Open Access

Seasonal Changes in the Sexual Size Dimorphisms of the Chelipeds and Pleons of the Porcellanid Crab *Petrolisthes japonicus*

Katsuyuki Hamasaki* 🕩 and Shigeki Dan 🕩

Department of Marine Biosciences, Tokyo University of Marine Science and Technology, Konan, Minato, Tokyo 108-8477, Japan. *Correspondence: E-mail: hamak@kaiyodai.ac.jp (Hamasaki) E-mail: sdan@kaiyodai.ac.jp (Dan)

Received 5 August 2020 / Accepted 5 February 2021 / Published 18 April 2021 Communicated by Benny K.K. Chan

Decapod crustaceans develop secondary sexual structures, such as large chelipeds for weaponry and/ or display in males and a wider pleon for incubating eggs in females. These structures should be costly to produce and maintain; hence, the crustacean reproductive strategy might have adapted to conserve energy for developing secondary sexual characteristics during the reproductive season. However, little is known about seasonal changes in the sexual size dimorphisms of the chelipeds and pleons of decapod crustaceans. Anomuran crabs from the family Porcellanidae exhibit a true crab-like body shape, with relatively large chelipeds for their body size and a well-developed pleon. They also show sexual size dimorphism (i.e., males with larger chelipeds and females with wider pleons); therefore, it was expected that seasonal changes in the sexual size dimorphisms of these organs would occur in porcellanid crabs. We tested this expectation using *Petrolisthes japonicus*, which is common on the intertidal cobble and boulder shores of the temperate and tropical regions of Japan. We employed allometric growth analyses of the cheliped and pleon dimensions of P. japonicus females and males collected over a year. Our analyses supported our expectation regarding the seasonal changes in the sexual size dimorphisms of the chelipeds and pleons in P. japonicus. Intersexual size dimorphism of the chelipeds and pleons was evident during the breeding season: females allocated more energy to pleon growth, while reducing cheliped growth, and investment in the pleon increased with increasing female body size, whereas males invested their energy in cheliped growth, and the investment in chelipeds increased with increasing male body size. During the nonbreeding season, females and males conserved energy by reducing the size of pleons and chelipeds relative to their respective body sizes. Our results highlighted the sex-specific and seasondependent resource allocation and reproductive strategies of porcellanid crabs.

Key words: Allometric growth, Life history, Reproductive strategy, Secondary sexual traits, Sexual maturity.

BACKGROUND

Decapod crustaceans show sexual dimorphisms in size or morphological traits (Davie et al. 2015); for example, in brachyuran crabs, females have a broad pleon for incubating eggs, which are attached to the second to fifth pleopods on the ventral pleomeres, whereas males have a relatively narrow pleon that covers the first and second pleopods, which are modified copulatory organs (*i.e.*, gonopods) (Davie et al. 2015). Some decapods have enlarged chelipeds that are used to manipulate food organisms and weaponry in predator avoidance and contest competition (Lee 1995; Davie et al. 2015; Lavalli and Spanier 2015). Although decapod

Citation: Hamasaki K, Dan S. 2021. Seasonal changes in the sexual size dimorphisms of the chelipeds and pleons of the porcellanid crab *Petrolisthes japonicus*. Zool Stud **60:**18. doi:10.6620/ZS.2021.60-18.

chelipeds principally exhibit similar functions in both sexes, the chelipeds of males are generally larger than those of females (Crane 1975; Lee 1995; Mariappan et al. 2000; Emlen 2008; Hamasaki et al. 2020a).

Sexual dimorphism in decapod cheliped size is thought to be a consequence of sexual selection (Baeza and Asorev 2012; Cothran 2020): males win the competition for females by having larger chelipeds; for instance, in male fiddler crabs, the cheliped greatly enlarges and functions as both a weapon to fight competitive males and as an ornament to court receptive females through claw waving display (Crane 1975; Christy 1982 1983; Pope 2000). The males of some brachyuran crabs have larger chelipeds, which they use to protect receptive females from other males during pre- and postcopulatory mate-guarding behaviour, and embrace females from behind with their walking legs (van den Brink and McLay 2010; Soundarapandian et al. 2013; Waiho et al. 2015). 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 (Hazlett 1968 1972; Yasuda et al. 2011 2012).

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); hence, their reproductive strategy might have adapted to conserve energy for developing secondary sexual characteristics during a reproductive season, and thus sexual dimorphism may change seasonally in these organisms. Secondary sexual characteristics become evident after pubertal moult in decapod crustacean species (Hartnoll 1974 1978); therefore, the growth of secondary sexual characteristics, such as chelipeds and pleons, relative to a reference body dimension was measured to elucidate their size at the onset of sexual maturity in numerous decapod crustaceans (McLay 2015), and these analyses highlighted the sexual size dimorphisms of the chelipeds and pleons. Only a few studies have documented seasonal changes in the sexual dimorphism of decapod crustaceans: adult females reduced pleon growth after the breeding season in the shore crab Pachygrapsus transversus Gibbes 1850 (Flores and Negreiros-Fransozo 1999), and adult males increased cheliped growth during the reproductive season in the anomuran crab Aegla franca Schmitt 1942 (Bueno and Shimizu 2009) and hermit crabs Diogenes nitidimanus Terao 1913 (Koga et al. 2010) and Pagurus minutus Hess 1865 (Yasuda et al. 2017).

Anomuran crabs, which belong to the family Porcellanidae Haworth 1825, exhibit a brachyuran crablike body shape; broad and dorsoventrally flattened, relatively large chelipeds for their body size; and a well-developed, symmetrical pleon that is carried bent under the cephalothorax and held against the thorax (Jones 1977; Barría and González 2008; Osawa and McLaughlin 2010). Sexual size dimorphisms of the chelipeds and pleons have been documented in some porcellanid crab species (*i.e.*, males with larger chelipeds and females with wider pleons) (Miranda and Mantelatto 2010; Baeza and Asorey 2012; Wassick et al. 2017); it is therefore likely that the relatively large chelipeds and well-developed pleons of porcellanid crabs are costly to produce and maintain, and that seasonal changes in sexual size dimorphism occur in their chelipeds and pleons.

In the present study, we aimed to test this expectation of seasonal changes in the sexual size dimorphisms of the chelipeds and pleons of porcellanid crabs using *Petrolisthes japonicus* (De Haan 1849). This crab is a free-living species, common on the intertidal cobble and boulder shores of the temperate and tropical regions of Japan (Miyake 1998). We examined the sexual size dimorphisms of the chelipeds and pleons and their seasonal changes using allometric growth analyses of *P. japonicus* specimens collected over one year on an intertidal cobble and boulder shore on the Boso Peninsula, Japan.

MATERIALS AND METHODS

Measurement of crabs

We collected 1,259 *P. japonicus* specimens through monthly sampling, conducted from April 2008 to March 2009 in an intertidal cobble and boulder zone $(34^{\circ}58'N, 139^{\circ}46'E)$ on the Boso Peninsula, Japan (Table 1). These crab specimens were used in our previous study to investigate the reproductive traits and population structure of a *P. japonicus* population (Hamasaki et al. 2020b).

The carapace width (CW; the widest measurement between the lateral margins of the carapace) of the crabs was measured using a digital calliper (CW > \sim 3 mm, accuracy 0.05 mm) or a stereomicroscope with the aid of a micrometre (CW < \sim 3 mm, accuracy 0.01 mm). The crabs with > 2.3 mm CW were sexed based on the position of the gonopores (*i.e.*, at the coxae of the third pereiopods in females and at the coxae of the fifth pereiopods in males) (Osawa and McLaughlin 2010) because the minimum body size of females has been found to be 2.3 mm CW (Nakasone 1972; Hamasaki et al. 2020b). Each female was then classified according to the presence or absence of eggs attached to the pleopods (ovigerous or non-ovigerous females, respectively).

Our crab specimens comprised 568 females (including 156 ovigerous females), 585 males and 106 unsexed juveniles (Table 1). Porcellanid crabs easily autotomize their first pereiopods (i.e., chelipeds) due to physical stress (Wasson et al. 2002). In our crab specimens, 112 females, 126 males (including three males with noticeably small regenerated chelipeds) and 35 unsexed juveniles had lost one or both chelipeds naturally and/or due to physical stress during the sampling procedure (Table 1). We therefore measured several body parts of intact specimens (456 females, 459 males and 71 unsexed juveniles; Table 1) using a digital calliper or a stereomicroscope as follows: propodus length (from the tip of the propodus to the carpal joint) and width (the widest part of the propodus) of the right and left chelipeds, and pleon width (the widest part of the fifth pleonite). Heterochely is known in some porcellanid crab species (Baeza and Asorey 2012), and one of the chelipeds was larger than the second in the pair of P. japonicus in the present study, as shown in figure S1; therefore, we selected the largest measurement between the right and left chelipeds as the cheliped dimension.

Sexual size dimorphisms of chelipeds and pleons

In the present study, the statistical analyses were performed with the statistical software R (R4.0.2; R Core Team 2020) at a 5% significance level. The sexual size dimorphisms of the chelipeds and pleons were evaluated based on allometric growth analyses. The growth of the body dimensions relative to a reference dimension (CW) was examined using the following allometric growth equation (Huxley 1932): $v = ax^{b}$, where x is CW, y is the measurement for another body part (cheliped propodus length and width, and pleon width), b is the allometric growth coefficient and ais the initial growth constant. The relative growth patterns were defined as follows: b > 1 indicated positive allometric growth, or faster growth of v than x; b = 1 indicated isometric growth, or the same growth rate for y and x; and b < 1 indicated negative allometric growth, or slower growth of y than x. The coefficients and standard errors were estimated by applying a general linear model to the log-transformed equation $\ln y = \ln a + b \ln x$ using the *lm* function, and the statistical significance of the coefficient estimates and the linear model were evaluated with *t*-tests and *F*-tests, respectively.

To statistically infer the intersexual dimorphisms as the differences between females and males in the allometric growth coefficients of the cheliped and pleon sizes, using overall specimens, we compared two models that included a continuous explanatory variable (CW) and a categorical explanatory variable (Sex: female or male) in the allometric growth analyses, as follows: Model 1, $lny \sim lnCW + lnCW \times Sex$; and Model 2, $\ln y \sim \ln CW$, where y is the cheliped or pleon size; we then selected the model with the lower AIC value (Akaike 1973). The models showed whether the allometric growth equation had the same intercept and different slopes (Model 1) or the same intercept and slope (Model 2) between the different sexes. When Model 1 was selected, intersexual dimorphism was detected.

Table 1. Collection records for porcellanid crab *Petrolisthes japonicus* specimens, collected from April 2008 to March2009 on an intertidal cobble and boulder shore on the Boso Peninsula, Japan

Sampling date	Total number of crabs	Number of females	Number of ovigerous females	Number of lost cheliped females	Number of intact females	Number of males	Number of lost cheliped males	Number of intact males	Number of unsexed juveniles	Number of lost cheliped juveniles	Number of intact juveniles
April 21	86	40	0	4	36	46	6	40	0	0	0
May 19	190	86	6	19	67	104	25	79	0	0	0
June 19	142	74	59	11	63	68	15	53	0	0	0
July 18	120	61	52	15	46	57	7	50	2	0	2
August 19	107	41	29	10	31	32	14	18	34	16	18
September 16	125	47	9	4	43	44	2	42	34	9	25
October 16	73	15	0	6	9	27	8	19	31	10	21
November 26	25	12	0	5	7	10	4	6	3	0	3
December 14	104	39	0	9	30	64	15	49	1	0	1
January 17	111	60	0	10	50	50	8	42	1	0	1
February 14	91	49	1	14	35	42	9	33	0	0	0
March 16	85	44	0	5	39	41	13	28	0	0	0
Total	1259	568	156	112	456	585	126	459	106	35	71

To evaluate the monthly changes in intersexual size dimorphism, allometric growth Model 1 was applied using monthly data from April 2008 to March 2009. In this analysis, the data from October and November were pooled due to the small sample size in November (Table 1). Additionally, to detect the intrasexual dimorphism during the breeding and nonbreeding seasons, the allometric growth analyses were conducted separately for females and males based on the following model: $\ln y \sim \ln CW + \ln CW \times Season$, where *y* is the cheliped or pleon size and Season is the categorical explanatory variable (breeding season or non-breeding season). In our sample population of P. japonicus, ovigerous females were found from May to September and in February, but only one was detected in February (Table 1); therefore, the breeding and nonbreeding seasons were defined as the period from May

to September and the period from December to April, respectively.

RESULTS

The relationships among CW, cheliped propodus length and width, and pleon width are shown for the overall specimens of females, males and unsexed juveniles in figure 1. The data plots for unsexed juveniles were placed on the same line as those for smaller females and males. Of the two log-transformed allometric growth equation models applied to the cheliped and pleon dimensions of females and males, Model 1 was selected (Table 2), indicating the existence of intersexual size dimorphisms of the chelipeds and pleons of *P. japonicus*. The chelipeds had a larger

Table 2. Intersexual size dimorphism evaluated using a log-transformed allometric growth equation model for some body parts of the porcellanid crab *Petrolisthes japonicus*. Two models were applied: Model 1, $\ln y \sim \ln CW + \ln CW \times$ Sex and Model 2, $\ln y \sim \ln CW$, where CW is the carapace width, y is the measurement for another body part (cheliped propodus length and width, and pleon width) and Sex is female or male. The coefficient estimate with a standard error (SE) for each explanatory variable, including the Sex, was the output for males, 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.

Response variable	Coefficients and statistics		Мо	del 1		Model 2			
		Estimate	SE	t value	Р	Estimate	SE	t value	Р
Chela propodus length	Intercept	0.0292	0.0091	3.205	0.0014	0.0024	0.0113	0.212	0.8320
	InCW	1.1966	0.0057	209.346	< 0.0001	1.2398	0.0068	183.356	< 0.0001
	$lnCW \times Sex-Male$	0.0522	0.0023	22.856	< 0.0001				
	AIC	-2628				-2216			
	R^2	0.9832				0.9736			
	F	266670				33620			
	df	2, 912				1, 913			
	Р	< 0.0001				< 0.0001			
Chela propodus width	Intercept	-0.8382	0.0105	-79.690	< 0.0001	-0.8589	0.0117	-73.480	< 0.0001
	InCW	1.1794	0.0066	178.980	< 0.0001	1.2127	0.0070	174.010	< 0.0001
	$lnCW \times Sex-Male$	0.0403	0.0026	15.320	< 0.0001				
	AIC	-2368				-2161			
	R^2	0.9767				0.9707			
	F	19130				30280			
	df	2, 912				1, 913			
	Р	< 0.0001				< 0.0001			
Pleon width	Intercept	-0.4941	0.0089	-55.610	< 0.0001	-0.8589	0.0117	-73.480	< 0.0001
	InCW	1.1666	0.0056	209.560	< 0.0001	1.2127	0.0070	174.010	< 0.0001
	$lnCW \times Sex-Male$	-0.0921	0.0022	-41.410	< 0.0001				
	AIC	-2677				-2161			
	R^2	0.9800				0.9707			
	F	22390				30280			
	df	2,912				1, 913			
	Р	< 0.0001				< 0.0001			

allometric growth coefficient estimate in males (propodus length, b = 1.25; propodus width, b = 1.22) than in females (propodus length, b = 1.20; propodus width, b = 1.18), whereas the pleon width had a larger allometric growth coefficient estimate in females (b = 1.17) than in males (b = 1.07; Table 2).

Considering the relationships among CW, the cheliped propodus length and width, and the pleon width of females and males on a monthly basis (Figs. 2–4), the intersexual size dimorphisms of the

chelipeds and pleons appeared to be distinct during the breeding season from May to August, regardless of the reproductive status of the females (non-ovigerous or ovigerous). The seasonal changes in intersexual size dimorphism could be evaluated quantitatively by calculating the monthly coefficient estimates for the explanatory variable, including the Sex (*i.e.*, lnCW × Sex), which represented the degree of difference between the allometric growth coefficients of males and females (Fig. 5; Tables S1–S3). The coefficient



Fig. 1. Growth of the cheliped propodus length (A), cheliped propodus width (B) and pleon width (C) relative to the carapace width in overall specimens of the porcellanid crab *Petrolisthes japonicus*, collected from April 2008 to March 2009. Data are shown for females, males and unsexed juveniles.



Fig. 2. Growth in the cheliped propodus length relative to the carapace width in specimens of the porcellanid crab *Petrolisthes japonicus*, collected monthly from April 2008 (A) to March 2009 (K). Data are shown for females, ovigerous females and males. The data for October and November were pooled because of the small sample size in November.



Fig. 3. Growth of the cheliped propodus width relative to the carapace width in specimens of the porcellanid crab *Petrolisthes japonicus*, collected monthly from April 2008 (A) to March 2009 (K). Data are shown for females, ovigerous females and males. The data for October and November were pooled because of the small sample size in November.



Fig. 4. Growth in the pleon width relative to the carapace width in specimens of the porcellanid crab *Petrolisthes japonicus*, collected monthly from April 2008 (A) to March 2009 (K). Data are shown for females, ovigerous females and males. The data for October and November were pooled because of the small sample size in November.

estimates for the cheliped dimensions increased starting in April and peaked between June and July; they then declined, and the significant differences between the sexes in these coefficient estimates generally disappeared between December and March. The coefficient estimates of pleon width fluctuated similarly to those of the cheliped dimensions, but the differences between the sexes were still evident during the period from December to March. The intrasexual size dimorphisms of the chelipeds and pleons of females and males during the breeding (May to September) and non-breeding seasons (October to April) could be evaluated quantitatively by calculating the estimates of the explanatory variable, including the Season (*i.e.*, $lnCW \times Season$), which represented the degree of difference in the allometric growth coefficient between the breeding season and the non-breeding season (Fig. 6; Table S4). The coefficient



Fig. 5. Monthly changes in the intersexual size dimorphisms of the chelipeds and pleons of the porcellanid crab *Petrolisthes japonicus* specimens, collected from April 2008 to March 2009. Intersexual size dimorphism was represented by the coefficient estimates for the explanatory variable, including the Sex ($lnCW \times Sex$), in the log-transformed allometric growth equation model: $lny \sim lnCW + lnCW \times Sex$, where CW is carapace width, *y* is the measurement for another body part (cheliped propodus length and width, and pleon width) and Sex is female or male. The coefficient estimate of $lnCW \times Sex$ was the output for males, representing changes in the response variable relative to the baseline category (female) (Tables S1–S3), and thus also representing the degree of difference in the allometric growth coefficient between males and females. Vertical lines indicate standard errors. The dotted bars indicates the estimates that were not significantly different between sexes. The data for October and November were pooled because of the small sample size in November.



Fig. 6. Intrasexual size dimorphisms of the chelipeds and pleons during the breeding and non-breeding seasons of the porcellanid crab *Petrolisthes japonicus*, collected from April 2008 to March 2009. Intrasexual size dimorphism was represented by the coefficient estimate of the explanatory variable, including the Season ($InCW \times Season$), in the log-transformed allometric growth equation model: $Iny \sim InCW + InCW \times Season$, where CW is carapace width, *y* is the measurement for another body part (cheliped propodus length (PrL) and width (PrW), and pleon width (PlW)), and Season is the breeding season (May to September) or non-breeding season (October to April). The coefficient estimate of $InCW \times Season$ was the output for the breeding season, representing the change in the response variable relative to the baseline category (non-breeding season) (Table S4), and thus also representing the degree of difference in the allometric growth coefficient between the breeding season and non-breeding season. Vertical lines indicate standard errors. The dotted bar indicates an estimate that was not significantly different between the breeding season and non-breeding season.

estimates were significant positive values for the pleon widths of females and cheliped sizes of males, and they were significant negative values for the cheliped sizes of females, but not significantly different from zero in the pleon widths of males; thus, females increased pleon growth, but decreased cheliped growth, during the breeding seasons, whereas males increased the cheliped growth during the breeding season, but their pleon width remained unchanged regardless of the season.

DISCUSSION

The present study revealed the distinct intersexual size dimorphisms of the chelipeds and pleons of the porcellanid crab P. japonicus (Fig. 1); these dimorphisms were previously known for some porcellanid crab species inhabiting different oceans (Miranda and Mantelatto 2010; Baeza and Asorey 2012; Wassick et al. 2017). Overall, the chelipeds of males were larger than those of females, while the cheliped dimensions showed positive allometric growth in both sexes (b = 1.18 - 1.25). The pleon widths exhibited positive allometric growth in females (b = 1.17), but near-isometric growth in males (b = 1.07; Table 2). The ontogenetic changes in the allometric growth patterns appeared to be indistinct for the cheliped and pleon dimensions of female and male P. japonicus (Fig. 1), which matched one of the relative growth patterns in brachyuran crabs classified by McLay (2015), being only a single allometric phase of growth. The minimum CW value for the ovigerous P. japonicus females was 3.80 mm in our sampling population (Hamasaki et al. 2020b), and this was considered to be the size at the onset of sexual maturity in females. When observing the monthly plots of cheliped dimensions against the CW in females and males, particularly from May to July (Figs. 2 and 3), sexual size dimorphisms in the chelipeds appeared to increase after the crabs grew to about 4 mm CW; thus, the size at the onset of sexual maturity of males appeared to be similar to that of females.

Our analyses supported our expectation that seasonal changes in the sexual size dimorphisms of the chelipeds and pleons might occur in *P. japonicus* because of the high cost of producing and maintaining such large organs (Allen and Levinton 2007; Wilson et al. 2009; Doake et al. 2010). In *P. japonicus*, the intersexual size dimorphisms of the chelipeds and pleons began to increase starting in April, peaked in June and July, declined from October to November, and then disappeared (chelipeds) or steadied (pleon) during the overwintering period from December to March (Fig. 5). Intrasexual size dimorphisms of the chelipeds and pleons were also identified in both sexes during the breeding season, from May to September, and non-breeding season, from October to April (Fig. 6), highlighting that the sex-specific resource allocation and reproductive strategies depended on the season. During the breeding season, females allocated more energy to pleon growth, while reducing cheliped growth, and the investment in pleon growth increased with increasing female body size (b = 1.23), whereas males invested their energy in cheliped growth, an investment that increased with increasing body size (propodus length, b = 1.29; propodus width, b = 1.24), but their pleon width remained unchanged, regardless of the season. In the nonbreeding season, females and males saved their energy by reducing the sizes of their pleons and chelipeds relative to their respective body sizes.

We used crab specimens collected for our previous study, which investigated the reproductive traits and population structure of a P. japonicus population (Hamasaki et al. 2020b). In the studied population of P. japonicus, when August (in which the first main recruitment occurred) was considered as the age transition month, three age groups (*i.e.*, 0+, 1+, and 2+ age groups) were detected. The crabs in the 0+age group began to breed in the year after hatching; therefore, it was presumed that 0+ aged P. japonicus females and males began to increase their pleon and cheliped growth, respectively, through moulting just before the breeding season in the year after hatching. After the breeding season, the crabs in the 1+ age group invested more energy in somatic growth than in the growth of these organs; then, during the next breeding season, 1+ aged crabs likewise allocated more energy to their pleon and cheliped growth; finally, the crabs in the 2+ age group died at the end of this next breeding season. To further elucidate the sex-specific and season-dependent resource allocation and reproductive strategies in P. japonicus, future laboratory culture experiments will be required to trace seasonal changes in the relative growth patterns of the chelipeds and pleons in individual male and female crabs.

The porcellanid pleon functions as an egg incubatory chamber, and eggs are attached to the paired pleopods on each of the pleomeres 3-5 (Jones 1977; Osawa and McLaughlin 2010). Regarding the allometric growth analysis of fecundity (*i.e.*, the number of eggs attached to the female pleopods), the allometric growth coefficient was categorised as positive allometry (b > 3), isometry (b = 3), or negative allometry (b < 3) (Bauer 1991). The fecundity of *P. japonicus* generally showed positive allometric growth (Hamasaki et al. 2021), linked to a wider pleon with positive allometric growth in females during the breeding season (b = 1.23). Female pleons exhibited a greater allometric growth coefficient, even during the nonbreeding season (b =

The chelipeds of the porcellanid crabs are broad, dorsoventrally flattened and large relative to their body size (Jones 1977; Barría and González 2008; Osawa and McLaughlin 2010). These chelipeds are known to be involved in intraspecific agonistic and sexual communications in porcellanid crabs. Molenock (1976) examined agonistic behaviour in four intertidal freeliving Petrolisthes species, P. cabrilloi Glassell 1945, P. cinctipes (Randall 1840), P. eriomerus Stimpson 1871 and P. manimaculis Glassell 1945, reporting that the crabs forcefully extended one or both chelipeds, often repeatedly, and pushed nearby crabs out of their space with their chelae. Baeza et al. (2002) documented that the sea anemone-dwelling species Allopetrolisthes spinifrons (H. Milne Edwards 1837) displayed the merus of the chelae closest to the opponent, subsequently attempting to push this opponent crab away from the host sea anemone, and if the interactions escalated, the crab grasped both the chelae of the other crab. During these agonistic interactions, the majority of larger crabs gained or retained the space or host (Molenock 1976; Baeza et al. 2002). Molenock (1975) investigated the courtship behaviour of the four Petrolisthes species mentioned above and reported that a male guarded a receptive female or females before copulation by marking a territory; the females deposited eggs on their pleopods within a few hours of copulation, and males displayed their chelae to the courting females. Accordingly, selection might favour a large body with large chelipeds in porcellanid crabs to monopolize resources in intraspecific agonistic and sexual interactions. The males of P. japonicus grew larger than the females and the sexual dimorphism of their body sizes became evident after the beginning of their first breeding season (Hamasaki et al. 2020b), and, also, males had an ability to change energy allocation to produce larger chelipeds with more positive allometric growth during the breeding season (the present study). Consequently, the sexual size dimorphisms of the bodies and chelipeds of *P. japonicus* might be the consequence of sexual selection (*i.e.*, male-male competition).

The importance of male sexual competition as an evolutionary force driving sexual size dimorphisms of the bodies and chelipeds of porcellanid crabs was supported by a study by Baeza and Asorey (2012) that used two closely related species of symbiotic porcellanid crabs (which they treated as *Petrolisthes*). In *Liopetrolisthes mitra* (Dana, 1852), which inhabits sea urchins as dense aggregations, male sexual competition was recurrent and sexual size dimorphisms of the bodies and chelipeds were evident, whereas in solitary *A. spinifrons*, which inhabit sea anemones, male sexual competition was negligible, such sexual dimorphism of body size was not detected, and differences in relative cheliped size were small (Baeza and Asorey 2012). Baeza and Asorey (2012) also argued that alternative mechanisms to explain the sexual size dimorphisms of these two species remain to be explored (*e.g.*, female mate choice).

CONCLUSIONS

Our allometric growth analyses revealed seasonal changes in the sexual size dimorphisms of the chelipeds and pleons of the porcellanid crab Petrolisthes japonicus. In the porcellanid crab species, pleons can function as a brood chamber in females, and chelipeds can act as weaponry and/or display features in intraspecific agonistic and sexual communications, particularly in males. During the breeding season, P. japonicus females allocate more energy to pleon growth, whereas males invest their energy in cheliped growth, and they save energy by reducing the relative size of these organs during the non-breeding season; thus, the present study highlights the sex-specific and season-dependent resource allocation and reproductive strategies of P. japonicus. To further elucidate the reproductive ecology of *P. japonicus*, the relative growth patterns of the chelipeds and pleons should be traced for individual crabs, and sexual selection, including malemale competition and female mate choice, should be evaluated using laboratory experiments.

Acknowledgments: We thank Minako Ishii for collecting and measuring crab specimens. We are grateful to the anonymous reviewer and the editor for their valuable comments and suggestions, which have improved the manuscript.

Authors' contributions: KH designed the study. KH and SD analysed the data and prepared the manuscript. All authors approved the final manuscript.

Competing interests: The authors declare that they have no conflicts of interests.

Availability of data and materials: All data are provided within the manuscript and supplementary materials.

Consent for publication: Not applicable.

Ethics approval consent to participate: The

present study complied with current Japanese laws.

REFERENCES

- Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. *In*: Petrov BN, Csaki F (eds) 2nd international symposium on information theory, Tsahkadsor, Armenia, USSR, September 2–8, 1971. Akadémiai Kiadó, Budapest, pp. 267–281.
- Allen BJ, Levinton JS. 2007. Costs of bearing a sexually selected ornamental weapon in a fiddler crab. Funct Ecol **21:**154–161. doi:10.1111/j.1365-2435.2006.01219.x.
- Baeza JA, Asorey CM. 2012. Testing the role of male-male competition in the evolution of sexual dimorphism: a comparison between two species of porcelain crabs. Biol J Linn Soc 105:548–558. doi:10.1111/j.1095-8312.2011.01803.x.
- Baeza JA, Stotz W, Thiel M. 2002. Agonistic behaviour and development of territoriality during ontogeny of the sea anemone dwelling crab *Allopetrolisthes spinifrons* (H. Milne Edwards, 1837) (Decapoda: Anomura: Porcellanidae). Mar Fresh Behav Physiol **35**:189–202. doi:10.1080/1023624021000003817.
- Barría EM, González MI. 2008. Effect of autotomy and regeneration of the chelipeds on growth and development in *Petrolisthes laevigatus* (Guérin, 1835) (Decapoda, Anomura, Porcellanidae). Crustaceana 81:641–652. doi:10.1163/156854008784513447.
- Bauer RT. 1991. Analysis of embryo production in a caridean shrimp guild from a tropical seagrass meadow. *In*: Wenner AM, Kuris A (eds) Crustacean issues 7: crustacean egg production. AA Balkema, Rotterdam, pp. 181–191.
- Bueno SLS, Shimizu RM. 2009. Allometric growth, sexual maturity, and adult male chelae dimorphism in *Aegla franca* (Decapoda: Anomura: Aeglidae). J Crust Biol 29:317–328. doi:10.1651/07-2973.1.
- Christy JH. 1982. Burrow structure and use in the sand fiddler crab, Uca pugilator (Bosc). Anim Behav 30:687–694. doi:10.1016/ S0003-3472(82)80139-5.
- Christy JH. 1983. Female choice in the resource-defense mating system of the sand fiddler crab, *Uca pugilator*. Behav Ecol Sociobiol 12:169–180. doi:10.1007/BF00343209.
- Cothran RD. 2020. Sexual selection and sexual conflict in crustaceans. *In*: Cothran RD, Thiel M (eds) The natural history of the crustacea: reproductive biology, Vol 6. Oxford University Press, New York, NY, USA, pp. 305–331.
- Crane J. 1975. Fiddler crabs of the world: Ocypididae: genus *Uca*. Princeton University Press, New York, NY, USA.
- Davie PJF, Guinot D, Ng PKL. 2015. Anatomy and functional morphology of Brachyura. *In*: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (eds) Treatise on zoology anatomy, taxonomy, biology. The crustacea, Vol. 9 Part C (71-2). Brill, Leiden, pp. 11–163. doi:10.1163/9789004190832 004.
- Doake S, Scantlebury M, Elwood RW. 2010. The costs of bearing arms and armour in the hermit crab *Pagurus bernhardus*. Anim Behav 80:637–642. doi:10.1016/j.anbehav.2010.06.023.
- Emlen DJ. 2008. The evolution of animal weapons. Annu Rev Ecol Evol Syst 39:387–413. doi:10.1146/annurev.ecolsys.39.110707.173502.
- Flores A, Negreiros-Fransozo ML. 1999. Allometry of the secondary sexual characters of the shore crab *Pachygrapsus transversus* (Gibbes, 1850) (Brachyura, Grapsidae). Crustaceana 72:1051– 1066. doi:10.1163/156854099504013.
- Hamasaki K, Ishii M, Dan S. 2020b. Reproductive traits and population structure of the porcellanid crab *Petrolisthes*

japonicus (Decapoda: Anomura: Porcellanidae). Crust Res **49:**121–132. doi:10.18353/crustacea.49.0_121.

- Hamasaki K, Ishii M, Dan S. 2021. Seasonal variability in fecundity and egg size in the porcellanid crab *Petrolisthes japonicus* (Decapoda: Anomura: Porcellanidae). Crust Res **50**:17–27. doi:10.18353/crustacea.50.0_17.
- Hamasaki K, Osabe N, Nishimoto S, Dan S, Kitada S. 2020a. Sexual dimorphism and reproductive status of the red swamp crayfish *Procambarus clarkii*. Zool Stud **59:**7. doi:10.6620/ZS.2020.59-07.
- Hartnoll RG. 1974. Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). Crustaceana 27:131–136. doi:10.1163/156854074X00334.
- Hartnoll RG. 1978. The determination of relative growth in crustacea. Crustaceana **34:**281–293. doi:10.1163/156854078X00844.
- Hazlett BA. 1968. The sexual behavior of some European hermit crabs (Anomura: Paguridae). Pub Staz Zool Napoli **36:**238–252.
- Hazlett BA. 1972. Shell fighting and sexual behavior in the hermit crab genera *Paguristes* and *Calcinus*, with comments on *Pagurus*. Bull Mar Sci **22**:806–823.
- Huxley JS. 1932. Problems of relative growth. Dial Press, New York, NY, USA.
- Jones MB. 1977. Breeding and seasonal population changes of *Petrolisthes elongatus* (Crustacea, Decapoda, Anomura) at Kaikoura, New Zealand. J Roy Soc New Zeal 7: 259–272. doi:1 0.1080/03036758.1977.10419428.
- Koga T, Yoshino K, Fukuda Y. 2010. Temporal changes in the reproductive population structures and male's secondary sexual character of the hermit crab *Diogenes nitidimanus*. Ecol Res 25:1007–1017. doi:10.1007/s11284-010-0727-x.
- Lavalli KL, Spanier E. 2015. Predator adaptations of decapods. In: Thiel M, Watling L (eds) The natural history of the Crustacea: lifestyles and feeding biology, Vol 2. Oxford University Press, New York, NY, USA, pp. 190–228.
- Lee SY. 1995. Cheliped size and structure: the evolution of a multifunctional decapod organ. J Exp Mar Biol Ecol **193**:161–176. doi:10.1016/0022-0981(95)00116-6.
- Mariappan P, Balasundaram C, Schmitz B. 2000. Decapod crustacean chelipeds: an overview. J Biosci 25:301–313. doi:10.1007/ BF02703939.
- McLay CL. 2015. Moulting and growth in Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (eds) Treatise on zoology - anatomy, taxonomy, biology. The crustacea, Vol. 9 Part C (71-5). Brill, Leiden, pp. 245–316. doi:10.1163/9789004190832_007.
- Miranda I, Mantelatto FL. 2010. Sexual maturity and relative growth of the porcellanid crab *Petrolisthes armatus* (Gibbes, 1850) from a remnant mangrove area southern Brazil. Nauplius **18**:87–93.
- Miyake S. 1998. Japanese crustacean decapods and stomatopods in color, Vol I. Macrura, Anomura and Stomatopoda, 3rd Print. Hoikusha, Osaka. (in Japanese)
- Molenock J. 1975. Evolutionary aspects of communication in the courtship behavior of four species of anomuran crabs (*Petrolisthes*). Behaviour **53**:1–29. doi:10.1163/156853975X00524.
- Molenock J. 1976. Agonistic interactions of the crab *Petrolisthes* (Crustacea, Anomura). Z Tierpsychol **41:**277–294. doi:10.1111/j.1439-0310.1976.tb00483.x.
- Nakasone Y. 1972. Observations of the reproductive cycle of *Petrolisthes japonicus* (De Haan) (Anomura: Porcellanidae). Bull Sci Engin Div Univ Ryukyus, Math Nat Sci **15:**127–135.
- Osawa M, McLaughlin PA. 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part II Porcellanidae. Raffles Bull Zool Suppl **23**:109–129.

- Pope DS. 2000. Testing function of fiddler crab claw waving by manipulating social context. Behav Ecol Sociobiol **47:4**32–437. doi:10.1007/s002650050687.
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/. Accessed 22 June 2020.
- Soundarapandian P, Varadharajan D, Ilavarasan N, Kumar J, Kumar A. 2013. Mating behaviour of flower crab, *Charybdis feriata* (Linnaeus). J Mar Sci Res Dev **3**:127. doi:10.4172/2155-9910.1000127.
- van den Brink AM, McLay CL. 2010. Competing for last place: mating behaviour in a pill-box crab, *Halicarcinus cookii* (Brachyura: Hymenosomatidae). Zool Anz **249:**21–32. doi:10.1016/j.jcz.2010.01.002.
- Waiho K, Mustaqim M, Fazhan H, Norfaizza WIW, Megat FH, Ikhwanuddin M. 2015. Mating behaviour of the orange mud crab, *Scylla olivacea*: the effect of sex ratio and stocking density on mating success. Aquacult Rep 2:50–57. doi:10.1016/ j.aqrep.2015.08.004.
- Wassick A, Baeza JA, Fowler A, Wilber D. 2017. Reproductive performance of the marine green porcelain crab *Petrolisthes armatus* Gibbes, 1850 in its introduced range favors further range expansion. Aquat Invasions 12:469–485. doi:10.3391/ ai.2017.12.4.05.
- Wasson K, Lyon BE, Knope M. 2002. Hair-trigger autotomy in porcelain crabs is a highly effective escape strategy. Behav Ecol 13:481–486. doi:10.1093/beheco/13.4.481.
- Wilson RS, James RS, Bywater C, Seebacher F. 2009. Costs and benefits of increased weapon size differ between sexes of the slender crayfish, *Cherax dispar*. J Exp Biol **212**:853–858. doi:10.1242/jeb.024547.
- Yasuda C, Suzuki Y, Wada S. 2011. Function of the major cheliped in male-male competition in the hermit crab *Pagurus nigrofascia*. Mar Biol **158**:2327–2334. doi:10.1007/s00227-011-1736-1.
- Yasuda C, Takeshita F, Wada S. 2012. Assessment strategy in malemale contests of the hermit crab *Pagurus middendorffii*. Anim Behav 84:385–390. doi:10.1016/j.anbehav.2012.05.007.
- Yasuda CI, Otoda M, Nakano R, Takiya Y, Koga T. 2017. Seasonal change in sexual size dimorphism of the major cheliped in the hermit crab *Pagurus minutus*. Ecol Res **32**:347–357. doi:10.1007/s11284-017-1438-3.

Supplementary materials

Fig. S1. Scatter plots for the propodus length (A) and width (B) of the right and left chelipeds of the porcellanid crab *Petrolisthes japonicus*. The line indicates the same size for the right and left cheliped dimensions. (download)

Table S1. Monthly analyses of intersexual size dimorphism, evaluated with a log-transformed allometric growth equation model for the chela propodus length (PrL) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: $lnPrL \sim lnCW + lnCW \times Sex$, where CW is the carapace width and Sex is female or male. The coefficient estimate with a standard error (SE) for the explanatory variable, including the Sex, was the output for males, 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. The data for October and November were pooled because of the small sample size in November. (download)

Table S2. Monthly analyses of inter-sexual size dimorphism, evaluated with a log-transformed allometric growth equation model for the chela propodus width (PrW) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: $lnPrW \sim lnCW + lnCW \times Sex$, where CW is the carapace width and Sex is female or male. The coefficient estimate with a standard error (SE) for the explanatory variable including the Sex, was the output for males, 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. The data for October and November were pooled because of the small sample size in November. (download)

Table S3. Monthly analyses of inter-sexual size dimorphism, evaluated with a log-transformed allometric growth equation model for the pleon width (PlW) of the porcellanid crab *Petrolisthes japonicus*. The linear equation model was as follows: lnPIW $\sim \ln CW + \ln CW \times Sex$, where CW is the carapace width and Sex is female or male. The coefficient estimate with a standard error (SE) for the explanatory variable including the Sex, was the output for males, 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. The data for October and November were pooled because of the small sample size in November. (download)

Table S4. Intrasexual size dimorphism during the breeding and non-breeding seasons, evaluated with a log-transformed allometric growth equation model for some body parts of the porcellanid crab Petrolisthes japonicus. The linear equation model was as follows: $\ln y \sim \ln CW + \ln CW \times Season$, where CW is the carapace width, y is the measurement for another body part (cheliped propodus length and width, and pleon width), and Season is the breeding season (May to September) or non-breeding season (October to April). The coefficient estimate with a standard error (SE) for the 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. (download)