Reproductive traits and population structure of the porcellanid crab
*Petrolisthes japonicus* (Decapoda: Anomura: Porcellanidae)

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**Abstract.**— We investigated the reproductive traits and population structure of a *Petrolisthes japonicus* population through monthly sampling for one year on an intertidal cobble and boulder shore on the Boso Peninsula, Japan. The main reproductive season lasted for four months, from June to September. The sex ratios were approximately 0.5. Newly recruited juveniles were found mainly from August to October, and three age groups were detected using body size histograms. The growth curves of both sexes were significantly different, and males grew larger than females. Our analyses suggest that females and males in the 0+ age group begin to breed in the year after hatching and that a relatively large proportion of 0+ aged individuals die during the end of or after the reproductive season. A relatively small proportion of 0+ aged individuals survive even after the reproductive season and breed in the next year as the 1+ age group; then, individuals that reach the 2+ age group likely die by the end of summer. Consequently, the longevity of *P. japonicus* is estimated to be 1–2 years.

**Key words:** Reproductive seasonality, growth equation, size structure, sexual size dimorphism, longevity

**Introduction**

Anomuran crabs of the family Porcellanidae Haworth, 1825 exhibit a brachyuran crab-like body shape with broad and dorsoventrally flattened chelipeds and a well-developed symmetrical pleon that is carried bent under the cephalothorax and held against the thorax (Jones, 1977; Osawa & McLaughlin, 2010). They comprise 30 genera with 277 species (Osawa & McLaughlin, 2010) and inhabit intertidal and shallow waters throughout tropical and temperate regions (Werding *et al*., 2003; Rodríguez *et al*., 2005). Most porcellanid crabs are free-living and inhabit hard substrates such as crevices among cobbles, boulders and rocks; some species are associated with other organisms, including sessile colonial invertebrates such as sponges, corals, sea anemones, sea urchins, and tubeworms (Haig, 1960; Werding, 1983; Baeza & Thiel, 2000, Baeza *et al*., 2001).

Porcellanid crabs exhibit a unique feeding habit: they are filter feeders, trapping suspended detritus and plankton by using the long setae of their third maxillipeds (Trager & Genin, 1993; Achituv & Pedrotti, 1999; Zimba *et al*., 2016). They may therefore compete with sympatric filter feeding invertebrates for suspended prey organisms (Hollebone & Hay, 2008). Additionally, porcellanid crabs are known to be preyed on by fish and crabs (Randall, 1967; Hollebone & Hay, 2008; Knope & Larson, 2014).

Consequently, porcellanid crabs may play an important ecological role as competitors and/or prey organisms within the benthic community (Hollebone & Hay, 2008). Basic biological and ecological information about porcellanid crab populations would provide a better understanding of their ecological impacts on benthic com-
munities. To date, most biological and ecological studies of porcellanid crab populations have been conducted in the Southern Hemisphere (e.g., Jones, 1977; Baeza & Thiel, 2000; Gebauer et al., 2007; Miranda & Mantelatto, 2009; Baeza et al., 2011, 2013; Wehrtmann et al., 2012; Pinheiro et al., 2017).

*Petrolisthes japonicus* (De Haan, 1849) is one of the most common porcellanid crabs in Japan and is found on intertidal cobble and boulder shores in temperate and tropical regions (Miyake, 1998). However, biological and ecological information about this species is limited to observations of the female reproductive cycle (Nakasone, 1972), their zoeal morphology (Muraoka & Konishi, 1987; Osawa, 1995), and their distribution patterns on intertidal shores (Asakura, 1991). The aim of the present study was to investigate the reproductive traits and population structure of a *P. japonicus* population by conducting monthly sampling for one year on an intertidal cobble and boulder shore on the Boso Peninsula, Japan.

### Materials and Methods

**Crab sampling**

Samples of *Petrolisthes japonicus* were collected monthly from April 2008 to March 2009 in an intertidal cobble and boulder zone (34°58′N, 139°46′E) on the Boso Peninsula, Japan (Table 1). Two people collected crabs by hand for one hour during low tide. The crabs were individually packed in small plastic bags on site to avoid the autotomy of chelipeds by agonistic interactions between crabs. The crab specimens were then brought to the laboratory and kept in the freezer.

**Crab measurements**

We collected 1259 crabs during the sampling period. Additionally, 77 crabs (31 females and 36 males) that had been infected with parasitic isopods of the family Entoniscidae Kossmann, 1881 were collected. These crabs were not used in the present study because the crabs exhibited substantial swelling of the carapace (Williams & Boyko, 2012).

After thawing the frozen specimens, the carapace width (CW, the widest portion between the lateral margins of the carapace) of the crabs was recorded. The data were then tabulated as shown in Table 1.

### Table 1. Collection records for the porcellanid crab *Petrolisthes japonicus* from April 2008 to March 2009 on an intertidal cobble and boulder shore on the Boso Peninsula, Japan

| Sampling date | Total number of crabs | Total number of females | Number of ovigerous females | Number of males | Number of unsexed juveniles |
|---------------|-----------------------|-------------------------|-----------------------------|----------------|-----------------------------|
|               |                       |                         | Total | Non-eyed egg stage | Eyed egg stage | Hatching egg stage |                       |               |
| April 21      | 86                    | 40                      | 0     | 0                 | 0              | 0                  | 46                   | 0              |
| May 19        | 190                   | 86                      | 6     | 6                 | 0              | 0                  | 104                  | 0              |
| June 19       | 142                   | 74                      | 59    | 30                | 24             | 5                  | 68                   | 0              |
| July 18       | 120                   | 61                      | 52    | 30                | 19             | 3                  | 57                   | 2              |
| August 19     | 107                   | 41                      | 29    | 12                | 12             | 5                  | 32                   | 34             |
| September 16  | 125                   | 47                      | 9     | 2                 | 6              | 1                  | 44                   | 34             |
| October 16    | 73                    | 15                      | 0     | 0                 | 0              | 0                  | 27                   | 31             |
| November 26   | 25                    | 12                      | 0     | 0                 | 0              | 0                  | 10                   | 3              |
| December 14   | 104                   | 39                      | 0     | 0                 | 0              | 0                  | 64                   | 1              |
| January 17    | 111                   | 60                      | 0     | 0                 | 0              | 0                  | 50                   | 1              |
| February 14   | 91                    | 49                      | 1     | 1                 | 0              | 0                  | 42                   | 0              |
| March 16      | 85                    | 44                      | 0     | 0                 | 0              | 0                  | 41                   | 0              |
| **Total**     | **1259**              | **568**                 | **156** | **81**            | **61**        | **14**            | **585**             | **106**        |
was measured using a digital calliper (CW > 3 mm, accuracy 0.05 mm) or a stereomicroscope with the aid of a micrometer (CW < 3 mm, accuracy 0.01 mm). The carapace length (CL, from the tip of the rostrum to the posterior margin of the carapace) was also measured for the crabs collected from April to August 2008, and for comparison with previous work the following linear regression equation between CW and CL was determined: CL = 0.2163 + 1.0144CW (n = 645, R² = 0.9945, F₁, 643 = 116200, P < 0.0001).

Nakasone (1972) documented that *P. japonicus* females are easily distinguished by the presence of gonopores at the coxae of the third pair of pereiopods, and the minimum body size of females was 2.5 mm CL (≈ 2.3 mm CW, converted value using the equation in the present study). Therefore, crabs with > 2.3 mm CW were sexed based on the position of the gonopores (i.e., at the coxae of the third pereiopods in females and at the coxae of the fifth pereiopods in males) (Osawa & Mclaughlin, 2010). Each female was classified according to the presence or absence of eggs attached to the pleopods (ovigerous or non-ovigerous females, respectively). The eggs were then sampled from each ovigerous female using forceps, and their embryonic development was classified into three stages under the stereomicroscope according to the following characteristics: non-eyed eggs, embryos without eye pigmentation; eyed eggs, embryos with eye pigmentation; and hatching eggs, fully developed embryos with little or no yolk and any embryos that had emerged from the egg membrane.

**Data analysis**

Statistical analyses were performed with R statistical software (R3.6.2; R Core Team, 2019) at a 5% significance level. The size of females at the onset of sexual maturity was estimated as the minimum CW value (3.80 mm) of ovigerous females; the size of males at the onset of sexual maturity was not determined in the present study. In decapod crustacean species, sexual size dimorphism in chelipeds occurs in relation to sexual maturity (Hartnoll, 1974, 1978; McLay, 2015), and the chelipeds of *P. japonicus* males become disproportionately larger after reaching approximately 4 mm CW (K. Hamasaki., unpublished data). Therefore, we considered that females and males with ≥ 3.8 mm CW had reached sexual maturity (i.e., the adult stage). To infer the temporal changes in the population structure, the proportions of adult females and males and of unsexed juveniles in the total crab sample were calculated, and the proportion of ovigerous females among adult females was also calculated. The sex ratio was calculated as the [number of males/number of total crabs], and a binomial test (*binom.test* function) was used to test the null hypothesis for the sex ratio in each month and in the total sampling period (H₀; sex ratio = 0.5).

The monthly size-frequency distributions were constructed using 1 mm CW intervals (e.g., 0.5 ≤ CW < 1.5 mm) for both sexes. Unsexed juveniles were divided equally into female and male histograms because the sex ratio was considered to be 0.5 in our *P. japonicus* population (see the Results section). We assumed that the *P. japonicus* population was composed of different cohorts with different mean body sizes and that the body size of each cohort exhibited a normal distribution; i.e., the respective CW histograms comprised a mixture of normal distributions. We estimated the parameters (mixing proportion, mean and standard deviation) for each component of the mixed normal distributions using a nonlinear least squares method with Microsoft Excel Solver (Gorie, 2002). The standard deviation was assumed to be equal for the mixed normal distributions in each CW histogram, because the Excel Solver analysis did not converge in some cases. The analysis was not performed for crabs collected in November because of the small sample size.
We successfully distinguished 2–3 cohorts and defined 0+, 1+ and 2+ age groups based on the size frequency distributions of females and males (see the Results section). To trace and compare the growth trends of females and males from ages 0+ to 2+ (1–25 months), the logistic growth equation (Ricker, 1975) was applied to the mean CW estimates through successive months starting in August, when the first main recruitment occurred. The logistic growth equation is expressed as \( CW_t = CW_\infty \left(1 + \exp\left(-K(t - t_0)\right)\right)^{-1} \), where \( CW_t \) is the size estimated at age \( t \) (1–25 months), \( CW_\infty \) is the asymptotic size, \( K \) is a relative growth rate (with unit month \(^{-1}\)) and \( t_0 \) corresponds to the inflection point of the sigmoidal curve. Coefficients with standard errors of the growth equation were estimated with a nonlinear least squares method using the \textit{nls} function with a \textit{t}-test. The growth equations were then compared between sexes using an \textit{F}-test according to the method of Chen et al. (1992). Additionally, the overall mean CW values of females and males were compared with Welch’s \textit{t}-test (\textit{t.test} function).

**Results**

We collected 568 females, including 156 ovigerous females (81 non-eyed, 61 eyed, and 14 hatching egg stages), 585 males and 106 unsexed juveniles during the sampling period (Table 1). The mean ± standard deviation (range) of the CW values of the specimens was as follows: overall females, 5.18 ± 1.56 (2.31–9.65) mm; ovigerous females, 6.21 ± 1.10 (3.80–9.65) mm; males, 5.67 ± 2.01 (2.31–11.00) mm; and unsexed juveniles, 1.80 ± 0.24 (1.37–2.25) mm. The CW values of males were significantly higher than those of overall females \( (t = -4.636, df = 1100.1, P < 0.0001) \).

Ovigerous females were found from May to September and in February (Table 1). The proportion of ovigerous females among adult females was 7.3% in May, peaked at 74.4–85.2% from June to August and then declined to 60.0% in September (Fig. 1). Egg hatching oc-
curred from June to September, and the proportion of developed eggs, including eyed eggs and hatching eggs, increased from approximately 45% to 78% during this period (Fig. 2). In February, only one ovigerous female (8.25 mm CW) with non-eyed eggs was detected. Unsexed juveniles were found from July to January (Fig. 1). The proportion of unsexed juveniles increased from July (1.7%) through August to October (27.2–42.5%) and then declined from November (12%) to December (1%) and January (0.9%) (Fig. 1). Accordingly, the proportions of adult females and males fluctuated inversely with that of unsexed juveniles. The sex ratios were approximately 0.5, and significantly unbalanced sex ratios were not detected except in December ($P = 0.0176$) (Fig. 1).

The size frequency distributions of females and males with information on ovigerous females and/or unsexed juveniles are shown in Figs. 3 and 4, respectively. We detected three (August) or two normal distributions (other months) in the CW histograms of both sexes.
The mixing proportion and the mean and standard deviation were successfully estimated for each component, and the calculated normal distribution curves were superimposed on the respective CW histograms in Figs. 3 and 4. When the mean CW estimates were plotted against the sampling months, and August, in which the first main recruitment occurred, was considered the age transition month, three age groups, i.e., 0+, 1+, and 2+ age groups, could be detected (Fig. 5). To trace crab growth from the 0+ to 2+ age groups, the successive CW estimates from 1–25 months are shown in Fig. 6. The growth of the crabs could be expressed as the logistic growth equations with significant coefficient estimates for both sexes (Table 2). Significant difference was detected in the growth equations between sexes ($F_{3,40} = 3.533, P = 0.0231$). The asymptotic CW estimate was larger in males (9.08 mm) than females (7.94 mm). Based on the estimates of the mixing proportions of the respective cohorts in the CW histograms (Fig. 7), the 0+ age group was dominant in both sexes, excluding males.
Discussion

Our field surveys detected the presence of ovigerous females of *Petrolisthes japonicus* from May to September 2008 and in February 2009 (Fig. 1). Considering the proportions of ovigerous females, the main reproductive season of this species lasted for approximately four months during the spring and summer seasons, from June to September, at this intertidal cobble and boulder shore on the Boso Peninsula, Japan.

Nakasone (1972) conducted monthly surveys to investigate the reproductive cycle of *P. japonicus* from June 1966 to May 1967 in the intertidal zone at Tsuyazaki (33°47′N, 130°27′E), Fukuoka Prefecture, Japan. He detected ovigerous females from May to November and reported that the main reproductive season was five months from June to October, which was longer than that of the *P. japonicus* population on the Boso Peninsula (34°58′N, 139°46′E) in the present study. The body size of female specimens (2.3–9.7 mm CW) and the minimum body size of ovigerous females (3.8 mm CW) of the Boso population were slightly larger than those of the Tsuyazaki population (females, 2.3–8.2 mm CW; smallest ovigerous females, 3.5 mm CW) (Nakasone, 1972). Thus, intraspecific variability was observed in some reproductive traits of the *P. japonicus* populations.

Intraspecific variability in reproductive traits has been documented in decapod crustaceans (Henmi, 1993; Kyomo, 2000; Ituarte *et al*., 2006; Bas *et al*., 2007; Silva *et al*., 2009; Baldanzi *et al*., 2018), including porcellanid crab species (Jones, 1977; Wehrtmann *et al*., 2012). It has been suggested that regional environmental conditions such as temperature, salinity, photoperiod, and food availability may affect such trait variations among populations. The reproductive season of the porcellanid crab *Petrolisthes elongatus* (H. Milne-Edwards, 1837) showed a latitudinal gradient and ranged...
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from 6 to 12 months in southern to northern locations of New Zealand, probably due to the influence of latitudinal temperature gradients (Jones, 1977). *P. japonicus* is distributed from northern Japan (40°N) to subtropical islands of southern Japan (24°N) (Miyake, 1998). Future studies targeting *P. japonicus* populations from northern to southern locations would contribute to understanding the interpopulation variability and its causes in the life history traits of this species, which has a broad geographical distribution.

Nakasone (1972) suggested that females produced three broods per year after examining the occurrence pattern of non-ovigerous and ovigerous females with or without developed ovarian eggs in the Tsuyazaki *P. japonicus* population. According to a laboratory experiment by Osawa (1995), the larval development of *P. japonicus* comprises two zoeal stages before metamorphosis into the megalopa stage, and the zoeal stage duration is 12–15 days at 24–25°C, which is equivalent to the natural temperature conditions during August and September (Fig. 8). The zoeal duration of *P. japonicus* may be longer than 0.5 months during June and July considering the temperature conditions (\( \text{\( \beta \)} 19.5–23°C) (Fig. 8). In the present study, the egg hatching season lasted for four months from June to September and unsexed juveniles mainly occurred from August to October (Figs. 1, 3, and 4). Taken together, the data suggest that *P. japonicus* megalopae may require approximately 0.5–1 months to grow into unsexed juveniles with \( \text{\( \beta \)} 1.4–2.3 \text{ mm} \).

Fig. 7. Monthly changes in mixture proportion estimates for the 0+, 1+, and 2+ age groups in carapace width histograms for female (A) and male (B) *Petrolisthes japonicus* from April 2008 to March 2009. The first main recruitment occurred in August, and dotted vertical lines show the boundaries between age groups. See Figs. 3 and 4 for carapace width histograms. The analysis was not performed for crabs collected in November because of the small sample size.

Table 2. Coefficient estimates of logistic growth equations \( \text{CW}_t = \text{CW}_\infty (1 + \exp(-K(t - t_0)^{-1})) \) for females and males of porcellanid crab *Petrolisthes japonicus*. CW, carapace width (mm) at age \( t \) (month, 1–25); CW\( \infty \), the asymptotic CW (mm); \( K \) is a relative growth rate (with unit month\(^{-1}\)); and \( t_0 \) corresponds to the inflection point of the sigmoidal curve.

| Sex   | Coefficients | Estimate | SE  | \( t \) value | \( P \) |
|-------|--------------|----------|-----|---------------|-------|
| Female | \( \text{CW}_\infty \) | 7.9370   | 0.5239 | 15.150         | <0.0001 |
|        | \( K \)      | 0.1500   | 0.0272 | 5.525          | <0.0001 |
|        | \( t_0 \)    | 6.9687   | 1.0963 | 6.357          | <0.0001 |
| Male   | \( \text{CW}_\infty \) | 9.0808   | 0.7162 | 12.679         | <0.0001 |
|        | \( K \)      | 0.1548   | 0.0290 | 5.341          | <0.0001 |
|        | \( t_0 \)    | 8.6752   | 1.3138 | 6.603          | <0.0001 |
significantly larger than those of females. After settling on the cobble and boulder shore, females and males of *P. japonicus* grew from 2 mm to 5–5.6 mm CW by the next spring (May); then, a significant difference appeared in the growth rates between sexes, and the males grew larger than the females. After two years of settlement, males and females reached approximately 8.7 mm and 7.8 mm CW on average, respectively. Thus, *P. japonicus* males grew larger than females, demonstrating sexual dimorphism in body size, which has been observed in decapod crustacean species (e.g., Pinheiro & Hattori, 2006; Koga et al., 2010; Gonçalves et al., 2017; Miazaki et al., 2019), including porcelain crab species (Jones, 1977; Miranda & Mantelatto, 2009; Pinheiro et al., 2017). The sexual dimorphism in body size is often attributed to sex-specific resource allocation strategies (Hartnoll, 1982; Pinheiro & Hattori, 2006; Koga et al., 2010; Baeza et al., 2013; Miazaki et al., 2019): females invest their energy into egg production and incubation, whereas males allocate more energy into somatic growth because a larger body size is advantageous in male-male competition for acquiring mates. This may also be the case in *P. japonicus* because sexual size dimorphism became evident after the crabs reached the beginning of their first reproductive season (May).

Our mixed normal distribution analyses also inferred the life span of *P. japonicus*. Females and males of 0+ aged *P. japonicus* begin to breed in the year after hatching (Figs. 3 and 4). Considering the proportions of the respective age groups in the population, i.e., the dominance of the 0+ age group (except for males in April 2008, which was probably caused by sampling bias (Fig. 7)), a relatively high proportion of 0+ aged individuals appear to die during the end of or after the reproductive season. A relatively small proportion of 0+ aged individuals may survive even after the reproductive season and breed in the next year as the 1+ age group. Then, the individuals that reach the 2+ age group likely die by the end of the reproductive season. Consequently, the longevity of *P. japonicus* is estimated to be 1–2 years.

Information on the life span of porcelain crab species is scarce, but *Liopetrolisthes mitra* (Dana, 1852) has been suggested to live for at least one and a half years based on size frequency distributions (Baeza & Thiel, 2000).

The larval hatching period lasted for four months, and recruitment occurred over a period longer than four months in the *P. japonicus* population. To further elucidate the population dynamics of *P. japonicus*, intensive surveys with more crab samples and shorter sampling intervals are required for future studies.

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