



## Life history of the ghost shrimp, *Callinassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan

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### Abstract

Growth, density, survival, and reproduction were examined for the population of the ghost shrimp, *Callinassa japonica* Ortmann, inhabiting an intertidal sandflat in western Kyushu, Japan, based on samples collected from May, 1989 to April, 1991. During the breeding season (June–October) each year, there were two discrete periods of egg production by females. The post-larval settlement, with a time-lag of 1–1.5 months (brooding plus larval developmental periods), generated two major recruitment cohorts, occurring in July–August (1st cohort) and September–November (2nd cohort). The higher growth rate of individuals after recruitment in the 1st cohort enhanced the separation of the two cohorts. Between sexes, the subsequent life history patterns and population characteristics were, for the most part, similar. In females, the majority of individuals of each of the two cohorts matured after approximately one year, respectively, at around a 20-mm total body length, and a portion of these cohorts survived as a fused cohort until June of the second year, breeding again prior to dying off by the end of September. The pattern of growth was an indeterminate type. For each of the two cohorts, the growth rates changed at two transition points of their life history, at around the beginning of their two breeding seasons. The growth rate for the 1st cohort slowed down at the first transition point, while that for the 2nd cohort speeded up there. This led to the approach and fusion of the two cohorts near the second transition point, when growth stopped. During periods other than the breeding seasons, high survival rates were exhibited by the two cohorts. During the first breeding season, a significantly low survival rate was observed for the 1st cohort, but not for the 2nd cohort. The degree of participation in breeding activity may be responsible for the above differences between cohorts. In the two male cohorts, while the cost of reproduction did not reduce the growth rates during the first breeding season, it lowered their survival rates more severely compared to those of females. This may be responsible for the slightly female-biased sex ratio in the population (1.06:1). The density of the population as a whole was stable throughout the study period, with the mean  $\pm$ SD

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being  $901 \pm 157/\text{m}^2$  ( $n = 27$ ); the adult population declines during the breeding seasons were effectively replenished by recruitment each year. ©1997 Elsevier Science B.V.

**Keywords:** *Callianassa japonica*; Intertidal sandflat; Growth; Density; Survival; Reproduction

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## 1. Introduction

In recent ecological studies on marine soft-sediment communities, increased attention has been paid to callianassid ghost shrimps (Decapoda: Thalassinidea). In particular, their bioturbating activities (e.g. Roberts et al., 1982; Vaugelas and Buscail, 1990; Rowden and Jones, 1993) and consequent effects on the benthic community structure (e.g. Murphy, 1985; Tamaki, 1994; Wynberg and Branch, 1994) have been the central themes. In contrast, the number of studies on their life history and population dynamics is far fewer, and an overall synthesis of the life history remains limited [*Trypaea australiensis*—Hailstone and Stephenson, 1961; *Callianassa filholi*—Devine, 1966; *Callianassa kraussi*—Forbes, 1977; *Neotrypaea californiensis*—Bird, 1982; *Lepidophthalmus louisianensis*—Felder and Lovett (1989) and Felder and Griffis (1994); *Callianassa japonica*—Tamaki and Ingole, 1993; *Callichirus islagrande*—Felder and Griffis, 1994; *Callianassa subterranea*—Rowden and Jones, 1994]. This is, in part, due to difficulties in regularly obtaining samples from the entire sediment columns inhabited by the animals. Scarcity of information on life history and population dynamics is also a bottleneck for the development of both bioturbation and community studies.

On an intertidal sandflat in western Kyushu, Japan, where sediment thickness is fairly thin (up to 60 cm: Tamaki, 1984), various ecological aspects of *Callianassa japonica* Ortmann have been investigated such as: its influences on sediment properties (Tamaki, 1984); interspecific effects on other macrobenthos as regards amensalism (Tamaki, 1988, 1994) and commensalism (Tamaki and Suzukawa, 1991); interactions with predators (Tamaki et al., 1992b); intraspecific relationships (Tamaki et al., 1992a; Tamaki and Ingole, 1993); and brooding and larval developmental periods (Tamaki et al., 1996). However, a detailed presentation of its life history and population characteristics has not been made. The purpose of this paper is to detail aspects of the life history based on a two-year survey and to compare them with other studies of callianassid ghost shrimps.

## 2. Materials and methods

### 2.1. Study area

The study area was an intertidal sandflat situated on the northwestern corner of Amakusa-Shimoshima Island (130° 02' E; 32° 31' N), western Kyushu, Japan (Fig. 1). The sandflat faces Tomioka Bay in the westernmost part of Ariake Sound, and extends about 4 km along the shore, where it is exposed for 150 to 700 m seaward at extreme

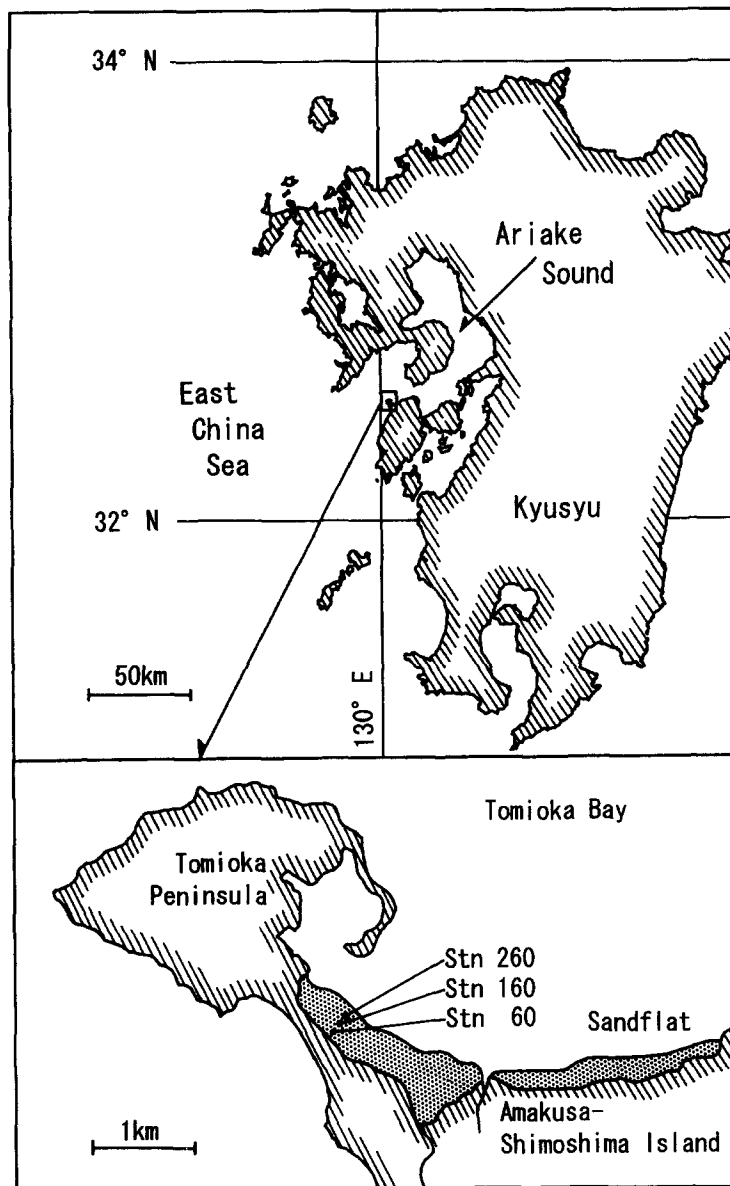


Fig. 1. Location of the transect stations for sampling *Callinassa japonica* on the Tomioka Bay sandflat (dotted area), western Kyushu.

low water spring tide. *Callinassa japonica* inhabits almost the entire sandflat. The sediment at the study area is of well to moderately sorted, fine sand (*sensu* Folk, 1974), with the silt-clay content lower than 2.6% (Tamaki and Suzukawa, 1991). The water temperature and salinity of the sea surface was measured in the vicinity of the study area

(about 1 km apart) on a daily basis for at least 13 days per month (Goto and Kikuchi, unpubl.). During the entire period (January, 1989–April, 1991), the monthly averaged water temperature ranged between 12.7°C (February, 1991) and 27.8°C (August, 1990) (Fig. 2). Although the extremes of monthly averaged salinity were 31.95‰ (September, 1989) and 38.1‰ (August, 1989), both values, especially the latter one, appear to be exceptions in light of long-term data; during the study period, all other monthly values were between 32.5‰ (May, 1989) and 34.5‰ (December, 1989) (Goto and Kikuchi, pers. comm.).

## 2.2. Some biological information about *Callianassa japonica*

Based on previous studies, several biological characteristics of *Callianassa japonica* in the study area, a necessary prerequisite for the present study, are summarized below. Animals live in Y-shaped burrows occupying the entire sediment column, under which lies an accumulation of large-shell remains. Each adult burrow has two openings on the sandflat surface and is inhabited by a single adult only (Tamaki et al., 1992a). The animal is a deposit feeder, sediment being extruded through one burrow opening and deposited as a mound on the sandflat surface; on average, about 5–10-ml sediment (3–5-cm diameter mound) per individual is discarded per day (Tamaki, 1988, 1994). Reproductive and recruitment characteristics shown below are based on Tamaki et al. (1996). Maturity in females is marked by a well-developed, orange or red ovary visible through the translucent integument. Ovigerous females, which release planktonic larvae, occur from June to October. The spherical diameters of eggs, which are attached to the 1st and 2nd pleopods, are about 0.5–0.6 mm. The brooding period ranges between 13 and 22 days, most frequently 14 days and lengthening toward both beginning and end of the breeding season (characterized by lower water temperatures: Fig. 2). The time-lag between the first appearance of eyed eggs and the hatching of larvae is 4 to 6 days during most of the breeding season (from June to September; values in October are undetermined as yet). Female ovarian content decreases with egg deposition, but usually

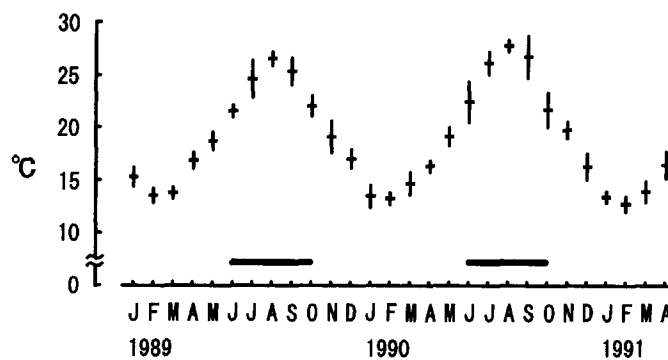


Fig. 2. Monthly mean  $\pm$ SD temperature of the surface waters measured about 1 km from the study area during January, 1989 to April, 1991 (number of the measurement per month=13–23). From Goto and Kikuchi (unpubl.). Stout horizontal bars denote breeding seasons of *Callianassa japonica* (see Section 3.1).

it begins to increase during subsequent brooding, leading to a further deposition of eggs 1–5 days after the release of larvae (iteroparous reproduction). Mating appears to occur immediately prior to deposition of a successive brood. The duration of the planktonic development—six zoeal and one post-larval (= decapodid) stages—is estimated to last 20 to 25 days during mid-June to mid-August, while that during the latter half of the breeding season is undetermined.

### 2.3. Sampling of *Callinassa japonica* population

Sampling of the *Callinassa japonica* population was conducted on a total of 27 occasions (spring tides) during the period from 6 May 1989 to 17 April 1991. Sampling dates are indicated in Figs. 5 and 6 (Section 3.2). The study period can be grouped into three parts with regards to the sampling intervals: (1) during 6 May 1989 to 11 May 1990, every 1 to 2 months; (2) during 11 May 1990 to 2 November 1990, every 2 weeks; and (3) during 2 November 1990 to 17 April 1991, every 1 to 2 months. During low tide on each occasion, individuals of *C. japonica* were collected at three stations placed along a permanent transect which extended perpendicularly from the shore (Fig. 1). The lower end of the transect was at the mean low water spring tide level, 310 m from the shore. The stations were 60 m (Stn 60), 160 m (Stn 160), and 260 m (Stn 260) from the shore, respectively. At each station, 10 to 24 sediment columns reaching the substratum bottom were extracted using a cylindrical corer (100-cm<sup>2</sup> × 50-cm long acrylic tube). On each occasion, the number of samples taken from each station was equal or nearly equal, and the total number of samples from all stations ranged from 31 (28 May 1990) to 52 (13 October 1989)—most frequently 48. The mean ± SD depth of collected sediment columns at each station throughout the study period was 32.0 ± 4.7 cm (Stn 60, *n* = 435), 29.9 ± 3.9 cm (Stn 160, *n* = 408), and 39.0 ± 3.9 cm (Stn 260, *n* = 394). Sampling plots were marked each time to ensure non-overlapped sampling on different occasions. Sediment columns were sieved individually through a 0.5-mm mesh sieve, and the contents on the sieve fixed with 10-% neutralized formalin solution. During the breeding season (June–October) in 1990, individual ovigerous females were fixed separately in a small polyethylene bag to prevent any loss of their eggs.

### 2.4. Laboratory treatments

In the laboratory, individuals of *Callinassa japonica* were sorted out from the sieved samples and categorized initially as ‘complete’, ‘semicomplete’, or ‘damaged’. ‘Complete’ individuals were defined as those whose total mid-dorsal length (abbreviated as TL: from the tip of the rostrum to the posterior margin of the telson) could be measured. ‘Semicomplete’ ones were those whose carapace mid-dorsal length (CL: from the tip of the rostrum to the posterior margin of the cardiac region) could be measured. Measurements were made to the nearest 0.1 mm under a stereomicroscope. For ‘complete’ individuals collected on 13 October 1989, both TL and CL were measured to obtain a linear regression equation of TL on CL. This sample was chosen because in October, the animals constituting the population had a wide range of body sizes—from newly-recruited individuals to their full-grown adults (Tamaki and Ingole, 1993; Tamaki

et al., 1996). The TL's for the 'semicomplete' individuals were estimated using this equation. 'Damaged' individuals were those whose TL and CL dimensions could not be obtained. In the enumeration of these animals, care was taken to avoid an overlapped count of heads and telsons by matching them as carefully as possible. Sex was determined according to the presence (in females) or absence (in males) of the 2nd pair of pleopods, unless evident by the conspicuous presence of ovaries. The minimum TL of females detected over the course of the study was 5.4 mm, and no determination of sex was made for animals smaller than this size. For 'semicomplete' and 'damaged' individuals, sex-determination was dependent on the conditions of the above-mentioned characteristics. For ovigerous females collected in 1990, the number of eggs, of which the developmental stages were classified as either uneyed or eyed, was counted. Due to the less frequent sampling occasions in 1989, population characteristics as regards breeding performance and recruitment were examined mainly on the basis of data collected in 1990.

Body-size (TL)-frequency distributions were made separately for females and males for each sampling occasion, in which all data from the three stations were pooled. The reason for the pooling is to ensure a sufficient number of specimens for the subsequent cohort analysis. Size-class interval was set at 2.0 mm. For individuals whose sex could not be determined, they were allocated equally to both sexes one by one; the minimum-sized animal being placed in the female category in the first place. This is based on the nearly equal sex ratio recorded for the rest of the population (see Section 3.1). Each TL-frequency distribution was divided into multiple normal-distribution groups (cohorts) based on a computer program using Cassie's (1954) and Taylor's (1965) methods (Tsutsumi and Tanaka, 1987). In the procedure, the larger-sized cohorts were isolated from an original TL-frequency distribution one by one. When sampling occurred during the process of population recruitment, the remaining group of the larger-sized cohorts (several smallest size classes) was not established as a newly-recruited cohort corresponding to a normal distribution (i.e. a size distribution with its left edge truncated). In the present study, this group was also regarded as an (incomplete) newly-recruited cohort when carrying out further analyses [see (2) and (3) in the following paragraph]: (1) the TL-'mode' of the cohort was operationally defined as the halfway point of the largest size-class number of the constituent size classes; and (2) the density of the cohort defined as the total number of individuals belonging to all these size classes.

Based on the results of the above cohort separation (shown in Figs. 5 and 6), the life history pattern and six population characteristics [(1)–(6) below] were examined. The 'damaged' individuals were not used in the analyses. In cases where multiple cohorts shared any one size class (no. of such cohorts = 2 or 3), the animals belonging to the class were allocated to the respective cohorts in proportion to the number of individuals under each corresponding normal-distribution curve crossing that class. With regard to the densities [values in (1), (3), (4), and (5) below], they were converted to those per m<sup>2</sup> of the sandflat. (1) The recruitment pattern following egg production during the breeding season of 1990. The egg density on each sampling occasion was defined as the total number of uneyed (or eyed) eggs held by all ovigerous females pooled from the three stations. Newly-recruited individuals (both sexes combined) were defined as those belonging to the smallest size class of the TL-frequency distributions. (2) The growth

curves for each sex. These were made by following the progression of the TL-modes of the normal distributions of the corresponding cohorts through time. (3) The survivorship curves for each sex. These were made by tracking the total number of individuals under each of the normal-distribution curves of the corresponding cohorts through time. In practice, the density of a cohort was expressed as transformed data;  $\log_{10}$  (density value + 1). Moreover, [and also in (2)], each curve was regarded as a combination of several lines derived from the linear regression of density (or TL-mode) on the sampling date; the transition points between the lines were determined by eye. (4) The degree of participation in breeding by females from the different cohorts. This was evaluated in terms of both the densities of ovigerous females (and their proportion in the female population) and the densities of eggs produced by those females. (5) The temporal change in the 'total' densities of each cohort (all animals of both sexes from the three stations pooled) during the study period. (6) The temporal change in the density (both sexes combined) at each of the three stations throughout the study period. The whole study period was divided into five parts, either between- or during-recruitment seasons: May and June in 1989 (between), July–December in 1989 (during), February–June in 1990 (between), July–December in 1990 (during), and February–April in 1991 (between). For each part, the mean  $\pm$ SD densities were calculated using all the samples collected throughout the period. In particular, for each during-recruitment season, the densities of the newly-recruited cohorts (defined in the preceding paragraph) and those of the 1+ -year-old cohorts (defined in Section 3.2) were calculated separately to examine whether the spatial difference in recruitment was reflected in the older animals' densities. For the between-recruitment seasons, the densities of the population as a whole were calculated. The densities were expressed as values per unit sampling area, 100 cm<sup>2</sup> [a 'true' density which is, in its strictest sense, different from those defined in (1), (3), (4), and (5)].

### 3. Results

#### 3.1. Notes on some basic population characteristics

In this section, several fundamental parameters of the *Callinassa japonica* population are given, which are the basis for the description in subsequent sections.

A total of 11 872 individuals were collected; 5688 females, 5345 males, and 839 sex-unidentified individuals, giving a slightly female-biased sex ratio (1.06: 1). TL values were available for 93.8% of the sampled animals, and of these 8.0% of the data were estimated from the CL data using a linear regression equation of TL on CL:  $TL = 4.68CL - 1.09$  ( $n = 604$ ;  $r^2 = 0.98$ ;  $p < 0.001$ ) (Fig. 3). The TL of the smallest animal was 4.1 mm. The TL of the largest female (46.8 mm) was greater than that of the largest male (46.1 mm), but the mean  $\pm$ SD TL-values of the largest individuals recorded from each sampling occasion ( $n = 27$ ) indicated that females ( $38.5 \pm 3.2$  mm) were significantly smaller than males ( $40.9 \pm 3.0$  mm) (Mann–Whitney  $U$ -test:  $0.001 < p < 0.01$ ).

In 1989 and 1990, almost all the ovigerous females occurred from June to October;

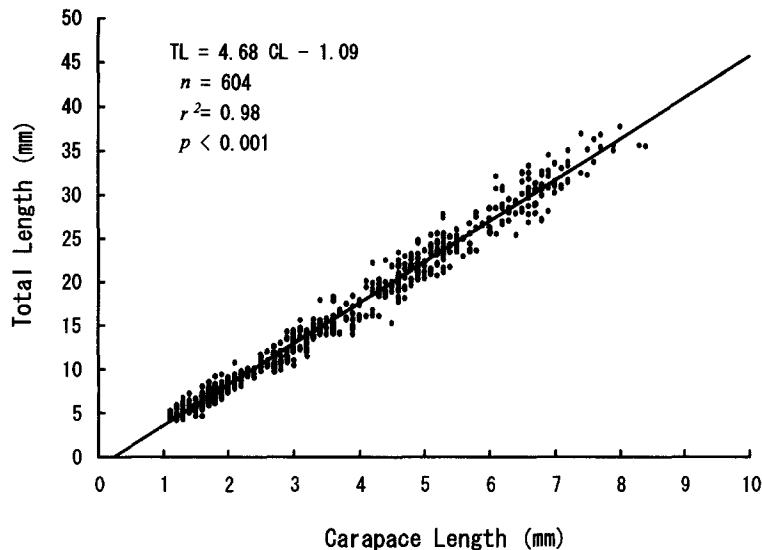


Fig. 3. Linear regression of total length (TL) on carapace length (CL) for the 'complete' individuals of *Callinassa japonica* collected on 13 October 1989 (see Section 2.4).

the only exceptions were single individuals collected on 11 May and 2 November 1990, respectively. Thus the breeding season accorded with the mean water temperatures exceeding 20°C (Fig. 2). The minimum TL of ovigerous females recorded throughout the study period was 17.9 mm (15 September 1989), and the mean  $\pm$ SD TL of the smallest ones from all sampling occasions during June to October in both 1989 and 1990 was  $20.9 \pm 2.0$  mm ( $n = 15$ ). There was a highly significant positive correlation between the number of eggs per female and the female's respective body size, expressed as TL cubed, for the ovigerous females with uneyed eggs collected during June to October in 1990:  $r = 0.81$ ;  $n = 289$ ;  $p < 0.001$  [only uneyed eggs were considered because eggs might have been lost during the incubation period (cf. Bird, 1982); and also, all the 'semicomplete' females and 'complete' females whose eggs indicated any evidence of drop-out and/or death were excluded]. The maximum no. of eggs per female was 962, and mean  $\pm$ SD  $333.1 \pm 212.7$ .

Fig. 4 illustrates the relationship between egg production by the female population and the subsequent recruitment by post-larvae in 1990; densities of uneyed eggs, eyed eggs, and newly-recruited individuals (4.05 to 6.05-mm TL: Fig. 5 Fig. 6) are plotted against the sampling dates. Two discrete groups of uneyed eggs were observed in the periods from 8 June to 5 August and from 5 August to 16 October, respectively. However, the two discrete groups of eyed eggs corresponding to those of the uneyed ones were not detected. One reason might be that some females with eyed eggs had already released larvae on respective sampling dates. In newly-recruited individuals, there were also two major discrete groupings, ranging from 9 July to 5 September and from 5 September to 2 December, respectively. The latter one could be subdivided into two components, before and after the 16 October. Both major groups of newly-recruited



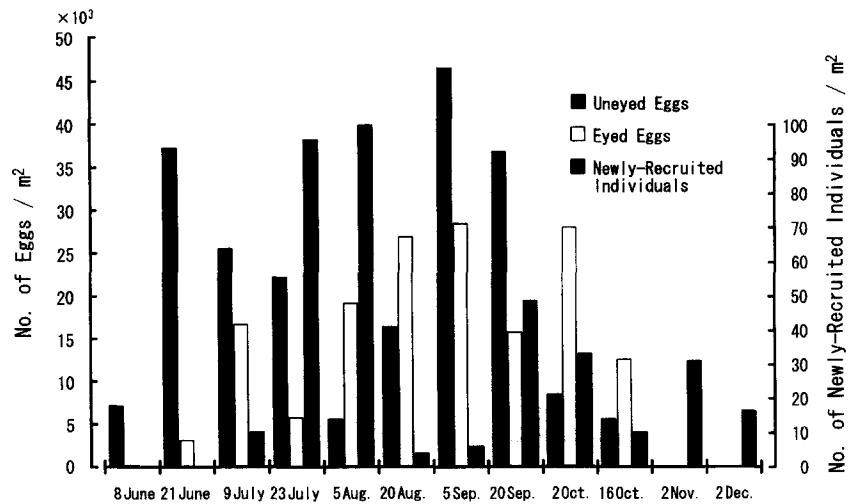


Fig. 4. Temporal changes in the densities of uneyed and eyed eggs per  $m^2$  on ovigerous females and of the newly-recruited individuals (from 4.05 to 6.05-mm TL: Figs. 5 and 6) of *Callinassa japonica* during the breeding and recruitment season of 1990. Data from the three stations were combined.

individuals corresponded well with the two groups of uneyed eggs, respectively, with a time-lag of about 1 month (during June to October) and 1.5 months (during October to December). These time-lag values are consistent with the brooding plus larval developmental periods estimated from samples from different years [33–47 days (Section 2.2)], although the larval period around the end of the breeding season is not available yet; probably it is reasonable to postulate that the length of the period will increase under continuing lower water temperatures during October to December (Fig. 2). The high densities of uneyed eggs on 5 and 20 September were not followed by comparable high densities of newly-recruited individuals.

### 3.2. Size-frequency distributions and life history

The TL-frequency distributions for females and males are shown in Fig. 5 and Fig. 6, respectively. The proportion of sex-unidentified specimens, which had been allocated equally to both sexes, was 4.4%. Multiple normal-distribution curves are superimposed on the TL-frequency distributions. The cohort analysis was performed fundamentally on the grounds of the recruitment pattern, as pointed out in Section 3.1 (Fig. 4). In 1990, three discrete recruitment cohorts were recognized, which occurred from 9 July to 20 August, from 5 September to 16 October, and from 2 November to 2 December. Hereafter these are termed the 1st, 2nd, and 3rd 0-(1990) year-old cohorts, respectively. The year in parentheses stands for the year of recruitment. No curve fitting was made to the 1st one in July and August, 1990, to the 2nd one in September and October, 1990, or to the 3rd one during November, 1990 to April, 1991. Although the recruitment pattern in 1989 was basically the same as that in 1990, there were several differences: (1) the 1st and 2nd 0-(1989) year-old cohorts were not so discrete from each other; (2)

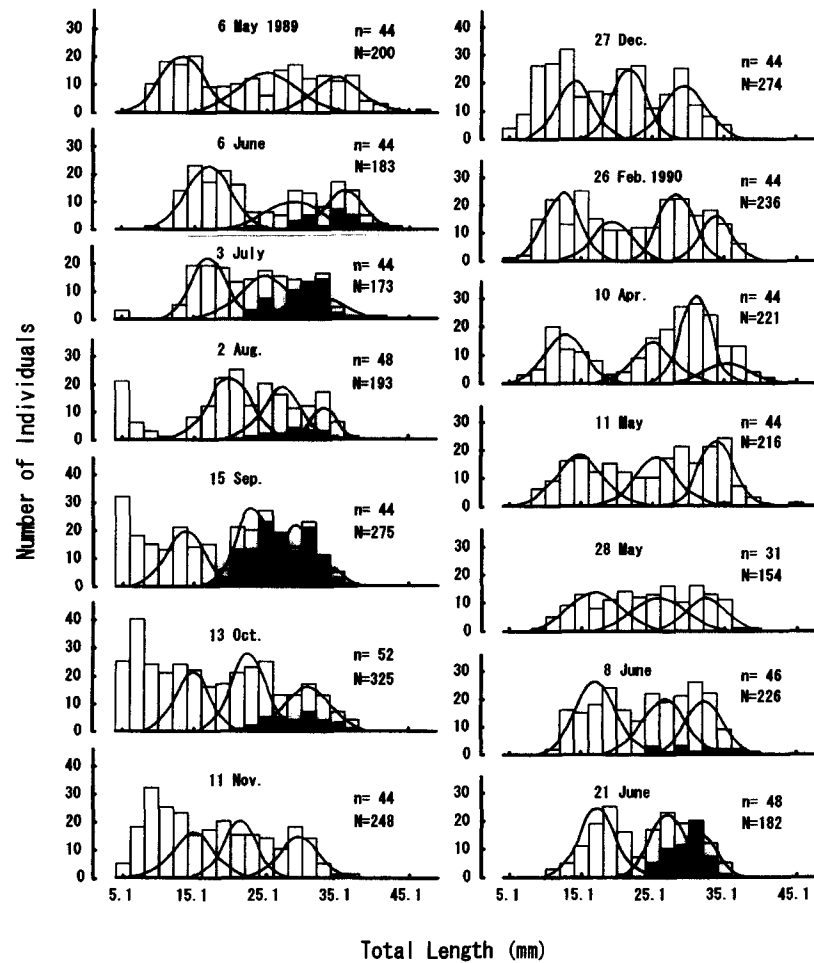


Fig. 5. Body size (TL)-frequency distributions for female *Callinassa japonica* throughout the study period. Data from the three stations are combined. Hatched parts indicate ovigerous females. Normal-distribution curves correspond to cohorts. For samples during the recruitment seasons of 1989 and 1990 and for those during February to April, 1991, no curve fitting is made to the group of several smallest size classes (see text). *n*, number of core samples; *N*, total number of individuals of *C. japonica*.

the density of the 2nd cohort was not low when compared with that of the 1st cohort; and (3) the density of the 3rd cohort was, if anything, negligible. In spite of (1) above, the two 0-(1989) year-old cohorts could still be recognized as separate cohorts even in the following year, 1990. For example, in the TL-frequency distribution of females on 9 July 1990 (Fig. 5), these constituted the second and third largest normal-distribution groups, respectively. Hereafter these are termed the 1st and 2nd 1-(1989) year-old cohorts [on any date in 1990, such cohorts as recruited in 1989 will be termed the 1-(1989) year-old cohorts irrespective of their precise ages]. The largest normal-distribution group in the figure, which was isolated initially in the cohort analysis, was

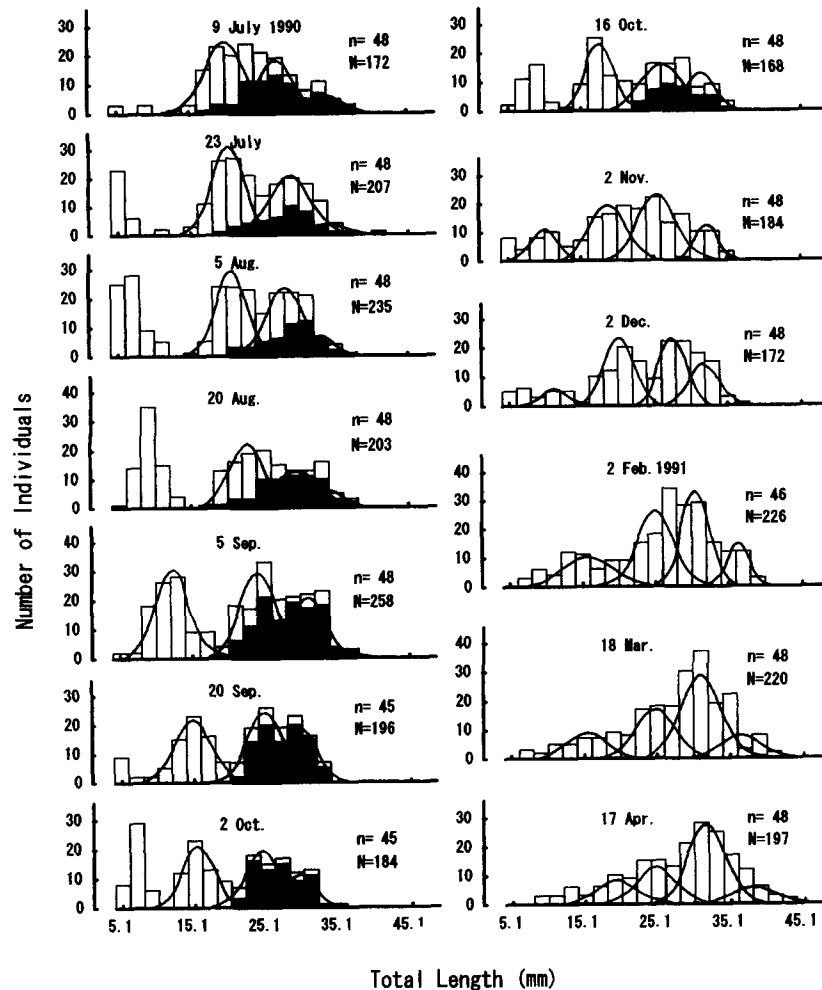


Fig. 5. (continued)

regarded as a composite cohort derived from the multiple cohorts (probably two major ones) that had been recruited in 1988; this is termed the fused, 2-(1988) year-old cohort. In fact, in 1990, the two cohorts recruited in 1988 could be distinguished from each other only as late as on the 10 April, for both sexes. In both 1989 and 1990, the presence of the fused, 2-year-old cohorts could be traced as late as September.

Fig. 7 shows the temporal change in the proportion of ovigerous females for each of the 1- and 2-year-old cohorts and for all females combined, during the breeding season of 1990. For the entire sample (combined cohorts), a bimodal pattern was observed, with the peaks on 9 July (43.7%) and 2 October (82.5%). This seems to be related with the two discrete peaks in egg production by the population (Fig. 4). The pattern in the entire sample occurred from the simultaneous peaks in percentage ovigerous shared among the

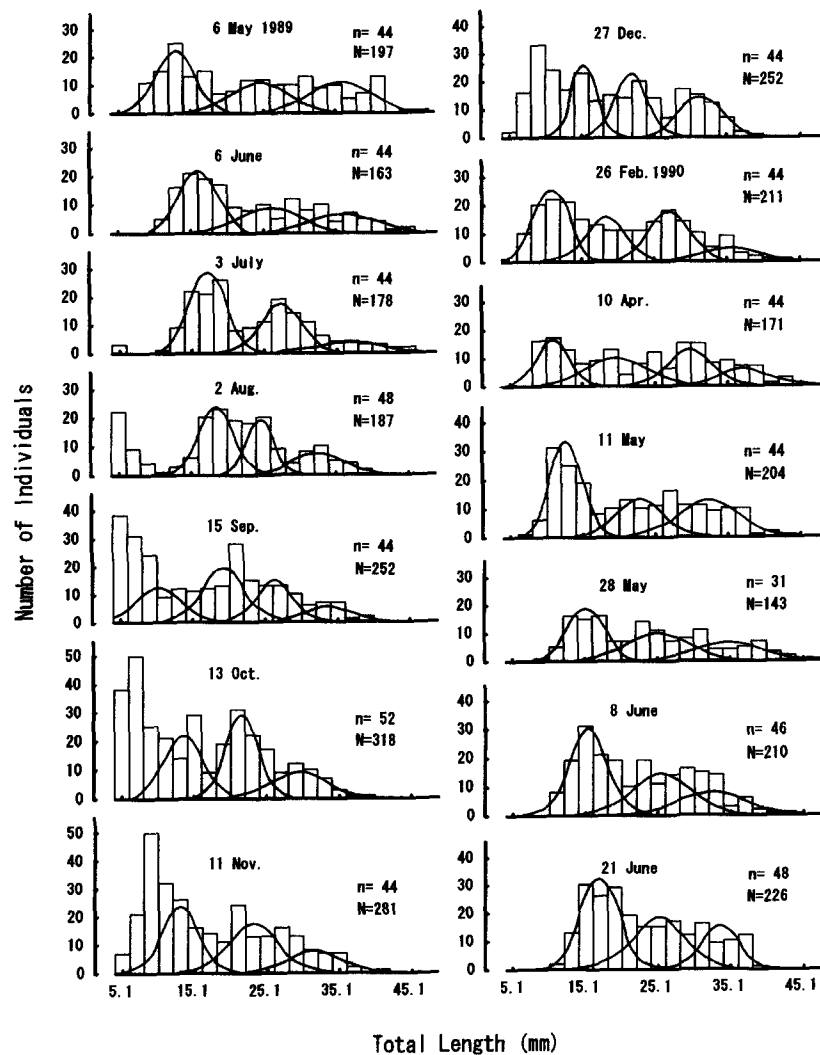


Fig. 6. Body size (TL)-frequency distributions for male *Callinassa japonica* throughout the study period. See the caption for Fig. 5.

three cohorts, although there were some differences, as follows: (1) the spawning of the fused, 2-year-old cohort occurred mainly in the former half of the breeding season prior to dying off; (2) that of the 1st 1-year-old cohort occurred throughout the breeding season, with the intensity higher in the latter half; and (3) that of the 2nd 1-year-old cohort was concentrated mostly in the latter half. These results highlight that, in the population, egg deposition was initiated by the larger-sized females in the beginning of the breeding season, while the smaller-sized females participated in reproduction later on.

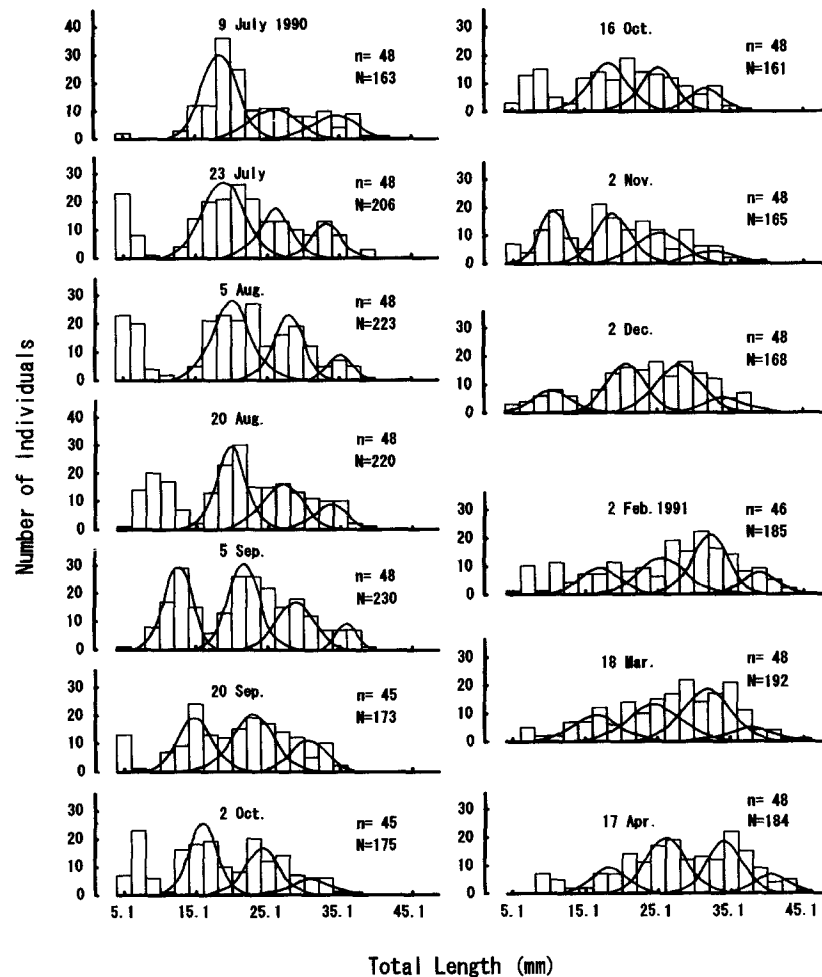


Fig. 6. (continued)

In females, as early as September, 1990, the size of the largest individuals of the 1st 0-(1990) year-old cohort had caught up with that of the smallest members of the 2nd 1-(1989) year-old cohort (Fig. 5). However, 0-year-old females, experimentally enclosed in the field, did not develop their ovaries in the same year as they were recruited (Tamaki et al., unpubl.).

From the preceding information, the life history of females is summarized as follows: the majority of each of the two major recruitment cohorts (those recruited in either the summer or the autumn) become mature in approximately one year, respectively at around a 20-mm TL, and a portion of these cohorts survive as a fused cohort until June of the second year, breeding again and dying off by the end of September. Further

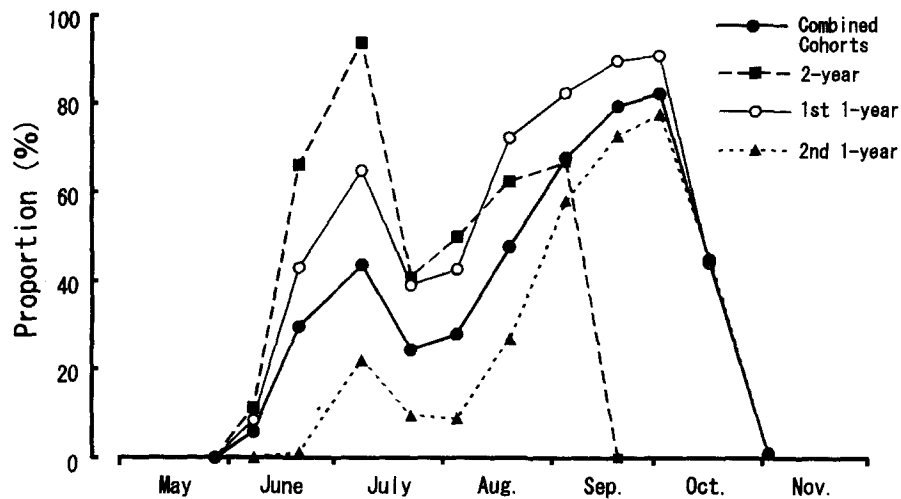


Fig. 7. Temporal change in the proportion of ovigerous females in each of the three competent cohorts and in the total female sample (combined cohorts) of *Callianassa japonica* during the breeding season of 1990. Data from the three stations are combined.

reproductive characteristics exhibited by the different cohorts are detailed in Section 3.3 Section 3.4 Section 3.5.

For males, their sexual maturity based on morphological characters was not examined in the present study. It has been demonstrated for several callianassid species that maturation is evident in the relative growth of the secondary sexual characters such as the major chela vs. carapace length (Hailstone and Stephenson, 1961; Devine, 1966; Rodrigues, 1985; Felder and Lovett, 1989; Rowden and Jones, 1994). In his unpublished study on the biology of *Callianassa japonica*, H. Tanoue (pers. comm.) found that the relative growth of the major chela length (from the tip of dactylus to the proximal end of carpus) vs. total body length (TL) in males changed at the transition point of about 20-mm TL, yielding strong positive allometric growth in the major chela beyond this body size. He pointed out that puberty in males occurs at around a 20-mm TL. Furthermore, comparing Fig. 5 and Fig. 6 in the present paper, it is apparent that between sexes cohort separations are the same in number (though not in shape) throughout the study period. Therefore we presume that the life history of males is similar to that of females.

### 3.3. Growth

In Fig. 8 (females) and Fig. 9 (males), the TL-modes of respective cohorts shown in Figs. 5 and 6 are plotted against the sampling dates; since the 1st and 2nd 2-(1988) year-old cohorts merge at 11 May 1990 in both sexes [the fused, 2-(1988) year-old cohorts], the modes thereafter are plotted as a single point on each date. Furthermore, a total of 11 and 10 linear regression lines, for females and males, respectively, are fitted to each series of points as the growth 'curves' (designated by the serial numbers in Table

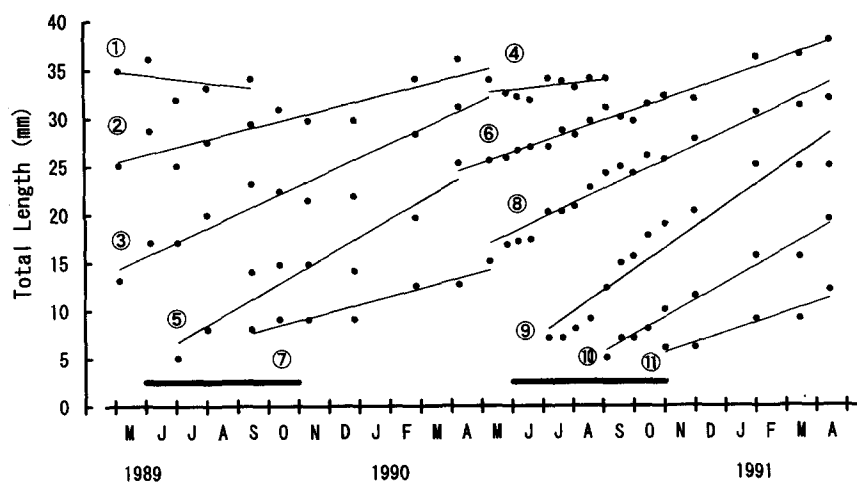


Fig. 8. Growth 'curves' for female cohorts of *Callinassa japonica*. Each dot corresponds to the TL-mode of each normal distribution shown in Fig. 5. Regression lines (No. 1–No. 11) are fitted to the respective data points based on the linear regression equation of TL-mode on sampling date (Table 1). No. 2 and No. 3 merge into No. 4 [fused, 2-(1988) year-old cohort] (see text). Stout horizontal bars denote breeding seasons.

1 and Figs. 8 and 9). The slopes of the two lines for each sex (Nos. 1 and 4 and Nos. 12 and 15) were not significantly different from zero, suggesting the cessation of growth. These correspond to the fused, 2-year-old cohorts during the breeding seasons of 1989 and 1990.

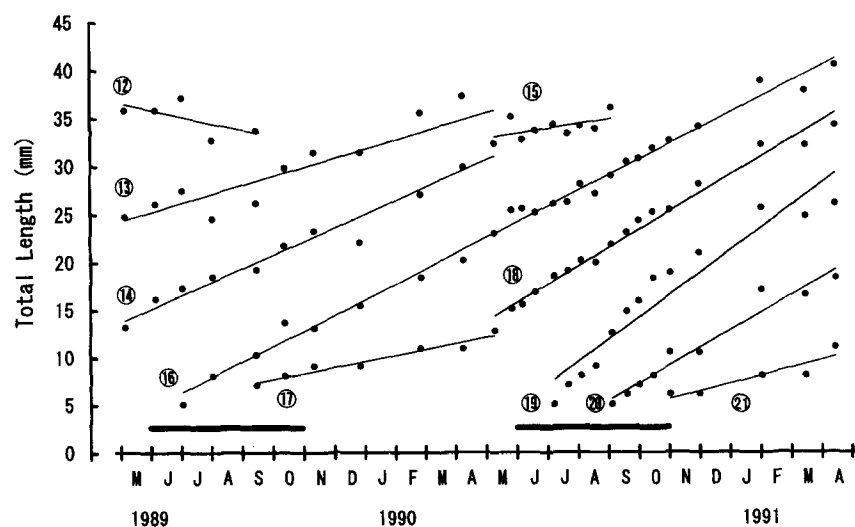


Fig. 9. Growth 'curves' for male cohorts of *Callinassa japonica* based on Fig. 6. See the caption for Fig. 8 and Table 1 (No. 12–No. 21). No. 13 and No. 14 merge into No. 15 [fused, 2-(1988) year-old cohort] (see text).

Table 1

Growth of each female (No. 1–No. 11) and male (No. 12–No. 21) cohorts of *Callinassa japonica* as shown in Fig. 8 and Fig. 9

No.	Cohort	Period	(a, b)	(n, r <sup>2</sup> , p)
1	2-(1987)	6 May '89–15 Sep. '89	(−0.0128, 34.8226)	(5, 0.17, 0.48)
2	1st 1-(1988)	6 May '89–11 May '90	(0.0258, 25.5591)	(11, 0.83, ***)
3	2nd 1-(1988)	6 May '89–11 May '90	(0.0478, 14.4150)	(11, 0.92, ***)
4	2-(1988)	11 May '90–5 Sep. '90	(0.0105, 32.6733)	(9, 0.22, 0.20)
5	1st 0-(1989)	3 July '89–10 Apr. '90	(0.0602, 6.7039)	(8, 0.88, ***)
6	1st 1-(1989)	10 Apr. '90–17 Apr. '91	(0.0359, 24.4870)	(18, 0.98, ***)
7	2nd 0-(1989)	15 Sep. '89–11 May '90	(0.0274, 7.6676)	(7, 0.90, ***)
8	2nd 1-(1989)	11 May '90–17 Apr. '91	(0.0488, 16.9866)	(17, 0.96, ***)
9	1st 0-(1990)	9 July '90–17 Apr. '91	(0.0719, 8.0872)	(13, 0.90, ***)
10	2nd 0-(1990)	5 Sep. '90–17 Apr. '91	(0.0584, 5.8605)	(9, 0.96, ***)
11	3rd 0-(1990)	2 Nov. '90–17 Apr. '91	(0.0340, 5.5636)	(5, 0.90, **)
12	2-(1987)	6 May '89–15 Sep. '89	(−0.0229, 36.4330)	(5, 0.42, 0.21)
13	1st 1-(1988)	6 May '89–11 May '90	(0.0307, 24.3741)	(11, 0.79, ***)
14	2nd 1-(1988)	6 May '89–11 May '90	(0.0462, 13.8776)	(11, 0.96, ***)
15	2-(1988)	11 May '90–5 Sep. '90	(0.0163, 32.9958)	(9, 0.31, 0.11)
16	1st 0-(1989)	3 July '89–17 Apr. '91	(0.0532, 6.3384)	(25, 0.98, ***)
17	2nd 0-(1989)	15 Sep. '89–11 May '90	(0.0207, 7.3261)	(7, 0.94, ***)
18	2nd 1-(1989)	11 May '90–17 Apr. '91	(0.0620, 14.3637)	(17, 0.98, ***)
19	1st 0-(1990)	9 July '90–17 Apr. '91	(0.0763, 7.6819)	(13, 0.90, ***)
20	2nd 0-(1990)	5 Sep. '90–17 Apr. '91	(0.0604, 5.6481)	(9, 0.96, ***)
21	3rd 0-(1990)	2 Nov. '90–17 Apr. '91	(0.0269, 5.5719)	(5, 0.83, *)

Each cohort is designated by reference to the initial date of the corresponding period.

The two coefficients of the linear regression equation of TL-mode (mm) on sampling date,  $TL = aX + b$  ( $X$  is the cumulative total days from the initial date), are listed.

Levels of statistical significance of  $p$  with regards to  $a$  are denoted as \* $<0.05$ ; \*\* $<0.01$ ; \*\*\* $<0.001$ .

In females, three major phases of growth could be recognized through their life history. The first phase characterizes the initial growth from recruitment until around the beginning of the first breeding season in the following year. For example, in 1990, the transition points for the two 1-(1989) year-old cohorts occurred just prior to the breeding season: on 10 April (Nos. 5 and 6) and 11 May (Nos. 7 and 8), respectively. During this phase, the growth rate was higher in the 1st cohort (No. 5) than in the 2nd cohort (No. 7). A similar difference was also observed between the three 0 (or 1)-(1990) year-old cohorts (Nos. 9, 10, and 11). In general, these differences in the initial growth rates for cohorts would accelerate the separation of the two major 0-year-old cohorts. The single line fitted to the 1st 0 (or 1)-(1990) year-old cohort (No. 9) could be subdivided into two lines: an earlier, faster-growth phase which lasts until 16 October 1990 and the later, slower-growth phase which lasts until 17 April 1991. In order to elucidate any yearly variations in the initial growth pattern for cohorts, further data will be needed. The second growth phase in life history occurs between the beginning of the first breeding season and the beginning of the second breeding season. During this phase, the growth rate for the 1st 1 (or 2)-year-old cohorts becomes lower than that in the first phase [e.g. the 1st 1-(1989) year-old cohort in 1990: No. 6 vs. No. 5]. In contrast, that for the 2nd 1



(or 2)-year-old cohorts was higher in the second phase [e.g. the 2nd 1-(1989) year-old cohort in 1990: No. 8 vs. No. 7]. Furthermore, during the second phase, the growth rates for the 2nd cohorts were higher than those for the 1st cohorts (No. 3 vs. No. 2 and No. 8 vs. No. 6), which eventually leads to the fusion of the TL-modes of these two cohorts near the beginning of the second breeding season. The third, final growth phase in life history is an ‘asymptote’ phase during the second breeding season [the fused, 2-(1987) year-old cohort in 1989 (No. 1) and the fused, 2-(1988) year-old cohort in 1990 (No. 4)].

In males, the growth patterns exhibited by the multiple cohorts were essentially the same as those observed for females; both patterns are indeterminate growth types. One difference between the sexes was that the male growth ‘curve’ for the 1st 0 (1, or 2)-(1989) year-old cohort could be approximated by a single line throughout the study period (No. 16 vs. Nos. 5 and 6). The other difference was that for each of the two cohorts recruited in 1989, the body size of females was larger than that of males until around the end of their first breeding season, after which males became larger (Section 3.1); dates of reversal, as calculated by the points of intersection of the regression lines, were 11 October 1990 for the 1st 1-(1989) year-old cohorts (No. 6 vs. No. 16) and 25 November 1990 for the 2nd 1-(1989) year-old cohorts (No. 8 vs. No. 18).

### 3.4. Survivorship

In Fig. 10 (females) and Fig. 11 (males), the temporal changes in log-transformed densities of the different cohorts throughout the study period are shown. Linear regression equations constituting each survivorship ‘curve’ are listed in Table 2. The starting point for the regression equation for a newly-recruited cohort is set at the earliest date when recruitment to the cohort was almost complete. For each of the fused, 2-year-old cohorts, the terminal point for the regression equation is set at the sampling date immediately prior to the disappearance of the cohort. Of the 24 regression equations (designated by the serial numbers in Table 2 and Figs. 10 and 11), the numbers of the equations with ‘slope’-coefficients significantly different from (lower than) zero were 4 for females and 5 for males (a zero-‘slope’ indicates 100-% survival rate). Any marked population declines would indicate critical phases in the life history. For each of these cases, the survival rate ( $S$ ) during the period can be calculated, using the following equation:  $S \equiv D_f/D_i \approx (D_f + 1)/(D_i + 1) = 10^{a(t_f - t_i)}$ , where  $D_i$  and  $D_f$  are densities ( $> 1/\text{m}^2$ ) on the initial date,  $t_i$  and the final date,  $t_f$ , respectively, and  $a$  is the ‘slope’ of the equation.

In females, significant population declines were observed for (1) the fused, 2-year-old cohorts during the breeding seasons of 1989 and 1990 ( $S=22.0\%$  and  $6.8\%$ : Nos. 1 and 5), (2) the 1st 1-(1989) year-old cohort during the breeding season of 1990 ( $S=45.9\%$ : No. 7), and (3) the 1st 1 (or 2)-(1988) year-old cohort between the end of the breeding season of 1989 and the beginning of the breeding season of 1990 ( $S=38.1\%$ : No. 3). The two 2nd recruitment cohorts that were recruited in 1988 and 1989, respectively, did not suffer significant mortalities until the beginning of their final breeding seasons in the second year (Nos. 4 and 9).

Variations in the survival pattern between years for corresponding cohorts (i.e. for

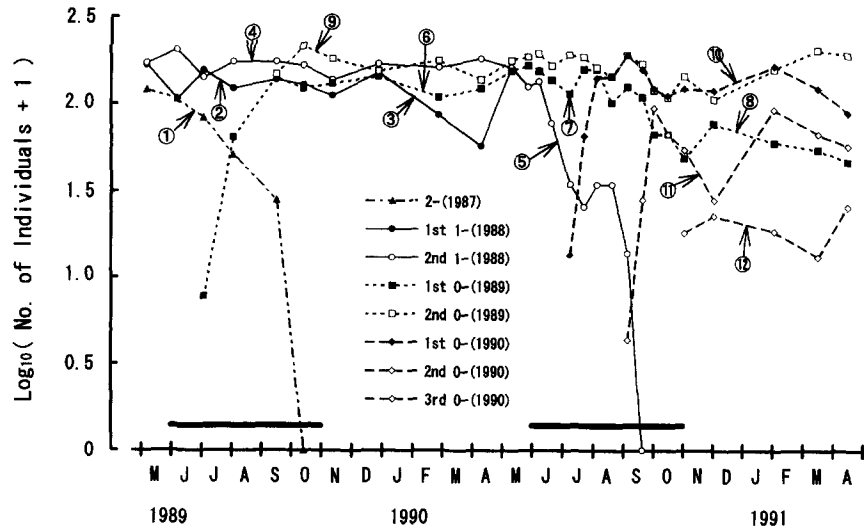


Fig. 10. Survivorship curves for each cohort of female *Callinassa japonica*. Each cohort is designated by reference to the data of the starting point of the curve. The number of individuals of each cohort on each sampling occasion was calculated from that under the corresponding normal-distribution curve (Fig. 5), and values converted to those per  $m^2$ . Linear regression equations of log-transformed density on sampling date (designated by the serial numbers) are listed in Table 2 (No. 1–No. 12). No. 3 and No. 4 merge into No. 5 [fused, 2-(1988) year-old cohort]. Stout horizontal bars denote breeding seasons.

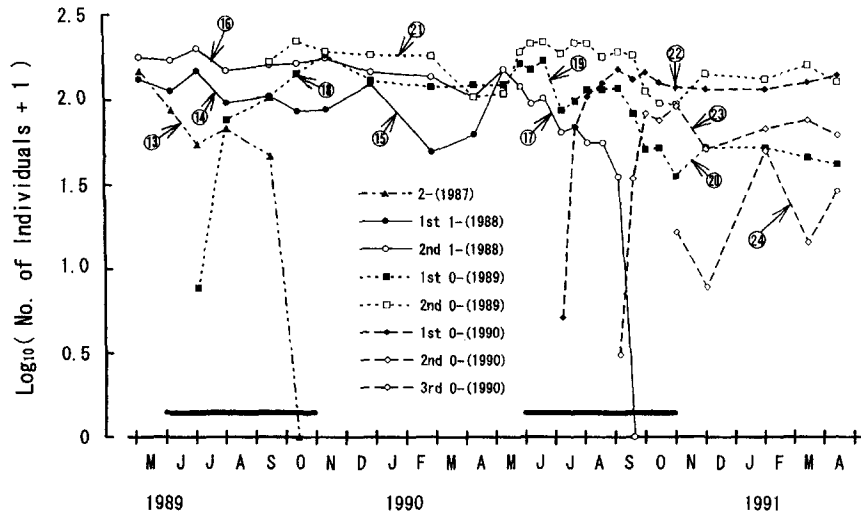


Fig. 11. Survivorship curves of each cohort of male *Callinassa japonica* based on Fig. 6. See the caption for Fig. 10 and Table 2 (No. 13–No. 24). No. 15 and No. 16 merge into No. 17 [fused, 2-(1988) year-old cohort].

Table 2

Survivorship of each female (No. 1–No. 12) and male (No. 13–No. 24) cohorts of *Callinassa japonica* as shown in Figs. 10 and 11

No.	Cohort	Period	(a, b)	(n, r <sup>2</sup> , p)
1	2-(1987)	6 May '89–15 Sep. '89	(−0.0050, 2.1457)	(5, 0.96, **)
2	1st 1-(1988)	6 May '89–27 Dec. '89	(−0.0001, 2.1384)	(8, 0.02, 0.76)
3	1st 1-(1988)	27 Dec. '89–10 Apr. '90	(−0.0040, 2.1817)	(3, 0.98, ***)
4	2nd 1-(1988)	6 May '89–11 May '90	(−0.0000, 2.2286)	(11, 0.01, 0.76)
5	2-(1988)	11 May '90–5 Sep. '90	(−0.0088, 2.2343)	(9, 0.88, ***)
6	1st 0-(1989)	15 Sep. '89–11 May '90	(0.0000, 2.1186)	(7, 0.00, 0.96)
7	1st 1-(1989)	11 May '90–16 Oct. '90	(−0.0021, 2.2543)	(12, 0.66, **)
8	1st 1-(1989)	16 Oct. '90–17 Apr. '91	(−0.0006, 1.8144)	(6, 0.25, 0.30)
9	2nd 0-(1989)	13 Oct. '89–17 Apr. '91	(−0.0001, 2.2542)	(22, 0.06, 0.28)
10	1st 0-(1990)	5 Aug. '90–17 Apr. '91	(−0.0006, 2.1784)	(11, 0.27, 0.10)
11	2nd 0-(1990)	2 Oct. '90–17 Apr. '91	(−0.0000, 1.7975)	(7, 0.00, 0.97)
12	3rd 0-(1990)	2 Nov. '90–17 Apr. '91	(−0.0000, 1.2857)	(5, 0.00, 0.98)
13	2-(1987)	6 May '89–15 Sep. '89	(−0.0034, 2.0798)	(5, 0.77, *)
14	1st 1-(1988)	6 May '89–27 Dec. '89	(−0.0005, 2.0919)	(8, 0.21, 0.25)
15	1st 1-(1988)	27 Dec. '89–10 Apr. '90	(−0.0031, 2.0289)	(3, 0.62, 0.33)
16	2nd 1-(1988)	6 May '89–11 May '90	(−0.0004, 2.2646)	(11, 0.53, **)
17	2-(1988)	11 May '90–5 Sep. '90	(−0.0048, 2.1509)	(9, 0.94, ***)
18	1st 0-(1989)	15 Sep. '89–11 May '90	(−0.0002, 2.1292)	(7, 0.04, 0.65)
19	1st 1-(1989)	11 May '90–16 Oct. '90	(−0.0026, 2.2127)	(12, 0.64, **)
20	1st 1-(1989)	16 Oct. '90–17 Apr. '91	(−0.0001, 1.6622)	(6, 0.01, 0.86)
21	2nd 0-(1989)	15 Sep. '89–17 Apr. '91	(−0.0003, 2.2907)	(23, 0.17, 0.052 ≈*)
22	1st 0-(1990)	5 Sep. '89–17 Apr. '91	(−0.0002, 2.1138)	(9, 0.08, 0.44)
23	2nd 0-(1990)	2 Oct. '90–17 Apr. '91	(−0.0004, 1.8793)	(7, 0.16, 0.37)
24	3rd 0-(1990)	2 Nov. '90–17 Apr. '91	(0.0019, 1.1150)	(5, 0.19, 0.44)

Each cohort is designated by reference to the initial date of the corresponding period.

The two coefficients of the linear regression equation of  $\text{Log}_{10}(\text{density value} + 1)$  on sampling date,  $\text{Log}_{10}(\text{density value} + 1) = aX + b$  ( $X$  is the cumulative total days from the initial date), are listed.

Levels of statistical significance of  $p$  with regards to  $a$  are denoted as \* $<0.05$ ; \*\* $<0.01$ ; \*\*\* $<0.001$ .

respective categories of the 1st or 2nd recruitment cohort) occurred. For example, in contrast to (2) in the preceding paragraph, the 1st 1-(1988) year-old cohort during the breeding season of 1989 did not decrease significantly (No. 2). Although a decline similar to that in (3) above was observed for the 1st 1-(1989) year-old cohort after the breeding season of 1990, it was not statistically significant (No. 8).

In males, significant population declines were observed for (1) the fused, 2-year-old cohorts during the breeding seasons of 1989 and 1990 ( $S=35.7\%$  and  $27.5\%$ : Nos. 13 and 17), (2) the 1st 1-(1989) year-old cohort during the breeding season of 1990 ( $S=38.7\%$ : No. 19), and (3) the two 2nd recruitment cohorts that were recruited in 1988 and 1989, respectively until the beginning of their final breeding seasons in the second year ( $S=68.7\%$  and  $65.3\%$ : Nos. 16 and 21). Between sexes, therefore, the patterns in population decline were, for the most part, similar. The major difference seems to be that survival rates were lower in males for the 2nd recruitment cohorts of 1988 and 1989, respectively, during the period from recruitment to the beginning of their final, second breeding seasons (No. 4 vs. No. 16; No. 9 vs. No. 21).

### 3.5. Comparison of participation in breeding by the different cohorts

For the breeding season of 1990, the degree of participation in breeding by the three competent cohorts of females [the fused, 2-(1988) year-old, the 1st, and 2nd 1-(1989) year-old cohorts] were evaluated in terms of densities of ovigerous females and egg (both uneyed and eyed eggs pooled) densities produced by them (Fig. 12). Both reveal a similar, bimodal pattern, with the lower peak occurring on 9 July and the higher one on 5 September. Not surprisingly, this pattern is consistent with the bimodal pattern observed for the proportion of ovigerous females in the population (Fig. 7), although the second peak in the latter was recorded on 2 October. With regard to the ovigerous female densities, the following characteristics were found: (1) in June, the 2-year-old cohort represented about 50% of the ovigerous population and subsequently decreased from 20 to 0% during September; (2) during June to August, the 1st 1-year-old cohort comprised about 50 to 70%; and (3) during September to October, the 2nd 1-year-old cohort's proportion became greater, accounting for between about 50 and 63%. These differences in the degree of participation are not directly reflected by the egg densities, in which the older cohorts' share is greatly enhanced due to the positive correlation between individual body-size and number of its eggs (Section 3.1): (1) during the earlier part of the breeding season (until 9 July), the contribution by the 2-year-old cohort represented 42 to 68%; (2) except for June, the contribution by the 1st 1-year-old cohort was the greatest throughout the season, representing 45% (9 July) to 62% (5 September); and (3)

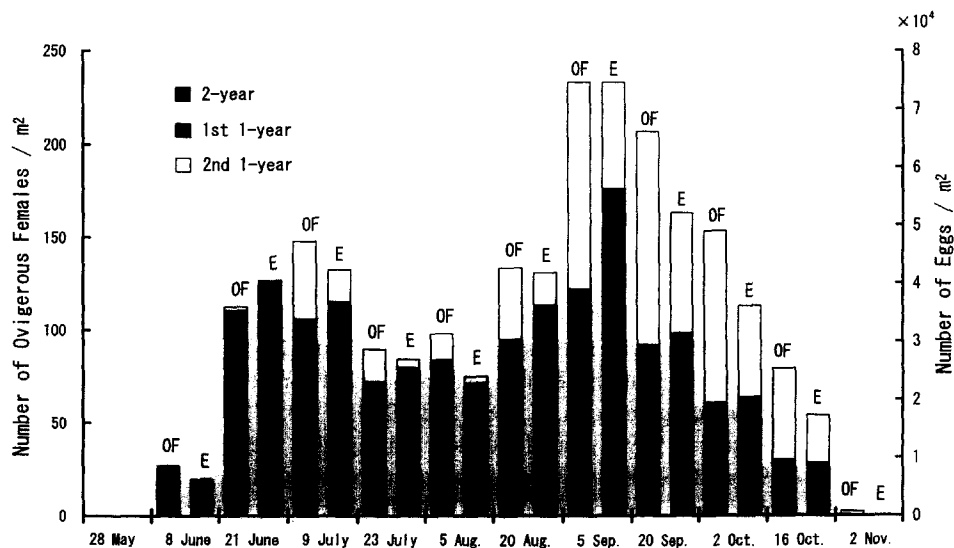


Fig. 12. Temporal changes in the ovigerous female density (OF) of each of the three competent cohorts of *Callinassa japonica* and in the egg density (E) held by each cohort during the 1990 breeding season. Data from the three stations are combined, with density values converted to those per  $\text{m}^2$ .

toward the end of the season, the contribution by the 2nd 1-year-old cohort became more prominent, representing 40% (20 September) to 48% (16 October).

### 3.6. Temporal change in the total densities of each cohort

The temporal change in densities of each cohort (both sexes combined; pooled for the three stations) throughout the study period is summarized in Fig. 13. Between each of the two major 0-year-old cohorts in 1988, 1989, and 1990, a comparison of the densities at the end of the recruitment season (December) can be made; for December 1988 data, densities for the 6 May 1989 [those for the 1st and 2nd 1-(1988) year-old cohorts] were used (as no data was available for December, 1988); and for the 1990 data, the 2nd and 3rd recruitment cohorts (Figs. 5 and 6) were combined as the 'latter' major recruitment cohort in the year (called the 2nd recruitment cohort here). The densities of the 1st recruitment cohorts were stable among the three years, i.e. 298.0, 269.1, and 232.9/m<sup>2</sup>, respectively. Those of the 2nd recruitment cohorts were also stable between 1988 and 1989, i.e. 347.8 and 334.9/m<sup>2</sup>, respectively, but that of 1990 was about 1/3 of these values, 105.1/m<sup>2</sup>. On the first sampling occasion in each of the three years, 1989, 1990, and 1991, the population densities as a whole were stable, i.e. 911.7, 1010.6, and 886.7/m<sup>2</sup>, respectively. Thus the population declines at the adult stage during the breeding seasons (Section 3.4) were effectively replenished by recruitment each year. In addition, throughout the entire study period, densities of the population as a whole were

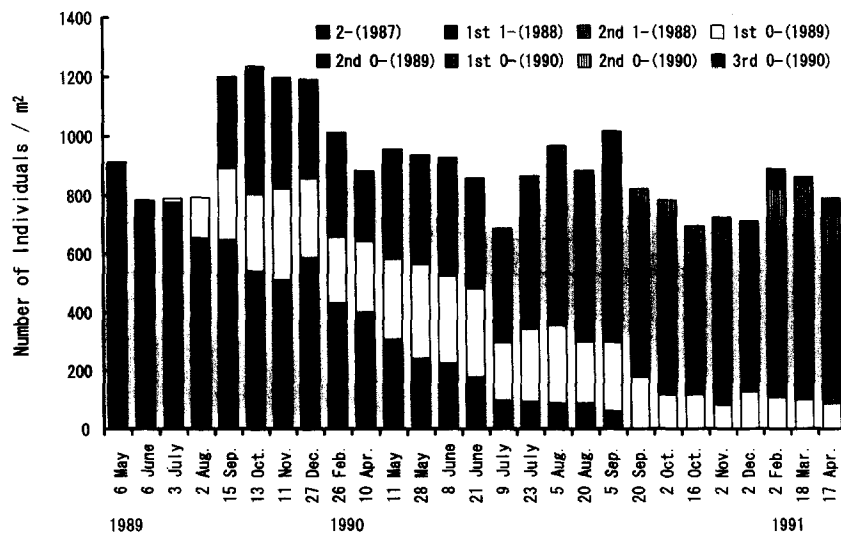


Fig. 13. Temporal changes in the total number of individuals (data from both sexes and the three stations combined) of each cohort of *Callianassa japonica* throughout the study period, with density values converted to those per m<sup>2</sup>. Each cohort is designated by reference to the date of its first appearance in the sampling period.

stable, varying between  $685.1/\text{m}^2$  (9 July 1990) and  $1232.6/\text{m}^2$  (13 October 1989), and the mean  $\pm$ SD being  $901.2 \pm 156.8/\text{m}^2$  ( $n=27$ ).

### 3.7. Temporal change in the densities at the three stations

The temporal change in densities (both sexes combined) at each of the three stations over the study period is shown in Fig. 14. In the two recruitment seasons, densities of

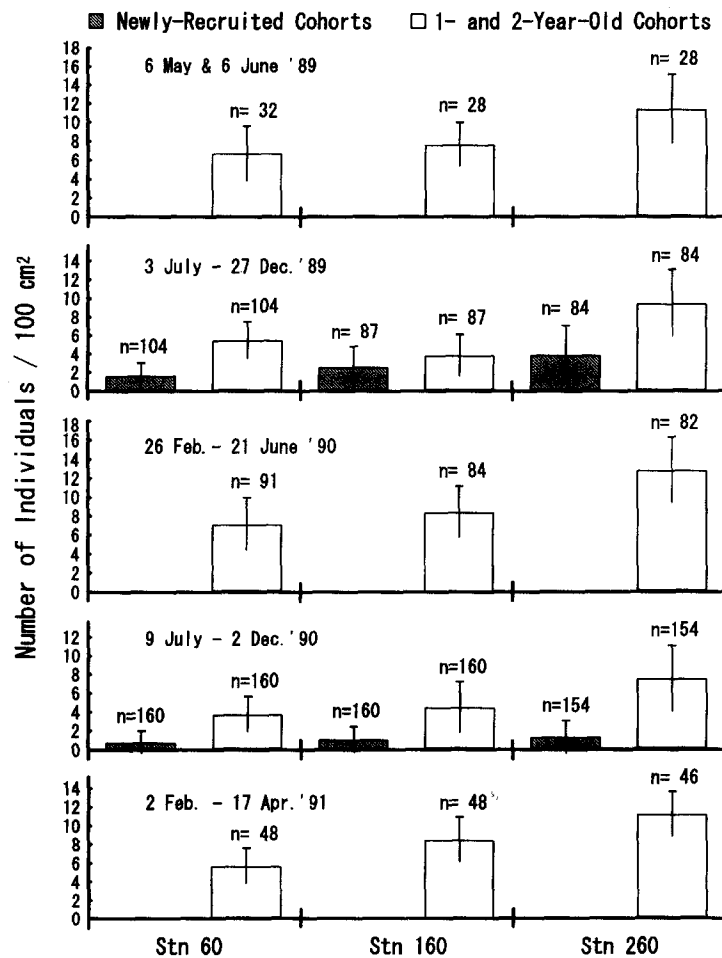


Fig. 14. Mean  $\pm$ SD densities (both sexes combined; expressed per unit sampling area;  $n$ , number of core samples) of the newly-recruited cohorts (the smallest-sized cohorts: see Section 2.4 in text) and the 1- and 2-year-old cohorts of *Callinassa japonica* at the three stations in the two recruitment seasons (July–December) and in the three between-recruitment seasons. Note that owing to the definition of the above cohorts, the older 0-year-old cohorts are not included in the figures for the recruitment seasons [e.g. 1st 0-(1990) year-old cohorts during 5 September to 2 December 1990 and 2nd 0-(1990) year-old cohorts during 2 November to 2 December 1990 (see Figs. 5 and 6)].

the newly-recruited cohorts were higher on the seaward side; differences between the stations were significant (Kruskal–Wallis test:  $p < 0.001$  in 1989 and  $0.02 < p < 0.05$  in 1990). Except for the 1- and 2-year-old cohorts in the recruitment season of 1989, the same tendency as above was found for both the densities of the 1- and 2-year-old cohorts in the recruitment season of 1990 and those in the three between-recruitment seasons (all,  $p < 0.001$ ); in the recruitment season of 1989, the density was significantly lower at Stn 160 than at Stn 60 (Mann–Whitney  $U$ -test:  $p < 0.001$ ). With regard to the densities in the three between-recruitment seasons, the mean values per 100 cm<sup>2</sup> at each station were stable, varying from 5.7 to 7.2 at Stn 60, from 7.8 to 8.6 at Stn 160, and from 11.2 to 12.9 at Stn 260; these density values are slightly higher than those described in Tamaki and Ingole (1993), in which a larger threshold size criterion for the ‘adult’ members of the population was used. Thus the stability of the total densities (Section 3.6) was derived from that at each station.

#### 4. Discussion

The present study has revealed various aspects of the life history and population characteristics of one callianassid species in more detail than any others investigated to date. The life history pattern of the *Callianassa japonica* population on the Tomioka Bay sandflat was basically characterized by the occurrence of two major recruitment cohorts each year [the 1st (summer) cohort and the 2nd (autumn) cohort]. The difference in the initial growth rates between the cohorts [i.e. that occurring during the first phase (Section 3.3)] initially enhanced their establishment as discrete cohorts. By the beginning of the breeding season (June–October) each year, three competent cohorts occurred: the fused 2-year-old, and the 1st, and 2nd 1-year-old cohorts. The bimodality in recruitment was essentially derived from the bimodal pattern of egg production, although the survival rate and/or success of settlement of the planktonic larvae seem to be variable within a breeding season [Fig. 4 (Section 3.1)]. Bimodal egg production was caused by two processes: (1) egg production by the fused, 2-year-old cohort and that by the 2nd 1-year-old cohort occurred mainly in the former and latter halves of the breeding season, due to the life span and body-size limitations on the onset of maturity, respectively; and (2) both the proportion and the density of ovigerous females in the population for each of the three competent cohorts dropped temporarily from the end of July to mid-August, during which time water temperatures reached a maximum for the year (Goto and Kikuchi, pers. comm.; Fig. 2). The latter process might have a physiological basis, because *C. japonica*, especially larger-sized individuals, seem to be extremely susceptible to heat stress and/or desiccation. For example, it was observed only during sunny low tide in summer that for animals placed on the sandflat surface, the burrowing activity was reduced considerably, often leading to death (pers. obs.). Under natural conditions, animals will remain in the deeper portions of the sediment column in which the lower water temperatures are less critical, even during the hottest daytime temperatures (Tamaki, 1984; Tamaki and Ingole, 1993). It is possible that during the hottest part of summer, the population would have a decreased reproductive performance

due to metabolic restriction to gonadal development, reduced feeding and/or mating activities, etc.

The life history patterns of the three callianassid species previously studied appear to be essentially similar to that of *Callianassa japonica*, in that (1) the appearance of two discretely recruited cohorts in a year, (2) maturity occurring 1–1.5 years after recruitment, and (3) their participation in breeding separately and/or jointly 2–3 times through a life span of 2–2.5 years, with the last breeding occurring just prior to death [Trypaea australiensis-Hailstone and Stephenson, 1961; *Callianassa kraussi*-Forbes, 1977; *Lepidophthalmus louisianensis*-Felder and Lovett (1989) and Felder and Griffis (1994)]. The breeding season of *L. louisianensis* is similar to that of *C. japonica* (May to September; Louisiana, USA). The initial distinction of two discretely recruited cohorts which subsequently merge have also been recorded for *C. kraussi*. However, two major differences exist: (1) the span of the breeding seasons for the two species are more extensive than that for *C. japonica*, being from winter to summer for *C. kraussi* (7 months-July to January; Port Elizabeth, South Africa) and from autumn to spring for *T. australiensis* (7 months-April to October; Brisbane, Australia); and (2) the periods of brooding and larval development, especially the latter, vary considerably among the species (see review by Tamaki et al., 1996).

In both sexes of the present *Callianassa japonica* population, the critical phases in the life history were associated with breeding activity. They were characterized by the lower growth rates (Section 3.3) and the lower survival rates (Section 3.4), although there were variations between different cohorts, sexes, and different years. Further long-term data will be needed to fully evaluate these variations. The occurrence of iteroparous egg deposition at an individual level during a single breeding season has been confirmed (Tamaki et al., 1996). Continual production of broods was suggested to occur in *Callianassa filholi* (Devine, 1966) and in *Lepidophthalmus louisianensis* (Felder and Lovett, 1989). In general, it is expected that such repeated egg depositions would reduce growth and decrease survival in females, functioning as the cost of reproduction. In males, their combatant behaviour when competing for females and the energy allocated for the development of the major chelae, for their use in such aggressive encounters, could be a cost of reproduction, as suggested for *C. filholi* (Devine, 1966), *Neotrypaea californiensis* (Bird, 1982), *L. louisianensis* (Felder and Lovett, 1989), and *Callianassa subterranea* (Rowden and Jones, 1994).

In the present *Callianassa japonica* population, the lowered growth rates, concomitant with the start of the breeding season, were observed for the fused, 2-year-old cohorts of both sexes and the female 1st 1-(1989) year-old cohort, but not for the male 1st 1-(1989) year-old cohort (a constant growth rate) and the 2nd 1-(1989) year-old cohorts of both sexes (higher growth rates)(Section 3.3). For males of the 1st 1-year-old cohort, the energy usage in the development of both the testes and the major chelae may not have significantly affected their body growth. As demonstrated in Figs. 7 and 12, because the majority of the female 2nd 1-year-old cohort were involved in reproduction only in the latter half of the breeding season which was characterized by decreasing water temperatures (Fig. 2)[this was also suggested for the male 2nd 1-year-old cohort (Section 3.2)], the cost of reproduction should have been lower in the 2nd cohorts than



in the 1st cohorts which bred throughout the season. Both decreased growth rates in females and an unchanged rate in males associated with breeding activity have also been reported for *Callianassa kraussi* (Forbes, 1977).

In the present *Callianassa japonica* population, the high survival rates exhibited by most cohorts of both sexes during the periods other than the breeding seasons are noteworthy (Section 3.4). The lower survival rates in the breeding season were observed for the 1st 1-(1989) year-old cohorts of both sexes and the male 2nd 1-(1988) and (1989) year-old cohorts as well as for the fused, 2-year-old cohorts of both sexes, but not for the female 2nd 1-(1988) and (1989) year-old cohorts (Table 2). These patterns would also be explicable from the degree of participation in the breeding activity: the 1st recruitment cohorts make their reproductive effort mostly during the first breeding season, while the 2nd ones' effort is more concentrated in the second breeding season. A corollary of this is that when the density at recruitment for the female 2nd cohort is greater than or equal to that for the 1st one [as observed for the two 1-(1988) year-old cohorts (No. 4 vs. No. 2 in Fig. 10) and the two 0-(1989) year-old cohorts (No. 9 vs. No. 6), but not for the two major 0-(1990) year-old cohorts (Nos. 11 and 12 vs. No. 10)], the former plays a central role in the second breeding season in life history. For males of the 2nd 1-year-old cohorts, combatant encounters with other males might lead to the lower survival rates. This would have resulted in the expulsion of the defeated males onto the sandflat surface, leading to their death due to predation, heat stress, wave disturbance, etc. (see Discussion in Tamaki and Ingole, 1993). Higher death rates in males than in females might explain the slightly female-biased sex ratio in the population (Section 3.1). Of reported callianassid species lower survival rates associated with the first as well as the second (final) breeding seasons through life history are suggested for both sexes of *Callianassa kraussi* (Forbes, 1977). Female-biased sex ratios are also recorded for *Callianassa filholi* (1:2-Devine, 1966), *Neotrypaea californiensis* (1:1.8-Bird, 1982), *Lepidophthalmus louisianensis* (1:1.02 to 1.13-Felder and Lovett, 1989; Felder and Griffis, 1994), and *Callichirus islagrande* (1:1.03 to 1.48-Felder and Griffis, 1994), while the reverse ratios recorded for *C. kraussi* (1.2 to 3.5:1-Forbes, 1977) and *Callianassa subterranea* (1.9:1-Rowden and Jones, 1994).

Throughout the present study period, the stability of the population densities of *Callianassa japonica* was remarkable (Section 3.6 Section 3.7). It is expected, a priori, that such stability would result from a circular chain of the population processes as follows: (1) stable egg production by the females [ Fig. 12 (seasonal trend); yearly variations were not investigated in the present study]; (2) yearly stable recruitment by post-larvae to the benthic population (Section 3.6; except for the lower recruitment levels of the 2nd plus 3rd recruitment cohorts in 1990); and (3) the high survival rates of individuals after recruitment until the beginning of the first breeding season and during non-breeding seasons (Section 3.4). A part of the above processes would be derived from both a positive intraspecific relationship and from the habitat used being in the deeper portion of the sediment column-where environmental conditions are more stable than in the shallower portion (Tamaki, 1984). Tamaki and Ingole (1993) suggested that the higher densities of newly-recruited individuals at the seaward stations and its reflection on adult densities as demonstrated in Fig. 14 in the present paper are

attributable to the facilitation of larval settlement by conspecific adults and to escape from potential high mortality occurring near the sediment surface. Settling post-larvae crossing the sandflat with the incoming tide would successfully burrow *en masse* into the adult-inhabited substrate as soon as it was encountered, with the remaining larvae settling progressively shoreward. Adults indirectly assist settlement by both softening the substrate resulting from the bioturbation (Tamaki and Suzukawa, 1991) and the presence of adult burrows acting as a conduit (Tamaki et al., 1992a) helping the larvae to easily burrow and reach the deeper portion of the sediment column. Recruiting post-larvae into the deeper portion of the sediment would reduce epibenthic predation, heat stress/desiccation, and washout by wave action. Besides such a positive intraspecific relationship, negative ones could also regulate the population density. Intraspecific competition for space regulating population densities has been suggested for other callianassid species (Hailstone and Stephenson, 1961; Bird, 1982; Felder and Lovett, 1989). For *C. japonica*, aggressive behavior when competing for burrow space in aquaria were often observed, irrespective of the opponents' sex (pers. obs.). Thus, even if densities at recruitment are far higher than those needed for the replacement of dead adults, a 'surplus' portion of the population might be eliminated due to death and/or emigration with the growth of juveniles. Assuming that the area of a mound extruded by one individual on the sandflat surface [3–5-cm averaged diameter (Section 2.2)] equals the exclusive two-dimensional area of its burrow extension, a carrying capacity on the sandflat with density varying from 509 to 1415/m<sup>2</sup> will be expected. The actual observed values referred to in Section 3.6 Section 3.7 were within this range. These were generally higher than the highest densities (/m<sup>2</sup>) recorded for several other callianassid species [*Trypaea australiensis*-500 (Hailstone and Stephenson, 1961); *Neotrypaea californiensis*-770 (Bird, 1982); *Lepidophthalmus louisianensis*-420 (Felder and Griffis, 1994); *Callichirus islagrande*-750 (Felder and Griffis, 1994)].

The present study was based on sampling conducted at an interval of 2 weeks to 2 months for two years. Results in Tamaki et al. (1996) clearly show the need for even more frequent sampling in order to detail the recruitment processes including the relationship between the egg production and the subsequent settlement by post-larvae. Moreover, the results of the present study suggest that acquisition of a longer-term data set is required to reveal the yearly variations in population characteristics examined above.

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