Heterochely and cheliped dimorphism in the porcellanid crab *Petrolisthes japonicus* (De Haan, 1849) (Decapoda: Porcellanidae)

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ABSTRACT

Cheliped dimorphism is common in decapod crustaceans, and many decapods have a pair of different-sized chelipeds, *i.e.*, one side being larger (major) than the other (minor), a phenomenon known as heterochely. Anomuran crabs from the family Porcellanidae exhibit a true crab-like body shape, with relatively large chelipeds for their body size, and they show a sexual size dimorphism of chelipeds (*i.e.*, males with larger chelipeds). However, very little is known about heterochely in porcellanid crabs. Therefore, we aim to elucidate heterochely and cheliped dimorphism in the porcellanid crab *Petrolisthes japonicus* (De Haan, 1849). We examined the laterality of the chelipeds and performed allometric growth analyses of the cheliped dimensions. Heterochely was observed in most of the specimens, and major chelipeds occurred randomly on either the right or left sides of the body, regardless of the crab size. Major and minor cheliped size of males surpassed female cheliped size, and males increased the growth of both major and minor chelipeds to the same degree during the breeding season, thereby inducing the distinct intersexual size dimorphism of the cheliped. This is probably attributable to sexual selection (*i.e.*, male–male competition). Intersexual dimorphism as an energy allocation strategy was also evident with females allocating their energy evenly to both major and minor cheliped growth without changing the chela shape; regardless of the body size, whereas males were investing more energy in major cheliped growth, resulting in wider chelae with increasing body size. Consequently, the major cheliped may have a greater role in male–male competition in *P. japonicus*.

KEYWORDS

Allometric growth, chela asymmetry, handedness, laterality, secondary sexual traits

INTRODUCTION

Cheliped dimorphism is common in decapod crustaceans, and many decapods have a pair of different-sized chelipeds, *i.e.*, one side being larger (major) than the other (minor), a phenomenon known as heterochely. Foraging, agonistic and sexual interactions have been considered important selection pressures that shape decapod cheliped size and structure (Lee, 1995; Mariappan *et al.*, 2000). In carnivorous brachyuran crabs, the major cheliped with molariform teeth is often used for crushing hard-shelled prey, while the minor cheliped with cutting teeth is used for manipulating and cutting food or grooming (Lee, 1995; Mariappan *et al.*, 2000; Masunari *et al.*, 2015). Decapod chelipeds are generally larger in males than in females, and males win competition for females by having larger chelipeds (Lee, 1995; Mariappan *et al.*, 2000; Emlen, 2008). For instance, in male fiddler crabs, either the right or left cheliped is greatly enlarged and functions as both a weapon to fight competitive males and as an ornament to court receptive females through claw-waving display (Crane, 1975; Perez *et al.*, 2012; 2015).

Anomuran crabs of the family Porcellanidae Haworth, 1825 exhibit a true crab-like body shape, with relatively large chelipeds for their body size and a well-developed pleon (Jones, 1977; Barría and González, 2008; Osawa and McLaughlin, 2010; Tudge *et al.*, 2012). They are primarily suspension feeders, trapping suspended detritus, phytoplankton and zooplankton using the long setae of their third maxillipeds (Caine, 1975; Kropp, 1981; Trager and Genin, 1993; Achituv and Pedrotti, 1999; Hollebone and Hay, 2008; McGlaun and Withers, 2012); however, they can use their chelipeds for foraging (Caine, 1975; Kropp, 1981). The chelipeds of porcellanid crabs are involved in intraspecific agonistic and sexual communications (Molenock, 1975; 1976; Baeza *et al.*, 2002). Therefore, it is likely that cheliped dimorphism occurs in porcellanid crabs.

Sexual size dimorphism of the secondary sexual characters, such as large male chelipeds and wider female pleons for incubating eggs, have been documented in some porcellanid crab species (Miranda and Mantelatto, 2010; Baeza and Asorey, 2012; Wassick *et al.*, 2017), including *Petrolisthes japonicus* (De Haan, 1849) (Hamasaki and Dan, 2021). *Petrolisthes japonicus* is common on the intertidal cobble and boulder shores of the Japanese temperate and tropical regions (Miyake, 1998). The selected sexual structures of decapod crustaceans should be costly to produce and maintain (Allen and Levinton, 2007; Wilson *et al.*, 2009; Doake *et al.*, 2010), and so the reproductive strategy of *P. japonicus* may adapt to conserve energy for developing large male chelipeds and wider female pleons during the reproductive season. In a previous study, we tested this hypothesis with allometric growth analyses for chelipeds and pleons of *P. japonicus* females and males collected over a year (Hamasaki and Dan, 2021). We selected the largest propodus length and width measurements between the right and left chelipeds as the cheliped dimension of *P. japonicus* and revealed that, in the breeding season, females allocated more energy to pleon growth while reducing cheliped growth, whereas males invested their energy in cheliped growth. Thus, our previous study highlighted the sex-specific and season-dependent resource allocation and reproductive strategies of *P. japonicus* (see Hamasaki and Dan, 2021).

However, very little is known about heterochely in porcellanid crabs. To the best of our knowledge, only Baeza and Asorey (2012) documented the laterality of the chelipeds, *i.e.*, proportions of crabs with larger chelipeds on the right side of the body in females and males of *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) and *Liopetrolisthes mitra* (Dana, 1852). In the present study, we aim to quantify heterochely and further elucidate cheliped dimorphism in *P. japonicus*. We examine the laterality of the chelipeds; then, allometric growth analyses were performed to evaluate the shape and size differences between major and minor chelipeds and quantify the intra-and intersexual dimorphism of shape and size in each cheliped type; considering the breeding and non-breeding seasons, as analyzed in our previous study (Hamasaki and Dan, 2021).

MATERIALS AND METHODS

Measurement of crabs

To investigate population ecology of *P. japonicus*, we collected 986 specimens through monthly sampling conducted from April 2008 to March 2009 in an intertidal cobble and boulder zone (34°58'N, 139°46'E) on the Boso Peninsula, Japan (Hamasaki *et al.*, 2020; 2021). The crabs were individually packed in small plastic bags on site to avoid the autotomy of chelipeds by agonistic interactions between crabs. The crab specimens were then brought to the laboratory and kept in the freezer. These crab specimens were used in our previous study to investigate seasonal changes in the sexual size dimorphism of the chelipeds and pleons of *P. japonicus* (Hamasaki and Dan, 2021). In our sample population of *P. japonicus*, ovigerous females were found from May to September; therefore, the breeding and non-breeding seasons were defined as the period from May to September and the period from December to April, respectively.

The crabs with > 2.3 mm carapace width (CW) were sexed based on the position of the gonopores (*i.e.,* on the coxae of the third pereiopods in females and on the coxae of the fifth pereiopods in males) according to Nakasone (1972). Our crab specimens comprised 456 females, 459 males and 71 unsexed juveniles. These crab specimens were measured using a digital caliper (CW > ~3 mm, accuracy 0.05 mm) or a stereomicroscope using a micrometer (CW < ~3 mm, accuracy 0.01 mm) as follows: CW (the widest measurement between the lateral margins of the carapace), propodus length (PrL) (from the tip of the propodus to the carpus joint) and propodus width (PrW) (the widest part of the propodus) of the right and left chelipeds.

Petrolisthes japonicus has no dentate structures along the inner margins of the dactylus and propodus of the chelipeds (Miyake, 1998). Therefore, both major and minor chelipeds could only be distinguished based on the size difference. To determine the major and minor chelipeds of each specimen, we used the geometric mean of PrL and PrW ($\sqrt{\text{PrL} \times \text{PrW}}$) as the cheliped dimension (chela size) because the laterality judged from the largest PrL and PrW dimensions between right and left chelipeds of the identical specimen differed in 52 cases.

Heterochely and cheliped dimorphism

Statistical analyses were performed using the statistical software R (R4.0.2; R Core Team, 2020) at a 5 % significance level. The sizes of the right and left chelae were the same (*i.e.,* homochely) in some specimens and one of the chelae surpassed the second in the pair (*i.e.,* heterochely) in other specimens. The frequencies of homochelous and heterochelous specimens were statistically compared among unsexed juveniles, females and males using Fisher's exact test. The chela size laterality of unsexed juveniles, females and males was tested from an expected random distribution of 1:1 using the *binom. test* function (binomial test). We used a generalized linear model (GLM) with a binomial distribution to evaluate the changes in chela size laterality [right major cheliped (1) or left major cheliped (0)] (response variable) regarding the body size (CW) (explanatory variable) of unsexed juveniles, females and males. In the GLM analyses, the statistical significance of the explanatory variable was evaluated using the *glm* and *anova* functions (likelihood ratio test).

The growth of PrW relative to the PrL (*i.e.,* chela shape) and the growth of chela size (ChS) relative to the body size (CW) were evaluated for major and minor chelipeds of unsexed juveniles, females and males using the following allometric growth equation (Huxley, 1932): $y = ax^b$, where x is PrL or CW, y is PrW or ChS, b is the allometric growth coefficient and a is the initial growth constant. The relative growth patterns were defined as follows: $b > 1$, indicating positive allometric growth or faster growth of y than x; $b = 1$, indicating isometric growth or the same growth rate for y and x; and $b < 1$, indicating negative allometric growth or slower growth of y than x. The coefficients with standard errors and their 95 % confidence intervals were estimated using a general linear model to the log-transformed regression equation (model 1, $\ln y = \ln a + b \ln x$) using the *lm* and *confint* functions, and the statistical significance of the coefficient estimates and the linear model were evaluated with *t*-tests and *F*-tests, respectively. Analysis of covariance was employed to compare differences in slopes and elevations between log-transformed regression equations estimated for major and minor chelipeds using the *covar.test* function (Aoki, 2021).

We further evaluated the intra-and intersexual dimorphism of the shapes and sizes of the major and minor chelipeds by considering the breeding and non-breeding seasons, as analyzed in our previous study (Hamasaki and Dan, 2021). To statistically infer the intrasexual dimorphism of each cheliped type between the breeding and non-breeding seasons in each sex, the allometric growth analyses were conducted using the following equation (model 2): $\ln y = \ln a + b \ln x + c \ln x \times$ Season, where Season is the categorical explanatory variable [breeding season (May to September) or non-breeding season (October to April)]. Additionally, to evaluate the intersexual dimorphism of each cheliped type in the breeding and non-breeding seasons, the allometric growth analyses were conducted based on the following equation (model 3): $\ln y = \ln a + b \ln x + c \ln x \times$ Sex, where Sex is the categorial explanatory variable (female or male).

In these allometric growth models, the initial growth constant was the same in each cheliped type regardless of the season and sex, and the coefficient estimate (c) for each explanatory variable, including the Season or Sex, was the output for the breeding season or male, representing changes in the response variable relative to the baseline category (non-breeding season or female), and thus also representing the degree of the intra-and intersexual dimorphisms in each cheliped type.

RESULTS

Cheliped laterality

The frequency of homochelous and heterochelous crabs varied significantly among unsexed juveniles, females, and males ($P < 0.0001$) (Fig. 1A; Tab. A1), and the proportion of homochelous crabs tended to be
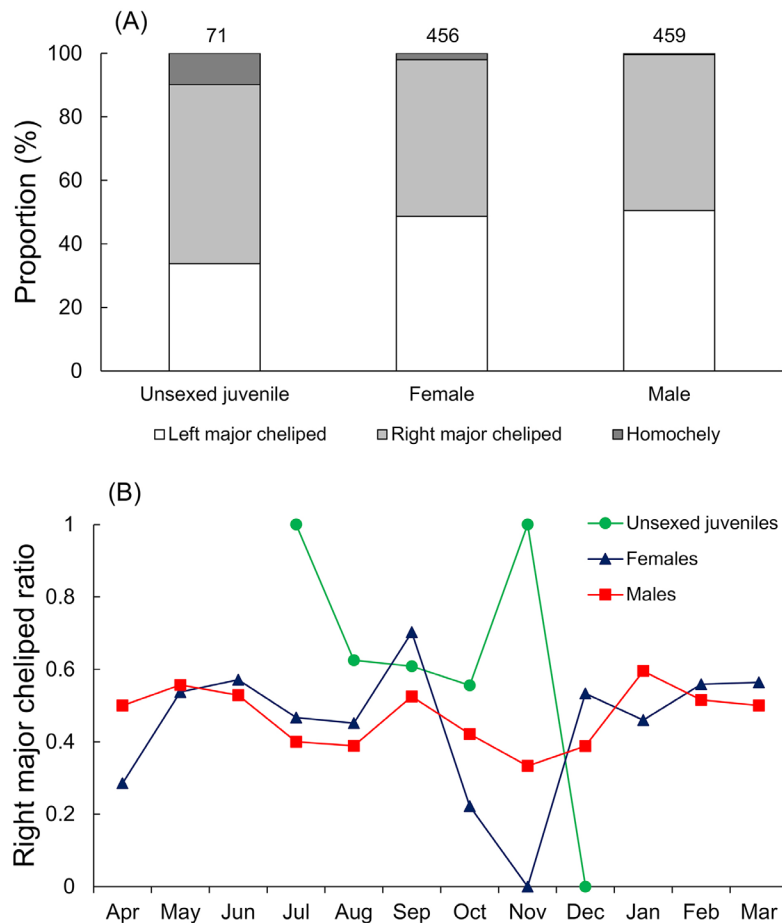

Figure 1. Overall proportions of specimens with either the left or right major chelipeds enlarged (heterochely) or identical-sized left and right chelipeds (homochely) (**A**) and monthly ratios of specimens with right major chelipeds (**B**) in unsexed juveniles, females and males of the porcellanid crab *Petrolisthes japonicus*. Numbers of specimens are shown above the bars.

higher in unsexed juveniles (10.9 %, 7/71) compared with females (2.0 %, 9/456) and males (0.4 %, 4/459). The ratio of crabs with a right major cheliped varied among sampling months, especially in unsexed juveniles and females (Fig. 1B; Tab. A1); however, the overall ratio of crabs with a right major cheliped did not significantly differ from an expected random distribution of 1:1 in all groups (Fig. 1A) (unsexed juveniles, $P = 0.0599$; females, $P = 0.9246$; males, $P = 0.7790$). The chela size laterality was not significantly influenced by the body size in unsexed juveniles ($\chi^2_1 = 1.0524, P = 0.3050$), females ($\chi^2_1 = 2.2837, P = 0.1307$) and males ($\chi^2_1 = 3.3758, P = 0.0662$).

Chela shape dimorphism

The PrL–PrW relationship is shown for the major and minor chelipeds of unsexed juveniles, females and males in Fig. 2A–C, respectively. All log-transformed allometric growth equations between these variables (model 1) were statistically significant (Tab. 1). The PrW showed positive allometric growth ($b > 1$), isometric growth ($b = 1$) and negative allometric growth ($b < 1$) relative to the PrL in both cheliped types of unsexed juveniles, females and males, respectively (see the 95 % confidence intervals for the allometric growth coefficient estimates in Tab. 1).

Unsexed juveniles had similar chela shapes between major and minor chelipeds, as exemplified by the same slope ($F_{1, 138} = 0.0472, P = 0.8283$) and same elevation ($F_{1, 139} = 0.2141, P = 0.6443$) of model 1 equations for respective cheliped types. Females and males exhibited different chela shapes between major and minor chelipeds because the model 1 equations for respective cheliped types had the same slope ($F_{1, 908} = 1.8713, P = 0.1717$) and different elevations ($F_{1, 909} = 21.739, P < 0.0001$) in females and different slopes ($F_{1, 914} = 12.267, P = 0.0004$) in males. These results indicate that major chelipeds exhibit wider chelae compared with minor chelipeds in both sexes (Fig. 2D), and the chelae shape difference between major and minor chelipeds did not change regardless of the PrL in females, but the chelae became wider in major chelipeds than in minor chelipeds with increasing PrL in males.

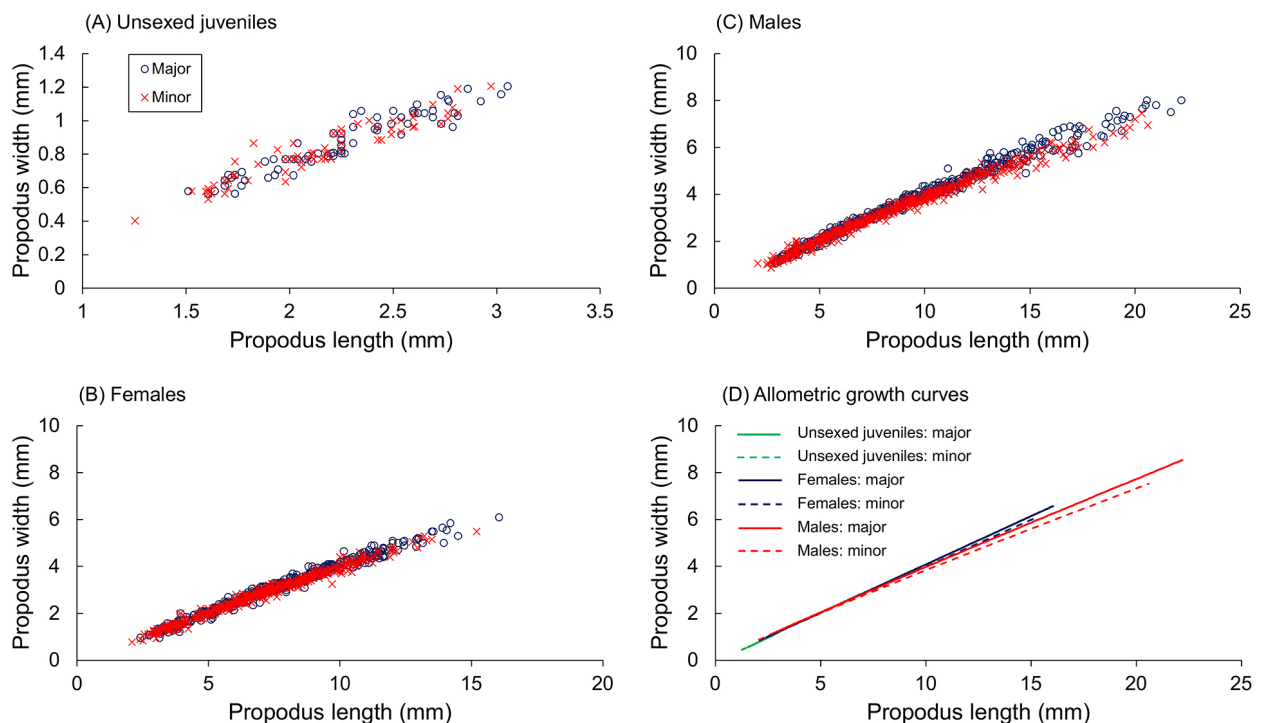**Figure 2.** Growth of the propodus width relative to the propodus length of the major and minor chelipeds in unsexed juveniles (**A**), females (**B**) and males (**C**) of the porcellanid crab *Petrolisthes japonicus*. Allometric growth curves derived from the log-transformed regression equations of major and minor chelipeds (Tab. 1) are shown for the respective groups (**D**).

Table 1. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) of log-transformed allometric growth equations ($\ln PrW = \ln a + b \ln PrL$) to evaluate the relationships between propodus length (PrL) and propodus width (PrW) of major or minor chelipeds of the porcellanid crab *Petrolisthes japonicus*. The statistical significance of the coefficient estimates and each model was evaluated with *t*-tests and *F*-tests, respectively.

Sex	Cheliped	Coefficient	Estimate	SE	95 % CI		*t*	*P*	R^2	*F*	d.f.	*P*
Unsexed juvenile	Major	Intercept	-1.0660	0.0358	-1.1373	-0.9947	-29.82	< 0.0001	0.9073	676	1, 69	< 0.0001
		lnPrL	1.1316	0.0435	1.0447	1.2184	25.99	< 0.0001				
	Minor	Intercept	-1.0608	0.0339	-1.1284	-0.9932	-31.30	< 0.0001	0.9009	628	1, 69	< 0.0001
		lnPrL	1.1180	0.0446	1.0290	1.2070	25.05	< 0.0001				
Female	Major	Intercept	-0.9101	0.0128	-0.9353	-0.8849	-70.96	< 0.0001	0.9816	24230	1, 454	< 0.0001
		lnPrL	1.0066	0.0065	0.9939	1.0193	155.65	< 0.0001				
	Minor	Intercept	-0.9023	0.0126	-0.9270	-0.8776	-71.80	< 0.0001	0.9807	23120	1, 454	< 0.0001
		lnPrL	0.9940	0.0065	0.9812	1.0069	152.10	< 0.0001				
Male	Major	Intercept	-0.8251	0.0107	-0.8462	-0.8040	-76.85	< 0.0001	0.9880	37700	1, 457	< 0.0001
		lnPrL	0.9580	0.0049	0.9483	0.9677	194.18	< 0.0001				
	Minor	Intercept	-0.8001	0.0118	-0.8233	-0.7770	-67.99	< 0.0001	0.9837	27650	1, 457	< 0.0001
		lnPrL	0.9319	0.0056	0.9208	0.9429	166.27	< 0.0001				

The intrasexual chela shape dimorphism was not evident for major and minor chelipeds in both sexes, as shown by the insignificant coefficient estimates (*c*) for the explanatory variable, including the Season (*i.e.*, lnPrL × Season) in the model 2 equations (Fig. 3A; Tab. A2). On the one hand, the intersexual chela shape dimorphism was evident for major and minor chelipeds in both breeding and non-breeding seasons, as exemplified by the significant coefficient estimates (*c*) with similar negative values for the explanatory variable, including Sex (*i.e.*, lnPrL × Sex) in the model 3 equations (Fig. 3B; Tab. A3), indicating that males had more slender chelae than females regardless of the cheliped types and seasons.

Chela size dimorphism

The relationship between CW and ChS are shown for the major and minor chelipeds of unsexed juveniles, females, and males in Fig. 4A–C, respectively. All log-transformed allometric growth equations between these variables (model 1) were statistically significant (Tab. 2). The coefficient of determination (R^2 values) in major chelipeds (unsexed juveniles, 0.8780; females, 0.9796; males, 0.9859) surpassed those in minor chelipeds (unsexed juveniles, 0.7206; females, 0.9528; males, 0.9579), indicating a larger size variation in minor chelipeds. The ChS showed positive allometric growth (*b* > 1) relative to the CW in both cheliped types of all groups, and the allometric growth

coefficients of males (*b* = 1.2316–1.2633) exceeded those of females (*b* = 1.1371–1.1535).

The chela size differences between major and minor chelipeds were stable, regardless of the CW, in unsexed juveniles and females because the model 1 equations for respective cheliped types had the same slope (unsexed juveniles, $F_{1, 138}$ = 0.1931, *P* = 0.6611; females, $F_{1, 908}$ = 1.3299, *P* = 0.2491) and different elevations (unsexed juveniles, $F_{1, 139}$ = 23.118, *P* < 0.0001; females, $F_{1, 909}$ = 232.37, *P* < 0.0001). In males, major chelipeds became larger than minor chelipeds following the CW, as the model 1 equations for respective cheliped types had different slopes ($F_{1, 914}$ = 5.3111, *P* = 0.02373). Overall, chela size was the largest in male major chelipeds, followed by male minor and female major chelipeds, and smallest in female minor chelipeds (Fig. 4D).

The intrasexual chela size dimorphism was evident for major and minor chelipeds in both sexes because the coefficient estimates (*c*) for the explanatory variable, including the Season (*i.e.*, lnCW × Season) in the model 2 equations of respective cheliped types, showed similar significant negative values in females and similar significant positive values in males (Fig. 5A; Tab. A4). These results indicate that males increased the growth of both major and minor chelipeds to the same degree during the breeding season, inducing the following intersexual size dimorphism of the chelipeds. The intersexual chela size dimorphism
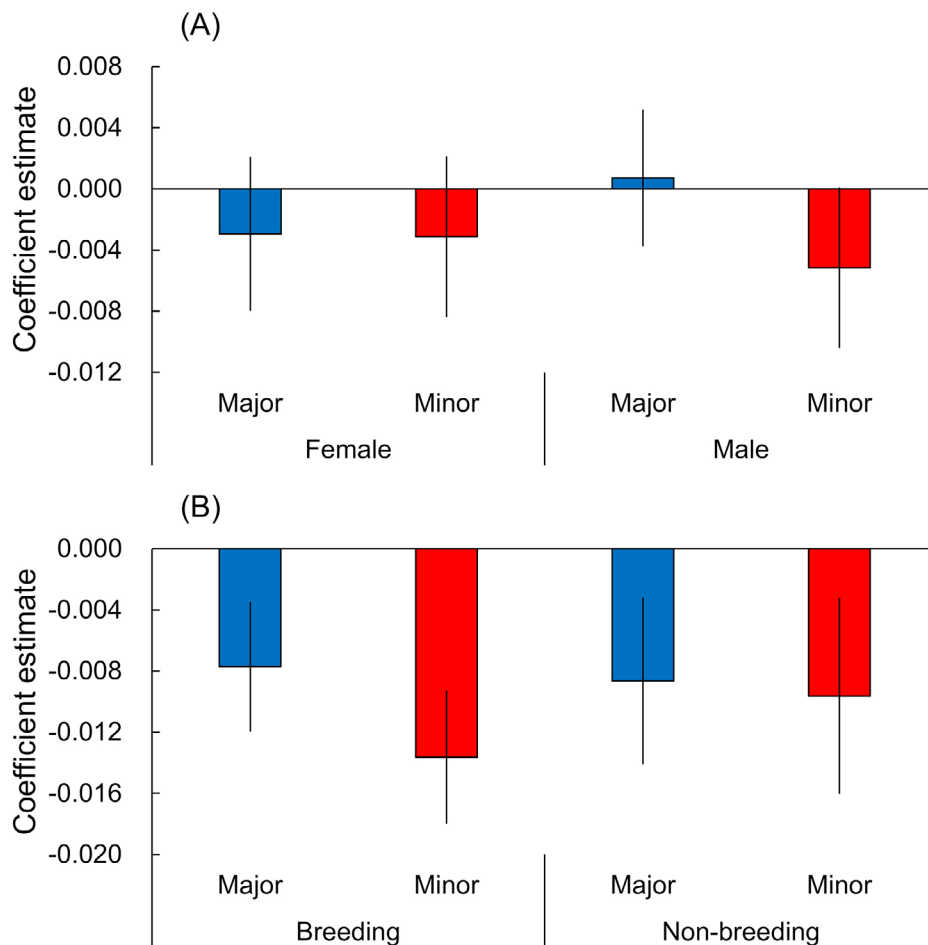
Figure 3. Intrasexual chela shape dimorphism between the breeding and non-breeding seasons in each sex (**A**) and intersexual chela shape dimorphism in the breeding and non-breeding seasons (**B**) for major and minor chelipeds of the porcellanid crab *Petrolisthes japonicus*, based on the respective log-transformed allometric growth equation models between propodus length (PrL) and propodus width (PrW) of the chelipeds: $\ln PrW = \ln a + b \ln PrL + c \ln PrL \times Season$, where Season is the categorical explanatory variable [breeding season (May to September) or non-breeding season (October to April)] and $\ln PrW = \ln a + b \ln PrL + c \ln PrL \times Sex$, where Sex is the categorial explanatory variable (female or male). The coefficient estimate for each explanatory variable, including the Season or Sex, was the output for the breeding season or male, representing changes in the response variable relative to the baseline category (non-breeding season or female), and thus also representing the degree of the intra-and intersexual dimorphisms in each cheliped type. Vertical lines indicate 95 % confidence intervals.

was evident for major and minor chelipeds during the breeding season, but it decreased or diminished in both cheliped types during the non-breeding season because the coefficient estimates (*c*) for the explanatory variable, including Sex (*i.e.*, lnCW × Sex) in the model 3 equations, exhibited similar significant positive values for both cheliped types during the breeding season, and it was significant, but small, for the major cheliped and insignificant for the minor cheliped during the non-breeding season (Fig. 5B; Tab. A5).

Discussion

The present study revealed that heterochely was a common phenomenon, and major chelipeds occurred randomly on either the right or left sides of the body regardless of the crab size in *P. japonicus* (Fig. 1). Decapod heterochely exhibits interspecific variability; major chelipeds occur predominately, or evenly, on the right or left sides of the body (Lee, 1995; Yamaguchi and Tokunaga, 1995; Mariappan *et al.*, 2000). Baeza and Asorey (2012) documented the cheliped laterality
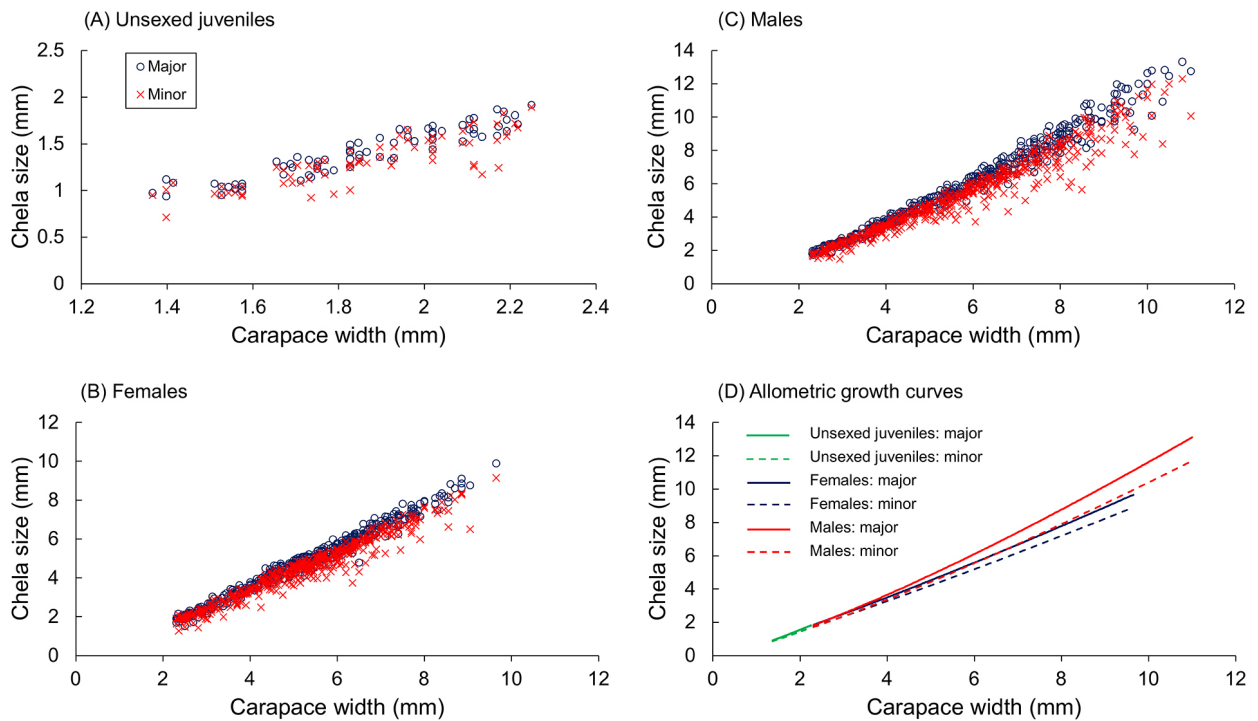
Figure 4. Growth of the chela size (geometric mean of the propodus length and width) of the major and minor chelipeds relative to the carapace width in unsexed juveniles (**A**), females (**B**) and males (**C**) of the porcellanid crab *Petrolisthes japonicus*. Allometric growth curves derived from the log-transformed regression equations of major and minor chelipeds (Tab. 2) are shown for the respective groups (**D**).

Table 2. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) of log-transformed allometric growth equations ($\ln ChS + \ln a = b \ln CW$) to evaluate the relationships between carapace width (CW) and chela size (ChS, geometric mean of the propodus length and width) of major or minor chelipeds of the porcellanid crab *Petrolisthes japonicus*. The statistical significance of the coefficient estimates and each model was evaluated with *t*-tests and *F*-tests, respectively.

Sex	Cheliped	Coefficient	Estimate	SE	95 % CI		*t*	*P*	R^2	*F*	d.f.	*P*
Unsexed juvenile	Major	Intercept	-0.5249	0.0388	-0.6023	-0.4475	-13.52	< 0.0001	0.8780	497	1, 69	< 0.0001
		lnCW	1.3849	0.0621	1.2610	1.5089	22.29	< 0.0001				
	Minor	Intercept	-0.5657	0.0624	-0.6902	-0.4411	-9.061	< 0.0001	0.7206	178	1, 69	< 0.0001
		lnCW	1.3332	0.0999	1.1339	1.5326	13.341	< 0.0001				
Female	Major	Intercept	-0.3475	0.0128	-0.3726	-0.3224	-27.23	< 0.0001	0.9796	21790	1, 454	< 0.0001
		lnCW	1.1535	0.0078	1.1381	1.1688	147.63	< 0.0001				
	Minor	Intercept	-0.3919	0.0194	-0.4300	-0.3538	-20.20	< 0.0001	0.9528	9165	1, 454	< 0.0001
		lnCW	1.1371	0.0119	1.1137	1.1604	95.73	< 0.0001				
Male	Major	Intercept	-0.4563	0.0122	-0.4802	-0.4324	-37.49	< 0.0001	0.9859	31860	1, 457	< 0.0001
		lnCW	1.2633	0.0071	1.2494	1.2772	178.49	< 0.0001				
	Minor	Intercept	-0.4943	0.0208	-0.5351	-0.4535	-23.78	< 0.0001	0.9579	10390	1, 457	< 0.0001
		lnCW	1.2316	0.0121	1.2078	1.2553	101.91	< 0.0001				

in two porcellanid crab species; in both males and females of *A. spinifrons* and females of *L. mitra*. The major chelipeds occurred randomly on either the right or left body sides, whereas in males of *L. mitra*, right major chelipeds predominated (72 %).

It has been suggested that handedness may be advantageous for feeding on hard-shelled prey in decapods (Seed and Hughes, 1995; Schenk and Wainwright, 2001; Masunari *et al.*, 2015). Particularly, right-handedness (*i.e.*, right crusher chela) predominates in carnivorous brachyuran crabs (Lee, 1995; Mariappan *et al.*, 2000; Masunari *et al.*, 2015), and this trait has been considered an adaptation for breaking dextrally coiled shells, a
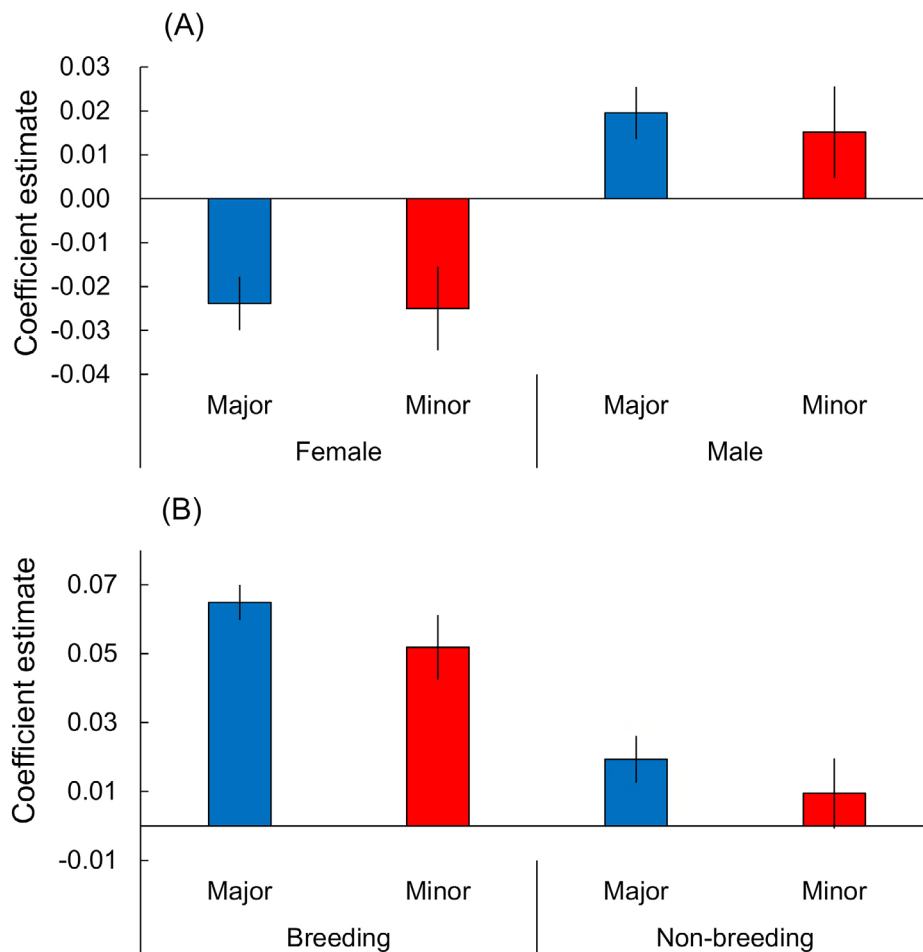
Figure 5. Intrasexual chela size dimorphism between the breeding and non-breeding seasons in each sex (**A**) and intersexual chela size dimorphism in breeding and non-breeding seasons (**B**) for major and minor chelipeds of the porcellanid crab *Petrolisthes japonicus*, based on the respective log-transformed allometric growth equation models between carapace width (CW) and chela size (ChS, geometric mean of the propodus length and width) of the chelipeds: $\ln ChS = \ln a + b\ln CW + c\ln CW \times Season$, where Season is the categorical explanatory variable [breeding season (May to September) or non-breeding season (October to April)] and $\ln ChS = \ln a + b\ln CW + c\ln CW \times Sex$, where Sex is the categorial explanatory variable (female or male). The coefficient estimate for each explanatory variable, including the Season or Sex, was the output for the breeding season or male, representing changes in the response variable relative to the baseline category (non-breeding season or female), and thus also representing the degree of the intra-and intersexual dimorphisms in each cheliped type. Vertical lines indicate 95 % confidence intervals.

predominant shell form in marine snails (Ng and Tan, 1985; Shigemiya, 2003; Dietl and Hendricks, 2006). However, porcellanid crabs are primarily suspension feeders, trapping suspended detritus and plankton using the long setae of their third maxillipeds (Caine, 1975; Kropp, 1981; Trager and Genin, 1993; Achituv and Pedrotti, 1999; Hollebone and Hay, 2008; McGlaun and Withers, 2012). It is known that the porcellanid crab *Petrolisthes cabrilloi* Glassell, 1945 can grasp particulate material with the chelipeds and transfer that material to the mouth parts (Kropp, 1981). *Petrolisthes japonicus* exhibit no dentate structures along the inner margins of the dactylus and propodus of both chelipeds (Miyake,

1998), as is typical in the porcellanid crabs (*e.g.*, Osawa and McLaughlin, 2010; Werding and Hiller, 2015). Considering feeding habits and chela structures, the heterochely of porcellanid crabs may not be an adaptation for manipulating food organisms.

Handedness may also play an important role in intraspecific agonistic and sexual interactions in decapods. The most iconic example of advantageous handedness is found in male fiddler crabs; one cheliped greatly enlarges and functions as both a weapon to fight competitive males and as an ornament to court receptive females through claw-waving displays (Crane, 1975; Perez *et al.*, 2012; 2015). The callianassid shrimps are known to exhibit

distinct sexual dimorphism of the major cheliped, and males are more aggressive using the major cheliped as a weapon for intraspecific fighting (Shimoda *et al.*, 2005). The males of some pagurid hermit crabs exhibit precopulatory guarding behaviour by grasping the aperture of the gastropod shell occupied by sexually mature females with their minor (*i.e.*, left) cheliped, while guarding males frequently use their major (*i.e.*, right) cheliped to defend females against intruders (Yasuda *et al.*, 2011; 2012).

The chelipeds are involved in intraspecific agonistic and sexual communications in four porcellanid species belonging to the genus *Petrolisthes* (see Molenock, 1975; 1976). During agonistic interactions, one or both of the chelipeds were forcefully extended, often repeatedly, and the chelae usually touched nearby crabs, pushing them from their space, and the majority of larger crabs gained or retained the space. Similarly, during sexual communication, the male crabs held a territory and the male nudged the courted female with his chelae just before copulation. Accordingly, selection might favor a large body with large chelipeds in porcellanid crabs to monopolize resources in intraspecific agonistic and sexual interactions, and the sexual size dimorphism in porcellanid chelipeds is thought to be a consequence of sexual selection (Baeza and Asorey, 2012). However, the exact functions of heterochely for intraspecific agonistic and sexual interactions are currently unknown in porcellanid crabs.

In the present study, we conducted allometric growth analyses for both major and minor chelipeds based on the chela size (*i.e.*, geometric mean of the PrL and PrW of the chelipeds) in *P. japonicus*. Major and minor chelipeds of males exceeded the female respective chelipeds, while chela size showed positive allometric growth in both cheliped types, regardless of sex. Additionally, the size variability was larger in minor chelipeds than in major chelipeds, probably because of the cheliped regeneration after autotomy, which functions as an anti-predator defence mechanism. *Petrolisthes japonicus* is ready to autotomize the cheliped when it is held by the cheliped, enabling it to escape the predator crab at high probabilities (Hamasaki *et al.*, 2022a; b). Our analyses clearly detected intra-and intersexual size dimorphism in both major and minor chelipeds, as observed in our previous study, based on the largest PrL and PrW

measurements between the right and left chelipeds as the cheliped dimension (Hamasaki and Dan, 2021). Males of *P. japonicus* increased the growth of both major and minor chelipeds to the same degree during the breeding season, causing distinct intersexual-size dimorphism in major and minor chelipeds (Figs. 4 and 5; Tab. 2). Females of *P. japonicus* decreased the growth of both major and minor chelipeds to the same degree during the breeding season. Thus, the present study further supports our view that the sexual size dimorphism of *P. japonicus* chelipeds might be the consequence of sexual selection (*i.e.* male–male competition) (Hamasaki and Dan, 2021).

Furthermore, our findings may provide the first insights into the ecological function of heterochely in the porcellanid crabs. Our allometric growth analyses revealed a chela shape dimorphism in *P. japonicus*. Males had more slender chelae than females, regardless of the cheliped types and seasons (Figs. 2 and 3); thus, males enlarged their chelae in the length dimension. Unsexed juveniles had similar chela shapes of major and minor chelipeds, and the chelae were wider in major chelipeds than in minor chelipeds in both sexes. The chela shape differences between major and minor chelipeds remained unchanged regardless of the chela length in females, but the chelae became wider in major chelipeds than in minor chelipeds with increasing chela length in males (Fig. 2; Table 1). Hamasaki *et al.* (2022a) reported that the chelipeds of *P. japonicus* exhibited a similar cheliped weight–length relationship regardless of the sex and cheliped type with larger or smaller chela lengths, based only on a few specimens (females: 23 large and 18 small chelipeds, males: 18 large and 18 small chelipeds). These results suggest that male major chelipeds may become thinner following the chela length while retaining a similar cheliped biomass–length relationship. This should be confirmed by measuring 3-dimensions and weight of chelipeds from many female and male specimens in future studies. Our analyses also revealed that the chela size differences between major and minor chelipeds were stable regardless of the body size in unsexed juveniles and females, whereas major chelipeds became larger than minor chelipeds following the body size in males (Fig. 4; Tab. 2). Thus, intersexual dimorphism of an energy allocation strategy was evident in *P. japonicus*; with females allocating their

energy evenly to major and minor cheliped growth without changing the chela shape, regardless of the body size. Males on the other hand, invested more energy to major cheliped growth, causing wider chelae with increasing body size. Overall, the major cheliped of *P. japonicus* may have a greater role in male–male competition. Our allometric growth analyses for the cheliped shape and size dimorphism could infer the advantage of male major chelipeds in regard to sexual selection in *P. japonicus*.

CONCLUSIONS

Heterochely was a common phenomenon, and major chelipeds occurred randomly on either the right or left sides of the body, regardless of the crab size in the Japanese porcellanid crab *P. japonicus*. The heterochely of *P. japonicus* may not be an adaptation for manipulating food particles because the crab is principally a suspension feeder and has no specific feeding structures on its chelae. Our allometric growth analyses also revealed the intra-and intersexual shape and size dimorphism in major and minor chelipeds; females had major and minor chelipeds with similar shaped chelae, whereas males enlarged their major chelipeds leading to wider chelae with increasing body size. This suggests that the major cheliped of *P. japonicus* may play a greater role in male-male competition for acquiring mates. However, the advantages of major chelipeds for females remains unknown. To elucidate the ecological functions of heterochely and whether handedness exists in *P. japonicus*, the behaviors of major and minor chelipeds involved in intraspecific agonistic and sexual communications should be detailed for both sexes using laboratory experiments.

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APPENDIX

Table A1. Cheliped laterality of the porcellanid crab *Petrolisthes japonicus* collected from April 2008 to March 2009. Numbers of crabs with heterochely (either the left or right major chelipeds) and homochely (identical sized left and right chelipeds) are summarized.

Sex	Month	Number of crabs			
		Left major cheliped	Right major cheliped	Heterochely	Homochely
Unsexed juvenile	Apr				
	May				
	Jun				
	Jul	0	2	2	0
	Aug	6	10	16	2
	Sep	9	14	23	2
	Oct	8	10	18	3
	Nov	0	4	4	0
	Dec	1	0	1	0
	Jan				
	Feb				
	Mar				
	Total	24	40	64	7
Female	Apr	25	10	35	1
	May	31	36	67	0
	Jun	27	36	63	1
	Jul	24	21	45	0
	Aug	17	14	31	0
	Sep	11	26	37	6
	Oct	7	2	9	0
	Nov	7	0	7	0
	Dec	14	16	30	0
	Jan	27	23	50	0
	Feb	15	19	34	1
	Mar	17	22	39	0
	Total	222	225	447	9
Male	Apr	20	20	40	0
	May	35	44	79	0
	Jun	25	28	53	0
	Jul	30	20	50	0
	Aug	11	7	18	2
	Sep	19	21	40	0
	Oct	11	8	19	0
	Nov	4	2	6	0
	Dec	30	19	49	0
	Jan	17	25	42	0
	Feb	16	17	33	0
	Mar	14	14	28	0
	Total	232	225	457	2

Table A2. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) for the explanatory variables of log-transformed allometric growth equation models to evaluate the intrasexual chela shape dimorphism of major or minor chelipeds between the breeding (May to September) and non-breeding seasons (October to April) in each sex of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: lnPrW = ln$a$ + $b$lnPrL+ $c$lnPrL× Season, where PrW is the cheliped propodus width, PrL is the cheliped propodus length, and Season is the breeding season or non-breeding season. The coefficient estimate for each explanatory variable, including the Season, was the output for the breeding season, representing changes in the response variable relative to the baseline category (non-breeding season). The statistical significance of the coefficient estimates and each model was evaluated with t-tests and F-tests, respectively.

Sex	Cheliped	Coefficient	Estimate	SE	95 % CI		t	P	R^2	F	d.f.	P
Female		Intercept	-0.9132	0.0131	-0.9390	-0.8875	-69.70	< 0.0001	0.9817	12120	2, 453	< 0.0001
	Major	lnPrL	1.0099	0.0071	0.9960	1.0237	143.00	< 0.0001				
		lnPrL × Season-Breeding	-0.0029	0.0026	-0.0080	0.0021	-1.15	0.2500				
		Intercept	-0.9053	0.0128	-0.9305	-0.8801	-70.65	< 0.0001	0.9808	11570	2, 453	< 0.0001
	Minor	lnPrL	0.9974	0.0071	0.9833	1.0114	139.76	< 0.0001				
		lnPrL × Season-Breeding	-0.0031	0.0027	-0.0084	0.0021	-1.17	0.2430				
Male		Intercept	-0.8243	0.0110	-0.8460	-0.8026	-74.72	< 0.0001	0.9880	18820	2, 456	< 0.0001
	Major	lnPrL	0.9572	0.0055	0.9464	0.9680	173.82	< 0.0001				
		lnPrL × Season-Breeding	0.0007	0.0023	-0.0037	0.0052	0.32	0.7490				
		Intercept	-0.8054	0.0120	-0.8290	-0.7817	-66.88	< 0.0001	0.9839	13910	2, 456	< 0.0001
	Minor	lnPrL	0.9373	0.0063	0.9250	0.9496	149.84	< 0.0001				
		lnPrL × Season-Breeding	-0.0052	0.0027	-0.0104	0.0001	-1.93	0.0545				

Table A3. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) for their explanatory variables of log-transformed allometric growth equation models to evaluate the intersexual chela shape dimorphism of major or minor chelipeds in the breeding (May to September) and non-breeding seasons (October to April) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: lnPrW ~ ln$a$ + $b$lnPrL + $c$lnPrL × Sex, where PrW is the cheliped propodus width, PrL is the cheliped propodus length, and Sex is female or male. The coefficient estimate for each explanatory variable, including the Sex, was the output for the male, representing changes in the response variable relative to the baseline category (female). The statistical significance of the coefficient estimates and each model was evaluated with t-tests and F-tests, respectively.

Season	Cheliped	Coefficient	Estimate	SE	95 % CI		t	P	R^2	F	d.f.	P
Breeding		Intercept	-0.8507	0.0116	-0.8734	-0.8280	-73.51	< 0.0001	0.9864	17740	2, 489	< 0.0001
	Major	lnPrL	0.9770	0.0057	0.9657	0.9883	170.01	< 0.0001				
		lnPrL × Sex-Male	-0.0077	0.0022	-0.0120	-0.0035	-3.57	0.0004				
		Intercept	-0.8207	0.0111	-0.8425	-0.7989	-73.9	< 0.0001	0.9857	16800	2, 489	< 0.0001
	Minor	lnPrL	0.9525	0.0057	0.9413	0.9637	167.20	< 0.0001				
		lnPrL × Sex-Male	-0.0136	0.0022	-0.0180	-0.0093	-6.13	< 0.0001				
Non-breeding		Intercept	-0.8736	0.0127	-0.8986	-0.8486	-68.63	< 0.0001	0.9829	12060	2, 420	< 0.0001
	Major	lnPrL	0.9893	0.0069	0.9757	1.0029	143.26	< 0.0001				
		lnPrL × Sex-Male	-0.0086	0.0028	-0.0141	-0.0032	-3.11	0.0020				
		Intercept	-0.8755	0.0140	-0.9031	-0.8480	-62.44	< 0.0001	0.9773	9045	2, 420	< 0.0001
	Minor	lnPrL	0.9815	0.0079	0.9660	0.9969	124.87	< 0.0001				
		lnPrL × Sex-Male	-0.0096	0.0033	-0.0160	-0.0032	-2.95	0.0033				

Table A4. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) for the explanatory variables of log-transformed allometric growth equation models to evaluate the intrasexual chela size dimorphisms of major or minor chelipeds between the breeding (May to September) and non-breeding seasons (October to April) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: lnChS = ln$a$ + $b$lnCW + $c$lnCW × Season, where ChS is the chela size (geometric mean of the propodus length and width), CW is the carapace width, and Season is the breeding season or non-breeding season. The coefficient estimate for each explanatory variable, including the Season, was the output for the breeding season, representing changes in the response variable relative to the baseline category (non-breeding season). The statistical significance of the coefficient estimates and each model was evaluated with t-tests and F-tests, respectively.

Sex	Cheliped	Coefficient	Estimate	SE	95 % CI		t	P	R^2	F	d.f.	P
Female	Major	Intercept	-0.3713	0.0124	-0.3957	-0.3470	-29.94	< 0.0001	0.9820	12330	2, 453	< 0.0001
		lnCW	1.1820	0.0082	1.1659	1.1982	143.50	< 0.0001				
		lnCW × Season-Breeding	-0.0238	0.0031	-0.0299	-0.0178	-7.71	< 0.0001				
	Minor	Intercept	-0.4169	0.0195	-0.4552	-0.3786	-21.39	< 0.0001	0.9554	4852	2, 453	< 0.0001
		lnCW	1.1670	0.0129	1.1416	1.1924	90.15	< 0.0001				
		lnCW × Season-Breeding	-0.0250	0.0049	-0.0345	-0.0154	-5.14	< 0.0001				
Male	Major	Intercept	-0.4416	0.0119	-0.4650	-0.4183	-37.18	< 0.0001	0.9871	17380	2, 456	< 0.0001
		lnCW	1.2438	0.0074	1.2292	1.2584	167.68	< 0.0001				
		lnCW × Season-Breeding	0.0195	0.0030	0.0136	0.0255	6.48	< 0.0001				
	Minor	Intercept	-0.4829	0.0210	-0.5242	-0.4416	-22.99	< 0.0001	0.9586	5277	2, 456	< 0.0001
		lnCW	1.2165	0.0131	1.1907	1.2422	92.72	< 0.0001				
		lnCW × Season-Breeding	0.0152	0.0053	0.0047	0.0256	2.84	0.0047				

Table A5. Coefficient estimates with standard errors (SE) and their 95 % confidence intervals (CI) for the explanatory variables of log-transformed allometric growth equation models to evaluate the intersexual chela size dimorphism of major or minor chelipeds in the breeding (May to September) and non-breeding seasons (October to April) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: lnChS ~ ln$a$ + $b$lnCW + $c$lnCW × Sex, where ChS is the chela size (geometric mean of the propodus length and width), CW is the carapace width, and Sex is female or male. The coefficient estimate for each explanatory variable, including the Sex, was the output for the male, representing changes in the response variable relative to the baseline category (female). The statistical significance of the coefficient estimates and each model was evaluated with t-tests and F-tests, respectively.

Season	Cheliped	Coefficient	Estimate	SE	95 % CI		t	P	R^2	F	d.f.	P
Breeding	Major	Intercept	-0.4370	0.0118	-0.4601	-0.4139	-37.18	< 0.0001	0.9865	17900	2, 489	< 0.0001
		lnCW	1.1960	0.0070	1.1822	1.2098	170.56	< 0.0001				
		lnCW × Sex-Male	0.0648	0.0026	0.0597	0.0700	24.81	< 0.0001				
	Minor	Intercept	-0.4743	0.0216	-0.5168	-0.4319	-21.95	< 0.0001	0.9534	5002	2, 489	< 0.0001
		lnCW	1.1751	0.0129	1.1498	1.2004	91.16	< 0.0001				
		lnCW × Sex-Male	0.0518	0.0048	0.0424	0.0613	10.79	< 0.0001				
Non-breeding	Major	Intercept	-0.3842	0.0126	-0.4090	-0.3594	-30.42	< 0.0001	0.9826	11830	2, 420	< 0.0001
		lnCW	1.1902	0.0084	1.1737	1.2068	141.13	< 0.0001				
		lnCW × Sex-Male	0.0194	0.0035	0.0126	0.0262	5.60	< 0.0001				
	Minor	Intercept	-0.4330	0.0190	-0.4703	-0.3957	-22.81	< 0.0001	0.9600	5044	2, 420	< 0.0001
		lnCW	1.1773	0.0127	1.1524	1.2022	92.88	< 0.0001				
		lnCW × Sex-Male	0.0094	0.0052	-0.0008	0.0197	1.89	0.0698				