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Temporal changes in the reproductive population structures and males' secondary sexual character of the hermit crab *Diogenes nitidimanus*

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Abstract We investigated the reproductive ecology of *D. nitidimanus* in the Waka-River estuary with special reference to temporal change in the relative size of chelae length for males, i.e., secondary sexual character. Ovigerous females were observed from April to October, peaking in June–July with over 90% of females being ovigerous. Adult female carapace size ranged from 3.5 to 8.5 mm, but with the majority of females falling between 5–6 mm. Male carapace length was more evenly distributed between 3.5 and 10 mm. Juvenile settlement occurred mostly in July, during which time the frequency of both large females (over 6.5 mm in carapace length) and large males (over 8.5 mm in carapace length) clearly decreased. The carapace length of precopulatory-guarded females varied from 4.8 to 8.0 mm, while guarding males were almost over 7 mm and always larger than their paired females. The relative growth of the major chelae differed significantly between small and large males during the early months of the year, including the reproductive peak months (April–June). During these early months, large males had relatively larger chelae for their body size than did small crabs. This difference, however, was not evident later in the year (July–September). Large males may grow their chelae relatively long in the early months in order to take advantage of the mating opportunities during April–June. This is the first report in animals, to our knowledge, that relative size of the secondary sexual character for males temporarily change during a single reproductive season.

Keywords Allometry · Diogenidae · Functional maturity · Reproductive strategy · Seasonal variation

Introduction

Sexual dimorphisms in size or morphology are found in the animal kingdom and are often the consequence of sexual selection (Andersson 1994). In animals in which males intensively compete for females, there is often inter-male variation in the relative size or morphology of particular traits that cannot be attributed to differences in body size (Eberhard 1985). In several cases, it is clear that the variations are due to differences in reproductive tactics or strategies (Shuster and Wade 2003). In indeterminate growing species (those that continue to grow even after maturation), there can be changes in reproductive tactics with age as individuals follow different life-history strategies (Koga and Murai 1997). However, there has been no research showing the change of relative size in the secondary sexual character during a single reproductive season in animals.

In many motile crustaceans, sexual differences are evident in morphology, distribution, and behavior. These differences can be explained as life-history and/or reproductive strategy variation between the sexes (Burggren and McMahon 1988; Bauer and Martin 1991; Koga 1995). Hermit crabs are also such taxa. In two major families of marine hermit crabs Diogenidae and Paguridae from temperate to tropical region, there are many studies reporting sexual dimorphisms in body size (e.g., Asakura 1987a; Wada et al. 1996; Wada 1999; Turra and Leite 2000; Mantelatto and Garcia 2000; Yoshino et al. 2001; Mantelatto and Dominciano 2002; Macpherson and Raventos 2004; Litulo 2005) and chela size (e.g., Asakura 1987b; Gherardi and Nardon 1997; Manjón-Cabeza and Garcia Raso 1999; Yoshino and Goshima 2002; Fransozo et al. 2003; Biagi and Mantelatto 2006).

Diogenes nitidimanus Terao is a small diogenid hermit crab inhabiting intertidal sandflats and shallow waters at a few meters of depth. According to a series of studies on

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this species in Amakusa Island, Kushu, Japan (Asakura and Kikuchi 1984; Asakura 1987a, 1987b, 1991, 1995a), the size-distribution patterns greatly differ between sexes, and the sex ratios within populations are biased towards females. Ovigerous females occur from April to October, and the occurrence reaches a peak in August. There is a polymorphism in the major chelae of males, and it is suggested that some males with larger chelae win competition for females when body size is matched between the rivals. Recently, Koga and Fukuda (2008) found in the Waka-River estuary in August that larger males of *D. nitidimanus* have relatively longer chelae than do smaller ones, i.e., the inter-male dimorphism of weapon size. August is a part of the reproductive season of this species, during which larger males with relatively large chelae may be advantageous of inter-male competition for female mates. However, we do not know exactly when larger males with relatively large chelae appear and disappear.

In this study, we examine the reproductive biology of the *D. nitidimanus* and describe (1) when and at what size the sexes reproduce and disappear from the population (2) what size of males show precopulatory mate guarding behavior, (3) relative growth of the male major chelae, and (4) its seasonal changes. We discuss life-history strategies of both sexes, especially focusing on the association between size variation of male chelae and timing of the reproductive season.

Methods

Study site was the Waka-River estuary located at the western side of Kii-peninsula along with Pacific coast in central Japan. We collected the hermit crab *D. nitidimanus* at sandy tidalflats close to mouth of the river (N 34°10'23", E 135°10'49") because many ovigerous females were observed there in our preliminary study (Koga and Fukuda 2008).

Samplings of the population were conducted from April to October in 2002, since the period is predicted to be the reproductive season of *D. nitidimanus* at our site from the result in Amakusa region (Asakura 1987b). In the period of spring tides of each month, we randomly cast a sieve (33 cm in diameter) turning it upside down four to six times and collected all the hermit crabs captured within the sieve. Hermit crabs were sexed based on the position of gonopores (i.e., the coxa of the third pereopods in females and fifth pereopods in males, Asakura 1995b) under a dissecting microscope, and their carapace length (hereafter CL) and the length of the major chelae (length from the basis of propodus to the tip of immovable dactylus: hereafter CHL) were measured using a caliper nearest to 0.05 mm. We also checked if eggs were attached on the pleopods in females.

In the reproductive season, males show precopulatory guarding behavior in which they grasp the rim of the shell of a receptive female with their minor chela. Males defend the female from other rival males using their major chelae until copulation to assure their

fertilization (Goshima 2002). If such mate-guarding pairs were detected during samplings in May–July, they were also collected and measured in the same way.

Statistical analyses

For analyzing the transition of population structures, we performed cohort separation assuming that the size distribution was composed of the mixture of several normal distributions. We fitted three models with different number of cohorts (i.e., one to three cohort models). Optimal model was fundamentally determined by the minimum AIC with a finit-size correction (AICc) for small sample size. However, if AICc differences between models were less than 2, more parsimonious model was selected (Burnham and Anderson 2002; Bolker 2008). Parameter estimation was made by the solver routine of Excel 2003 for each mixture model.

Differences in size-distribution patterns were analyzed by the Kolmogorov–Smirnov test (hereafter KS test). In many crustaceans, relative growth of body parts often changes with life-history stages, for example, from the juvenile to adult phase (e.g., Hartnoll 1978; Somerton 1980; Goshima et al. 2000; McQuaid et al. 2006). In this study, we focused on the difference in relative growth of male chelae between functionally mature and immature phases. Functional maturity was defined as the actual engagement in reproductive activity, which was evaluated by mate-guarding behavior in males as in the stone crab *Hapalogaster dentata* (Goshima et al. 2000). As most of the guarding males were larger than 7 mm CL (see “Results”), we considered males larger than this size as functionally mature and smaller than this size as being functionally immature. We separately fitted regression lines to the log-transformed data of CL and CHL for functionally mature and immature males, respectively. For each month, we tested whether the separate regressions were significantly better than single regression through the two phases according to the formula in Somerton (1980):

$$F = \frac{(\text{RSS}_{\text{single}} - \text{RSS}_{\text{separate}})/2}{\text{RSS}_{\text{separate}}/(n - 4)}$$

where $\text{RSS}_{\text{single}}$ is the residual sum of squares (RSS) of the single regression fit, $\text{RSS}_{\text{separate}}$ is the RSS of separate regressions fit (i.e., two lines fit) to the data, n is sample size. If single-line fit is better than separate two-lines fit, F follows F distribution with 2 and $n-4$ degrees of freedom. These analyses were made with freeware R ver. 2.8.1 (R Development Core Team 2008).

Results

Brooding frequency and size distribution

Ovigerous females were found in all the months investigated (Table 1), with the frequency reaching the

Table 1 Monthly percentages of ovigerous females during the reproductive season

Month	Ovigerous females (%)	<i>n</i>
April	1.8	56
May	74.7	99
June	90.3	217
July	90.3	227
August	57.4	115
September	47.4	190
October	9.9	101

n = total number of collected females with 3.5 mm or larger carapace length

maximum of over 90% in June–July and the minimum of about 2% in April. The frequency was still high in July, but afterward continued to decrease and finally became 9.9% in October (Table 1). The size of most ovigerous females was larger than 4 mm CL and the minimum size at brooding was 3.5 mm CL in August (Fig. 1), suggesting that crabs less than this size were juveniles.

The pattern of size distribution differed significantly between the sexes in all months (KS test, all $D > 0.24$, all $p < 0.0006$). The mode of adult female size falls between 5 and 6 mm CL in most months and few individuals over 7 mm CL were found except for May–June (Fig. 1). In contrast, such a mode was relatively unclear in adult males, which ranged from 3.5 mm to over 9 mm CL and was distributed in similar frequency in any month (Fig. 1). The frequency of individuals larger than 7 mm CL was higher in males than in females (Fig. 1).

Cohort curves were also overlain in the Fig. 1. The transition of population structures was complex, especially in males, because partial fusion and separation of cohorts were inferred. According to the transition from May to June in males, a part of crabs in the smaller-CL cohort grew to fuse with the larger-CL cohort. The male's smaller-CL cohort in August separated into two cohorts in September probably due to differences in growth rate among individuals within the same cohort. However, the cohort analyses detected several clear patterns of the transition of our population. The occurrence of cohort with small CL (1.5–3.5 mm) in July clearly showed many juvenile crabs of both sexes settled in July. A low rate of juvenile settlement in August was inferred from the separation of the cohort of females with small CL in September. Also, the cohort of large adults of males (8.5 mm or larger) and females (6.5 mm or larger) disappeared in July, when juvenile settlements occurred and constructed new cohorts of small body size (Fig. 1).

Guard pairs

A total of 27 pairs were collected from May to July when there were many ovigerous females and then it was relatively easy to detect the guard pairs. The size of the guarded females varied from 4.8 to 8.0 mm CL (Fig. 2),

which was consistent with the size range of ovigerous females in Fig. 1. In contrast, the size of almost all of the guarding males was larger than 7 mm CL, which corresponded to the males of the large size class. Guarding males were always larger than their female mates (Fig. 2). Guarded females mainly consisted of individuals that had molted recently or that had well-developed eggs attached to their pleopods (i.e., the yolk was well absorbed). This means that females reproduce more than once within a reproductive season. In only one pair, males less than 7 mm CL guarded females with less developed eggs.

Relationship between carapace length and chela length

Differences in the relative growth of male chelae were detected between the two phases in several months (Fig. 3; Table 2). In April, the two-lines fit was not significantly better than the single fit ($F_{2,43} = 1.98$, $p = 0.15$), but significantly better if one outlier was removed (Table 2). The two-lines fit was still significant even if the data were analyzed for individuals less than 8.5 mm CL ($F_{2,33} = 5.72$, $p = 0.007$; the same outlier was removed), considering the disappearance of large males in August and September (Fig. 1). Similarly, in May and June, the two-lines fits were significantly better than the single fits both for all data set (Table 2) and for data less than 8.5 mm CL (all $F > 3.31$, $p < 0.043$). The regressions for functionally matured (7.0 mm CL or larger) males were also significant both for all data set (all $F > 39.68$, all $r^2 > 0.65$, all $p < 0.0001$) and the data less than 8.5 mm CL (both $F > 6.93$, all $r^2 > 0.31$, all $p < 0.022$). In July and August, the two-lines fits were significantly better than single fit (Table 3), but the regressions for functionally matured males were not significant in both seasons ($F < 0.16$, $r^2 < 0.018$, $p > 0.69$). If data was restricted to less than 8.5 mm CL, the two-lines fit in July was not better than the single one ($F_{2,52} = 3.13$, $p = 0.052$), or the regression for functionally matured males was not significant ($F_{1,18} = 1.97$, $p = 0.18$, $r^2 = 0.1$), either. Hence, single-line fit is enough for explaining the relationships in July and August. In September, we found no improvement in reducing residuals by two-lines fit (Table 3). In October, the two-lines fit was significantly better than the single fit for all data set (Table 2). The regression for functionally matured males was significant ($F_{1,28} = 4.72$, $p = 0.038$, $r^2 = 0.14$), but the slopes of the two lines did not differ ($F_{1,133} = 0.002$, $p = 0.97$). The two-lines fit was still significant for the data less than 8.5 mm CL ($F_{2,131} = 8.49$, $p < 0.0005$), but the regression for functionally matured males was no longer significant ($F_{1,26} = 0.83$, $r^2 = 0.03$, $p = 0.37$).

We also compared male relative chela length (i.e., CHL/CL) between the early period (April–June pooled data, $n = 87$) and the later period (August–October pooled data, $n = 51$) of the reproductive season for males with 7.0 mm or larger CL. Relative chela lengths

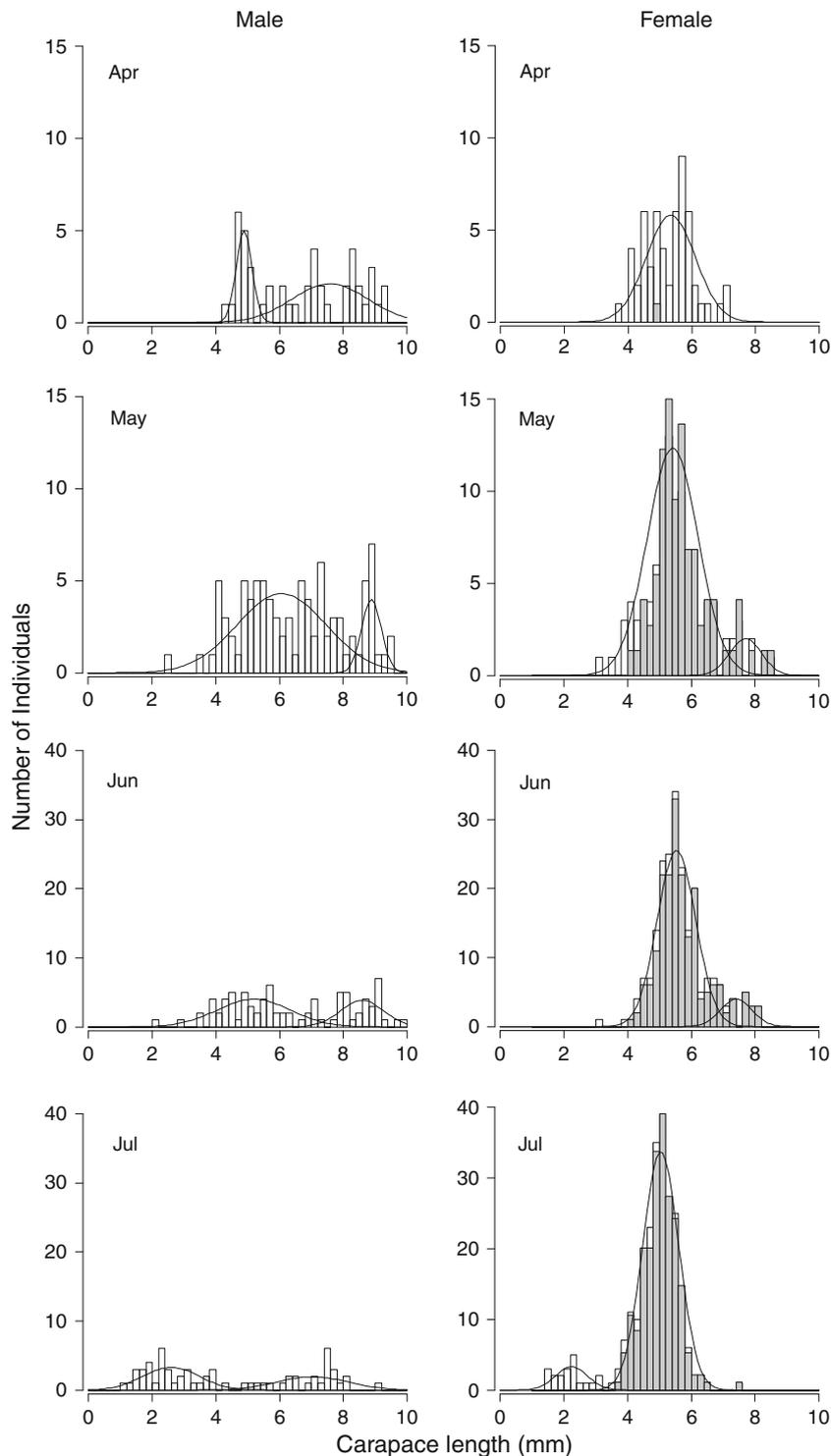


Fig. 1 Size distributions of male and female hermit crab *Diogenes nitidimanus* during reproductive season in 2002. Gray cells represent ovigerous females

significantly differed between the two periods (Mann–Whitney U test, $z = -4.94$, $p < 0.0001$), and the lengths of early period (mean \pm SD = 0.72 ± 0.11) were larger than those of the late period (0.62 ± 0.11). This difference was still significant even after CL of males were controlled from 7.0 to 8.4 mm because there

were few males with 8.5 mm or larger CL in August–October unlike in April–June (Mann–Whitney U test, $z = -2.54$, $p = 0.011$). Although mean CL and the standard deviation did not differ between the two periods after the range of male body size controlled (early: 7.7 ± 0.5 , $n = 46$; late: 7.7 ± 0.4 , $n = 49$), the relative

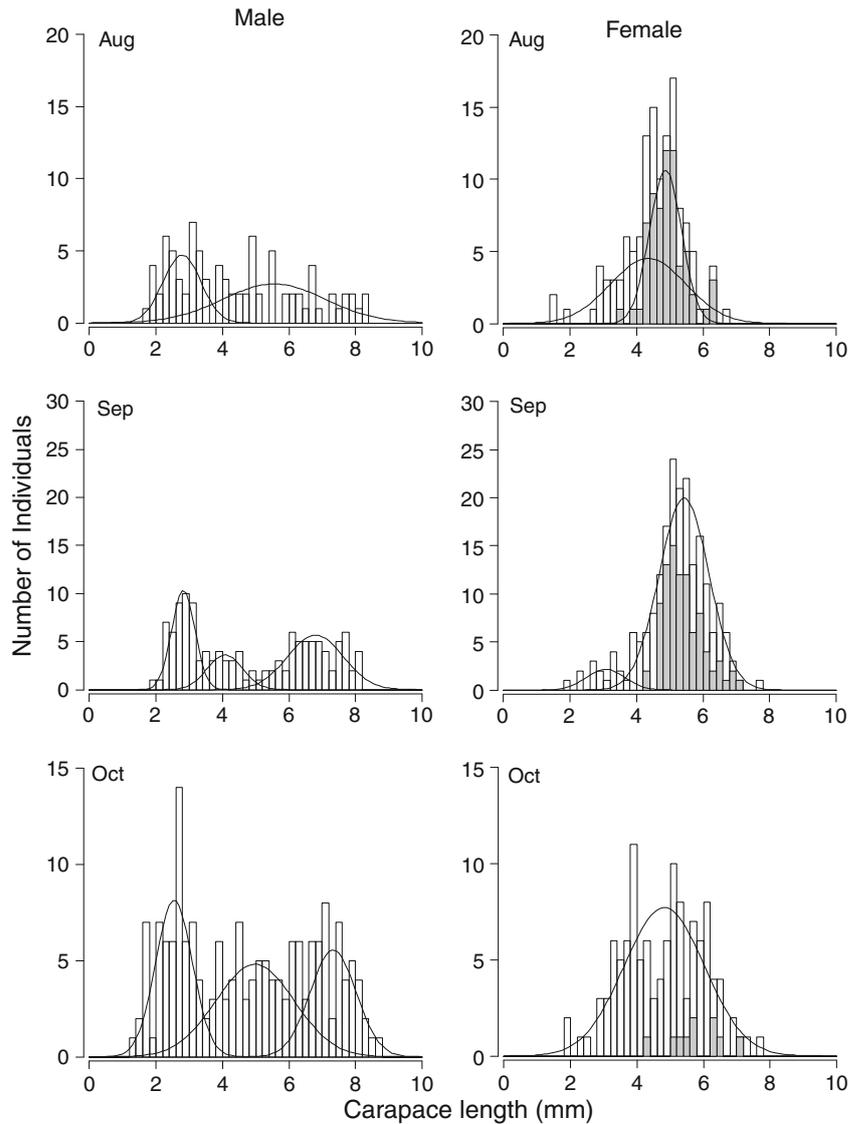


Fig. 1 continued

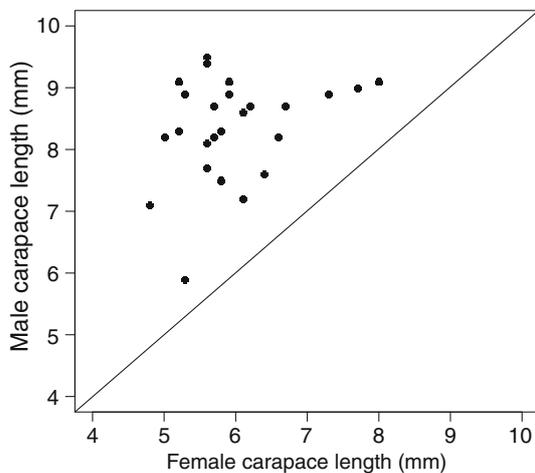


Fig. 2 Carapace lengths (CL) of the mate-guarding pairs in *Diogenes nitidimanus*

chela length of the early period (0.67 ± 0.10) was larger than that of later period (0.62 ± 0.11).

Contrary to males, we could not find clear phase differences in the allometry of female chelae from the plots of females in any month (Fig. 4). We compared chela size of crabs less than 7 mm CL between sexes using ANCOVA. Except for September and October, the regression slopes or intercept significantly differed between sexes, and the slopes or the intercepts were larger in males than in females (Fig. 4, Table 3).

Discussion

The reproductive patterns of hermit crabs differ between regions even in the same species (reviewed in Turra and Leite 2000). The peak period of reproductive activity of *D. nitidimanus* slightly differed between our site (i.e., the

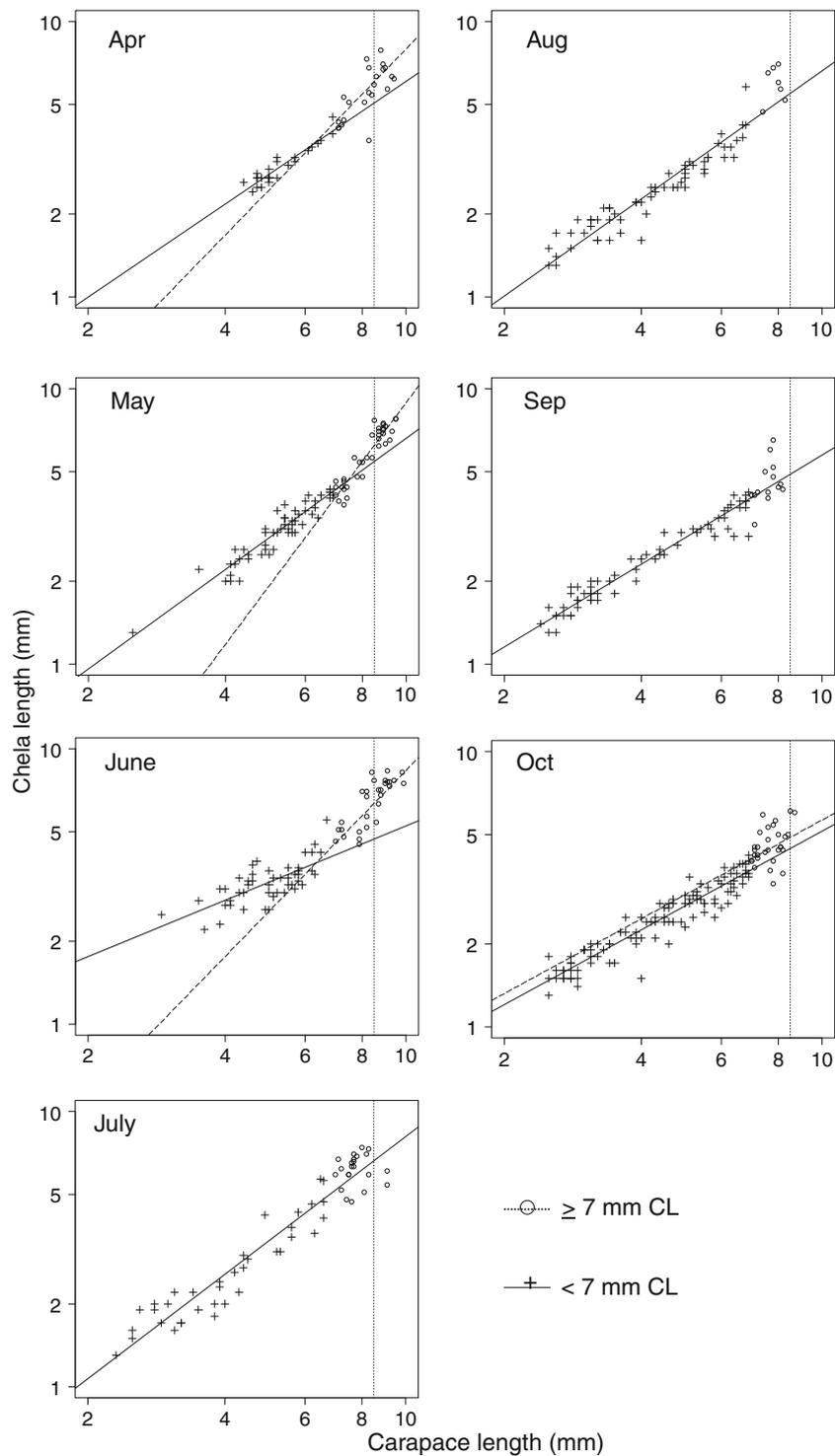


Fig. 3 Relationships between carapace length (CL) and chela length of male *Diogenes nitidimanus* larger (dashed line) or smaller (solid line) than 7 mm CL during reproductive season in 2002. Vertical dotted lines denote CL = 8.5 mm

Waka-River Estuary) and Amakusa Island, though the reproductive season was similar in both sites. At our site, the peak season (judged from the occurrence of ovigerous females) was June to July, while August was the peak in the Amakusa Islands (Asakura and Kikuchi 1984). The peak of juvenile settlement also shifted

probably due to the shift of the reproductive peak. The peak settlement in the Amakusa Islands occurred in August to September (Asakura and Kikuchi 1984; Asakura 1991), but our results showed a clear peak in July. One cause of this peak difference may be due to the geographical difference in climatic condition such as

Table 2 Monthly allometric relationship between carapace length (CL) and chela length

Month	Allometric relationship		F	p	n
	Small size class (< 7 mm CL)	Large size class (≥ 7 mm CL)			
April ^a	$\text{Log}_{10}(\text{chela}) = -0.34 + 1.121 \text{ log}_{10}(\text{CL})$	$\text{Log}_{10}(\text{chela}) = -0.8 + 1.7 \text{ log}_{10}(\text{CL})$	3.75	0.032	46
May	$\text{Log}_{10}(\text{chela}) = -0.38 + 1.2 \text{ log}_{10}(\text{CL})$	$\text{Log}_{10}(\text{chela}) = -1.26 + 2.21 \text{ log}_{10}(\text{CL})$	21.86	<0.0001	88
June	$\text{Log}_{10}(\text{chela}) = 0.04 + 0.68 \text{ log}_{10}(\text{CL})$	$\text{Log}_{10}(\text{chela}) = -0.78 + 1.7 \text{ log}_{10}(\text{CL})$	16.9	<0.0001	76
July ^b	$\text{Log}_{10}(\text{chela}) = -0.35 + 1.26 \text{ log}_{10}(\text{CL})$		5.08	0.0095	58
August ^b	$\text{Log}_{10}(\text{chela}) = -0.35 + 1.17 \text{ log}_{10}(\text{CL})$		12.1	<0.0001	67
September	$\text{Log}_{10}(\text{chela}) = -0.24 + 1.0 \text{ log}_{10}(\text{CL})$		2.25	0.112	77
October	$\text{Log}_{10}(\text{chela}) = -0.14 + 0.9 \text{ log}_{10}(\text{CL})$	$\text{Log}_{10}(\text{chela}) = -0.2 + 0.9 \text{ log}_{10}(\text{CL})$	4.72	0.0002	137

F values denote the significance on the justification of two-lines fit. n = sample size. See also text for details on ^a and ^b

^aResults when one outlier was removed

^bNo significant regression for large size class

Table 3 ANCOVA results on the comparison of chela lengths between sexes less than 7 mm CL

Source	df	MS	F	p
April				
Log ₁₀ (CL)	1	0.262	341.175	<0.0001
Sex	1	0.010	13.454	<0.0005
Residuals	74	0.001		
May				
Log ₁₀ (CL)	1	0.839	632.6584	<0.0001
Sex	1	0.025	18.4775	<0.0001
Log ₁₀ (CL) × sex	1	0.012	8.7636	0.004
Residuals	137	0.001		
June				
Log ₁₀ (CL)	1	0.342	235.479	<0.0001
Sex	1	0.094	64.723	<0.0001
Residuals	232	0.001		
July				
Log ₁₀ (CL)	1	1.206	610.3275	<0.0001
Sex	1	0.003	1.7352	0.189
Log ₁₀ (CL) × sex	1	0.112	56.546	<0.0001
Residuals	254	0.002		
August				
Log ₁₀ (CL)	1	1.769	1097.3756	<0.0001
Sex	1	0.002	1.4154	0.236
Log ₁₀ (CL) × sex	1	0.007	4.0806	0.045
Residuals	172	0.002		
September				
Log ₁₀ (CL)	1	2.322	2089.0543	<0.0001
Sex	1	0.000	0.2356	0.628
Residuals	183	0.001		
October				
Log ₁₀ (CL)	1	2.693	1627.9445	<0.0001
Sex	1	0.000	0.1486	0.700
Residuals	209	0.002		

If interaction between CL and sex was not found, the term was included into the residual

water temperature between the sites. However, it is clear that some other local conditions such as shell availability and inter-specific relationships are also important for shaping the reproductive patterns of hermit crabs (Turra and Leite 2000). Sympatric species often exhibit distinct reproductive activities (e.g., Wada et al. 2000; Macpherson and Raventos 2004), which situations cannot be explained by the difference of climatic condition. The

cause of the difference in reproductive peak of *D. nitidimanus* would also be intricately influenced by several factors. More information is needed to disentangle this topic.

Adult female body size ranged from 3.5 to 8.5 mm CL and peaked between 4 and 6 mm, while male size except recruited juveniles distributed from 3.5 to 10 mm CL in similar frequencies compared to females. Sexual differences in body-size distribution are found in other diogenid hermit crab species (e.g., Turra and Leite 2000; Mantelatto and Garcia 2000; Mantelatto and Dominiciano 2002; Macpherson and Raventos 2004; Litulo 2005) including *D. nitidimanus* from the Amakusa Islands (Asakura 1987b, 1995a). Such sexual differences in the size distribution may be ultimately viewed as a reflection of the different life history strategies between the sexes. According to Asakura (1992), the growth rate of female *D. nitidimanus* decreases with their body size, but males do not. They also report that the decrease in the size increment of females after molt is more pronounced during the reproductive season than in the other seasons (Asakura 1992). These findings suggest that larger females invest more energy into reproduction than growth and results in a population size distribution with a peak size. This female strategy would be favored since the fitness gain from increasing body size beyond a certain size may not be high (Harvey 1990). In males, however, sperm production is energetically less costly than the production of eggs (Krebs and Davis 1993) and body size is more important for mating success than it is in females (e.g., Asakura 1987b; Harvey 1990; Wada et al. 1999; Yoshino et al. 2002, 2004). Males would therefore invest more energy into growth and continue to grow consistently. This strategy would result in a male population with a more uniform size distribution than females.

While male size ranged from 3.5 to 10 mm CL, almost all guarding males were larger than 7 mm CL. This contrasted with adult females, in which a wide range of female sizes were guarded. Similar patterns in guarding pairs were also reported in Asakura (1987a). Although a

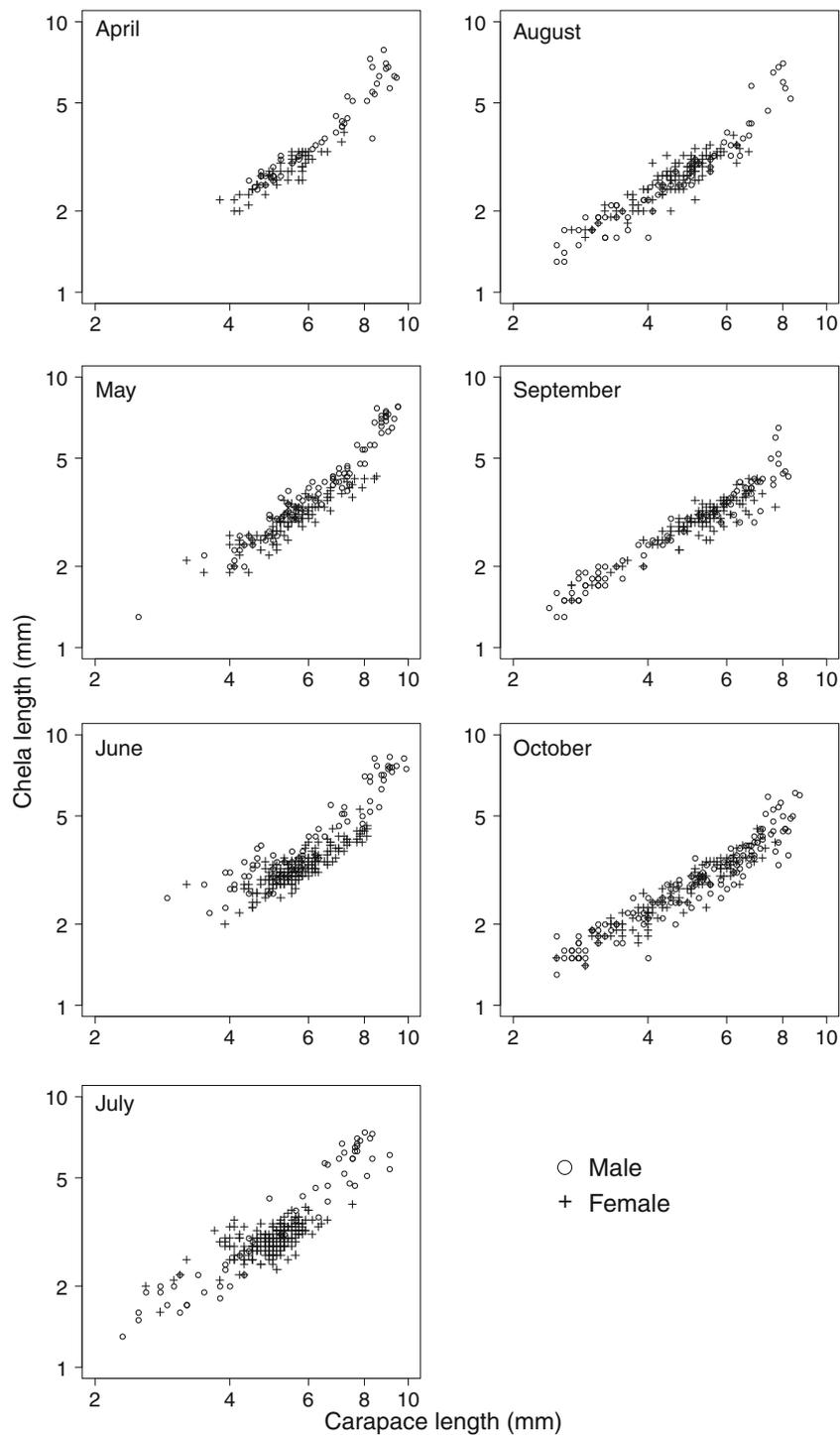


Fig. 4 Relationships between carapace length (CL) and chela length of male and female *Diogenes nitidimanus* during reproductive season in 2002

histological analysis has not been done, small adult males are considered to be mature enough for fertilizing eggs (Asakura 1987a). Nevertheless, the fact that large males can monopolize females indicates that large males are at an advantage in competing for females (Asakura 1987a; Wada et al. 1999; Yoshino et al. 2002, 2004). We found one pair whose male was less than 7 mm CL, but

this was unlikely to be a precopulatory guarding pair since the body size difference of the pair was small and the female had underdeveloped eggs. It is more likely that the male was found holding onto the female in order to exchange shells with her.

We found clear decreases in the abundance of males larger than 8.5 mm CL and females larger than 6.5 mm

CL in July. The simplest explanation for the decreases is natural mortality by longevity. However, density-dependent mortality may also be related to the decreases, since many juveniles were recruited in the same time period. A similar pattern was found in the mud crab *Macrophthalmus japonicus*. From a 7-year study, Henmi (1992a) detected that the longevity and growth of the adult is reduced in the year of which crab density is high due to high juvenile settlements. Field experiments on the mud crab indicated that the reduced longevity and growth are attributed to the remarkable decrease in the feeding activity of large crabs through interference interaction due to high density (Henmi 1992b). Large crabs actually avoid high-density sites for burrows (Henmi 1992b). Increased density by juvenile settlements may also have caused serious stress, especially on large, senescent individuals in *D. nitidimanus* and may have increased their mortality as a result. It is also likely that large individuals migrated to avoid the high-density conditions. In fact, adult *D. nitidimanus* in the Amakusa region migrate to the subtidal zone before juveniles were recruited to the sandflats, leading to habitat segregation between adults and juveniles (Asakura and Kikuchi 1984). Size-dependent migration has not been reported in this species.

Another possible reason for the drop in numbers of large crabs is seasonally specific predation, because large individuals are more visible and likely to suffer more risk of predation. Predation is seemingly an unlikely explanation since the 'missing' individuals were of different sizes in the two sexes. However, in sexually size-dimorphic species, such size-dependent mortality can occur through the difference in encounter rates to predators between sexes. From the size distribution pattern of the sexes of *D. nitidimanus*, predators are likely to encounter and prey upon females more often than males in around 6 mm CL, but males are more often eaten at around 8 mm CL. In our site, juvenile settlers of a predatory portunid crab *Portunus pelagicus*, occasionally grasping *D. nitidimanus*, are often observed in this season (T. Koga, pers. obs.). In addition, we are now investigating the seasonal change of prey preference of another portunid species of *Charybdis japonica* that are observed in the tidal flats throughout the year. *C. japonica* likely consumes a large amount of *D. nitidimanus* during summer in a laboratory (Koga et al., unpublished data). Hence, seasonally specific predation can also be attributable to the disappearance of the large individuals.

We found different chela growth rates between functionally mature and immature males in several months, though such a pattern was not found in females. Mature males had relatively larger chelae (relative to their body size) than immature males. This two-phase growth of *D. nitidimanus* is consistent with the description in Asakura (1987b) that gigantic chelae (he referred to as "broad type") were found in males of large body size, though quantitative data were not shown. It is reported that large chelae can efficiently serve as an

operculum for blocking shell opening (Blackstone 1985; Reddy and Biseswar 1993; Mantelatto and Martinelli 2001), which suggests the efficacy of large chelae in reducing the loss of shell internal water and risk of predation as a result. However, as these advantages are also applicable to females as well as males, those cannot explain well the sexual dimorphism of the relative growth in chelae. Another explanation is the one due to sexual selection. Large weapons are advantageous for competition for mates in various animals (Andersson 1994) and males with large chelae are at an advantage when guarding and overtaking females from rival males in *D. nitidimanus* (Asakura 1987a). The possible cause of sexual dimorphism in the relative growth of the major cheliped would be that males invest more energy into chela growth to achieve high mating success once they reached a threshold body size.

Interesting is the seasonal change in the relationships between carapace length and male chelae length. The two-phase growth patterns that were observed from April to June disappeared in July, and remained undetectable until September when the abundance of males larger than 7 mm CL recovered. One reason for the disappearance of the two-phase patterns is the drastic decrease of males larger than 8.5 mm CL in July. However, it is clear that the disappearance cannot be explained by the decrease of the large males alone, because the two-phase patterns in April–June were still maintained even when the large males are excluded from the analyses. Relative chela size was also significantly larger in the early reproductive season (i.e., April–June) than in the later season (August–September) for the data set in which large males were excluded. The different relative growth of chelae between juvenile and adult phases is reported in many crustaceans (e.g., Hartnoll 1978; Goshima et al. 2000; McQuaid et al. 2006) including hermit crabs (e.g., Mantelatto and Martinelli 2001; Biagi and Mantelatto 2006). However, our findings would probably be the first where the relative size of males' secondary sexual character within the same population changes plastically regardless of the reproductive season.

The life-history strategy employed by males may be expressed in the seasonal change in the relative growth of male chelae. We suspect that males tune their growth rates of the major chelae with seasons to maximize their lifetime reproductive success. It is true that large chelae enable males to enjoy high mating success in *D. nitidimanus* (Asakura 1987a), but might be maladaptive in terms of predation avoidance. In ocypodid crabs, large chelae function in predation avoidance in some species (Backwell et al. 1998), but not others. In *Uca beebei*, large chelae make males susceptible to their bird predators because of the conspicuousness of the large claw (Koga et al. 2001). If this is the case in *D. nitidimanus*, selection would favor males that grow their chelae large at the beginning of the reproductive season when male reproductive success is expected to be the highest. In the Waka-River Estuary, juveniles of the predatory port-

unid *P. pelagicus* are often found during and after July and adults of another portunid *C. japonica* are found year round and likely feed on a lot of hermits during the summer (Koga et al., unpublished data). The two-phase growth patterns disappeared at this time. Later in the year, after the breeding season, males may constrain their chelae growth in order to reduce predation risk. Keeping chelae small would increase their chances of surviving to the following breeding season when they can, again, increase the size of their chelae. Even if those portunids stop predation on the hermits in autumn or later, relatively large chelae may be costly for males in terms of loading during non-reproductive seasons. We are also currently investigating male chela allometry in more detail as well as predation pressures on the hermits by the carnivorous portunids to test those possibilities.

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