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Sexual size dimorphisms of the pleons and chelipeds of the varunid crab *Gaetice depressus* (Decapoda: Brachyura: Varunidae)

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Abstract

Using allometric growth analyses, we investigated the sexual size dimorphisms of the pleons and chelipeds of the varunid crab *Gaetice depressus*, wherein the carapace width (CW) values for females and males were 4.11–21.22 and 4.01–27.68 mm, respectively. Pleons were larger in females, which showed positive allometric growth, than in males, where negative allometric growth was observed. In females, three distinct groups based on pleon size were identified: small-sized individuals with <4.11–9.05 mm CW and narrow pleons, medium-sized individuals with 10.39–10.71 mm CW and intermediate-sized pleons, and large-sized individuals with >10.52–21.22 mm CW and wide pleons. These three groups correspond to the following classification: immature, subadult and mature crabs. As for the chelipeds, the females showed positive allometric growth or isometric growth across body sizes. In males, the isomeric growth in cheliped propodus length and merus length shifted to a positive allometric growth at 9.62–10.58 mm CW, whereas the cheliped propodus width showed positive allometric growth across body sizes. Overall, male chelipeds showed stronger positive allometric growth than the female chelipeds, and the sexual size dimorphism of chelipeds was evident after ~10–11 mm CW was reached, during which morphological sexual maturity may occur.

Keywords: allometric growth; sexual selection; secondary sexual characteristics; sexual maturity

Introduction

Brachyuran crabs develop secondary sexual structures, such as large chelipeds for courtship in males and wide pleons for egg incubation in females (Davie et al. 2015). In crabs, secondary sexual characteristics appear in early post-settlement instars (Luppi et al. 2002; Guimarães and Negreiros-Fransozo 2005; Guerao and Rottlant 2009; Hirose et al. 2010) and are more pronounced after the pubertal moult. To elucidate the sizes of pleons and chelipeds at the onset of sexual maturity, researchers have measured the growth of these structures relative to a reference body dimension (Hartnoll 1974, 1978; McLay 2015).

The varunid crab *Gaetice depressus* (De Hann 1833) (Decapoda: Brachyura: Varunidae) inhabits intertidal cobble and boulder shores from Hokkaido to Hong Kong in East Asia (Sakai 1976). The ontogeny of the sexual size dimorphisms of the pleons and chelipeds in *G. depressus* has been investigated based on the percent proportions of pleon and cheliped sizes to a reference body dimension (i.e. carapace width, CW) of crabs reared in a laboratory from first instar with ~2 mm CW to tenth (mainly eighth and ninth) instar with ~10–11 mm CW (Hamasaki et al. 2024). To infer the effects of bopyrid isopod infestation on the morphology of field-caught *G. depressus* with ~6–24 mm CW, Corral et al. (2019) applied linear regression equations to analyse the relationships between the following body dimensions: CW and cheliped propodus width in males and CW and pleon width (PW) in males and females. Sakai (2019) also determined the percent proportion of PW to the thoracic sternum width of field-caught female and male *G. depressus* with ~5–25 mm CW to assess crab size at the onset of sexual maturity; the results showed constant PW proportions in males, whereas a linear increase in PW proportions was observed up to maturity in females.

In *G. depressus*, sexual size dimorphism of chelipeds across body sizes is largely unknown. Furthermore, allometric growth analysis, a method commonly used to study the degree of sexual size dimorphism in decapod crustaceans (Hartnoll 1974, 1978; McLay 2015), has not yet been applied to examine this species. Therefore, we aimed to assess the sexual size dimorphisms of the pleons and chelipeds of *G. depressus* using allometric growth analysis, as well as elucidate the crab size at the onset of sexual maturity.

Materials and Methods

Crab specimens

We collected 30 non-ovigerous females and 30 males one spring tide during breeding season (2 June 2022) from an intertidal cobble and boulder shore (34°58′N, 139°46′E) of the Boso Peninsula, Japan. The sex of the crabs was determined based on the width of the pleon. The collected specimens were transported to a laboratory at the Tokyo University of Marine Science and Technology, Tokyo, Japan, and stored in a freezer at −20 °C. In addition, we used exuviae or specimens obtained from eight females and five males reared sequentially from first to eighth or tenth instar during our previous study (Hamasaki et al. 2024). To avoid pseudoreplication by taking measurements from exuviae or crab specimens obtained from the same individual, we arbitrarily selected one exuvia or crab specimen with >~4 mm CW from the eight females and five males. This criterion was used because *G. depressus* juveniles grow faster in CW than in carapace length up to ~4 mm CW, beyond which the CW growth rate stabilises (Hamasaki et al. 2024).

Crab measurements

We obtained the following five body dimensions from the exuviae and crab specimens (see Fig. 1 in Hamasaki et al. 2024): 1) CW, 2) width of the fifth pleonal somite (PW), 3) cheliped propodus length (CPL), 4) cheliped propodus width (CPW) and 5) cheliped merus length (CML). For the laboratory-reared crabs, measurements were obtained from intact body parts using a stereomicroscope equipped with a digital camera and image analysis system (Nikon Digital Sight and NIS-Elements Software, Nikon Corp., Tokyo, Japan), and the measurements were recorded to the nearest 0.01 mm. For the field-caught crabs, measurements were obtained using a digital calliper. Both chelipeds were measured, and the maximum size of either the right or left cheliped was used for analysis.

Statistical analysis

Statistical analyses were performed using R statistical software (R4.3.2; R Core Team 2023) at the 5% significance level. The sexual size dimorphisms of the pleons and chelipeds were assessed using allometric growth analysis. The growth of body parts relative to a reference (i.e. CW) was examined using the following allometric growth equation (Huxley 1932): $y = ax^b$, where x is the CW, y is another body dimension (PW, CPL, CPW or CML), b is the allometric growth coefficient and a is the initial growth constant. The relative growth rates are defined as follows: $b > 1$ indicates positive allometric growth, or faster growth of y than x; $b = 1$ indicates isometric growth, or the same growth rates for y and x; and $b < 1$ indicates negative allometric growth, or slower growth of y than x.

To infer changes in the relative growth rates of pleons and chelipeds, we performed piecewise regression analyses of the log-transformed allometric growth equation ($\ln y = \ln a + b \ln x$) using the *segmented* function of the segmented package (Muggeo 2017). Three distinct groups based on PW were observed in females, and the groups consisting of individuals with narrow and wide pleons were subjected to analysis; the three females with intermediate-sized pleons were excluded. To avoid model overfitting, we limited the maximum number of changes in the relative growth rates to one based on the scatter plots between the log-transformed variables. Piecewise linear regression models without and with a breakpoint (BP) were evaluated using the corrected Bayesian information criterion (BICc) (Schwarz 1978; McQuarrie 1999), which was generated by the *BICc* function of the greybox package (Svetunkov and Sagaert 2023). ΔBICc (BICc – BICc lower) between the models with and without BP was subsequently calculated. The model with a lower BICc value was selected as the better model, whereas the conservative model without BP was selected when ΔBICc was ≤2, indicating that the models were equivalent (Kass and Raftery 1995; Raftery 1995). The statistical significance of the regression equations was evaluated using an F-test. The relative growth patterns were determined according to the 95 % confidence intervals of the allometric growth coefficient estimates.

Results

Fig. 1 shows the relationships between CW and other body dimensions. The CW values for the females and males were 4.11–21.22 and 4.01–27.68 mm, respectively. Table 1 shows the BICc, ΔBICc and adjusted R^2 values of the corresponding log-transformed allometric growth models, and Table 2 summarises the coefficient estimates of the selected models.

In females, three distinct groups based on pleon size were found: 1) small-sized individuals with <4.11–9.05 mm CW and narrow pleons, 2) medium-sized individuals with 10.39–10.71 mm CW and intermediate-sized pleons and 3) large-sized individuals with >10.52–21.22 mm CW and wide pleons. For the first and third groups (small- and large-sized individuals), the model without BP was selected; moreover, PW showed positive allometric

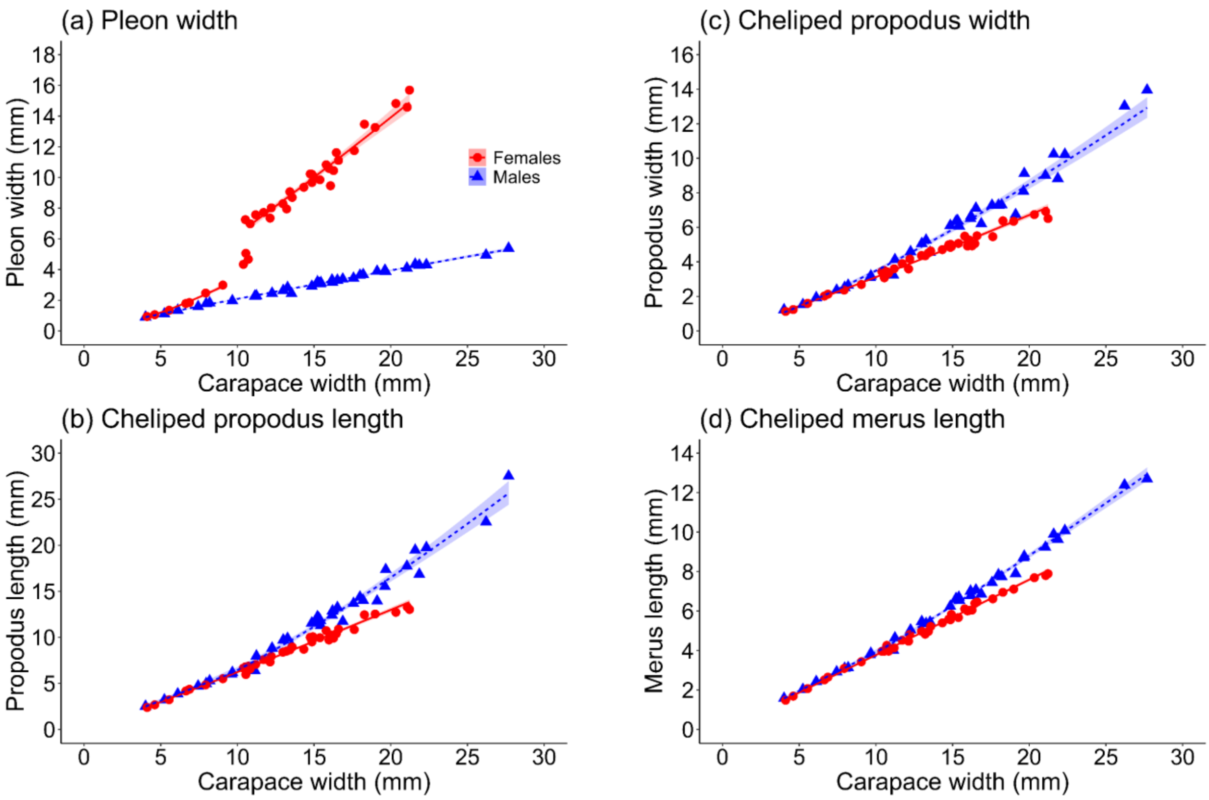

Fig. 1. Growth in pleon width (a), cheliped propodus length (b), cheliped propodus width (c), and cheliped merus length (d) relative to carapace width in female and male *Gaetice depressus*. Regression curves with 95 % confidence bands were drawn based on the allometric growth equations given in Table 2.

Table 1. Corrected Bayesian information criterion (BICc) and adjusted R^2 values of the log-transformed linear regression models (ln*y* = ln*a* + *b*ln*x*) with no breakpoint (BP) (0) and with one BP (1) for evaluating the allometric growth between carapace width (*x*) and four other body dimensions (*y*) of female and male *Gaetice depressus*. PW, pleon width; CPL, cheliped propodus length; CPW, cheliped propodus width; CML, cheliped merus length.

Dimensions	Sex	BP	BICc	ΔBICc	Adjusted R^2
PW	Small-sized female	0	−21.79	0.00	0.9913
		1	−12.89	8.90	0.9976
	Large-sized female	0	−83.22	0.00	0.9518
		1	−81.81	1.40	0.9599
	Male	0	−131.40	0.00	0.9940
		1	−123.69	7.71	0.9938
CPL	Female	0	−132.79	0.00	0.9916
		1	−129.11	3.68	0.9922
	Male	0	−81.82	4.53	0.9849
		1	−86.34	0.00	0.9890
CPW	Female	0	−117.62	0.86	0.9886
		1	−118.48	0.00	0.9906
	Male	0	−76.40	0.00	0.9836
		1	−75.21	1.18	0.9859
CML	Female	0	−173.91	0.30	0.9968
		1	−174.21	0.00	0.9974
	Male	0	−127.85	7.45	0.9948
		1	−135.30	0.00	0.9965

Table 2. Coefficient estimates with 95% confidence interval (CI) of the log-transformed linear regression models (ln*y* = ln*a* + *b*ln*x*) with one segment but without a breakpoint (BP) or with two segments with a BP for evaluating the allometric growth between carapace width (*x*) and four other body dimensions (*y*) of female and male *Gaetice depressus*. PW, pleon width; CPL, cheliped propodus length; CPW, cheliped propodus width; CML, cheliped merus length. The BP values in parentheses in the lowermost row for CPL and CML represent the antilogarithmic values in millimetres.

Dimension	Sex	N	Model segment	Coefficient estimate							F	df	p
				Intercept	Slope	95 % CI		BP	95 % CI				
PW	Small-sized female	7	1	−2.2116	1.4883	1.3419	1.6347	-	-	-	682.7	1, 5	<0.0001
	Large-sized female	28	1	−0.7876	1.1417	1.0402	1.2433	-	-	-	534.5	1, 26	<0.0001
	Male	34	1	−1.3787	0.9184	0.8932	0.9437	-	-	-	5493	1, 32	<0.0001
CPL	Female	38	1	−0.6084	1.0590	1.0264	1.0915	-	-	-	4366	1, 36	<0.0001
	Male	35	1	−0.5085	1.0243	0.8610	1.1877	2.2638	1.9849	2.5428	1020.5	3, 31	<0.0001
			2	−1.2609	1.3567	1.2653	1.4481	(9.62)	(7.28)	(12.71)			
CPW	Female	38	1	−1.4114	1.1068	1.0671	1.1465	-	-	-	3119	1, 36	<0.0001
	Male	35	1	−1.7125	1.2863	1.2283	1.3443	-	-	-	2037	1, 33	<0.0001
CML	Female	38	1	−0.9962	1.0091	0.9902	1.0280	-	-	-	11700	1, 36	<0.0001
	Male	35	1	−0.9403	1.0020	0.9284	1.0755	2.3591	2.1075	2.6107	3271.1	3, 31	<0.0001
			2	−1.3650	1.1820	1.1320	1.2319	(10.58)	(8.23)	(13.61)			

growth, being stronger in the small-sized individuals (*b* = 1.488 (95 % confidence interval, 1.342–1.635)) than in the large-sized ones (*b* = 1.142 (1.040–1.243)). The model without BP was also selected for male PW, which showed negative allometric growth (*b* = 0.918 (0.893–0.944)).

For female chelipeds, the model without BP was selected. In females, CPL and CPW showed positive allometric growth (*b* = 1.059 (1.026–1.092) and 1.107 (1.067–1.147), respectively), whereas CML exhibited isometric growth (*b* = 1.009 (0.990–1.028)). In males, the models with BP values of 9.62 mm (7.28–12.71 mm) and 10.58 mm (8.23–13.61 mm) were selected for CPL and CML, respectively. The CPL and CML in males initially showed isometric growth (*b* = 1.024 (0.861–1.188) and 1.002 (0.928–1.076), respectively) and subsequently showed positive allometric growth (*b* = 1.357 (1.265–1.448) and 1.182 (1.132–1.232), respectively). The CPW in males showed positive allometric growth without BP (*b* = 1.286 (1.228–1.344)).

Discussion

Corral et al. (2019) assessed the effects of bopyrid isopod infestation on the morphology of *G. depressus* collected from the intertidal shore (34°00′N, 135°09′E) of the Kii Peninsula, Japan. They used linear regression equations to analyse the relationships between CW and CPW in males, and

CW and PW in males and females, and found that only PW was marginally smaller in bopyrid-infested males than in uninfested males. In the present study, we did not examine bopyrid isopod infestation in *G. depressus* specimens due to the difficulty of visually detecting parasites under the carapace and the low prevalence of 3.6 % in the Kii Peninsula population (Corral et al. 2019). If our *G. depressus* specimens were infested with the bopyrid isopod, the impact on the allometric growth analyses would be negligible.

In *G. depressus*, the proportion of PW to CW is similar in both sexes up to ~4 mm CW, beyond which sexual size dimorphism of pleons begins to appear (Hamasaki et al. 2024). Our allometric growth analyses showed that at ~4–28 mm CW, the pleons were larger in females, which showed positive allometric growth, than in males, which exhibited negative allometric growth. In females, three distinct groups based on pleon size were identified (Fig. 1a): 1) small-sized individuals with narrow pleons, 2) medium-sized individuals with intermediate-sized pleons and 3) large-sized individuals with wide pleons. Sakai (2019) also recognised three female groups in *G. depressus* collected from the intertidal shore (37°18′N, 137°14′E) of the Noto Peninsula, Japan: immature crabs with pleons shaped like an isosceles triangle, subadult crabs with pleons not fully covering the thoracis sternites 5–7, and mature crabs (including ovigerous females) with pleons fully covering the thoracic sternites 5–7. The small-, medium- and large-sized female specimens in our study correspond to the immature, subadult and mature crabs as classified by Sakai (2019).

Although we did not analyse the allometric growth of the intermediate-sized individuals given their small number, pleon development in female *G. depressus* could be inferred as follows: in the immature phase, pleons develop with strong positive allometric growth, which further increases in the subadult phase; when the mature size is reached, the pleons subsequently show a relatively weak positive allometric growth. Sakai (2019) found that immature females had ~5–11 mm CW and subadult females had ~7–17 mm CW, and the ovigerous female with 8.2 mm CW was the smallest among the specimens collected. Fukui (1988) reported the smallest ovigerous *G. depressus* female with 7.2 mm CW collected from the intertidal shore (33°41–42′N, 135°20–21′E) of the Kii Peninsula, Japan. Thus, *G. depressus* females can undergo a pubertal moult over a wide range of body sizes (i.e. ~7–17 mm). However, in the study of Corral et al. (2019), the three distinct groups could not be easily distinguished in the scatter plots between CW and PW of the large number of *G. depressus* females. If a large number of female specimens are collected in our field on the Boso Peninsula, this may result in a wide range of body sizes being recorded for subadult females. The classification system used by Sakai (2019) may be useful to distinguish between immature, subadult and mature females of *G. depressus*.

In *G. depressus*, the proportions of CPL, CPW and CML to CW are known to be larger in males than in females from first instar crabs with ~2 mm CW to crabs with ~11 mm CW (Hamasaki et al. 2024). In the present study, the sexual size dimorphism of chelipeds was also evident in *G. depressus* with ~4–28 mm CW (Fig. 1b–d). Female chelipeds showed positive allometric or isometric growth across body sizes. In males, CPL and CML initially showed isometric growth and subsequently showed positive allometric growth at 9.6–10.6 mm CW, whereas CPW showed positive allometric growth across body sizes. Overall, male chelipeds showed stronger positive allometric growth than female chelipeds, and the sexual size dimorphism of chelipeds was evident after ~10–11 mm CW was reached. *G. depressus* males sometimes use their chelipeds to grasp females during courtship, and they extend their chelipeds and spread their fingers when other crabs approach a copulating pair (Fukui 1994). Thus, larger chelipeds appear to be advantageous for males in capturing sexually receptive females. Taken together, ~10–11 mm CW may indicate morphological maturity in *G depressus* males. This finding is supported by copulation experiments showing that *G. depressus* males measuring ~9–10 mm could already mate with females (Fukui 1994, 1995).

This study highlights the sexual size dimorphisms of the pleons and chelipeds of *G. depressus* assessed through allometric growth analyses. To further deepen our knowledge of the reproductive biology of *G. depressus*, we must analyse a large sample to estimate the size at which 50 % of females reach maturity, an important life history parameter in assessing the reproductive potential of a population.

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