

## Original Article

# Allometry and sexual dimorphism of the mangrove climbing crab *Metopograpsus latifrons* from Magnesia Mangrove Forest, Virac, Catanduanes Island, Philippines

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**Abstract:** Morphological adaptations associated with life history may be explained by studies on allometry and sexual dimorphism in animals. However, little is known about these concepts among the climbing crab species. Here, we investigated the allometric growth (relative growth) and sexual dimorphism of the mangrove climbing crab *Metopograpsus latifrons* from Magnesia Mangrove Forest, Catanduanes Island, Philippines in 2023 (April, September, and December) and 2024 (October). The results suggest that *M. latifrons* is positively allometric (both males and females) in the cheliped characters and abdomen. This reflects strategies in intrasexual resource competition (food and spatial resources) and abdominal adaptations related to reproductive systems, respectively. No sexual dimorphism is detected in the body size, indicating that the arboreal strategies of the species may not favor larger individuals. Sexual dimorphism, however, is present in the cheliped, which may be an advantage among males (confrontation, grasping, or courtship display) driven by sexual selection in its mangrove-related lifestyle.

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## Introduction

Crabs play a vital role in the mangroves' nutrient cycling, emphasizing their efficient contribution to the ecosystem's ecological dynamics. Fundamental to the functional integrity of the habitat's trophic system, their activities on litter and sediments (Kristensen, 2008; Gao and Lee, 2022) facilitate productivity resilience. Associated with these mechanisms, their survival tactics have been developed. For instance, the consumption of mangrove leaves and detritus (not readily available for other species) integrate into their foraging habit, demonstrating strategies in resource utilization (Giddens et al., 1986; Pinheiro et al., 2005; Robertson, 2021; Gao and Lee, 2022). In conjunction with other environmental gradients, morphological diversity results from these adaptive strategies shaped by selective pressures in the coastal environments.

Adaptive traits are exhibited by several crab species extending above the water surface (mangrove trees). Vannini et al. (1997) and Fratini et al. (2005)

categorized species of climbing crabs according to their degree of tree utilization and climbing abilities. These species are suggested to have undergone morphological convergence due to their climbing habit despite representing different brachyuran families (Fratini et al., 2005). Other species are adapted to utilize both mangrove trees and sediments near their host trees (Sivasothi, 2000). Drawing from these examples, the morphological adaptation of the climbing crabs (e.g., Sesarmidae) suggests influences by the nature of the mangrove forests (Jones, 1984).

The allometric concept offers valuable perspectives on understanding key roles in the evolution of these morphological structures. This includes (aside from morphological adaptations related to environmental factors) influence on the expression of sexual dimorphism driven by natural and sexual selection (Littleford-Colquhoun et al., 2019; Liang et al., 2022). Associated investigations among crustaceans are usually carried out to explain relative growth (Huxley,

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1924; Huxley and Tessier, 1936; Hartnoll, 1974), where several works have related morphometric relationships with sexual dimorphism in different species (Hartnoll, 1978; Felder and Lovett, 1989; Pinn et al., 2001; Itani and Uchino, 2005; Bueno and Shimizu, 2009; Claverie and Smith, 2010; El-Damhougy et al., 2018; Fazhan et al. 2021). As morphological variabilities in the population can be expounded by analyzing allometric relationships (Fairbairn, 1997; Costa and Soares-Gomes, 2008; Ribeiro et al., 2013; Griffen et al., 2018; Vermeirin et al., 2021), the role of allometry in describing the species' sexual dimorphism is emphasized. Allometry and sexual dimorphism (as a manifestation of allometric patterns) interplay in species' morphology, with implications on reproductive strategies, resource competition, aggression, and/or habitat adaptations.

Crustaceans are excellent morphometric models because they have firm exoskeletons that complement accurate data recordings (Hartnoll, 1978). Despite this advantage, there is a paucity of information on the allometry and sexual dimorphism in climbing crabs, possibly due to their enigmatic nature. Here, we aimed to elucidate these concepts in *Metopograpsus latifrons* (one of the least explored climbing crab species) by investigating its morphometric characteristics with interpretations in its mangrove-related lifestyle.

## Materials and Methods

Magnesia Mangrove Forest (with a nearby coastal village) is situated on the southwestern coast of Virac, Catanduanes Island, Philippines, facing the Lagonoy Gulf, an inlet of the Philippine Sea (Pacific Ocean) (Fig. 1). It is fed by a river, with our sampling stations located in the river mouth-estuary systems. Specifically, the starting point of sampling stations was 10 m from the zone where seawater enters the river (under the bridge), then inward of the mangrove forests, along the main river channel. Collections and observations were conducted in the margins of the mangrove forests (east and west corridors) ( $\leq 3$  m) bordering the river channel (river bank), and walking up to 100 m of the channel from the starting point. We also tracked the opposite bank (west corridor), but we

explored only 20 m from the starting point due to deep sediments and impassable pathways, hampering some of our sampling efforts.

We conducted a naturalistic observation survey during sampling and specimen collection. During our preliminary visits, we found that most crab individuals were on mangrove trees within the river channel's banks, where mangroves remain partially submerged in water even during spring low tides. This led us to select these stations as our study site. A transect line (center) was established to facilitate the survey, with observers tracking the line through visual observation. Stations (corridors) were positioned on the river channel strata (2 riverbank corridors [east and west]). Collection/observation was then conducted randomly. In addition, some encountered crab individuals outside the stations were also collected (opportunistic sampling within the station vicinities) to increase the number of samples due to the relative rarity of the species. Sampling activities were conducted in 2023 (April, September, and December) and 2024 (October) to facilitate additional visits, including both day and night collections over 2 hours (within three hours of the lowest tide).

Crab individuals were primarily collected from the mangrove trees, including those in the trunk corners. The collection did not include crabs at the larval stage (e.g., megalopa). We attempted to collect "juveniles" (smaller than those found climbing on the trees) by scooping the water column and scrubbing the sediments and pneumatophore networks, but finding them was challenging (obtaining only three individuals). In addition, a very small individual (9.02 mm CW) was found deeper in the pneumatophore networks, possibly a *Metopograpsus* sp., but the particular species and sex cannot be determined morphologically; thus, we excluded it from the data analysis. We identified the samples following the morphological characterizations based on White (1847), Miers (1880) (with comparisons between related species), Abraham and Prakasan (2020), and including information from databases such as the World Register of Marine Species (WoRMS) (2023) and Crab Database (2023). Samples were preserved in

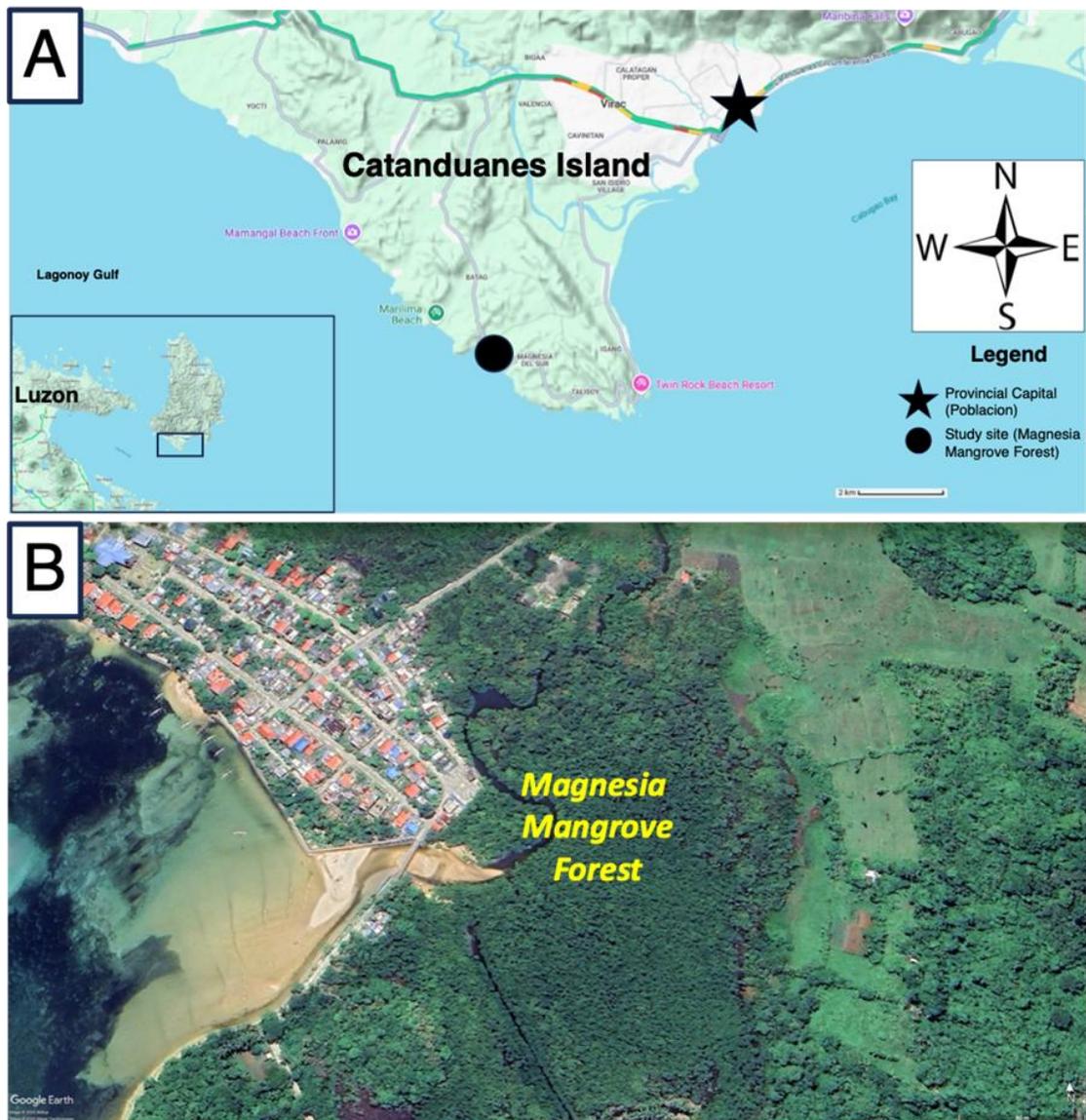


Figure 1. The study site. The location of the Magnesia Mangrove Forest in the southern portion of Catanduanes Island is represented by a black circle, 1A; Top view of the mangrove forest, 1B (the mangrove forest's boundary is not illustrated, which may extend beyond the areas depicted in the photo).

a 70% ethanol solution and deposited in the Science Laboratory Building of the College of Science, Catanduanes State University.

The samples were examined and measured at Catanduanes State University (ex-situ). Three specimens had damaged or missing chelipeds, so they were not included in the chela morphometric analyses. The following morphometric characters were measured: Carapace Width (hereafter, CW), Propodus Length (hereafter, PL), Propodus Height (hereafter, PH), and Abdomen Width (hereafter, AW) to the nearest 0.01 mm.

Analyses of the growth of the morphometric

characters relative to the growth of the carapace were performed using the linear regression equation of  $y = ax^b$ , fitted with standard least squares as adapted from Hartnoll (1974, 1978). The data were converted to linear form using the log transformation as  $\log y = \log a + b \log x$ , where  $x$  is the independent variable (in this case, the CW) and  $y$  is the dependent variable (the PL, PH, AW),  $a$  is the intercept (value of  $y$  when  $x = 0$ ), and  $b$  is regression line's slope. Allometry was determined by positive allometry ( $b > 1$ ), negative allometry ( $b < 1$ ), and isometry ( $b = 1$ ). The body size difference was determined through a t-test on the CW. We tested for significant differences in each morphometric

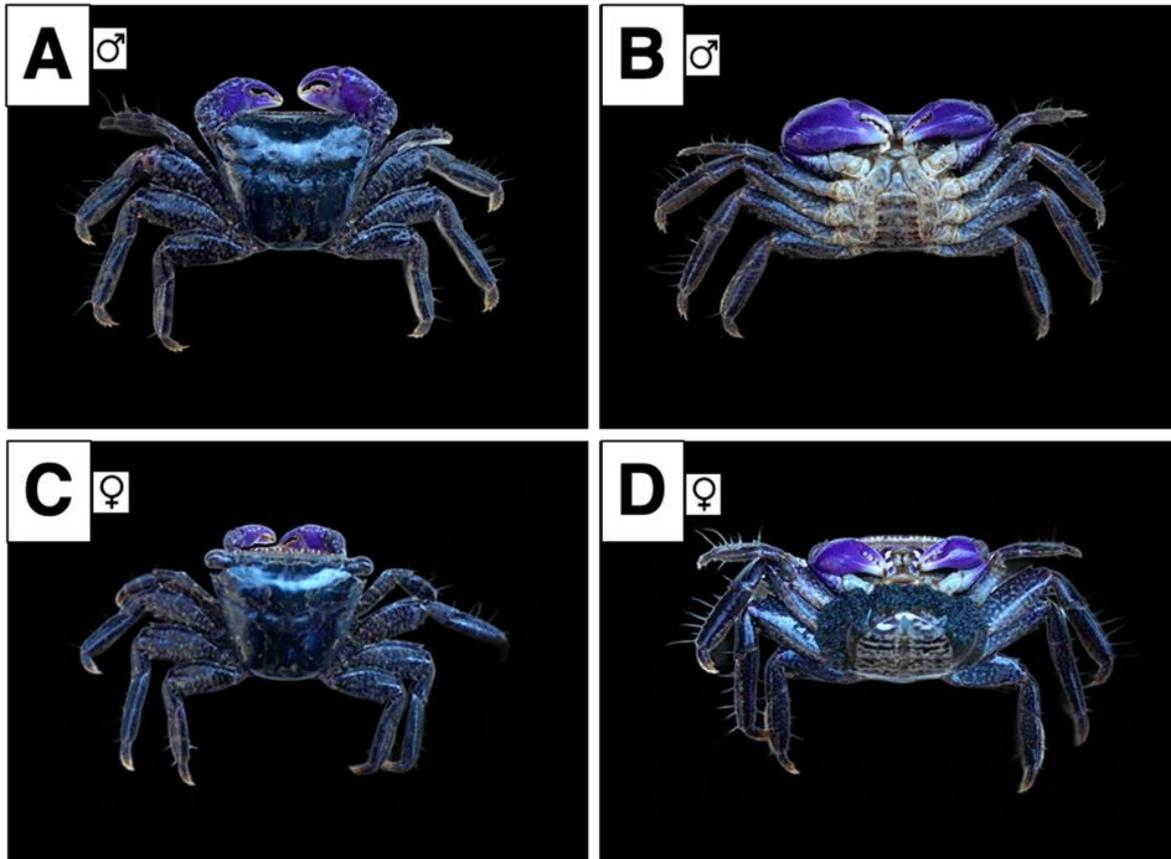


Figure 2. The climbing crab *Metopograpsus latifrons*: male with 30.19 mm CW (2A-B); female (ovigerous) with 29.84 mm CW (2C-D).

character between sexes (PL, PH, AW) (i.e., whether a morphological character of males is proportionally larger than that of females) using the Analysis of Covariance (ANCOVA). The Analysis of Covariance (ANCOVA) was used to investigate residuals of regression (comparison between morphometrics of the two variables). This analysis aimed to determine if the growth of a morphometric character (PL, PH, and AW) is significant between the two groups, considering the influence of the covariate (CW). Statistical analyses were performed in SAS-JMP software.

## Results

We collected a total of 87 *M. latifrons* individuals, of which 37 are males and 50 are females. Body size (CW) ranged from 13.76 to 34.22 mm in males (Mean = 25.81 mm, SD = 5.05, SE = 0.83) and 18.43 to 33.26 mm in females (Mean = 26.05 mm, SD = 3.29, SE = 0.46). The representative of each sex is shown in Figure 2 (male size, 30.19 mm; female size, 29.84

mm). The results revealed no significant difference in the body size (CW) between males and females (t-value = -0.56; DF = 55.12;  $P > 0.05$ ). The sizes of the smallest male and female observed with copulatory-mating behaviors were 26.13 and 26.04 mm, respectively, while the size of the smallest ovigerous female was 24.30 mm.

The morphometry of the crab is shown in Figure 3. Both sexes were generally represented in each group size of CW (except in  $\leq 15.00$  mm, which is represented only by a male) (Fig. 3A). The smallest record of the climbing individuals was 17.78- and 18.43-mm CW for males and females, respectively, indicating that *M. latifrons* may start the climbing habit roughly before attaining the size of 20 mm CW. The three “non-climbing individuals” (all males,  $\leq 17.40$  mm CW) were found in the sediments within or near the pneumatophore networks. The PL ranged from 5.46 to 22.02 mm in males (Mean = 14.85 mm, SD = 4.63, SE = 0.79) and 8.27 mm to 16.48 mm in females (Mean = 12.78 mm, SD = 2.17, SE = 0.31)

Table 1. Allometric scaling using the Regression analyses of the morphometric characters' data (PL= Propodus Length, PH= Propodus Height, and AW= Abdomen Width). Morphometric data were log-transformed.

Morphometric characters	Sex	Regression equation: $\text{Log } y = \text{log } a + b \text{ log } x$	R <sup>2</sup>	Allometric Scaling
PL	Male	$\text{LogPL} = -2.297 + 1.529\text{LogCW}$	0.92	Positively allometric
	Female	$\text{LogPL} = -1.588 + 1.267\text{LogCW}$	0.88	Positively allometric
PH	Male	$\text{LogPH} = -4.943 + 2.118\text{LogCW}$	0.96	Positively allometric
	Female	$\text{LogPH} = -2.643 + 1.353\text{LogCW}$	0.86	Positively allometric
AW	Male	$\text{LogAW} = -2.213 + 1.259\text{LogCW}$	0.90	Positively allometric
	Female	$\text{LogAW} = -1.587 + 1.310\text{LogCW}$	0.91	Positively allometric

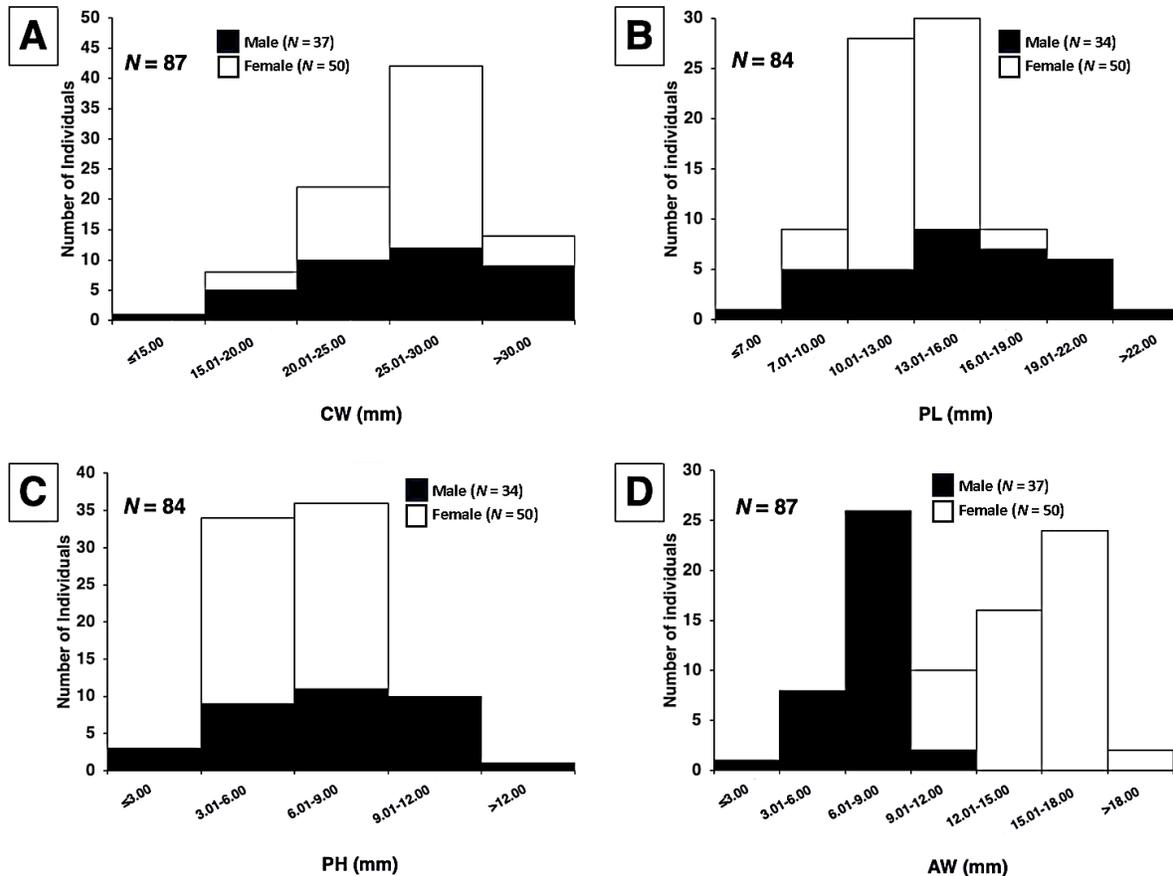


Figure 3. Morphometry of *Metopograpsus latifrons*: Carapace Width (CW), 3A; Propodus Length (PL), 3B; Propodus Height (PH), 3C; Abdomen Width (AW), 3D. Three males with missing or damaged chelipeds were not included in 3B and 3C.

(Fig. 3B). The PH ranged from 1.54 to 12.07 mm in males (Mean = 7.37 mm, SD = 2.92, SE = 0.50) and 3.48 to 7.79 mm in females (Mean = 5.90 mm, SD = 1.06, SE = 0.15) (Fig. 3C). The histogram shows that males have larger chela (PL, and PH), with the size of >19.00 mm in PL, and >9.00 mm in PH only recorded in males (heterochely is found in both sexes, but it is robust in males, slightly in females). Further, AW ranged from 2.81 to 10.09 mm in males (Mean = 6.62 mm, SD = 1.67, SE = 0.27) and 9.62 to 18.28 mm in females (Mean = 14.72 mm, SD = 2.50, SE = 0.35)

(Fig. 3D), which shows the larger abdomen among females. Starting with the AW range of 12.01-15.00 mm, all individuals were females.

All morphometric characters exhibited positive allometry: PL,  $y = -2.297 + 1.529x$  for male and  $y = -1.588 + 1.267x$  for female; PH,  $y = -4.943 + 2.118x$  for male and  $y = -2.643 + 1.353x$  for female; AW,  $y = -2.213 + 1.259x$  for male and  $y = -1.587 + 1.310x$  for female. Regression analyses were drawn from the morphometric data and are represented in Table 1. The results revealed that males have larger chelipeds than

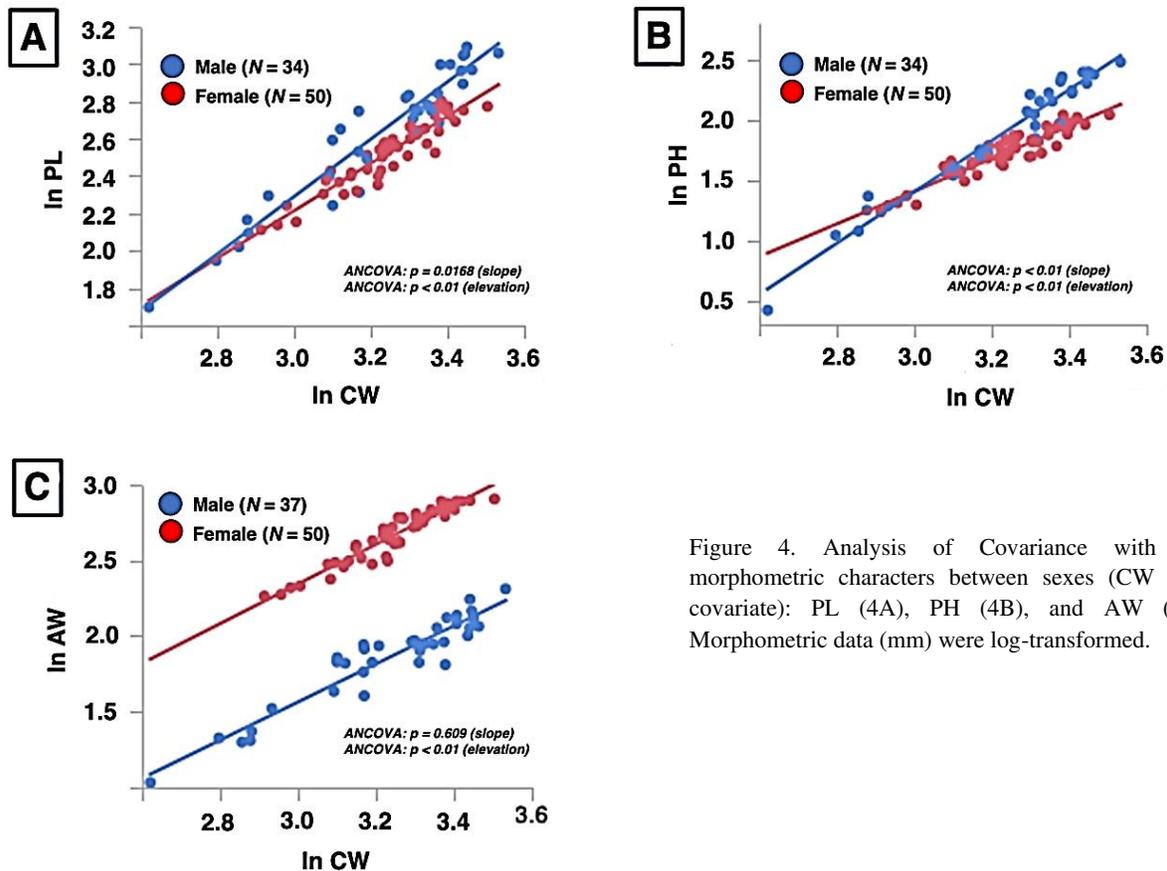


Figure 4. Analysis of Covariance with the morphometric characters between sexes (CW as a covariate): PL (4A), PH (4B), and AW (4C). Morphometric data (mm) were log-transformed.

females: PL (slope:  $F = 5.97$ ,  $P = 0.0168$ ; elevation:  $F = 56.13$ ,  $P < 0.01$ ), PH (slope:  $F = 45.36$ ,  $P < 0.01$ ; elevation:  $F = 58.87$ ,  $P < 0.01$ ). Females, on the one hand, have larger abdomens than males: AW (slope:  $F = 0.2630$ ,  $P = 0.609$ ; elevation:  $F = 2415.64$ ,  $P < 0.01$ ). Figure 4 shows the results of ANCOVA.

## Discussions

In many crustacean males, body size increases the likelihood of mating, a strategy primarily linked to sexual selection (Hartnoll, 1969; Bauer et al., 2014; Azizi et al., 2024). As the body serves as the platform for the cheliped, a larger male body (which may enhance cheliped development) is an advantage for male-male confrontation in many species (Fumis et al., 2007). This has also been regarded as productive among crabs that exhibit pre-copulatory and post-copulatory mating habits (Waiho et al., 2015; Fazhan et al., 2021). The body size of *M. latifrons*, however, does not follow the classic size dimorphism (classic body size dimorphism =  $M > F$ ), wherein in this case, there is no significant difference between sexes. This

also occurs in some species in the family Ocypodidae (Fransozo et al., 2003; Costa and Soares-Gomez, 2011) and in a species in the family Trichodactylidae (Williner et al., 2014). In a rare case, size dimorphism is female-biased, as shown in *Ilyograpsus nodulosus* in the family Macrophthalmidae (Nakayama and Wada, 2015). In that case, an experiment revealed no advantage of the large male size in the presence of random competition; all males (regardless of body size) successfully copulated. Our study did not investigate sex choice experiments; therefore, experimental studies in detail may be further explored. Additionally, exposure to various adaptations such as food resource access (Hines, 1989; Fransozo et al., 2003; Silaban, 2020; Colpo et al., 2022) and the nature of different populations (Hidayani et al., 2018; De Grande et al., 2021) may explain these variabilities. Relating to these conditions, the vertical habitats (and associated tree resources) are potential influences on the body size of *M. latifrons*. During the sampling, we observed the crab move or jump swiftly between trunks or branches. Given this mobility, the small size

may limit the risks of falling and improve the individual's maneuverability.

Males have larger chelipeds (PL and PH) relative to the growth of the body size (CW). This is similar to many crustacean species where males exhibit positive allometry in the cheliped development (PL and PH), providing an advantage in intrasexual competition. Males of many crustacean species invest more energy in claws (weaponry) due to competition for females, leading to levels of aggressive behaviors during male-male confrontations (Claverie and Smith, 2009; Swanson et al., 2013; Baeza et al., 2016). This is a possibility for *M. latifrons*, at least with some levels of combat displays, but perhaps an experimental study may be explored to confirm this trajectory. On one hand, sexual selection is also driven by the choice of mate (Azofeifa-Solano et al., 2022). During sampling, we observed a grasping mechanism of some paired individuals on the mangrove trunks (0-10 cm from the water surface). The males grasp the female using cheliped and pereopods, suggesting pre-copulatory and post-copulatory guarding positions, a behavior observed in other grapsid species (Brockerhoff and McLay, 2005). We do not have other information on the mating rituals of *M. latifrons*, but this portrays an advantage for having larger chelae, especially in vertical habitats, and thus a possible driving force for mate choice. In addition, we aimed to describe the handedness of the species as it may have implications for the feeding nature of the crab (Silva et al., 2014), but we observed that this feature is not present in the species.

An inflection point is not calculated in the regression line due to a small number of smaller individuals (only three "non-climbing" individuals). The three smallest males (all "non-climbing") have chelipeds of similar size. On the other hand, we recorded an asymmetric cheliped (heterochelous) in all males found climbing on the tree (the smallest climbing individual had 17.78 mm CW), which suggests that secondary growth of males occurs before attaining a size of 20 mm CW and probably coincides with the climbing behavior in males. However, there is no literature on the onset of maturity in *M. latifrons*.

Positive allometry in female chelipeds may be associated with intraspecific competition for food and spatial resources, as also exhibited by other crustacean species (Debusse et al., 2001; Claverie and Smith, 2009; Baeza et al., 2017). We observed individuals feeding on epiphytes on the trunk. This agrees with Shaw and Tibbetts (2004) and Vermeiren et al. (2015), describing the morphology of *Metopograpsus* spp. more suited for foraging and scraping macroalgae. The abundance of these resources is unknown, but accessing them (if abundant) may be limited, as increased climbing height poses a greater risk of avian predation (several predatory intertidal birds were present at the site). Related predator-prey interactions have been observed in gulls preying on species of intertidal crabs (Ellis et al., 2005). During a night sampling, we observed an individual "hunting or eating" beside the flowers of *Rhizophora* sp., adjacent to a moth. It was not determined if the crab was eating the flower or attempting to capture the moth as it splashed into the water immediately. However, access to either resource (flowers, insects) could be episodic, following seasonal timing or weather variabilities. The presence of most individuals observed on the narrow strip of mangroves along the river channel also potentially contributes to spatial constraints, but this requires studies on crab and mangrove distribution. Moreover, leaf and detritus consumption may occur in the nearby "drained" mangal floors at low tide, as observed in other species of climbing crabs in the family Sesamidae (Matillano et al., 2018). Information about competition for leaves and detritus between climbing crabs is limited, but it seems that if this feeding habit takes place (considering its feeding morphology), this constitutes selective pressure for the species. Figure 5 shows the crab in the natural mangrove environment (in situ).

Food resources may be occasionally found in the water (most individuals were found on the mangroves at the river channel banks, which are partially submerged even during spring low tide), but this appears less likely. Diving behaviors after being disturbed suggest that water (aside from its probable role in reproduction) is associated with predator

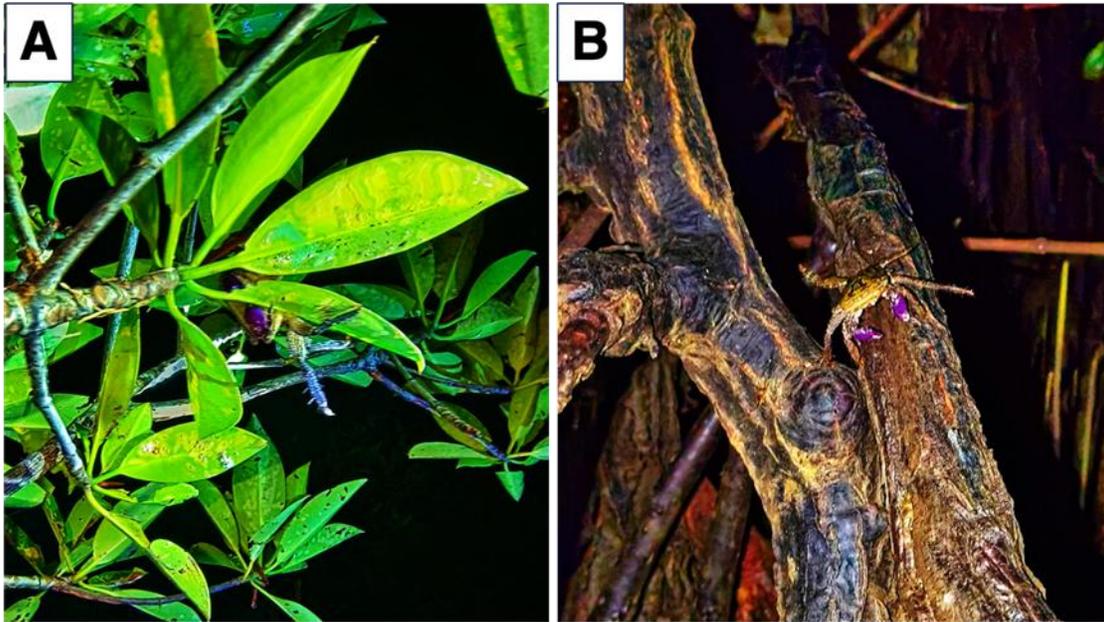


Figure 5. *Metopograpsus latifrons* found on the mangrove trees: on the leaves and branches, 5A; and on the trunk, 5B.

escape. Nonetheless, as some fishes are possible predators, there is a need to investigate fish assemblages to explain the magnitude of the diving trade-off, which is beyond the study's scope.

Females have a larger abdomen (AW) (as typically exhibited by female brachyurans) due to the space for the eggs and developing embryos (Araujo et al., 2012; Ribeiro et al., 2013). The result of our study is no exception to this usual trend. However, males of *M. latifrons* demonstrate relatively strong positive allometry in the abdomen ( $b = 1.259$ ) compared with males of other species, with the abdomen growth rate increasing approximately similarly between sexes (ANCOVA, slope:  $P = 0.609$ ). The association of this condition with sperm competition is unknown, but it is plausible. It was described earlier that the copulatory position of the species suggests sperm competition, where, in this case, the efficiency of a large ejaculate may increase male fitness (Jivoff, 1997; Cornwallis and Connor, 2009). However, there is another contrasting point: sexual dimorphism in size is not detected in the species. In general, large ejaculate, which fertilizes many eggs, is associated with large males (Jivoff, 1997; Sato et al., 2010), and in some species of stone crab, large males produce increasing ejaculates when copulated with females of

increasing body size (Sato and Goshima, 2007). Sperm production is energetically costly (Pretterebner et al., 2022), and in this species, energy spent in mating (copulation) also includes muscular energy for anchoring and maneuvering on the tree, as well as grasping females, which amplifies the cost. Thus, small-sized males (which may be suited for anchoring and maneuvering) with a positively allometric abdomen (potentially with a larger ejaculate) may be advantaged. A study is required to reveal the relationship between increasing male abdomen size and gonopod development and sperm production in this species. In addition, the enlargement of the abdomen to protect the gonopod (including retaining moisture) during prolonged climbing may also favor the male crab. Future investigations require a careful scientific process to obtain a concrete understanding of the male crab's abdominal evolution in complex environments.

### Conclusions

Larger bodies may not be an advantage for the arboreal nature of the species in the presence of intrasexual competition (with greater risks of falling for larger individuals and increased maneuverability for smaller individuals). Nonetheless, as the males'

cheliped develops larger than the females', this suggests that these structures are associated with sexual selection - a confrontation, grasping, or courtship advantage of males, especially in a vertical habitat. The female cheliped is probably used in intraspecific competition (food, spatial resources) in complex mangrove environments, and the male abdomen may be associated with sperm competition and gonopod protection (positive allometry in the male abdomen). While we have provided evidence of sexual dimorphism in cheliped characters, behavioral studies may be conducted to fully document the nature of dimorphism and its evolutionary drivers (combat display, mating, etc.). This study may guide future field observations and experiments on the crab's mangrove dynamics, and potentially, conservation initiatives for the species and its habitat.

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