

## Growth and reproduction of the pilumnid crab *Benthopanope indica* (Decapoda: Brachyura) in Tateyama Bay, Japan

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**Abstract:** The growth and reproduction of the pilumnid crab, *Benthopanope indica*, were examined from April 2001 to March 2002 in Tateyama Bay, central Japan. Oviparous females were mainly observed from June to August, whereas small juveniles were recruited from August to January. After settlement, juveniles (carapace width, CW, of less than 2 mm) grew to and exceeded the mature size (CW 5.80 mm in males and 4.54 mm in females) by the following April. Although large males had considerably larger major chelipeds, their relative growth did not correspond to sexual maturity. The relative growth rate of the male abdominal width decreased at the puberty molt. Enlargement of the abdomen occurred in the mature females, but it was difficult to distinguish postpubertal females from prepubertal females on the basis of abdominal width only, because some females had intermediate abdominal widths, between those of pre- and postpubertal females. Brood size correlated positively with CW, ranging from 120 to 1,700 eggs. After the reproductive season, many large individuals died of senescence, with a longevity of almost one year. However, from size frequency distributions and growth rate analysis, it is likely that some individuals survived until the next reproductive season.

**Keywords:** *Benthopanope indica*, Pilumnidae, growth, reproduction

### 1. Introduction

The pilumnid crab *Benthopanope indica* (Decapoda, Brachyura) is a small species that attains a carapace width (CW) of approximately 11 mm. It inhabits the branches or roots of the brown alga *Sargassum thunbergii* and under calcareous algae in the intertidal zone. It has been recorded from the temperate to subtropical region of the Indo-West Pacific Ocean (SAKAI, 1976; MIYAKE, 1998). DAVIE (1989) transferred this species from the genus *Pilumnopeus* (SAKAI, 1976; MIYAKE, 1998) to the new genus *Benthopanope* established by him. *Benthopanope* is distinguished from other genera by its postlarval morphological characteristics. KO (1995) described the complete larval development of *B. indica* and confirmed DAVIE's classification. The crab of this genus recorded in Japan is *B. indica* only (DAVIE, 1989).

The growth and reproduction of Xanthoidea have frequently been investigated, especially those of Menippidae (e.g., TWEEDALE *et al.*, 1993), Xanthidae (e.g., KNUDSEN, 1960), Panopeidae (e.g., McDONALD, 1982), and Eriphiidae (e.g., TOMIKAWA and WATANABE, 1992). No such studies of the Pilumnidae have been performed until recently, although there are 400 pilumnid species all over the world (NG and HUANG, 2002). The limited references to the Pilumnidae include reports of their embryonic and postembryonic development (WEAR, 1967; CLARK and NG, 2004), agonistic behavior (LINDBERG and FRYDENBERG, 1980), fecundity (ALMACA, 1987), size at sexual maturity (KUHLMANN and WALKER II, 1999), feeding (KYOMO, 1999), reproductive behavior (KYOMO, 2001), reproductive cycle (KYOMO, 2002; LITULO, 2005a), and population structure (LITULO, 2005a, b).

The mouth of Tokyo Bay is by the side of the Kuroshio Current and many aquatic organisms exist in this coastal area. Various crab species including warm-water species, also live on the

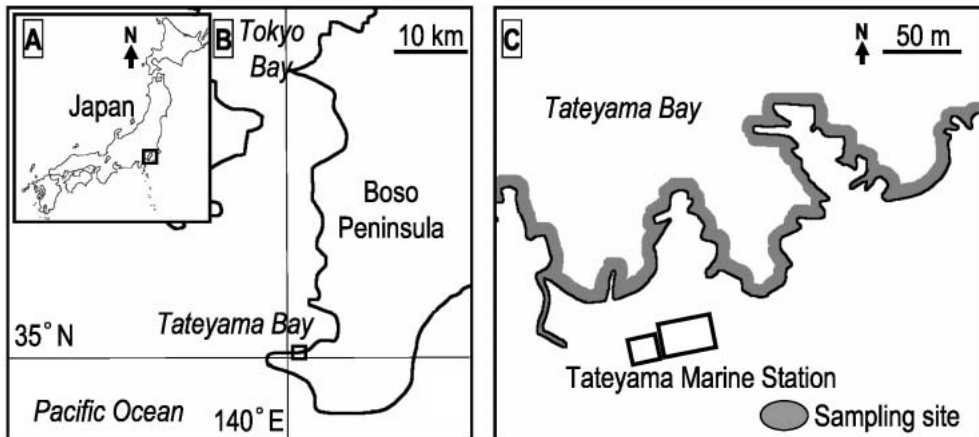


Fig. 1. Maps showing sampling site in Tateyama Bay. (A) – (C) show the site in increasing detail. Sampling of *Benthopanope indica* was carried out on the intertidal rock along the shoreline shown in (C).

reef. Therefore, basic ecological studies of these crabs have been undertaken: the majids *Tiarinia cornigera* (TSUCHIDA and WATANABE, 1991) and *Pugettia quadridens quadridens* (FUSEYA and WATANABE, 1993; FUSEYA *et al.*, 2001), the xanthid *Leptodius exaratus* (WATANABE *et al.*, 1990), the eriphiid *Eriphia smithii* (TOMIKAWA and WATANABE, 1992), the plagusiid *Plagusia dentipes* (TSUCHIDA and WATANABE, 1997; SAMSON *et al.*, 2007), the hymenosomatid *Rhynchoplax coralicola* (GAO *et al.*, 1994), the portunids *Thalamita sima* (NORMAN, 1996) and *Thalamita pelsarti* (as *T. prymna*; NORMAN *et al.*, 1997). Although *B. indica* is one of the dominant crabs in this area (personal observation), its life history has not yet been investigated.

In this study, monthly sampling over one year and the morphometric analysis of several body parts of the collected samples were used to clarify the patterns of growth and reproduction and size at sexual maturity. The life history of *B. indica* was inferred from the data.

## 2. Materials and Methods

Samples were collected monthly between April 2001 and March 2002 at upper intertidal zone on the rocky shore near the Tateyama Marine Station, Field Science Center of Tokyo University of Marine Science and Technology, located near the tip of Boso Peninsula, Chiba Prefecture, Japan (Fig. 1). Crabs attached to

the roots of the brown alga *S. thunbergii* or hidden below the calcareous algae were collected by hand and forceps during the day (April–October) or at night (November–March) during low tide. Sampling was performed in those algae associations randomly selected until up to about one hundred individuals were collected but the sample size could not reach the purpose in April and May in 2001. The specimens were preserved in 10% formaldehyde–sea water. The crabs were sexed based on the form of the pleopods and the location of the gonopores. The females were checked for the presence or absence of attached eggs in the pleopods. Ovigerous females were separated into those bearing early developing (nonpigmented–eyed) eggs and those with pigmented–eyed eggs. Carapace width (CW) to the nearest 0.01 mm was measured with digital calipers in all specimens and CW frequency distributions by sex for 1 mm intervals were constructed for each month.

Carapace width and the following body parts were measured to the nearest 0.01 mm with digital calipers and under a stereomicroscope using a micrometer: propodus length (PL) and height (PH) of the major chelipeds and the width of the fifth abdominal segment (AW). Cheliped handedness was determined by the size and dentition of the cheliped.

To detect quantitative morphological changes, the growth of some body parts

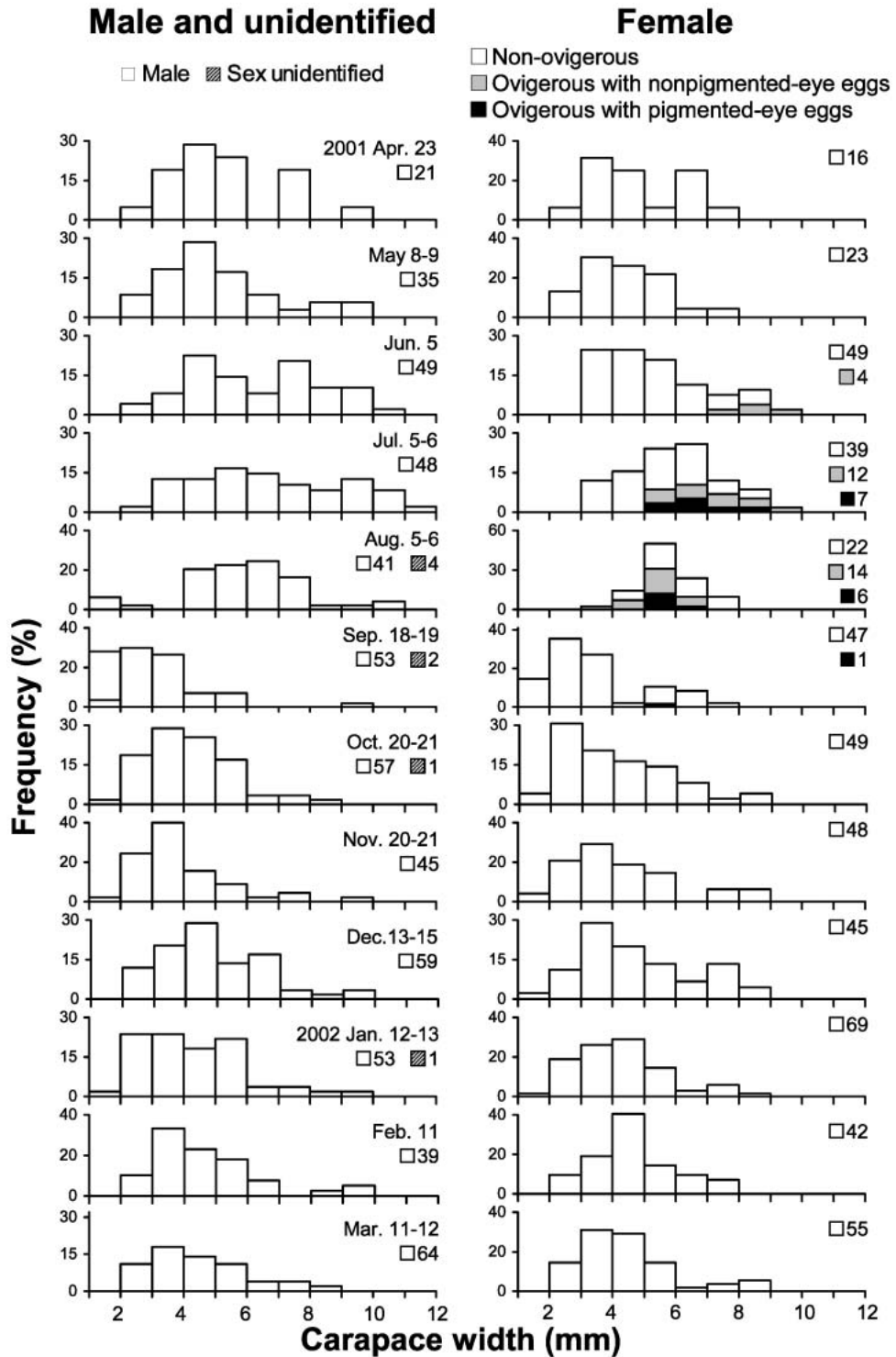


Fig. 2. Monthly changes in the size frequency distribution of *Benthopanope indica* from April 2001 to March 2002. Figures at the right side of each box indicate the number of individuals in each category.

relative to the CW was analyzed with regression lines. If a morphological change in a body part does not occur during growth, the relationship between the body part and CW is usually described by a single regression line. Conversely, when a morphological change occurs in a body part, two or more regression lines are possible. If the ranges of CW of the two regression lines do not overlap, we can estimate the parameter of the regression lines by searching statistically for the inflection point. We used the Akaike's information criterion (AIC) method (AKAIKE, 1973) as the criterion for detecting the best-fit inflection point between two regression lines (see DOI *et al.*, 2007). The inflection point was estimated by the stepwise calculation of each 0.10 mm. In the case of overlapping CW ranges in the regression lines, we tried to distinguish them using the body part/CW ratio.

The total numbers of external eggs (NE) attached to the pleopods of all ovigerous females were counted under a stereomicroscope. To evaluate the relationship between CW and NE, a power function was fitted by the nonlinear least square methods using Solver, a nonlinear optimization tool in Excel 2003 (Microsoft, Tokyo, Japan). To estimate mean egg diameter, the longest and shortest diameters closest to 0.025 mm were measured using a micrometer under a binocular microscope.

### 3. Results

#### Growth

The total number of crabs sampled was 1,128, consisting of 572 males, 548 females, eight small individuals of unidentified sex, and two intersex individuals. The CW ranged from 1.29 to 11.32 mm for males and from 1.32 to 9.51 mm for females. The CW frequencies were relative uniformly distributed over the entire size range from April to July (Fig. 2). The size frequency distribution showed that the population was composed of two size groups larger and smaller than ca 7.00 mm CW in June and July. The small crabs (CW < 7.00 mm) grew during this period. Whereas those adults comprised the main group in August, they almost disappeared and juveniles (CW < 4.00 mm) became the main group in September. The recruits

began to occur in August and comprised most of the population from September to March. Although alteration of the cohorts (year class) was clearly observed between August and September, few larger crabs of the previous cohort were observed to have survived.

#### Reproduction

A total of 44 ovigerous females were collected during the study and their sizes ranged from 4.54 to 9.51 mm CW (mean  $\pm$  SD,  $6.37 \pm 1.26$ ) (Fig. 2). Ovigerous females were found from June to September. Their frequency was low in June (7.6%), but increased abruptly to > 30% in July (32.8%) and August (47.6%). Only one specimen was sampled in September (2.1%). Females bearing eyed eggs were collected except in June and their frequencies were 12.1% and 14.3% in July and August, respectively. The mean CW ( $\pm$  SD) of ovigerous females in those months were  $8.30 \pm 0.93$  mm,  $6.82 \pm 1.23$  mm, and  $5.63 \pm 0.50$  mm in June, July, and August, respectively, and the CW of one ovigerous female in September was 5.06 mm.

#### Relative growth

AIC analysis of two relative size relations (PL to CW, PH to CW) produced two regression lines in males (Fig. 3, Table 1). The inflection points of PL and PH were at CW values of 7.50 mm and 7.60 mm, respectively. The secondary sexual characteristic, elongation of the cheliped, was more clearly observed in the PL value. The relative growth of AW in males was divided into two lines at the CW value of 5.80 mm (Fig. 4; Table 1). The gradient of the upper line was smaller than that of the lower line.

There was no marked increase of the cheliped in females. The increase in both PL and PH relative to CW was fitted to a single straight line (Table 1). The female abdominal segment showed considerable enlargement by the puberty molt (Fig. 5). An overlap of the mature, immature, and transition groups was observed from CW larger than 3.00 mm. Therefore, a single straight line representing the growth of AW relative to CW was fitted only for ovigerous females (Fig. 5, Table 1).

The minimum AW/CW value in ovigerous females was 0.293. Assuming this value to be the

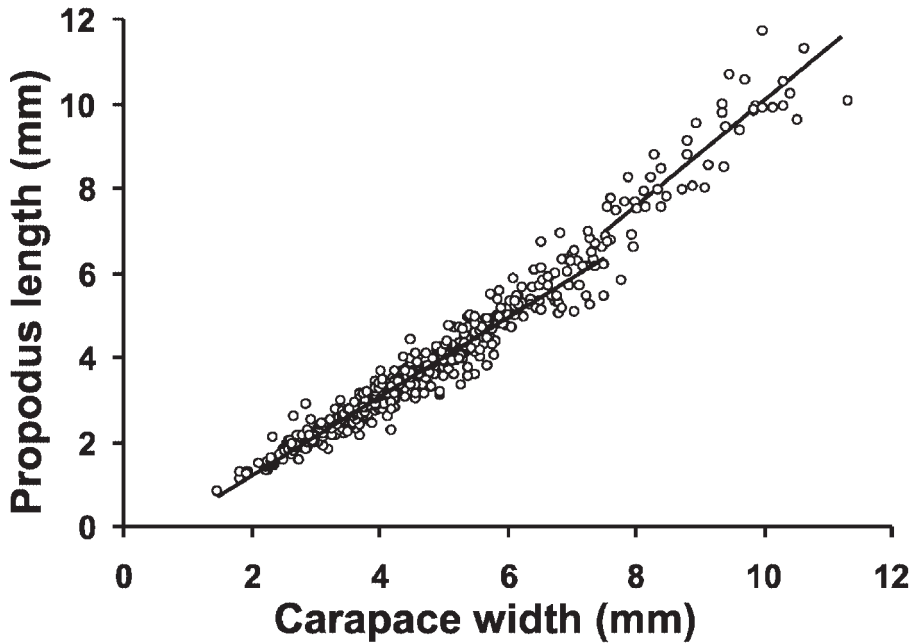


Fig. 3. Growth of propodus length relative to carapace width in male *Benthopanope indica*.

Table 1. Regression lines  $y = a + bx$  for the morphometric analysis of *Benthopanope indica*. Asterisk indicates that the slope ( $b$ ) is significant ( $t$  test; \*  $P < 0.001$ ). Dagger indicates that the slope ( $b$ ) is significantly different between sexes (ANCOVA; †  $P < 0.001$ ). AIC, Akaike's information criterion; AW, fifth abdominal segment width; CW, carapace width; IP, inflection point; NA, not applicable; PH, propodus height of the major cheliped; PL, propodus length of the major cheliped.

Sex	Dependent variables	No. regression lines	AIC	IP (mm, CW)	CW range	Parameter		N	R	Significance	
						Intercept (a)	Slope (b)			b	Between sexes
Male	PL	1	536	NA	1.47–11.32	-1.150	1.057	480	0.979	NA	†
		2	442	7.50	1.47–7.47	-0.675	0.939	431	0.970	NA	†
					7.50–11.32	-2.372	1.247	49	0.879	NA	†
	PH	1	-54	NA	1.47–11.32	-0.541	0.573	480	0.979	NA	†
		2	-113	7.60	1.47–7.57	-0.363	0.529	435	0.967	NA	†
					7.61–11.32	-0.432	0.580	45	0.846	NA	†
AW	1	-1374	NA	1.29–11.32	0.094	0.181	570	0.980	NA	†	
	2	-1447	5.80	1.29–5.79	0.004	0.205	421	0.965	NA	†	
Female	PL	1	NA	NA	5.81–11.32	0.205	0.165	149	0.933	NA	†
					1.32–9.41	-0.232	0.803	459	0.973	*	NA
	PH	1	NA	NA	1.32–9.41	-0.124	0.459	460	0.970	*	NA
	AW	1	NA	NA	4.54–9.51	-0.270	0.367	44	0.975	*	NA

puberty point, we distinguished nonovigerous females at two stages: postpuberty  $\geq 0.293$  and prepuppy  $< 0.293$  (Fig. 6). There were not only postpubertal females with broad abdomens, but also those with extremely narrow abdomens between June and September. Although the change of generations occurred after the main reproductive season (June to

August), postpubertal and mature-sized females were found with a mean CW that was greater than that of ovigerous females (6.37 mm CW). Whereas the postpubertal females were included in the group with large CW in most months, females at the postpuberty that were smaller than the smallest ovigerous female (4.54 mm CW) were found in December,

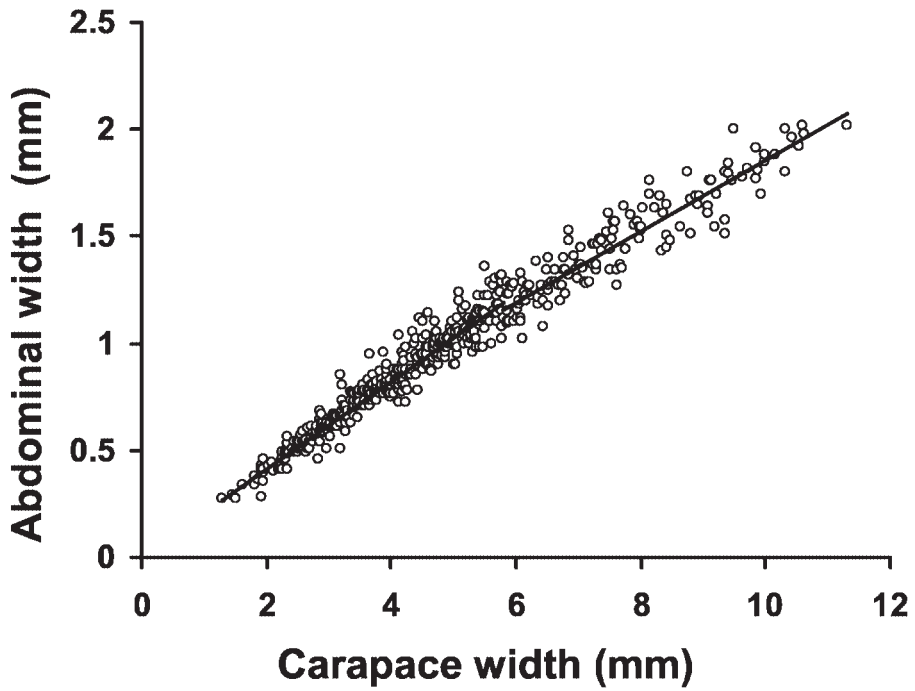


Fig. 4. Growth of fifth abdominal segment width relative to carapace width in male *Benthopanope indica*.

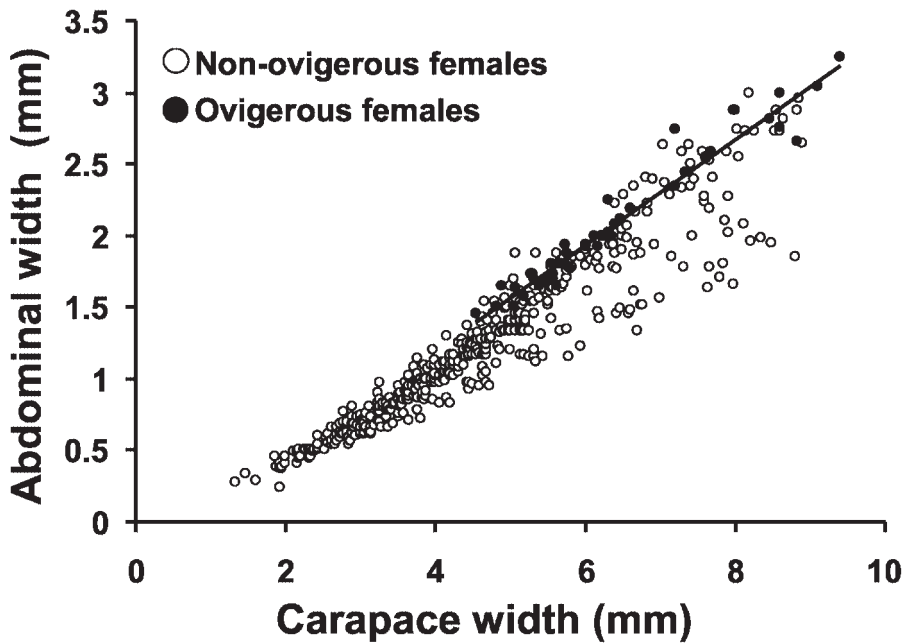


Fig. 5. Growth of fifth abdominal segment width relative to carapace width in female *Benthopanope indica*. Open and closed circles indicate nonovigerous and ovigerous females, respectively.

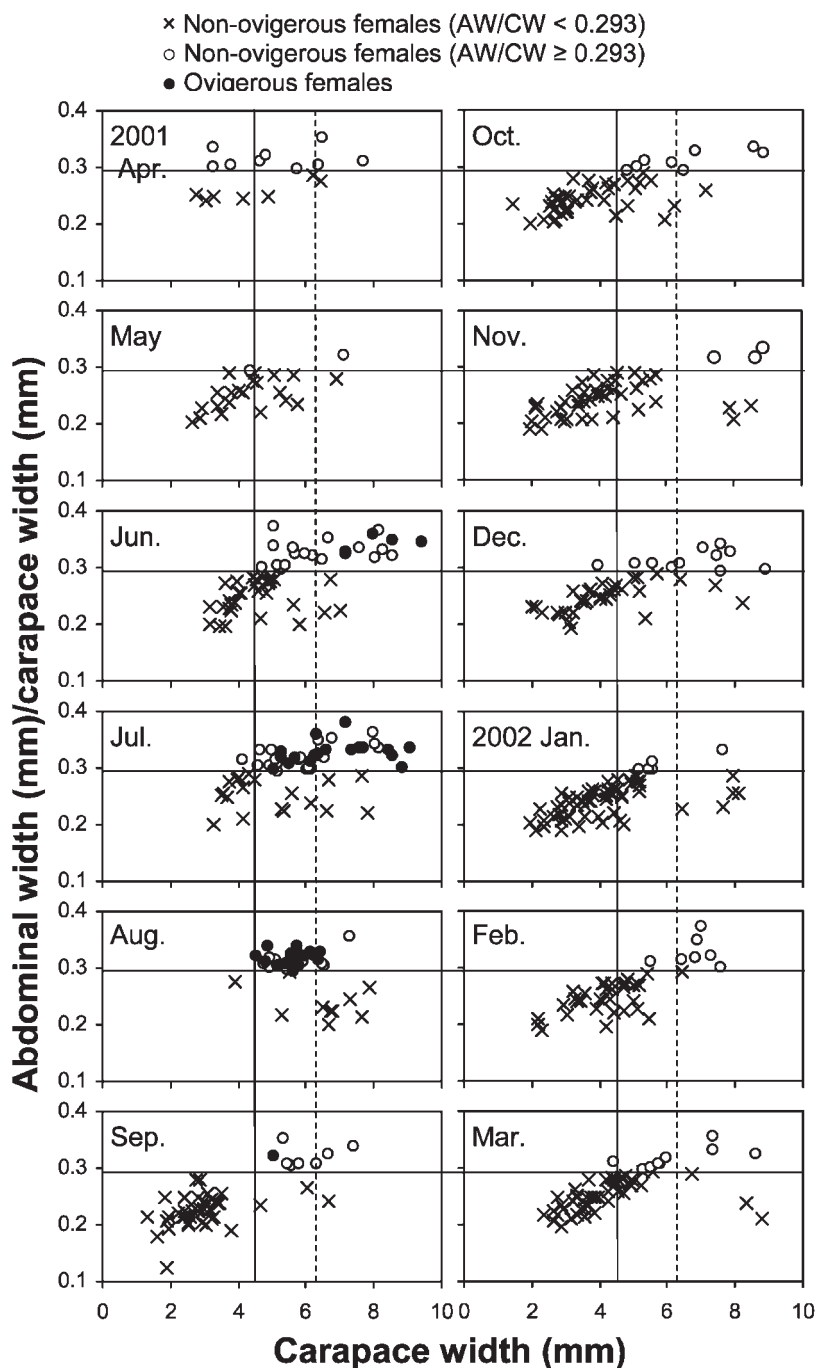


Fig. 6. Monthly changes in the relationship between carapace width (CW) and abdominal width (AW),  $AW/CW$ , in female *Benthopanope indica* from April 2001 to March 2002. Closed circles, open circles, and crosses indicate ovigerous females, nonovigerous females with wide abdomens ( $AW/CW \geq 0.293$ ), and nonovigerous females with narrow abdomens ( $AW/CW < 0.293$ ), respectively. Solid and dashed vertical lines indicate the smallest (4.54 mm) and mean CW of ovigerous females (6.37 mm), respectively. Horizontal lines indicate the puberty point ( $AW/CW = 0.293$ ).

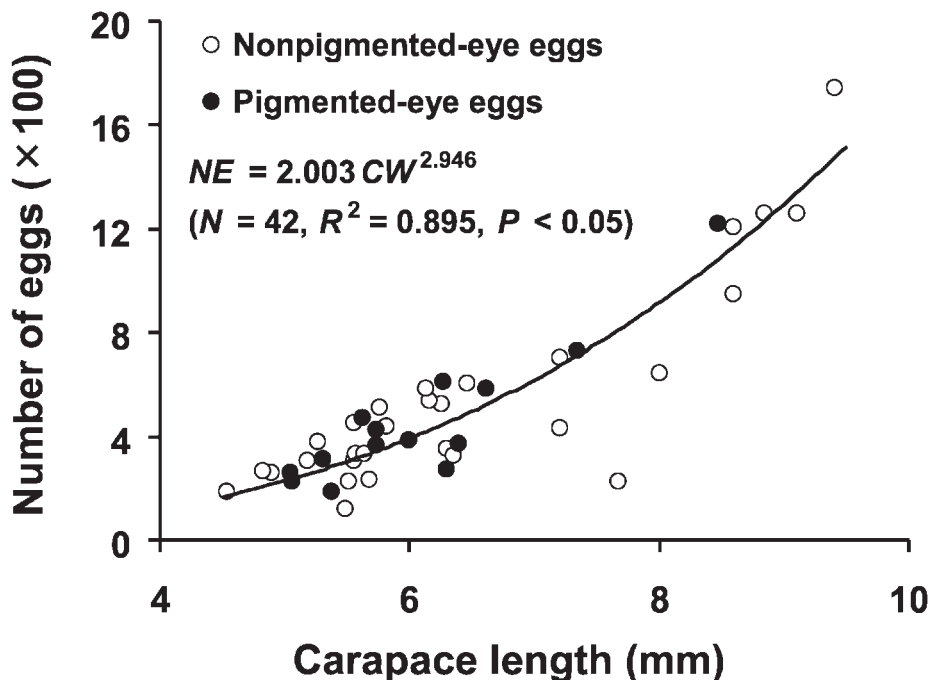


Fig. 7. Relationship between carapace width and number of eggs in the pleopods of *Benthopanope indica* females. Open and closed circles indicate noneyed and eyed eggs, respectively.

March, and especially in April. Sexual dimorphism in growth rates relative to CW was found for all parameters evaluated (Table 1).

#### Brood size and egg size

The numbers of eggs of the 44 ovigerous females (4.54–9.51 mm CW) ranged from 120 to 1,739. Egg number increased with CW (Fig. 7), and large females had large numbers of eggs. The relationship between brood size (number of eggs, NE) and CW is described as follows:  $NE = 2.003CW^{2.946}$  ( $N = 44, R^2 = 0.895, P < 0.05$ ). The mean diameter of noneyed eggs was  $0.38 \pm 0.03$  mm ( $N = 300, 10$  broods), and was significantly smaller than that of eyed eggs, with a mean diameter of  $0.42 \pm 0.03$  mm ( $N = 360, 12$  broods) ( $t$  test,  $P < 0.01$ ).

#### 4. Discussion

Newly settled crabs (CW < 2.00 mm) were found from August, and the smallest males and females (CW 1.32 mm and CW 1.29 mm, respectively) were collected in September. From these results, we infer that the beginning of recruitment of the small crabs occurred in August or

early September. KO (1995) reported that the period from the first zoea to the first juvenile crab of *B. indica* was at least 24–28 days (20–25 °C) and that the size of the megalopa was 0.87 mm. QUINTANA (1986) showed that the CWs of the megalopa and the first-, second-, and third-stage crabs in the related pilumnid, *Parapilumnus trispinosus*, were 0.83, 1.28, 1.58, and 1.77 mm, respectively. Therefore, these small crabs of *B. indica* might constitute the first postlarval stage one month after hatching, and the earliest hatching females might be from the preceding June or early July. This corresponds to the earliest month (June) in which we collected ovigerous females (Fig. 2).

It is difficult to estimate the final reproductive season from our current data because of inconsistencies in the results. Ovigerous females were collected until September, whereas several crabs of the small size group were sampled in January (Fig. 2). If the period from hatching to recruitment was also one month in the final reproductive season, the small crabs of the final season would have been born around December or late November. However, it was only



three months before we collected the final ovigerous females. This inconsistency is remarkable. There are three possible explanations of this discrepancy. First, the recruits could be transported from the southern populations with the longer reproductive season through the warm oceanic current. For instance, the tropical and sub-tropical hermit crabs, *Calcinus* spp., could be collected in this area (MURATA *et al.*, 1991). The larval transportation through the oceanic current would play an important role in the source of the recruits of *B. indica* in this area. Second, the actual pelagic larval period could be longer because the described period was measured in the warmer season. Further research into the relationship between larval development and environmental conditions should clarify this. Third, samples of ovigerous females would not have been caught later in the reproductive season because the main reproductive season had already finished. As we will explain in a later section, this species has two forms of life history. Thus, several mature or mature-like females do not die out, but live beyond the main reproductive season. Occasionally, the surviving females produce eggs until the end of autumn. These results lead us to hypothesize that the reproductive season of this species extends at least from June to September (three months), or slightly longer, until October or November in this area. This seasonality and the duration of the reproductive period are similar to those of the xanthid crab *Leptodiis exaratus* (WATANABE *et al.*, 1990), the eriphiid crab *Eriphia smithii* (TOMIKAWA and WATANABE, 1992), the majid crab *Tiarinia*

*cornigera* (TSUCHIDA and WATANABE, 1991), the portunid crab *Thalamita pelsarti* (NORMAN *et al.*, 1997), and the hymenosomatid crab *Rhynchoplax coralicola* (GAO *et al.*, 1994) in the same study area. *B. indica* and these five species are warm-water species and the present study area is the northern limit in their distributions except for *R. coralicola* (SAKAI, 1976; MIYAKE, 1998). The reproductive season of all warm-water species are limited in about three warmer months in this area. In contrast, other temperate species with the northward distribution have longer reproductive period and/or different seasonality in this area: February–August in the majid crab *Pugettia quadridens quadridens* (FUSEYA and WATANABE, 1993), October–December in the plagusiid crab *Plagusia dentipes* (TSUCHIDA and WATANABE, 1997). These patterns of reproductive seasons are possibly related to physiological difference between warmer and temperate species.

In September 2001, a considerable number of small crabs appeared and grew. In the same month, the number of large crabs decreased, although they had comprised the major proportion of the population in previous months. Most individuals that have completed their reproductive activity probably die from senescence. Therefore, their longevity is almost one year. However, some crabs might live for more than one year. From September onwards, a few large crabs were distinguishable from the juveniles recruited in August. To confirm the age of those large crabs, we analyzed their growth rates as follows. We assumed that all the crabs settled on September 1 and calculated the growth rate ( $\Delta CW$ ),

Table 2. Growth rate ( $\Delta CW$ ) analysis based on the assumption that all crabs were recruited on September 1, 2001, in *Benthopanope indica*.  $\Delta CW_i$  was calculated as follows,  $\Delta CW_i = CW_i - \overline{CW}_{t-1}$ , where  $\Delta CW_i$  and  $CW_i$  are the growth rate and carapace width of individual  $i$  in month  $t$ , respectively.  $\overline{CW}_{t-1}$  is the mean carapace width in month  $t-1$ . Individuals with  $-\Delta CW_i$  were excluded from the analysis because they hatched after September 1, 2001.

Month	Male $\Delta CW_i (> 0)$			Female $\Delta CW_i (> 0)$		
	Mean	Range	$N$	Mean	Range	$N$
Oct.	1.61	0.04–5.70	47	1.88	0.19–5.40	26
Nov.	1.35	0.01–4.79	14	1.69	0.07–4.74	21
Dec.	1.57	0.01–5.43	43	1.73	0.02–4.60	24
Jan.	1.25	0.06–4.22	19	1.29	0.13–3.36	19
Feb.	1.50	0.13–5.03	28	1.17	0.05–3.34	25
Mar.	1.25	0.19–3.98	28	1.37	0.05–4.31	23

$$\Delta CW_{it} = CW_{it} - \overline{CW}_{t-1},$$

where  $\Delta CW_{it}$  and  $CW_{it}$  are the growth rate and CW of individual  $i$  in month  $t$ .  $\overline{CW}_{t-1}$  is the mean CW in month  $t-1$ .  $\Delta CW_{it}$  values that were  $<0$  were excluded from the analysis because those individuals had hatched after September 1, 2001. Although the mean  $\Delta CW$  ranged from 1.17 to 1.88, the maximum  $\Delta CW$  showed a considerably higher value (3.34–5.70) in each month (Table 2). Individuals with extremely high  $\Delta CW$  could have been members of the previous year class that had survived after the reproductive season. However, their size frequency distributions were unclear because the sample size was small. The presence of two longevity forms is similar to those of the majid crabs *T. cornigera* (TSUCHIDA and WATANABE, 1991) and *P. quadridens quadridens* (FUSEYA and WATANABE, 1993) in the same study area.

The relative growth rates of male PL and PH increased at the inflection points of 7.50 mm and 7.60 mm CW, respectively. Although both inflection points were close, it is doubtful that these changes reflect physiological maturity. The growth of Brachyura displays two patterns relative to the timing of the puberty molt: one in which the puberty molt is the terminal molt and the other in which molts occur more than once after the puberty molt (HARTNOLL, 1985). In the former type, considerable changes in relative growth were observed at the puberty molt, but in the latter type, these changes are not clear. *Benthopanope indica* is the latter type, like most xanthoid crabs (HARTNOLL, 1985), because the ovigerous females molt after larval hatching in captivity.

In panopeid crabs such as the male *Panopeus austrobesus*, the growth of the cheliped dimensions relative to CW provides a much higher estimate of the mature sizes than that calculated with gonad analysis. The measurement of the length of the first gonopod is consistent with gonad development (NEGREIROS-FRANZOZO and FRANZOZO, 2003). Moreover, the pattern of relative growth of the first gonopod length corresponds to the relative increase in AW (HARTNOLL, 1974). Therefore, the inflection point for the male AW (5.80 mm CW) probably

indicates the size at physiological maturity in *B. indica* males.

For the relative growth of female AW, a straight line could only be fitted to data from ovigerous females. It was difficult to rigidly divide nonovigerous females into immature and mature groups because many females had a transitional AW.

Morphologically mature females with broad abdomens were found throughout the year. However, our limited data do not show whether the females that survived into the second reproductive season had already spawned in the first reproductive season. We did not examine their ovaries because their body size was small. In future studies, histological observation will be required to confirm their reproductive cycle. Females with narrow abdomens were observed, which exceeded the mean CW of ovigerous females during and after the reproductive season. These females may not have attained sexual maturity. A parasitic epicaridean isopod, *Xanthion spadix*, causes the narrowing of the abdomen of female *L. exaratus* and inhibits their reproductive ability (MIZOGUCHI *et al.*, 2002). It must be confirmed in a future study whether *B. indica* females with narrow abdomens are parasitized by epicaridean isopods. Some small females with broad abdomens were found in December, March, and April, indicating that the puberty molt also occurs during winter and spring, before the reproductive season in females.

Our study area is located at the extreme northern limit of the distribution of *B. indica* (SAKAI, 1976; MIYAKE, 1998). In female *Panopeus herbstii*, the size at sexual maturity, the mean size of the mature crabs, and the proportion of large crabs were less in the northern part of its distribution than in southern areas (HINES, 1989). HINES (1989) attributed this to the cessation of the molt during the cold season. This interpretation may explain why there are two longevity forms and so much variation in size at maturity in *B. indica*.

Brood size was positively related to body size. The relationship between the number of the eggs per brood and CW in crabs that have the same reproductive season as *B. indica* at Banda are as follows: 610–10,110 (11.80–26.20

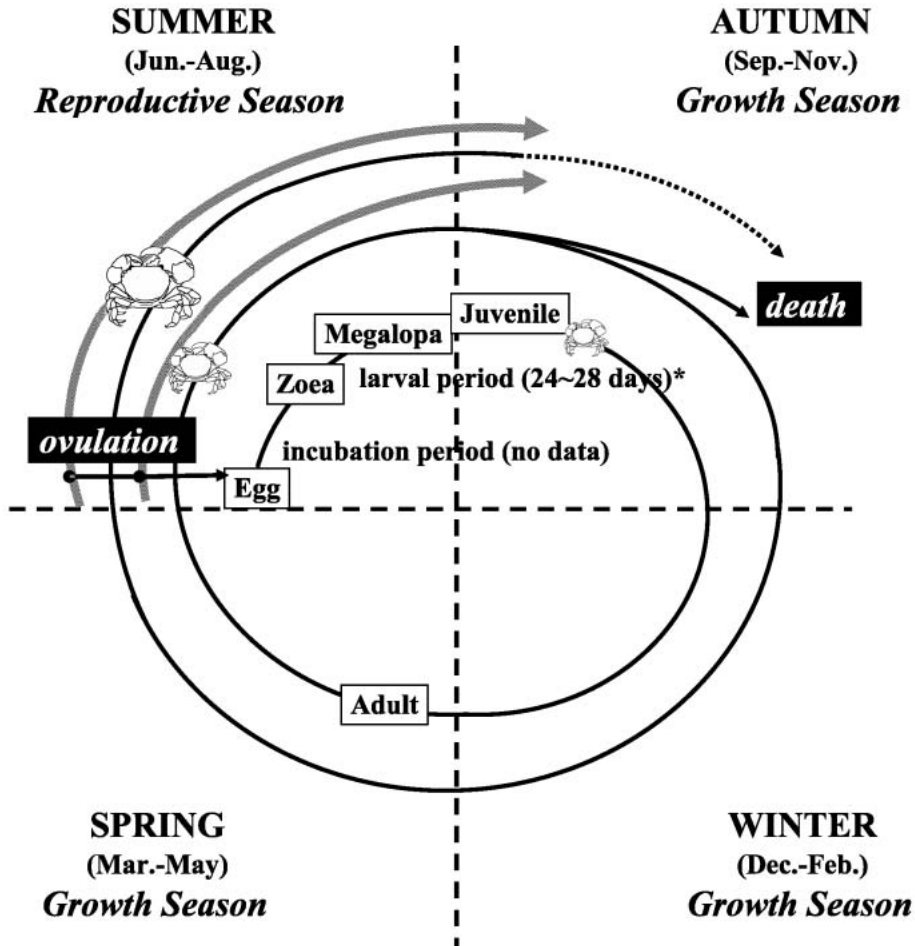


Fig. 8. Scheme of the life history of *Benthopanope indica*. In August–January, juveniles are recruited. The carapace width of juveniles increases to above 6.00 mm by June. From June to early September, these crabs start to spawn and incubate their eggs. After the reproductive season, most individuals die. Part of the population survives until the next reproductive season. (\* Ko (1995))

mm) in *L. exaratus* (WATANABE *et al.*, 1990), 5,293–73,501 (25.10–52.60 mm) in *E. smithii* (TOMIKAWA and WATANABE, 1992), 1,000–2,000 (17.00–25.00 mm) in *T. cornigera* (TSUCHIDA and WATANABE, 1991), and 23–230 (2.65–3.90 mm) in *R. coralicola* (GAO *et al.*, 1994), respectively. The mean number of eggs of *B. indica* is relatively smaller than that of these species because its body size is smaller (HINES, 1982; REID and COREY, 1991). *B. indica* and the latter two species with the relative smaller brood size inhabit in colonies of the algae, while the former two species occur under cobbles and inside crevices. The habitat stability (FUKUI and WADA, 1986) and complexity (LOHRER *et al.*, 2000) are

related to the different reproductive effort of the brachyurans and opportunistic species adapt unstable and low complex habitats (FUKUI and WADA, 1986; LOHRER *et al.*, 2000). The habitat characteristic of the colonies of the algae is still unknown, but they may contribute to the low mortality of crabs inhabiting them. It is necessary to investigate the survival rates of such crabs living in the algae. The accurate number of spawnings per female in the annual reproductive season is still unknown, and must be clarified before the reproductive efforts of these species can be compared. *B. indica* has relative small brood size and restricted spawning season in this area. Further studies are

needed to clarify that how degree do the population of Tateyama Bay and that of the southern area contribute to the maintenance of the population of this area.

The life history of *B. indica* can be deduced from previously published data and the results of this study (Fig. 8). In August–January, the juveniles appear after the larval stage in the colony of brown algae and under calcareous algae. Juveniles with CWs of around 3 mm reach the size of morphological maturity for males (CW 5.80 mm) and the minimum size of ovigerous females (CW 4.54 mm) by the following April. During the reproductive season, from June to early September, the mature females spawn 127–1,739 eggs at a time. Thereafter, most individuals die out, but a few survive into the second year after recruitment and reproduce.

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#### References

- AKAIKE, H. (1973) : Information theory and an extension of the maximum likelihood principle. *In* 2nd International Symposium on Information Theory. Petrov, B.N. and F. Csáki (eds.), Akadémiai Kiadó, Budapest, p.267–281.
- ALMAÇA, C. (1987) : Crabs of the *Sabellaria alveolata* (Linnaeus, 1767) community. Egg number and population size in *Pilumnus hirtellus* (Linnaeus, 1761) and *Porcellana platycheles* (Pennant, 1777). *Arq. Mus. Bocage*, **1**, 19–32.
- CLARK, P.F. and P.K.L. NG (2004) : The larval development of *Actumnus setifer* (de Haan, 1835) (Brachyura: Xanthoidea: Pilumnidae) described from laboratory reared material. *Crust. Res.*, **33**, 27–50.
- DAVIE, P.J.F. (1989) : A re-appraisal of *Heteropanope* Stimpson, and *Pilumnopeus* A. Milne Edwards (Crustacea: Decapoda: Pilumnidae) with descriptions of new species and new genera. *Mem. Queensland Mus.*, **27**, 129–156.
- DOI, W., T.T. LWIN, M. YOKOTA, C.A. STRÜSSMANN and S. WATANABE (2007) : Maturity and reproduction of goneplacid crab *Carcinoplax vestita* (Decapoda, Brachyura) in Tokyo Bay. *Fish. Sci.*, **73**, 331–340.
- FUKUI, Y. and K. WADA (1986) : Distribution and reproduction of four intertidal crabs (Crustacea, Brachyura) in the Tonda River Estuary, Japan. *Mar. Ecol. Prog. Ser.*, **30**, 229–241.
- FUSEYA, R. and S. WATANABE (1993) : Growth and reproduction of the spider crab, *Pugettia quadridens quadridens* (De Haan) (Brachyura: Majidae). *Crust. Res.*, **22**, 75–81.
- FUSEYA, R., K. YOKOKURA and S. WATANABE (2001) : Morphology and distribution of setae used for decorating on the dorsal carapace of the spider crab, *Pugettia quadridens quadridens* (De Haan) (Brachyura: Majidae). *Crust. Res.*, **30**, 154–159.
- GAO, T., S. TSUCHIDA and S. WATANABE (1994) : Growth and reproduction of *Rhynchoplax coralicola* Rathbun (Brachyura: Hymenosomatidae). *Crust. Res.*, **23**, 108–116.
- HARTNOLL, R.G. (1974) : Variation in growth pattern between some secondary sexual characters in crabs (Decapoda Brachyura). *Crustaceana*, **27**, 131–136.
- HARTNOLL, R.G. (1985) : Growth, sexual maturity and reproductive output. *In* *Crustacean Issue 3: Factors in adult growth*. Wernner, A. M. (ed.), A. A. Balkema, Rotterdam, p.101–128.
- HINES, A.H. (1982) : Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.*, **69**, 309–320.
- HINES, A.H. (1989) : Geographic variation in size at maturity in brachyuran crabs. *Bull. Mar. Sci.*, **45**, 356–368.
- KNUDSEN, J.W. (1960) : Reproduction, life history, and larval ecology of the California Xanthidae, the pebble crabs. *Pac. Sci.*, **14**, 3–17.
- KO, H.S. (1995) : Larval development of *Benthopanope indica* (de Man, 1887) (Decapoda: Brachyura: Pilumnidae) in the laboratory. *J. Crust. Biol.*, **15**, 280–290.
- KUHLMANN, M.L. and R.E. WALKER II (1999) : Geographic variation in size structure and size at maturity in the crab *Pilumnus sayi* (Crustacea: Decapoda: Xanthidae) in the northern Gulf of Mexico. *Bull. Mar. Sci.*, **64**, 535–541.
- KYOMO, J. (1999) : Feeding patterns, habits and food storage in *Pilumnus vespertilio* (Brachyura: Xanthidae). *Bull. Mar. Sci.*, **65**, 381–389.
- KYOMO, J. (2001) : Reproductive behavior of the play-dead hairy *Pilumnus vespertilio* (Crustacea: Brachyura: Pilumnidae) with respect to carapace size. *Bull. Mar. Sci.*, **68**, 37–46.
- KYOMO, J. (2002) : Timing and synchronization of the breeding period in *Pilumnus vespertilio* (Crustacea: Pilumnidae) in subtropical Okinawa, Japan. *Pac. Sci.*, **56**, 317–328.
- LINDBERG, W.J. and R.B. FRYDENBERG (1980) : Resource centered agonism of *Pilumnus sayi* (Brachyura, Xanthidae), an associate of the

- bryozoan *Schizoporella pungeus*. Behaviour, **75**, 235–250.
- LITULO, C. (2005a) : Reproductive biology of the hairy crab *Pilumnus vesperitilio* (Brachyura: Pilumnidae) in the East African region. J. Mar. Biol. Assoc. UK, **85**, 877–881
- LITULO, C. (2005b) : Population structure and breeding biology of the hairy crab *Pilumnus vesperitilio* (Fabricius, 1793) (Crustacea: Brachyura: Pilumnidae) in southern Mozambique. J. Nat. Hist., **39**, 1359–1366.
- LOHRER, A.M., Y. FUKUI, K. WADA and R.B. WHITLATCH (2000) : Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab, *Hemigrapsus sanguineus* (de Haan). J. Exp. Mar. Biol. Ecol., **244**, 203–217.
- MCDONALD, J. (1982) : Divergent life history patterns in the co-occurring intertidal crabs *Panopeus herbstii* and *Eurypanopeus depressus* (Crustacea: Brachyura: Xanthidae). Mar. Ecol. Prog. Ser., **8**, 173–180.
- MIYAKE, S. (1998) : Japanese Crustacean Decapods and Stomatopods in Color, Vol. 2. Brachyura (crabs). Hoikusha, Osaka, 277pp. (in Japanese).
- MIZOGUCHI, K., Y. HENMI and T. YAMAGUCHI (2002) : Parasitic status of epicaridean isopods (Crustacea: Malacostraca) and the effects on their brachyuran crab hosts. Jap. J. Benthol., **57**, 79–84 (in Japanese with English abstract).
- MURATA, K., S. WATANABE and A. ASAKURA (1991) : Hermit crabs of genus *Calcinus* (Crustacea: Decapoda: Anomura) from Boso Peninsula. J. Nat. Hist. Mus. Inst., Chiba., **1**, 21–23 (in Japanese with English abstract).
- NEGREIROS-FRANZOZO, M.L. and V. FRANZOZO (2003) : A morphometric study of the mud crab, *Panopeus austrobesus* Williams, 1983 (Decapoda, Brachyura) from a subtropical mangrove in South America. Crustaceana, **76**, 281–294.
- NG, P.K.L. and J.-F. HUANG (2002) : The Indo-Pacific Pilumnidae XV. On two rare species of Rhizopinae (Decapoda, Brachyura) from Taiwan. Crustaceana, **74**, 1379–1385.
- NORMAN, C.P. (1996) : Reproductive biology and evidence for hard-female mating in the brachyuran crab *Thalamita sima* (Portunidae). J. Crust. Biol., **16**, 656–662.
- NORMAN, C.P., Y.J. HIRANO and T. MIYAZAKI (1997) : Hard-female mating in the brachyuran crab *Thalamita prymna* (Portunidae). Crust. Res., **26**, 62–69.
- QUINTANA, R. (1986) : On the megalopa and early crab stages of *Parapilumnus trispinosus* SAKAI, 1965 (Decapoda, Brachyura, Xanthidae). Proc. Japan. Soc. Syst. Zool., **34**, 1–17.
- REID, D.M. and S. COREY (1991) : Comparative fecundity of decapod crustacean, II The fecundity of fifteen species of anomuran and brachyuran crabs. Crustaceana, **61**, 175–189.
- SAKAI, T. (1976) : Crabs of Japan and the adjacent seas. Kodansha, Tokyo, 773pp.
- SAMSON, A.S., M. YOKOTA, C.A. STRÜSSMANN and S. WATANABE (2007) : Natural diet of grapsoid crab *Plagusia dentipes* De Haan (Decapoda: Brachyura: Plagusiidae) in Tateyama Bay, Japan. Fish. Sci., **73**, 171–177.
- TOMIKAWA, N. and S. WATANABE (1992) : Reproductive ecology of the xanthid crab *Eriphia smithii* McLeay. J. Crust. Biol., **12**, 57–67.
- TSUCHIDA, S. and S. WATANABE (1991) : Growth and reproduction of the spider crab, *Tiarina cornigera* (Latreille) (Brachyura: Majidae). Res. Crust., **20**, 43–55.
- TSUCHIDA, S. and S. WATANABE (1997) : Growth and reproduction of the grapsid crab *Plagusia dentipes* (Decapoda: Brachyura). J. Crust. Biol., **17**, 90–97.
- TWEEDALE, W.A., T.M. BERT and S.D. BROWN (1993) : Growth of postsettlement juveniles of the Florida stone crab, *Menippe mercenaria* (Say) (Decapoda: Xanthidae), in the laboratory. Bull. Mar. Sci., **52**, 873–885.
- WATANABE S., H. YAMANA and N. TOMIKAWA (1990) : Reproduction of the xanthid crab, *Leptodius exaratus* (H. Milne Edwards). Res. Crust., **19**, 73–78.
- WEAR, R.G. (1967) : Life-history studies on New Zealand Brachyura I. Embryonic and post-embryonic development of *Pilumnus novaezealandiae* Filhol, 1886, and of *P. lumpinus* Bennett, 1964 (Xanthidae, Pilumninae). N.Z. J. Mar. Freshwat. Res., **1**, 482–535.

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