Regeneration of major cheliped after the mating season in the hermit crab Pagurus middendorffii

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Abstract.—Males of the hermit crab Pagurus middendorffii use their major cheliped in male–male contests during the reproductive season. This study examined whether autotomized major chelipeds were regenerated before, during or after the mating season. We reared males that were experimentally induced to autotomize just before the mating season (October). During the mating season (November), few males molted even if they had autotomized their major cheliped. In contrast, males initiated a molt at the end of and after the mating season, and most of the autotomized males regenerated their major cheliped before the end of the rearing period (December). This suggests that regenerated major chelipeds in this study affect events other than mating, particularly perhaps future shell acquisition associated with general activities such as predator avoidance, physiological tolerance and growth.

Key words: Anomura, autotomy, major chela, molt, regrowth

Introduction

Chelipeds in decapod crustaceans are used in various contexts such as feeding (Lee & Seed, 1992; Lee, 1995), predator avoidance (Robinson et al., 1970) and reproduction (Muray & Backwell, 2005, 2006). In some species, chelipeds are weapons and can be predictors of fighting success in male–male contests (Emlen, 2008; Briffa, 2013). For example, Orconectes crayfish actively use their major chelipeds to grab and/or hold opponent during fighting (Moore, 2007). Males of Carcinus maenas perform cheliped displays during contests (Sneddon et al., 1997). The frequency of displays increases with cheliped length, and winners perform this display more often than losers (Sneddon et al., 1997). Yoshino et al. (2011) demonstrated that males with a larger cheliped than their opponent are more likely to win in male–male contests of the hermit crab Diogenes nitidimanus.

Because of the importance of the major cheliped, its loss could have negative impacts on male mating success in crustaceans. Individuals in many crustacean species can shed their appendages (i.e. autotomy, Juanes & Smith, 1995; Maginnis, 2006; Fleming et al., 2007) as a strategy to escape from predatory attacks (Robinson et al., 1970; Wasson et al., 2002). Crabs without the major cheliped, however, are less likely to win in male–male contests compared with intact crabs (Smith, 1992; Abello et al., 1994; Juanes & Smith, 1995; Daleo et al., 2009; Yasuda et al., 2011). Sekkelsten (1988) reported that crabs with cheliped loss show a lower mating success in the field.

Individuals with a regenerated major cheliped are expected to improve their competitive performance compared with those without a major cheliped (e.g. Backwell et al., 2000; Reney et al., 2008; Lailvaux et al., 2009). For example, in the fiddler crab Uca annulipes, males with a regenerated major cheliped use their chelipeds as a bluff against intruders in male–male contests for a territory (Backwell et
Neil (1985) demonstrated that, in the hermit crab *Pagurus bernhardus*, crabs with a regenerated major cheliped show a higher probability of winning than crabs without a major cheliped in contests over gastropod shells. Therefore, for males without a major cheliped, the regeneration of a major cheliped would be of considerable importance. We then hypothesized that males without a major cheliped would regenerate their lost major cheliped before the fighting events including male–male contests in the reproductive season.

*Pagurus* hermit crabs possess a larger right (i.e. major) cheliped, and males use it as a weapon during male–male contests during the reproductive season (Yasuda et al., 2011, 2012). Since the presence and/or the size of a major cheliped strongly affects the probability of winning in male–male contests (e.g. *P. nigrofascia*, Yasuda et al., 2011; *P. filholi*, Matsuo et al., in press; *P. middendorffii*, Yasuda et al., 2012), regeneration of the major cheliped would be effective to overcome, in part, the disadvantage of loss of the major cheliped by males in this group. Yasuda et al. (2014) demonstrated that males of *P. middendorffii* could largely regenerate their major cheliped in the first molt after autotomy requiring an average of 28 days. This study was conducted in the laboratory from late June to September. In the present study, we experimentally induced males of this species to autotomize the major cheliped in October. Since the mating season of *P. middendorffii* is from late October to early December in the study site (Wada et al., 1995), males in this study are considered to have autotomized the major cheliped just before the mating season. We predicted that autotomized males would invest more energy to regenerate the major cheliped during the mating season since the claw is important for mate actuation and defense. We further predicted that males would regenerate the major cheliped within a shorter period compared with a prior experiment.

### Materials and Methods

#### Experimental design

Males of *Pagurus middendorffii* were collected from the intertidal rocky shore on 18 and 19 October (i.e. just before the mating season) 2013 at Kattoshi, southern Hokkaido, Japan (41°44′N, 140°36′E). All crabs were brought back to the laboratory in a bucket with natural seawater. In the laboratory, each male was examined to check that they had all appendages. Intact males were randomly assigned to two experimental groups: regeneration (*N* = 90; R-males) or control (*N* = 50; C-males). Autotomy treatment was conducted on 24 October 2013 which formed the start of the rearing experiment. R-males were induced to autotomize their major cheliped by grasping it with forceps, and autotomy usually happened within three minutes. No crabs lost other appendages during this experimental procedure. There was no treatment for C-males. We measured the autotomized major cheliped for the propodus length (total length of propodus; PL) and width (maximum width; PW) in R-males to the nearest 0.01 mm under a stereomicroscope and used the data as the original size of the major cheliped for each crab.

Crabs in both groups were kept individually in small containers (14.3 × 10.8 × 7.2 cm) filled with natural seawater at 15°C and a depth of about 3 cm. They were fed each day artificial food (TETRA, Tetra Plankton) and *ad libitum* red alga (*Neorhodomela aculeata*, collected from the study site). The seawater was changed each day. We observed all crabs once a day and recorded whether the crab had molted or not. We measured PL and PW of the molted exoskeleton in R-males. The shield length (calcified anterior portion of the cephalothorax; SL) was also recorded as an index of the body size in both R- and C-males to the nearest 0.01 mm under a stereomicroscope. The rearing experiment ended on 25 December 2013, and final
measurements were made of SL, PL and PW of males in R-males and SL in C-males. The above experimental procedures were the same as our previous study (Yasuda et al., 2014) except no acclimation period was used in the present study.

Analyses

We compared the duration from autotomy to molt between groups using a Cox’s proportional hazard model (Cox, 1972) since 10 R-males and 23 C-males did not molt during the rearing period. The response variable was the duration until the molt (days) and the explanatory variables were the experimental manipulation (R- or C-male) and the initial SL (SL at the start of the experiment). Since 13 R-males did not regenerate the major cheliped at the molt (see Results), we examined the factors affecting regeneration of the major cheliped by using a generalized linear model (GLM) with a binomial error distribution. The response variable was whether or not the male regenerated the major cheliped (Yes = 1, No = 0, N = 80), and the explanatory variables were the initial SL and the number of days until molt.

In R-males, the original and regenerated PL or PW were compared using GLM with a normal error distribution (N = 67). The response variables were PL or PW, and the explanatory variables were SL and category (size of original or regenerated) and interaction between SL and category.

The growth in body size (difference between SL after the molt and initial SL) was compared between R- and C-males. Since all R-males regenerated the major cheliped after 33 days, to analyze the data on growth in SL, we used a subset of data in which the molt occurred after 33 days (R-males, N = 79; C-males, N = 26). The response variable was growth in body size (mm), and the experimental variables were the experimental manipulation, initial SL and the duration until molt. Also, we examined the effect of the major cheliped regeneration on SL growth by a GLM with a normal error distribution. The response variable was the same as above, and the explanatory variable was PL or PW. All statistical analyses were performed using R ver. 3.0.1 (R Core Team 2013).

Results

Although a small number of males molted during November (i.e. mating season) in both groups, most males molted after this month (Fig. 1). The occurrence of molting in R-males (88.9%) was significantly higher and of a shorter duration than C-males (54.0%) (Cox’s proportional hazard model; z = 5.523, P < 0.001; Fig. 1): 44.0 days (± 6.78 SD, N = 80)
from experiment initiation for R-males; 51.3 days (±7.89 SD, N = 27) for C-males. The frequency of molting in all males significantly decreased with increasing initial SL (z = -3.276, P = 0.001). Frequency of regeneration significantly decreased with the number of days (GLM; z = -2.542, P = 0.013; Fig. 1) but had no relationship with initial SL (z = 1.125, P = 0.264).

Most R-males regenerated their major cheliped during the molt after the experimental autotomy. The mean PL regeneration rate (regenerated PL as a percentage of original PL) was 72.72 (±11.02 SD) % (N = 67), and the mean duration from the day of autotomy to regeneration was 43.3 days ± 6.26 SD. There was a significant interaction between body size (SL) and category (original PL or regenerated PL) (GLM; Table 1a). The gradient of the linear regression between SL and PL is lower for regenerated PL than for the original (Fig. 2), indicating a clear decrease in the PL regeneration rate at the molt in relation to body size. Similarly, the mean regeneration rate in PW as a percentage of the original PW at the first molt was 66.22 (±11.67 SD) %, with a significant interaction between SL and category (original PW or regenerated PW) (GLM; Table 1b), and a shallower gradient for the regenerated compared with original PW (Fig. 3).

Growth in SL at the molt significantly decreased with initial SL in all males (GLM; t = -2.436, P = 0.017) while there was no difference between R-males (0.27 ± 0.34 SD mm, N = 79) and C-males (0.29 ± 0.20 SD mm, N = 26) (t = -0.263, P = 0.793). Duration until the molt also had no effect on the growth in SL (t = -0.456, P = 0.649). Both PL and PW of the regenerated major cheliped had no effect on SL growth (GLM; N = 67; PL, t = 1.492, P = 0.140; PW, t = 1.439, P = 0.155).

Discussion

Since we induced males of Pagurus midden-dorffii to autotomize their major cheliped just
before the mating season (i.e. October), we predicted that males would regenerate their major cheliped within a shorter period than a prior experiment in the non-mating season (Yasuda et al., 2014). However, the results in this study were opposite (Table 2). Yasuda et al. (2014) found that autotomized males initiated to regenerate on the 16th day and all of the males molted with an average of 28 days. In contrast, we found that the first major cheliped regeneration occurred on the 33rd day after autotomy and the mean duration until molting was about 44 days. 10 autotomized males did not molt during the rearing period. Males with a major cheliped loss in *P. middendorffii* therefore required a longer duration to regenerate major cheliped in the mating season than in the non-mating season, suggesting a lower investment for major cheliped regeneration in the mating season.

Although most R-males regenerated the major cheliped, the first male molted in late November and most molting occurred after the mating season. This, in part, can be explained as a conflict of interest between reproduction and growth. Kendall & Wolcott (1999) suggest that once males initiate their interest in mating, their physiological status might change causing a reduction of interest in molting to continue mating behavior. In *P. middendorffii* and *P. nigrofascia*, their mating seasons are limited to about one month and females produce only one clutch per year (Wada et al., 1995; Goshima et al., 1996), and almost all males immediately guard receptive females (Wada et al., 2011; Suzuki et al., 2012). On the other hand, *P. filholi* have a longer reproductive season (about 8 months) with laying several clutches (Goshima et al., 1998), and males do not guard receptive females especially when the males would molt within 5 days (Hasaba et al., 2015). Therefore in *P. middendorffii* and *P. nigrofascia* the opportunity for mating is more limited than *P. filholi*, and an investment for major cheliped regeneration in the mating season in *P. middendorffii* would potentially be restricted by constraints related to the physiological reproductive status. Alternatively, due to the softness of

Table 1. Comparisons between original and regenerated major cheliped analyzed by generalized linear model with a normal error distribution

(a) Relationship between PL and SL

| Estimate | SE   | t      | P    |
|----------|------|--------|------|
| Intercept| 0.223| 0.383  | 0.583| 0.561|
| SL       | 1.653| 0.087  | 19.013| < 0.001|
| Regeneration| 0.456| 0.563  | 0.810| 0.419|
| SL × Regeneration| −0.652| 0.124  | −5.260| < 0.001|

(b) Relationship between PW and SL

| Estimate | SE   | t      | P    |
|----------|------|--------|------|
| Intercept| 0.307| 0.243  | 1.262| 0.209|
| SL       | 0.875| 0.055  | 15.865| < 0.001|
| Regeneration| 0.461| 0.357  | 1.290| 0.200|
| SL × Regeneration| −0.463| 0.079  | −5.892| < 0.001|

PL, PW and SL indicate the propodus length and width of major cheliped and shield length (index of body size), respectively. Males were experimentally induced major cheliped autotomy and regenerated this appendage (*N* = 67).
Table 2. Summary of molting experiments conducted on males in *P. middendorffii* collected in Hakodate Bay

| Date        | Rearing period | Water temperature (°C) | N       | Molting frequency (%) | The number of days until molting | SL growth (mean ± SD, mm) | Regenerated major cheliped | Reference                  |
|-------------|----------------|------------------------|---------|------------------------|---------------------------------|---------------------------|---------------------------|----------------------------|
|             |                |                        |         |                        | Mean (± SD, days)              | The first day of regeneration | PL (mean ± SD, %)         | PL (mean ± SD, %)          |                            |
| Intact crab |                |                        |         |                        |                                 |                           |                          |                            |                            |
| Every month | 3 days         |                        | Nov.: 142 | less than 10           | —                               | —                         | —                         | —                          | Wada (2000)                |
| July. to Sep.| 2 month       |                        | Dec.: 129 | 91                     | 100.0                           | 27.5 ± 12.24               | 0.42 ± 0.16               | —                          | Yasuda *et al.*, (2014)    |
| Oct. to Dec.| 2 month       |                        | 15       | 150.0                  | 51.3 ± 7.89                     | 0.29 ± 0.20               | —                          | —                          | Present study              |
| Autotomized crab |       |                        | 15       | 150.0                  | 28.2 ± 6.76                     | 16th                      | 0.35 ± 0.14               | 86.63 ± 17.12             | Yasuda *et al.*, (2014)    |
| July. to Sep.| 2 month       |                        | 15       | 150.0                  | 44.0 ± 6.78                     | 33rd                      | 0.27 ± 0.34               | 72.72 ± 11.02             | Present study              |
| Oct. to Dec.| 2 month       |                        | 15       | 150.0                  |                                 |                           |                          |                            |                            |

PL, PW and SL indicate the propodus length and width of the major cheliped and shield length (index of body size), respectively.
the new exoskeleton (Duffy & Thiel, 2007), newly molted crabs have an ineffective weapon and/or armor and are less likely to win competitive interactions (e.g. Caldwell, 1987). In the field, precopulatory guarding males without a major cheliped can be found in Pagurus hermit crabs (Yasuda et al., 2011; CI Yasuda, personal observation). Taken together, males of *P. middendorffii* would show a lower investment for molting to regenerate the major cheliped during the mating season even if such males without a major cheliped are expected to become subordinate in male–male contests.

In general, individuals of *P. middendorffii* actively molt from spring to summer whereas few crabs molt during winter including their mating season (Wada, 2000; Table 2). However, males in this study initiated to molt at the end of and after the mating season, and finally most R-males and about a half of C-males molted before the end of rearing period (i.e. December; Table 2). The frequency of molting in our study is therefore considered to be clearly higher than that in the previous report by Wada (2000), although the methodology differed between the two studies. The higher molting frequency in the present study would be associated with the rearing environment. For example, the physiological cycle of reared males might be accelerated under the relatively higher water temperature (15°C) than the natural field (less than 10°C; Takahashi & Goshima, 2012) due to the positive relationship between temperature and metabolic rate in ectotherms (Angilletta, 2009). R-males, moreover, molted more often than C-males, suggesting that major cheliped autotomy still facilitates the next molt. This is consistent with the prior study of *P. middendorffii* (Yasuda et al., 2014) as well as other studies on crustacean (Hopkins, 1982; Juanes & Smith, 1995), and our results also suggest this facilitation of molting occurs even in seasons when the molting frequency is very low.

Although R-males autotomized major cheliped just before the mating season, they initiated to regenerate their major cheliped after the peak of the mating season. This suggests that the regenerated major cheliped in males after the mating season affects events other than achieving mating opportunities. For crustaceans, major chelipeds contribute to general activities other than reproduction such as feeding, predatory avoidance and agonistic interactions in the context of natural selection (e.g. Sneddon et al., 1997; Giraud, 2011). Regeneration of the major cheliped would therefore always be needed to overcome negative impacts during such activities by autotomy of this appendage. Especially in hermit crabs, the importance of the major cheliped has also been demonstrated during the assessment for unoccupied shells (Elwood & Neil, 1992) and competitions for shells (Neil, 1985; Imafuku, 1989; Elwood et al., 2006), and characteristics of occupied shells (e.g. size or species) often affect physiological tolerance (Davenport et al., 1980), predatory avoidance (Vance, 1972; Mima et al., 2003) and body size growth (Fotheringham, 1976; Blackstone, 1985). Regeneration of the major cheliped after the mating season could therefore be considered as an investment for future events related to natural selection by improving future shell acquisition. Moreover, an advantage of larger body size has been also reported in the contest outcomes of shell fights (Neil, 1985) and the degree of physiological tolerance (Davenport, 1972), suggesting body size growth is important regardless of major cheliped autotomy. If the molting after mating season is for such general activities, this could partly explain the lack of difference in body size growth between R- and C-males in this study. Further experimental studies will be needed to examine these possibilities.

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