Intermolt duration and postembryonic growth of two sympatric species of *Hyalella* (Amphipoda, Dogielinotidae) in laboratory conditions

Daniela da Silva Castiglioni; Deise Garcia-Schroeder;
Daniela Ferreira Barcelos; Georgina Bond-Buckup

(DSC; DG-S; DFB; GB-B) Laboratório de Carcinologia, Departamento de Zoologia, PPG Biologia Animal, Universidade Federal do Rio Grande do Sul, Avenida Bento Gonçalves, 9500, prédio 43435-2, sala 214, CEP: 91501-970, Porto Alegre, RS, Brasil.
E-mail: danielacastiglioni@yahoo.com.br

Abstract

This study was designed to test the hypothesis that two sympatric species of freshwater gammaridean, *Hyalella pleoacuta* and *H. castroi*, might show differences at the intermolt duration and postembryonic growth in laboratory conditions. Ovigerous females were collected with a net in April 2005 and April 2006, in a trout culture pond in the Vale das Trutas, municipality of São José dos Ausentes, southern Brazil. These specimens were cultured in the laboratory (19° C and 12-hour light-dark photoperiod), and examined for signs of release of juveniles at the same time each day. The culture water was changed twice a weak. Juveniles that emerged from the brood pouch were separated and classified as stage I; the subsequent stages were identified by each successive molt. All the amphipods were observed twice a day until their death. There was no significant difference between the mean total intermolt period of males (9.68 days) and females (9.03 days) of *H. pleoacuta*. However, in *H. castroi,* the males showed a longer mean total intermolt period (12.18 days) than did females (10.68 days). Sexual dimorphism was observed at stage V in both species (*H. pleoacuta* – males: 25.6 ± 0.65 days and females: 24.7 ± 0.40 days; *H. castroi* – males: 28.4 ± 1.29 days and females: 27.1 ± 0.56 days). Sexual maturity (stage VIII) was attained after 52.3 ± 1.1 days in males and 51.5 ± 1.1 days in females of *H. pleoacuta*. In *H. castroi* the males and females attained sexual maturity after 56.7 ± 2.5 and 53.2 ± 1.3 days, respectively. Males and females attained a maximum cephalothorax length of 0.85 and 0.79 mm, respectively in *H. pleoacuta,* and 0.89 and 0.86 mm, respectively in *H. castroi*. The mean longevity of males and females was 124.8 ± 10.32 and 121.8 ± 9.31 days, respectively in *H. pleoacuta,* and 164.0 and 139.5 days, respectively in *H. castroi*.

Key words. Intermolt duration; molt frequency; sexual maturity; growth; *Hyalella*.

Introduction

The bodies of crustaceans are limited by rigid exoskeletons that determine a peculiar type of growth. The growth appears as a discontinuous phenomenon that takes place in staggered increments, whose most evident manifestation is the molting process or ecdysis. Each ecdysis is followed by a post-molt uptake of water and, as consequence, a rapid increase in body size during the short soft-skinned period (Hartnoll, 1982). The increase in weight and size after each molting event obeys to an increase in the volume of the body fluids and the subsequent tissue growth. The neurohormonal regulation of the molt cycle is affected by diverse external and internal factors,

being temperature and photoperiod the most relevant ones among the first group, and age, sex, and gonad maturity the most important ones among the second group (Hartnoll, 1982; Lipcius, 1985). Besides, these animals allocate energy between growth and reproduction many times throughout adult life (Stearns, 1992).

The genus *Hyalella* Smith, 1874 occurs in freshwater environments in southern Brazil. Most of the *Hyalella* species usually found associate to macrophytes, being that others species are found swimming at the water column or burrowing at the sediment of permanent reservoir, lakes, and streams (Kruschwitz, 1978; Wellborn, 1995). These species are important members of the benthos, because they are used as food by aquatic birds, fishes and other crustaceans (Kruschwitz, 1978; Wellborn, 1995).

Development of the species of *Hyalella* occurs in the marsupium (Cooper, 1965). These crustaceans, as well all amphipods, have direct development, and their eggs hatch into juveniles that have the general adult morphology, although they still lack secondary sex characteristics (Strong, 1972; Borowsky, 1991; Steele and Steele, 1991). Development in these species is divisible into an embryonic period, extending from ovulation to hatching; and a juvenile period (postembryonic period), extending from hatching to emergence from the marsupium (Borowsky, 1980a; 1980b). Sexual dimorphism in species of *Hyalella* is identified by adult larger body size and enlarged second gnathopod of males and oostegites of females (Nelson and Brunson, 1995).

The life cycles of the species of *Hyalella* that occur in Brazil are not known. The majority of studies on *Hyalella* in Brazil have emphasized the taxonomy of the group (Pereira, 1989; Bond-Buckup and Araujo, 1998; Pereira, 2004; González *et al.,* 2006). However, the biological traits of species of *Hyalella* were recently investigated by Castiglioni and Bond-Buckup (2007), Castiglioni and Bond-Buckup (in press a and b). This work was developed with the aim to test the hypothesis that two sympatric species of freshwater gammaridean, *Hyalella pleoacuta* González, Bond-Buckup and Araujo, 2006 and *H. castroi* González, Bond-Buckup and Araujo, 2006 might show differences at the intermolt duration and postembryonic growth in laboratory conditions. For these, the time to first molt, intermolt duration, molt frequency, age of the sex recognition, age of the sexual maturation and growth were analyzed in males and females of these two sympatric species of *Hyalella.*

Material and Methods

Ovigerous females of two *Hyalella* species were collected with a net in April 2005 and April 2006 in one culture pond holding trout – *Oncorhynchus mykiss* (Walbaum, 1792) in the Vale das Trutas near the headwaters of the Rio das Antas in the municipality of São José dos Ausentes, state of Rio Grande do Sul, Brazil (28°47'00"S, 49°50'53"W). Both species were found together, living under the roots of aquatic macrophytes of the genera *Senecio* Linnaeus, *Hydrocotile* Linnaeus, *Ludwigia* Linnaeus, and *Callitriche* Linnaeus along the sides of the ponds. The regional climate is characterized as medium mesotherm, with cold winters and mild summers because of the altitude (1,100 m) (Nimer, 1989).

The amphipods collected were placed in plastic bags and kept in a cooler during transportation to the laboratory where the animals were identified. The ovigerous females were cultured in the laboratory at a temperature of 19° C with a 12-hour light-dark photoperiod. During the embryonic and postembryonic periods, the specimens of both species were kept in containers with a volume of water of 100 ml each. The water used in laboratory cultures was collected together with the amphipods, from the trout culture pond. *Salvinia* sp. was added to the container to serve as a substrate as well as food for both species of *Hyalella.* Every other day, fish food (TetraDiskus® – 43% protein) was added *ad libitum* to the cultures as a food supplement for the females. Ovigerous females were examined for signs of release of juveniles at the same time each day. Juveniles that emerged from the brood pouch were placed individually into 50 ml containers, and classified as stage I. The subsequent stages were identified by each successive molt. These amphipods were fed twice a week with three drops of the algae *Ankistrodesmus* sp. Corda, 1838 (3.5 x 10^6 cells/ml) and a small leaf (about 0.009 g) of the macrophyte *Cal-*

litriche rimosa Fasset, 1951. This macrophyte was collected together with the ovigerous females in the trout culture ponds. The water in the cultures was changed twice a week. After the 8th stage, the specimens were transferred to 100 ml containers. All the amphipods were observed twice a day until their death.

The duration (days) of each molt stage was calculated for each amphipod. Next the total mean time between each molt (± SE) was calculated for males and females individually, for each species. Analyses of variance, complemented by a Bonferroni *test,* were used to compare the mean time between molt stages of each sex of species of *Hyalella* ($\alpha = 0.05$) (Zar, 1996). Each molt stage was compared between males and females of *H. pleoacuta* and *H. castroi* (ANOVA; Bonferroni *test;* $\alpha = 0.05$) (Zar, 1996).

Some amphipods were measured for cephalothorax length using a micrometer eyepiece in a stereoscopic microscope (0.01 mm), two days after each molt during the life cycle. This measurement was performed to determine the growth and molt increment in each molt stage of males and females of both species. The molt increment in each molt stage of males and females of each species was compared by analysis of variance (ANOVA) complemented by a Bonferroni *test* ($\alpha = 0.05$) (Zar, 1996). We also compared the molt increment between males and females of each species, and between males and females of both species (ANOVA; Bonferroni *test;* $\alpha = 0.05$) (Zar, 1996).

The longevity (days) was recorded for each specimen. Next the mean longevity of males and females for each species was calculated. The mean longevity (days) of amphipods was compared between sex and species, using a *t* test ($\alpha = 0.05$) (Zar, 1996).

Results

The life cycle of *H. pleoacuta* and *H. castroi* can be divided into an immature stage (consisting of the first 5 stages), a juvenile stage (stages VI and VII) and an adult stage (stage VIII and older). The duration of each stage differed between species.

Mortality in the first juvenile stages was high: 107 (51.2%) and 83 (35.3%) juveniles died before their sex could be determined, in *H. pleoacuta* and *H. castroi,* respectively. The first molt occurred at 7.1 ± 0.13 days (mean ± SE) (n = 152) in *H. pleoacuta* and 6.8 ± 0.09 days (n = 103) in *H. castroi.*

There was no significant difference between the mean total intermolt period (± SE) of males (9.68 ± 0.31 days) and females (9.03 ± 0.21 days) of *H. pleoacuta* ($t = 1.749$; $p < 0.05$). However, in *H. castroi,* the males showed a longer mean total intermolt period than the females (males: 12.18 ± 0.50 days; females: 10.68 ± 0.29 days) ($t = 2.628$; $p < 0.05$). Males and females of *H. castroi* showed a longer mean intermolt period than did males and females of *H. pleoacuta* (males: $t = -4.268$; females: $t = -4.675$; $p < 0.05$). Males and females of *H. pleoacuta* molted 9.8 and 9.7 times (means), respectively, whereas males and females of *H. castroi* molted 11.3 and 10.5 times along of life cycle, respectively.

The duration (days) of each stage of males and females of *H. pleoacuta* and *H. castroi* is shown in Table I. Males and females molted with more frequency at the 5th stage in *H. pleoacuta* ($p < 0.05$) and at the 6th stage in *H. castroi* ($p < 0.05$). However, males and females of both species showed a longer mean intermolt period in the later stages than in the first stages ($p < 0.05$).

Sexual dimorphism, identified by the enlarged second gnathopods of males and by the oostegites of females, was first observed at the 5th stage in both species of *Hyalella.* This stage was reached after about 25.6 ± 0.65 and 24.7 ± 0.40 days in males and females, respectively, in *H. pleoacuta.* In *H. castroi* sexual dimorphism was attained after 28.4 ± 1.29 days in males and 27.1 ± 0.56 days in females. The sex could be determined at sizes of about 0.35 and 0.37 mm CL in *H. pleoacuta* and *H. castroi,* respectively. Stage VIII (sexual maturity) was attained after 52.3 ± 1.1 days (mean ± SE) and 51.5 ± 1.1 days in males and females, respectively, in *H. pleoacuta.* In *H. castroi* the males and females attained sexual maturity after 56.7 ± 2.5 days and 53.2 ± 1.3 days, respectively. The males and females of *H. pleoacuta* attained sexual maturity at 0.51 and 0.48 mm CL, respectively. In *H. castroi,* males and females were sexually mature at 0.55 and 0.53 mm CL, respectively.

The molt increment in each molt stage of males and females of both species is shown in

Table I. Duration (days) (mean ± SE) of each stage of males and females of *Hyalella pleoacuta* and *H. castroi.*

Stages	*Hyalella pleoacuta*		*Hyalella castroi*	
	Juveniles		Juveniles	
I	7.1 ± 0.13 (213) ef / DE		6.8 ± 0.09 (200) ef / EF	
II	6.0 ± 0.13 (200) f / E		6.7 ± 0.11 (168) f / F	
III	6.0 ± 0.11 (152) f / E		6.8 ± 0.19 (145) ef / EF	
IV	6.6 ± 0.17 (152) ef / DE		7.1 ± 0.17 (124) ef / EF	
	Males	Females	Males	Females
V	8.1 ± 0.27 (58) ed	7.7 ± 0.25 (94) CD	7.4 ± 0.49 (25) ef	7.7 ± 0.26 (78) EF
VI	8.6 ± 0.31 (57) d	9.0 ± 0.38 (87) C	9.1 ± 0.74 (25) de	8.5 ± 0.38 (68) DE
VII	10.1 ± 0.40 (46) d	10.9 ± 0.44 (66) B	11.1 ± 0.90 (22) d	10.4 ± 0.61 (58) D
VIII	12.9 ± 0.86 (34) c	12.6 ± 0.75 (42) B	15.0 ± 1.28 (21) c	14.3 ± 1.02 (47) C
IX	17.3 ± 2. 11 (19) b	17.5 ± 2.23 (25) A	20.4 ± 1.55 (19) b	19.4 ± 1.64 (29) B
X	19.2 ± 1.74 (17) ab	18.1 ± 2.01 (20) A	20.3 ± 1.78 (16) b	22.8 ± 1.72 (25) A
XI	21.4 ± 1.93 (14) a	17.4 ± 1.12 (15) A	20.6 ± 2.30 (14) b	24.2 ± 1.83 (22) A
XII	22.0 ± 3.55 (10) a	19.8 ± 2.17 (12) A	25.5 ± 2.79 (11) a	24.9 ± 1.70 (18) A
XIII	22.3 ± 4.37 (4) a	20.8 ± 2.23 (9) A	25.6 ± 2.69 (8) a	25.4 ± 1.22 (13) A
XIV	25.7 ± 4.26 (3) a	23.6 ± 3.23 (7) A	29.0 ± 1.00 (2) a	28.4 ± 1.51 (7) A
XV	26.0 (1) a	23.7 ± 0.88 (3) A		
XVI		26.0 ± 6.00 (2) A		

Note: Juvenile stages I to IV were not separated into males and females, since these juveniles could not be sexed because their secondary sexual characters are not yet developed. Numbers between parentheses are number of individuals analyzed. Small letters correspond to the comparisons of males each species of *Hyalella* and capital letters correspond to the comparisons of females of each species of *Hyalella.* Values with at least one letter in common did not differ statistically ($\alpha = 0.05$).

Figure 1. Although the males showed a high molt increment, there was no significant difference in the molt increment in each molt stage of males and females of both species ($p > 0.05$). Besides, there was no observed significant difference in the molt increment between both sex of the species ($p > 0.05$). In Figure 2 indicates the cephalothorax length of males and females of *H. pleoacuta* and *H. castroi* at each stage. The cephalothorax length of males and females of both species is represented by a sigmoid curve, but males became larger than females with each successive stage, mainly in *H. pleoacuta.* The males and females attained a mean maximum size (cephalothorax length) of 0.85 and 0.79 mm, respectively in *H. pleoacuta,* and 0.89 and 0.86 mm in *H. castroi.* Figure 3 represents the growth curve of males and females of *H. pleoacuta* and *H. castroi* constructed by integrating data on molt increment and intermolt duration.

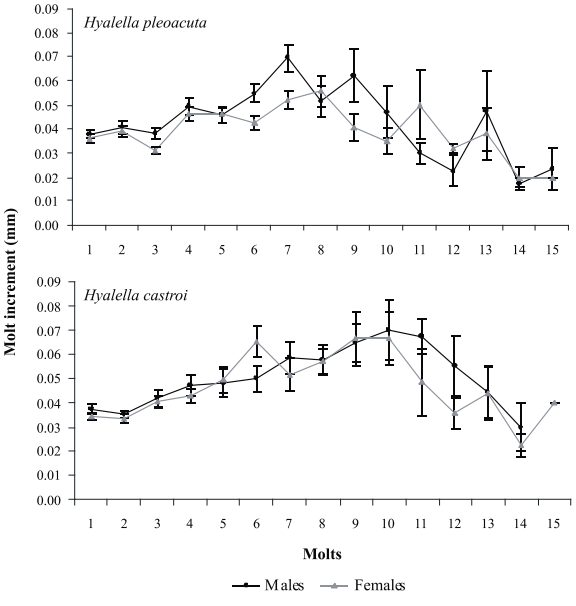

Figure 1. Mean molt increment (± SE) of males and females of *Hyalella pleoacuta* and *H. castroi* in each development stage.

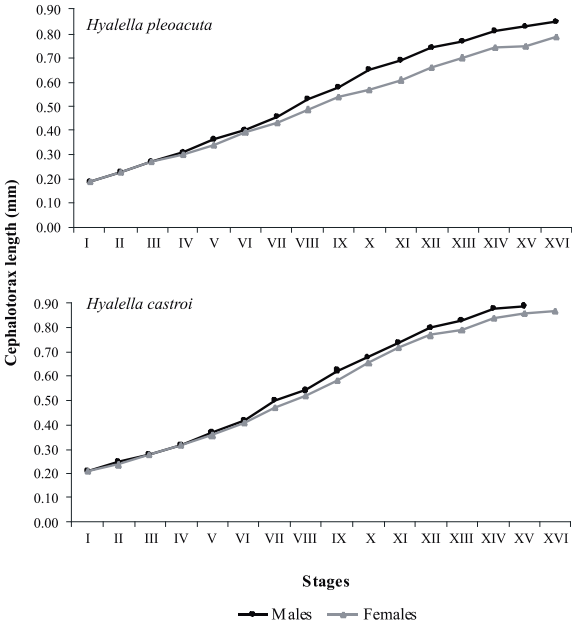

Figure 2. Mean cephalothorax length of males and females of *Hyalella pleoacuta* and *H. castroi* at each stage of their life cycle.

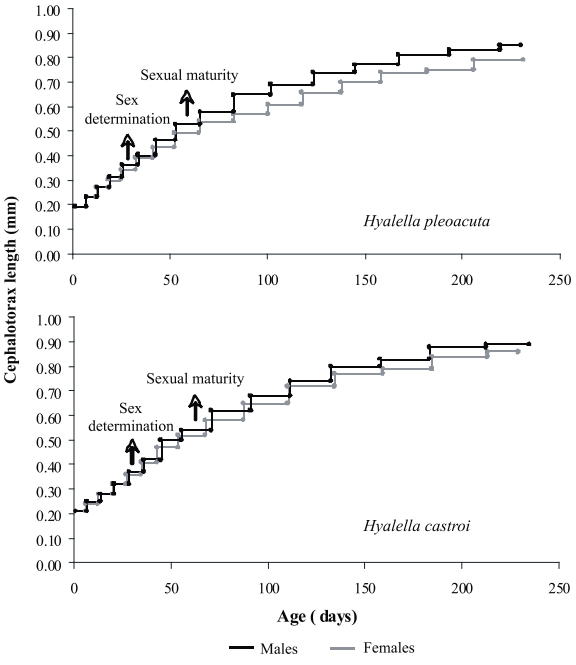

Figure 3. Growth curve of males and females of *Hyalella pleoacuta* and *H. castroi* in laboratory conditions constructed by integrating data on molt increment and intermolt duration.

The longevity of males of *H. pleoacuta* ranged from 58 to 259 days, and that of females from 51 to 266 days. There was no significant difference between the mean longevity (± SE) of males (124.8 ± 10.32 days; n = 33) and females (121.8 ± 9.31 days; n = 42) of *H. pleoacuta* ($t = 0.014$; $p > 0.05$). In *H. castroi,* the longevity of males ranged from 62 to 240 days and that of females from 56 to 262 days, i.e., males showed greater mean longevity than females (males: 164.0 ± 42.5 days; n = 21; females: 139.5 ± 10.39 days; n = 46) ($t = 1.230$; $p < 0.05$). Males and females of *H. castroi* showed greater mean longevity than did males and females of *H. pleoacuta* (males: $t = 2.509$; females: $t = -1.296$; $p < 0.05$).

Discussion

The stages of the life cycle identified in *H. pleoacuta* and *H. castroi* were the same as observed in *H. azteca* Saussure, 1858 by Cooper (1965). However, the duration of each stage and the age at sexual maturity of the species of *Hyalella* analyzed in the present work differed from *H. azteca*. Probably the duration of each stage of life cycle is directly influenced by the environmental conditions under which the animals are raised or exposed, especially the temperature and photoperiod (Bovee, 1950; Cooper, 1965; Strong, 1972; Kruschwitz, 1978). The intermolt periods in females of *H. pleoacuta* and *H. castroi* were very similar to that observed in *H. azteca* (11 days) by Othman and Pascoe (2001). However, the total intermolt period in males of these two species was lower than that of *H. azteca* studied by Kruschwitz (1978) (17.17 days) and by Othman and Pascoe (2001) (20 days).

Sexual dimorphism is often pronounced in amphipods. The sexes of gammarideans can usually be distinguished by differences in secondary sexual characters, including body size, gnathopods (Moore and Wong, 1996), oostegites (Kruschwitz, 1978), and antennae (Tsoi and Chu, 2005). Development of these secondary sexual characters reflects sexual differentiation and maturation (Hartnoll, 1982). The time of sex recognition in *H. pleoacuta* and *H. castroi* was very similar to the results reported by Nelson and Brunson (1995) and Othman and Pascoe (2001) in *H. azteca* (see Table II).

The age of sexual maturity of males and females of *H. pleoacuta* was similar to *H. castroi.* However, *H. azteca* became sexually mature at different ages than the species of *Hyalella* analyzed in the current work, as observed in Table II. It should be noted, however, that these variations in the age of sexual maturity may be attributed to the different ambient or laboratory conditions to which different species or populations were exposed. In the case of *H. azteca,* its growth and development are affected by several environmental factors, particularly temperature (Bovee, 1950; Cooper, 1965; De March, 1977; Kruschwitz, 1978), but also photoperiod (De March, 1977; Kruschwitz, 1978), dissolved oxygen (Nebeker *et al.,* 1992), pH (Pilgrim and Burt, 1993), and food quantity and quality (Hargrave, 1970; Moore and Farrar, 1996; Wellborn, 1994). For example, this species reared at lower temperatures can take longer to mature and grow larger than animals reared at higher temperatures.

The growth of individuals of *H. pleoacuta* and *H. castroi* was found to be continuous throughout life, in laboratory conditions. Nevertheless, growth rates were higher in the early phases (juvenile phases) in both species, when it is commonly accepted that individuals grow exponentially (Wel-

Table II. Comparison of age at sex recognition and age at sexual maturity of some species of *Hyalella.*

	Age of the sex recognition (days)	Age of the sexual maturity (days)	Laboratory conditions (temperature and photoperiod light/dark)	Authors
Hyalella azteca	_	60-65	20° C-22° C	Bovee (1950)
Hyalella azteca	_	26-41	26° C-28° C	Bovee (1950)
Hyalella azteca	_	36	20° C and 15 h / 9 h	Cooper (1965)
Hyalella azteca	_	24	20° C and 16 h / 8 h	Nelson and Brunson (1995)
Hyalella azteca	19-21	23	22° C and 16 h / 8 h	Othman and Pascoe (2001)
Hyalella pleoacuta	Males: 24.7* Females: 25.6*	Males: 52.3* Females: 51.5*	19° C and 12 h / 12 h	Present study
Hyalella castroi	Mals: 27.1* Females: 28.4*	Males: 56.7* Females: 53.2*	19° C and 12 h / 12 h	Present study

* = means

ton and Clarke, 1980). Similar data were reported by Othman and Pascoe (2001) for *H. azteca* and by Maranhão and Marques (2003) for *Echinogammarus marinus* (Leach, 1815), also in laboratory conditions.

Males and females of *H. pleoacuta* and *H. castroi* molted about the same time until sexual maturity. However, in adult males, the intermolt period was longer than in females. This observation is similar to those of Geisler (1944), Strong (1973), Kruschwitz (1978), and Othman and Pascoe (2001), who found that adult females molted more frequently than adult males of *H. azteca.* This is probably because the female are involved in producing and releasing the juveniles, and so they need to molt more frequently than the males.

In the case of gammaridean amphipods, the females have no mechanism for sperm storage and typically produce a clutch of eggs at each molt (Cooper, 1965; Strong, 1973). One to a few days prior to the female molt, males use their anterior gnathopods to grasp the female's second coxal segment, in a pre-copulatory mate-guarding behavior (Borowsky, 1984). Pairs remain attached in this way (male dorsal to female) throughout the female's molt, at which time the first-instar offspring are released and the new clutch of eggs is fertilized by the guarding male as eggs pass into the marsupium. Pairs separate after fertilization (Cooper, 1965; Strong, 1973). The pre-copulatory mate-guarding behavior guarantees that males and females are together during this phase of the female life cycle. The males of *H. pleoacuta* and *H. castroi* carry the females for about 6 days (Castiglioni and Bond-Buckup, 2007). The embryonic and postembryonic periods take about 15 days in *H. pleoacuta* and 16 days in *H. castroi* (Castiglioni and Bond-Buckup, 2007). Adding the time that the females of *H. pleoacuta* and *H. castroi* remain together with the males, to the time the females require to incubate the eggs and carrying the hatching juveniles in the marsupium, sums to about 20 days of their reproductive cycle. Thus, the somatic growth of the females is compromised, and they do not molt during this life phase. Afterwards, the females need to molt more frequently than males to compensate for the increase in body size. Besides, it must be taken into account that the body size of the female is correlated with the number of eggs produced, that is, the larger the female, the more eggs that she will can produce and carry in the marsupium during the course of embryonic development (Castiglioni and Bond-Buckup, submitted).

The body sizes at which sex can be identified, and maximum body size attained by individuals of *H. pleoacuta* and *H. castroi* under laboratory conditions were all smaller than in field conditions (see Castiglioni and Bond-Buckup, in press *b*). Hargrave (1970) and Moore and Farrar (1996) observed that diet quality and quantity are clearly important in determining growth and reproduction in *H. azteca.* Probably the food quality and quantity influence the growth of *H. pleoacuta* and *H. castroi.* A smaller body size under laboratory conditions was also observed in the amphipod *Echinogammarus marinus* by Maranhão and Marques (2003). In addition to the influence that the quality of the food may have had on these results, the lower body size reached by individuals under laboratory conditions could also be attributable to a decrease in the scope for growth in response to stress. Chen *et al.* (1990) recorded higher mortalities and lower growth rates of penaeid shrimps in culture, because of the deterioration of water quality caused by metabolic

wastes, mainly ammonia and nitrite, which can be toxic to crustaceans. It is possible that water-quality problems caused by wastes since the food was supplied *ad libitum* and the water was changed only twice per week, may have influenced the present results for growth of *H. pleoacuta* and *H. castroi*.

The time to first molt, molt frequency, sex determination, and sexual maturation were very similar between these sympatric species, *H. pleoacuta* and *H. castroi*. However, the species differed in the total intermolt period, maximum body size and longevity of males and females in laboratory conditions. Probably these differences in the life cycle observed in laboratory conditions are sufficient to allow the two species to coexist in the trout pond. Knowledge of these biological traits is essential to understanding of the life cycle of these freshwater gammarideans, and for their future utilization in tests of environmental quality.

Acknowledgments

To the CNPq for the fellowship to the first author and financial support to second author (Proc. 47259/2003-3). We are grateful to Adriano Martins for her help during field work, to colleagues of the Laboratory of Carcinology of UFRGS for their relief during field and laboratory activities and to Dr. J. W. Reid for English language review. This work was carried out according to state and federal laws concerning wild animal sampling. Contribution number 531 of the Departamento de Zoologia, Programa de Pós-graduação em Biologia Animal, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil.

References

Bond-Buckup, G. and Araujo, P. B. 1998. *Hyalella montenegrinae* sp. n., um Amphipoda de águas continentais do sul do Brasil (Crustacea, Peracarida, Hyalellidae). Nauplius, 6:53-59.

Borowsky, B. 1980a. Factors that affect juvenile emergence in *Gammarus palustris* (Bousfield, 1969). Journal of Experimental Marine Biology and Ecology, 42:213-223.

Borowsky, B. 1980b. Reproductive patterns of three intertidal salt-marsh gammaridean amphipods. Marine Biology, 55:327-334.

Borowsky, B. 1984. Effects of receptive females' secretions on some male reproductive behaviors in the amphipod *Microdeutopus gryllotalpa*. Marine Biology, 84:183-187.

Borowsky, B. 1991. Patterns of reproduction of some amphipod crustaceans and insights into the nature of their stimuli. Pp. 33-66 *In* Bauer, R. T. and Martin, W. eds. Journal of Crustacean Sexual Biology. Columbia, New York, 355p.

Bovee, E. C. 1950. Some effects of temperature on the rates of embryonic, postembryonic, and adult growth in *Hyalella azteca*. Proceedings of the Iowa Academy of Science, 57:439-444.

Castiglioni, D. S. and Bond-Buckup, G. 2007. Reproductive strategies of two sympatric species of *Hyalella* Smith, 1874 (Amphipoda, Dogielinotidae) in laboratory conditions. Journal of Natural History, 41:1571-1584.

Castiglioni, D. S. and Bond-Buckup, G. Size, pairing and reproductive success in two sympatric species of *Hyalella* (Crustacea, Amphipoda, Dogielinotidae) from southern Brazil. Acta Oecologica (in press a).

Castiglioni, D. S. and Bond-Buckup, G. Ecological traits of two sympatric species of *Hyalella* Smith, 1874 (Crustacea, Amphipoda, Dogielinotidae) from southern Brazil. Acta Oecologica (in press b).

Chen, J. C.; Ting, Y. Y.;. Lin, J. N. and Lin, M. N. 1990. Lethal effects of ammonia and nitrite on *Pennaeus chinensis* juveniles. Marine Biology, 107:427-431.

Cooper, W. E. 1965. Dynamics and production of a natural population of a freshwater amphipod *Hyalella azteca*. Ecological Monographs, 35(4):377-394.

De March, B. G. E. 1977. The effects of photoperiod and temperature on the induction and termination of reproductive resting phase in the freshwater amphipod *Hyalella azteca* (Saussure). Canadian Journal of Zoology, 55:1595-1600.

Geisler, S. S. J. 1944. Studies on the postembryonic development of *Hyalella azteca* (Saussure). Biological Bulletin, 86:6-22.

González, E. R.; Bond-Buckup, G. and Araujo, P. B. 2006. Two new species of *Hyalella* from southern Brazil (Amphipoda: Hyalellidae) with a taxonomic key. Journal of Crustacean Biology, 26(3):355-365.

Hargrave, B. T. 1970. Distribution, growth, and seasonal abundance of *Hyalella azteca* (Amphipoda) in relation to sediment microflora. Journal of the Fisheries Research Board Canada, 27:685-699.

Hartnoll, R. G. 1982. Growth. Pp. 11-196 *In* Bliss, D. E. (ed.). The Biology of Crustacea: embryology, morphology and genetics. Academic Press, New York, 440p.

Jenio, F. 1980. The life cycle and ecology of *Gammarus troglophilus* Hubricht and Mackin. Crustaceana 6(Suppl.):204-215.

Kruschwitz, L. G. 1978. Environmental factors controlling reproduction of the amphipod *Hyalella azteca*. Proceedings of the Oklahoma Academy of Science, 58:16-21.

Lipcius, R. N. 1985. Size-dependent reproduction and molting in spiny lobsters and other long-lived decapods. Pp. 129-148 *In* Wenner, A. M. (ed.). Crustacean Issues. Factors in adult growth. A. A. Balkema. Rotterdam.

Maranhão, P. and Marques, J. C. 2003. The influence of temperature and salinity on the duration of embryonic development, fecundity and growth of the amphipod *Echinogammarus marinus* Leach (Gammaridae). Acta Oecologica, 24:5-13.

Moore, D. W. and Farrar, J. D. 1996. Effect of growth on reproduction in the freshwater amphipod, *Hyalella azteca* (Saussure). Hydrobiologia, 328:127-134.

Moore, P. G. and Wong, Y. M. 1996. Observations on the life history of *Orchomene nanus* (Kroyer) (Amphipoda:

Lysionanassoidea) at Millport Scotland as deduced from baited trapping. Journal of Experimental Marine Biology and Ecology, 195:53-70.

Nebeker, A. V.; Onjukka, S. T.; Stevens, D. G.; Chapman, G. A. and Dominguez, S. E. 1992. Effects of low dissolved oxygen on survival, growth and reproduction of *Daphnia, Hyalella* and *Gammarus*. Environmental Toxicology and Chemistry, 11:373-379.

Nelson, M. K. and Brunson, E. L. 1995. Postembryonic growth and development of *Hyalella azteca* in laboratory cultures and contaminated sediments. Chemosphere, 31(4):3129-3140.

Nimer, E. 1989. Climatologia do Brasil. IBGE, Rio de Janeiro, 421p.

Othman, M. S. and Pascoe, D. 2001. Growth, development and reproduction of *Hyalella azteca* (Saussure, 1858) in laboratory culture. Crustaceana, 74(2):171-181.

Pereira, V. F. G. 1989. Uma espécie de anfípode cavernícola do Brasil – *Hyalella caeca* sp. n. (Amphipoda, Hyalellidae). Revista Brasileira de Zoologia, 6:49-55.

Pereira, V. F. G. C. 2004. *Hyalella dielaii* sp. nov. from São Paulo Brazil (Amphipoda, Hyalellidae). Revista Brasileira de Zoologia, 21(2):179-184.

Pilgrim, W. and Burt, M. D. B. 1993. Effect of acute pH depression on the survival of the freshwater amphipod *Hyalella azteca* at variable temperatures: field and laboratory studies. Hydrobiologia, 254:91-98.

Stearns, S. C. 2002. The evolution of life histories. Oxford University Press, New York, 249p.

Steele, D. H. and Steele, V. J. 1991. Morphological and environmental restraints on egg production in amphipods. Pp. 157-170 *In* Wenner, A. and Kuris, A. (eds.). Crustacean Egg production – Crustacena Isses 7. A. A. Balkema, Rotterdam.

Strong, Jr. D. R. 1972. Life history variation among populations of an amphipod *(Hyalella azteca)*. Ecology, 53(6):1103-1111.

Strong, Jr., D. R. 1973. Amphipod amplexus, the significance of ecotypic variation. Ecology, 54:1384-1388.

Tsoi, K. and Chu, K. 2005. Sexual dimorphism and reproduction of the amphipod *Hyale crassicornis* Haswell (Gammaridea: Hyalidae). Zoological Studies, 44(3):382-392.

Wellborn, G. A. 1994. Size-biased predation and the evolution of prey life histories: a comparative study of freshwater amphipod populations. Ecology, 75:2104-2117.

Wellborn, G. A. 1995. Determinants of reproductive success in freshwater amphipod species that experience different mortality regimes. Animal Behavior, 50:353-363.

Welton, J. S. and Clarke, R. R. 1980. Laboratory studies on the reproduction and growth of the amphipod *Gammarus pulex* (L.). Journal of Animal Ecology, 49:581-592.

Zar, J. H. 1996. Biostatistical analysis. Prentice Hall, Upper Saddle

Received: February 2007
Accepted: Autust 2007