

Research Article

Allometric Growth of the Freshwater Crab *Potamon algeriense* (Bott, 1967) (Decapoda, Brachyura, Potamidae) in Oued Zegzel, a Mountain Stream, in the Northeast of Morocco

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Received 30 January 2019; Revised 4 April 2019; Accepted 27 June 2019; Published 1 August 2019

Academic Editor: Thomas Iliffe

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A morphometric study has been carried out for the first time on the population of the freshwater crab *Potamon algeriense* inhabiting Oued Zegzel, a tributary of the Lower Moulouya River, in the northeast of Morocco. Crabs were collected monthly over one year (October 2017 to September 2018) by excavating burrows and searching under blocks. A total of 669 crabs were obtained, 291 females and 378 males. Regression analysis was performed among carapace width (CW), as the reference dimension, and wet weight (WW), carapace length (CL), length and width of abdomen (AL and AW), and length and width of the cheliped (ChL and ChW) were chosen as dependent variables, using the allometric method. Based on Somerton's technique, the onset of sexual maturity was estimated to occur at around 27mm CW for males and 32mm CW for females. The growth patterns recorded for *P. algeriense* are associated with the species reproductive strategy, i.e., preparation of body parts involved in female acquisition and egg incubation, like the male cheliped and the female abdomen, respectively. Among the 291 females sampled, 10.20% were left-handed and 89.80% were right-handed, while among the 378 males examined, 10.32% were left-handed and 89.68% were right-handed. It was concluded that the cheliped width and the abdominal width of *P. algeriense* are the morphometric variables most appropriate to estimate the size at the beginning of the sexual maturity for males and females of this species, respectively.

1. Introduction

Allometry, which is the oldest of the approaches and still widely applied in biology, is a well-known phenomenon concerning the study of the relationship between the size and function of organs of the body and growth or size of the whole body [1]. Allometry is often divided into three principal types: ontogenetic (when shape changes with ontogenetic stage or age), static (when shape correlates with size independently of age), and evolutionary (when shape correlates with size among species) [2].

Relative growth in brachyuran crabs has been commonly studied since the earlier decades of the century [3–5], but only in more recent work were these allometric patterns reviewed for the group [6]. It can be used in species identification [7, 8]

and to establish sexual maturity as well as contributing to the identification of “handedness” occurrence [9–12].

Size at which sexual maturity is attained is important in crab life history, because both age and size at maturity are associated with a species' reproductive output [13]. An assemblage of morphological, physiological, and behavioral changes through which immature individuals become able to produce and transfer gametes marks the onset of maturity [14].

The growth pattern of some specific body parts such as chelipeds, abdomen, and gonopods shows variations in the degree of allometry during the course of development, which may coincide with gonad maturation, providing an important estimate for the size at which these animals are ready for reproduction [15, 16].

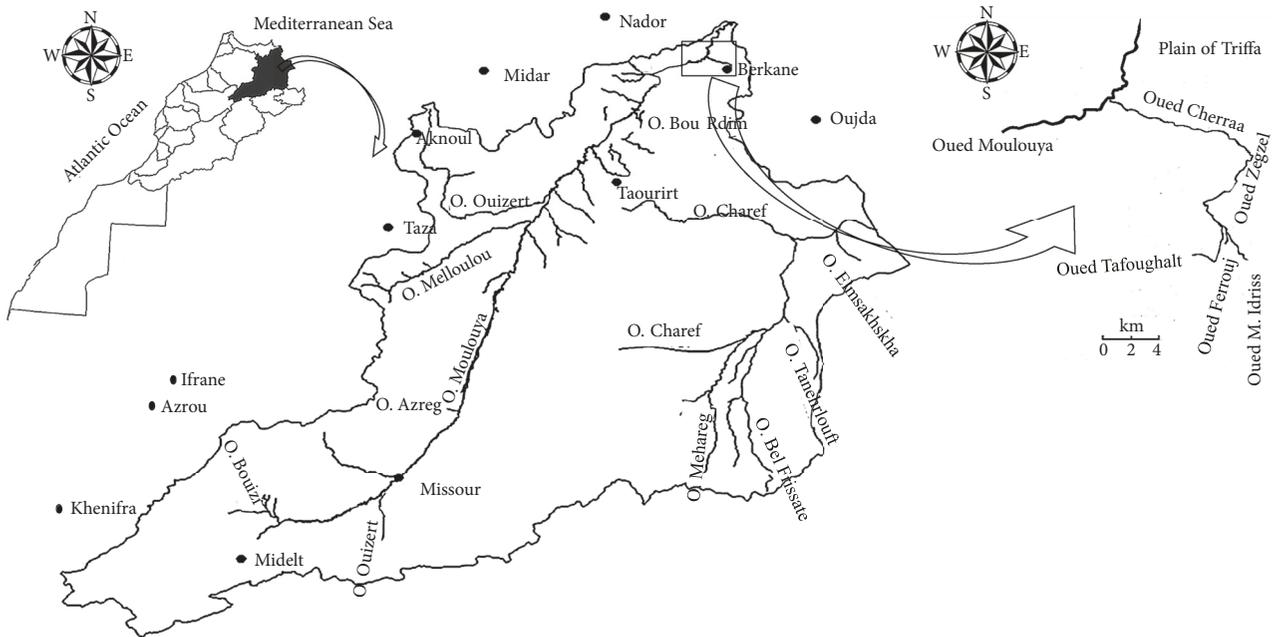


FIGURE 1: Localization of the study area, Oued Zegzel, Morocco.

Crabs of the infraorder Brachyura are among the most diverse groups of crustaceans with more than 7000 described species in 98 families, occurring in various habitats: marine, freshwater, and terrestrial [17–20].

Freshwater crabs are found exclusively in freshwater or terrestrial ecosystems and never enter brackish or marine waters for reproduction [21]. Approximately, 1400 species are known with additional species being regularly discovered reviewed in [16, 17].

Potamon algeriense belongs to the family of the Potamidae which is the largest of all freshwater crab families and comprises 95 genera and over 505 species distributed throughout the southern Palaearctic and Oriental zoogeographical regions from Morocco as far east as Japan and as far south as Indonesia [21, 22]. In fact, it is the only Maghrebian representative of this family. The species could be found exclusively in three countries: Morocco, Algeria, and Tunisia [23]. In Morocco, the species has been reported from the north in the watershed of the Oued Laou near Chefchaouen, from the northeast in watershed of Moulouya, and from the Middle Atlas in the Oued Oum er Rbia watershed near Khenifra.

Despite the wide distribution of *P. algeriense*, its occurrence drastically declined during the last two decades due to human impacts (sewage, industrial waste, and agricultural pesticides). Consequently, *P. algeriense* is included in the IUCN red list as least concern species. Comprehensive biological information about this species is incomplete, as previous studies have only treated its geographic distribution and taxonomic status [24].

This study aims to analyze for the first time the relative growth of *P. algeriense*, inhabiting Oued Zegzel, a mountain

stream, in the northeast of Morocco, focusing on the morphometric relationships between carapace width and the size of other body components. Through the analyses of these parameters, it is possible to characterize the allometry levels and to make inferences about the sizes at which males and females reach sexual maturity, thus evidencing their puberty molt. The frequency of handedness (major cheliped) in each sex and its growth are also studied.

2. Material and Methods

2.1. Study Area. The study was performed in Oued Zegzel ($34^{\circ} 50' 29.4''$ N, $2^{\circ} 21' 19.8''$ W), a tributary of the Lower Moulouya River, in the northeast of Morocco (Figure 1). The region is characterized by a Mediterranean climate.

Shrublands that mark the study area were composed mainly of *Nerium oleander*, *Tamarix africana*, *Salix pedicellata*, *Rubus ulmifolius*, *Rubus ulmifolius*, and *Crataegus monogyna*. Thus, a group of submerged plants (*Nasturtium officinale*, *Veronica catenata*, and *Scrophularia aquatica*) is individualized on the banks of the Oued, while in the central waters *Potamogeton natans* or *Potamogeton pectinatus* are often overgrown.

2.2. Crab Sampling and Measurement. The crabs were collected monthly over one year (October 2017 to September 2018) by excavating burrows and searching under blocks. The crabs could be caught by plunging an arm into the burrow. However, as the depth of the burrow can reach more than 50 cm it was not always possible to catch the crabs before they escaped to the greater depths. Consequently, the individuals assessed here represent a random sample.

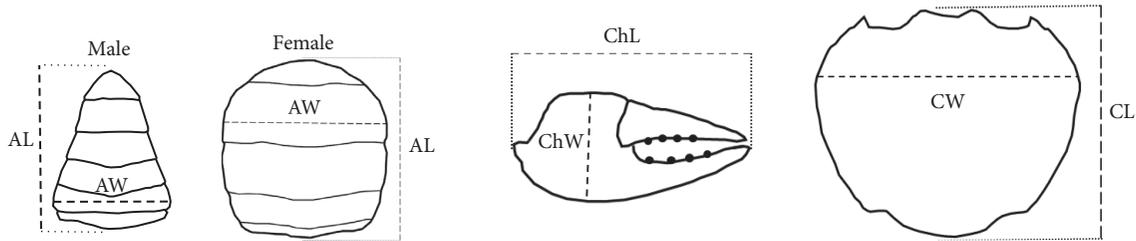


FIGURE 2: Position of measurements in *Potamon algeriense*. CW: carapace width; CL: carapace length; ChL: cheliped length; ChW: cheliped width; AW: abdomen width; AL: abdomen length.

All measurements were made to the nearest (0.01 mm) using a vernier caliper: carapace width (CW) used as the reference dimension, measured at the widest part; carapace length (CL); abdominal width (AW); abdominal length (AL) (taken from the widest segment); and cheliped width (ChW) and length (ChL). The position of these measurements is indicated in Figure 2.

The specimens were also weighted, wet weight (WW), using an analytical pocket balance to the nearest 0.01 g.

Sex determination was based on the morphology of the abdomen (considerably wider in females than in males) and the number of pleopods. The presence of eggs and juvenile in the abdomen of females was also recorded. Chelipeds were designated as major or minor by their size.

Only complete and sexed specimens were used in this study.

2.3. Statistical Analyses. Relative growth was examined following the method of Huxley [25] to describe most patterns of relative growth in animals in general and in brachyuran crabs especially [15, 26, 27].

The logarithmic transformation $\log Y = \log a + b \log X$ was linearized from the traditional allometric growth equation $Y = aX^b$, where (Y) and (X) are morphological dimensions and (a) and (b) are growth constraints. The computer programs Mature I and II [28, 29] were used to delimit the size at which 50% of the individuals reached maturity.

Analysis of covariance (ANCOVA) was performed to compare slopes and intercepts of the obtained regressions within each allometric relationship and between sexes [30, 31]. Carapace width (CW) was chosen as the reference dimension (independent variable), since this has been widely used for recent studies on decapods including the Potamidae [32].

Departures from isometry ($H_0: b = 3$) for wet weight and ($H_0: b = 1$) for the other measurements were tested using a Student's *t*-test on the obtained slope values ($\alpha = 0.05$) [31]. If $b > 1$, then the dimension (Y) increases in size relatively more rapidly than the reference dimension (X) does and growth is said to be positively allometric. A condition of $b < 1$ indicates negative allometry, and $b = 1$ indicates a condition of isometry that means there is no change in the relative shape with increasing size. Handedness between sexes was analyzed using a two-tailed χ^2 test to determine whether the frequencies of right- and left-handed males were similar.

3. Results

A total of 669 specimens of *P. algeriense* were collected, and their CW sizes ranged from 5.40 to 26.9 mm for juvenile males (N=323), from 27 to 60.30 mm CW for adult males (N=55), 11.80 to 31.9 mm for juvenile females (N=158), and 32 to 50.10 mm for adult females (N=133).

According to Somerton's technique [28, 29], the relationships that best indicate the change in the allometric coefficient between juveniles and adults phase and the distinction between male and female growth are CW vs. AW for females and CW vs. ChW for males. In fact, the size at which 50% of the females reached maturity is 32 mm of CW based on the CW vs. AW relationship. At this size, females present a noticeable growth of the abdomen width resulting in an increase of the allometric coefficient (1.38). On the other hand, the relationship between ChW and CW in males showed a remarkable increase of the cheliped width soon after the puberty molt, which may occur in crabs of approximately 27 mm CW, resulting in an increase of the allometric coefficient (1.38) (Figure 3).

The regressions parameters (slope and intercept) and the relative growth equations of the morphometric relationships obtained for both sexes in juveniles and adults, and their departures from isometry (*t*-test) are shown in Tables 1 and 2, respectively.

The relationships of WW, AW, ChW, and ChL with CW as an independent variable indicate that there are significant differences in growth between juveniles and adults in both sexes.

Concerning handedness, right-handed considerably outnumbered left-handed ones; from 669 crabs examined, 10.31% (69 of 669) had the left propodus and dactylus enlarged (left-handed) and 89.69% (600 of 669) had the right propodus and dactylus enlarged (right-handed). No homochealous individuals were found. Among the 291 females sampled, 10.20% (30 of 291) were left-handed and 89.80% (261 of 291) were right-handed, while among the 378 males examined, 10.32% (39 of 378) were left-handed and 89.68% (339 of 669) were right-handed. No significant difference in handedness between sexes was observed ($\chi^2 = 4.16$; $P > 0.05$).

4. Discussion

In crustaceans, some aspects such as gonadal development, presence of ovigerous females, and morphometric data are

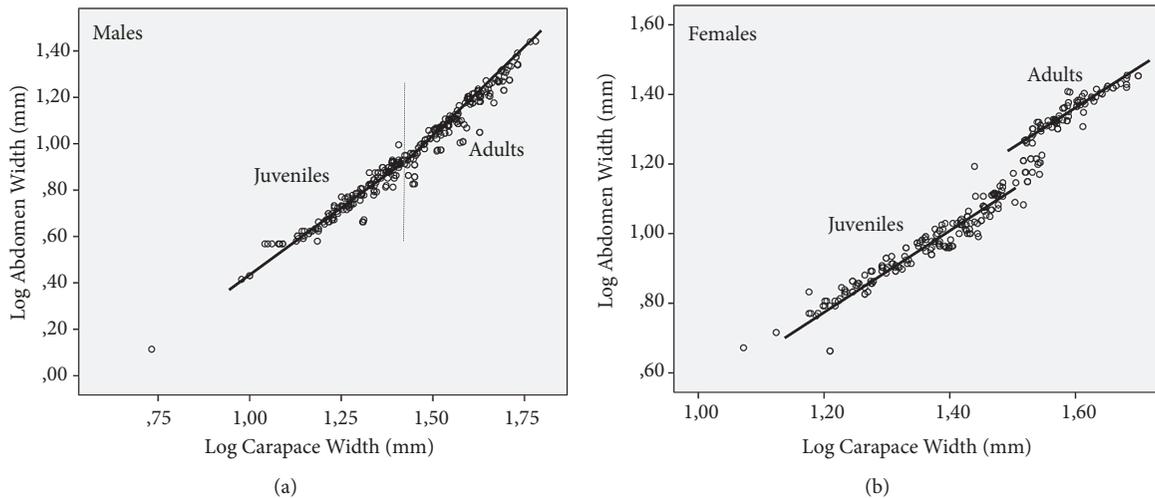


FIGURE 3: Dispersion points and adjusted curve of the relationships: (a) ChW vs. CW; (b) AW vs. CW for males and females of *Potamon algeriense*, respectively.

used to calculate the mean size at the onset of sexual maturity. In fact, the estimation of puberty size may vary according to the body part analyzed. In the present study, the mean size of maturity was calculated according to the relationships of ChW vs. CW and AW vs. CW for males and females, respectively. These relationships provide the best fit of sexual maturity of *P. algeriense*. Gherardi and Micheli [33] remarked that freshwater crabs mate during the intermolt phase when the male grabs the female within its chelipeds, pointing out the importance of chelipeds for the reproductive process and confirming the choice of this body part as the reference for the analysis of size at sexual maturity.

The patterns of relative growth by abdomen, cheliped, and heterochely in *P. algeriense* follow those already remarked in most crab species studied so far [6], and the adaptive value of the allometry exhibited by these organs has already been largely discussed [6, 10, 15, 34]. In this context, the results for relative growth in the *P. algeriense* female abdomen are as expected, with the abdomen width still growing during the adult phase. In fact, this phenomenon could provide an extra space for the fixation of eggs on the setose pleopods and thus act as an incubation chamber for the developing eggs, which is similar to the general pattern of female abdominal growth of most freshwater, marine, and terrestrial crabs [6, 35, 36].

On the other hand, Hartnoll [36] noted that the male abdomen forms a single protecting cover for the gonopods. Finney and Abele [10] are of the opinion that abdomen width growth in males does not have any reproductive benefits. Thereby, after the complete gonopod development, the abdomen growth assumes the isometric, or even a negative, allometry pattern, as previously observed for other freshwater crabs such as the potamid *Potamon potamios palestinensis* [33] and the *P. fluviatile* [37]; the trichodactylids *Dilocarcinus pagei*, *Sylviocarcinus australis* [38], and *Trichodactylus fluviatilis* [39].

In the literature, besides the abdomen width, there are frequent citations about the importance of morphometry and

growth of cheliped dimensions (generally cheliped width) to characterize a possible sexual dimorphism and maturation in crabs [6, 34].

The size at the onset of sexual maturity of *P. algeriense* from Oued Zegzel was greater in females than in males, and similar results have been found in the populations of *Mithraculus forceps*, *Mithrax tortugae*, and *Grapsus adscensionis* [40–42]. On the contrary, the onset of sexual maturity for the populations of *T. fluviatilis* and *D. pagei* [39, 43] from south-eastern Brazil occurred at the same size interval, as estimated based on chelipeds and abdomen growth for males and females, respectively. Delayed sexual maturity could allow females of *P. algeriense* to live longer, grow larger, and therefore have higher rate of fecundity [44]. Furthermore, the size at onset of maturity depends on multitude of exogenous factors, such as temperature and/or food availability. Therefore, it is not a constant character and may vary in different populations of the same species [45].

Marine [15] and freshwater [46, 47] crabs show the well-known, although not well-understood [48], phenomenon of cheliped asymmetry. Researchers sometimes seem to discard this asymmetry focusing mainly on investigating the functional use of the large cheliped.

Potamon algeriense is heterochelous, with right-handedness in both sexes being the most dominant (89.68% of males and 89.80% of females). According to Scalici and Gherardi [48], this pattern can be found in most brachyuran species that present handedness, as previously reported for some potamonautid crab species (for details see [47]), as well as marine crabs (e.g., [49, 50]).

The cheliped of males is larger than that of the females of the same size, suggesting its behavioral utilization, including sexual signaling during courtship, intermale fighting for the access of females, and the defense of resources such as food and territories [15, 33, 51–57]. Males with larger cheliped might increase the likelihood of winning during agonistic interactions for access to receptive females, considering that

TABLE 1: Results of allometric relationships studied in *Potamon algeriense*: analyses of covariance (ANCOVA) carried out to test slope and intercept for both sexes that indicate the beginning of maturity in relation to body size. Significance was indicated by an asterisk.

Relationship	Morphometric measure	Factor: Sex/maturity	Parameter	F
Females	WW	Juveniles vs. Adults	Slope	24.157*
			Intercept	32.452*
	CL	Juveniles vs. Adults	Slope	4.873
			Intercept	6.486
	AW	Juveniles vs. Adults	Slope	789.149*
			Intercept	848.941*
	AL	Juveniles vs. Adults	Slope	4.623
			Intercept	3.453
	ChW	Juveniles vs. Adults	Slope	468.157*
			Intercept	518.614*
	ChL	Juveniles vs. Adults	Slope	432.181*
			Intercept	495.214*
Males	WW	Juveniles vs. Adults	Slope	3.121
			Intercept	2.867
	CL	Juveniles vs. Adults	Slope	12.342
			Intercept	18.658
	AW	Juveniles vs. Adults	Slope	2.032
			Intercept	1.091
	AL	Juveniles vs. Adults	Slope	1.456
			Intercept	1.017
	ChW	Juveniles vs. Adults	Slope	761.646*
			Intercept	803.558*
	ChL	Juveniles vs. Adults	Slope	698.154*
			Intercept	645.167*
Females/males	WW	Females vs. Males	Slope	5.314
			Intercept	6.185
	CL	Females vs. Males	Slope	3.194
			Intercept	4.684
	AW	Females vs. Males	Slope	64.235*
			Intercept	61.489*
	AL	Females vs. Males	Slope	4.135
			Intercept	5.354
	ChW	Females vs. Males	Slope	82.318*
			Intercept	84.343*
	ChL	Females vs. Males	Slope	75.156*
			Intercept	76.685*

*P < 0.05

WW: wet weight; CL: carapace length; AW: abdomen width; AL: abdomen length; ChW: cheliped width; ChL: cheliped length.

dominance in crabs is largely determined both by body size (described earlier) and by relative cheliped size [6, 58, 59].

The handedness recorded for females is not a rare situation for freshwater crabs, as it was previously reported for some other species such as *Candidiopotamon rathbunae* in Taiwan [56] and *T. fluviatilis* [39] and *Potamonautes warreni* in South Africa [47]. The use of large cheliped for fights has also been proposed for ovigerous females. In fact, freshwater crabs are well known to be direct developers with long incubation periods (for up to three months in *Potamonautes sidneyi*) and extensive maternal care [51]. Consequently,

females with larger cheliped have a better chance of defending the developing young against attacks from predators [56].

5. Conclusions

Estimates for the beginning of morphological sexual maturity may provide various results when different body structures are studied, or even when different mathematical methods are applied. Thereby, bioassays for mating are suggested for assessing the importance of body parts as a reference to estimate the beginning of sexual maturity for crabs, as

TABLE 2: Regression analyses of morphometric data of *Potamon algeriense*. Carapace width (CW) was used as the independent variable.

Variable	Sex/Stage	N	Power Equation $Y=a.X^b$	$\log Y = \log a + b \log X$	R^2	$t (b=1)$	Allometry level*
WW	JM	187	$WW=9.772CW^{2.87}$	$\log WW=2.87 \log CW+0.990$	0.961	2.91	=
	AM	191	$WW=3.890CW^{3.17}$	$\log WW=3.17 \log CW+0.590$	0.988	3.67*	+
	JF	181	$WW=5.129CW^{2.95}$	$\log WW=2.95 \log CW+0.710$	0.984	3.05	=
	AF	110	$WW=8.710CW^{2.81}$	$\log WW=2.81 \log CW+0.940$	0.957	2.89	=
CL	JM	187	$CL=1.071CW^{1.02}$	$\log CL=1.02 \log CW+0.029$	0.993	1.09	=
	AM	191	$CL=1.015CW^{1.04}$	$\log CL=1.04 \log CW+0.006$	0.991	1.14	=
	JF	181	$CL=0.955CW^{0.97}$	$\log CL=0.97 \log CW-0.020$	0.993	0.94	=
	AF	110	$CL=1.230CW^{0.90}$	$\log CL=0.90 \log CW+0.090$	0.982	0.89	=
AW	JM	187	$AW=0.602CW^{0.99}$	$\log AW=0.99 \log CW-0.220$	0.972	1.01	=
	AM	191	$AW=0.741CW^{0.93}$	$\log AW=0.93 \log CW-0.130$	0.969	0.72*	-
	JF	181	$AW=0.275CW^{1.12}$	$\log AW=1.12 \log CW-0.560$	0.910	1.12	=
	AF	110	$AW=0.100CW^{1.47}$	$\log AW=1.47 \log CW-1.000$	0.813	4.65*	+
AL	JM	187	$AL=0.436CW^{1.00}$	$\log AL=1.00 \log CW-0.361$	0.958	1.00	=
	AM	191	$AL=0.602CW^{0.89}$	$\log AL=0.89 \log CW-0.220$	0.927	0.95	=
	JF	181	$AL=0.309CW^{1.19}$	$\log AL=1.19 \log CW-0.510$	0.939	1.15	=
	AF	110	$AL=0.380CW^{1.15}$	$\log AL=1.15 \log CW-0.420$	0.887	1.10	=
ChW	JM	187	$ChW=0.741CW^{1.03}$	$\log ChW=1.03 \log CW-0.130$	0.926	1.02	=
	AM	191	$ChW=0.245CW^{1.38}$	$\log ChW=1.8 \log CW-0.611$	0.913	9.89*	+
	JF	181	$ChW=0.182CW^{1.17}$	$\log ChW=1.17 \log CW-0.740$	0.908	1.17	=
	AF	110	$ChW=0.097CW^{1.36}$	$\log ChW=1.36 \log CW-1.013$	0.797	7.34*	+
ChL	JM	187	$ChL=0.213CW^{1.17}$	$\log ChL=1.17 \log CW-0.672$	0.952	1.16	=
	AM	191	$ChL=0.067CW^{1.52}$	$\log ChL=1.52 \log CW-1.174$	0.945	8.56*	+
	JF	181	$ChL=0.501CW^{1.11}$	$\log ChL=1.11 \log CW-0.300$	0.962	1.10	=
	AF	110	$ChL=0.380CW^{1.20}$	$\log ChL=1.20 \log CW-0.420$	0.876	8.20*	+

* t -test; $\alpha = 0.05$.

WW: wet weight; CL: carapace length; AW: abdomen width; AL: abdomen length; ChW: cheliped width; ChL: cheliped length; JM: juvenile males; AM: adult males; JF= juvenile females; AF: adult females; N: number of specimens.

(=) isometry; (+) positive allometry; (-) negative allometry.

observed for *P. algeriense*. In fact the exaggeration of body parts relevant for reproduction, such as those listed here (abdomen width and cheliped size), before or at the onset of sexual maturity is considered an adaptation for increasing reproductive output (e.g., in females) or mating success (e.g., in males), allowing individuals to optimize fitness over their lifetime.

Data Availability

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

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this work.

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