Bull. Fac. Fish. Hokkaido Univ.
51(1), 1-11, 2000.

Seasonal Growth Pattern and the Effect of Gastropod Shells on Sexual Growth Rates in the Hermit Crab *Pagurus middendorffii*

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Abstract

I described the seasonal growth pattern of male and female of the hermit crab *Pagurus middendorffii* and examined the effect of shell size on the growth rate in laboratory experiments. Both sexes showed high molt frequencies during spring and summer, and low frequencies in winter. Significant differences in sexual molting frequencies were in March, May and December. Sexual differences in increment rate of molting varied depending on size and season: the difference was significant in the large size class. Neither size nor season affected the increment rates of the small size class. The effects of shell size relative to crab size were found, and males grew faster than females in adequate shell size.

Key words: Growth, Seasonal pattern, Sexual difference, Hermit crab, *Pagurus middendorffii*

Introduction

While growth of crustaceans is usually affected by various intrinsic and environmental factors, such as maturity, temperature and amount of food (Conan, 1985; Hartnoll, 1985), the most important factor affecting growth rate in hermit crabs is gastropod shells that crabs occupy (Fotheringham, 1976a). Growth rate affects the fitness of hermit crabs because growth is directly and indirectly related to fitness components, such as body size, survival rate, female fecundity and male competitive ability to obtain mates (Wada et al., 1995, 1999a, b). Several authors have pointed out that hermit crabs suppress their growth when they occupy small shells (Markham, 1968; Fotheringham, 1976a, b; Asakura, 1992).

How do hermit crabs suppress their growth rate? Three ways are possible: long duration between molts, low increment rate per molt, or both of them. Experimental studies showed that both shell size and type (i.e., gastropod species) affect the growth rate of hermit crabs (Markham, 1968; Fotheringham, 1976a, b). However, they measured neither molt duration nor increment rate per molt. Although sexual difference in the growth rate was reported in these experiments, and sexual size dimorphism in which males are larger than females was reported in many hermit crabs (e.g., Harvey, 1990; Wada, 1999), how males grow faster than females in hermit crabs remains unclear. This study examined these questions for *Pagurus middendorffii*.

Shell resource may determine the population structure of hermit crabs and the degree of sexual size dimorphism (e.g., Wada, 1999). However, few studies have

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described the seasonal molting pattern of hermit crabs (but see, Asakura, 1992). In this paper, I describe the seasonal molting pattern of male and female *P. middendorffii*, and also estimated the shell-size adequacy of each individual with "shell adequacy index (SAI)" proposed by Vance (1972).

Materials and Methods

Study Site and Animals

The study site was at Kattoshi, on the west side of Hakodate Bay, along the coast of southern Hokkaido, Japan. Wada et al. (1995) describe the physical features of this site.

Pagurus middendorffii is a common hermit crab in Hakodate Bay. Its distribution extends to the Sea of Okhotsk and the Bering Sea (Miyake, 1982). In Hakodate, females spawn a clutch per year in November and carry it for 3.5 months (Wada et al., 1995). Sexual selection affects male body size (Wada et al., 1996, 1999a, b) and the yearly molting frequency of males is higher than that of females (Wada et al., 1995).

Estimation of SAI

To assess the shell condition of hermit crabs in the field, I calculated SAI (Vance, 1972). First, I determined the shell size preferred by the crabs for each species of gastropod shell. As *P. middendorffii* generally uses four gastropod species, *Homalopoma sangarense*, *Reticunassa fratercula*, *Cantharidus japonicus*, and *Chlorostoma argyrostomum* at this study site, these four type shells were used for the experiment. I allowed crabs free access to about 300 shells of various sizes in a plastic aquarium (42 cm × 32 cm × 15 cm) for 48 hours so that the crabs could select shells according to their shell size preference. After the experiment, the shield length (the calcified anterior portion of the cephalothorax, SL) of the crabs and the aperture width of the occupied shells (AW) were measured. The relationship between SL and AW was analyzed using the following regression model:

$$\log SL = a + b \log AW \quad (1),$$

where a and b are constants.

I sampled *P. middendorffii* at Kattoshi in August 1993, identified the sex and the species of occupied shells, and measured the SL and AW. Then, I calculated the crab size for each shell by using the regression model. The quality of shell size for each crab in the field was assessed using SAI. The SAI is defined as:

$$SAI = (\text{suitable SL})/(\text{actual SL}) \quad (2).$$

Therefore, $SAI = 1$ indicates a crab occupying a suitable shell, $SAI > 1$, when a crab occupies a shell larger than the preferred size, and $SAI < 1$, when a crab occupies a shell smaller than the preferred size. I also used SAI in the following experiments to control the shell quality for size.

Short-Term Rearing Experiment

I made monthly short-term rearing experiments from January 1993 to January 1994 to estimate the seasonal growth pattern of *P. middendorffii* in the field. The

crabs were maintained individually in acrylic plastic cylinders (diameter × height = 52 mm × 85 mm) that were completely submerged in the plastic aquariums (42 cm × 32 cm × 15 cm in height) for 3 days. The crabs were unfed and seawater was not changed during the 3 days in captivity. When I found the empty exoskeletons of molting individuals, I fixed them in 5% formalin-seawater. Individuals that molted continued rearing at least for 1 day after molting. The molting frequency was calculated for each sex using:

(Molting frequency) = 100 × (number of molted crabs)/{(number of unmolted crabs) + (number of molted crabs)}.

After the experiment, I fixed all crabs in 5% seawater-formalin, identified the sex, and I measured the SL. The increment in SL per molt was calculated by the following equation:

(Increment rate) = (SL after molt)/(SL for exoskeleton) − 1 (3).

I assumed that crabs rearing for 3 days in the laboratory reflected the molting pattern in the field. This method was similar to that of Asakura (1992).

Long-Term Rearing Experiment

To examine the effect of shell size both on increment rate per molt and molt cycle of *P. middendorffii*, I made a long-term rearing experiment in which crabs were maintained until they molted twice. I randomly collected crabs in May 1993. First, I carefully cracked each crab's shell using a stationary vise. I then placed each crab in a small aquarium (17 cm × 13 cm × 8 cm) and provided a *H. sangarense* shell without attachment of calcareous algae to promote the crab taking off the crashed shell. As soon as the crab abandoned its old shell, I quickly removed both old and newly provided shell to obtain naked crabs for a short time. This procedure did not appear to injure the crabs.

I supplied immediately a new shell for each crab, and reared the crabs individually in a numbered small plastic aquarium with two net surfaces (78 mm × 48 mm × 69 mm). Each small aquarium was completely submerged in a large, aerated tank with a flow of filtered natural seawater. I observed the crabs daily and maintained each crab until it molted twice. During the rearing period, I supplied the crabs with sufficient food: dry shrimp every two days and fresh pieces of the sea weed *Neorhodomela larix* every week.

Every time a crab molted, I recorded the date and its molt was fixed in 5% formalin-seawater. After the experiment, I recorded the duration from the start of the experiment to each molting, measured the crab's SL and shell's AW, and calculated the increment rate. The growth rate per day of each individual was calculated as follows:

(Growth rate) = (Increment rate at second molt)/(Time between the first and second molt (day)) (4)

I used a total of 146 individuals for the experiments.

Table 1. Shell species used for free access experiment and coefficients for logarithmic function ($\log_{10}(SL)=a+b\log_{10}(AW)$). Ns and Nc are the number of shells and the number of crabs, respectively.

Shell species	Ns	Nc	a	b	r^2
Homalopoma nocturnum	340	41	−0.101	0.888	0.766*
Cantharidus japonicus	270	21	−0.061	0.759	0.772*
Chlorostoma argyrostomum	280	20	−0.077	0.762	0.783*
Reticunassa fraterculas	280	36	0.176	0.795	0.813*

*; $p<0.001$

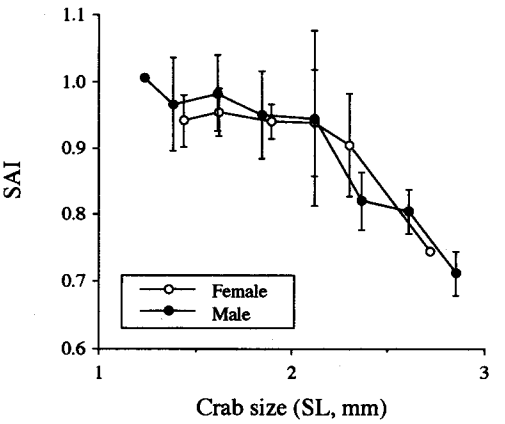

Fig. 1. Mean SAI by size classes for males and females of *Pagurus middendorffii* collected at Kattoshi. Vertical bars are 95% confidence intervals.

Results

SAI in the Field

Crab size and preferred shell size were positively and highly correlated in all shells of gastropod species tested (Table 1). I used equations (1) and (2) to calculate the SAI of individuals. The mean SAI in the field decreased with increasing crab size in both sexes (Fig. 1), and a significant correlation between SAI and crab size was found ((SAI)=1.203−0.145(SL), $r^2=0.268$, $n=237$, $p<0.001$). Although no sexual difference in SAI was found in most of the size classes, the SAI of females was better than that of males in the large size class (SL: 2.2-2.5 mm) (Mann-Whitney U-test, Table 2).

Short-Term Rearing Experiment

Figure 2 shows the monthly frequencies of molting in short-term rearing experiments. Male molting frequency per year was significantly higher than female frequency (χ^2-test, $p<0.05$). With monthly molting frequencies, males showed the highest frequency in May, while females peaked in March. Both sexes showed high molt frequencies during spring and summer, and low frequencies during winter. Comparing the molting frequencies between the sexes for each month, significant

Table 2. Comparisons of sexual SAI in each size class (Mann-Whitney U-test).

Size class (mm)	Sex	N	Mean SAI	p
1.24-1.6	male	17	0.963	0.402
	female	22	0.949	
1.6-1.9	male	13	0.972	0.426
	female	46	0.944	
1.9-2.2	male	5	0.956	0.495
	female	72	0.938	
2.2-2.5	male	19	0.827	0.005
	female	14	0.919	
2.5-3.0	male	28	0.779	0.503
	female	1	0.740	

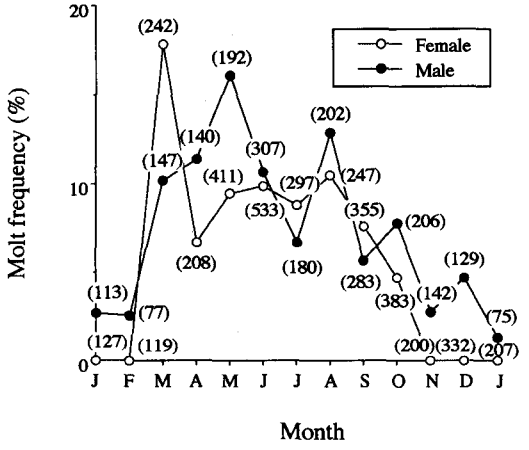

Fig. 2. Seaonal changes in molt frequency of *Pagurus middendorffii* from January 1993 to January 1994. Parentheses indicate the number of individuals for each sample.

differences were in March, May, and December (Fisher's exact probability test, $p<0.05$).

I classified the data of increment rate of molting in the short-term rearing experiment into four seasons: spring (March-May), summer (June-August), fall (September-November), and winter (December-February); the molt frequencies of males and females during winter were very low and zero, respectively (Fig. 2). Figure 3 shows the relationships of increment rate and crab size. Significant correlations existed in the relationships for females (spring: $Y=0.132\times0.035X$, $r^2=0.066$, $n=51$, $p<0.05$, summer: $Y=0.161-0.056X$, $r^2=0.186$, $n=74$, $p<0.001$, fall: $Y=0.117-0.038X$, $r^2=0.127$, $n=38$, $p<0.05$) but no significant correlations existed for males. The seasonal effect on increment rate was significant for males (ANOVA, Table 3), and, except for the difference between summer and winter and between fall and winter, significant differences were detected among seasons (Scheffe's post hoc comparison, Table 4). However, no significant effect of season

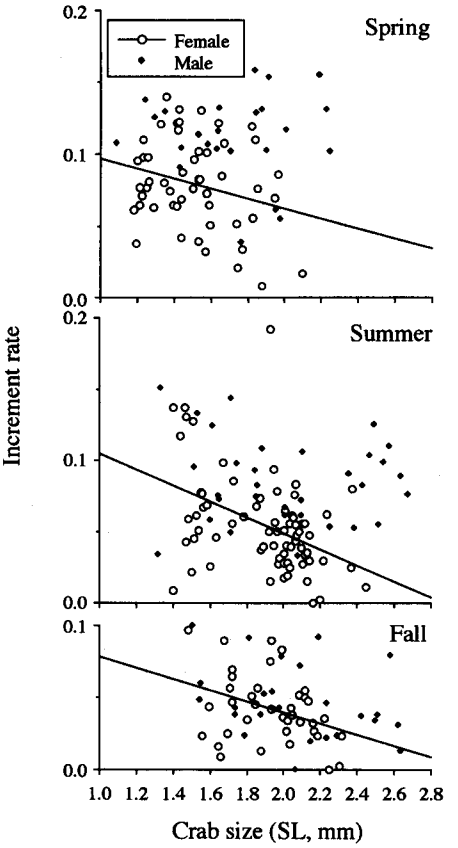

Fig. 3. Relationships between the increment rate of molting individuals and crab size (SL, mm) in short-term rearing experiments. In all three seasons, there were significant correlations (solid lines) between the increment rate and female size; $Y=0.132-0.035X$ ($r^2=0.066$, $p<0.05$), $Y=0.161-0.056X$ ($r^2=0.186$, $p<0.05$), $Y=0.161-0.056X$ ($r^2=0.127$, $p<0.05$), respectively. No significant correlation was detected in males.

Table 3. Results of ANOVA for the shor-term rearing experiments to examine the seasonal effect on the increment rate of male *Pagurus middendorffii*.

Source	*df*	Sum of Squares	Mean Square	*F*	*p*
Season	3	0.058	0.019	23.471	<0.001
Residual	83	0.069	0.001		

Dependent: Increment rate of male

was detected in the increment rate for females (ANCOVA, Table 5), although the probability is near to the significant level ($p=0.056$). Sexual differences in increment rate varied depending on size and season: The difference was significant in the large size class (SL: 1.8-2.3 mm) in spring and summer, but not in the fall. Neither size nor season affected the increment rates of the small size class (1.3-1.8 mm) (Mann-Whitney *U*-test, Table 6).

Table 4. Results of Scheffe's test for the short-term rearing experiment.

	Versus	Difference	Critical difference	
Summer	Spring	0.027	0.022	S
Fall	Spring	0.065	0.023	S
	Summer	0.038	0.022	S
Winter	Spring	0.004	0.040	S
	Summer	0.034	0.040	
	Fall	0.004	0.040	

S=Significantly different at $p<0.05$.

Table 5. Results of ANCOVA for the short-term rearing experiments to examine the seasonal effect on the increment rate of femle *Pagurus middendorffii*.

Source	*df*	Sum of Squares	Mean Square	*F*	*p*
Season	2	0.005	0.002	2.935	0.056
Crab Size	1	0.021	0.021	24.755	<0.001
Residual	159	0.134	0.001		

Dependent: Increment rate of female

Table 6. Sexual difference in increment rate.

Season	Size Class		Mean increment rate	*p*
Spring	1.3-1.8	male	0.105	0.732
		female	0.082	
	1.8-2.3	male	0.118	0.021
		female	0.067	
Summer	1.3-1.8	male	0.094	0.178
		female	0.073	
	1.8-2.3	male	0.080	0.021
		female	0.046	
Fall	1.3-1.8	male	0.052	0.802
		female	0.049	
	1.8-2.3	male	0.048	0.464
		female	0.042	

Table 7. Multiple regression analyses: correlations for SAI versus crab increment rate and time between start of experiment and molting.

	Coefficient	Standard coefficiest	*p*
Intercept	0.87		
Increment rate	2.09	0.53	0.0001
Time	−0.01	−0.29	0.0001

Table 8. Results of 3-way ANOVA for the long-term rearing experiment of examine the effect of shell size on growth of the hermit crab *Pagurus middendorffii*.

Source	*df*	Sum of Squares	Mean Square	*F*	*P*
Sex	1	3.00 (10^{-5})	29.97 (10^{-6})	14.49	<0.001
Size	3	0.41	1.37	0.66	0.576
SAI	2	6.09	30.45	14.72	<0.001
Sex* Size	3	0.56	1.86	0.90	0.443
Sex* SAI	2	0.93	4.65	2.25	0.110
Size* SAI	6	0.83	1.38	0.66	0.675
Sex* Size* SAI	3	0.57	1.89	0.91	0.436
Residual	121	25.02	2.07		

Dependent varibale: Growth rate

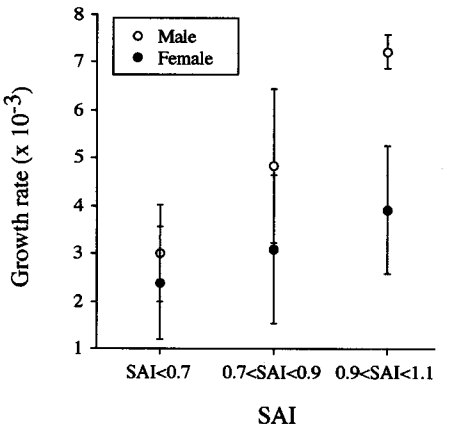

Fig. 4. The relationship between growth rate and SAI in the long-term rearing experiments. Error bars mean standard deviation.

Long-Term Rearing Experiment

SAI affected the time from the start of the experiment to first molting and the increment rate of first molting (multiple regression analysis, Table 7). After first molting of all individuals ($1.82<SL<2.53$ mm, $0.63<SAI<1.10$), I categorized them into four SL groups ($1.8<SL<2.0$, $2.0<SL<2.2$, $2.2<SL<2.4$, $2.4<SL<2.6$ mm) and three groups for SAI ($SAI<0.7$, $0.7<SAI<0.9$, $0.9<SAI<1.1$) and analyzed the effect of SAI and sex on growth rate during the period between the first and second moltings using three-way ANOVA. Clear sexual and SAI effects on the growth of *P. middendorffii* showed, but not for body size (ANOVA, Table 8). While the fact is clear that males grew faster than females in an adequate shell size, this sexual difference was vague for those in inadequate smaller shells ($SAI<0.7$, Fig. 4).

Discussion

Molting frequencies of both sexes varied seasonally, and the lowest frequency

Table 9. The existence of female molting just before copulation in the genus Pagurus. The references marked by * are shown after Hazlett (1975).

Species	Female molt	Reference
Pagurus miamensis	Usually	Hazlett 1966*
P. pygmaeus	Usually	Hazlett 1966*
P. bonairensis	No (ovigerous)	Hazlett 1966*
P. marshi	Yes	Hazlett 1966*
P. bernhardus	No (ovigerous)	Hazlett 1968*
P. cuanensis	No (ovigerous)	Hazlett 1968*
P. anachoretus	No	Hazlett 1968*
P. alatus	No (ovigerous)	Hazlett 1968*
P. prideauxi	No (ovigerous)	Hazlett 1968*
P. filholi	Usually	Goshima et al., 1998
P. lanuginosus	Yes	Wada et al., 1999
P. nigrofascia	Yes	Kanazawa unpublished

was observed in winter. The seasonal pattern of female molting frequency reflected their reproductive context in which females do not molt just before copulation, and during spawning (October to December) and egg incubation periods (about 3 months). I found no molting individuals from November to February, and the high molting frequency in March was the result of many females renewing their old exoskeletons. Although a frequently mentioned rule of crustacean reproductive behavior is that the female is soft from a recent molt just before copulation (thereby having a "soft" exoskelton), copulation without molting is not rare in the genus *Pagurus* (Table 9).

Lancaster (1990) suggested that females of *P. bernhardus* have lower growth rates than males because of molt suppression due to reproduction. Since the egg incubation period of *P. middendorffii* is longer than *P. bernhardus* (Lancaster, 1990), the difference in maximum size between males and females might partially be the result of female growth suppression during the egg incubation period. However, in *P. middendorffii*, both sexes show similar seasonal growth variation, and males also show lower molting frequencies and a lower increment rate during winter than other seasons, possibly due to environmental factors such as low temperature (Conan, 1985; Hartnoll, 1985).

I suggest that two components of sexual growth difference and effects of the shell would be important to proximately generate sexual size dimorphism of *P. middendorffii* in the field. One component is that males have a higher molting frequency throughout the year than females. The other factor is the higher increment rate for males that was especially observed in the large size class. Furthermore, results from the long-term rearing experiments suggest that SAI clearly affect the growth rate of *P. middendorffii*, and the degree of sexual difference in the growth rate. The SAI of each crab would also affects sexual size dimorphism of this species. Although males grew faster than females in the field, no significant sexual differences existed in the SAI for most size classes in the field, except for a large size class, suggesting that males change their shells into larger shells more frequently than

females and might be a superior competitor for shell resource.

Males often occupy different gastropod species shells from females in other hermit crabs (Abrams, 1988; Elwood and Kennedy, 1988; Gherardi, 1991; Asakura, 1995). Gastropod species of shells occupied by male hermit crabs might be more adequate for growth than shells occupied by females although my research has not examined this for *P. middendorffii*. Further studies are needed to clarify the effects of shell resource on the growth of hermit crabs in the field.

Acknowledgements

This study was partly supported by Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists.

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