



# From natural coexistence to artificial colonisation: habitat use, competition and population structure of sympatric *Aegla* species

Harry Boos<sup>1,2</sup> · Marcio C. A. João<sup>2,3</sup> · Gilson Stanski<sup>4</sup> · Marcelo A. A. Pinheiro<sup>2,5</sup>

Received: 14 November 2025 / Accepted: 12 March 2026  
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## Abstract

Aeglids are among the most threatened freshwater crustaceans worldwide, restricted to South American watersheds and largely confined to lotic environments. Occurrences in artificial canals have not yet been documented. Here, we investigated two sympatric species, *Aegla jarai* and *Aegla muelleri*, in Espingarda Creek, a natural lotic stream, and in an adjacent artificial canal. We assessed population structure, abundance and spatial relationships between the species through monthly sampling from June 2001 to July 2002. We hypothesised that their distinct microhabitat preferences would translate into measurable differences in population parameters between the natural stream and the artificial canal. In Espingarda Creek, *A. jarai* was consistently more abundant and reached larger sizes than *A. muelleri*. In the canal, only *A. jarai* appeared regularly, spanning all ontogenetic stages and attaining larger sizes than conspecifics from the creek. Size–frequency distributions of both species were bimodal, and modal comparisons supported competitive asymmetry under sympatry. The contrasting size structure of *A. jarai* in the absence of congeners reinforces this hypothesis. Our findings suggest that the apparent dominant competitor in natural streams can also be a successful coloniser in artificial habitats. This pattern does not strictly conform to the classical expectation of a strict competition–colonisation trade-off and is consistent with extensions of the competition–colonisation theory and with ecological plasticity in *A. jarai*. Overall, this study provides novel insights into coexistence mechanisms in freshwater decapods and highlights the importance of incorporating artificial habitats into conservation strategies for threatened aquatic invertebrates.

**Keywords** Competition–colonisation trade-off · Conservation · Freshwater decapods · Population structure

## Introduction

Aeglids constitute a monogeneric family of anomuran crustaceans that has achieved remarkable success in colonising and diversifying within freshwater habitats in South America (Bartholomei-Santos et al. 2020). Currently, the genus *Aegla* Leach, 1821, comprises 94 described species, although this number is probably underestimated, given frequent reports of parapatry and cryptic species complexes (Jara et al. 2018; Zimmermann et al. 2021; Mollmann et al. 2024). Their global distribution is restricted to watersheds in Argentina, Bolivia, Chile, Paraguay, Uruguay and Brazil, with southern Brazil harbouring the greatest diversity (Santos et al. 2017). Alarming, nearly 70% of *Aegla* species are currently classified in some extinction risk category according to the International Union for Conservation of Nature (IUCN) criteria (Bueno et al. 2016; Santos et al. 2017; Boos et al. 2020). Population declines have been documented in recent years, and their high endemism, coupled with a strong

✉ Harry Boos  
harry.boos-junior@icmbio.gov.br

<sup>1</sup> Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul, CEPSUL, Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio, Itajaí, SC, Brazil  
<sup>2</sup> Grupo de Pesquisa em Biologia de Crustáceos (CRUSTA), São Vicente, SP, Brazil  
<sup>3</sup> Instituto de Biociências, Programa de Pós-Graduação em Ecologia, Evolução e Biodiversidade, Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil  
<sup>4</sup> Instituto Federal Catarinense (IFC), Campus Santa Rosa do Sul, Santa Rosa do Sul, SC, Brazil  
<sup>5</sup> Departamento de Ciências Biológicas e Ambientais, Campus do Litoral Paulista (IB/CLP), Instituto de Biociências (IB), Universidade Estadual Paulista (UNESP), São Vicente, SP, Brazil

dependence on well-oxygenated environments, renders aeglids particularly vulnerable to anthropogenic change in freshwater systems (Maia et al. 2013; Bueno et al. 2014).

An important aspect of aeglid biology is their highly stenotopic nature and restricted geographical distribution. Several species occupy very limited areas or are known only from their type localities (Bond-Buckup and Buckup 1994; Bueno et al. 2007, 2014; Santos et al. 2010, 2012, 2014). In general, aeglids are confined to lotic habitats such as rivers and streams characterised by fast-flowing, well-oxygenated water over rocky substrates (Bueno et al. 2016 and references therein). Only two species have so far been reported from lentic environments: *Aegla prado* Schmitt, 1942, and *Aegla denticulata lacustris* Jara, 1898 (Jara 1989; Bond-Buckup et al. 2008). These exceptions highlight the narrow ecological amplitude of the group and reinforce their sensitivity to environmental alteration.

Across their distribution, several *Aegla* species occur in sympatry, with nearly 23 species in such conditions to date (Bond-Buckup and Buckup 1994; Santos et al. 2012). Among them, *A. jarai* Bond-Buckup and Buckup 1994 is the most frequently observed and appears to be particularly well-adapted to coexistence with congeners (Dalosto and Palaoro 2020; Boos et al. 2021). In sympatric situations, strong competition is expected because freshwater decapods are ecologically similar: they are generalist feeders, are mainly nocturnal, use shelters beneath rocks, and often are found at high densities while exhibiting aggressive behaviour (Bueno and Bond-Buckup 2000; Santos et al. 2008; Ayres-Peres et al. 2011a, 2015; Palaoro et al. 2013). Under such conditions, sympatric species are expected to display similar environmental requirements and/or some degree of spatial segregation, yet few studies have formally tested these patterns (Baumart et al. 2015; Colusso 2017).

The competition–colonisation (CC) trade-off offers a valuable framework to understand coexistence. This concept, which describes how species balance competitive ability against colonisation capacity, was originally developed for plants and microbes (Tilman 1994; Amarasekare 2003) but has since been applied more broadly. It is particularly relevant to freshwater crustaceans, which inhabit fragmented and dynamic habitats. For aeglids, clarifying how competition and colonisation shape population structure and habitat use is essential for interpreting their distribution patterns and guiding conservation measures.

In southern Brazil, *Aegla jarai* and *A. muelleri* Bond-Buckup and Buckup 2010 coexist in Espingarda Creek, a well-preserved lotic stream within Serra do Itajaí National Park (Boos et al. 2021). Bond-Buckup and Buckup showed that the two species occur throughout the year, probably facilitated by microhabitat partitioning: the larger aeglid (*A. jarai*) tends to occupy spaces between boulders, whereas the smaller species (*A. muelleri*) shelters in narrower crevices

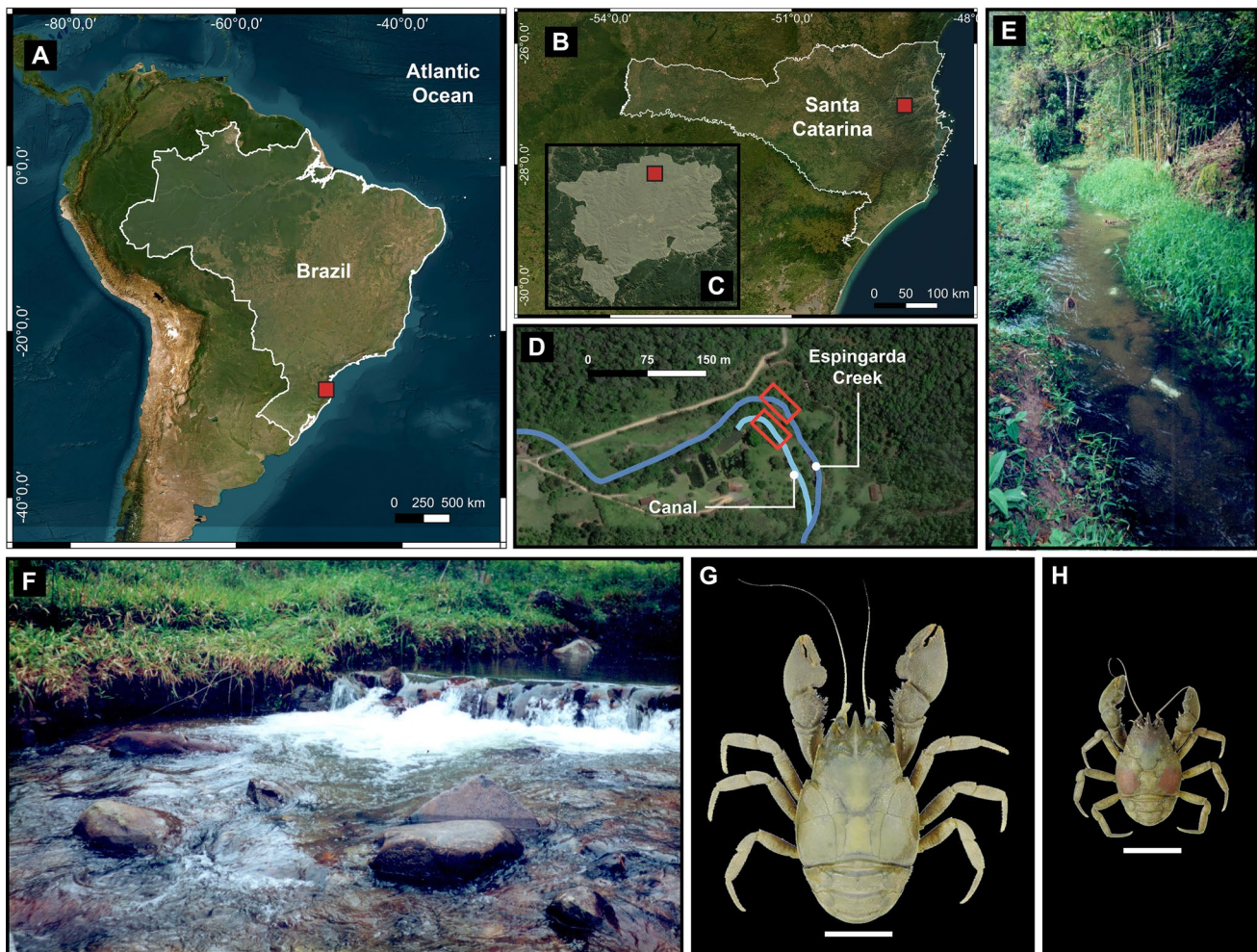
among pebbles. Adjacent to Espingarda Creek, there is an artificial canal constructed in the 1950s (before the establishment of the National Park) to operate a water wheel for local electricity generation (Zimmermann 1999). Water diverted from the creek flows through this artificial canal, which is characterised by reduced current and a sandy–loamy substrate, conditions that differ markedly from those of the natural stream. To date, little is known about how both *Aegla* species interact with such altered environments (Boos 2003).

With this in mind, the present study aimed to assess the population parameters of *A. jarai* and *A. muelleri* in both the natural stream (Espingarda Creek) and the adjacent artificial canal. Specifically, we describe population structure, abundance and spatial relationships between the two sympatric species. Data for *A. jarai* and *A. muelleri* in Espingarda Creek were previously published by Boos et al. (2021), but are re-analysed here to place them in the context of artificial canal creation and its implications for endemic taxa. Given the conservation concerns surrounding aeglids, expanding knowledge of these unique and geographically restricted crustaceans is essential to guide management strategies, particularly regarding their distribution and habitat use (Boos et al. 2020). We hypothesised that the distinct microhabitat preferences of *A. jarai* and *A. muelleri* would result in measurable differences in population parameters, such as abundance, spatial distribution and size structure, between the natural stream and the adjacent artificial canal. Ultimately, this study contributes to the broader debate on how the competition–colonisation trade-off operates in freshwater decapods, offering empirical evidence from an endemic group that includes some of the most threatened crustaceans worldwide.

## Methods

### Sampling sites and methods

Sampling was conducted monthly from June 2001 to July 2002 in Serra do Itajaí National Park (Santa Catarina State, Brazil), at Espingarda Creek (27°01'24" S, 49°09'06" W) and an adjacent artificial canal (27°01'24.2" S, 49°09'09" W) (Fig. 1A–D). Espingarda Creek (Fig. 1F) is a lotic system with water velocities ranging from 0.03 to 0.6 m/s, and substrates varying from fine gravel (2–20 mm) to small rocks (20–200 mm) (Boos et al. 2021). The sampling stretch is located in the Atlantic forest biome, within ombrophilous dense forest (Floresta Ombrófila Densa), montane formation (Cristo et al. 2018). By contrast, the canal (Fig. 1E) was constructed in the 1950s, prior to the creation of the National Park, to drive a water wheel for local electricity generation (Zimmermann 1999). It is an artificial system characterised by reduced current, a constant water velocity



**Fig. 1** Location of the study area and sampling sites in southern Brazil. **A** Map of Brazil with Santa Catarina State highlighted (red square). **B** Map of Santa Catarina showing the study region. **C** Serra do Itajaí National Park (white polygon); **D** Espingarda Creek (dark

blue) and the artificial canal (light blue), with sampling site marked (red rectangles). **E** View of the artificial canal. **F** View of Espingarda Creek. **G** Dorsal view of *Aegla jarai*. **H** Dorsal view of *A. muelleri*. Scale bars = 10 mm

of approximately 0.03 m/s, a sandy–loamy substrate and a near absence of rocky refuges. The site is largely unshaded, and its margins are colonised by grasses (*Brachiaria* sp.), resulting in environmental conditions that differ markedly from those observed in the creek. Consequently, the canal represents an environment with lower substrate heterogeneity, lower structural complexity and lower flow velocity, which favours greater retention of organic detritus and nutrients (i.e., food resources). However, no differences were observed between the canal and the creek with respect to water temperature, dissolved oxygen saturation, pH and electrical conductivity ( $\mu\text{S}/\text{cm}$ ) (Boos 2003; Boos et al. 2021).

Previous records confirm the sympatric occurrence of *A. jarai* and *A. muelleri* (Fig. 1G and H, respectively) in the Espingarda Creek (Boos et al. 2021). Because the environmental contrasts between the creek and the canal strongly influence capture efficiency, we applied active sampling in

the creek and passive traps in the canal. These procedures, adapted from established protocols (Shimizu and Bueno 2020), were designed to optimise detection in each habitat but also differ in their selectivity, especially for size classes. Therefore, results were analysed separately, and no direct statistical comparisons between habitats were performed.

In Espingarda Creek, individuals were collected using dip nets positioned on the streambed. The substrate upstream of the nets was manually disturbed to dislodge organisms sheltering beneath rocks and gravel, which were then transported by the current into the nets. In the canal, where rocky substrates are absent, we deployed cylindrical traps baited with chicken meat along the entire stretch. Traps were polyvinyl chloride (PVC) and installed in the late afternoon, remaining overnight to take advantage of the predominantly nocturnal activity of aeglids (Ayres-Peres et al. 2011b). They were retrieved the following morning. All captured individuals

were transported in plastic bags with creek or canal water, processed in the laboratory and released at the site of capture following recommended procedures for aeglid studies (Shimizu and Bueno 2020).

### Specimen processing

All specimens were identified morphologically using diagnostic characters (Bond-Buckup and Buckup 1994; Santos et al. 2012). Sex was determined by the presence of functional pleopods and registry of gonopores on the coxae of the third pair of pereopods, which are well-developed in females but absent or vestigial in males (Martin and Abele 1988). Observations were made with a magnifying lens or a stereomicroscope. Carapace length (CL; mm) of each individual was measured with a digital calliper (0.01 mm) from the internal orbital margin to the posterior edge of the carapace, excluding the rostrum.

### Statistical analyses

Population parameters were analysed separately for Espingarda Creek (*A. jarai* and *A. muelleri*) and the canal (*A. jarai* only). Departures from the expected 1:1 sex ratio (male:female) were tested using chi-squared tests (Wilson and Hardy 2002) to assess whether sex ratios in both environments were consistent with the hypothesis of balance between sexes (1:1, Fisher 1930). Because sex ratios in aeglids may be influenced by sampling method, with active collections usually being unbiased and passive collections often male-skewed, we interpreted the results with caution (Shimizu and Bueno 2020).

Because male aeglids are generally larger than females (Boos et al. 2006; Cohen et al. 2011) and individuals of *A. jarai* tend to be larger than *A. muelleri*, we tested for differences in body size (CL, mm) to confirm these expected contrasts. Assumptions of normality and homoscedasticity of the CL data were assessed by inspecting histograms and quantile–quantile (Q–Q) plots of model residuals. Generalised linear models (GLMs) with a Gaussian distribution were fitted for each environment, providing a flexible framework for comparing mean CL among groups while accommodating deviations from strict normality. For Espingarda Creek, CL was modelled with sex and species as fixed factors, whereas for the canal, only sex was included.

Size structure was described using frequency histograms with 2 mm CL intervals. Since no significant differences were detected between sexes, data were pooled by species and environment. Fisher's coefficient of skewness ( $SK$ ) was calculated (Sokal & Rohlf 2012), with the distributions categorised as symmetric when  $-0.5 \leq SK \leq 0.5$ , indicating similar proportions of juveniles and adults; positively skewed when  $SK > 0.5$ , indicating juvenile dominance; and

negatively skewed when  $SK < -0.5$ , indicating adult dominance (Pinheiro et al. 2022).

Modal composition was assessed by fitting finite mixture models using the function *normalmixEM* from the package *mixtools* (Benaglia et al. 2009). Each model was set to estimate two normal components ( $k=2$ ) with a maximum of 1000 iterations, and Welch's  $t$ -tests were applied to compare component means within species at a site and between species in Espingarda Creek.

Finally, monthly variation was explored by plotting abundance ( $N$ ) and mean CL for each species and site. The association between abundance and mean CL was tested with Pearson's correlation coefficient ( $r$ , degrees of freedom [ $df$ ] =  $n - 2$ ). All analyses were performed in R (R Core Team 2024). Because of the distinct selectivity of the sampling methods, habitats were not compared statistically as factors.

### Results

We recorded a total of 859 aeglid captures during the study period, including 335 from Espingarda Creek and 524 from the canal. In the Espingarda Creek, *A. jarai* was more abundant than *A. muelleri*, accounting for 58.8% ( $n = 197$ ) and 41.2% ( $n = 138$ ) of the captures, respectively. In the canal, the sample was almost entirely comprised of *A. jarai* (99.6%,  $n = 522$ ), with only two individuals of *A. muelleri* (0.4%) recorded throughout the sampling period. Therefore, all subsequent results from Espingarda Creek included both species, while analyses for the canal referred only to *A. jarai*.

Regarding population parameters from Espingarda Creek, the sex ratio of *A. jarai* was balanced (male:female = 1:1.1,  $\chi^2 = 0.3$ ,  $p = 0.60$ ), whereas *A. muelleri* showed a female-biased ratio (1:1.4,  $\chi^2 = 4.2$ ,  $p = 0.04$ ) (Table 1). The body size (CL) of individuals from Espingarda Creek did not differ significantly between sexes (likelihood ratio [LR]  $\chi^2 = 0.01$ ,  $p = 0.90$ ) or species (LR  $\chi^2 = 2.0$ ,  $p = 0.20$ ). When pooling sexes, CL ranged from 1.5 to 19.0 mm in *A. jarai* (mean  $\pm$  standard deviation:  $9.1 \pm 4.3$  mm), and from 1.5 to 13.0 mm in *A. muelleri* ( $8.5 \pm 2.8$  mm) (Table 1; Fig. 2). For *A. jarai* individuals sampled in the canal, CL ranged from 2.6 to 27.4 mm ( $12.7 \pm 5.2$  mm), with males being significantly larger than females (LR  $\chi^2 = 9.07$ ,  $p = 0.003$ ; Fig. 2). The only two *A. muelleri* individuals found in the canal had CL values of 2.6 and 11.1 mm.

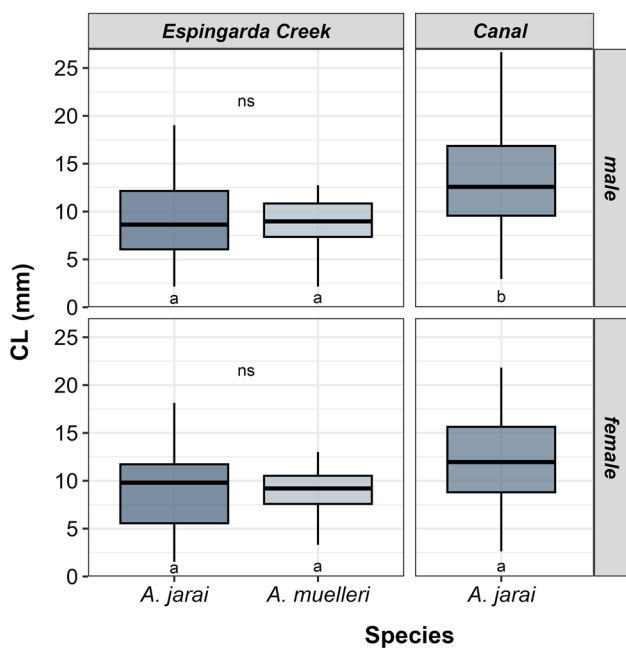
The size–frequency histograms for *A. jarai* from both Espingarda Creek and the canal indicated populations balanced between juveniles and adults ( $SK = 0.23$  at both sites). In contrast, *A. muelleri* individuals from Espingarda Creek showed a negatively skewed distribution ( $SK = -0.84$ ), suggesting a population biased towards adults. Regardless of site, both species exhibited a bimodal size distribution, with

**Table 1** Demographic parameters of *Aegla jarai* and *Aegla muelleri* sampled in Espingarda Creek and the canal

Site	Species	Sex	N	CL (mm)	Sex ratio (male:female)	$\chi^2$ (p-value)
Espingarda Creek	<i>Aegla jarai</i>	Male	93	9.1 ± 4.3	1: 1.1	0.3 (0.60 <sup>NS</sup> )
		Female	104	9.2 ± 4.2		
	<i>Aegla muelleri</i>	Male	57	8.5 ± 2.7	1: 1.4	
		Female	81	8.5 ± 2.8		
Canal	<i>Aegla jarai</i>	Male	289	13.3 ± 5.5	1: 0.8	6.0 (0.01 <sup>*</sup> )
		Female	233	11.9 ± 4.5		
	<i>Aegla muelleri</i>	Male	2	6.8 ± 6.0	NA	
		Female	—	—		

Carapace length (mm) is shown in mean ± standard deviation, SR sex ratio (M:F=Male:Female). Chi-squared test and corresponding p-values are for the sex ratio. Nonsignificance at  $p > 0.05$ . CL carapace length; NA not applicable; NS not significant

\*Significant ( $p < 0.05$ )



**Fig. 2** Variation in carapace length (CL; mm) of males and females of *Aegla jarai* and *Aegla muelleri* in Espingarda Creek (sympatric) and of *A. jarai* (allopatric). Lines inside the boxes indicated medians, boxes interquartile range (IQRs); whiskers are the lowest and highest values within 1.5 × IQRs. Different letters indicate significant differences between sexes within species at the same site ( $p \leq 0.05$ ), while identical letters indicate nonsignificant differences ( $p \geq 0.05$ ). Comparisons between species in the same site are shown by “ns” (nonsignificant)

two statistically distinct components representing smaller and larger individuals, respectively (Table 2; Fig. 3). When comparing species in Espingarda Creek, the first modal component did not differ significantly ( $t = 0.72, p = 0.48$ ), whereas the second mode, representing larger individuals, was significantly greater in *A. jarai* than in *A. muelleri* ( $t = 2.44, p = 0.015$ ).

When examining monthly variation, the relationship between the number of individuals (N) and carapace length (CL) showed species-specific patterns. For *A. jarai*, a significant negative correlation was detected between N and CL in both Espingarda Creek ( $r = -0.60, p = 0.031$ ) and the canal ( $r = -0.55, p = 0.041$ ), suggesting that months with fewer individuals were associated with larger CL values (Fig. 4A, B). For *A. muelleri*, no significant association was found between N and CL ( $r = -0.31, p = 0.35$ ), despite similar trends in some months. When comparing the two species in Espingarda Creek, visual inspection showed similar patterns of fluctuation in N and CL, although no significant correlation was detected between their monthly N ( $r = -0.06, p = 0.86$ ) or CL values ( $r = 0.52, p = 0.10$ ).

### Discussion

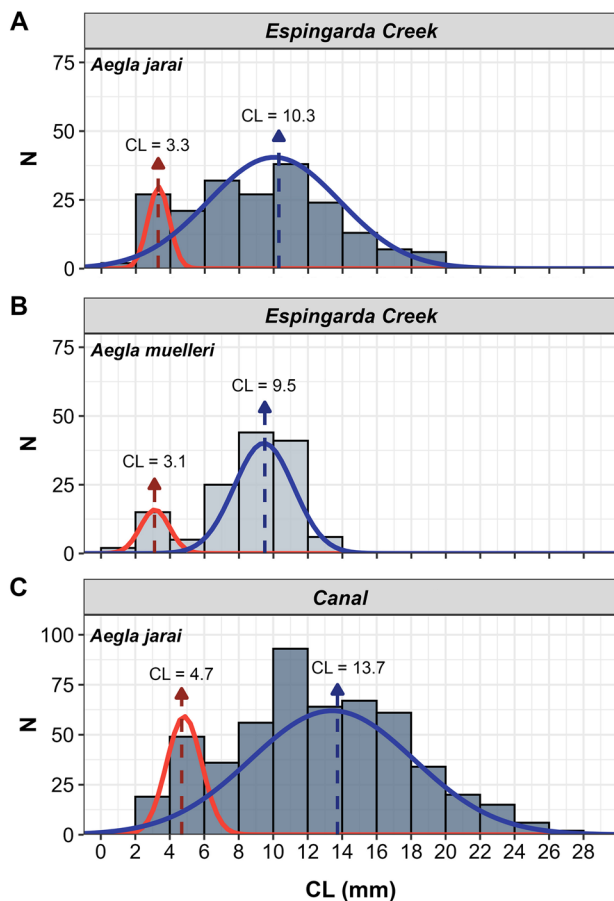
Our results provide new insights into the sympatry between *Aegla jarai* and *A. muelleri* in Espingarda Creek, expanding upon previous findings by Boos et al. (2021). Despite several ecological similarities, multiple indicators suggest that *A. jarai* is the dominant species in this stream, particularly due to its higher abundance and larger body sizes. Moreover, we report for the first time in Aeglidae a consistent occurrence and/or colonisation of an artificial canal by one species. Only *A. jarai* was found consistently in the canal, despite the presence of *A. muelleri* in the natural stream, raising hypotheses about interspecific differences in colonisation capacity, ecological plasticity or competitive advantages. These findings contribute to understanding aeglid interactions with artificial habitats and broaden knowledge on their distribution and habitat use, crucial aspect for conservation (Boos et al. 2020).

**Table 2** Modal decomposition of the size–frequency distribution of sympatric species *Aegla jarai* and *A. muelleri* analysed from individuals sampled in Espingarda Creek and the canal

Site	Species	Modal component	<i>N</i> (%)	CL (mm)	<i>t</i>
Espingarda Creek	<i>Aegla jarai</i>	Mode 1	32 (16.2%)	3.3 ± 0.6	22.1*
		Mode 2	165 (83.8%)	10.3 ± 3.7	
	<i>Aegla muelleri</i>	Mode 1	20 (14.5%)	3.1 ± 0.8	27.7*
		Mode 2	118 (85.5%)	9.5 ± 1.7	
Canal	<i>Aegla jarai</i>	Mode 1	62 (11.9%)	4.7 ± 0.8	38.3*
		Mode 2	460 (88.1%)	13.7 ± 4.5	

The two modal components were extracted by datasets pooled for sexes and months. carapace length (mm) is shown as mean ± standard deviation. CL, carapace length (mean ± standard deviation, in millimetres); *t*, Welch *t*-test.

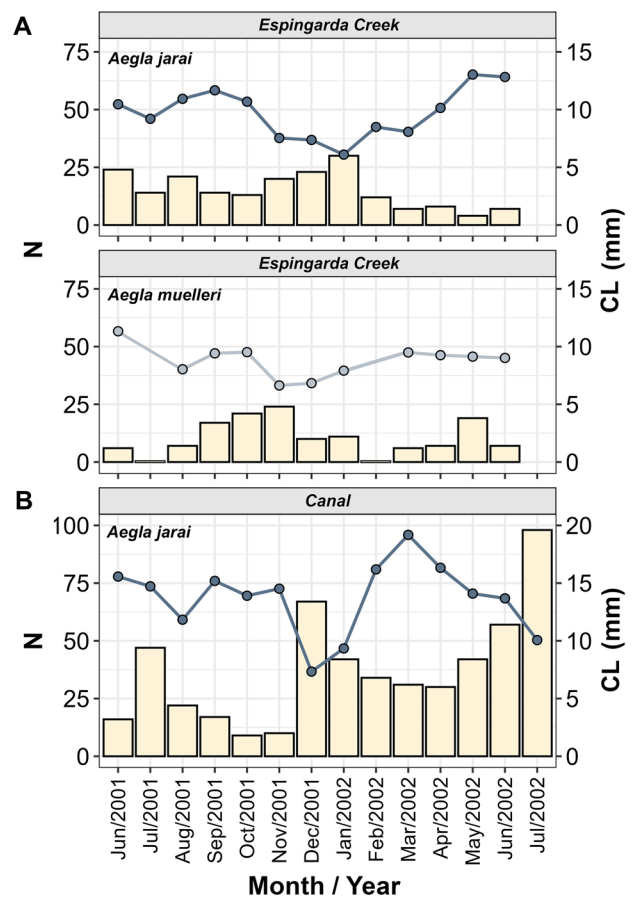
\*Significant ( $p < 0.05$ )



**Fig. 3** Size–frequency histograms and modal composition based on carapace length (CL, mm) in 2 mm class intervals for **A** *Aegla jarai* in Espingarda Creek, **B** *A. muelleri* in Espingarda Creek and **C** *A. jarai* in the canal. Curves represent fitted modal components, with significantly distinct modes shown in different colours and mean CL values indicated by arrows

### Aeglids from Espingarda Creek

The high abundance and wide representation of size classes of both species suggest that Espingarda Creek



**Fig. 4** Monthly variation in abundance (bars, *N*) and mean carapace length (line with dots, CL, mm) of **A** *Aegla jarai* in Espingarda Creek, **B** *Aegla muelleri* in Espingarda Creek and **C** *A. jarai* in the canal

offers environmental conditions conducive to stable coexistence. Environmental parameters recorded by Boos et al. (2021) in this stream are highly similar to those of other habitats successfully colonised by aeglids (Bueno and Bond-Buckup 2000; Swiech-Ayoub and Masunari 2001; Noro and Buckup 2002; Bueno et al. 2016; Masunari 2020). Habitat

complexity, particularly the heterogeneous gravel substrate, may facilitate sympatry by reducing direct competition (Boos et al. 2021), similar to what has been observed in other aeglid pairs, such as *A. obtao* and *A. denticulata*, which co-occur through spatial partitioning of microhabitats (Parra et al. 2011; Colusso 2017). In such cases, coexistence may be mediated by niche segregation, with dominant species occupying structurally favourable zones and subordinate species restricted to marginal habitats, as described by Bovbjerg (1970) for crayfish species. Our data suggest that a similar mechanism may occur between *A. jarai* and *A. muelleri*.

Differences in sex ratio, body size and cheliped morphology in *A. jarai* and *A. muelleri* are consistent with asymmetric interactions, although direct evidence for competitive mechanisms is limited. Active sampling methods are expected to provide unbiased sex ratios (1:1; Shimizu and Bueno 2020). *Aegla jarai* exhibited a balanced sex ratio and attained larger maximum sizes than *A. muelleri*, suggesting a potential advantage in resource acquisition or agonistic encounters.

Most males (64%) and females (58%) of *A. jarai* displayed a larger left chela, indicating left-biased cheliped laterality (Boos 2003), a pattern also reported in other *Aegla* species (López 1965; Rodrigues and Hebling 1978). By contrast, *A. muelleri* males more frequently exhibited a larger left chela (48%), whereas most females (60%) had chelae of equal size (Boos 2003).

Aeglids are generally aggressive, and dominance by the more abundant species may influence the spatial distribution of subordinate populations (Dalosto and Palaoro 2020). The combination of larger body size and left-biased chela dominance in *A. jarai* may confer a competitive advantage in agonistic interactions, allowing individuals to occupy the most favourable microhabitats. In contrast, *A. muelleri*, being smaller and less lateralised, appears restricted to marginal zones, suggesting that chela lateralisation, together with size and aggressiveness, structures habitat use and reduces direct competition. In Espingarda Creek, such spatial segregation likely facilitates coexistence, consistent with niche differentiation theory (Hutchinson 1957; Chesson 2000), while acknowledging that direct data on interspecific interactions are limited.

While microhabitat heterogeneity likely reduces direct competition, stabilising mechanisms (e.g. spatial partitioning, differential resource use) and equalising mechanisms (e.g. overlapping physiological tolerances) may together sustain sympatry. This integrative perspective suggests that asymmetric dominance by *A. jarai* does not preclude the persistence of *A. muelleri*, provided specific ecological filters are operating. Therefore, the female bias, smaller size and under-representation of adult males in *A. muelleri* may reflect displacement or higher male mortality due to

competition with *A. jarai* (Silva-Gonçalves et al. 2006, 2009; Boos et al. 2006). Such demographic asymmetries may be intensified by the greater robustness of *A. jarai* chelipeds, which increase success in aggressive interactions (Palaoro et al. 2014). Our results are consistent with broader evidence that aeglid assemblages are strongly shaped by microhabitat availability (Dalosto & Santos 2011; Zimmermann et al. 2016). Dominant species tend to monopolise central habitats with higher oxygen and structural refuge, relegating subordinate taxa to marginal or less suitable zones (Parra et al. 2011). This process may explain the reduced representation of large *A. muelleri* males, which could suffer higher mortality when excluded from optimal refuges.

Despite the general expectation of aeglid males being larger than females (Cohen et al. 2011; Bueno et al. 2016), individuals of both species from Espingarda Creek did not show sexual dimorphism in body size (CL). However, in the size distribution, males of *A. jarai* (19.0 mm CL) attained higher CL values than females (18.1 mm CL), consistent with previous reports that males grow faster and reach larger asymptotic sizes (Boos et al. 2006). For *A. muelleri*, the highest CL values of males (12.8 mm CL) and females (13.0 mm CL) were very close, indicating a lack of sexual dimorphism in this species.

Independent of sex, the symmetry of the histograms shows a balanced population for *A. jarai* and a distribution biased towards adults in *A. muelleri*. Although the capture of juvenile and small individuals is rare in many aeglid population studies (Bueno et al. 2014), our data show a good representation of the smaller size classes. However, in *A. jarai* the proportion of juvenile individuals was higher than in *A. muelleri*. Samples biased towards adults do not necessarily indicate a population with low recruitment rates. Still, they generally suggest that small individuals live in other refuges, especially to avoid cannibalism and competition with adults (Masunari 2020). Within the context of competition, it is plausible that *A. muelleri* juveniles are doubly disadvantaged, facing both conspecific adults and the more competitive *A. jarai*.

Monthly sampling of both species shows fluctuations in abundance and CL across the year. For *A. jarai*, we observed a significant negative correlation, with smaller CL values in months with higher abundance. This pattern was not confirmed for *A. muelleri*. Between the species, however, in some months we observed that when *A. jarai* abundance began to increase (e.g. October 2001 to January 2002), the opposite trend was recorded for *A. muelleri*.

### ***Aegla jarai* from the canal**

The colonisation of the canal highlights important ecological trends in aeglid habitat use. Based on our results, only *A. jarai* successfully established in this habitat, as

only two individuals of *A. muelleri* were recorded. This pattern suggests that *A. jarai* is more tolerant of altered environments characterised by lower substrate heterogeneity, reduced structural complexity and lower flow velocity. Such conditions may promote the accumulation of organic detritus and nutrients, potentially increasing the availability of food resources for aeglids, which commonly feed on detrital material and associated organic matter.

The successful establishment of *A. jarai* in the canal also indicates considerable ecological plasticity, contrasting with the more restricted tolerance observed for *A. muelleri*. Physiological resilience to variation in oxygen availability and temperature (Cerezer et al. 2020a, b), together with behavioural flexibility in diel activity (Dalosto and Santos 2011), may facilitate the colonisation of modified habitats. Similar patterns have been reported in other studies, where aeglids occupy atypical habitats or extend their distribution beyond expected environmental limits (Correa-Araneda et al. 2022; Zimmermann et al. 2018, 2021).

There are no apparent barriers preventing movement between the creek and the canal, suggesting that individuals likely belong to a single interconnected population. Therefore, the markedly higher abundance of *A. jarai* in the canal compared with *A. muelleri* is more plausibly related to species-specific ecological traits than to dispersal limitation.

The canal environment differs markedly from Espingarda Creek, being characterised by a sandy–clayey substrate, grassy margins and the absence of riparian vegetation (Boos et al. 2021). In this habitat, marginal grasses appear to provide the main refuge for *A. jarai*, offering both shelter and potential food resources. Although substrate composition and riparian shading are recognised ecological filters affecting aeglid distribution (Bueno et al. 2007, 2014; Cerezer et al. 2020a), no differences were observed between the canal and the creek in water temperature, dissolved oxygen saturation, pH, or electrical conductivity ( $\mu\text{S}/\text{cm}$ ) (Boos 2003; Boos et al. 2021). Together, these results suggest that habitat structure, rather than physicochemical conditions, plays a key role in explaining the high abundance and persistence of *A. jarai* in this altered environment.

Abundance and size composition differed between environments. Although higher abundance in the canal may reflect its smaller area, individuals tended to be larger, with the maximum (27.4 mm CL) exceeding by 44.2% the maximum from Espingarda Creek (19.0 mm CL). Passive sampling tends to over-represent large individuals (Shimizu and Bueno 2020), but the capture of all ontogenetic stages, including small size classes, indicates a stable population. Larger individuals may benefit from the absence of competition with *A. muelleri*, preferentially using the canal and reaching sizes close to the asymptotic length estimated for the species ( $\text{CL}_\infty = 25.11$  mm; Boos et al. 2006).

The sex ratio also varied: the canal showed a male bias, whereas Espingarda Creek was balanced. This may reflect sampling bias, as males are more easily captured due to competition for bait (Shimizu and Bueno 2020), but could also suggest habitat-related differences. Future studies using active sampling methods are needed to clarify whether sex ratio differences are artefacts of sampling or reflect genuine ecological selection pressures. Monthly fluctuations in abundance and CL were similar in both habitats, with higher abundance coinciding with smaller sizes, consistent with recruitment periods. This pattern was previously observed for *A. jarai* in the same area (Boos et al. 2021), indicating that reproductive seasonality remains stable despite environmental differences.

Our findings engage with the classical competition–colonisation trade-off model (Tilman 1994; Amarasekare 2003). While this framework predicts that dominant competitors are poor colonisers, *A. jarai*, dominant in Espingarda Creek, was also a successful coloniser of the canal. This apparent exception may reflect hydrological connectivity, habitat conditions (sandy–loamy substrate, reduced flow) or simply the ecological plasticity of *A. jarai*. Similar exceptions have been reported in other systems (Kneitel and Chase 2004; Calcagno et al. 2006).

Artificial streams may function as “novel ecosystems” (Hobbs et al. 2006) or even as potential ecological traps (Hale and Swearer et al. 2016), where native species establish but face long-term risks due to unstable resources, altered predator–prey dynamics or higher invasion probabilities. Thus, although *A. jarai* appears to thrive in the canal, conservation assessments should consider whether such environments genuinely support viable populations or merely provide temporary refuges.

From a conservation perspective, artificial habitats may extend the range of native species but also increase the risk of exotic species establishing. Studies elsewhere show that such habitats often become dominated by alien taxa (Katano et al. 1998; Karádi-Kovács et al. 2023). This is concerning for aeglid conservation, given predation and competition risks from salmonids (Bond-Buckup et al. 2008) and invasive crayfish such as *Procambarus clarkii* (Moraes et al. 2016). Thus, monitoring programmes should precede management actions to prevent the establishment of exotic species and safeguard native populations, particularly in protected areas such as Serra do Itajaí National Park.

Considering projected climate change impacts on freshwater decapods (Toh et al. 2022), populations such as those in Espingarda Creek and the canal may experience compounded pressures from hydrological alteration and invasive species. Long-term monitoring integrating population parameters, habitat quality and climatic drivers is essential to evaluate whether aeglids can maintain stable populations under rapid environmental change. This is especially

relevant for species with restricted ranges, where local extirpation could represent a significant conservation risk (Tumini et al. 2019; Silva et al. 2024).

## Broader implications

While we do not provide direct evidence of interspecific competition, the observed distribution patterns are consistent with the competition–colonisation framework, yet the outcome does not strictly conform to its classical expectation: the apparent dominant competitor in the creek, *A. jarai*, also performs as a successful coloniser in the canal. This context-dependent pattern is consistent with extended formulations of the competition–colonisation trade-off and with ecological plasticity in *A. jarai*. *Aegla muelleri* remains largely confined to the structurally complex creek environment. Differences in body size, cheliped morphology and behavioural traits may further influence habitat use, contributing to spatial segregation and potential coexistence.

These results underscore the importance of both natural and artificial habitats in aeglid conservation. By linking population patterns to ecological theory, we demonstrate that *A. jarai* exhibits higher ecological tolerance, plasticity and colonisation potential than *A. muelleri*. Future research should focus on (1) the role of microhabitat partitioning and niche segregation in maintaining sympatry, (2) phenotypic plasticity of *A. jarai* in disturbed environments, (3) the function of artificial habitats as novel ecosystems, balancing persistence of native species with invasion risks and (4) integrating aeglid ecology into freshwater biodiversity conservation under human-altered landscapes.

**Acknowledgements** We express our sincere gratitude in memoriam to Dr Georgina Bond-Buckup, retired professor at the Federal University of Rio Grande do Sul (UFRGS), whose dedicated guidance and scientific insight were instrumental in conducting the research that gave rise to this article. Her legacy continues to inspire our work. We are also grateful to Karin Schacht for her assistance with sampling and the anonymous reviewers for their valuable contributions. H.B. acknowledges the fellowship provided by Coordination for the Improvement of Higher Education Personnel (CAPES), and M.A.A.P. acknowledges the research grants awarded by the National Council for Scientific and Technological Development (CNPq) (grants #303286/2016–4 and #305957/2019–8).

**Author contributions** H.B. was responsible for the conceptualisation of the study, all sampling, measurements and data curation. All authors (H.B., M.C.A.J., G.S. and M.A.A.P.) contributed to the writing of the main manuscript, preparation of figures and critical revision of the content. All authors have approved the final version for publication and agree to be accountable for all aspects of the work.

**Funding** Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Brasil, Conselho Nacional de Desenvolvimento Científico e Tecnológico, #303286/2016–4 and #305957/2019–8.

**Data availability** Data will be made available upon request.

## Declarations

**Conflict of interest** The authors declare no competing interests.

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