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Weaponry Investment in the Socially Monogamous Snapping Shrimp *Alpheus brasileiro* (Decapoda: Alpheidae)

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ABSTRACT

Weapons are morphological structures used by animals in various contexts, especially in intra-specific contests and visual displays. In snapping shrimps of the genus *Alpheus*, particularly the monogamous species *Alpheus brasileiro*, both sexes bear enlarged chelipeds, potentially conferring advantages in mate competition or territorial defence. However, little is known about sex-specific weapon investment value (WIV) in socially monogamous species. This study investigated WIV in males and females of *A. brasileiro* through monthly sampling from April 2015 to March 2016 in a southeastern Brazilian estuary. Shrimps were measured for carapace and chela (propodus + dactyl) dimensions, and allometric analyses were performed to assess relative growth patterns. WIV was quantified by comparing the dry weight of the major chela to total body dry weight. Both sexes showed positive allometry for weapon growth, indicating increased energy allocation to chela development. However, males invested significantly more ($\approx 26\%$) of their body weight in weaponry compared to females ($\approx 20\%$). These findings suggest that males face stronger selective pressures favouring larger weapons, possibly due to intra-sexual competition, predatory defence or display behaviours. Our results provide new insights into sex-based differences in weapon development in *Alpheus*, emphasising the relevance of investigating morphological traits in socially monogamous crustaceans.

1 | Introduction

Different animal groups possess morphological structures that can be disproportionately large and serve various functions. One such example is weaponry, which consists of structures used in intra-specific combat to gain or defend access to resources, or as a mechanism for aggressive signalling to assess and deter potential rivals or attract potential mates (Emlen 2008; Rico-Guevara and Hurme 2019; McCullough

and O'Brien 2022). Animal weapons are thought to have evolved in response to natural and sexual selective pressures, enhancing the performance of their bearers and allowing their use in multiple contexts, including prey capture, predator defence, signalling and various agonistic interactions (Emlen 2008; Lane 2018). Typically, the evolution of these structures has occurred in diverse body regions across invertebrates, for example, such as the enlarged mandibles and horns of coleopterans, the legs or heads of orthopterans, the

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chelicerae of arachnids and the claws or mandibles of crustaceans, as well as in vertebrates, such as the antlers of mammals and the beaks of birds (Emlen 2008; Rico-Guevara and Hurme 2019; Palaoro and Peixoto 2022).

Some crustacean groups possess structures that can function as weapons, such as amphipods, isopods, stomatopods and especially decapods (Emlen 2008; Bywater et al. 2008; Callander et al. 2013; Hughes et al. 2014; Nogueira et al. 2022). The morphology of these weapons is highly diverse and includes large, robust chelipeds as well as elongated or modified appendages with claws (Emlen 2008; Vittori et al. 2024). Exaggeratedly developed chelipeds can be used both in predatory behaviours and in agonistic interactions (Bauer 2004, 2023). In addition, these structures may play a crucial role in visual displays, serving to attract potential mates or to induce rivals to retreat, thereby reducing the energetic costs associated with direct confrontation and minimising the risk of body injuries, which often demand high energetic investment for regeneration (Emlen 2008; Muramatsu 2011; Palaoro and Peixoto 2022).

Historically, many studies on weapon-like structures have focused primarily on male–male competition, leading to a bias in biological research towards the development of weapons specifically in males (Rico-Guevara and Hurme 2019; Dalosto et al. 2019; Graham et al. 2023). However, some groups do not exhibit evident sexual dimorphism, and in such cases, both males and females may develop structures that potentially function as weapons. In this context, studies that investigate female weaponry are of great importance, as they provide valuable insights into the evolutionary patterns underlying weapon development in both sexes (Dalosto et al. 2019). Crustacean taxa are frequently used as model systems to investigate weapon development and sexual differences, whether behavioural or morphological (Sneddon et al. 1997; Yamada and Boulding 1998; Palaoro and Briffa 2017; Dinh 2022; Nogueira et al. 2022).

Caridean shrimps exhibit four types of mating systems: neighbourhoods of dominance, pure search, search and attend, and monogamy, the latter being the most common among alpheid shrimps (Correa and Thiel 2003). In shrimp species with a monogamous mating system, it is particularly challenging to determine the degree of sexual fidelity, due to the complex analyses required to assess this trait, as demonstrated, for example, in *Alpheus angulosus* McClure 2002 (Mathews 2007). Since it is speculated that the level of fidelity may vary greatly among some species, and in certain cases may not even be obligatory, most studies on the topic refer to this mating system as social monogamy. Social monogamy in caridean shrimps involves mutual cooperation between two heterosexual adults engaged in a social system in which pair formation promotes behaviours such as territorial cohabitation and prolonged partner guarding (Subramoniam 2023). Pair stability is maintained only as long as conditions remain favourable for both individuals and may be disrupted by external factors such as predation pressure or the availability of partners with greater reproductive and competitive potential (Knolton 1980; Mathews 2002). Once paired, individuals gain benefits that enhance their reproductive success, including reduced exposure to predation and lower energetic costs due to a decreased need for resource searching (Bauer 2023).

Studies on the mating systems of various *Alpheus* Fabricius 1798 species, including *A. angulosus*, *Alpheus bouvieri*, *A. Milne-Edwards* 1878, *Alpheus carlae* (Anker 2012) (Costa-Souza et al. 2022), and *Alpheus brasileiro* (Anker 2012) (Pescinelli, Davanzo, and Costa 2017), the focal species of the present study, have indicated that these taxa exhibit social monogamy. In socially monogamous species, a pattern of monomorphism or reduced sexual dimorphism is expected; however, the selective pressures acting on each sex may lead to some degree of dimorphism, depending on the individual costs involved (Hughes et al. 2014). Therefore, to better understand the mechanisms underlying sexual dimorphism in weaponry among shrimps, such as those of the genus *Alpheus*, it is essential to redirect efforts towards identifying functional differences in weapon use between the sexes (Hughes et al. 2014).

Alpheus brasileiro is a species within the *Alpheus armillatus* H. Milne Edwards 1837 species complex, endemic to Brazil and widely distributed along the Brazilian coast (Anker 2012). Social monogamy has been documented for this species, and pairing between the sexes is considered size-assortative, that is, individuals of similar body size tend to form pairs (Pescinelli, Davanzo, and Costa 2017). This strategy can reduce the costs associated with basic tasks, such as territory defence, even though females may still allocate greater effort to additional functions, such as burrow construction and maintenance (Mathews 2002). Although several studies have investigated the ecological, morphological and behavioural aspects of *A. brasileiro* (Pescinelli, Davanzo, and Costa 2017; Pescinelli, Pantaleão, et al. 2017; Pescinelli et al. 2018, 2020), gaps remain in the literature regarding weapon investment value (WIV) and weapon size in this species.

Given that both sexes of *A. brasileiro* possess large chelipeds (Pescinelli et al. 2018), the importance of this structure in their life history becomes evident, particularly in reproductive success and in the defence and maintenance of their shelters. Therefore, *A. brasileiro* can be considered an excellent model for evaluating the development and investment in weaponry in species that do not exhibit pronounced sexual dimorphism in body size. In this study, we provide the first estimates of WIV in *A. brasileiro*, aiming to gather relevant biological data that contribute to a better understanding of weaponry development and allocation in a socially monogamous species. Based on previous records reporting sexual monomorphism in body size and dimorphism in the size of weapon-like structures in different *Alpheus* species (Costa-Souza et al. 2019; Ghizelli-Fraga et al. 2021), we tested the hypothesis that males and females of *A. brasileiro* exhibit divergent weaponry investment, likely shaped by sex-specific selective pressures acting on this structure.

2 | Material and Methods

2.1 | Study Area

Sampling was conducted in the intertidal zone of the Cananéia-Iguape Estuarine-Lagoon Complex, located on the southern coast of São Paulo State, Brazil (25°04'11.2" S, 48°03'08.9" W; Figure 1).

2.2 | Sampling

Specimens of *A. brasileiro* (Figure 2) were collected from April 2015 to March 2016, during periods of maximum exposure of the intertidal zone, according to tidal retreat. Three 1 m² sampling plots (20 mm × 5 mm) were established in the intertidal area, each separated by 10 m. Within each plot, multiple 1 m² quadrats were subdivided, and three were randomly selected for investigation.

Sampling was performed through active search, in which two collectors conducted sampling efforts for 2 h. After collection, the shrimps were stored in thermal containers and preserved in 70% ethanol. In the laboratory, individuals were

sexed following the methodology described by Bauer (2004) and measured using an image analysis system attached to a Zeiss Stemi 2000C trinocular stereomicroscope (accuracy: 0.01 mm). The following structures were measured (in mm): carapace length (CL), major cheliped length (MaCL), major cheliped height (MaCH), minor cheliped length (MiCL) and minor cheliped height (MiCH).

2.3 | Relative Growth

To determine the distribution pattern of the data, the Shapiro–Wilk test was applied. Depending on the results, appropriate

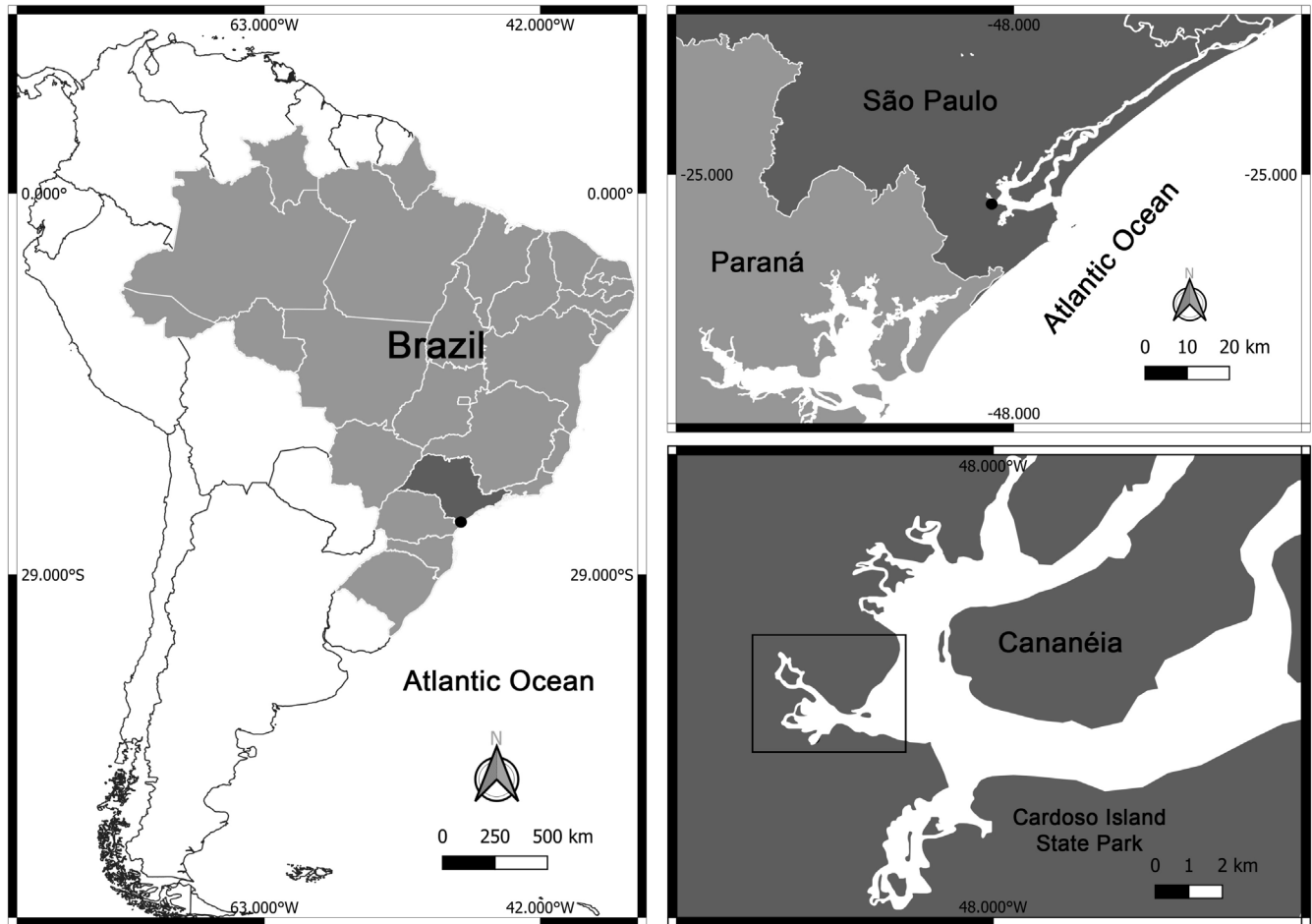


FIGURE 1 | Location of the study area in the estuarine zone of Cananéia, São Paulo, south-eastern Brazil.

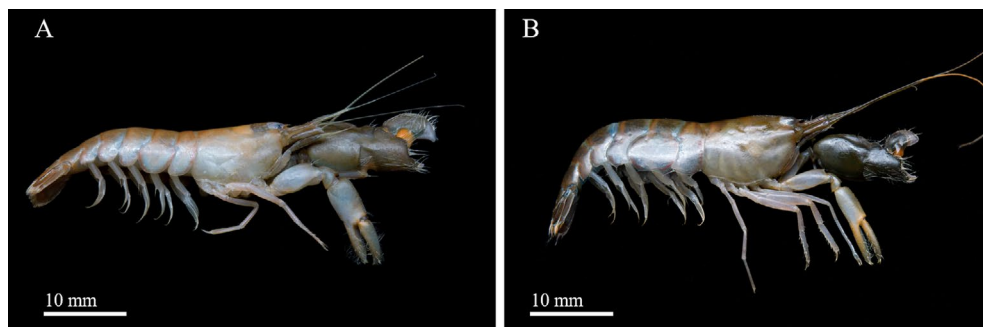


FIGURE 2 | Lateral view of (A) male and (B) female of *Alpheus brasileiro* (Anker 2012). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/azo.12009)]

statistical tests were employed for each data set. To evaluate changes in the relative growth pattern of body structures in relation to the independent variable (CL), the data points were fitted to the allometric equation ($y = ax^b$) (Huxley 1950; Hartnoll 1974, 1978), using its linearised form ($\log y = \log a + b \times \log x$). In this equation, y represents the dependent variable, x represents the independent variable (CL), a is the intercept and b is the slope (allometric coefficient). The allometric coefficient indicates whether the growth is positive allometric ($b > 1$), negative allometric ($b < 1$) or isometric ($b = 1$). To test the null hypothesis, a Student's t -test was applied ($H_0: b = 1; \alpha = 0.05$).

An analysis of covariance (ANCOVA) was used to test the angular and linear coefficients of each morphometric relationship between the sexual groups (males and females), indicating whether each relationship was better described by a single or two distinct linear equations.

2.4 | Weaponry Investment

To estimate WIV, we analysed the proportion of energetic allocation directed towards the development of the chela (propodus + dactyl) of both the major and minor chelipeds. This was calculated following the methodology proposed by Clarke et al. (1991) and Paschoal and Zara (2022). Both studies use the dry weight of a specific structure in relation to the total body dry weight to evaluate the energy allocation directed towards the development of such structures, often associated with reproduction.

To obtain dry weight measurements, shrimp were placed individually in Petri dishes and dried in an oven at 60°C for 24 h. The total dry mass of each individual (TW), as well as the dry weight of the major (MaC) and minor (MiC) chelae, was recorded. All weight measurements were obtained using a precision balance (0.0001 g).

WIV was calculated using the formula: $WIV (\%) = (\text{dry weight of chelae} / \text{total body dry weight}) \times 100$. The Mann-Whitney test ($\alpha = 0.05$) was used to compare the mean chela weight and WIV between males and females. Spearman's rank correlation was used to analyse the relationship between body size (CL in mm) and WIV.

3 | Results

A total of 224 individuals were analysed, comprising 127 females and 97 males. The mean values of the morphometric variables associated with weapon structures (MaCL, MaCH, MiCL and MiCH) were higher in males than in females (Table 1). Morphometric data did not follow a normal distribution (Shapiro-Wilk test, $p < 0.05$), except for carapace length (Shapiro-Wilk, $W = 0.99; p = 0.13$). All growth equations showed significant differences in growth patterns between males and females (ANCOVA, $p < 0.05$) (Table 2).

With the exception of the isometric growth observed for the MaCL in females, a pattern of positive allometric growth was

TABLE 1 | Mean size (M), standard deviation (SD), minimum (Min) and maximum (Max) of the morphometric variables for each sex of *Alpheus brasiliensis* (Anker 2012). Carapace length (CL), length of the major (MaCL) and minor (MiCL) chela; height of the major (MaCH) and minor (MiCH) chela. Measurements in millimetres.

Sex group	Variable	Mean	SD	Minimum-maximum
Males	CL	6.23	1.44	3.53–10.15
	MaCL	8.44	2.71	4.11–15.56
	MiCL	5.69	1.77	2.29–10.26
	MaCH	3.58	1.19	1.66–6.47
	MiCH	1.57	0.60	0.56–3.21
Females	CL	5.83	1.64	1.94–10.53
	MaCL	6.97	2.12	2.22–12.13
	MiCL	4.77	1.47	1.51–8.08
	MaCH	2.95	0.97	0.49–5.18
	MiCH	1.21	0.41	0.34–2.16

TABLE 2 | Analysis of covariance (ANCOVA) between males and females of *Alpheus brasiliensis* (Anker 2012) for each morphometric relationship: carapace length (CL); length of the major and minor chela (MaCL and MiCL); height of the major and minor chela (MaCH and MiCH).

Morphometric relationship	Group	Par. (log)	<i>F</i>	<i>p</i>
CL vs. MaCL	M × F	<i>a</i>	—	—
		<i>b</i>	19.91	<0.05
CL vs. MiCL	M × F	<i>a</i>	—	—
		<i>b</i>	6.81	<0.05
CL vs. MaCH	M × F	<i>a</i>	—	—
		<i>b</i>	14.30	<0.05
CL vs. MiCH	M × F	<i>a</i>	—	—
		<i>b</i>	26.32	<0.05

Note: Statistical differences = $p < 0.05$.

Abbreviations: *F* = statistical values, Par. = parameter.

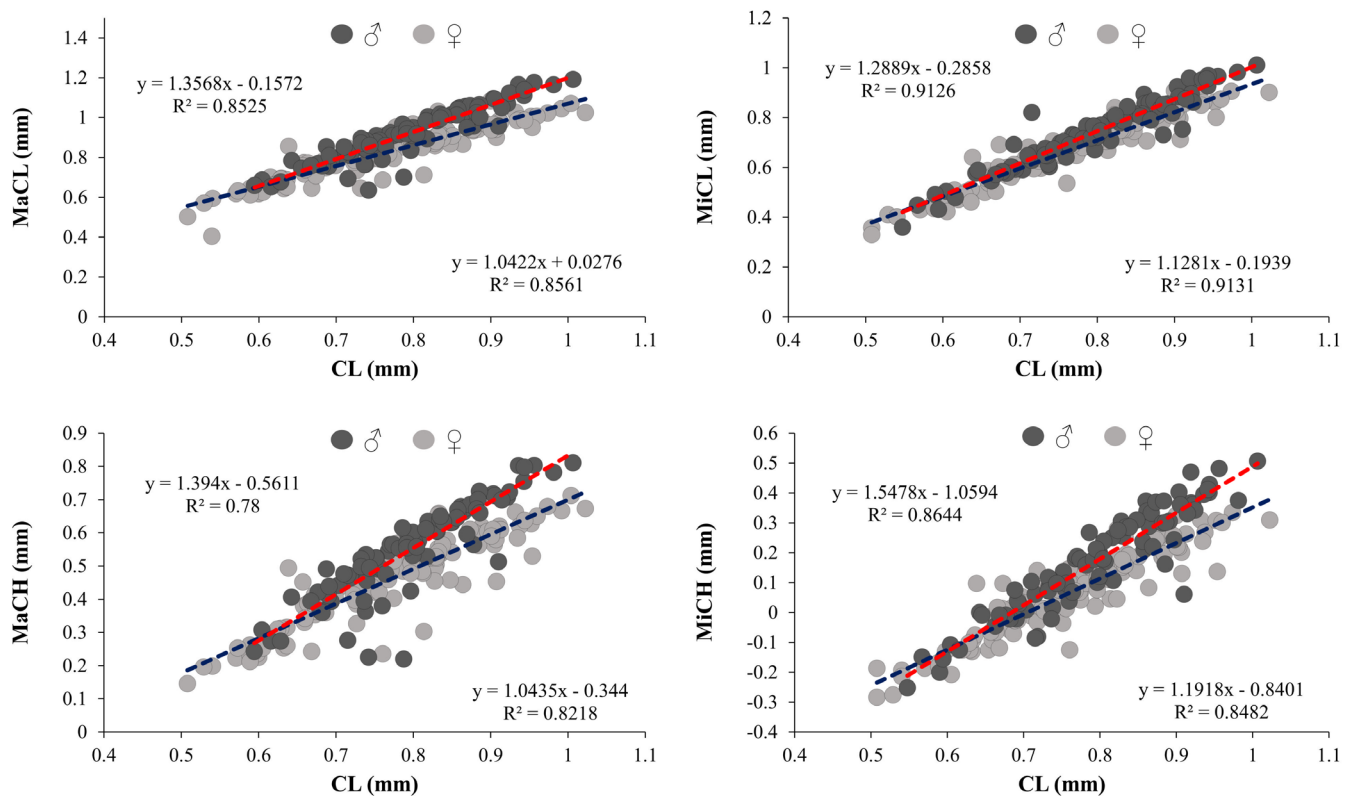
found in the other relationships tested for both sexes, indicating greater energy allocation towards chela growth relative to carapace length (Table 3). However, males exhibited a higher allometric constant (b) compared to females (Figure 3). No statistical difference in carapace length was found between sexes (T -test, $t = 2.01; p = 0.05$). In contrast, significant differences were observed in all other structures compared between males and females (Mann-Whitney, $p < 0.05$), with males showing larger chelae than females.

The estimated WIV indicated a mean percentage of $26.35 \pm 8.51\%$ and $20.25 \pm 6.1\%$ for males and females, respectively, in relation to the chela of the major cheliped (MaC).

TABLE 3 | Analysis of morphometric data using carapace length (CL) as the independent variable.

Relationship	Sex	N	a	b	r ²	T (b=1)	p	Allometry
CL vs. MaCL	M	97	-0.1572	1.3409	0.8525	6.56	<0.05	+
	F	127	0.0276	1.0410	0.8561	1.06	<0.05	=
CL vs. MaCH	M	97	-0.5611	1.3788	0.78	5.72	<0.05	+
	F	127	-0.344	1.0914	0.8218	1.79	<0.05	+
CL vs. MiCL	M	93	-0.2858	1.2870	0.9126	7.18	<0.05	+
	F	126	-0.1939	1.1075	0.9131	3.57	<0.05	+
CL vs. MiCH	M	93	-1.0594	1.5471	0.8644	8.91	<0.05	+
	F	126	-0.8401	1.1870	0.8482	4.18	<0.05	+

Abbreviations: + = positive allometry, = = isometry, a = intercept, b = allometric coefficient, MaCL = length of the major chela, MaCH = height of the major chela, MiCL = length of the minor chela, MiCH = height of the minor chela, r² = coefficient of determination, p = significance, T = statistical values.

**FIGURE 3** | Linear regressions between carapace length (CL) and the length and height, respectively, of the major (MaCL and MaCH) and minor (MiCL and MiCH) chela in males and females of *Alpheus brasiliensis* (Anker 2012). [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

Additionally, a mean WIV of $4.72\% \pm 1.96\%$ and $3.48\% \pm 1.17\%$ was recorded for the chela of the minor cheliped (MiC) in males and females, respectively. The median WIV for the MaC was significantly higher in males (29.1%) than in females (19.72%) (Mann–Whitney, $U = 3067$, $p < 0.001$) (Figure 4). The same pattern was observed for the MiC, with males showing a higher median value (4.64%) compared to females (3.57%) (Mann–Whitney, $U = 3015$, $p < 0.001$) (Figure 4).

A positive correlation was observed between body size (CL) and WIV in males (Spearman, $\rho = 0.39$, $p < 0.001$), indicating that increases in WIV are associated with increases in CL. In contrast, the correlation between CL and WIV in females was

weak and not significant (Spearman, $\rho = 0.13$, $p = 0.15$), suggesting a likely absence of a relationship between these variables (Figure 5).

4 | Discussion

A distinct pattern of growth and investment in weaponry was observed between males and females of the snapping shrimp *A. brasiliensis*, supporting the initial hypothesis proposed in this study. Significant sexual differences were found in both the size and investment of the major and minor chelae, with males exhibiting more developed structures and higher investment.

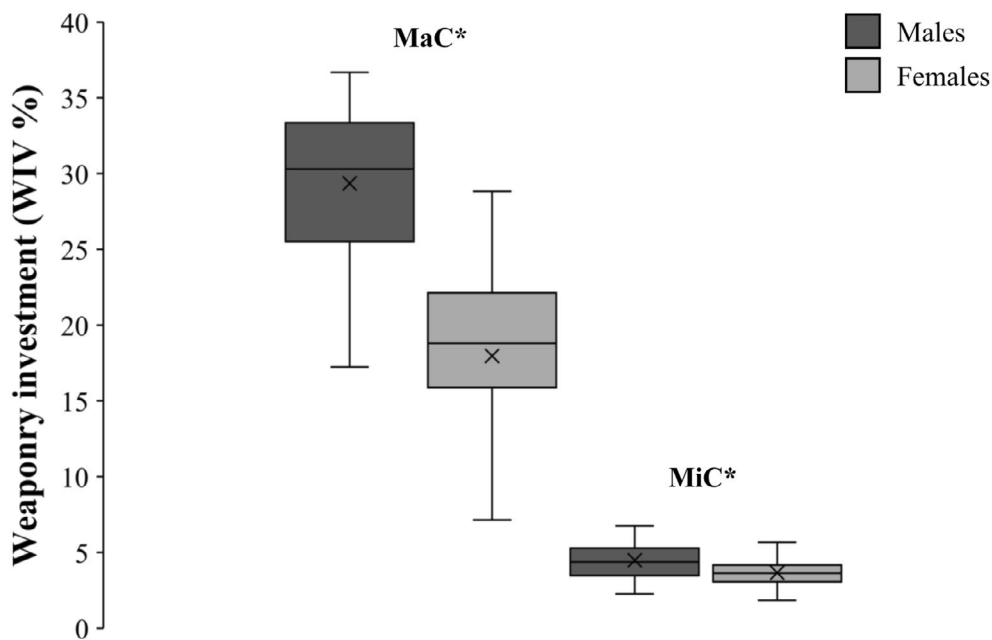


FIGURE 4 | Comparison of the weaponry investment (WIV) between males and females of *Alpheus brasiliensis* (Anker 2012). MaC = investment in the major chela; MiC = investment in the minor chela. The line inside the box indicates the median, the boxes represent the first and third quartiles, and the whisker indicates the minimum and maximum variation. × represents the mean value of the data. *Significant differences (Mann–Whitney, $p < 0.05$).

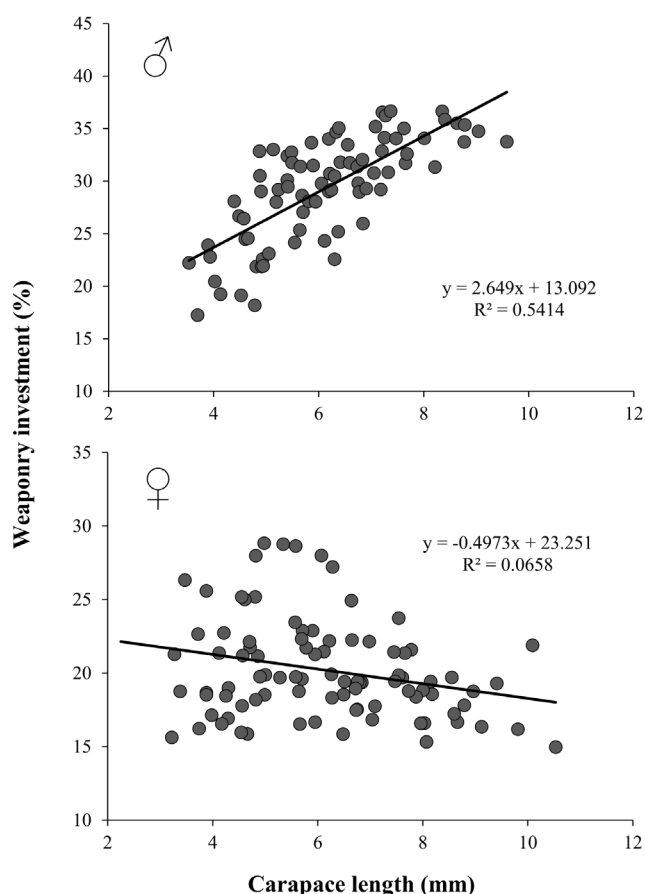


FIGURE 5 | Correlation between carapace length and weaponry investment of males and females of *Alpheus brasiliensis* (Anker 2012).

These findings indicate that, although the species exhibits a sexually monogamous system, it adopts sex-specific strategies of energy allocation, which are consistent with previous findings for *A. brasiliensis* (Pescinelli et al. 2018) as well as for other species of the genus (Costa-Souza et al. 2019; Ghizelli-Fraga et al. 2021; Dinh and Patek 2023).

In socially monogamous mating systems, the formation of heterosexual pairs is beneficial for shrimp, as this interaction may ensure mutual cooperation, whether territorial, such as in the maintenance of shelters, or reproductive, throughout part or all of the reproductive cycle (Mathews 2002; Pescinelli, Davanzo, and Costa 2017). Species that exhibit social monogamy are expected to show certain morphological traits, such as sexual monomorphism or only slight dimorphism, usually related to body size (Bauer 2004, 2023). These traits may facilitate the mating pattern (Costa-Souza et al. 2019), as observed in species such as *A. brasiliensis*, which exhibits size-assortative mating, a phenomenon in which pairs form with individuals of very similar body size (Pescinelli et al. 2020), a pattern also reported in other species of the genus (Rahman et al. 2003; Costa-Souza et al. 2019). However, when comparing the results of the present study with previous studies (Costa-Souza et al. 2019; Azoifeifa-Solano et al. 2020; Nascimento et al. 2025), it becomes clear that only body size is similar between sexes, while conspicuous differences are observed in cheliped size, with males bearing significantly larger weapons.

The morphometric relationships of the major chela, CL versus MaCL and CL versus MaCH, showed intersexual allometric differences. In the CL versus MaCL relationship, females and males exhibited isometric and positive allometric growth, respectively.

In contrast, for CL versus MaCH, both sexes displayed positive allometric growth, although females showed a lower allometric coefficient. Interestingly, our results differ from the pattern observed in congeneric species, in which adult females exhibited negative allometry in the development of the major chela (Costa-Souza et al. 2019; Ghizelli-Fraga et al. 2021). Based on studies of caridean shrimps, there appears to be no general allometric pattern among organisms that use their chelipeds as a form of weaponry or share the same socially monogamous behaviour, as such groups exhibit varying allometric trends. This indication is supported by the findings of Baeza (2008) for other socially monogamous shrimp, such as the palaemonid *Pontonia margarita* Verrill 1869, in which isometric growth was recorded in males and negative allometry in females. Similar results have also been reported for another species, *Conchodytes placunae* (Johnson 1967), which exhibited negative allometry in chela size in both sexes (Baeza and Marin 2023).

It was observed that male weapon can represent approximately 26% of the individual's total body mass, which may be associated with the cost minimisation hypothesis proposed by Dinh (2022). This hypothesis suggests that the development of large weapons occurs as a mechanism to increase fitness efficiency while reducing the energetic costs of carrying exaggerated structures, potentially providing greater advantages, especially in male–male interactions (Dinh 2022). Larger weapons may offer a biomechanical advantage, as they can produce longer-lasting cavitation bubbles with greater pressure capacity. Individuals that develop such structures may proportionally reduce their investment in muscle tissue while increasing investment in exoskeleton (Dinh 2022; Dinh and Patek 2023). Based on these findings and on our results for *A. brasileiro* males, we suggest that a higher WIV and, consequently, more developed weapons could be associated with potential benefits for male reproductive success, as larger weapons may increase the individual's offensive capacity during conspecific contests, as well as enhance fitness by effectively deterring predators and heterospecific intruders (Dinh and Patek 2023).

In a recent study by Nascimento et al. (2025) on propodus shape variation in three *Alpheus* species (*A. angulosus*; *A. carlae*; and *A. nuttingi* Smith 1924), sexual dimorphism in both shape and size between males and females was evidenced. The authors observed that males possess a greater projection on the pollex (fixed finger) of the major propodus, making this region more robust compared to females. This morphological trait is indicative of an efficient aggressive signalling mechanism, which may benefit males during agonistic encounters. Given such advantages, as males develop relatively larger weapons, they tend to bear proportionally lower energetic costs to maintain them (Somjee et al. 2018), which could explain the higher investment in armament observed in *A. brasileiro* males.

The lower investment in weaponry observed in females (approximately 20%) may be associated with the energetic demands directed towards reproduction, including oocyte production and embryo incubation, particularly given that this species can reproduce continuously throughout the year (Pescinelli et al. 2018). As a result, excessively developed weapons may eventually be

too costly for females due to the energy already allocated to these reproductive events, which are essential for achieving reproductive success (Dinh and Patek 2023). Nevertheless, although to a lesser extent, females still invest energy in weapon growth, reflecting the importance of this structure within the social monogamous mating system, as it may contribute primarily to territorial defence, predatory defence and enhance the chances of reproductive success (Hughes et al. 2014).

The degree of dimorphism in *Alpheus* shrimp can be influenced by different factors, including seasonal variations, as described by Heuring and Hughes (2019). The authors observed that during the reproductive season, males tend to invest more in larger weapons, while females may exhibit an opposite pattern, displaying larger claws during the non-reproductive season and prioritising an increase in body size rather than weapon size during the reproductive season. Furthermore, behavioural factors also play an important role in modulating dimorphism. Interestingly, Hughes et al. (2014) recorded more aggressive behaviour in females, who exhibited sex-specific aggression by being more aggressive towards other females than towards males. Based on this information, the differential investment in weaponry observed here in *A. brasileiro* may reflect distinct selective pressures between the sexes, with males potentially investing in larger weapons as a strategy to maximise success in conspecific contests and predator deterrence, while females, although investing less due to other energetic trade-offs, may maintain a certain degree of investment in weaponry to ensure fitness in territorial maintenance and in securing reproductive partners.

Typically, studies addressing weaponry in *Alpheus* have focused on the snapping cheliped (major chela), resulting in a scarcity of information in the literature regarding morphological variation in the cutting cheliped (minor chela) (Costa-Souza et al. 2019; Nascimento et al. 2025). In alpheid shrimps, the loss of the snapping chela can lead to asymmetry reversal, whereby the minor chela transforms into a functional snapping cheliped (Pereira et al. 2014). Nevertheless, the higher investment of males in the minor cheliped, even if only slightly greater than that of females, does not necessarily suggest a male advantage in the event of asymmetry reversal. Previous evidence (Azofeifa-Solano et al. 2020), as well as findings from the present study, indicate that males of different *Alpheus* species invest more than females in the development of the minor chela. In general, the minor chelipeds of decapod crustaceans are used for tasks such as grooming, prey capture and food manipulation (Mariappan et al. 2000). However, in alpheids, this structure may also play a role in agonistic behaviours, serving to hold opponents during fights (Hughes 1996, 2000). Therefore, in males, this slight increase in investment could be related to this function and may confer an advantage during male–male interactions. In contrast, considering the reproductive trade-off observed in females (Hughes et al. 2014), this group may prioritise other energy demands such as vitellogenesis and parental care (Bauer 2004).

The positive correlation between body size and WIV provides clearer evidence of the substantial energetic investment of males in secondary sexual traits, such as weapons. Thus, potentially, the larger the individual, the proportionally higher

its WIV, and possibly the greater its chances of pairing with a receptive female, as well as increasing its success in agonistic encounters (Hughes et al. 2014). Another factor to consider is that when these organisms feel threatened, they may autotomise one of their chelae. However, if this process involves the major chela, the shrimp may undergo asymmetry reversal, which imposes significant costs due to the need for successive moults (Cooney et al. 2017). The absence of a significant correlation between body size and WIV in females further supports the idea that energy is more specifically directed towards reproductive events or structures directly associated with reproduction, such as the second pleonal pleuron, which maximises egg incubation capacity (Bauer 2004). This assertion is supported by the positive correlation between fecundity and the size of this structure in *A. brasileiro* females (Pescinelli, Davanzo, and Costa 2017).

Our findings indicate that the specific roles of each sex, as well as pressures beyond sexual selection, may contribute to the differences observed in WIV in *A. brasileiro*, a species with a socially monogamous mating system. Although males with larger weapons may benefit in contests over resources and mating opportunities, these structures may also serve anti-predatory functions, expanding our interpretation beyond intra-specific competition. Given the intense reproductive effort of females and the high energetic demands associated with it, this group exhibited lower levels of WIV, likely due to the substantial energy allocated to reproductive events, from gonadal maturation to embryo incubation and maintenance (Correa and Thiel 2003; Pescinelli et al. 2018). These characteristics likely reflect the combined influence of sexual selection pressures and a highly competitive environment acting on these shrimps. Therefore, the application of diverse investigative approaches is essential to advance our understanding of the morphological and behavioural traits of shrimp species that possess some form of weaponry.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

- Anker, A. 2012. "Revision of the Western Atlantic Members of the *Alpheus armillatus* H. Milne Edwards, 1837 Species Complex (Decapoda, Alpheidae), with Description of Seven New Species." *Zootaxa* 3386: 1–109. <https://doi.org/10.11646/zootaxa.3386.1.1>.
- Azofeifa-Solano, J. C., J. A. Sibaja-Cordero, and I. S. Wehrtmann. 2020. "Sexual Dimorphism of the Major Chela and Sex Ratio as Indicators of the Mating System in the Estuarine Snapping Shrimp *Alpheus colombiensis* Wicksten, 1988 (Decapoda: Caridea: Alpheidae)." *Journal of Crustacean Biology* 40: 649–656. <https://doi.org/10.1093/jcobiol/ruaa069>.
- Baeza, J. A. 2008. "Social Monogamy in the Shrimp *Pontonia marginata*, a Symbiont of *Pinctada mazatlanica*, off the Pacific Coast of Panama." *Marine Biology* 153: 387–395. <https://doi.org/10.1007/s00227-007-0815-9>.
- Baeza, J. A., and I. Marin. 2023. "Mating System of the Symbiotic Shrimp *Chernocaris placunae* (Decapoda: Palaemonidae) in Vietnam: Social Monogamy and Differences Between Two Sites With Contrasting Environmental Conditions." *Symbiosis* 90: 159–169. <https://doi.org/10.1007/s13199-023-00926-8>.
- Bauer, R. T. 2004. *Remarkable Shrimps: Adaptations and Natural History of the Carideans*. University of Oklahoma Press.
- Bauer, R. T. 2023. "Shrimps: Their Diversity, Intriguing Adaptations and Varied Lifestyles." *Fish & Fisheries Series* 42: 1–720. <https://doi.org/10.1007/978-3-031-20966-6>.
- Bywater, C. L., M. J. Angilletta, and R. S. Wilson. 2008. "Weapon Size Is a Reliable Indicator of Strength and Social Dominance in Female Slender Crayfish (*Cherax dispar*)." *Functional Ecology* 22: 311–316. <https://doi.org/10.1111/j.1365-2435.2008.01379.x>.
- Callander, S., A. T. Kahn, T. Maricic, M. D. Jennions, and P. R. Y. Backwell. 2013. "Weapons or Mating Signals? Claw Shape and Mate Choice in a Fiddler Crab." *Behavioral Ecology and Sociobiology* 67: 1163–1167. <https://doi.org/10.1007/s00265-013-1541-6>.
- Clarke, A., C. C. E. Hopkins, and E. M. Nilssen. 1991. "Egg Size and Reproductive Output in the Deep-Water Prawn *Pandalus borealis* Kroyer, 1838." *Functional Ecology* 5: 724–730.
- Cooney, P., C. A. Korey, and M. Hughes. 2017. "Autotomy and Recovery in the Snapping Shrimp, *Alpheus angulosus* McClure, 2002 (Caridea: Alpheidae)." *Journal of Crustacean Biology* 37: 701–708. <https://doi.org/10.1093/jcobiol/rux082>.
- Correa, C., and M. Thiel. 2003. "Mating Systems in Caridean Shrimps (Decapoda: Caridea) and Their Evolutionary Consequences for Sexual Dimorphism and Reproductive Biology." *Revista Chilena de Historia Natural* 76: 187–203. <https://doi.org/10.4067/S0716-078X2003000200006>.
- Costa-Souza, A. C., J. R. B. Souza, and A. O. Almeida. 2019. "Growth, Sexual Maturity and Dimorphism in Six Species of Snapping Shrimps of the Genus *Alpheus* (Decapoda: Alpheidae)." *Thalassas* 35: 451–464. <https://doi.org/10.1007/s41208-019-00146-2>.
- Costa-Souza, A. C., J. R. B. Souza, and A. O. Almeida. 2022. "Populational Evidence Supports a Monogamous Mating System in Five Species of Snapping Shrimps of the Genus *Alpheus* (Caridea: Alpheidae)." *Zoological Studies* 61: 1–14. <https://doi.org/10.6620/zs.2022.61-01>.
- Dalosto, M. M., L. Ayres-Peres, P. B. Araujo, S. Santos, and A. V. Palaoro. 2019. "Pay Attention to the Ladies: Female Aggressive Behavior and Weapon Allometry Provide Clues for Sexual Selection in Freshwater *Anomurans* (Decapoda: Aeglididae)." *Behavioral Ecology and Sociobiology* 73: 1–11. <https://doi.org/10.1007/s00265-019-2741-5>.
- Dinh, J. P. 2022. "Large and Exaggerated Sexually Selected Weapons Comprise High Proportions of Metabolically Inexpensive

- Exoskeleton." *Biology Letters* 18: 20210550. <https://doi.org/10.1098/rsbl.2021.0550>.
- Dinh, J. P., and S. N. Patek. 2023. "Tradeoffs Explain Scaling, Sex Differences, and Seasonal Oscillations in the Remarkable Weapons of Snapping Shrimp (*Alpheus* spp.)." *eLife* 12: e84589. <https://doi.org/10.7554/eLife.84589>.
- Emlen, D. J. 2008. "The Evolution of Animal Weapons." *Annual Review of Ecology, Evolution, and Systematics* 39: 387–413. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173502>.
- Ghizelli-Fraga, B., R. C. Costa, and R. A. Pescinelli. 2021. "Life History Traits of the Snapping Shrimp *Alpheus carlae* (Decapoda: Alpheidae) From the South-Eastern Coast of Brazil." *Zoological Studies* 60: 1–12. <https://doi.org/10.6620/ZS.2021.60-62>.
- Graham, Z. A., M. B. Stubbs, and Z. J. Loughman. 2023. "Reproductive Season-Based Plasticity in the Size and Strength of Female Crayfish (*Faxonius obscurus*) Claws." *Journal of Morphology* 284: e21614. <https://doi.org/10.1002/jmor.21614>.
- Hartnoll, R. G. 1974. "Variation in Growth Pattern Between Some Secondary Characters in Crabs (Decapoda: Brachyura)." *Crustaceana* 27: 131–136. <https://doi.org/10.1163/156854074X00334>.
- Hartnoll, R. G. 1978. "The Determination of Relative Growth in Crustacea." *Crustaceana* 34: 281–293. <https://doi.org/10.1163/156854078X00844>.
- Heuring, W. L., and M. Hughes. 2019. "It Takes Two: Seasonal Variation in Sexually Dimorphic Weaponry Results From Divergent Changes in Males and Females." *Ecology and Evolution* 9: 5433–5439. <https://doi.org/10.1002/ece3.5136>.
- Hughes, M. 1996. "Size Assessment via a Visual Signal in Snapping Shrimp." *Behavioral Ecology and Sociobiology* 38: 51–57. <https://doi.org/10.1007/s002650050216>.
- Hughes, M. 2000. "Deception With Honest Signals: Signal Residuals and Signal Function in Snapping Shrimp." *Behavioral Ecology* 11: 614–623. <https://doi.org/10.1093/beheco/11.6.614>.
- Hughes, M., T. Williamson, K. Hollowell, and R. Vickery. 2014. "Sex and Weapons: Contrasting Sexual Dimorphisms in Weaponry and Aggression in Snapping Shrimp." *Ethology* 120: 982–994. <https://doi.org/10.1111/eth.12270>.
- Huxley, J. S. 1950. "Relative Growth and Form Transformation." *Proceedings of the Royal Society of London* 137: 465–469. <https://doi.org/10.1098/rspb.1950.0055>.
- Knolton, N. 1980. "Sexual Selection and Dimorphism in Two Demes of a Symbiotic, Pair-Bonding Snapping Shrimp." *Evolution* 34: 161–173. <https://doi.org/10.2307/2408325>.
- Lane, S. M. 2018. "What Is a Weapon?" *Integrative and Comparative Biology* 58: 1055–1063. <https://doi.org/10.1093/icb/icy083>.
- Mariappan, P., C. Balasundaram, and B. Schmitz. 2000. "Decapod Crustacean Chelipeds: An Overview." *Journal of Biosciences* 25: 301–313. <https://doi.org/10.1007/BF02703939>.
- Mathews, L. M. 2002. "Territorial Cooperation and Social Monogamy: Factors Affecting Intersexual Behaviours in Pair-Living Snapping Shrimp." *Animal Behaviour* 63: 767–777. <https://doi.org/10.1006/anbe.2001.1976>.
- Mathews, L. M. 2007. "Evidence for Restricted Gene Flow Over Small Spatial Scales in a Marine Snapping Shrimp *Alpheus angulosus*." *Marine Biology* 152: 645–655. <https://doi.org/10.1007/s00227-007-0718-9>.
- McCullough, E. L., and D. M. O'Brien. 2022. "Variation in Allometry Along the Weapon-Signal Continuum." *Evolutionary Ecology* 36: 591–604. <https://doi.org/10.1007/s10682-022-10158-9>.
- Muramatsu, D. 2011. "The Function of the Four Types of Waving Display in *Uca lactea*: Effects of Audience, Sand Structure, and Body Size." *Ethology* 117: 408–415. <https://doi.org/10.1111/j.1439-0310.2011.01884.x>.
- Nascimento, W. M., A. P. Pinheiro, and A. O. Almeida. 2025. "Size as a Determinant of Robustness: Exploring Sexual Dimorphism in the Size and Shape of the Snapping and Cutting Claws in *Alpheus* (Caridea: Alpheidae)." *Zoologischer Anzeiger* 314: 1–9. <https://doi.org/10.1016/j.jcz.2024.11.008>.
- Nogueira, C. S., A. R. Silva, and A. V. Palaoro. 2022. "Fighting Does Not Influence the Morphological Integration of Crustacean Claws (Decapoda: Aeglididae)." *Biological Journal of the Linnean Society* 136: 173–186. <https://doi.org/10.1093/biolinnean/blac026>.
- Palaoro, A. V., and M. Briffa. 2017. "Weaponry and Defenses in Fighting Animals: How Allometry Can Alter Predictions From Contest Theory." *Behavioral Ecology* 28: 328–336. <https://doi.org/10.1093/beheco/arw163>.
- Palaoro, A. V., and P. E. C. Peixoto. 2022. "The Hidden Links Between Animal Weapons, Fighting Style, and Their Effect on Contest Success: A Meta-Analysis." *Biological Reviews* 97: 1948–1966. <https://doi.org/10.1111/brv.12877>.
- Paschoal, L. R. P., and F. J. Zara. 2022. "Is There a Trade-Off Between Sperm Production and Sexual Weaponry in the Amazon River Prawn *Macrobrachium amazonicum* (Heller, 1862)?" *Zoology* 153: 1–13. <https://doi.org/10.1016/j.zool.2022.126029>.
- Pereira, A., E. Tracey, P. C. Cooney, C. A. Korey, and M. Hughes. 2014. "Post-Autotomy Claw Regrowth and Functional Recovery in the Snapping Shrimp *Alpheus angulosus*." *Marine and Freshwater Behaviour and Physiology* 47: 147–159. <https://doi.org/10.1080/10236244.2014.928460>.
- Pescinelli, R. A., A. O. Almeida, and R. C. Costa. 2018. "Population Structure, Relative Growth and Morphological Sexual Maturity of the Snapping Shrimp *Alpheus brasileiro* Anker, 2012 (Caridea: Alpheidae) From the South-Eastern Coast of Brazil." *Marine Biology Research* 14: 610–620. <https://doi.org/10.1080/17451000.2018.1472383>.
- Pescinelli, R. A., T. M. Davanzo, and R. C. Costa. 2017. "Social Monogamy and Egg Production in the Snapping Shrimp *Alpheus brasileiro* (Caridea: Alpheidae) From the South-Eastern Coast of Brazil." *Journal of the Marine Biological Association of the United Kingdom* 97: 1519–1526. <https://doi.org/10.1017/S0025315416000904>.
- Pescinelli, R. A., L. F. Miazaki, and R. C. Costa. 2020. "Growth, Age at Sexual Maturity, Longevity and Natural Mortality of *Alpheus brasileiro* (Caridea: Alpheidae) From the South-Eastern Coast of Brazil." *Nauplius* 28: e2020011. <https://doi.org/10.1590/2358-2936e2020011>.
- Pescinelli, R. A., J. A. F. Pantaleão, F. L. Mantelatto, and R. C. Costa. 2017. "Morphological Description of Early Zoeal Stages of *Alpheus brasileiro* Anker, 2012 Reared in the Laboratory, Including a Revision of the Larval Morphology of the First Zoeal Stage of the Genus *Alpheus fabricius*, 1798 (Caridea: Alpheidae)." *Zootaxa* 4269: 265–276. <https://doi.org/10.11646/zootaxa.4269.2.5>.
- Rahman, N., D. W. Dunham, and C. K. Govind. 2003. "Social Monogamy in the Big-Clawed Snapping Shrimp, *Alpheus heterochaelis*." *Ethology* 109: 457–473. <https://doi.org/10.1046/j.1439-0310.2003.00885.x>.
- Rico-Guevara, A., and K. J. Hurme. 2019. "Intrasexually Selected Weapons." *Biological Reviews* 94: 60–101. <https://doi.org/10.1111/brv.12436>.
- Sneddon, L. U., F. A. Huntingford, and A. C. Taylor. 1997. "Weapon Size Versus Body Size as a Predictor of Winning in Fights Between Shore Crabs, *Carcinus maenas* (L.)." *Behavioral Ecology and Sociobiology* 41: 237–242. <https://doi.org/10.1007/s002650050384>.

Somjee, U., H. A. Woods, M. Duell, and C. W. Miller. 2018. "The Hidden Cost of Sexually Selected Traits: The Metabolic Expense of Maintaining a Sexually Selected Weapon." *Proceedings of the Royal Society B: Biological Sciences* 285: 20181685. <https://doi.org/10.1098/rspb.2018.1685>.

Subramoniam, T. 2023. "Sexual Biology and Mating Behaviour in Decapod Crustaceans: A Case Study With Coral Reef Dwelling Caridean Shrimps." *Journal of Endocrinology and Reproduction* 27: 1–14. <https://doi.org/10.18311/jer/2023/31247>.

Vittori, M., V. Srot, B. Bussmann, F. Predel, P. A. van Aken, and J. Štrus. 2024. "Claws of Terrestrial Crustaceans: Structure, Composition and Mechanics." *Microscopy and Microanalysis* 30: 959–960. <https://doi.org/10.1093/mam/ozae044.472>.

Yamada, S. B., and E. G. Boulding. 1998. "Claw Morphology, Prey Size Selection and Foraging Efficiency in Generalist and Specialist Shell-Breaking Crabs." *Journal of Experimental Marine Biology and Ecology* 220: 191–211. [https://doi.org/10.1016/S0022-0981\(97\)00122-6](https://doi.org/10.1016/S0022-0981(97)00122-6).