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Author(s)	Wada, Satoshi; Yasuda, Chiaki I.; McLay, Colin
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Sexual size dimorphism in two endemic hermit crabs, *Pagurus traversi* and *P. novizealandiae*, in New Zealand

Satoshi WADA[1], Chiaki I. YASUDA[1] and Colin MCLAY[2]

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Abstract

The evolutionary factors of sexual size dimorphism and reproductive characters in *Pagurus traversi* and *P. novizealandiae,* are discussed. Investigations and sample collection were conducted in the intertidal area around Kaikoura peninsula, southern island of New Zealand from 22 February to 23 March 2012. The number of crabs collected was 1198 *P. traversi* and 318 *P. novizealandiae*. The degree of size dimorphism ((mean male size)/(mean female size)) was 1.09 and 1.03 in *P. traversi* and *P. novizealandiae*, respectively. The fecundity relationship between clutch size and female body size (shield length, mm) in *P. traversi* was estimated as $\log_{10}$[clutch size] $=1.010+0.794 \times \log_{10}$[female size^3], indicating that clutch size approximately increase as an isometric relationship. All males guarded females smaller than themselves in nine precopulatory guarding pairs of *P. traversi*. However, difference in the mean size between the guarding males (4.79 mm) and other males (4.50 mm) was small (0.29), suggesting that large size advantage might be weak in mate acquisition compared with other species of the genus *Pagurus*. Weak evolutionary selection pressure acting on male body size may explain relatively small degree of sexual size dimorphism in *P. traversi*.

Key words : crustacean, reproduction, sexual selection

Introduction

Sexual dimorphism in body size is known in many animals (Andersson, 1994 ; Prenter et al., 1999 ; Fairbairn et al., 2009). While females are typically larger than males in copepods (Bayly, 1978 ; Geddes and Cole, 1981), males are often larger than females in other crustaceans, such as amphipods (Naylor and Adams, 1987 ; Cothran, 2008), isopods (Adams et al., 1985) and decapods (e.g., Smith et al., 2009) including hermit crabs (Bertness, 1981 ; Abrams, 1988 ; Harvey, 1990 ; Wada, 1999).

Like other animals (Andersson, 1994 ; Prenter et al., 1999 ; Fairbairn et al., 2009), sexual selection on male body size should be a major determinant of the direction and degree of dimorphism of hermit crabs (Wada et al., 1999a). Large males have an advantage in male-male contest competition for mates in many hermit crabs (Abrams, 1988 ; Wada et al., 1999b ; Yasuda et al., 2011, 2012 ; Suzuki et al., 2012 ; Tanikawa et al., 2012). However, Harvey (1990) has suggested that the weak natural selection for fecundity acting on female body size, rather than sexual selection on male body size, would lead to sexual size dimorphism in the hermit crab *Clibanarius digueti*.

Pagurus traversi and *P. novizealandiae* are endemic hermit crabs in New Zealand, which are common in intertidal and shallow subtidal area throughout New Zealand (Osborne & McLay, 1986 ; Forest & McLay, 2001). Male longevity is estimated to be longer than that of females, and females grow faster than males in these two species (McLay, 1985). The sexual differences are unique because in other hermit crabs males show higher growth rate (e.g., Markham, 1968 ; Wada, 2000) and lower survival rate (e.g., Asakura, 1995). Although there is a short report for the mating behavior of *P. traversi* (Hazlett, 1986), there are few ecological or behavioral descriptions of these two species. We here describe the population structure and some behavioral and reproductive characters of *P. traversi* and *P. novizealandiae*, focusing on sexual size dimorphism.

Materials and Methods

We collected hermit crabs of *P. traversi* and *P. novizealandiae* in the intertidal area around Kaikoura peninsula, South Island of New Zealand from 22 February to 23 March 2012. They occurred under rocks, around sea algae and in runnels of rocky flat. The crabs were brought back to the laboratory at the Edward Perceval Field Station, University of Canterbury, and kept in an aquarium with running seawater

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[1] *Laboratory of Marine Biology, Graduate School of Fisheries Science, Hokkaido University, 3-1-1 Minato-cho, Hakodate, Hokkaido, 041-8611, Japan (e-mail : wadas@fish.hokudai.ac.jp)*
(北海道大学大学院水産科学研究院海洋生物資源科学部門海洋生物学分野)
[2] *School of Biological Sciences, University of Canterbury, Christchurch, New Zealand*

for four days. Within the four days, we measured the shield length (SL, the calcified anterior portion of the cephalothorax) of all specimens under a stereoscopic microscope. The sex of each crab was identified on the basis of the degeneration (male) or enlargement (female) of the first pleopod, and female crabs were further classified into ovigerous and non-ovigerous.

While the number of ovigerous females was 262 in *P. traversi*, the number was only three in *P. novizealandiae* (see Results and Discussion). The following procedures then applied to *P. traversi*. To estimate the spawning and larval release patterns of *P. traversi* in the field, we identified the developmental stages of eggs attached to the female pleopods, based on the amount of yolk and the development of the eye pigment. Eggs were differentiated into four developmental stages as follows : Stage A, newly-deposited eggs, completely filled with yolk ; Stage B, less than 70% of the egg volume composed of yolk, no eye pigment present ; Stage C, incompletely developed, suboval eye pigment visible ; and Stage D, well-developed oval eye pigment visible. Egg development was synchronous within clutches of all females seen in this study. We also counted the number of eggs for 22 ovigerous females that had eggs of Stage A or B to examine the relationship between female SL and clutch size in *P. traversi*. After the measurements, all crabs were returned to the sea.

We also collected all precopulatory guarding pairs of *P. traversi* that we found. Each pair was placed in a small vinyl pouch with some seawater in the field, and brought back to the laboratory. In the laboratory, we placed each pair in a small container (95 × 95 × 70 (height) mm) with some natural seawater for an hour. When the male guarded the female after an hour, we regarded them as precopulatory guarding pairs. To examine whether the females of guarding pairs breed multiple clutches per year, we turned over the female with tweezers in a small container, waited for the time that the female tried to right herself, and then observed the female's pleopods (and eggs on the pleopods) using a stereoscopic microscope in order to check for clean pleopod setae, and for developing eggs (i.e., stage IV). We thus defined the females of continuous and discontinuous breeding as follows : females in precopulatory mate guarding with old eggs on their pleopods were designated "continuous breeding" and those with clean pleopods as "discontinuous breeding" (Wada et al., 2007). Each pair was kept in a small container (174 × 174 × 35 (height) mm or 95 × 95 × 70 mm) in the laboratory for five days or until the female laid eggs. We checked every day whether the females had molted and/or laid eggs or not. Pairs were not fed during the rearing period and the seawater was exchanged everyday. After the rearing period, we measured SLs of all pairs and returned them to the sea.

Results and Discussion

We collected 1,198 and 318 individuals of *P. traversi* and *P. novizealandiae*, respectively. While the mean SL of males (4.50 ± 1.40 SD mm) was significantly larger than that of females (4.14 ± 1.19 SD mm) in *P. traversi* (Welch's *t*-test, $t = -4.75$, $P < 0.001$) (Fig. 1), there was no significant difference in the mean body size between males (6.57 ± 2.09 SD mm) and females (6.39 ± 1.42 SD mm) in *P. novizealandiae* (Welch's *t*-test, $t = -0.90$, $P = 0.37$) (Fig. 2). The degree of sexual size dimorphism, which was calculated as (the mean SL of males)/(the mean SL of females), was 1.09 and 1.03 in *P. traversi* and *P. novizealandiae*, respectively.

The degrees of sexual size dimorphism of *P. traversi* and *P. novizealandiae* seem to be relatively small but typical in comparing with other *Pagurus* species. Wada et al. (2005) have described variation in sexual dimorphism in body size (SL) among nine species of hermit crabs, which ranged from 1.01 to 1.34. The degrees of dimorphism ranged from 1.13 to 1.51 in five local sites of *P. middendorffii* (Wada, 1999). Those of *P. hirsutiusclus* in two study sites were 1.12 and 1.10 while those of *P. granosimanus* were 1.01 and 0.96 (Abrams, 1988).

Frequencies (%) of ovigerous females on 22 February, 5 March and 23 March 2012 were 57.14 ((number of ovigerous females)/(number of females) = 12/21), 58.86 (196/333) and 31.58 (54/171), respectively, in *P. traversi*, and the minimum SL of ovigerous females was 2.16 mm (Fig. 1). Those of *P. novizealandiae* were 1.79 (1/56), 8.33 (2/24) and 0 (0/40) on each sampling date. The minimum SL of ovigerous females

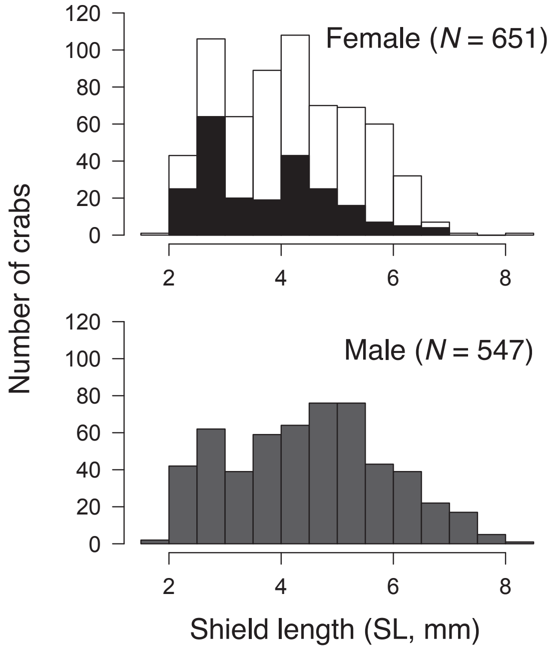

Fig. 1. Size distribution of the hermit crab *Pagurus traversi*. The solid and the open bars indicate ovigerous and non-ovigerous females, respectively.

was 8.14 mm in *P. novizealandiae* (Fig. 2). The interspecific difference in the frequency of ovigerous female indicates a difference in reproductive season between the two species. Mating season of *P. novizealandiae* may be earlier than late February while we collected nine precopulatory guarding pairs of *P. traversi* in our survey.

Fig. 3 shows model II regression (major axis regression) between clutch size and female body size in *P. traversi* ($\log_{10}$[clutch size]$= 1.01+0.79\times\log_{10}$[female SL^3]). Although the positive slope of the regression, 0.79, was significantly different from zero ($r = 0.84$, $N = 22$, $P < 0.01$), it did not differ from 1.0 ($r = -0.34$, $P = 0.12$), indicating that clutch size increases isometrically. Moderate natural selection for fecundity would act on female body size in *P. traversi*. This seems to be consistent with faster growth rate of females than males in *P. traversi* (McLay, 1985). However, we should also take account of annual number of clutches, which may depend on female body size, for estimating the strength of natural selection on the female size. All egg stages were found in the samples collected in February and March in *P. traversi* (Fig. 4), and the guarded females often had eggs with Stage D (Table 1), indicating that they have multiple clutches during a reproductive season. Frequency of ovigerous females tended to be higher in small females than in larger females (Fig. 1). If smaller females have more clutches during the reproductive season, natural selection for fecundity on female body size would be weaker than the above estimation.

All nine males guarded smaller females than themselves in *P. traversi* (Table 1). Larger males should have an advantage in mating with larger, more fecund females. However, the mean SL of guarding males was 4.79 (mm), and the difference in the mean SL between guarding males and population males was 0.29. Selection intensity due to guarding, which was calculated as the difference divided by the standard deviation of the population's SL (1.40), was 0.21. When a male encountered a guarding pair in a small container, active male–male contest for female was not observed in *P. traversi* although the replication of the experiment was only four (S. Wada, personal observation). McLay (1985) has also

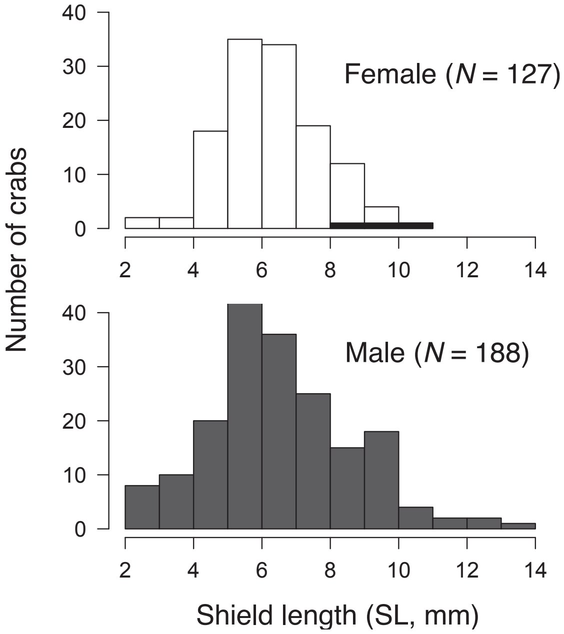

Fig. 2. Size distribution of the hermit crab *Pagurus novizealandiae*. The solid and the open bars indicate ovigerous and non-ovigerous females, respectively.

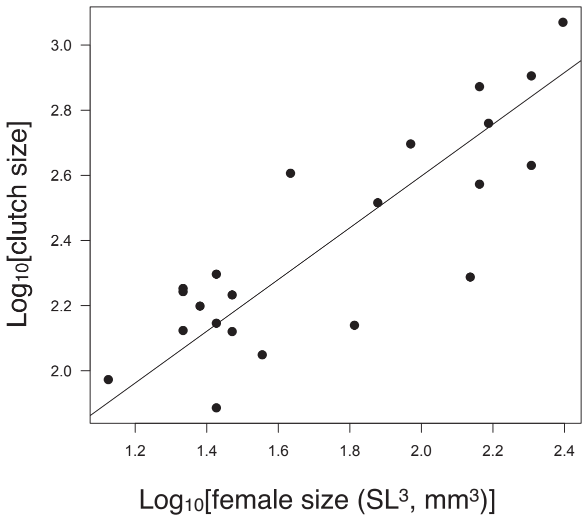

Fig. 3. Relationship between clutch size (number of eggs) and female size (shield length^3, mm^3) for *Pagurus traversi* ($\log_{10}$[clutch size] $= 1.010 + 0.794\times\log_{10}$[female SL^3]) (major axis regression analysis, $r = 0.84$, $N = 22$, $P < 0.01$). The slope of the regression was not significantly different from 1.0 ($r = -0.34$, $P = 0.12$).

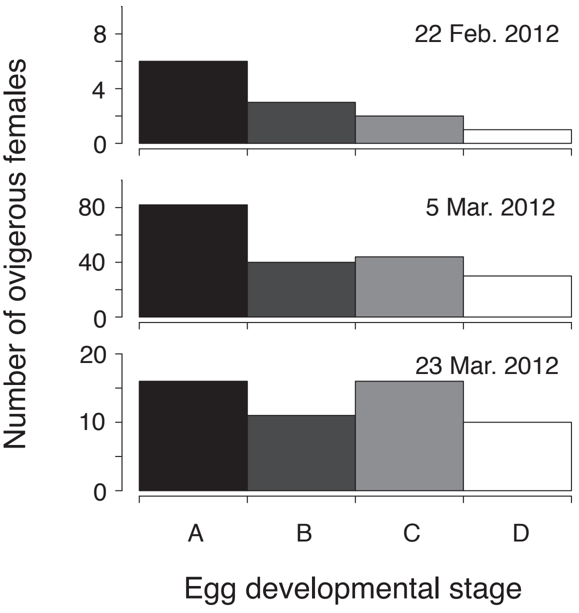

Fig. 4. Monthly distributions in developmental stage of eggs on pleopods of female *Pagurus traversi*. See text for explanation of developmental stages A–D.

Table 1. Data of precopulatory guarding pairs collected in the field. SL means shield length (the calcified anterior portion of the cephalothorax) of crabs. Continuous and molting means whether the female carries well-developed eggs (i.e., breed the susequent clutch continuously) and whether the female molt as the prenuptial molt during observation period, respectively. See text for further explanation.

	Male SL	Female SL	Breeding	Continuous	Molting
1	3.92	2.47	Yes	No	Yes
2	6.70	3.30	Yes	No	No
3	3.30	2.27	Yes	No	No
4	6.60	5.05	Yes	Yes	No
5	4.64	2.47	Yes	Yes	No
6	3.51	2.89	Yes	Yes	No
7	4.18	2.68	No	No	Yes
8	6.49	5.46	No	Yes	No
9	3.81	2.78	No	No	No

implied that *P. traversi* may have unusual precopulatory and/or copulatory behavior. These suggest that large size advantage in the contest competition might be weak in *P. traversi*. Selection intensities due to guarding in males of *P. lanuginosus* and *P. middendorffii* are 0.43 and 5.92 (Wada et al., 1996, 1999a). Males of other species, such as *P. filholi*, *P. lanuginosus*, *P. middendorffii* and *P. nigrofascia*, show active male–male contest under experimental conditions, supporting large size advantage in male–male competition (Wada et al., 1999b ; Suzuki et al., 2012 ; Tanikawa et al., 2012 ; Yasuda et al., 2012). While males grow faster than females in *P. bernhardus* (Markham, 1968 ; Lancaster, 1990), *P. filholi* (Matsuo et al., unpublished) and *P. middendorffii* (Wada et al., 1995 ; Wada, 2000), females grow faster than males in *P. traversi* and *P. novizealandiae* (McLay, 1985). Sexual selection acting on male body size would therefore be weak in the New Zealand hermit crabs. The weak evolutionary selection pressure may explain relatively small degree of sexual size dimorphism in the two species although further studies are needed especially in *P. novizealandiae*.

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