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Temporal allocation pattern between reproduction and growth within a breeding season of the hermit crab *Pagurus nigrivittatus*

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Abstract.—Allocation of energy between reproduction and growth is a fundamental principle in life history theory. In a seasonal environment, animals with indeterminate growth are predicted to change their allocation between reproduction and growth according to the season. We examined the seasonal variation in the allocation to reproduction and growth within a breeding season in the hermit crab *Pagurus nigrivittatus*. Females of *P. nigrivittatus* produced smaller clutches during the early part of the reproductive period than later although the frequency of prenuptial molting was lower early in the period. We suggest that environmental factors, such as temperature, may affect the development rate of embryos, as well as the metabolism and surplus energy in females, which have consequences for seasonal variation in the energy allocation to reproduction and growth.

Introduction

Energetic allocation between reproduction and growth is a fundamental tenet in life history theory (Roff, 1992; Stearns, 1992). The reason for this is because growth and reproduction compete for a limited supply of energy. The allocation pattern is relatively simple in annual animals with determinate growth, because the two processes are sequential rather than competitive and the only decision to be made is when to switch from growth to reproduction. However,

when perennial animals show indeterminate growth, they must optimize the use of resources to growth, or to reproduction, or to some combination of the two demands (Heino & Kaitala, 1999). In a seasonal environment, where abiotic and biotic conditions vary during a year, animals with indeterminate growth can partition energy between reproduction and growth according to season.

Females of some *Pagurus* hermit crabs, such as *P. filholi*, *P. minutus* and *P. nigrivittatus*, are considered to allocate energy to both reproduction and growth during a breeding season (Wada *et al.*, 2007, 2008). Females of these species have multiple clutches during each breeding season (Wada *et al.*, 2005), copulate before producing every clutch, and sometimes perform molting immediately prior to the copulation, which has been named as a prenuptial molt (Wada *et al.*, 2007). Males of *Pagurus* hermit crabs show precopulatory guarding behavior in which males grasp the aperture of the shell occupied by a mature female with their left chela for a period of up to several days (Hazlett, 1972, 1975; Wada *et al.*, 1995, 1996, 1999). By examining the pleopods of guarded females, the breeding continuity between clutches can be divided into two types; continuous and discontinuous breeding (Wada *et al.*, 2007, 2008; see Materials and Methods). Although females can grow larger with the prenuptial molt in *P. minutus* (Wada *et al.*, 2007) and *P. nigrivittatus* (Wada *et al.*, 2008), the frequency of prenuptial molts increases when females have discontinuous breeding. Thus, females that

breed with prenuptial molting tend to have a prolonged rest period from the last breeding in the hermit crabs.

Since both breeding and molting entail energetic costs, we hypothesize that females may try to avoid simultaneously channeling energy into reproduction and growth even within a reproductive season; i.e., they may divide the reproductive season into a molting period with discontinuous breeding and a non-molting period with continuous breeding. Alternatively, females may reduce their clutch size in the period of high frequency of the prenuptial molting. Temporal variation in the allocation pattern between reproduction and growth during a reproductive season remains unknown in hermit crabs. We here examine the seasonal allocation pattern between reproduction and growth within a reproductive season of *P. nigrivittatus*. This species is distributed on rocky shores in southern coast of Japan, from the Boso Peninsula southward to Kyushu (Komai, 2003). Females of *P. nigrivittatus* mature at the smallest size among the sympatric congeners in our study site and have the longest reproductive season, from October to June, in which they produce several clutches (Wada *et al.*, 2005). This study investigates the seasonal changes in clutch size, breeding continuity and prenuptial molting frequency.

Materials and Methods

Males of *P. nigrivittatus* show precopulatory guarding behavior typical of *Pagurus* species (Hazlett, 1968, 1972), in which they grasp the aperture of the shell occupied by a mature female with their left chela over a period of several days. We collected guarding pairs of *P. nigrivittatus* during low tides on a rocky intertidal area along coast of Hane-Cape (33°26'N 134°05'E), southern Shikoku, Japan. Each pair was placed into a small vinyl pouch (14 × 10 cm) with natural seawater and brought back to the laboratory. Sampling was carried out in 2003 on 26th November, 10th, 22th and 23th December; and

in 2004 on 20th, 21th January, 6th, 7th and 19th February and 8th March, which is the season showing the high and constant frequency of ovigerous females (Wada *et al.*, 2005). We treated data from the consecutive sampling dates as group data, and seven groups of data (from group-I of the sample on 26th November to group-VII on 8th March, respectively) were compared in the following analyses to examine seasonal variations.

We defined the females of continuous and discontinuous breeding as follows: females in precopulatory guarding with well-developed eggs or remnants of egg cases of the last clutch on their pleopods were designated as “continuous breeding”, and those with clean pleopods as “discontinuous breeding” (Wada *et al.*, 2007). Soon after arriving at the laboratory we turned over the female, waited until the female tried to right herself, and then observed the female's pleopods using a stereoscopic microscope and checked whether the female of each pair had pleopods with well-developing eggs and/or empty egg capsules or had clean pleopods. Then, each pair was kept in a small container (14 × 9 × 7 cm height) or in a polystyrene cylinder (200 ml) in the laboratory for a week or until the female spawned eggs. We checked daily whether the females had molted or not, and observed the pleopods of females under a stereoscopic microscope to determine whether the females spawned eggs or not. Pairs were not fed during the rearing period and the seawater was exchanged every two days. Females that did not spawn during a one week period, were returned to the sea along with their partners.

After the females spawned eggs, we counted the number of eggs dislodged on the bottom of the container, and measured the shell width of the gastropod shell that the female occupied. The females were then fixed in 5% seawater formalin to count the number of eggs attach to their pleopods and measure the shield length (the calcified anterior portion of the cephalothorax; hereafter SL) under a stereoscopic microscope.

Clutch size was calculated as the sum of the number of dislodged eggs and the number of eggs attached to the pleopods although the number of dislodged eggs was zero in most cases.

To examine the effects of season on continuity of breeding and frequency of prenuptial molting, we compared the frequencies of continuous breeding and prenuptial molting of the seven groups with a χ^2 test and post-hoc multiple comparison (Ryan method). We also analyzed seasonal variations in female SL with ANOVA after the variance homogeneity was checked using Bartlett's test. ANCOVA was used to examine a seasonal effect on clutch size that was correlated with female SL, based on the finding that the interaction between sampling group and female SL was not significant. Before the ANCOVA, both female SL and clutch size were log-transformed because a power-law relationship was expected between female SL and clutch size.

Results

We collected 416 guarding pair of *P. nigrivittatus* during the sampling period, and 384 of the females spawned eggs in the pairs. Since the number of eggs of eleven females could not be determined because of

firm sticking of eggs on each other, we used the remaining 373 females for the following analyses.

Female SL did not differ among sampling groups (ANOVA, $F_{6,366} = 1.41$, $P = 0.21$, Table 1). However, we found a seasonal difference in the power-law relationships between clutch size and female SL (ANCOVA, $F_{6,365} = 15.54$, $P < 0.01$, Fig. 1), and the post-hoc test (Bonferroni-Dunn test) of the ANCOVA indicated that females produced larger clutches in late groups than early groups (Fig. 1); i.e., females of groups-I and -II had significantly smaller clutches than those of other groups (Bonferroni-Dunn test, $\alpha = 0.0024$, $P < 0.0024$), and females of groups-III and -IV also had significantly smaller clutches than those of group-V (Bonferroni-Dunn test, $\alpha = 0.0024$, $P < 0.0020$).

Frequencies of continuous breeding and prenuptial molting varied among sampling groups (χ^2 test, continuous breeding: $\chi^2 = 14.79$, $P = 0.02$, prenuptial molting: $\chi^2 = 7.87$, $P < 0.01$, Fig. 2). The frequency of continuous breeding of group-I was significantly lower than that of group-III (Ryan method, $\alpha = 0.0024$, $P = 0.0017$). The frequency of prenuptial molting in group-I was significantly lower than frequencies in group-VI ($\alpha = 0.0024$, $P < 0.001$).

Table 1. Mean shield length (SL) of females and linear regressions of female SL on clutch size in seasonal groups. Both female SL and clutch size was log-transformed, and the regression is given by $\log(\text{clutch size}) = a + b \log(\text{female SL})$. Significance of linear model (R^2) and the coefficients in each group were indicated with asterisks (**; $P < 0.01$, *; $P < 0.05$). Min, Max and SE in parentheses indicate minimum, maximum and standard error, respectively.

	<i>N</i>	Mean SL (Min–Max)	Regression coefficients		R^2
			<i>a</i> ($\pm$ SE)	<i>b</i> ($\pm$ SE)	
group-I	27	2.01 (1.66–2.69)	1.00 ($\pm$ 0.36)*	2.14 ($\pm$ 1.20)	0.08
group-II	42	1.98 (1.44–2.50)	1.95 ($\pm$ 0.28)**	1.39 ($\pm$ 0.95)	0.03
group-III	56	1.96 (1.31–2.96)	1.53 ($\pm$ 0.15)**	1.03 ($\pm$ 0.49)*	0.06*
group-IV	74	1.96 (1.40–2.74)	1.30 ($\pm$ 0.12)**	2.00 ($\pm$ 0.41)**	0.24**
group-V	82	2.06 (1.43–3.12)	1.39 ($\pm$ 0.11)**	2.03 ($\pm$ 0.36)**	0.28**
group-VI	54	1.97 (1.32–2.65)	1.53 ($\pm$ 0.16)**	1.48 ($\pm$ 0.56)*	0.10*
group-VII	38	2.01 (1.43–2.53)	1.78 ($\pm$ 0.25)**	0.64 ($\pm$ 0.82)	0.02

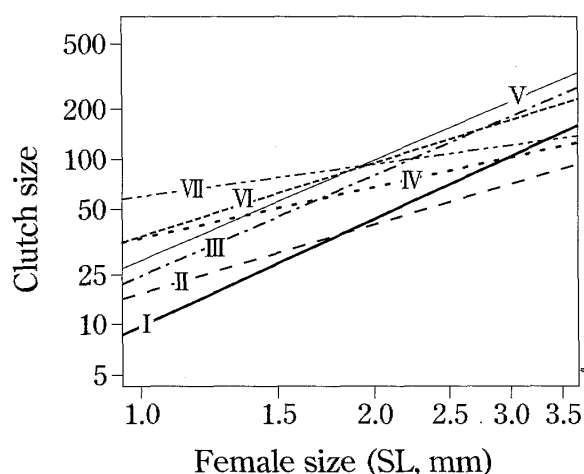


Fig. 1. Temporal variation in the relationships between female size (SL, mm) and clutch size in the hermit crab, *Pagurus nigrivittatus*. Data from the consecutive sampling dates was treated as a group (in 2003 on 26th November, 10th, 22th and 23th December and in 2004 on 20th, 21th January, 6th, 7th, 19th February and 8th March), and data were divided into seven groups. Group-I and -II had significantly smaller clutches than other groups, and groups-III and -IV also had smaller clutches than group-V (Bonferroni-Dunn test, $\alpha = 0.0024$, $P < 0.0024$).

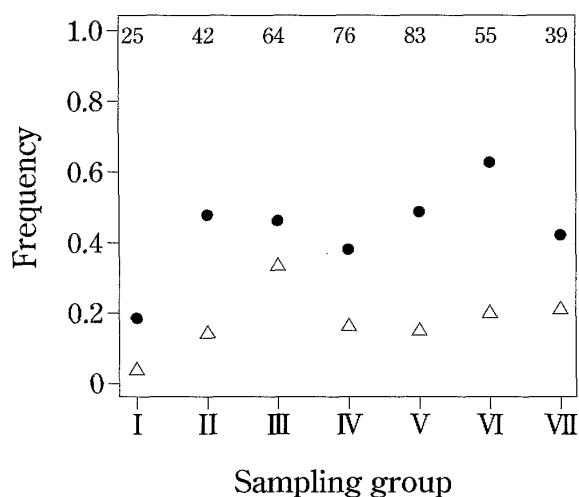


Fig. 2. Temporal change of frequencies of pre-nuptial molting (solid circles) and continuous breeding (open triangles) in the hermit crab, *Pagurus nigrivittatus*. Data from the consecutive sampling dates was treated as a group (in 2003 on 26th November, 10th, 22th and 23th December and in 2004 on 20th, 21th January, 6th, 7th, 19th February and 8th March), and data were divided into seven groups. Numbers at the top of the graph represent sample sizes.

Discussion

Our results are not consistent with the prediction that females may divide the reproductive season into a molting period with discontinuous breeding and a non-molting period with continuous breeding, and that females may reduce their clutch size in the period of higher frequency of the pre-nuptial molting. Females of *P. nigrivittatus* showed lower frequencies of pre-nuptial molting and continuous breeding early in the breeding season (group-I) than females breeding later. Furthermore, females produced smaller clutches during the early part of the reproductive period (groups-I, II) than during the late part of the period.

Female size generally affects both reproduction and growth in hermit crabs (e.g., Hazlett, 1981; Elwood & Neil, 1992). Several studies have demonstrated that temporal reproductive activity during a reproductive season depends on female body size. Large females breed earlier than small females in *P. middendorffii* (Wada *et al.*, 1996) and *P. filholi* (Yoshino *et al.*, 2002) while in *P. ochotensis* small females breed earlier than large females (Wada, 2001). The frequency of pre-nuptial molting decreases with female size in *P. nigrivittatus* (Wada *et al.*, unpublished). However, in this study, we found no significant temporal effects of female size in *P. nigrivittatus*.

Growth rate is generally considered to increase with temperature in crustaceans because a higher rate of metabolism is realized under high temperature (Hartnoll, 1985; Conan, 1985; Brylawski & Miller, 2006). Asakura (1992) has reported that females molt more often during the reproductive season, which is a high temperature season, than the non-reproductive season in the hermit crab *Diogenes nitidimanus*. Molting frequency and size increment per molt is higher in the warmer seasons of spring and summer than in winter in the hermit crab *P. middendorffii* (Wada, 2000). However, this was not true in our results because while the molting frequency tended

to be higher in the late period of the breeding season than in the early period (group-I), water temperature was in fact lower in the late periods. Monthly average temperatures of seawater collected at AM10:00 at the fishery port of Muroto City, about 20km distance from our study site, were 22.7, 19.3, 16.6, 16.5 °C in November, December 2003, and January, February 2004, respectively (from online database of Japan Oceanographic Data Center). Therefore, temperature does not in itself explain the temporal change in molting frequency in our results.

On the other hand, low temperature late in the breeding season may be enable females to accumulate more energy, and relax the energetic limitation for both reproduction and growth. Temperature changes affect the incubation period of ovigerous female in *Pagurus* hermit crabs (Wada *et al.*, 2005). In *P. nigrivittatus*, mean incubation periods were 32.2 and 18.7 days at 16 and 22 °C, respectively (Wada *et al.*, 2005). Since the breeding interval of females with continuous breeding varies with the incubation period, it should be short early in the season. We therefore suggest that females could devote less energy to both producing a clutch and molting in the early period than in the late period, due to the short breeding interval. Short breeding interval is related with a reduction of clutch size in some multi-voltine (*i.e.*, multiple broods in a single season) terrestrial animals, such as the pygmy grasshopper (Forsman, 2001) and barn swallow (Møller, 2007). Thus, although a short breeding interval can increase the number of clutches during a breeding season, it may increase the energetic constraints for females (Reznick & Yang, 1993; Forsman, 2001; Harris & Ludwig, 2004; Møller, 2007).

Additionally, the cost of parental care can also influence energetic allocation. Fernández *et al.* (2000) have demonstrated that brooding behavior of brachyuran crabs (*i.e.*, abdomen flapping and use of chelae) provide oxygen to embryos, so there is a cost to brooding. Female hermit crabs also

incubate eggs on their pleopods until the larvae hatch out, and we observed that females often flicked their pleopods while incubating eggs. The flicking may provide oxygen to the incubated eggs. Although higher temperature induces faster development of embryos, it should in turn require more parental effort to supply sufficient oxygen to embryos and females need to flick more frequently. The effect of temperature on parental care and its consequence on allocation between reproduction and growth should be examined in laboratory experiments.

Seasonal variation in food availability may also cause the seasonal variation in clutch size and molt frequency in our study. Availability of food is an important determinant of energetic allocation between reproduction and growth in aquatic animals (Jokela & Mutikainen, 1995; Ito & Wada, 2005; Yoneda & Wright, 2005). For example, in marine bivalves, reproduction is often sacrificed for maintenance and growth under less favorable food conditions (Bayne *et al.*, 1983; MacDonald & Thompson, 1985). Peterson and Fegley (1986) observed seasonal differences in the growth rate of the hard clam, *Mercenaria mercenaria*, was most likely to be due to increased allocation to stored energy as they prepared for the oncoming reproductive season. Hard clams may change their energy allocation between growth and reproduction in response to seasonal demands (Peterson & Fegley, 1986). Food resources also affect the breeding interval in many animals such as fish (Reznick & Yang, 1993; Rideout *et al.*, 2005; Jørgensen & Fiksen, 2006; Jørgensen *et al.*, 2006) and amphibians (Harris & Ludwig, 2004). In a salamander *Hemidactylium scutatum* with parental care, females under high food levels reproduce more frequently than females under low food levels (Harris & Ludwig, 2004). Food availability may especially determine the performance in species with parental care because of the additional energy expended on caring for offspring (Roff, 1992).

We suggest that environmental factors, such as temperature and food availability, may affect the development rate of embryos, as well as the metabolism and surplus energy for females, which have consequences for the seasonal variation in energetic allocation to reproduction and growth. However, there is little evidence to support these ideas in hermit crabs. Further investigations and experiments are needed to evaluate the environmental effects on life history traits in hermit crabs.

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