

**Comparative Studies on the Life History of the Grapsid
Crabs (Crustacea, Brachyura) Inhabiting Intertidal
Cobble and Boulder Shores**

By

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Abstract Growth, survivorship and reproduction of seven species of grapsid crabs inhabiting intertidal cobble and boulder shores were investigated in Shirahama, Wakayama Prefecture, Japan. In general, growth rate decreased with age, was similar between the sexes for the immature crabs, and was lower in mature females than in mature males within a species. Growth rate showed considerable variations among species, which seemed to be mainly due to the interspecific differences in intermolt period. Survival rate was similar between the sexes, and tended to be lower in mature crabs than in immature crabs within a species. Survival rate varied considerably among species, and an apparent trade-off relationship to an index of reproductive activity existed. This brood index was calculated by multiplying the ratio of brood weight per body weight by the number of broods per year. Egg size and the ratio of brood weight per body weight were constant within a species regardless of body size of parent female crabs, whereas the number of eggs per brood was nearly proportional to the third power of their carapace width. Among species, mean number of eggs per brood and size at maturity were correlated with mean adult body size of the species, whereas egg size, the number of broods per year, brood index and age at maturity were not. A model which shows the relationships between the expected value of the number of eggs laid per life per female and some life history traits was made on the basis of the general rules followed by the present grapsid crabs in the intraspecific and interspecific variations in life history traits. Using this model, the factors influencing the evolution of age at maturity and brood index were analyzed. Delayed maturity and smaller brood index were predicted to be favored as survival rate in immature period increases and/or relative growth rate to maximum body size decreases.

Recently the information on the life history traits of brachyuran crabs has been accumulated using laboratory and field studies. Since brachyuran crabs grow through molts, some studies have analyzed their growth rate from molt increment and intermolt period (Hartnoll, 1982). Molting makes it almost impossible to mark an individual crab for a long time in order to follow its growth under natural conditions. Probably for the same reason, there are few studies on survival rate of individual brachyuran crabs. Likewise, the number of broods per year and age at maturity are relatively difficult to estimate, thereby being studied for a few species (Pillay & Ono, 1978; Seiple, 1979; McDonald, 1982). In contrast, some reproductive traits, e.g., egg size, the number of eggs per brood and reproductive cycle, have been studied for many species (e.g., Knudsen, 1964; Pillay & Nair, 1971; Hines,

1982). Thus there are great differences in the amount of information among life history traits according as the trait is measured easily or not. Most of the studies on the evolution of life history pattern of brachyuran crabs have dealt with only a fraction of the life history traits, and have given little consideration to the relationship among those traits.

This paper compares the life history pattern of seven species of intertidal grapsid crabs, *Hemigrapsus sanguineus* (De Haan), *Hemigrapsus penicillatus* (De Haan), *Gaetice depressus* (De Haan), *Acmaeopleura parvula* Stimpson, *Nanosesarma gordonii* (Shen), *Cyclograpsus intermedius* Ortmann, and *Cyclograpsus* sp., which exploit different but overlapping habitats on cobble and boulder shores in Shirahama, Wakayama Prefecture, Japan. The purpose of this paper is threefold. First, the life history traits of the seven species are estimated from the data of field survey and laboratory rearing. This paper particularly aims at elucidating all aspects of growth rate, survival rate and reproductive traits for each species. Second, the general rules followed by the grapsid crabs are searched for in the intraspecific and interspecific variations of the observed life history traits. For example, the relationship of each trait to body size is examined. It has been indicated that some life history traits are subjected to allometric constraints (Hines, 1982, 1986). The relationships among traits, e.g., the effect of reproductive effort on the other traits, are also examined. Finally, using a model based on these general rules obtained, the factors influencing the evolution of life history pattern in the present grapsid crabs are analyzed and discussed.

Materials and Methods

1. Monthly sampling.

To follow temporal changes of densities and size-frequency distributions, quantitative samplings were carried out on the south coast of Tanabe Bay, Shirahama, Wakayama Prefecture, central Japan, for 7 species of intertidal grapsid crabs, *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula*, *Nanosesarma gordonii*, *Cyclograpsus intermedius* and *Cyclograpsus* sp. On the basis of the results of preliminary researches, relatively high density areas were selected as sampling sites for each species (Fig. 1). Samplings were conducted approximately monthly at spring low tide, and the collected crabs were measured (maximum carapace width [CW]) to the nearest 0.1 mm with hand calipers or a micrometer under a binocular microscope, sexed and, in female crabs, examined for eggs. Specimens smaller than the following size in carapace width were difficult to sex, and were arbitrarily classed as juveniles; 8 mm for *H. sanguineus*; 6 mm for *H. penicillatus*, *G. depressus* and *C. intermedius*; 3 mm for *A. parvula* and *C. sp.*; 2 mm for *N. gordonii*. As a rule, specimens of *H. sanguineus*, *C. intermedius* and *C. sp.* were measured in the field and returned to the sampling site afterward. Specimens of the other species were fixed immediately in 10% formalin and measured in the laboratory. Since the sampling area was estimated to be 0.03 to 3.7% of the whole boulder area at each sampling site, it seemed that sampling had little effects on the density of crab populations there. More detailed notes on sampling area and method for each species are shown as follows.

Hemigrapsus sanguineus: Crabs were sampled from May 1981 to September 1982 at Site G, where a gently-sloping rock bed with scattered angular boulders (>26 cm in diameter) and cobbles (6 to 26 cm in diameter) spread out at the foot of the cliff. Boulders and cobbles were accumulated to make a cross-shore strip of stone pile as the sampling site of this species. The stone pile was 1 m in width, 0.3 m in height and 16 m in length, with the height being from 30 to 140 cm above chart datum. Boulders and cobbles scattered within 10 m on both sides of the pile were removed. The pile was divided into 8 sections of 2 m length, numbered 1 to 8 seaward, and the even-numbered sections

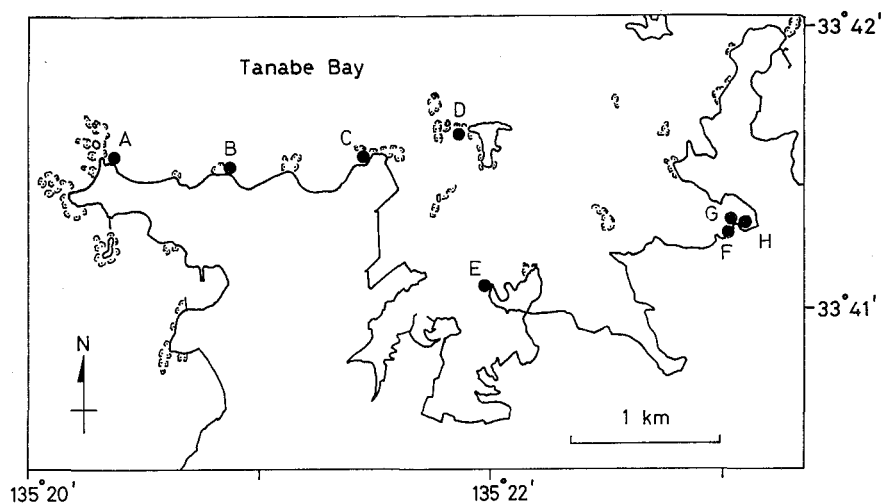


Fig. 1. Map of the south coast of Tanabe Bay, showing location of sampling sites (A-H).

were selected to be sampled. In sampling at each section, a barrier was built between sections using a vinyl cloth, and then all boulders in the section were turned over to capture crabs. After sampling, boulders and cobbles were piled up again as before.

Hemigrapsus penicillatus: Crabs were sampled from April 1981 to May 1982 at Site H, where angular boulders and cobbles covered nearly half of the sandy mud bottom of the middle to lower intertidal zone at the foot of the cliff. A quadrat of 50×50 cm was set at 2 m intervals along an intertidal cross-shore line of 16 m in length. The sampling points were numbered 0 to 8 seaward, with the height being 20 to 120 cm above chart datum. In each quadrat, boulders and cobbles within a depth of 20 cm were turned over to capture crabs.

Gaeticus depressus: Crabs were sampled from December 1977 to January 1979 at Site A; from July 1977 to January 1979 at Site B; and from August 1977 to May 1979 at Site D. At Site A a cobble shore was located from 20 to 50 cm above chart datum among rock reefs. Angular cobbles and boulders covered nearly all over the sandy bottom. At Site B a cobble shore was located from 10 to 110 cm above chart datum among rock reefs at the foot of artificial concrete embankment. Angular cobbles and boulders covered about half of the sandy bottom. At Site D a gently-sloping cobble shore was located from 30 to 120 cm above chart datum. Angular cobbles and boulders covered nearly all over the sandy bottom. At all sampling sites, quadrats of 50×50 cm were set at random from the middle to lower intertidal zone, and in each quadrat cobbles and boulders within a depth of 20 cm were turned over to capture crabs. The number of quadrats set for samplings was 3 to 10 at Site A, 6 to 15 at Site B, and 3 to 5 at Site D.

Acanoepleura parvula: Crabs were sampled from March 1981 to April 1982 at Site F, where a cobble shore spread out throughout the intertidal zone. Angular cobbles and boulders covered nearly all over the sandy bottom and cobbles dominated the upper shore and boulders dominated the lower shore. Two quadrats of 20×20 cm were set at 2 m intervals along a cross-shore line of 20 m in length. The sampling points were numbered 0 to 10 seaward, with the height being from 10 to 210 cm above chart datum. In each quadrat, cobbles and boulders within a depth of 20 cm were turned over to capture crabs.

Nanosesarma gordonii: Crabs were sampled from April 1979 to May 1980 at Site E, where a boulder shore was located from 10 to 60 cm above chart datum. Angular boulders were piled up, and barnacles (*Chthamalus challengeri* Hoek and *Balanus amphitrite* Darwin) and tube-dwelling polychaetes (*Pomatoleios krausii* (Baird)) were abundant on the surface of boulders. In each monthly sampling, 15-minute collection was repeated 8 times in different places. Adjoining boulders were turned over in turn, and all individuals of this species found on the surface were captured. Since the search area

per 15-minute collection ($Y \text{ m}^{-2}$) was linearly negatively related to the number of collected crabs (X) ($Y = -0.0246 X + 1.91$, $r = -0.823$, $p < 0.05$), the density of crabs was estimated using this equation for each monthly sampling.

Cyclograpsus intermedius and *Cyclograpsus* sp.: Crabs were sampled from June 1983 to June 1984 at Site C, where a relatively steeply-sloping cobble shore spread out throughout the intertidal zone at the foot of the cliff. Round and smooth cobbles and boulders were piled up about 3 fold on the sandy bottom. A quadrat of $50 \times 50 \text{ cm}$ was set at 1 m intervals in the upper 5 m and at 2 m intervals in the lower 10 m along a cross-shore line of 15 m in length. The sampling points were numbered 0 to 10 seaward, with the height being 30 to 240 cm above chart datum. In each quadrat, cobbles and boulders within a depth of 10 cm were turned over to capture crabs.

2. Growth rate and survival rate.

Growth rate of crabs after settlement was estimated from the monthly size-frequency distributions obtained from the samples. In the species *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*, whose histograms of size distributions showed relatively distinct modes, the monthly group of collected crabs was divided into size groups using the size-frequency analysis described by Cassie (1954). The age of the size group was determined on the assumption that crabs were born in the middle month of the breeding season: in July for *H. sanguineus*, *H. penicillatus*, *G. depressus* and *N. gordonii*; and in January for *A. parvula*. Growth rate was estimated separately for the immature and mature periods, using temporal change in the size mode of the estimated age group. Mean monthly growth rate (=growth rate per 30 days) was calculated from the slope of the regression line between time (day) and the size mode of the age group in carapace width (mm).

Survival rate after settlement was estimated separately for the immature and mature periods, using temporal change in the density of estimated age groups. The period from December to March, when crab density was often extraordinarily low, was omitted from estimation of survival rate. Mean annual survival rate (=survival rate per 365 days) was calculated from the slope of the regression line between time (day) and the natural logarithm of density (m^{-2}).

3. Reproductive traits.

The wet weights of ovigerous females with and without eggs were measured, and the weight of a brood was calculated from these 2 values. The number of eggs per brood was determined by direct counting and wet weight estimation. For the wet weight estimation, sample eggs of 30 to 60 mm^3 were counted and weighed. The number of eggs were calculated from the total brood weight and the reference sample weight. The developmental stages of eggs were categorized as: (1) Stage I—newly deposited, filled with yolk; (2) Stage II—a yolk-free part present; (3) Stage III—eye pigment visible, still containing much yolk; (4) Stage IV—yolk reducing to 2 small patches. Egg size was measured in the living crab. For each species, 6–16 ovigerous females with Stage I eggs and 4–11 ones with Stage IV eggs were collected, and 10 eggs were taken at random for each brood. The length and width of an egg were measured, and the egg volume was calculated on the assumption that an egg is a spheroid. The number of broods per year (N) was estimated by the following equation:

$$N = \sum_{i=a}^b \frac{Mi}{Ii} Ri$$

where Ii = the mean incubation period (days) in the i th month; Mi = the length (days) of the i th month; Ri = the ratio of ovigerous females to total females of the age group in the i th month; a and b = the first and the last month, respectively, of the breeding season. The incubation period in each month was calculated from the regression equation between the incubation period and temperature, obtained from the laboratory rearing (see the next section), using the surface water temperature measured near the field (Wakayama Prefecture Fishery and Culture Station, 1984).

4. Laboratory rearing.

The 5 species of *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula*, and *Nanosesarma gordonii* were reared in the laboratory to investigate molt increment, intermolt period

and incubation period. The rearing was conducted from April to October 1981 for *H. sanguineus*, *H. penicillatus* and *N. gordonii*; from July 1978 to July 1979 for *G. depressus*; and from November 1981 to November 1982 for *A. parvula*. Crabs, marked individually by sticking numbered tape on the carapace, were kept in the tank measuring $50 \times 30 \times 20$ cm. The number of crabs per tank was about 10 in *H. sanguineus*; about 20 in *H. penicillatus*, *G. depressus* and *N. gordonii*; and about 40 in *A. parvula*. *H. penicillatus* was reared in 1 tank, and the other species were reared in 2 tanks. Sex ratio of the crabs in the tank was nearly 1:1. When reared crabs died, new crabs collected from the field were supplied. Sea water was left running continuously, and water temperature was not controlled but was measured every day. Crabs were fully fed on shrimps or mysids 2 or 3 times a week. Every time crabs molted, they were marked again and measured in carapace width after the body hardened. Female crabs were examined at about 3 day intervals to note oviposition and hatching, from which the incubation period was calculated.

Results

1. Growth.

1-1. *Hemigrapsus sanguineus*.

Early juveniles ($< CW$ 4 mm) occurred from August to May with the highest peak in November (Fig. 2). The minimum size of collected crabs was CW 2.0 mm. There was little seasonal change in growth rate after settlement (Fig. 4(1)). In either of immature crabs (crabs younger than 22 months old; see p. 141) and mature crabs, mean growth rate was not significantly different between the sexes (analysis of covariance (=ANCOVA), $p > 0.5$) (Table 1); males and females reached CW 19.0 mm and CW 18.4 mm, respectively, at 22 months old. Growth rate was significantly lower after maturity for both sexes (ANCOVA, $p < 0.05$). The maximum size of collected crabs was CW 42.4 mm for males and CW 39.0 mm for females.

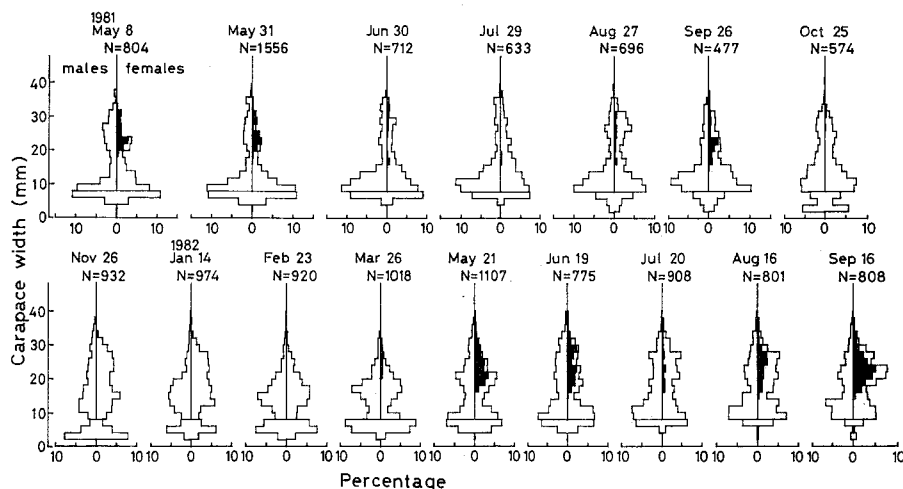


Fig. 2. *Hemigrapsus sanguineus*. Size-frequency distributions at Site G from May 1981 to September 1982. Solid histograms represent ovigerous females. N=Number of individuals in each collection.

Table 1. Estimate of monthly growth rate (mm/month). Growth rate was calculated from the slope of the regression line between time and the size mode of the age group in carapace width based on the monthly samplings.

			male		female	
			immature	mature	immature	mature
<i>Hemigrapsus sanguineus</i>		May 1981–May 1982	0.82	0.16	0.85	0.23
		Oct 1981–Sep 1982	0.74		0.70	
<i>Hemigrapsus penicillatus</i>		Sep 1981–May 1982	0.62		0.73	
		Jun 1981–May 1982		0.82		0.62
<i>Gaetice depressus</i>	Site A	Dec 1977–May 1978	0.79		0.78	
		Jun 1978–Jan 1979		0.91		0.27
	Site B	Oct 1977–May 1978	0.64		0.66	
		Jul 1977–May 1978		0.92		0.61
	Site D	Jun 1978–Jan 1979		0.82		0.22
		Feb 1978–Jun 1978	1.37		1.36	
		Nov 1978–May 1979	0.72		0.78	
		Aug 1977–Jun 1978		0.48		0.33
	Jun 1978–May 1979		0.66		0.30	
<i>Acmaeopleura parvula</i>		Mar 1981–Apr 1982	0.24		0.23	
		Mar 1981–Nov 1981	0.26	0.15	0.24	0.16
		Dec 1981–Apr 1982		0.07		0.09
<i>Nanosarma gordonii</i>		Aug 1979–Nov 1979	0.72		0.64	
		Jun 1979–Sep 1979		0.25		0.22

1–2. *Hemigrapsus penicillatus*.

Early juveniles (<CW 4 mm) were collected throughout the year with the highest peak in October (Fig. 3). The minimum size of collected crabs was CW 1.6 mm. Since sample sizes were too small from December 1981 to March 1982,

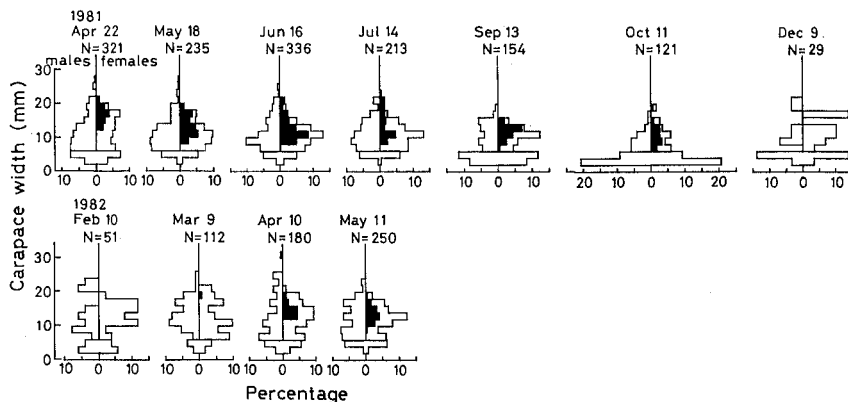


Fig. 3. *Hemigrapsus penicillatus*. Size-frequency distributions at Site H from April 1981 to May 1982. Legend as in Fig. 2.

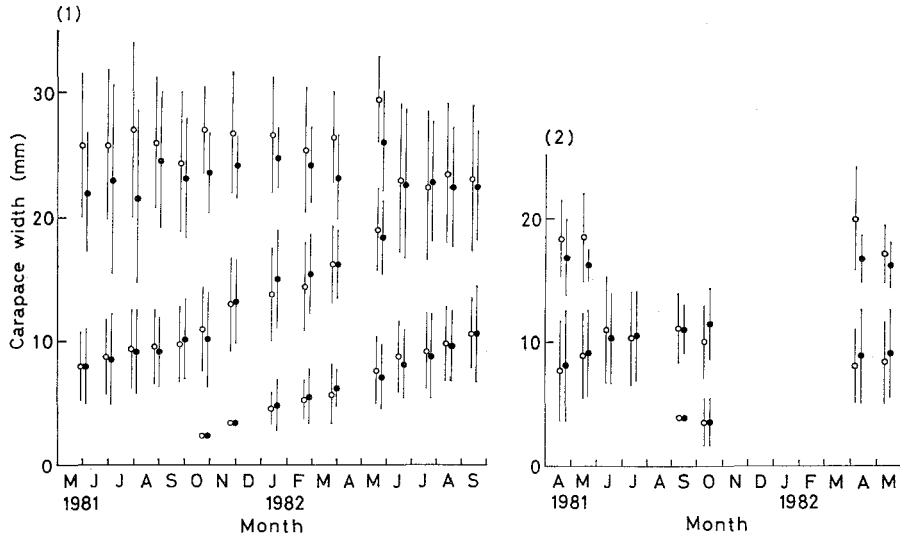


Fig. 4. (1) *Hemigrapsus sanguineus*. Growth patterns at Site G. (2) *Hemigrapsus penicillatus*. Growth patterns at Site H. Mode and standard deviations of carapace width are shown for each age group obtained from the size-frequency distribution data. Open circles represent males, solid circles females.

the size distributions in this period could not be divided into size groups and were omitted from calculation of growth rate. For that reason, seasonal change in growth rate after settlement could not be followed either (Fig. 4(2)). In either of immature crabs (crabs younger than 11 months old; see p. 141) or mature crabs, mean growth rate was not significantly different between the sexes (ANCOVA, $p > 0.5$) (Table 1);

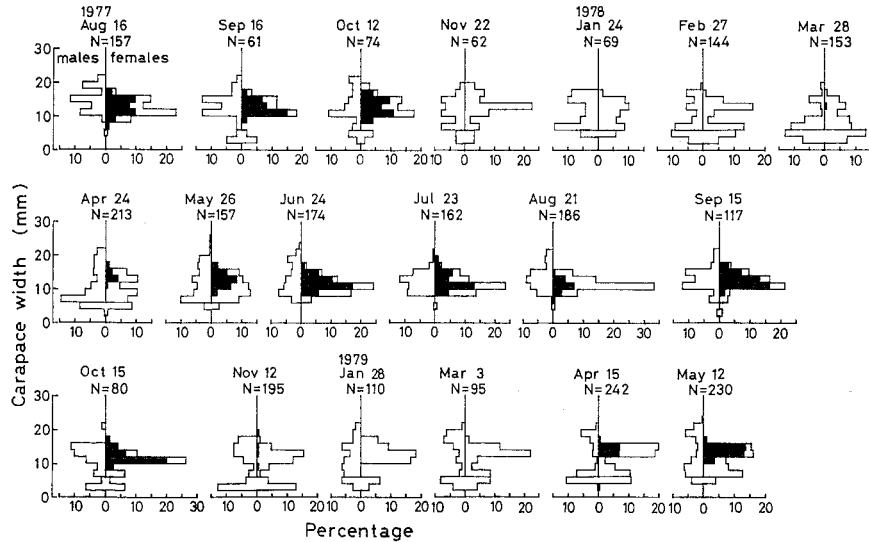


Fig. 5. *Gaetice depressus*. Size-frequency distributions at Site D from August 1977 to May 1979. Legend as in Fig. 2.

males and females reached CW 11.0 mm and CW 10.3 mm, respectively, at 11 months old. Between immature and mature crabs, growth rate was not significantly different for either sex (ANCOVA, $p > 0.1$). The maximum size of collected crabs was CW 30.6 mm for males and CW 22.0 mm for females.

1-3. *Gaetice depressus*.

Early juveniles (<CW 4 mm) occurred nearly throughout the year with the higher peak in September to March, though there were slight differences in the recruitment period between years (Fig. 5). The minimum size of collected crabs was CW 2.2 mm. Growth pattern was similar among sampling sites (Fig. 6). Growth rate after settlement changed more or less seasonally, being highest from late spring to early summer and lowest in winter. In immature crabs (crabs younger than 11 months old; see p. 141) mean growth rate was not significantly different between the sexes (ANCOVA, $p < 0.5$) (Table 1); for example at Site D, males and females reached CW 10.3 mm and CW 10.1 mm, respectively, at 11 months old. In mature crabs (equal to or older than 11 months old), mean growth rate of females

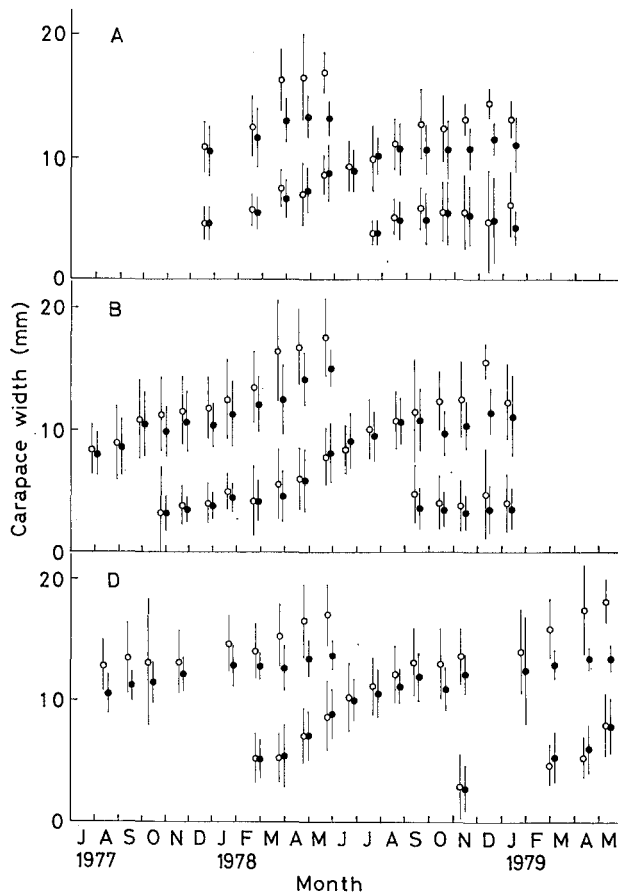


Fig. 6. *Gaetice depressus*. Growth patterns at Sites A, B and D. Legend as in Fig. 4.

was significantly lower than that of males (ANCOVA, $p < 0.05$). Between immature and mature crabs, growth rate was not significantly different for males (ANCOVA, $p > 0.05$), whereas it was significantly lower after maturity for females (ANCOVA, $p < 0.05$). The maximum size of collected crabs was CW 28.1 mm for males and CW 23.4 mm for females.

1-4. *Acmaeopleura parvula*.

Early juveniles ($< CW$ 2.5 mm) occurred from December to April with the higher peak in January to March (Fig. 7). The minimum size of collected crabs was CW 1.7 mm. There was little seasonal change in growth rate after settlement (Fig. 9(1)). In either of immature crabs (crabs younger than 22 months old; see p. 141) or mature crabs, growth rate was not significantly different between the sexes (ANCOVA, $p > 0.5$) (Table 1); males and females reached CW 7.8 mm and CW 7.9 mm, respectively, at 22 months old. Growth rate was significantly lower after maturity (ANCOVA, $p < 0.05$ for males; $p < 0.01$ for females). The maximum size of collected crabs was CW 14.4 mm for males and CW 12.8 mm for females.

1-5. *Nanosesarma gordonii*.

Juveniles ($< CW$ 2 mm) occurred from August to April with the highest peak in August (Fig. 8). The minimum size of collected crabs was CW 1.1 mm. Growth rate after settlement showed seasonal change, being nearly zero from November to April (Fig. 9(2)). In either of immature crabs (crabs younger than 11 months old; see p. 141) or mature crabs, growth rate was not significantly different between the sexes (ANCOVA, $p > 0.5$) (Table 1); males and females reached CW 4.8 mm

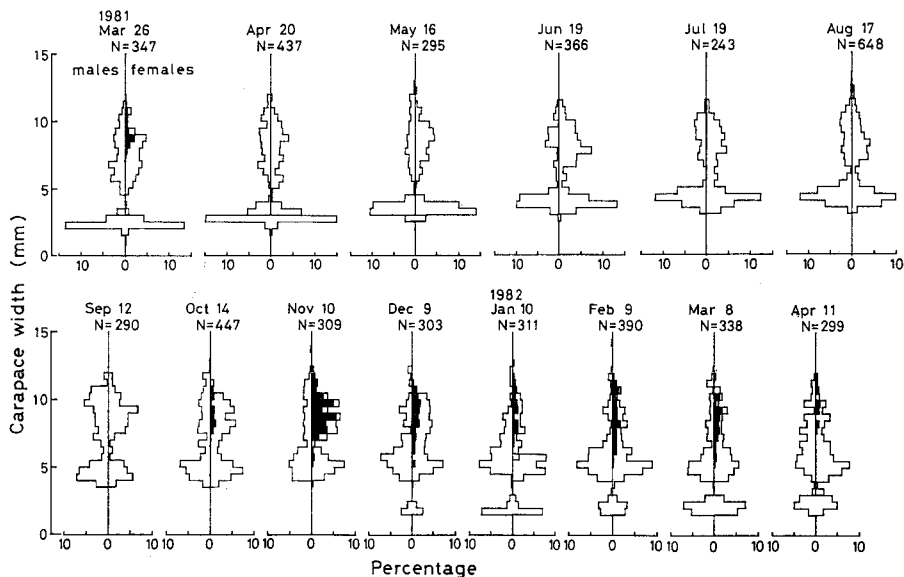


Fig. 7. *Acmaeopleura parvula*. Size-frequency distributions at Site F from March 1981 to April 1982. Legend as in Fig. 2.

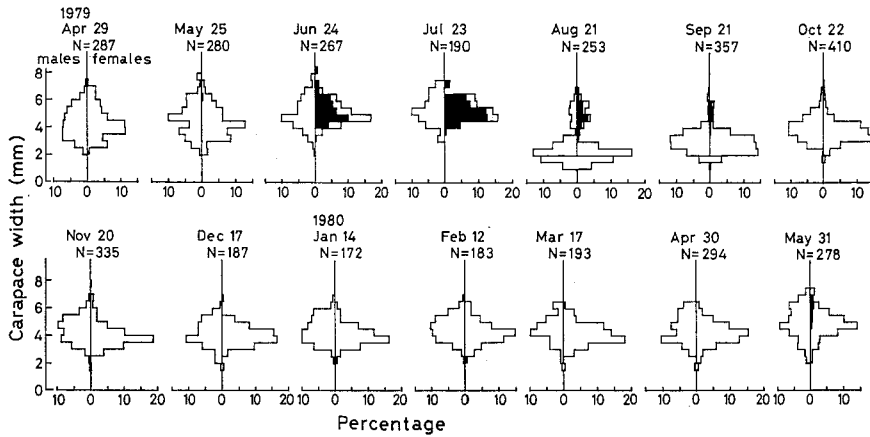


Fig. 8. *Nanosesarma gordonii*. Size-frequency distribution at Site E from April 1979 to May 1980. Legend as in Fig. 2.

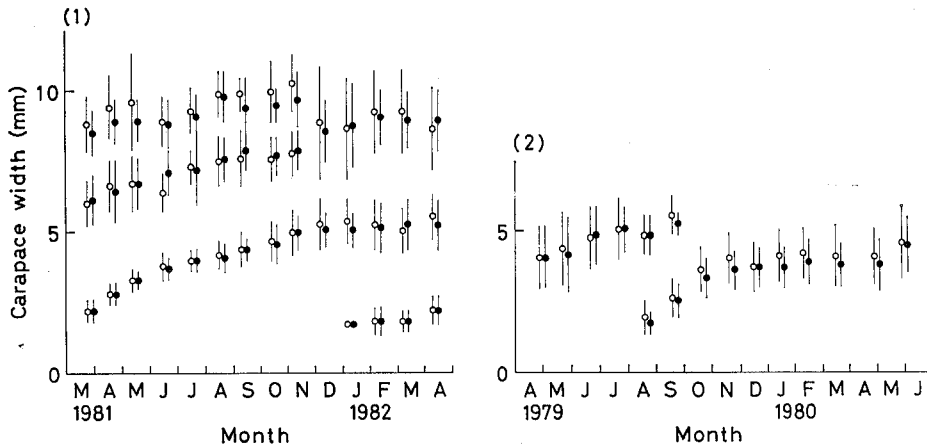


Fig. 9. (1) *Acmaeopleura parvula*. Growth patterns at Site F. (2) *Nanosesarma gordonii*. Growth patterns at Site E. Legend as in Fig. 4.

and CW 4.9 mm, respectively, at 11 months old. Growth rate was significantly lower after maturity (ANCOVA, $p < 0.05$ for males and females). The maximum size of collected crabs was CW 7.7 mm for males and CW 8.0 mm for females.

1-6. *Cyclograpsus intermedius*.

Growth pattern could not be estimated from the monthly change in the size distribution of crabs. Early juveniles ($< CW 4$ mm) occurred throughout the year with a marked peak in November (Fig. 10). This peak of juveniles, however, could not be followed afterward. The minimum size of collected crabs was CW 1.7 mm. The maximum size of collected crabs was CW 28.9 mm for males and CW 25.8 mm for females.

1-7. *Cyclograpsus* sp.

Growth pattern could not be estimated from the monthly change in the size

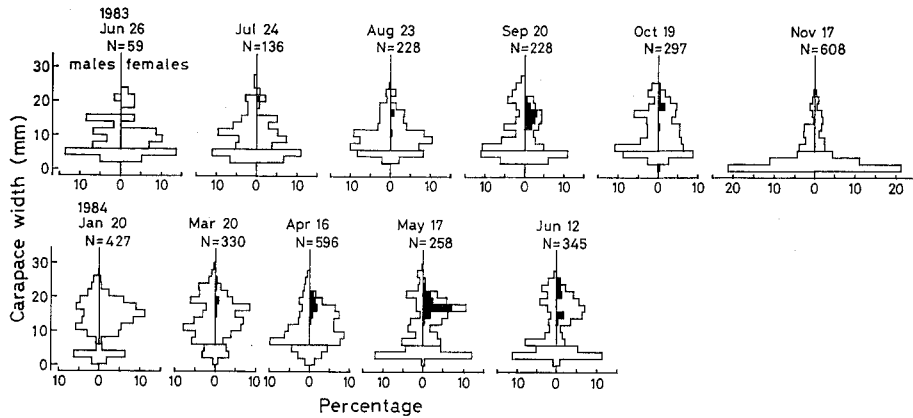


Fig. 10. *Cyclograpsus intermedius*. Size-frequency distribution at Site C from June 1983 to June 1984. Legend as in Fig. 2.

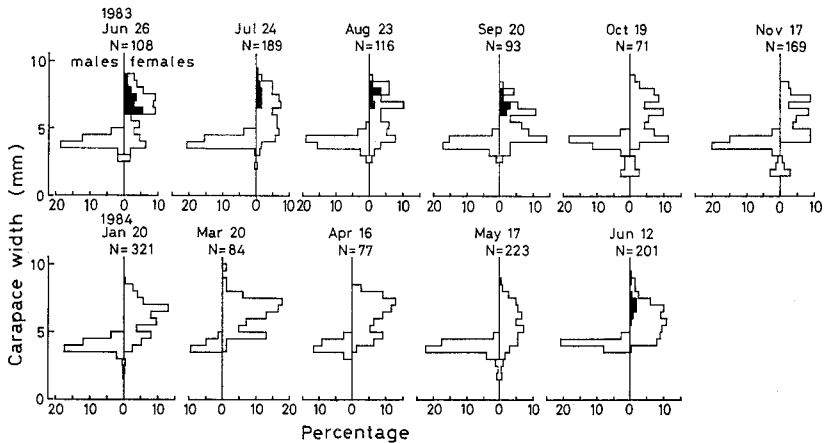


Fig. 11. *Cyclograpsus* sp. Size-frequency distribution at Site C from June 1983 to June 1984. Legend as in Fig. 2.

distribution of crabs. Juveniles ($<CW$ 3 mm) occurred from May to January without distinct abundance peak (Fig. 11). The minimum size of collected crabs was CW 1.6 mm. The size distribution of males was unimodal throughout the year, and the size mode was nearly changeless (approximately CW 4.0 mm). The size distribution of females was often polymodal, but the peak of new recruits was not recognized. The maximum size of collected crabs was markedly larger in females than in males; it was CW 5.0 mm for males and CW 9.5 mm for females.

2. Temporal density change.

2-1. *Hemigrapsus sanguineus*.

The new recruits born in 1981 occurred at all sampling sections, being more abundant at the upper sections in spring in 1982 (Fig. 12(1)). The total density

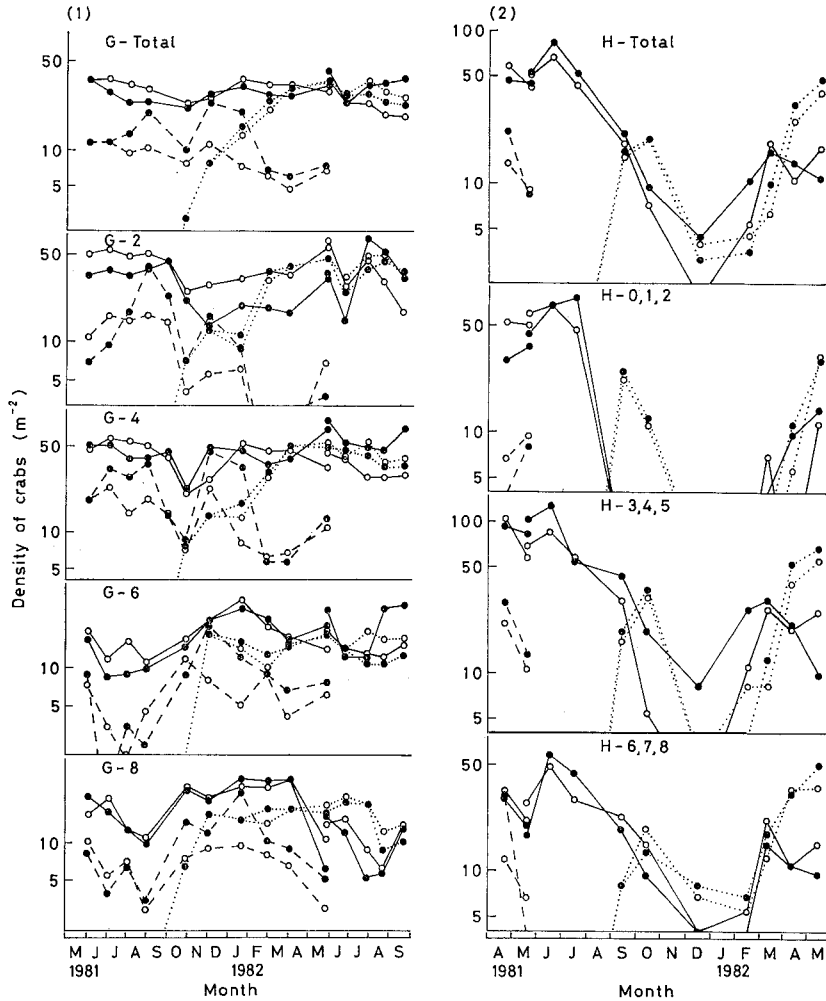


Fig. 12. (1) *Hemigrapsus sanguineus*. Temporal change of the density of each age group. Intertidal heights of sampling sections were lowered from G-2 to G-8. Dotted lines represent the 1981 generation, solid lines the 1980 generation, and dashed lines the older generations. Open circles represent males and solid circles females. (2) *Hemigrapsus penicillatus*. Temporal change of the density of each age group. Intertidal heights of sampling points were lowered from H-0 to H-8. Dotted lines represent the 1981 generation, solid lines the 1980 generation, and dashed lines the older generations. Open circles represent males and solid circles females.

of the new recruits increased rapidly from October 1981 to March 1982, and reached a peak in May 1982. Both age groups of the crabs born in 1980 and in and before 1979 were also generally more abundant at the upper sections. Their densities of each section showed seasonal changes, being high from spring to summer at the upper and from autumn to winter at the lower. The total density of the crabs born in 1980 showed a slight decrease from May 1981 to May 1982. Males and females showed a similar density change. Compared with this age group, the

total density of the crabs born in and before 1979 decreased more distinctly. The density of males decreased gradually from May 1981 to May 1982, whereas that of females varied monthly and was extraordinarily high in August, November 1981 and January 1982.

2-2. *Hemigrapsus penicillatus*.

The new recruits born in 1981 occurred at all sampling points in September 1981 (Fig. 12(2)). Although their total density reached a peak in October 1981, in December 1981 and February 1982 it was markedly lowered, and afterward it increased again until May 1982. The total density of the crabs born in and before 1980 decreased considerably from June to December 1981, and increased afterward until March 1982, returning nearly to the density recorded in September 1981. The decrease of crab density in winter was more rapid in the upper sampling points for both age groups. In each age group, males and females showed a similar density change.

2-3. *Gaeticte depressus*.

The density of new recruits usually increased rapidly from summer to autumn at all sampling sites (Fig. 13). Their density, however, was occasionally markedly

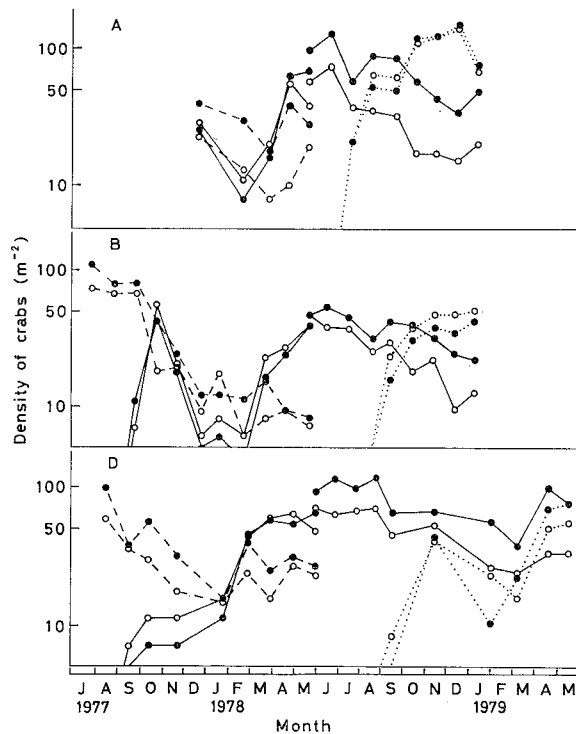


Fig. 13. *Gaeticte depressus*. Temporal change of the density of each age group at sampling sites of A, B and D. Dotted lines represent the 1978 generation, solid lines the 1977 generation, and dashed lines the older generations. Open circles represent males and solid circles females.

low from December to March of the following year, and afterward it increased again until May. After May, two size groups of the crabs born in and before the preceding year were combined into one group. Their density decreased gradually but the decrease rate was more or less different with years and with sampling sites. In each age group, males and females showed a similar density change.

2-4. *Acmaeopleura parvula*.

The new recruits born from autumn in 1981 to spring in 1982 began to occur in December 1981 at almost all sampling points of the intertidal zone, being most abundant in the middle sampling points (Fig. 14(1)). Their total density increased rapidly from December 1981 and reached a peak in March 1982. The density of the crabs born from autumn in 1980 to spring in 1981 was highest and most stable at the upper sampling points. Their total density fluctuated monthly but did not apparently decrease from March 1981 to April 1982. At the upper sampling points,

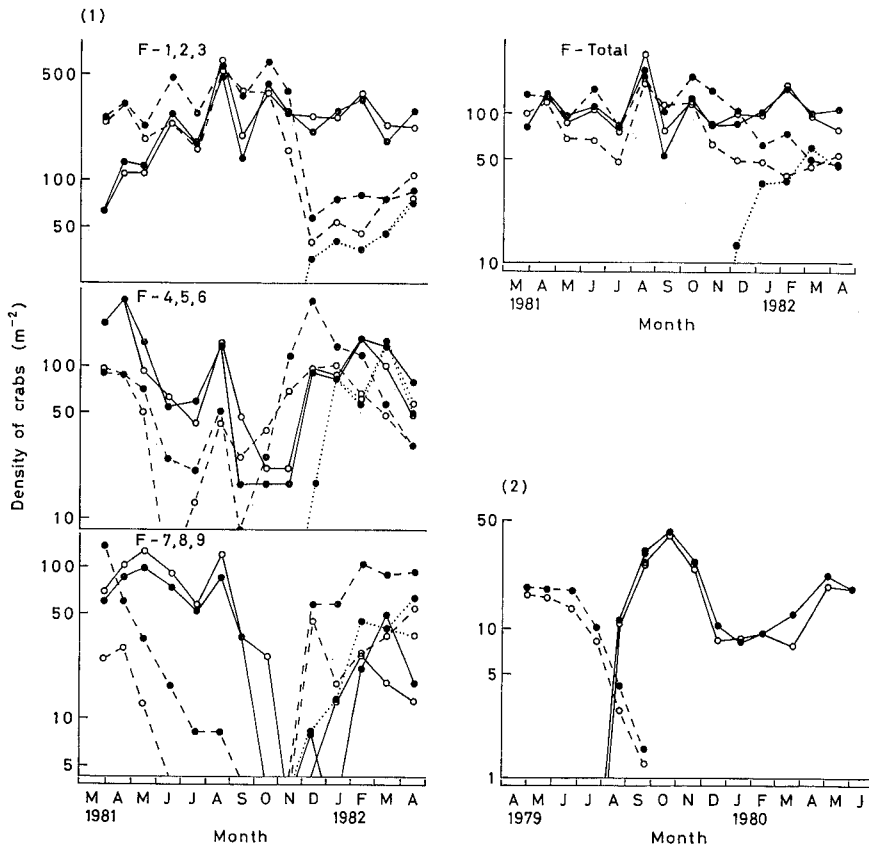


Fig. 14. (1) *Acmaeopleura parvula*. Temporal change of the density of each age group. Intertidal heights were lowered from F-1 to F-9. Dotted lines represent the 1982 generation, solid lines the 1981 generation, and dashed lines the older generations. Open circles represent males and solid circles females. (2) *Nanosesarma gordonii*. Temporal change of the density of each age group. Solid lines represent the 1979 generation and dashed lines the older generations. Open circles represent males and solid circles females.

the density of the crabs born before spring in 1980 was high and slightly increased from March to October 1981, but decreased rapidly in December 1981. At the lower sampling points, on the other hand, their density tended to be high from winter to spring and low from summer to autumn. Their total density decreased obviously from March 1981 to April 1982. In each age group, males and females showed a similar density change.

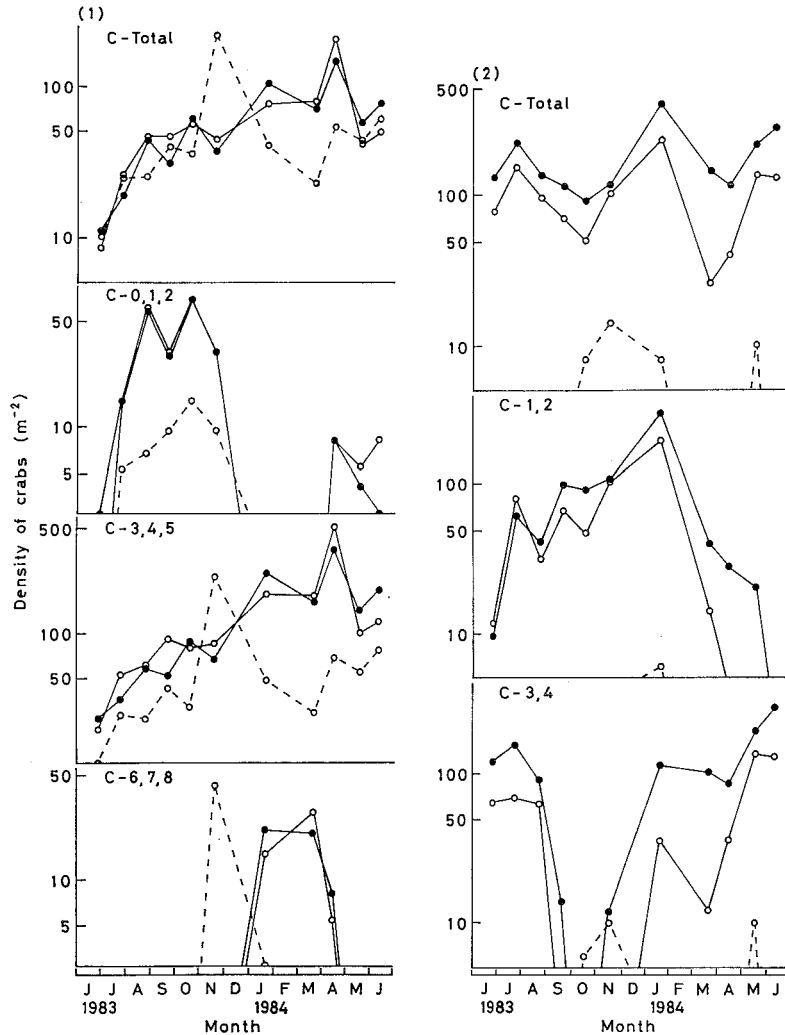


Fig. 15. (1) *Cyclograpsus intermedius*. Temporal change of the density. Intertidal heights were lowered from C-0 to C-8. Dashed lines represent the unsexable crabs (< CW 6 mm). Solid lines represent the sexable crabs (\geq CW 6 mm), and open circles represent males and solid circles females. (2) *Cyclograpsus* sp. Temporal change of the density. Intertidal heights were lowered from C-1 to C-4. Dashed lines represent the unsexable crabs (< CW 3 mm). Solid lines represent the sexable crabs (\geq CW 3 mm), and open circles represent males and solid circles females.

2-5. *Nanosesarma gordonii*.

The density of the new recruits born in 1979 increased rapidly from summer to autumn, and reached a peak in October 1979 (Fig. 14(2)). Their density decreased afterward, and remained low from December 1979 to March 1980. It increased again in April 1980, returning nearly to the density recorded in November 1979. The density of the crabs born in and before 1978 was nearly constant from April to June 1979, and afterward it decreased sharply until September 1979. In each age group, males and females showed a similar density change.

2-6. *Cyclograpsus intermedius*.

This species was collected from sampling points 0 to 9 of the upper to middle intertidal zone, but 87.5% of juveniles (<CW 6 mm), 84.2% of males and 84.1% of females were collected from sampling points 3 to 5 (Fig. 15(1)). The total density of juveniles fluctuated monthly, being lowest in June 1983 and highest in November 1983. The vertical distribution range of sexable crabs (>CW 6 mm) changed seasonally; they occurred from summer to autumn at the upper sampling points, and from winter to spring at the lower sampling points. Their total density tended to increase from June 1983 to June 1984. Males and females showed a similar density change.

2-7. *Cyclograpsus* sp.

This species was collected only at sampling points 1 to 4 of the upper intertidal zone. The density of juveniles (<CW 3 mm) was markedly low throughout the year, and any distinct peak of new recruits was not recognized (Fig. 15(2)). The total density of sexable crabs (>CW 3 mm) varied considerably with monthly sam-

Table 2. Estimate of annual survival rate. Survival rate was calculated from the slope of the regression line between time and the natural logarithm of density of the age group based on the monthly samplings.

		male		female	
		immature	mature	immature	mature
<i>Hemigrapsus sanguineus</i>	May 1981–May 1982	0.692	0.529	0.889	0.627
<i>Hemigrapsus penicillatus</i>	Jun 1981–May 1982		0.247		0.161
<i>Gaetice depressus</i>	Site A Jun 1978–Nov 1978		0.055		0.207
	Site B Jul 1977–May 1978		0.055		0.042
	Jun 1978–Nov 1978		0.160		0.402
	Site D Aug 1977–May 1978		0.464		0.310
	Jun 1978–May 1979		0.432		0.783
<i>Acmaeopleura parvula</i>	Apr 1981–Apr 1982	0.665	0.642	0.814	0.475
<i>Nanosesarma gordonii</i>	Jun 1979–Sep 1979		<0.001		<0.001
	Sep 1979–May 1980	0.424		0.392	

plings. Males and females showed a similar density change.

3. Survival rate.

Estimated survival rates were similar between the sexes within species, and the differences were not significant (ANCOVA, $p > 0.1$) (Table 2). Survival rates of immature crabs could be estimated only in *Hemigrapsus sanguineus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*. In *H. sanguineus* and *A. parvula*, survival rates of the mature crabs tended to be lower than those of the immature crabs, but the differences were not significant (ANCOVA, $p > 0.05$ for female *A. parvula*; $p > 0.5$ for *H. sanguineus* and male *A. parvula*). In *N. gordonii*, although the period for estimating survival rates was different between immature and mature crabs, survival rates of mature crabs were significantly lower than those of immature crabs (ANCOVA, $p < 0.005$). Among species, annual survival rate of immature crabs was relatively high in *H. sanguineus* and *A. parvula* (from 0.6 to 0.9) compared with *N. gordonii* (approximately 0.4). Annual survival rate of mature crabs was also highest in *H. sanguineus* and *A. parvula* (from 0.5 to 0.6), followed by *Gaetice depressus* and *Hemigrapsus penicillatus*, and it was lowest (less than 0.001) in *N. gordonii*.

4. Infestation of rhizocephalans

In *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus* and *Cyclograpsus intermedius*, some collected crabs were infested by rhizocephalans (*Sacculina* spp.). The crab with the externa of *Sacculina* in the abdomen was regarded as an infested individual. Infested crabs were collected nearly throughout the year, but the rate of infestation was mostly less than 1% in all species (Table 3). The rate of infestation showed slight seasonal changes, being relatively high in autumn in *H. sanguineus*, *G. depressus* and *C. intermedius*. The size of infested crabs ranged from CW 7.9 to 27.0 mm for *H. sanguineus*, from CW 12.1 to 17.6 mm for *H. penicillatus*, from CW 8.0 to 18.1 mm for *G. depressus*, and from CW 15.4 to 26.8 mm for *C. intermedius*.

Table 3. Percentage of the crabs infested by *Sacculina*. —: Infested crab was not collected.

		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>Hemigrapsus sanguineus</i>	1981					—	0.3	0.2	0.1	1.1	1.4	0.1	
	1982	0.1	—	0.1		0.4	0.1	0.4	0.1	0.6			
<i>Hemigrapsus penicillatus</i>	1981				0.6	0.4	0.3	—		—	—		—
	1982	—	2.0	—	0.6	0.4							
<i>Gaetice depressus</i>	Site A												0.6
	1977												
	1978		—	—	—	0.3	—	—	0.3	0.6	1.4	0.9	0.6
	1979	—											
	Site B							—	—	0.7	0.4	—	—
	1977												
	1978	—	—	—	—	0.3	—	0.4	1.0	1.3	0.6	0.2	—
	1979	0.3											
<i>Cyclograpsus intermedius</i>	1983						—	—	0.4	1.3	0.7	—	
	1984	0.5		0.3	0.5	0.4	0.6						

Both males and females were found to be infested.

5. Molting.

5-1. Molt increment.

In *Hemigrapsus sanguineus* and *Hemigrapsus penicillatus*, the records of molt increments was too few to show the relationship between molt increment and body size, though the values of *H. penicillatus* were similar to those of *Gaetice depressus* (Fig. 16). In the immature crabs of *G. depressus*, percentage molt increment was not correlated with premolt carapace width (correlation coefficient, $p > 0.1$), and mean percentage increment was not significantly different between the sexes (t-test, $p > 0.5$, mean value: 24.5% for males and 23.4% for females). In the mature crabs of *G. depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*, log percentage molt increment decreased linearly with the premolt carapace width (correlation coefficient, $p < 0.05$). In *G. depressus*, the slope of the regression line was significantly smaller in females than in males (ANCOVA, $p < 0.05$). In *A. parvula* and *N. gordonii*, percentage molt increment for the same body size tended to be smaller in females than in males, but neither the slope nor the elevation was significantly different between the sexes (ANCOVA, $p > 0.1$).

5-2. Intermolt period.

In *Hemigrapsus sanguineus*, 12 crabs (CW 26.1 to 34.9 mm for males and CW

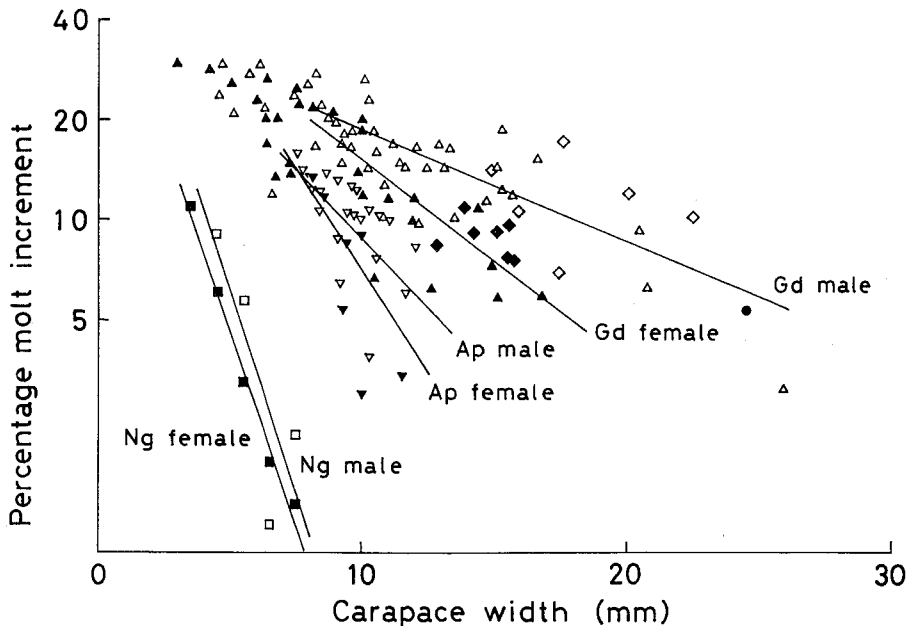


Fig. 16. Percentage molt increment on log scale plotted against carapace width. Circles represent *Hemigrapsus sanguineus*, slanting squares *Hemigrapsus penicillatus*, triangles *Gaetice depressus* (Gd), inverted triangles *Acmaeopleura parvula* (Ap), and squares *Nanosesarma gordonii* (Ng). Open symbols represent males and solid symbols females.

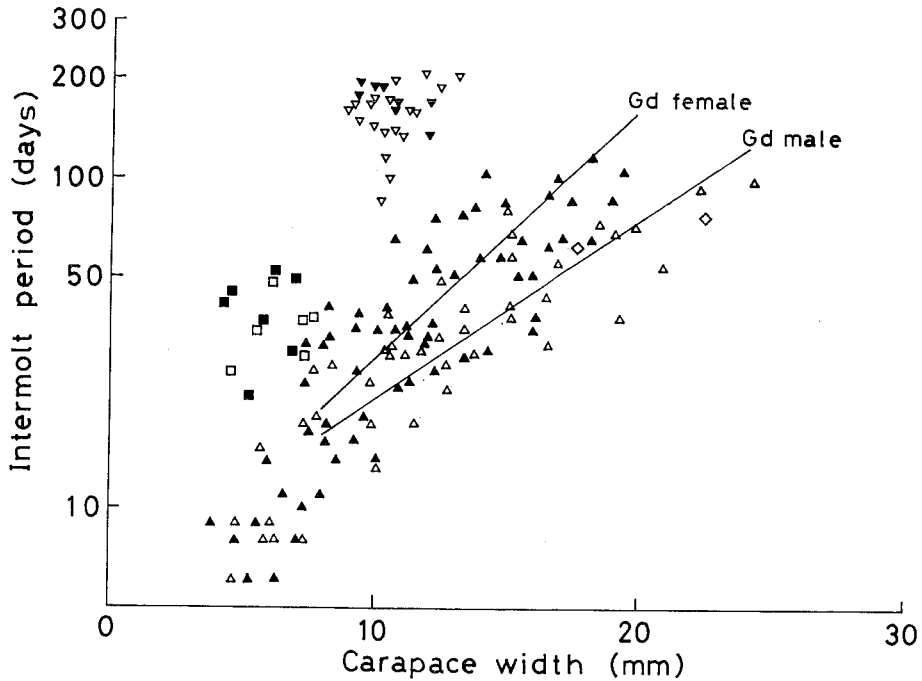


Fig. 17. Intermolt period on log scale plotted against carapace width. Legend as in Fig. 16.

27.2 to 32.1 mm for females) of 20 crabs reared did not molt during the laboratory rearing, which shows that their intermolt periods were more than 200 days. In *Hemigrapsus penicillatus*, only few data were obtained, since molt crabs were often cannibalized. The intermolt period of *Gaeticus depressus* ranged from 6 to 98 days for males (CW 4.7 to 28.3 mm) and from 4 to 117 days for females (CW 3.9 to 20.6 mm) (Fig. 17). In the immature crabs of *G. depressus*, the correlation between log intermolt period and carapace width was not significant (correlation coefficient, $p > 0.1$), and mean intermolt period was not significantly different between the sexes (t-test, $p > 0.1$, mean value: 9.2 days for males and 8.3 days for females). In the mature crabs of *G. depressus*, log intermolt period increased linearly with carapace width (correlation coefficient, $p < 0.01$ for males and females). The slope of the regression line was slightly larger in females than in males but the difference was not significant (ANCOVA, $0.05 < p < 0.1$). Since the elevation of the regression line was significantly larger in females than in males (ANCOVA, $p < 0.05$), the intermolt period of females tended to be longer than that of similar-sized males. The intermolt period of *Acmaeopleura parvula* ranged from 86 to 211 days for males (CW 8.0 to 13.2 mm) and from 136 to 197 days for females (CW 7.4 to 13.1 mm). It was much longer than that of similar-sized *G. depressus*. The intermolt period of *Nanosesarma gordonii* ranged from 26 to 49 days for males (CW 4.6 to 7.4 mm) and from 22 to 53 days for females (CW 4.3 to 7.0 mm). It was also longer than that of similar-sized *G. depressus*. In the mature crabs of *A. parvula* and *N. gordonii*, the correlation between log inter-

molt period and premolt carapace width was not significant (correlation coefficient, $p > 0.1$). Their mean intermolt period was longer in females than in males, but the differences were not significant (t-test, $p > 0.1$, mean value: *A. parvula*, 158.2 days for males and 174.4 days for females, *N. gordonii*, 35.7 days for males and 39.9 days for females).

6. Reproduction.

6-1. Breeding season.

In this paper, the period when ovigerous females occur is regarded as breeding season. The percentage of ovigerous females in each species showed similar seasonal

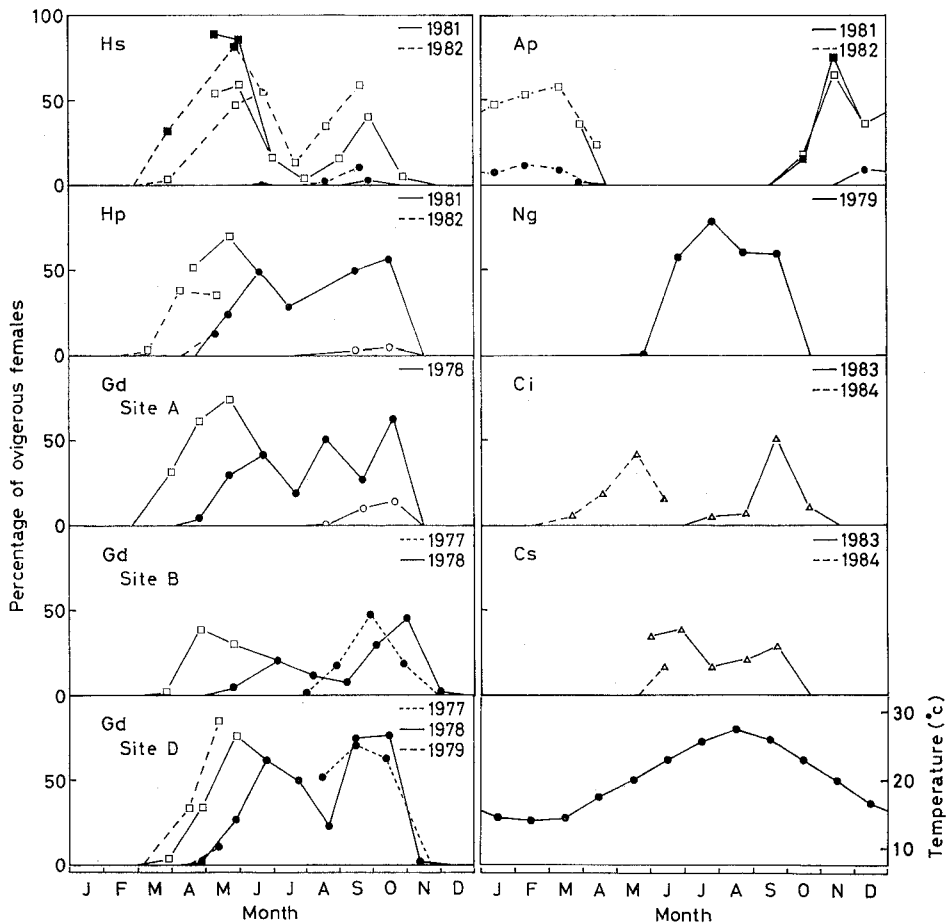


Fig. 18. Seasonal change in percent ovigerous females. Open circles represent 0+ year group, solid circles 1+ year group, open squares 2+ year group, and solid squares 3+ year group. Triangles represent the mature-sized groups for *Cyclograpsus intermedius* and *Cyclograpsus* sp. Seasonal change in surface water temperature measured in Tanabe Bay (Wakayama Prefecture Fishery and Culture Station, 1984) is also shown. Hs: *Hemigrapsus sanguineus* Hp: *Hemigrapsus penicillatus* Gd: *Gaeticia depressus* Ap: *Acmaeopleura parvula* Ng: *Nanosesarma gordonii* Ci: *Cyclograpsus intermedius* Cs: *Cyclograpsus* sp.

changes between years and between stations (Fig. 18). The breeding season of the 7 species studied was classified into 3 groups: spring to autumn breeding, summer breeding, and autumn to spring breeding. *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus* and *Cyclograpsus intermedius* belonged to the spring to autumn breeding group; their breeding period lasted about 8 months from March to October or November. The percentage of the ovigerous females showed similar seasonal changes among species, with two peaks from May to June and from September to October. *Nanosarma gordonii* and *Cyclograpsus* sp. belonged to the summer breeding group; their breeding period lasted about 4 months from late May to late September. The seasonal change in percentage of ovigerous females showed a peak in July in *N. gordonii*, whereas it showed two peaks in June and September in *Cyclograpsus* sp. *Acmaeopleura parvula* belonged to the autumn to spring breeding group; its breeding period lasted about 6 months from mid-October to mid-April. The ovigerous females appeared in high percentage in November and March.

6-2. Age at maturity.

In the 5 species of *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula* and *Nanosarma gordonii*, age at maturity was estimated from the seasonal change in percentage of ovigerous females for each age group (Fig. 18). In *H. sanguineus*, the percentage of ovigerous females in the monthly samplings was less than 15% for the age group having overwintered once (1+ year group). About 50% females were ovigerous in April to June for the age group having overwintered twice (2+ year group). The age group having overwintered at least three times (3+ year group) showed higher percentages of ovigerous females than 2+ year group, and more than 80% females were ovigerous in April and May. In *H. penicillatus* and *G. depressus*, ovigerous females were less than 15% for the age group having not overwintered (0+ year group). About 50% females were ovigerous in June for the age group having overwintered once (1+ year group). The age group having overwintered at least twice (2+ year group) began to breed in March and showed higher percentages of ovigerous females than 1+ year group, and about 70% females were ovigerous in May. In *A. parvula*, the percentage of ovigerous females was about 10% before their second summer (1+ year group), and after the following October (2+ year group) the value reached about 50%. In *N. gordonii*, female crabs began to breed from late May after their first winter (1+ year group). About 80% females were ovigerous in June.

Mean age at maturity in female of each species was calculated from the period between the mean birth month of an age group and the month when about 50% of females became ovigerous. It was 11 months old, i.e. about 1 year old, for *H. penicillatus*, *G. depressus* and *N. gordonii*, and 22 months old, i.e. about 2 years old, for *H. sanguineus* and *A. parvula*. In the 2 species of *Cyclograpsus intermedius* and *Cyclograpsus* sp., age at maturity could not be determined.

6-3. Size at maturity.

In this paper, the minimum body size of ovigerous individuals is regarded as

the size at maturity of females. From the field samples (Figs 2, 3, 5, 7, 8, 10 & 11), the size at maturity of females was as follows: CW 14.0 mm for *Hemigrapsus sanguineus*, CW 6.4 mm for *Hemigrapsus penicillatus*, CW 7.2 mm for *Gaetice depressus*, CW 5.0 mm for *Acmaeopleura parvula*, CW 3.5 mm for *Nanosesarma gordonii*, CW 11.0 mm for *Cyclograpsus intermedius*, and CW 5.5 mm for *Cyclograpsus* sp.

6-4. Incubation period.

Within each species of *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*, incubation period showed a little variation at a given water temperature, but shortened obviously with rising temperature (Fig. 19(1)). Log incubation period was significantly linearly related to log water temperature (correlation coefficient, $p < 0.001$ for all species) (Table 4). Although the range of water temperature during the breeding season was different between *A. parvula* and the other 4 species, both the slope and the elevation of the regression lines were similar among species.

6-5. The number of broods per year and per month.

Estimated number of broods per year was different with age groups (Table 5). The age groups younger than mean age at maturity showed less than one brood per year. In *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus* and *Gaetice depressus*, since

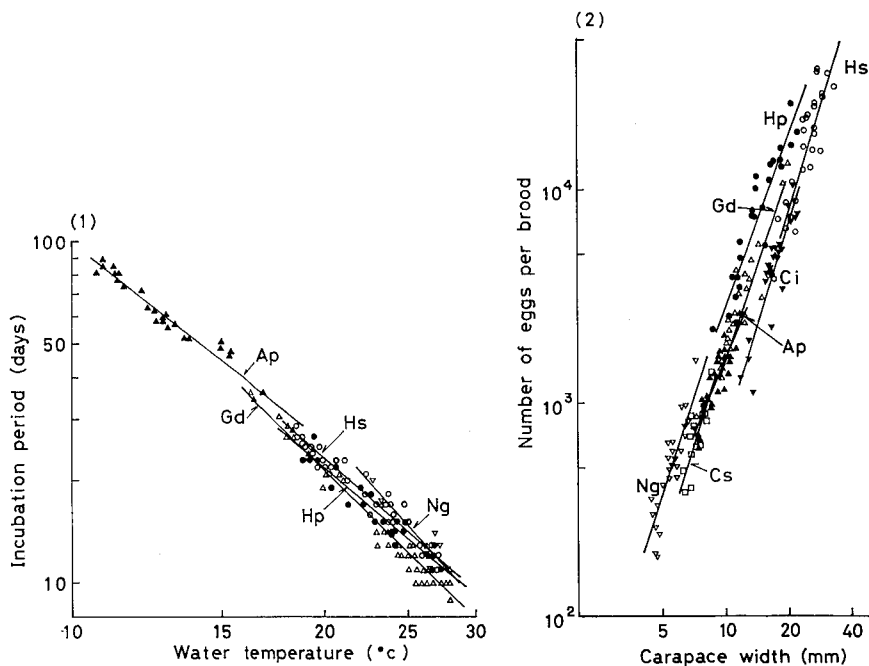


Fig. 19. (1) Incubation period versus water temperature. (2) Number of eggs per brood versus carapace width on both log scales. Open circles represent *Hemigrapsus sanguineus*, solid circles *Hemigrapsus penicillatus*, open triangles *Gaetice depressus*, solid triangles *Acmaeopleura parvula*, and open inverted triangles *Nanosesarma gordonii*. Abbreviations of species name as in Fig. 18.

Table 4. The relationship between incubation period and water temperature. X =log mean water temperature ($^{\circ}\text{C}$); Y =log incubation period (day); n =sample size; r = regression coefficient.

	equation	n	r
<i>Hemigrapsus sanguineus</i>	$Y = -2.14 X + 4.15$	44	-0.974
<i>Hemigrapsus penicillatus</i>	$Y = -2.08 X + 4.04$	30	-0.967
<i>Gaetice depressus</i>	$Y = -2.44 X + 4.50$	53	-0.978
<i>Acmaeopleura parvula</i>	$Y = -1.97 X + 3.97$	26	-0.979
<i>Nanosesarma gordonii</i>	$Y = -2.73 X + 4.98$	13	-0.901
total	$Y = -2.28 X + 4.31$	166	-0.988

Table 5. Estimated number of broods per year and per month.

		Number of broods per year					Number of broods per month
		0+	1+	2+	3+	Mean	
<i>Hemigrapsus sanguineus</i>		0	0.30	4.51	5.48	5.00	0.63
<i>Hemigrapsus penicillatus</i>		0.16	5.39	6.61	—	6.00	0.74
<i>Gaetice depressus</i>	Site A	0.62	5.43	6.89	—		
	Site B	0.00	2.83	3.62	—		
	Site D	0.03	7.26	8.36	—		
	Mean	0.22	5.17	6.28	—	5.73	0.72
<i>Acmaeopleura parvula</i>		0	0.24	2.49	2.58	2.54	0.43
<i>Nanosesarma gordonii</i>		0	5.74	—	—	5.74	1.43
<i>Cyclograpsus intermedius</i>						2.88	0.36
<i>Cyclograpsus</i> sp.						2.93	0.73

females of mean age at maturity started to lay eggs from the middle month of breeding season, their number of broods per year was smaller than that of the older groups by about one. Mean number of broods per year of each species was calculated from the two values of the group of mean age at maturity and the older group. It ranged from 2.54 for *Acmaeopleura parvula* to 5.74 for *Nanosesarma gordonii*. *H. sanguineus*, *H. penicillatus*, *G. depressus* and *N. gordonii* had 5 to 6 broods per year, whereas *A. parvula*, *Cyclograpsus intermedius* and *Cyclograpsus* sp. had 2 to 3 broods per year. The frequency of laying broods per month was calculated by dividing the number of broods per year by the period (month) of breeding season. Mean number of broods per month varied considerably among species, ranging from 0.36 for *C. intermedius* to 1.43 for *N. gordonii* (Table 5).

6-6. Egg size.

Within a species, egg size at a given developmental stage showed little variation within or among broods. All eggs of a brood were at the same developmental stage. The mean egg volume of Stage I ranged from $9.8 \times 10^{-3} \text{ mm}^3$ for *Nanosesarma gordonii* to $3.73 \times 10^{-2} \text{ mm}^3$ for *Cyclograpsus intermedius* (Table 6). Egg volume increased during

Table 6. Egg volume (mm³).

	Stage I			Stage IV			IV/I
	Mean	SD	(n)	Mean	SD	(n)	
<i>Hemigrapsus sanguineus</i>	0.0155	0.0019	(6)	0.0240	0.0018	(4)	1.55
<i>Hemigrapsus penicillatus</i>	0.0106	0.0019	(14)	0.0174	0.0014	(8)	1.65
<i>Gaetice depressus</i>	0.0144	0.0019	(16)	0.0253	0.0038	(11)	1.76
<i>Acmaeopleura parvula</i>	0.0188	0.0017	(10)	0.0345	0.0038	(11)	1.84
<i>Nanosarma gordonii</i>	0.0098	0.0006	(13)	0.0162	0.0010	(11)	1.65
<i>Cyclograpsus intermedius</i>	0.0373	0.0041	(14)	0.0622	0.0072	(8)	1.67
<i>Cyclograpsus</i> sp.	0.0160	0.0014	(8)	0.0264	0.0023	(7)	1.65

Table 7. Comparison of egg volume at Stage I data from Table 6 using t-test. Abbreviations of species name as in Fig. 18. ns: not significant; **: p<0.01.

	Ci	Ap	Cs	Hs	Gd	Hp
Ap	**					
Cs	**	ns				
Hs	**	ns	ns			
Gd	**	**	ns	ns		
Hp	**	**	**	**	**	
Ng	**	**	**	**	**	ns

embryonic development, and the increase in volume from Stage I to Stage IV ranged from 55% for *Hemigrapsus sanguineus* to 84% for *Acmaeopleura parvula*. The order of egg size among the 7 species was the same at Stage I and IV, except between *H. sanguineus* and *Gaetice depressus*. At Stage I, egg volume was largest in *C. intermedius*, followed in order by *A. parvula*, *Cyclograpsus* sp., *H. sanguineus*, *G. depressus*, *Hemigrapsus penicillatus* and *N. gordonii* (Tables 6 & 7).

6-7. The number of eggs per brood.

The number of eggs per brood ranged from about 190 for small *Cyclograpsus* sp. to about 56000 for large *Hemigrapsus sanguineus*. Log egg number per brood was

Table 8. The number of eggs per brood. X=log carapace width (mm); Y=log egg number per brood; n=sample size; r=regression coefficient.

	equation	n	r
<i>Hemigrapsus sanguineus</i>	Y=3.20 X-0.255	30	0.930
<i>Hemigrapsus penicillatus</i>	Y=2.63 X+0.832	26	0.943
<i>Gaetice depressus</i>	Y=2.93 X+0.271	30	0.877
<i>Acmaeopleura parvula</i>	Y=2.41 X+0.813	29	0.869
<i>Nanosarma gordonii</i>	Y=2.99 X+0.480	30	0.862
<i>Cyclograpsus intermedius</i>	Y=3.17 X-0.275	25	0.909
<i>Cyclograpsus</i> sp.	Y=3.10 X+0.168	13	0.816

linearly related to log female carapace width for all species (Fig. 19(2), Table 8). The slope of the regression line ranged from 2.41 to 3.20, but was not significantly different between species (ANCOVA, $p > 0.05$). In contrast, the elevation was different between some pairs of species, from which the 7 species were classified into 3 groups: *Hemigrapsus penicillatus* and *Nanosesarma gordonii*; *Gaetice depressus*, *Acmaeopleura parvula* and *C. sp.*; and *H. sanguineus* and *Cyclograpsus intermedius*. Within each group, the elevation was not significantly different between species (ANCOVA, $p > 0.1$), but between groups it decreased significantly in the above order (ANCOVA, $p < 0.05$). The number of eggs per brood of the mean sized ovigerous female was treated as the mean number of eggs per brood of each species, which was largest in *H. sanguineus*, followed in order by *H. penicillatus*, *C. intermedius*, *G. depressus*, *A. parvula*, *C. sp.* and *N. gordonii*.

6-8. The ratio of brood weight per body weight and brood index.

Within a species, the ratio of brood weight per body weight was not significantly correlated with the body size (correlation coefficient, $p > 0.05$ for *Gaetice depressus* and $p > 0.1$ for the other species) (Fig. 20). The mean value ranged from 7.4% to 17.0% (Table 9). It was highest in *Nanosesarma gordonii*, followed in order by *Hemigrapsus penicillatus*, *Cyclograpsus sp.*, *Acmaeopleura parvula*, *G. depressus*, *Cyclograpsus intermedius* and *Hemigrapsus sanguineus* (Tables 9 & 10). "Brood index" which is defined as the

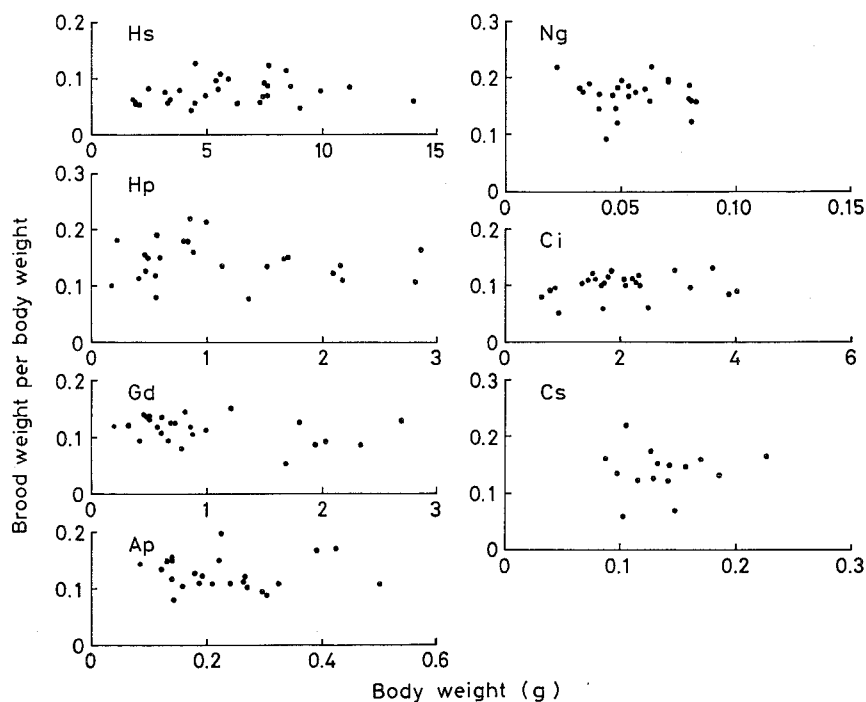


Fig. 20. The ratio of brood weight per body weight versus body weight. Abbreviations of species name as in Fig. 18.

Table 9. The ratio of brood weight per body weight and brood index.

	The ratio of brood weight per body weight			Brood index
	Mean	SD	n	
<i>Hemigrapsus sanguineus</i>	0.074	0.023	30	0.37
<i>Hemigrapsus penicillatus</i>	0.140	0.038	26	0.84
<i>Gaetice depressus</i>	0.114	0.023	25	0.65
<i>Acmaeopleura parvula</i>	0.123	0.028	25	0.31
<i>Nanosesarma gordonii</i>	0.170	0.029	25	0.98
<i>Cyclograpsus intermedius</i>	0.100	0.021	25	0.29
<i>Cyclograpsus</i> sp.	0.138	0.039	15	0.40

Table 10. Comparison of the ratio of brood weight per body weight data from Table 9 using t-test. Abbreviations of species name as in Fig. 18. ns: not significant; *: $p < 0.05$; **: $p < 0.01$

	Ng	Hp	Cs	Ap	Gd	Ci
Hp	**					
Cs	**	ns				
Ap	**	ns	ns			
Gd	**	**	*	ns		
Ci	**	**	**	**	*	
Hs	**	**	**	**	**	**

total annual brood weight per body weight (Graham & Branch, 1985) was calculated by multiplying the ratio of brood weight per body weight by the number of broods per year. Brood index was highest in *N. gordonii*, followed in order by *H. penicillatus*, *G. depressus*, *C. sp.*, *H. sanguineus*, *A. parvula* and *C. intermedius* (Table 9).

Discussion

1) Growth.

Crustaceans have an inextensible exoskeleton and grow through successive molts. The growth rate through molting is determined by two factors, molt increment and intermolt period. In this section, on the basis of the relationships between molting factors and body size obtained from the laboratory rearing and of the growth rate estimated from the field data, I discuss the general feature of growth curve in the grapsid crabs, the differences in growth rate between males and females within a species, and the differences in growth rate among species.

Within a species, the percentage molt increment tends to be nearly constant before maturity in some brachyuran crabs (Suzuki, 1981, Hartnoll, 1982). In this study, the molting of immature crabs was investigated only for *Gaetice depressus*, in which the percentage molt increment was not correlated with body size. According to my calculation of the data from Kurata (1962), *Hemigrapsus sanguineus* shows

nearly constant percentage molt increment before maturity. After maturity, the percentage molt increment generally decreases with size (Broekhuysen, 1941; Hiatt, 1948; Warner, 1967; Bennett, 1974), and significant negative correlation has been found between log percentage molt increment and premolt carapace width in some brachyuran crabs, including *H. sanguineus* (Hartnoll, 1982). Such a negative correlation has been obtained for the mature crabs of *G. depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*. On the other hand, the intermolt period generally lengthens with body size within a species, and the positive correlation between log intermolt period and the body size has been found in some brachyuran crabs, including *H. sanguineus* (Kurata, 1962; Hartnoll, 1982). In this study, log intermolt period increased significantly with carapace width in the mature crabs of *G. depressus*.

The relationships of two molting factors and body size indicates that growth rate in carapace width decreases with age in the grapsid crabs. Mean growth rate estimated from the field data was higher in immature crabs than in mature crabs in males and females of *Hemigrapsus sanguineus*, *Acmaeopleura parvula* and *Nanosesarma gordonii* and in females of *Gaetice depressus*, which supports that their growth rate decreases with age.

The growth rate of immature crabs estimated from the field data was similar between males and females in *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii* (Table 1). In *G. depressus*, both molt increment and intermolt period of immature crabs were also similar between males and females (Figs 16 & 17). After maturity, however, the growth rate estimated from the field data was apparently lower in females than in males in *H. penicillatus* and *G. depressus*. The difference between the sexes was significant in *G. depressus*, in which females showed smaller molt increment and longer intermolt periods than males. Some reasons for such sexual differences in growth have previously been indicated. Since the ovary is much larger than the testis in brachyuran crabs (Pillay & Nair, 1971; Yamaguchi & Takamatsu, 1980), the production of large amount of reproductive matter in females seems to result in the low energy investment into growth. In addition, since moltings are inhibited by hormonal effect during egg brooding (Adiyodi & Adiyodi, 1970), the intermolt period of mature females may become longer than that of mature males. Nevertheless the results of this study showed that the degree of sexual differences in growth varied with species.

Among species, the percentage molt increment seems to be related to the mean body size of the species (=mean carapace width of ovigerous females). The percentage molt increment of early juvenile crabs is similar among species in grapsid crabs; it was from 17.4 to 30.0% (calculated from the data of Hiatt, 1948; Kurata, 1962, 1968; Muraoka, 1963; Suzuki, 1981; and Fig. 16). The size at maturity tends to increase with the mean body size of the species. The percentage molt increment of mature crabs decreases more slowly with carapace width as the mean body size of the species becomes large. Consequently, at a given body size, the larger species tends to have larger percentage molt increment. However, the growth rate estimated from the field data was not correlated with the mean body size among species (Fig.

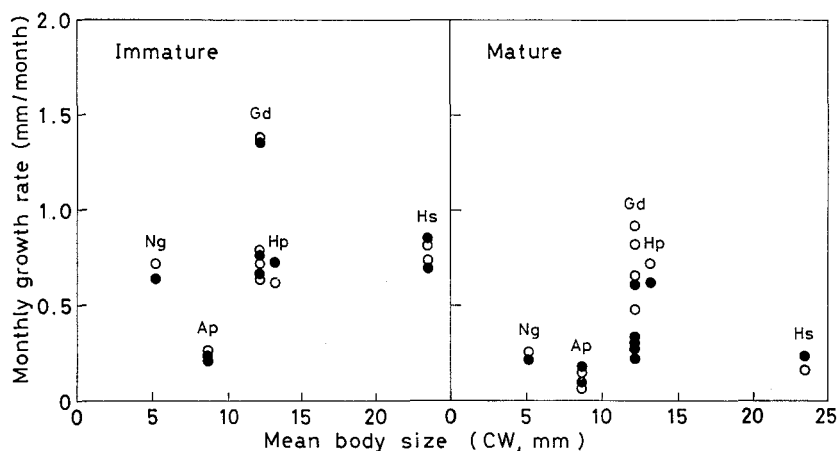


Fig. 21. The relationship between growth rate and mean body size of the species. Open circles represent males and solid circles females. Abbreviations of species name as in Fig. 18.

21). The interspecific differences in growth rate seem to be more greatly influenced by those in intermolt period than by those in molt increment. *Acmaeopleura parvula* had much longer intermolt periods and smaller growth rates than *Gaetice depressus* and *Nanosesarma gordonii*. The intermolt period did not show a distinct relationship to the body size of the species. The factors determining the interspecific differences in intermolt period have not been made clear, but they may include seasonal periodicity of molting which is considerably influenced by the susceptibility to temperature and the reproductive cycle of the species (Conan, 1985). It was confirmed through laboratory observation that the mature crabs of *G. depressus* molted almost all the year round including the breeding season though their molt frequency tended to decrease in winter, whereas the mature crabs of *A. parvula* molted in the two restricted periods of autumn and spring.

2) Survivorship.

There are numerous mortality factors for grapsid crabs after settlement. Birds, fishes and crabs have been recorded to prey upon grapsid crabs occasionally (Hiatt, 1948; Williason, 1981; Abele et al., 1986). However, I have never observed predation in the field. It is probably because the surveys were carried out mainly at daytime low tides, when the present crabs were mostly inactive under or within the cobbles and boulders.

Infestation of rhizocephalans (*Sacculina* spp.) was found in *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus* and *Cyclograpsus intermedius*. The crabs infested by *Sacculina* not only cease to molt or rarely molt, but lose the ability of reproduction owing to parasitic castration (Overstreet, 1983). Hiraiwa (1924) has recorded that in a species of grapsid crabs, *Pachygrapsus crassipes*, 42 of 80 individuals (52.5%) were infested in Misaki, Japan. In contrast, no infested *P. crassipes* was found among 150

individuals collected at Monterey, California (Hiatt, 1948). The influence of rhizocephalans on grapsid crabs, therefore, seems to vary considerably with locations. In this study, the percentage of infested crabs was mostly less than 1% for all the 7 species, which shows that the crab populations in Shirahama suffered little or no damage from rhizocephalans.

Loss of the refuges may heighten the mortality of the crabs. The present grapsid crabs utilize the spaces under or among the cobbles and boulders and the small concavities on the boulder as their refuges. These areas would provide protection from heat and desiccation at low tide and from predators. In the Shirahama shore exposed to the open sea, the surface cobbles and boulders may be covered with sand or moved around under the influence of strong wave, especially by typhoons in autumn and atmospheric depressions in winter. Those substrate disturbances may directly kill the crabs, or may indirectly heighten the mortality of the crabs through reducing the refuges suitable for them. During the present study, some parts of the cobble shore at Site B were covered with sand from autumn to winter in 1977, and the density of *Gaeticte depressus* decreased rapidly coincidentally at this sampling site (Fig. 13). Fukui & Wada (1986) have suggested that in the estuarine environment the surface cobble movements caused by swift currents at the heavy rainfall heighten the mortality of the crabs.

Besides these extrinsic mortality factors, it is possible that growth and reproductive activity have some influences on survivorship. Growing through a succession of molts involves danger. Crabs may possibly fail in molting or, if molting successfully, the soft body after molting may be easily injured by environmental stress and predators. In addition, increase in growth rate needs more feeding activities outside the refuge, which may increase the risk of being preyed upon. However, the apparent trade-off relationship between growth rate and survival rate was not recognized among species (Fig. 22). In males of *Gaeticte depressus*, high growth rates tended to lower survival rates. On the other hand, the following results suggest that the

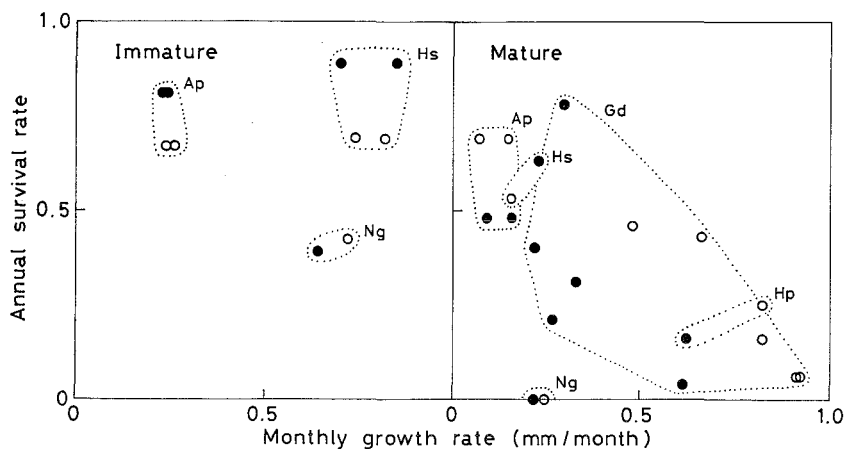


Fig. 22. The relationship between growth rate and survival rate. Legend as in Fig. 21.

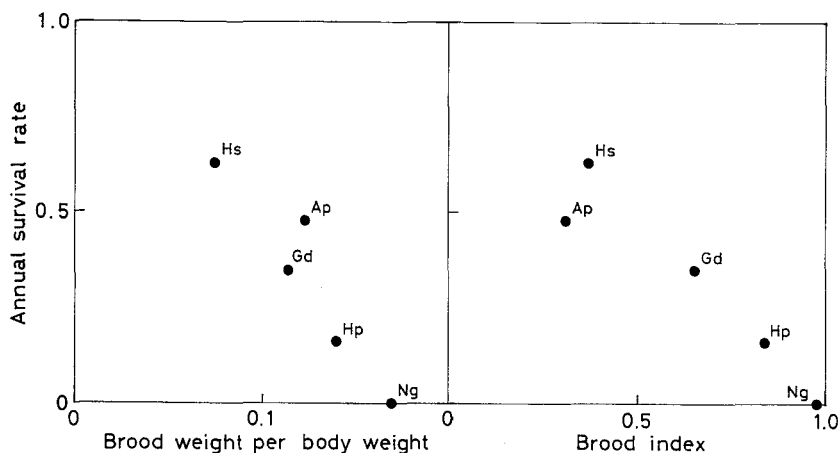


Fig. 23. The relationship between survival rate of mature females and the indices of reproductive effort. Abbreviations of species name as in Fig. 18.

reproductive activity reduces the survival rate in mature period. The estimated survival rates tended to be lower in the mature period than in the immature period in *Hemigrapsus sanguineus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*. The density of mature crabs began to decrease sharply after the beginning of their breeding seasons particularly in *A. parvula* and *N. gordonii*. Furthermore, the estimated survival rates of mature crabs tended to be negatively correlated with the indices of reproductive activity, such as the ratio of brood weight per body weight and brood index (correlation coefficient, $p < 0.05$) (Fig. 23). Although brood index may be proper as a measure of reproductive effort of females, it does not apply to males. Since, as previously stated, the testis is much smaller than the ovary in brachyuran crabs, production of male reproductive matter should not greatly influence the survival rate of mature males. Nevertheless there were no significant differences in survival rate between the sexes. In males, other forms of energy cost or behavioral constraints may be in counterpoise to the effect of female reproductive effort on their survivorship. For example, chelipeds grow larger proportionally in mature males than in mature females in many brachyuran crabs (Teissier, 1960; Seiple & Salmon, 1987). Fight between mature males for a female as a copulation partner has been observed in some grapsid crabs (Wright, 1966). Furthermore, a large amount of energy may be allocated to territorial defense, burrow maintenance and courtship behavior by males (Warner, 1975; Seiple & Salmon, 1982; Christy, 1983; Salmon, 1984).

3) Reproduction.

Within a species, egg size was constant regardless of body size of female parent crabs in all 7 species. In crustaceans, intraspecific variation in egg size occurs with respect to latitude (Barns & Barns, 1965; Efford, 1969; Nishino, 1980), with respect to season (Diaz, 1980), and between marine and estuarine shores (Nelson, 1980), but no significant correlation between egg size and parent body size has been re-

ported. It has been shown theoretically that the expected value of offspring number per parent is maximized when egg size is constant regardless of parent body size, assuming that survival rate of an egg depends only on egg size (Iwasa, 1981).

The ratio of brood weight per body weight was also constant regardless of parent body size in each of all 7 species. Hines (1982) has shown that the brood volume is primarily determined by the body cavity volume in brachyuran crabs. In addition, the habit of brood-bearing in the abdomen of female crabs seems to limit the brood volume. The brood volume, as well as each part of the body structure, may be under the control of relative growth.

The number of eggs per brood was, in all the 7 species examined, nearly proportional to the third power of carapace width. Such correlation has been observed widely in brachyuran crabs (Hines, 1982). Considering that body weight is generally nearly proportional to the third power of body length, it is suggested that the correlation between the number of eggs per brood and body size results from invariability in both egg size and the ratio of brood weight per body weight within a species.

Among the 7 species, egg size showed some differences, but was not correlated with the mean body size of the species (Kendall's τ , $p > 0.5$) (Fig. 24). Although the interspecific correlation between egg size and mean body size has been found in various crustacean groups such as cladocerans, mysids, amphipods, brachyuran crabs and stomatopods (Mauchline, 1973; Reaka, 1979; Lynch, 1980; Nelson, 1980; Hines, 1982), egg size has considerable variations among similar-sized species in all the groups. It has been indicated that habitat environments have some influences on the evolution of egg size in crustaceans (Shokita, 1979; Thurman II, 1985). *Cyclograpsus intermedius* had by far the largest eggs of the 7 species studied. Its habitat after settlement is the upper intertidal zone and is similar to those of *Acmaeopleura parvula* and *Cyclograpsus* sp., and body size of new recruits is also similar among these species. The large egg size of *C. intermedius*, therefore, does not seem to be related to habitat conditions after settlement. Egg size may be related to the habitat environment at the larval stage, and this possibility has been indicated for some crustaceans (Shokita, 1979), but information on larval life of the present grapsid crabs is lacking.

The mean number of eggs per brood was correlated with the mean body size of the species among the 7 species (Kendall's τ , $p < 0.05$) (Fig. 24). The interspecific correlation between egg number and mean body size of the species is common in crustacean groups such as cladocerans, mysids, cumaceans, amphipods, brachyuran crabs and stomatopods (Mauchline, 1973; Reaka, 1979; Lynch, 1980; Nelson, 1980; Corey, 1981; Hines, 1982). This is probably because both egg size and the ratio of brood weight per body weight are relatively similar among species of each group. Nevertheless egg size and the ratio of brood weight per body weight had some variations among species in the present crabs, which led to the differences in the number of eggs per brood of the same-sized females. The species with small eggs and/or large ratio of brood weight per body weight (*Hemigrapsus penicillatus* and *Nanosesarma gordonii*) had approximately three times as many eggs per body size as the species

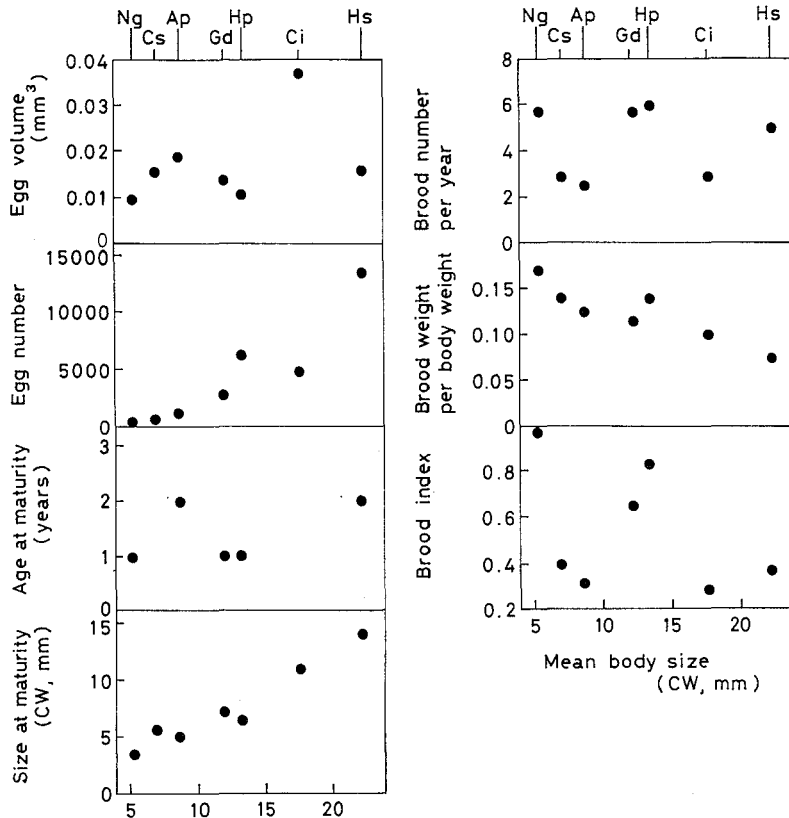


Fig. 24. The relationship between reproductive traits and mean body size of the species. Abbreviations of species name as in Fig. 18.

with large eggs and/or small ratio of brood weight per body weight (*Hemigrapsus sanguineus* and *Cyclograpsus intermedius*).

The mean number of broods per year was not correlated with the mean body size of the species (Kendall's τ , $p > 0.5$) (Fig. 24). The laboratory rearing showed that incubation period became long as temperature declined within species and that at a given temperature it was similar among species. From this relationship, the frequency of laying broods seems to be restricted to a lower level in winter-breeding than in summer-breeding. This may be why *Acmaeopleura parvula*, the only winter-breeding species, had the smallest number of broods per year. The frequency of laying broods, however, varied considerably among summer-breeding species, which suggests that this frequency is not determined only by the relationship between incubation period and temperature.

The ratio of brood weight per body weight ranged from 0.074 to 0.175 among the 7 species, and it was negatively correlated with the mean body size of the species (Kendall's τ , $p < 0.05$) (Fig. 24). Hines (1982), however, has shown that this ratio is not correlated with body size among 20 species of brachyuran crabs. This ratio has often been used as an index of reproductive effort (Tinkle, 1969; Pianka & Parker,

1975). Although Hirshfield & Tinkle (1975) has indicated that the ratio of brood weight per body weight does not show the reproductive effort in the sense of the proportion of energy investment into reproduction, this ratio seems to be convenient when the intensity of reproductive activity is compared among closely related species of different body sizes. In the comparison among the species with different numbers of broods per year, "brood index", i.e. the ratio of brood weight per body weight multiplied by the number of broods per year, is considered to be more appropriate (Hirshfield & Tinkle, 1975; Graham & Branch, 1985). Brood index ranged from 0.29 to 0.98 among the 7 species, and it was not correlated with the mean body size of the species (Kendall's τ , $p > 0.1$) (Fig. 24).

Age at maturity of females was not correlated with the mean body size of the species (Kendall's τ , $p > 0.5$) though size at maturity of females was so (Kendall's τ , $p < 0.05$) (Fig. 24). Regarding the selective pressures that have driven the evolution of delayed maturity of females, some hypotheses have been suggested (Stearns & Crandall, 1981). (1) When the trade-off relationship between growth and reproduction exists, delayed maturity increases body size, which may result in the increase in fecundity. (2) When the trade-off relationship between survivorship and reproduction exists, delayed maturity increases adult survival rate. (3) When the parent progresses in breeding the offsprings with age, delayed maturity increases juvenile survival rate. Hypotheses (1) and (2) may be applicable to the present grapsid crabs, since the decreases of growth rate and survival rate after maturity were observed.

4) Analysis of the relationships between life history traits using a model.

On the basis of the observed intraspecific and interspecific variations of life history traits in the present grapsid crabs, a model was made which predicts the number of eggs laid through life by a female. Previously models have been proposed for the evolution of life history traits based upon aspects of the fitness of an organism. However, they occasionally use hypotheses which are not supported by the available facts (Gadgil & Bossert, 1970; Stearns & Crandall, 1981; Stearns & Koella, 1986). In this section, the set of life history traits that is favored for female crabs will be discussed using the model.

The expected value of the number of eggs per life per female on its settling (N) is given by

$$N = \sum_{x=\alpha}^{\infty} l(x) m(x)$$

where $l(x)$ = probability of surviving to age x (year) after settlement, $m(x)$ = the number of eggs laid at age x and α = age at maturity (year). In the present grapsid crabs, $l(x)$ and $m(x)$ were formulated on the following assumptions. The survival rates of immature and mature periods were assumed to be constant, respectively. The number of eggs per year is determined by multiplying the number of eggs per brood by the number of broods per year. It was assumed that the number of eggs

per brood is proportional to the third power of carapace width and the number of broods per year is constant. Then

$$\begin{aligned} l(x) &= s_i^x & (x < \alpha) \\ l(x) &= s_i^\alpha s_m^{x-\alpha} & (x \geq \alpha) \\ m(x) &= k B \{c(x)\}^3 \end{aligned}$$

where s_i =annual survival rate in immature period, s_m =that in mature period, $c(x)$ =mean carapace width (mm) at age x , B =brood index, and k =constant of each species. Regarding $c(x)$, since the growth rate of the present grapsid crabs tended to decrease with age, a modified von Bertalanffy's growth curve, which took into account that growth rate may possibly decrease after maturity, was used.

$$\begin{aligned} c(x) &= K(1-g_i^x) + L g_i^x & (x < \alpha) \\ c(x) &= K(1-g_i^\alpha g_m^{x-\alpha}) + L g_i^\alpha g_m^{x-\alpha} & (x \geq \alpha) \end{aligned}$$

where K =the maximum carapace width (mm), L =the minimum carapace width (mm), g_i =the index of growth in immature period, and g_m =that in mature period. Relative growth rate to maximum body size increases as the index of growth decreases. In this model, s_m/s_i and g_m/g_i can be regarded as survival cost and fecundity cost associated with reproduction, respectively. The value of each parameter which maximizes N was considered "optimal"; if crab populations do not increase or decrease, N can be regarded as showing the reproductive success of the crab. Five species of *Hemigrapsus sanguineus*, *Hemigrapsus penicillatus*, *Gaetice depressus*, *Acmaeopleura parvula* and *Nanosesarma gordonii* were used for analysis, since most of the parameters were estimated for these species (Table 11). The indices of growth, g_i and g_m , were estimated from the growth curve based on the field data.

First, the effects of some life history traits on the optimal age at maturity were tested. When survival rate in immature period ranges over the estimated values in the field (see Table 2), the optimal age at maturity (year) was 4, 3, and 1 for *Hemigrapsus sanguineus*, *Acmaeopleura parvula* and *Nanosesarma gordonii*, respectively (Figs. 25, 26). Although these values tended to be higher than the true ages at maturity, the prediction by this model, that delayed maturity is favored for *H. sanguineus* and *A. parvula* compared with *N. gordonii*, corresponded to the observed interspecific dif-

Table 11. The value of the parameters estimated for females from the field data. As with each parameter, see the text.

	K (mm)	L (mm)	k	B	α (year)	s_i	s_m	g_i	g_m
<i>Hemigrapsus sanguineus</i>	39.0	2.0	13.5	0.37	2	0.89	0.63	0.69	0.69
<i>Hemigrapsus penicillatus</i>	22.0	1.6	17.8	0.84	1	—	0.16	0.45	0.45
<i>Gaetice depressus</i>	23.4	2.2	13.2	0.65	1	—	0.35	0.46	0.66
<i>Acmaeopleura parvula</i>	12.8	1.7	13.2	0.31	2	0.81	0.48	0.62	0.72
<i>Nanosesarma gordonii</i>	8.0	1.1	17.6	0.98	1	0.39	0.00	0.41	0.41

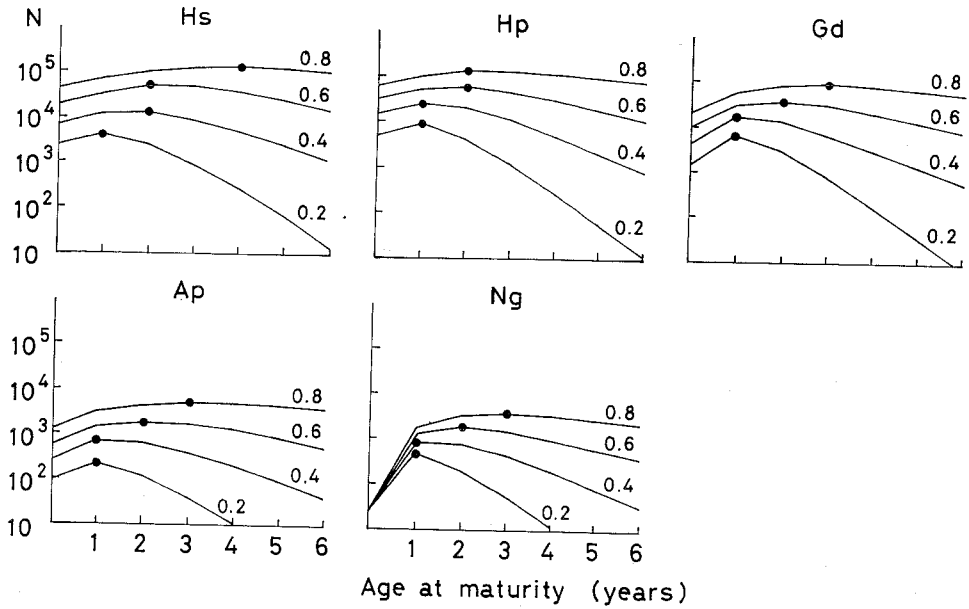


Fig. 25. The number of eggs per life (N) as a function of age at maturity for different survival rates in immature period (0.2-0.8). Points represent the optimal age at maturity. Abbreviations of species name as in Fig. 18.

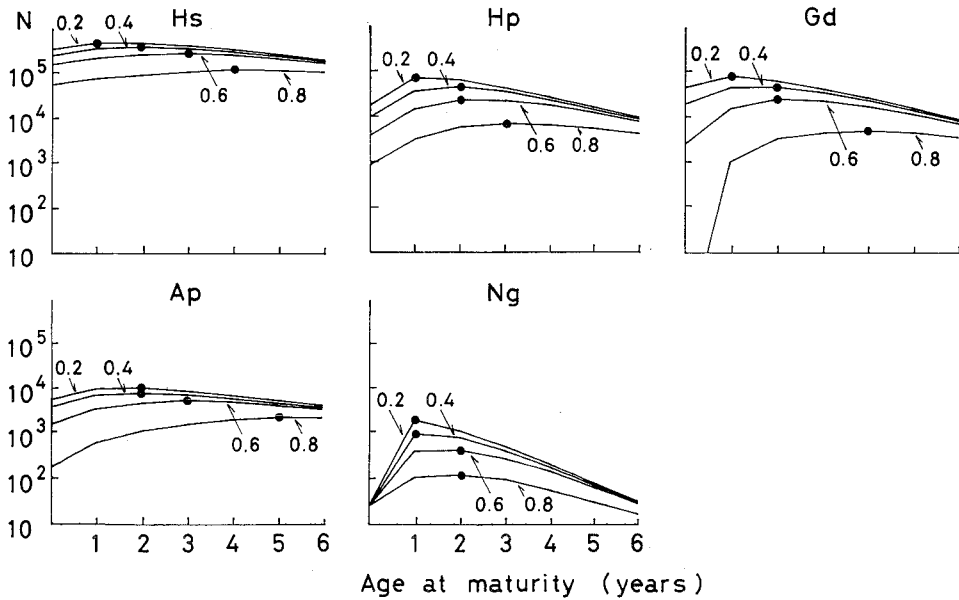


Fig. 26. The number of eggs per life (N) as a function of age at maturity for different indices of growth (0.2-0.8). Points represent the optimal age at maturity. Abbreviations of species name as in Fig. 18.

ferences. Disagreements between the estimated values and the observed ones may arise from the fact that survival rate in immature period is underestimated, survival rate decreases with age, or the present grapsid crabs have physiological longevity. If growth rates or survival rates do not decrease after beginning of reproduction, the number of eggs laid through life increases with decrease in age at maturity. In other words, the fact that the optimal age at maturity is not zero in this model is due to the existence of survival cost or fecundity cost associated with reproduction. It corresponds to the theoretical predictions stated previously. However, *Gaetice depressus* had the highest fecundity cost and *N. gordonii* had the highest survival cost among the 5 species, but these species showed relatively early maturity. Fecundity costs or survival costs therefore do not explain the observed differences in age at maturity. This model shows that two life history traits change the optimal age at maturity. One is the survival rate in immature period (s_i). The optimal age at maturity tends to become earlier as survival rate in immature period decreases (Fig. 25). This means that even if a crab grows rapidly without any cost of reproduction to heighten its fecundity, low probability of surviving to the age at maturity may negate the achieved high fecundity. The other trait which changes the optimal age at maturity in the model is the index of growth (g_i). The optimal age at maturity tends to be delayed as the index of growth increases (Fig. 26). This means that if a crab has a high expectancy of growing more and getting larger fecundity in the future, delayed maturity is optimal. In fact, delayed maturity species, *H. sanguineus* and *A. parvula*, had higher immature survival rates and larger indices of growth than early maturity species, *Hemigrapsus penicillatus*, *G. depressus* and *N. gordonii* (Table 11). This analysis suggests that the age at maturity of these species has been determined in the course of evolution in connection with survival rate and/or the index of growth in immature period.

Secondly, the effects of some life history traits on the optimal brood index were tested. In the field data, survival rate in mature period tended to decrease as brood index increased among species (Fig. 23), which suggests that survival cost associated with reproduction increases with reproductive effort. Although s_m/s_i was estimated for only a few species (Fig. 27), the following relationship between survival rates and brood index was assumed.

$$s_m = (1-B) s_i \quad (0 \leq B \leq 1)$$

On the basis of this relationship, this model shows that the optimal brood index also depends on survival rate and the index of growth in immature period (Figs 28, 29). The optimal brood index increases with decrease in survival rate in immature period or with decreasing value of the index of growth. This means that if a crab has a low probability to attain the age at maturity or a low expectancy to get high fecundity in the future, it is optimal to invest much into the current reproduction. This also corresponds to the observed combinations of brood index, survival rate in immature period and the index of growth in the present grapsid crabs (Table 11).

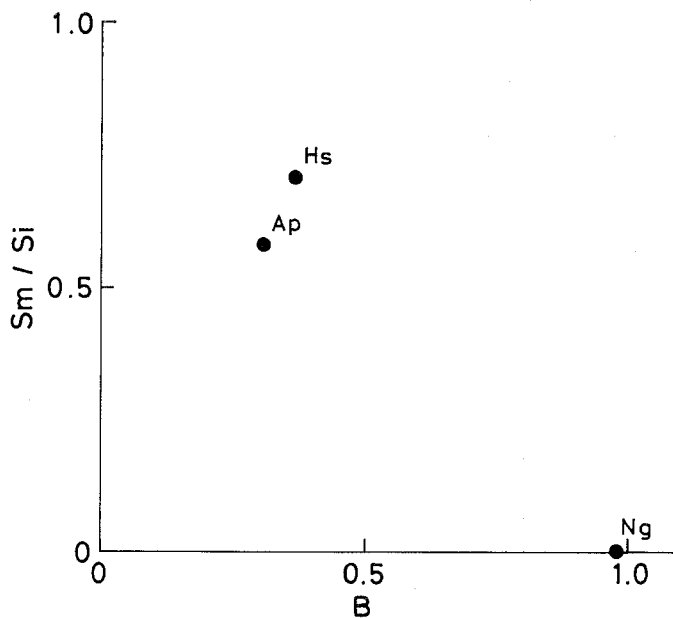


Fig. 27. The relationship between the ratio of survival rate in mature period to that in immature period (s_m/s_i) and brood index (B). Abbreviations of species name as in Fig. 18.

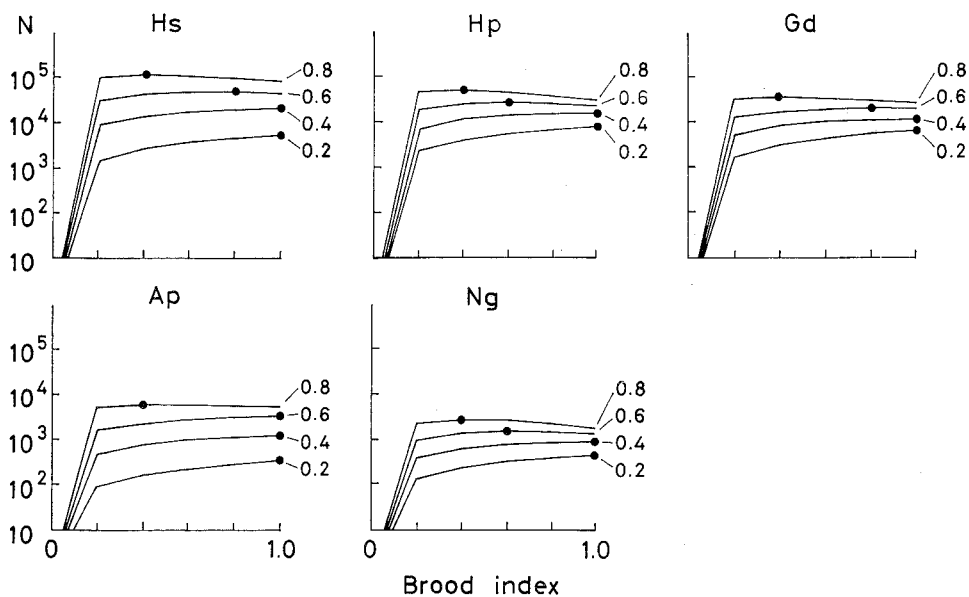


Fig. 28. The number of eggs per life (N) as a function of brood index for different survival rates in immature period (0.2-0.8). Points represent the optimal brood index. Abbreviations of species name as in Fig. 18.

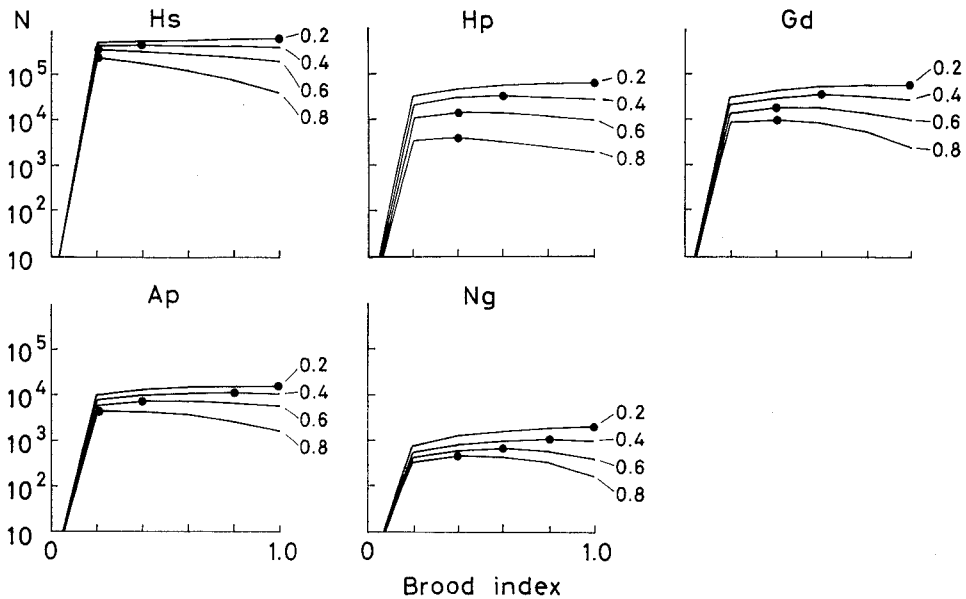


Fig. 29. The number of eggs per life (N) as a function of brood index for different indices of growth (0.2–0.8). Points represent the optimal brood index. Abbreviations of species name as in Fig. 18.

In addition, assuming that age at maturity and brood index change freely, the optimal set of the two was obtained (Table 12). In age at maturity, the optimal values calculated tended to be higher than the observed ones but the predicted interspecific differences corresponded to those observed. In brood index, on the other hand, the optimal value was calculated to be always 1.0 in this analysis. This may suggest that age at maturity is determined earlier than brood index and works as one of the factors determining the brood index. Or it may be due to a rough estimate of the relationship between brood index and survival rates in immature and mature periods.

Consequently, the evolution of the following two sets of life history traits were predicted by this model, and those sets were recognized among the present grapsid crabs. (1) high survival rate in immature period, small relative growth rate to maxi-

Table 12. The optimal set (age at maturity (year), brood index) in different annual survival rates and indices of growth in immature period.

	annual survival rate (s_i)			index of growth (g_i)			
	0.4	0.6	0.8	0.4	0.5	0.6	0.7
<i>Hemigrapsus sanguineus</i>	(2, 1.0)	(3, 1.0)	(5, 1.0)	(3, 1.0)	(4, 1.0)	(5, 1.0)	(6, 1.0)
<i>Hemigrapsus penicillatus</i>	(2, 1.0)	(2, 1.0)	(3, 1.0)	(2, 1.0)	(2, 1.0)	(3, 1.0)	(3, 1.0)
<i>Gaeticus depressus</i>	(2, 1.0)	(2, 1.0)	(3, 1.0)	(2, 1.0)	(2, 1.0)	(3, 1.0)	(3, 1.0)
<i>Acmaeopleura parvula</i>	(2, 1.0)	(3, 1.0)	(4, 1.0)	(3, 1.0)	(3, 1.0)	(4, 1.0)	(5, 1.0)
<i>Nanosesarma gordonii</i>	(1, 1.0)	(2, 1.0)	(3, 1.0)	(1, 1.0)	(2, 1.0)	(2, 1.0)	(2, 1.0)

imum body size in immature period, delayed maturity and low reproductive effort, and (2) low survival rate in immature period, large relative growth rate to maximum body size in immature period, early maturity and high reproductive effort. This accords with the predictions in the evolution of life history traits by r- and K-selection theory; Set (1) corresponds to K-selection and Set (2) to r-selection, respectively (Pianka, 1970; Stearns, 1976). The r- and K-selection theory predicts that unstable and unpredictable habitat environments which cause high density-independent mortality favor Set (2) of life history traits. Low survival rate in immature period can be considered as the effect of high density-independent mortality, which may be the reason for such accordance between the predictions by this model and by r- and K-selection theory. However, this model shows that the relative growth rate to maximum body size also can be a factor determining which set of life history traits will be favored in the present grapsid crabs. The theoretical studies on the evolution of life history pattern of organisms, the r- and K-selection theory and the bet-hedging theory, emphasize the importance of survival rate and its relationship to age (Stearns, 1976, 1977). Survival rate has indeed a great influence on the expected value of the number of offsprings laid through life in all species of organisms. Growth pattern, however, should not be depreciated with respect to its effect on the evolution of life history, especially for those brachyuran crabs which continue to grow after the beginning of reproduction and whose number of offsprings depends on the parent body size.

In view of the importance of two life history traits, survival rate and relative growth rate in immature period, habitat conditions and morphological or physiological constraints may possibly have the following effects on the evolution of life history pattern of grapsid crabs. Although the cause of the interspecific differences in survival rate of immature period in the present grapsid crabs has not been determined, the interspecific differences in habitat conditions may be related to them. *Hemigrapsus sanguineus* use the space between rocky reef and boulders or between boulders as refuges, which seldom seems to change in structure. *Hemigrapsus penicillatus* and *Gaetice depressus* usually hide under the cobbles and boulders at low tide. *H. penicillatus* is distributed on the muddy bottom of the inner bay or estuary, and *G. depressus* on the sandy bottom of the protected or open coast (Kikuchi et al., 1981; Fukui & Wada, 1983). In the habitats of the latter two species, surface cobbles and boulders may be covered with sand and mud or moved themselves under the influence of wave and riverflow. In this manner, the persistency of refuges seems to have considerable variations with the size of cobbles and boulders, the feature of substratum and the influence of wave and riverflow. The refuges of *H. penicillatus* and *G. depressus* seem to be unstable, and these species showed Set (2) of life history traits compared with *H. sanguineus*. In addition, some grapsid crabs like *Ptychognathus ishii* and *Ptychognathus capillidigitatus*, inhabiting the intertidal cobble shore in the estuary where the cobbles are prone to be moved by riverflow, also show early maturity and high reproductive effort (Fukui & Wada, 1986). If the persistency of refuges limits the survival rate of inhabitants, it may be a key factor for diversifying life history patterns among

these species.

On the other hand, the relative growth rate to maximum body size may be related with the evolution of life history pattern to the following effect. Among *H. sanguineus*, *G. depressus* and *Nanosesarma gordonii*, since growth rate in immature period is similar, the interspecific differences of the maximum body size are related to those of the relative growth rate. In the grapsid crabs which utilize the space under or among the cobbles and boulders as refuges, the miniaturization of body size seems to enable to use small, and relatively abundant, spaces as refuges. If some small-sized species have evolved to use such small spaces under the competition for refuges, the miniaturization of body size may possibly have determined the direction of evolution of their life history pattern. In addition, small relative growth rate in *Acmaeop-leura parvula* is considered to be due to its extremely slow growth rate itself. The interspecific differences in growth rate was mainly affected by the intermolt period of the species, which suggests that the physiological characteristics of the species play an important role on determining growth rate. Although why the intermolt period of *A. parvula* is so long is not known, it is suggested that this characteristic of slow growth is connected with delayed maturity and small brood index of this species.

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