Reproductive biology of the hermit crab *Pagurus middendorffii* Brandt (Decapoda: Anomura: Paguridae)

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*Abstract.* — Reproductive biology of the hermit crab *Pagurus middendorffii* was studied from August 1992 to January 1994 in Kattoshi, located along the west side of Hakodate Bay, Hokkaido, Japan. Its mating season was from late October to early December with a peak in early November. Ovigerous females were observed from October to March, with highest frequencies occurring from December to February (mean: 91.3%). Developmental stages of incubated eggs were synchronized within the population. Females were found to be able to reproduce in their first year and laying a single clutch each following year. Incubation period was about 3.5 months. While ovigerous females did not molt from November to March, male molting frequency was also low during the female incubation period. The covariation of male and female molt frequencies suggests that females do not necessarily have a growth disadvantage due to molt cessation during incubation.

*Introduction*

Hermit crabs have a unique character which is the occupation of empty snail shells to protect their soft abdomens. Many ecological and behavioral studies in hermit crabs have been presented, particularly focused on the relationship between the crabs and gastropod shells. However, most of these studies dealt with tropical or south-temperate hermit crab species (Ameyaw-Akumfi, 1975; Fotheringham, 1976a, b, 1980; Bertness, 1980, 1981a, b, c, d; Abrams, 1982a, b; Asakura & Kikuchi, 1984; Imafuku, 1984; Asakura, 1987, 1992; Hazlett, 1990), and studies of north-temperate hermit crabs are rare, except for *Pagurus bernhardus* (Neil & Elwood, 1985; Elwood & Stewart, 1987; Jackson & Elwood, 1989; Lancaster, 1990; Elwood & Neil, 1992). Furthermore, few studies give sufficient information on the reproductive biology of hermit crabs. Many studies showed only the temporal variation in the frequency of ovigerous females and, for example, did not investigate the temporal variation in the number of precopulatory pairs. The annual breeding time in most hermit crab species remains unknown.

*Pagurus middendorffii* Brandt is the common intertidal hermit crab in Hokkaido, which has been known to distribute in the Sea of Okhotsk and Bering Sea (Miyake, 1982). No ecological studies of reproduction have been conducted on this north-temperate species. The present paper aims to describe the reproductive biology of *P. middendorffii*. We describe the following data: temporal variation in the number of precopulatory pairs, frequencies of ovigerous and post-ovigerous females, pattern of molting, and developmental synchrony of incubated eggs among individuals. From these data it was possible to infer the strict breeding times in *P. middendorffii*.
Materials and Methods

Study site

The study site was located at Kattoshi, situated on the west side of Hakodate Bay, along the coast of southern Hokkaido, Japan (Fig. 1). The low-tide-platform is about 250 m offshore, and composed of a sand and pebble area, rocky flat area and boulder area. The slope of the platform is very gentle, and 80% of the platform is exposed at spring low tide. A detailed description of the biological and physical features of this site was provided by Nagata (1983).

Field sampling

We conducted monthly line transect sampling from August 1992 to July 1993. The arrangement of the sampling points is shown in Fig. 1. Three transects were positioned parallel to the shore line. A quadrat sample (50 cm x 50 cm) was taken at each sampling point. All P. middendorffii collected were fixed in 5% seawater formalin. In the laboratory crabs were removed by breaking open the shell and the shield length (the calcified anterior portion of the cephalothorax; hereafter, SL) was measured under a stereoscopic microscope with an ocular micrometer to 0.01 mm accuracy. Since all the crabs just after settlement had an undeveloped first pleopod, we referred to them as “unsexed”. We were able to identify the sex when the first pleopod was clearly developed (female) or degenerated (male).

To determine the incubation period for
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Fig. 2. Seasonal change of the size distribution of Pagurus middendorffii from August 1992 to July 1993. S.R. means sex ratio (Number of males / Total number of crabs).
Fig. 3. Reproductive season of *Pagurus middendorffii*: A, changes in the number of pairs for each sample; B, monthly changes in the frequency (%) of ovigerous females (●) and post-ovigerous females (○).

*P. middendorffii*, all females in the quadrats were classified into three categories: non-ovigerous, ovigerous, and post-ovigerous. Non-ovigerous females had neither eggs nor egg capsules on the pleopods and ovigerous females had eggs (and egg capsules). Post-ovigerous females had only egg capsules on the pleopods. Egg capsules were observed for some duration after the eggs hatched. We counted the eggs of 56 females collected on 20 November 1992 to determine the relationship between female SL and clutch size.

Like many other hermit crabs, *P. middendorffii* shows precopulatory guarding, in which the male primarily grasps the aperture of the shell occupied by the mature female with his left chela.
We also set up 3 permanent quadrats (one of them is 0.5 m x 50 m, and others 0.5 m x 20 m as drawn in Fig. 1) and counted the number of pairing crabs monthly from August 1992 to July 1993, except for from October to December. From October to December, we increased the counting frequency, with counts made on the following dates: October 13, 24, 26, and 29, November 9, 12, and 25, and December 9, 15, and 25.

Egg development
From November 1992 to February 1993, except for January 1993, we increased the sampling from monthly to semi-monthly and randomly selected 87 to 130 ovigerous females to examine the developmental stage of the eggs attached to the pleopods. Five stages of egg development were microscopically judged based on the amount of yolk and the development of the eye pigment. Stage A eggs were newly-deposited and completely filled with yolk. Stage B eggs had not less than 80% of their egg volume composed of yolk. Stage C eggs had 50-80% of their volume composed of yolk and no eye pigment was present. Stage D eggs had less than 50% composed of yolk and incompletely developed sub-oval eye pigment visible. Stage E eggs had well-developed oval eye pigment visible. We decided the egg stage for each individual as the egg stage of more than 50% of the clutch.

Seasonal variation in molt frequency
From January 1993 to January 1994 we randomly sampled hermit crabs during each spring low tide and individually maintained them in an incubator for 3 days. All specimens were sexed and the number of males, females, and individuals which molted were counted. Molting frequencies (i.e., 100 x (number of molted crabs) / ((number of molted crabs) + (number of unmolted crabs))) were calculated monthly for each sex. Crabs were unfed during the 3 days in captivity.

Results
Fig. 2 shows the monthly size structure of the P. middendorffii population from August 1992 to July 1993. Newly
settled crabs were observed from April to July. Sex ratios (i.e., the monthly percentages of males into each population) were significantly different from the expected 50% (p < 0.05, $\chi^2$-test) except for August 1992, February, and April 1993. Maximum sizes of males were always larger than those of females, and the mean sizes of males were also larger than those of females except during May. The mean sizes of males were not significantly larger than those of females in November and from June to September, significantly larger in October and from December to April, and mean female size was significantly larger in May (p < 0.05, Mann-Whitney $U$-test).

Pairs were found during the period from late October to early December with a peak in early November (Fig. 3A). All pairing females were non-ovigerous. Ovigerous females were observed from late October to early March, and post-ovigerous females from late February to late March (Figs. 2, 3B). Frequencies of ovigerous females were nearly constant from late November to early February (mean: 91.3%) and even the smallest females usually had a clutch at the same time (Fig. 2). Developmental stages of the incubated eggs were directly synchronized within the population (Fig. 4). Females did not molt just before copulation (Wada, personal observation) and clutch size increased as a function of female body size: Log[clutch size] = 0.85 + 3.59 Log[SL, mm] ($r^2 = 0.78$, p < 0.001, n = 56) (Fig. 5).

Table 1 shows the monthly frequencies of molting. Male molting frequency per year was significantly higher than female frequency ($\chi^2 = 4.1$, p < 0.05). Concerning monthly molting frequencies, males showed the highest frequency in May, while females peaked in March. Both sexes showed low molt frequencies during winter. Comparing the molting frequencies between the sexes for each month, there were significant differences in March, May, and December (Fisher's exact probability test, p < 0.05).

Fig. 5. Relationship between clutch size (Number of eggs) and female size (SL in mm) for *Pagurus middendorffii*. The equation of the regression line is $Y = 0.85 + 3.59X$ ($r^2 = 0.78$, n = 56, p < 0.001).
Table 1. Molt frequencies (%) of Pagurus middendorffii from January 1993 to January 1994. Numbers of individuals for each sample are indicated in parentheses.

<table>
<thead>
<tr>
<th>Month</th>
<th>Male</th>
<th>Female</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1993</td>
<td>2.7 (113)</td>
<td>0.0 (127)</td>
<td>1.3 (240)</td>
</tr>
<tr>
<td>Jan</td>
<td>2.6 (77)</td>
<td>0.0 (119)</td>
<td>1.0 (196)</td>
</tr>
<tr>
<td>Feb</td>
<td>10.2 (147)</td>
<td>17.8 (242)</td>
<td>14.9 (389)</td>
</tr>
<tr>
<td>Mar</td>
<td>11.4 (140)</td>
<td>6.7 (208)</td>
<td>8.6 (348)</td>
</tr>
<tr>
<td>Apr</td>
<td>16.1 (192)</td>
<td>9.5 (411)</td>
<td>11.6 (603)</td>
</tr>
<tr>
<td>May</td>
<td>10.7 (307)</td>
<td>9.9 (533)</td>
<td>10.2 (840)</td>
</tr>
<tr>
<td>Jun</td>
<td>6.7 (180)</td>
<td>8.8 (297)</td>
<td>8.0 (477)</td>
</tr>
<tr>
<td>Jul</td>
<td>12.9 (202)</td>
<td>10.5 (247)</td>
<td>11.6 (449)</td>
</tr>
<tr>
<td>Aug</td>
<td>5.7 (283)</td>
<td>7.6 (355)</td>
<td>6.7 (638)</td>
</tr>
<tr>
<td>Sep</td>
<td>7.8 (206)</td>
<td>4.7 (383)</td>
<td>5.8 (589)</td>
</tr>
<tr>
<td>Oct</td>
<td>2.8 (142)</td>
<td>0.0 (200)</td>
<td>1.2 (342)</td>
</tr>
<tr>
<td>Nov</td>
<td>4.7 (129)</td>
<td>0.0 (332)</td>
<td>1.3 (461)</td>
</tr>
<tr>
<td>Dec</td>
<td>1.3 (75)</td>
<td>0.0 (207)</td>
<td>0.4 (282)</td>
</tr>
<tr>
<td>1994</td>
<td>8.3</td>
<td>6.7</td>
<td>7.3</td>
</tr>
</tbody>
</table>

Discussion

While some hermit crab females molt just before copulation (Hazlett, 1975; Asakura, 1987), this is not the case in P. middendorffii. Concentrated pair occurrence and highly synchronized egg development in the present study (Figs. 3A, 4) suggest that each female spawns only once a year and has an incubation period of approximately 3.5 months. These data also suggest that the absence of molting females observed during November and December would result from their breeding and incubation. The high molting frequency of females in March (Table 1) would result in many crabs renewing their old exoskeleton. Lancaster (1990) suggested that females of P. bernhardus would have lower growth rates than males because of molt suppression due to reproduction. Since the incubation period of P. middendorffii seems to be long relative to P. bernhardus (Lancaster, 1990), the difference in maximum size between males and females (Fig. 2) might partially be the result of their long incubation period. However, in P. middendorffii, males also showed low molting frequencies during winter (Table 1), possibly due to low temperature (Hartnell, 1985; Conan, 1985). Although male molting frequency per year is significantly higher than female molting frequency, growth rate is determined by both molt frequency and molt increment (McLay, 1985). Furthermore, sexual size dimorphism would be the result of not only the sexual difference of growth but also that of survival. Some factors might affect the sexual size difference observed in P. middendorffii.

Fig. 2 shows that all size classes of females contained >50% ovigerous females during the incubation period. Therefore, females would have a clutch in their first year, when they are very small. Almost all hermit crabs live within empty gastropod shells, which are often available only in limited quantities (Vance, 1972a; Bach et al., 1976; Bertness, 1980). Shell utilization by hermit crabs affects their population size (Vance, 1972a), growth rate
(Markham, 1968; Fotheringham, 1976a, b; Bertness, 1981a, b), clutch size (Childress, 1972; Fotheringham, 1976b, 1980; Bertness, 1981a, b) and survival rate since inadequate shells cannot protect them well from various mortality factors, such as predation (Vance, 1972b). Lancaster (1990) has suggested that precocious breeding might be an adaptation enabling hermit crabs to overcome the problems of shell-limitation. Precocious breeding could help females avoid the need to attain a specific age or size before reproducing, which could result in the high mortality when large shells are scarce. Our results are consistent with this hypothesis.

The relationship between female size and clutch size in P. middendorffii (Log[clutch size] = 0.85 + 1.20 Log[SL]; \( r^2 = 0.78, p < 0.001, n = 56 \)) (Fig. 5) is more positive than those in other hermit crabs; e.g., Clibanarius digueti, Log[clutch size] = 2.41 + 0.44 Log[SL], \( r^2 = 0.50, p < 0.005, n = 15 \) (Harvey, 1990), and Diogenes nitidimanus, Log[clutch size] = 1.56 + 1.02 Log[SL], \( r^2 = 0.88, p < 0.001, n = 41 \) (Asakura, 1984). Many hermit crabs in nearshore waters containing C. digueti and D. nitidimanus seem to have more than one brood per year (Asakura, 1987; Harvey, 1990; Elwood & Neil, 1992). To have larger annual fecundity, the female in those species can increase either number of clutches per year or number of eggs per clutch. P. middendorffii females, however, lay eggs only once a year, and can only increase number of eggs per clutch. Therefore, the more positive relationship between egg number and female size observed in P. middendorffii might be an adaptation to have larger annual fecundity under the constraint of limited breeding season.

Ovigerous P. bernhardus, a north-temperate hermit crab species, usually occur in the same season as P. middendorffii (Elwood & Stewart, 1987; Lancaster, 1990; Elwood & Neil, 1992). However, as Elwood & Neil (1992) suggest, the breeding period in P. bernhardus varies with locality. Furthermore, other sympatric hermit crabs in the present study site show a variety of the seasonality (Wada, personal observation), as has been reported at other sites (Reese, 1968; Hazlett, 1981). We cannot easily consider the reproductive pattern observed in the present study as the typical pattern of north-temperate hermit crabs or the specific pattern of P. middendorffii. Further detailed ecological studies of this animal are needed to determine what factors are responsible for determining the reproductive season of the hermit crab P. middendorffii.

Acknowledgments

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