Temporal size covariation of mating pairs of the hermit crab *Pagurus middendorffii* (Decapoda: Anomura: Paguridae) during a single breeding season

Satoshi Wada, Takeshi Sonoda, and Seiji Goshima

**Abstract.** — Temporal size variation of precopulatory guarding males and females of the hermit crab *Pagurus middendorffii* were described from field data collected during a single breeding season, and the advantage of large size to males competing for mates was examined in a laboratory experiment. Larger males won in mate competition, and size assortative mating occurred in the peak and the late periods of the breeding season, but not in the early period. Both mating male and female sizes declined with time during the breeding period. The decrease in size of mating males with time might be caused by the trade-off between the present and future reproductive success, or by physiological constraints. Decreasing size of breeding females might be due to size-dependent variation in the allocation of reproduction and growth, or to physiological constraints experienced by small females.

**Introduction**

Recent behavioral studies have presented evidence that both external factors, such as predation risk and operational sex ratio, and internal factors, such as energy allocation and past experience, influence the mating behavior of various animals (Berglund, 1993, 1994, 1995; Downhower & Lank, 1994; Collins, 1995; Vepsäläinen & Savolainen, 1995; Godin & Briggs, 1996). Since these factors vary not only yearly, but also within a single breeding season (e.g., Grant *et al.*, 1995), some aspects of mating, such as the intensity of male-male competition, mate choice and size assortative mating, might vary within a single breeding season. A quantitative investigation throughout the breeding season is needed to clarify the details of the mating system of an organism in the field.

*Pagurus middendorffii* Brandt is a common hermit crab in the intertidal and shallow subtidal areas of Hokkaido in northern Japan. In Hakodate Bay, females of this species are iteroparous and typically spawn a single clutch per year during a restricted mating season from late October to early December, with a distinct peak in early November (Wada *et al.*, 1995). Like other hermit crabs (Asakura, 1987; Harvey, 1990; Elwood & Neil, 1992; Goshima *et al.*, 1996), *P. middendorffii* males perform precopulatory guarding behavior, in which a male grasps the rim of a shell occupied by a mature female with his left chela for several days before copulation. Although there are many ecological and behavioral studies dealing with guarding behavior in various crustacean species (e.g., Wellborn, 1995; Goshima *et al.*, 1995), few investigations have examined the temporal variation of this behavior throughout one mating season.

In this paper, we describe the temporal mating pattern of *P. middendorffii*, including the size distributions of guarding pairs and the degree of size assortative mating, and suggest possible causes of the temporal variation. Although a precopulatory guarding pairs is not synonymous
with a mating pair, since a pairing male might lose the female its guarding to another male, or one of the pair might be preyed upon, in this study we assume a guarding pair to be a mating pair.

Materials and Methods

Sampling was done on a flat, intertidal, rocky shore located along the southwest side of Hakodate Bay, southern Hokkaido, Japan (41°44'N, 140°36'E). The low-tide platform extends about 250 m offshore and has a very gentle slope. On 10 November, 25 November and 8 December 1992, we conducted line transect sampling with six quadrats (0.5 m × 0.5 m) located 100 m from and parallel to the shoreline to survey the variation in the frequency of ovigerous females among different size classes. All females collected were fixed in 10% seawater formalin and removed from their shells after the shell was broken. We determined whether each female had a clutch on the pleopods and measured the shield length (the calcified anterior portion of the carapace; hereafter, SL) under a stereoscopic microscope with an ocular micrometer to the nearest 0.01 mm. On 5 November and 5 December 1995, we conducted similar line transect sampling with ten quadrats and measured the SL of all specimens to determine the size distribution of both sexes in the area.

In 1995, to determine the temporal variation of male and female size during precopulatory guarding, we set up four permanent quadrats (0.5 m × 10 m), with two located 90 m from shore, and two located 110 m from shore. From the results of an investigation in 1992 in the same area (Wada et al., 1995), we distinguished the mating season into three periods: Early, period from the first observation of guarding behavior to when the total number of guarding pairs within the four quadrats reached 50; Peak, period when more than 50 pairs occurred within the four quadrats; and Late, period when the number of pairs fell below 50. We counted the number of precopulatory pairs present on 27 October, 4, 15, 25 November, and 4 December 1995, and collected guarding pairs on 6, 13, and 22 November 1995. We sampled once on each date. Collected pairs were fixed in 10% seawater formalin and the SL of each individual was measured.

We conducted a laboratory experiment to examine male competition for mates and the advantage of large size to males. Two males that had paired with females in the field were used for each set of experiments. First, a male (pairing male) and its mate were placed in an aquarium (17 cm × 13 cm × 8 cm). Another male (unpaired male), that was separated from its mate, was then introduced into the aquarium. After ten minutes observation, we recorded the result of the competition (i.e., which male won and guarded the female), and measured the SL of the males but not of the females. A total of 122 different males were examined in 61 sets of experiments.

Results

Since the minimum size of pairing males collected in the Peak period was 1.6 mm and the ovigerous frequency in the smallest size class of females (SL = 1.2 mm) was over 50% (see below), we determined the maturity size of males and females to be 1.6 mm and 1.2 mm, respectively. The mean SLs and standard deviations (hereafter, SD) of mature males in November and December 1995 were 1.92 ± 0.24 mm and 2.00 ± 0.33 mm, respectively, and those of mature females were 1.73 ± 0.24 mm and 1.73 ± 0.25 mm, respectively. There was no significant difference in the size distributions between the two months for either sex (Mann-Whitney U-test, P > 0.05).

Figure 1 shows the occurrence pattern of guarding pairs in 1995. We collected 22,
117, and 25 pairs from the four permanent quadrats in the Early, Peak, and Late periods, respectively. Throughout the mating season, males were significantly larger than their mates (Mann-Whitney U-test, $P < 0.001$), and size assortative mating was clearly detected (Fig. 2) ($P < 0.001$, $N = 164$, $r^2 = 0.319$). Assortative mating was observed in the Peak ($P < 0.001$, $N = 117$, $r^2 = 0.318$) and Late periods ($P < 0.001$, $N = 25$, $r^2 = 0.364$), but not in the Early period ($P > 0.05$, $N = 22$, $r^2 = 0.141$).

Although there was no significant change in the mean size of the whole population, temporal size decrease was detected in both males and females performing precopulatory guarding. The mean SLs ± SD of pairing males in the Early, Peak, and Late periods were $4.57 ± 1.43, 3.34 ± 1.39, 3.14 ± 1.10$ mm, respec-

---

**Fig. 1.** Temporal variation in the number of precopulatory guarding pairs of *Pagurus middendorffii* observed in the permanent quadrats. Three periods, Early (E), Peak (P) and Late (L), were determined by whether the number of pairs exceeded 50 pairs.

---

**Fig. 2.** The relationship between male SL (mm) and female SL (mm) in guarding pairs of *P. middendorffii*. Regression lines of Peak and Late periods are represented by solid line ($Y = 1.3944 + 0.1315X$, $N = 117$, $r^2 = 0.318$, $P < 0.001$) and dashed line ($Y = 0.2280 + 0.1383X$, $N = 25$, $r^2 = 0.364$, $P < 0.001$), respectively. Although a significant regression was also observed throughout the breeding season ($Y = 1.3787 + 0.1356X$, $N = 164$, $r^2 = 0.319$, $P < 0.001$), it is not shown because it largely overlaps to the line of the Peak period.
MATING OF PAGURUS MIDDENDORFFII

Fig. 3. Size frequency distribution of pairing males in the three breeding periods, Early, Peak, and Late.

Discussion

Size assortative mating is a common mating pattern in crustaceans (Crespi, 1989) and is well studied, particularly in the amphipod Gammarus pulex (e.g., Elwood & Dick, 1990; Ward & Porter, 1993). The present study demonstrates that P. middendorfii also shows size assortative mating throughout its breeding season (Fig. 2). Crespi (1989) classified all the hypotheses for size assortative mating into three types: those based on mate choice, mate availability, and constraints. In the present study, the assortative mating is due to a mate availability hypothesis, temporal covariation in male and female availability, in which assortative mating occurs as pairing male and female size covaries during the breeding season. Figures 3 and 4 show that this hypothesis is consistent with our results. Ridley & Thompson (1979) described a similar temporal covariation in male and female size for Aselus isopods. The present study is the first description in hermit crabs. However, the temporal covariation of male and female availability cannot explain all of the mating pattern of P. middendorfii, which showed a tendency toward size.
assortative mating in the Peak and Late periods, but not in the Early period (Fig. 2). This mating pattern variation among periods suggests that the mating system of *P. middendorffii* might vary within a single breeding season.

The most important pattern in this study is the temporal decline of guarding male size (Fig. 3). Most theoretical models for precopulatory guarding assume, for simplicity, that all mature males can always mate with mature females (e.g., Yamamura, 1987). If this were the case in *P. middendorffii*, a decrease in the number of receptive females would result in a more male biased operational sex ratio, and stronger sexual selection for male body size where large males have an advantage in mate competition. Since the Early and Late periods are considered to have more male biased sex ratios than the Peak period because fewer receptive females are present, large males should monopolize mates in these periods. However, the observed pattern in *P. middendorffii* is inconsistent with the prediction; there was no significant difference in guarding male size between the Peak and
Late periods. Furthermore, it would not result from the temporal decrease of mean male size for the whole population.

A possible cause of this inconsistency is the trade-off between present reproductive success and that of future success, e.g., the success during the next breeding season. Since Late-period females of small size can produce only a small clutch (Wada et al., 1995) and large males would have already mated with large females, the cost of decreasing the expected reproductive success in the future might override the benefit of further mating with small females. Another possibility is that large males in the Late period might not be able to continue reproductive activity due to energetic and/or sperm limitation.

Figure 4 shows that larger P. middendorffii females breed earlier than smaller individuals, and the size-dependent occurrence of ovigerous females also supports this phenomenon (Fig. 5). Why do P. middendorffii females show this breeding pattern? Bertness (1981) suggested that, in the tropical hermit crabs Clibanarius albidigitus, Calcinus obscurus, and Pagurus sp., females allocate their energy to reproduction when shell availability is low and that the growth of females is limited by the size of their shells. Because reproduction and growth of hermit crabs are both affected by shell characters (e.g., Childress, 1972; Fortheringham, 1976). At our study site, larger P. middendorffii females tend to occupy shells smaller than their preferred size, which limits their growth (Wada, in preparation). Small females occupy adequate-sized shells and can grow larger, although they have low fecundity due to their small gonads. On the other hand, most small females belonged to the first age class, which hatched from February to March and settled from April to May (Wada et al., 1995). Therefore, small females could become larger and increase their fecundity by delaying the timing of breeding, or they might be unable to develop gonads, due to physiological constraints, at the same time as the larger ones.

In P. middendorffii, sizes of both male and female participants for mating seem to vary temporally even within one breeding season. Further work about this phenomenon is needed to assess and clarify the causes of these findings.

Acknowledgments

We are grateful to A. W. Harvey and A. Asakura for their invaluable comments on the manuscript. We thank S. Nakao, T. Noda and all other members of the Laboratory of Mariculture, Faculty of Fisheries, Hokkaido University for their advice in the laboratory. Discussions with K. Ito and H. Ohmori were most helpful, and S. Kitano assisted with the field sampling. We also thank them for their critical readings of earlier manuscripts.

Literature Cited


Address: Laboratory of Benthos Ecology, Faculty of Fisheries, Hokkaido University, 3-1-1 Minato-cho, Hakodate 041, Japan.
E-mails: (SW) swada@fish.hokudai.ac.jp; (TS); choho@fish.hokudai.ac.jp; (SG) goshima @fish.hokudai.ac.jp