

## Population structure and habitat occupation in two sympatric *Aegla* species (Decapoda, Anomura, Aeglidae) in Atlantic Forest, Brazil

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### ABSTRACT

This study deals with population structure and habitat sharing of two sympatric aeglid species, *Aegla jarai* Bond-Buckup and Buckup, 1994 and *Aegla muelleri* Bond-Buckup and Buckup, 2010 at Espingarda Creek, Serra do Itajaí National Park, Rio Itajaí-Açu basin, Santa Catarina, Brazil. Individuals of *A. jarai* (n = 190) and *A. muelleri* (n = 131) were captured from June/2001 to May/2002 in monthly collection. A total of 89 males and 101 females (2 ovigerous) of *A. jarai* were collected with a sex ratio of 1:1, and 56 males and 75 females (2 ovigerous) of *A. muelleri*, with a predominance of females. *Aegla jarai* was larger than *A. muelleri* and the reproductive period of *A. jarai* was in the winter and spring, while that of *A. muelleri* was in the spring. Three cohorts were observed throughout the year, and both species have a recruiting period in the spring and summer. Both species perform their entire life cycle in the Espingarda Creek and their coexistence is attributed to space partitioning: the larger *A. jarai* lives in the large spaces formed between boulders, while the smaller *A. muelleri* shelters in the small spaces between pebbles.

### KEYWORDS

*Aegla jarai*, *Aegla muelleri*, distribution, freshwater crustacean, Neotropical region, sex ratio

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## INTRODUCTION

Species of the family Aeglididae Dana, 1852 live mostly in small streams close to springs and many are endemic (Bond-Buckup, 2003). Among them, *Aegla jarai* Bond-Buckup and Buckup, 1994 occurs in the watersheds of the Itajaí-Açú River, Canoas, and Pelotas, in southern Brazil (Fig. 1), while *Aegla muelleri* Bond-Buckup and Buckup, 2010 has a known distribution only in the Itajaí-Açú River basin (Fig. 1) (Boos *et al.*, 2012; Santos *et al.*, 2019). Both species occur in sympatry in Espingarda Creek, Serra do Itajaí National Park, Santa Catarina, Brazil, type-locality of *A. muelleri*. The growth of *A. jarai* was examined by Boos *et al.* (2006) in Espingarda Creek.

Sympatry is common among aeglids and is recorded in 23 species. *Aegla jarai* shows the highest records of sympatry involving the following species: *Aegla brevipalma* Bond-Buckup and Santos, 2012, *Aegla leachi* Bond-Buckup and Santos, 2012, *Aegla oblata* Bond-Buckup and Santos, 2012, *Aegla odebrechtii* Müller, 1876, *Aegla spinosa* Bond-Buckup and Buckup, 1994, and *A. muelleri* (see Dalosto and Palaoro, 2019).

For sympatric species to coexist, at least one must adopt a strategy to decrease competitiveness (Musil *et al.*, 2010). When studying sympatric species, it is

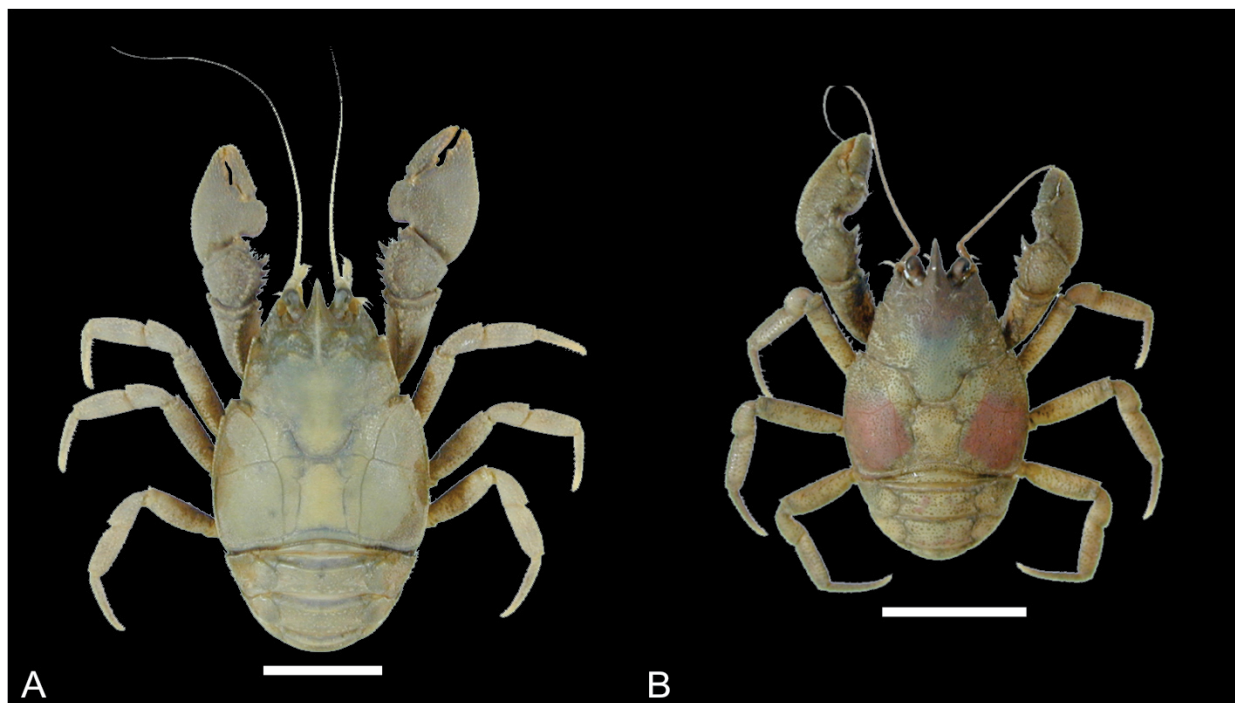
necessary to evaluate temporal and spatial distribution to accurately predict ecological and behavioral inferences about each species (Scopel *et al.*, 2009). Only by understanding these relationships, can it be inferred whether competition occurs between the species studied (Colwell and Futuyma, 1971).

Therefore, this study involves the analysis of the population structure of *A. jarai* and *A. muelleri* through the analysis of sex ratio, reproductive period, recruitment, and size range. We also assess habitat occupation and sharing.

## MATERIAL AND METHODS

Sampling took place in Espingarda Creek (27°01'24"S 49°09'06"W), Serra do Itajaí National Park, Rio Itajaí-Açú basin, Santa Catarina, Brazil. The vegetation cover of the park is classified as tropical, ombrophilous dense forest, located in the Atlantic rainforest of Brazil (GAPLAN, 1986).

A 45 m stretch was chosen at Espingarda Creek and divided into three sections of 15 m. The sections were designated 1, 2, and 3, from the most downstream region to the most upstream. The choice of Espingarda Creek was based on a pilot sampling where two species belonging to the family Aeglididae were observed.



**Figure 1.** *Aegla jarai* (A) and *Aegla muelleri* (B) collected in Espingarda Creek (27°01'24"S 49°09'06"W), Serra do Itajaí National Park, Rio Itajaí-Açú basin, Santa Catarina, Brazil. Scale bar: 10 mm.

The substrate of each sampled site was classified according to Leinz and Amaral (1970). Water velocity was measured with a float (Tucci, 1993) at several locations, in rapids and backwaters, during a rainless period of approximately 10 days in September 2002.

Samplings were monthly for 12 months, from June 2001 to May 2002, using dip nets (3 mm mesh) at points 1, 2, and 3. The dip net was placed on the bottom of the stream and the substrate was turned over upstream of the net so that any aeglids were carried by the water flowing into the net.

The aeglids were sorted by species and sex, and the cephalothorax length (CL) was measured with a digital caliper (0.01 mm), from the internal portion of the orbit to the posterior end of the carapace (rostrum excluded). After measuring, the individuals were returned to the point they were captured.

Sexing was done through the inspection for the presence of functional pleopods and genital pores on the coxae of the third pair of pereopods in females and the absence of these structures in males, using a magnifying glass (5 times magnification) (Martin and Abele, 1988). The reproductive period was evaluated based on the presence of ovigerous females throughout the sampling period.

The annual sex ratio was obtained by the ratio of the total number of males to the total number of females collected. The variation in the percentage of males and females was also observed at each season of the year, and the difference between the number of males and females was evaluated by the Binomial test ( $p < 0.05$ ) (Wilson and Hardy, 2002).

At each sampling period, temperature, dissolved oxygen saturation, pH, and electrical conductivity of the water were measured using an oximeter (oxi 330/SET WTW), pH meter (Hanna), and conductivity meter (33 YSI).

#### Statistical analysis

The Binomial test ( $p < 0.05$ ) was used to compare the sex ratio of each species at the Espingarda Creek per season and to compare the proportion of individuals between species by seasons and sampling point. The Mann-Whitney test estimated the difference in size between the species ( $p < 0.05$ ), since the assumptions

of variance and normality of the data were not found using the Levene and Shapiro-Wilks tests, respectively.

A Mann-Whitney test ( $p < 0.05$ ) evaluated differences in size of the sampled species and the size between males and females for each species (Zar, 1999).

To describe the population structure in size, individuals were grouped in size classes (minimum to maximum CL) following the method suggested by Sturges (1926).

## RESULTS

The sampled stretch in Espingarda Creek, where points 1, 2, and 3 were established, was composed of fine gravel substrate (2 – 20 mm in diameter), areas of accumulation of coarser gravel/small rocks (20 – 200 mm), sand (0.02 – 2 mm) and plant debris. The average water velocity at point 1 was 0.1 m/s, with a minimum of 0.03 m/s and a maximum of 0.3 m/s. Sampling points 2 and 3 had an average velocity of 0.3 m/s and a minimum velocity of 0.2 m/s. The highest speed recorded in sections 2 and 3 was 0.5 and 0.6 m/s, respectively.

The water temperature varied between 16 °C in autumn and 22.7 °C in summer, with the lowest average recorded in winter (16.45 °C) and the highest in summer (20.35 °C). Dissolved oxygen saturation in the water averaged 80 % annually, the pH was close to neutrality, and the average electrical conductivity was 24.25  $\mu\text{S}/\text{cm}$ . No statistical difference was recorded between sampling points (Tab. 1).

**Table 1.** Espingarda Creek (27°01'24"S 49°09'06"W), Serra do Itajaí National Park, River Itajaí-Açú basin, Santa Catarina, Brazil. Oscillations of the abiotic variables of the water during the seasons: water temperature (°C), oxygen content (%), pH, and conductivity ( $\mu\text{S}/\text{cm}$ ).

Season	Range	Water temperature (°C)	Oxygen content (%)	pH	Conductivity ( $\mu\text{S}/\text{cm}$ )
Winter	Min.	16.2	70	7.36	25
	Max.	16.6	98		
Spring	Min.	18.2	73	6.95	20
	Max.	19.0	75		
Summer	Min.	18.0	51	7.4	25
	Max.	22.7	103		
Autumn	Min.	16.0	85	7.9	27
	Max	20.7	91		

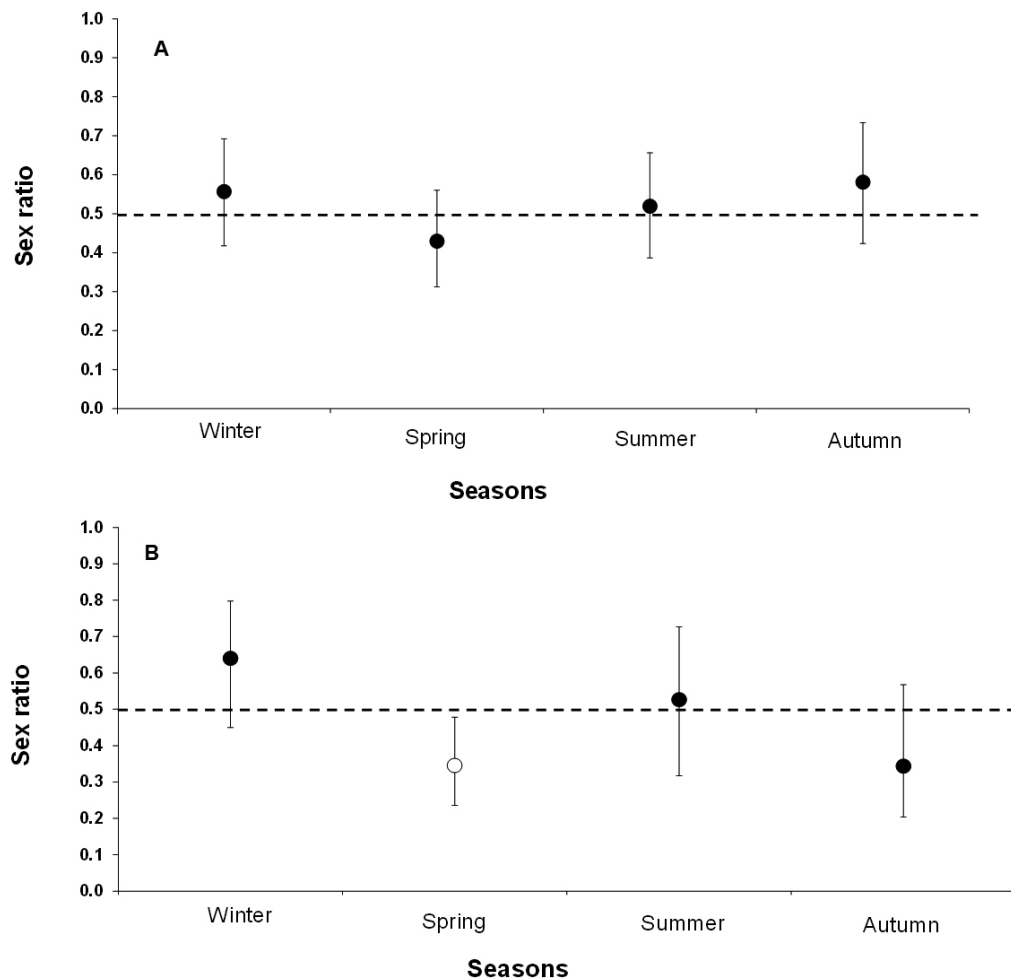
*Aegla jarai* individuals were captured throughout the study period, with 190 specimens in total, 89 males and 101 females (2 ovigerous); 47 % and 53 %, respectively. The sex ratio was 1:1 (Binomial test,  $p > 0.05$ ) for all seasons. A similar pattern occurred with *A. muelleri*, with 131 specimens captured, 56 males and 75 females (2 ovigerous); 43 % and 57 %, respectively. Overall, the sex ratio was dominated by females (Binomial test,  $p < 0.05$ ), and especially in the spring and autumn (Binomial test,  $p < 0.05$ ) (Fig. 2).

*Aegla jarai* had, on average, a larger CL than *A. muelleri*, ranging from 2.16 to 19.02 mm, while *A. muelleri* measured from 1.53 to 13.02 mm (Mann-Whitney,  $p < 0.05$ , Fig. 3). No sexual dimorphism in size was observed in either species at the statistical level (Mann-Whitney,  $p > 0.05$ , Figs. 4, 5), however,

*A. jarai* showed males that were larger than females in absolute size (Fig. 5).

The only two ovigerous females of *A. jarai* measured 16.27 mm CL (obtained in spring) and 19.00 mm (in winter), at points 1 and 3, while those of *A. muelleri* were 11.05 mm and 11.37 mm (both in spring) and from points 1 and 2.

There were three recognizable cohorts throughout the year. Both species showed the smallest individuals in the spring and summer, representing the cohort of juveniles recently recruited into the population. Later, the second cohort composed of intermediate size aeglids appeared in autumn and winter, and the third cohort of oldest and largest individuals with a lower frequency was present in various seasons (Figs. 6, 7).



**Figure 2.** Espingarda Creek. Sex ratio of *Aegla jarai* (A) and *Aegla muelleri* (B) by season during the sampling period, from June/2001 to May/2002. White circles indicate deviations from the sex ratio of 1:1, Binomial test,  $p < 0.05$ , and the bars correspond to the monthly variation amplitude.

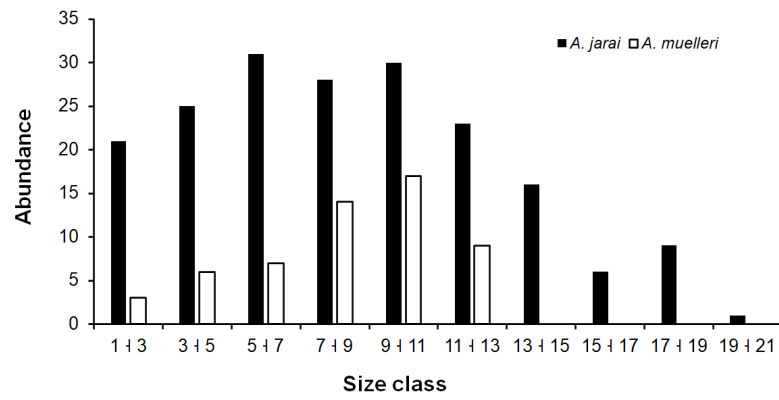


Figure 3. Espingarda Creek. Distribution of the population of *Aegla jarai* and *Aegla muelleri* into CL size class (mm).

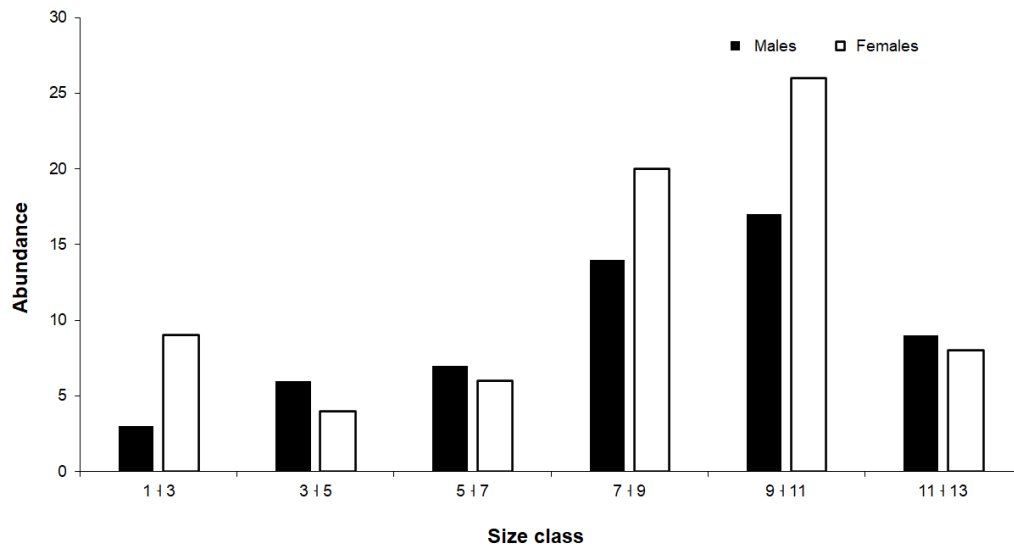


Figure 4. Espingarda Creek. Distribution of males and females (including the two ovigerous females) of *Aegla muelleri* into CL size class (mm).

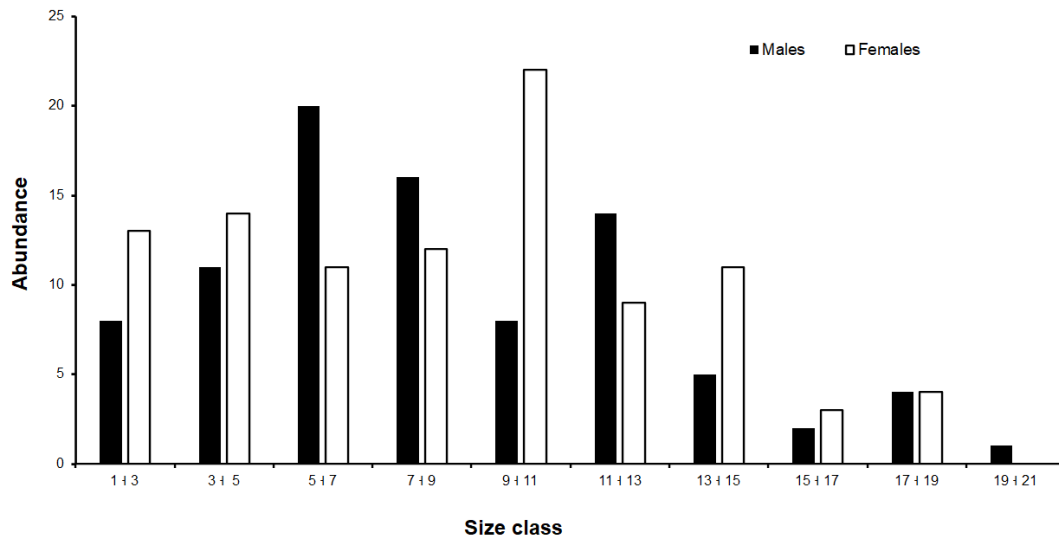
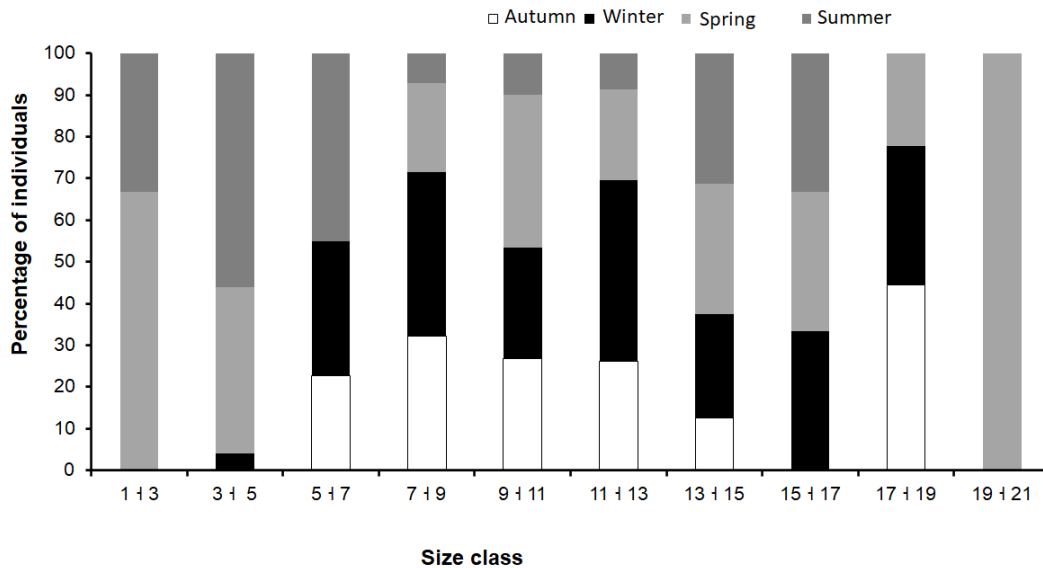
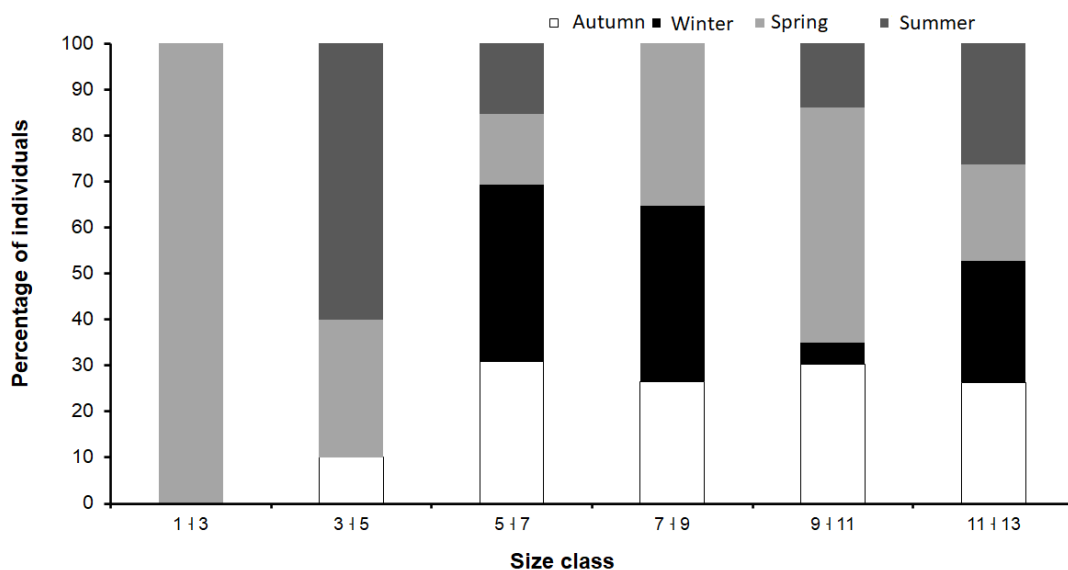


Figure 5. Espingarda Creek. Distribution of males and females (including the two ovigerous females) of *Aegla jarai* into CL size class (mm)



**Figure 6.** Espingarda Creek. Distribution of the population of *Aegla jarai* obtained in different seasons into CL size class (mm).



**Figure 7.** Espingarda Creek. Distribution of the population of *Aegla muelleri* obtained in different seasons into CL size class (mm).

We observed habitat sharing by the two species in all seasons and at all sampling points, except for *A. muelleri* which was absent at point 3 in the winter (Tab. 2; Figs. 8, 9).

## DISCUSSION

In lotic environments, such as Espingarda Creek, the temperature oscillates daily and seasonally, and between locations, altitude, and vegetation cover

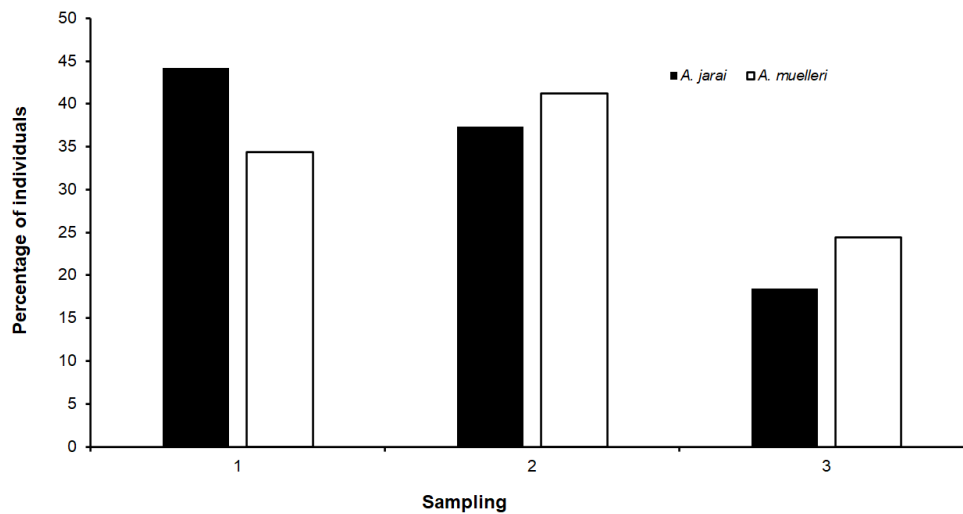
(Allan, 1995). In the analyzed and sampled stretch, Espingarda Creek was shown to have adequate oscillation of abiotic variables (temperature, pH, dissolved oxygen, type of substrate, and water speed).

The sampling location in Espingarda Creek has riverbanks with no forest cover, and so the solar radiation directly affects the water body. Therefore, water temperature and oxygen saturation are directly influenced by daily and seasonal climatic fluctuations.

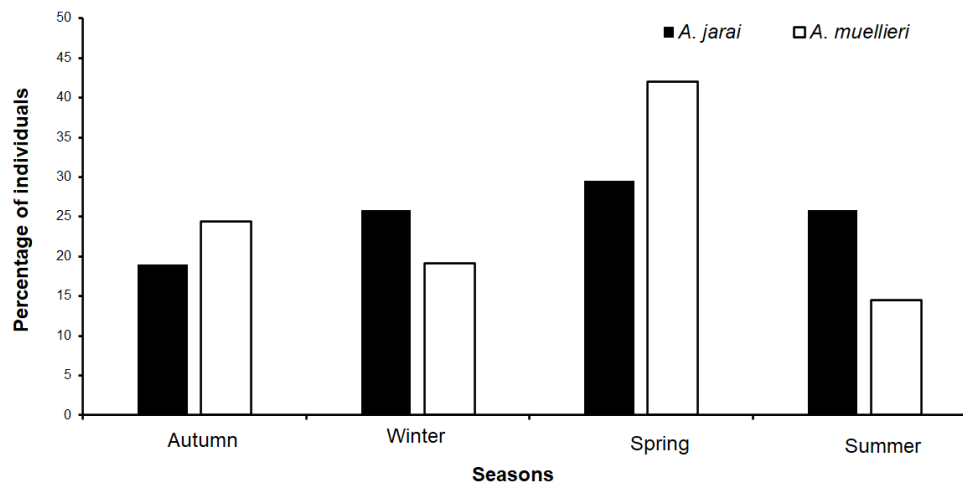
**Table 2.** The abundance of *Aegla muelleri* and *Aegla jarai* per point sampled in relation to the season from June/2001 to May/2002 in Espingarda Creek (27°01'24"S 49°09'06"W), Serra do Itajaí National Park, Rio Itajaí-Açú basin, Santa Catarina, Brazil. (\* =  $p < 0.05$  statistically different abundances).

Winter	<i>A. muelleri</i>	<i>A. jarai</i>	<i>p</i>	Spring	<i>A. muelleri</i>	<i>A. jarai</i>	<i>p</i>
1	5	26	0.03*	1	18	19	0.97
2	9	21	0.004*	2	24	14	0.12
3	0	12	0.0003*	3	20	14	0.35
Summer	<i>A. muelleri</i>	<i>A. jarai</i>	<i>p</i>	Autumn	<i>A. muelleri</i>	<i>A. jarai</i>	<i>p</i>
1	9	28	0.002*	1	13	11	0.76
2	8	29	0.002*	2	13	7	0.22
3	6	8	0.23	3	6	1	0.09

\* = significant



**Figure 8.** Espingarda Creek. Percentage of *Aegla jarai* and *Aegla muelleri* at each sampling point.



**Figure 9.** Espingarda Creek. Percentage of *Aegla jarai* and *Aegla muelleri* in each season.

This creek is characterized by a high saturation of oxygen, low temperatures, variable water speed, and substrates composed of gravel (fine gravel) and pebbles (coarse gravel), according to Schäfer (1985). Previous studies on aeglids also recorded similar abiotic characteristics in other water courses (López, 1965;

Jara, 1977; Rodrigues and Hebling, 1978; Bueno and Bond-Buckup, 2000; Swiech-Ayoub and Masunari, 2001a; Noro and Buckup, 2002; Masunari, 2019).

Both populations of the two species in the present study are under the influence of the same abiotic variables and no competition for space is visible: both species occurred in all sampling points and in all seasons. This coexistence of *A. jarai* and *A. muelleri* may be related to the structurally complex substrate of Espingarda Creek, that is composed of mixed gravel of varied size. This kind of substrate gives rise to a multiplication of substrates (Downes *et al.*, 1998), making numerous refuges for different sizes of aeglids available. The juveniles and small aeglid species would be sheltered in the smaller spaces between pebbles, while the adults and larger aeglid species, can shelter in the spaces between larger boulders.

*Aegla jarai* is a species previously known to share its habitat with several other aeglid species (Boos *et al.*, 2012; Santos *et al.*, 2019; Dalosto and Palaoro, 2019), showing a high adaptive capacity to live in sympatry.

The equal sex ratio of 1:1 recorded for *A. jarai* has already been previously recorded for *Aegla laevis* (Latreille, 1818), *Aegla platensis* Schmitt, 1942, and *A. castro* Schmitt, 1942 (Bahamonde and López, 1961; Bueno and Bond-Buckup, 2000; Swiech-Ayoub and Masunari, 2001b).

However, in *A. muelleri* the sex ratio was unbalanced (1.4: 1), with a predominance of females in the spring and autumn. This result could possibly suggest a higher predation rate on males compared to females, because males are active for longer periods when feeding and courting females, exposing themselves to potentially more predation and environmental adversities (Silva-Castiglioni *et al.*, 2006; Silva-Gonçalves *et al.*, 2009).

This unequal sex ratio in *A. muelleri* could also be related to the distinct distribution of males and females in the environment, as already pointed out by Bueno and Bond-Buckup (2000) and Swiech-Ayoub and Masunari (2001b). Observations in the laboratory showed that during the incubation period, ovigerous females do not feed (Swiech-Ayoub and Masunari, 2001a). Therefore, it is expected that in different periods of the year, more males would be sampled than females or vice versa affecting the sampled sex ratio.

There may be an intraspecific difference, since each species is subject to a complexity of environmental

factors, such as rainfall, type of substrate, current speed, availability of food and shelter, predators, which can influence habitat occupation. However, it seems more likely that an improvement in the collection effort could record a balanced sex-ratio, as the population of *A. muelleri* is visibly less abundant than that of *A. jarai*.

The sexual dimorphism in size observed in *A. jarai* was already recorded by Boos *et al.* (2006), and it could be a consequence of the lower growth rate in females. Growth in crustaceans is, in general, similar between the sexes until sexual maturity is reached. After that, periods of intermolt are longer in females, due to the cost of laying and incubating eggs (Warner, 1967; Díaz and Conde, 1989).

Therefore, the smaller size of females of *A. jarai* could be related to a higher investment of energy in reproduction (gonad maturation, egg production, and incubation) (Hartnoll, 1982; 1985), compared to the male investment in somatic growth. The same pattern has already been observed in other aeglids, such as *A. laevis*, *Aegla paulensis* Schmitt, 1942, *Aegla perobae* Hebling and Rodrigues, 1977, *A. platensis*, *A. castro*, *Aegla leptodactyla* Buckup and Rossi, 1977, and *Aegla longirostri* Bond-Buckup and Buckup, 1994 (Bahamonde and López, 1961; López, 1965; Rodrigues and Hebling, 1978; Bueno *et al.*, 2000; Swiech-Ayoub and Masunari, 2001b; Noro and Buckup, 2003; Colpo *et al.*, 2005). However, this pattern previously seen in most aeglids (Masunari, 2019) was not seen in *A. muelleri* in this study, resulting in similar-sized males and females.

In both species, there was a marked decrease in the frequency of animals in the larger size classes, starting from 16 mm CL in *A. jarai* and 12 mm in *A. muelleri*, probably because of an increase in the natural mortality rate (see Fig. 3).

The record of ovigerous females in two distinct size classes (16.27 mm CL and 19.00 mm CL) may indicate that *A. jarai* constitutes a multiparous species, with the smaller one representing the first reproductive event and the larger one, a second one. This pattern has previously been reported in the growth curve of *A. jarai* (Boos *et al.*, 2006). Reproduction in two consecutive years (and size classes) has already been observed in *A. laevis*, *A. platensis*, *A. paulensis*, *A. leptodactyla*, and *A. castro* (see Bahamonde and López, 1961; López,



1965; Bueno and Bond-Buckup, 2000; Swiech-Ayoub and Masunari, 2001a; Noro and Buckup, 2002).

Conversely, the two ovigerous females of *A. muelleri* obtained in the present study were very close in size (11.05 mm and 11.37 mm CL), and therefore were probably in the same reproductive cohort.

The reproductive period observed in the colder seasons for both *A. jarai* (winter and spring) and for *A. muelleri* (spring), is similar to that seen in other aeglids such as *A. paulensis* and *A. leptodactyla* (autumn and spring) (López, 1965; Noro and Buckup, 2002), and for *A. perobae* and *A. castro* (winter and spring) (Rodrigues and Hebling, 1978; Swiech-Ayoub and Masunari, 2001a). On the other hand, in *A. platensis*, ovigerous females are found in all seasons, except November and December, constituting an exception (Bueno and Bond-Buckup, 2000).

Although the peak reproductive period in most aeglids coincides with the coldest months, it is likely that the temperature, together with photoperiod, availability of food and shelter, rainfall, and oxygen saturation, act in synergy to induce the spawning (Sastry, 1983). Therefore, it is expected that differences in the reproductive period will occur between different species and populations of aeglids.

Recruitment occurred in spring and summer for *A. jarai* and *A. muelleri* as a consequence of the presence of the ovigerous females in the winter and spring. In most aeglid species, recruitment has been recorded in the spring, as in *A. paulensis*, *A. perobae*, and *A. leptodactyla* (see López, 1965; Rodrigues and Hebling, 1978; Noro and Buckup, 2002), however, juveniles of *A. castro* were recorded in all seasons (Swiech-Ayoub and Masunari 2001a), indicating continuous reproduction.

The results here suggest that the coexistence of *A. jarai* and *A. muelleri* is most likely due to their occupation of distinct microhabitats, or space partitioning, and the distinct size ranges of these species help to support this assumption. Competing species have been known to choose different microhabitats in the same area or concentrate their activity at different periods of the day (Rosas *et al.*, 1994; Castro-Souza and Bond-Buckup, 2004; Baumart *et al.*, 2015). Niche overlap between sympatric species of the genus *Aegla* has been reported in other studies (de Castro-Souza and Bond-Buckup, 2004). They studied the stomach contents

of sympatric *Aegla camargoi* Buckup and Rossi, 1977 and *A. leptodactyla*, and found niche overlap that is seasonally independent, with a higher overlap in the winter, based on competition for food between the two species. Future studies on the natural diet and circadian rhythm of *A. jarai* and *A. muelleri* will assist in elucidation of the main factors that enable their apparent sympatric coexistence.

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