigerous females and pre-copula pairs were separated from other individual in the field and preserved (70% ethanol) in microtubes, and the other specimens were taken to the laboratory, sorted and preserved in 70% ethanol. Later, specimens were identified and the cephalothorax (i.e. head) length (CL, in mm) was measured using a micrometer eyepiece in a stereoscopic microscope.

Specimens were classified into four categories: juveniles (individuals lacking secondary sexual characteristics), males (individuals with the second pair of gnathopods well developed, larger than first pair), females (individuals with marsupium developed and a small second pair of gnathopods, subequal in size as the first pair) and ovigerous females (females carrying eggs or juveniles inside the marsupium) (Borowsky, 1991; Castiglioni and Bond-Buckup, 2008a).

The total frequency distribution in size classes was estimated in relation to CL of males and females (including ovigerous females). For each category, the width of the size classes was determined using the value of 1/4 of the standard deviation from the mean values of cephalothorax (Markus, 1971). Normality of the frequency distributions was analyzed using Shapiro-Wilk test ($\alpha = 0.05$) (Zar, 1996).

Minimum, maximum and mean cephalothorax lengths were estimated for males and females (including both ovigerous and non-ovigerous females). Size was compared among sexes using t-test (α =0.05) (Zar, 1996).

Size at the sexual maturity was estimated for both sexes based on the size of the smallest male and the smallest female found forming couples in pre-copula (Castiglioni and Bond-Buckup, 2008b; Wellborn *et al.*, 2005).

Sex ratio was estimated as the total number of males divided by the total number of females (includes both ovigerous and non-ovigerous females) sampled. Besides, sex ratio was calculated by season and size classes (using CL). Later, the goodness of fit test (chi-square) was used to verify that the ratio found for sexual *H. bonariensis* follows the ratio of 1:1 (males: females) (Zar, 1996).

To estimate the reproductive period, we calculated the frequency of females that were ovigerous in relation of adult females. All females that were as large as or larger than the smallest female found in pre-copula (i.e. estimated size at sexual maturity) were included in this analysis. Then, the proportion of ovigerous females was compared between seasons using multinomial proportion test (MANAP; α =0.05) (Curi and Moraes, 1981). We also calculated the relative frequency (%) of pairs in precopulatory behavior and then compared between seasons using multinomial proportion test (MANAP; α = 0.05) (Curi and Moraes, 1981).

To evaluate the recruitment period (juveniles entry in population), we calculated the juvenile proportion in relation to adults for each season and we used a Chi-Square goodness of fit test (Chi-Square, $\chi 2$) (α =0.05) (Zar, 1996), in order to check if the proportion follows the pattern 1:1 ratio (juveniles: adults). We considered juveniles the specimens with CL smaller than 0.3 mm, i.e., those individuals where the enlargement of the second pair of gnathopods could not be observed (male diagnostic characteristic) and the presence of a marsupium (female diagnostic characteristic) (Borowsky, 1991). Subsequently, we estimated the juvenile relative frequency by season and compared using multinomial proportion test (MANAP) (α =0.05) (Curi and Moraes, 1981).

All statistical analyses were performed using the software Statistica 7.0.

A total of 5,266 individuals were collected: 1,878 males, 2,073 females (including 240 ovigerous females) and 1,315 inveniles. Table 1 presents the number of males.

RESULTS

1,315 juveniles. Table 1 presents the number of males, females, ovigerous females and juveniles sampled in each season.

The frequency distribution in size classes of CL of males and females was not considered normal (males W=0.95; females W=0.92; p<0.05). Besides, frequency distribution of males and females was polymodal and bimodal, respectively (Fig. 1).

The CL of males of *H. bonariensis* ranged from 0.30 to 0.92 mm and that of females from 0.30 to 0.74 mm. CL of males (0.49 ± 0.11 mm) was significantly larger than females (0.46 ± 0.08 mm) (t=9.80; p<0.05). Sexual maturity of males and females was estimated at 0.40 and 0.38 mm for CL, respectively.

Sex ratio favored females (0.91 male: 1 female) ($\chi 2=9.62$; p<0.05), which were more frequent in all seasons, except in summer when males were more abundant (p<0.05) (Tab. 1). For the sex ratio analysis by size classes of CL, females predominated in intermediate classes and males predominated in larger size classes (p<0.05; Fig. 2).

Ovigerous females were sampled in all seasons, but in greater abundance in the winter (65.4% of females were ovigerous) (p<0.05) (Fig. 3). Couples in pre-copula also occurred in all seasons, being more frequently collected in the winter (p<0.05) (Fig. 3).

Juveniles were found in all seasons, being more abundant in winter and spring (MANAP; p<0.05) (Fig. 4). They represented only 25% of the total sampled population, in a way that the adult specimens were more abundant in summer (80.82%; χ 2=691.69; p<0.05), autumn (84.9%; χ 2=364.28; p<0.05) and winter (76.64%; χ 2=531.27; p<0.05).

DISCUSSION

For frequency distribution in size classes in amphipods, bimodality and polymodality are apparently the most common distributions, and could be the result of a reduced growth rate in immature stage, juvenile recruitment pulses, migration, mortality or a differential distribution (Díaz and Conde, 1989). This pattern was observed in the population of *H. bonariensis* that showed a bimodal and polymodal distribution for females and males, respectively. This result may indicate that this population has reproduction peaks, with a

	Males	Females (ovigerous females)	Juveniles	Total	M: F	χ^2
Summer	1,018	453 (23)	349	1,820	2.25:1	217.01*
Autumn	292	343 (34)	113	748	0.85:1	4.10*
Winter	424	1010 (157)	437	1,871	0.42:1	239.47*
Spring	144	267 (26)	416	827	0.54: 1	36.81*
Total	1,878	2,073 (240)	1,315	5,266	0.91:1	9.62*

Table 1. Number of males, females, ovigerous females, juveniles and total specimens of *Hyalella bonariensis*, sex ratio (males: females) and results of the χ^2 test by sampling seasonal in Silveira Martins, state of Rio Grande do Sul, Brazil.

Note.: "*" indicate significant difference in sex ratio (p<0.05).

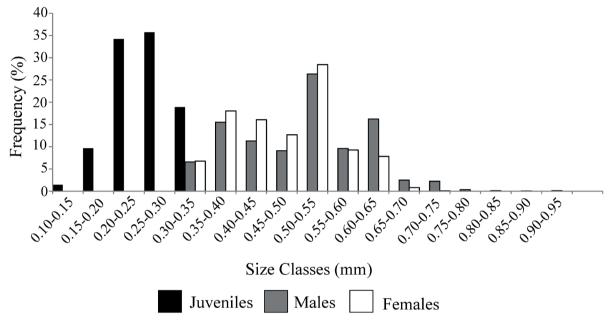
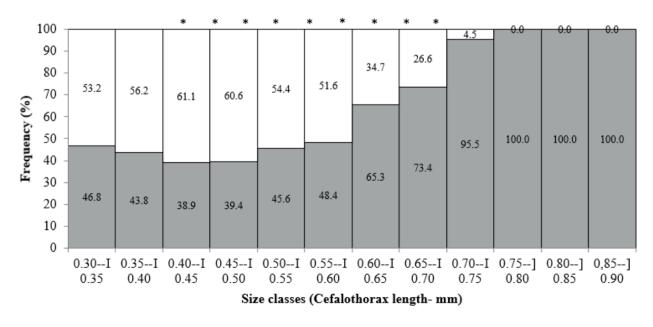


Figure 1. Frequency distribution in size classes of cephalothorax length (CL in mm) for males and females from a population of *Hyalella bonariensis* of Silveira Martins, state of Rio Grande do Sul, Brazil.



■Males □Females

Figure 2. Sex ratio of *Hyalella bonariensis* by size classes of cephalothorax length (CL in mm), from Silveira Martins, state of Rio Grande do Sul, Brazil. "*" indicate significant difference in sex ratio (p<0.05).

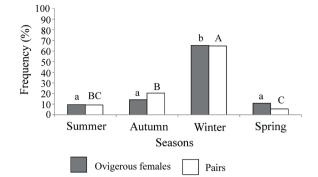


Figure 3. Relative frequency (%) of ovigerous females and couples in pre-copula of *Hyalella bonariensis* from Silveira Martins, state of Rio Grande do Sul, Brazil. Lower case letters indicate the comparison of ovigerous females frequency between seasons and capital letters compare the frequency of the couples. Columns with at least one letter in common are not significantly different (p>0.05).

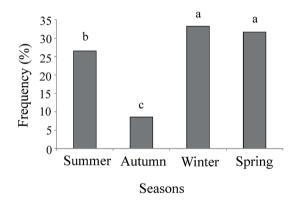


Figure 4. Relative frequency (%) of juveniles of *Hyalella bonariensis* from Silveira Martins, state of Rio Grande do Sul, Brazil. Columns with at least one letter in common are not significantly different (p>0.05).

consequent input of juveniles throughout the year. Besides, this assumption can be supported by the fact that juveniles and pre-copula pairs were found in all seasons.

These types of distribution have already been observed for other species of *Hyalella*, such as *H. pleocuta*, *H. castroi* (Castiglioni and Bond-Buckup, 2008b) and *H. azteca* (Saussure, 1858) (Pickard and Benke, 1996). For other amphipods, bimodal distribution also appears to be common as, for example, in *Corophium multisetosum* Stock, 1952 (Cunha *et al.*, 2000), *Echinogammarus longisetosus* Pinkster, 1973 (Guerao, 2003), *Talorchestia brito* Stebbing, 1891 (Gonçalves *et al.*, 2003) and *Gammarus chevreuxi* Seston, 1913 (Subida *et al.*, 2005).

In crustaceans, it is well documented that generally males reach larger sizes than females, especially in freshwater amphipods as, for example, in *H. pleocuta*, *H.* castroi (see Castiglioni and Bond-Buckup, 2008b), H. azteca (see Pickard and Benke, 1996), Gammarus pulex (Linnaeus, 1758) (Adams and Greenwood, 1983), Gammarus leopoliensis Jadzewski & Konopacka, 1989 (Zielinski, 1998) and *E. longisetosus* (see Guerao, 2003). According to Low (1978), males and females have similar growth rates until they reach sexual maturity, and then, later, they develop different reproductive and ecological demands, resulting in different growth rates. Thus, males invest energy in body growth, while females need to divide their energy between growth and reproduction, resulting in more prolonged intermolt periods and a minor increase in body size (Hartnoll, 1982; Borowsky, 1991; Wen, 1992; Thiel, 1999).

In addition, it is noteworthy that in some amphipods, including *Hyalella*, there is a pre-copula behavior in which males carry females for a few days before the copula occurs (Strong, 1972; Wellborn, 1995). So, the fact that males are larger than females enables them to carry females in an easily way (Adams and Greenwood, 1983; Adams *et al.*, 1985). Furthermore, larger males may present a higher pairing success, once females prefer these individuals (Castiglioni and Bond-Buckup, 2008a). The population analyzed in this paper follows this pattern, in order that sexual dimorphism in relation to body size was observed, with males larger than females.

Sex ratio, along with the assessment of body size and distribution in size classes, is a population parameter estimated for several crustaceans. All parameters evaluated by such analyses have a direct influence on the population dynamics, especially in reproductive potential (Emmerson, 1994), which highlights the importance of being studied.

Females were more frequent than males, a result also observed for *H. pleoacuta, H. castroi* (see Castiglioni and Bond-Buckup, 2008b) and other amphipods (Powell and Moore, 1991; Cardoso and Veloso, 1996; Appadoo and Myers, 2004; Kevrekidis, 2004; 2005). Deviations observed in sex ratio of *H. bonariensis*, as has been observed in other species of *Hyalella*, appear to be related to their reproductive behavior (Wellborn, 1994; 1995; Wellborn and Cothran, 2007; Castiglioni and Bond-Buckup, 2008b). Males spend more time exposed in the environment by choosing a female that they will carry during the pre-copula, which turn them more susceptible to predation, resulting in a population with greater abundance of females. Furthermore, it has been observed that predators, such as fish and Odonata larvae, always prefer to feed the largest specimens of *Hyalella*, in this case the males, favoring sex ratio for females (Wellborn, 1994). In amphipods, female-biased sex ratios can also be related to variations in temperature, type of vegetation, growth rates, maturity, mortality, longevity, habitat fragmentation, occupation of different microhabitats, food availability and presence of parasites (Wilson and Pianka, 1963; Strong, 1972; Wenner, 1972; Wildish, 1979; Moore, 1981; Powell and Moore, 1991).

Predominance of females in intermediate size class of body size and males in the larger size classes, framed the population of *H. bonariensis* in the anomalous pattern described by Wenner (1972). This result may be related to the greater investment in reproduction by females (Cardoso and Veloso, 1996), as also observed in other species of *Hyalella* from Brazil (Castiglioni and Bond-Buckup, 2007). Other reason could be the fact that female amphipods incubate the eggs in the marsupium (Borowsky, 1991), and often even juveniles, developing a parental care behavior, which results in a molt prolongation, limiting their growth (Thiel, 2003).

In H. bonariensis, the presence of couples in precopula and ovigerous females was recorded throughout the year, but more often in winter, in a way that, consequently, juveniles were also found in greater frequency in winter and spring. Similarly, H. castroi and H. pleoacuta, which occur in the highland region of state of Rio Grande do Sul, also reproduce with higher intensity in winter (Castiglioni and Bond-Buckup, 2008a), a pattern also observed in Gammarus duebeni Lilljeborg, 1951, Gammarus oceanicus Segerstrale, 1947, Gammarus salinus Spooner, 1947 (Kolding and Fenchel, 1981) and Corophium multisetosum (see Cunha et al., 2000). Differently from the Brazilian species of Hyalella, H. azteca, a North American species, has a reproduction peak in summer, which could be influenced by temperature (Cooper, 1965; Strong, 1972; Kruschwitz, 1978; March, 1978; Wen, 1992), photoperiod (March, 1977) and oxygen concentration (Nebeker, et al., 1992).

Occurrence of a peak of ovigerous females seems to be related to a greater abundance of aquatic macrophytes on the edge of aquatic environments, because these plants provide food and shelter for Hyalella populations (Castiglioni and Bond-Buckup, 2008b). Hargrave (1970) states that H. azteca feeds primarily on algae and bacteria associated with sediment and macrophytes, as well as decomposing animals and plants (Cooper, 1965). At the sampling site of *H. bonariensis* population, a greater abundance of macrophytes was verified in the colder months of the year (D.S. Castiglioni et al., pers. obs.), coinciding with the period of greatest occurrence of ovigerous females. Therefore, future studies about the relation between the presence of aquatic plants and ovigerous females can show the importance of conservation of these microhabitats for the population dynamics of freshwater amphipods.

Juveniles were found throughout the year, probably due to the continuous reproduction of *H. bonariensis*, as mentioned above. Furthermore, juveniles occurred in greater abundance in winter and spring, which may be due to the reproductive peak of the species in winter, resulting in a higher recruitment at this period of the year. Likewise, continuous recruitment was also observed in *H. pleocuta* and *H. castroi* (see Castiglioni and Bond-Buckup, 2008b), and other amphipods as *Corophium multisetosum* (see Cunha *et al.*, 2000), *Echinogammarus marinus* (Leach, 1815) (Maranhão *et al.*, 2001), *E. longisetosus* (see Guerao, 2003) and *G. chevreuxi* (see Subida *et al.*, 2005).

The population of *H. bonariensis* studied in this paper was different when compared to other species of *Hyalella*, mainly regarding to reproductive peak. Differences in population aspects between *H. bonariensis* and the North American species of *Hyalella* enhance the urgent necessity in studying the Brazilian species. Then, the creation of environmental quality assessment protocols based in organisms adapted to aquatic ecosystems from Brazil can be a reality. Furthermore, the present study highlights the importance of known the population dynamics of Brazilian species of *Hyalella*, in order to create a pattern of cultivation in laboratory and, in the future, use these species in ecotoxicology tests. Besides, more studies on the population dynamics of *H. bonariensis* are needed to better understand its life cycle, ecology and reproductive aspects, also including other populations from the same species. Later, this species can be used in ecotoxicology testing and evaluation of environmental quality, in order to help the conservation and preservation of freshwater environments in Brazil.

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