Comparative Studies on Life History Traits and Reproductive Ecology of Epiphytic Caprellids(Crustacea,Amphipoda)in a Sargassum patens Agardh Bed

青木, 優和
九州大学理学研究科生物学専攻

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Masakazu AOKI

CONTENTS

Abstract

Comparative studies on life history traits and reproductive ecology of epiphytic caprellids in a *Sargassum patens* bed were carried out in Amakusa, west Kyushu. Long term samplings of field population at the permanent quadrats in the *S. patens* bed, observation of reproductive behavior, and rearing experiments both at laboratory and *in situ* natural condition were conducted.

Caprellids are one of the most dominant taxa in the epiphytic fauna of *S. patens*. Nineteen species belonging to 4 genera were recorded in the present study. Among the species, peculiar reproductive behavior, that is maternal care for the juveniles was observed in 3 species. In most of the caprellid species, the juveniles disperse immediately after the emergence from the mother's brood pouch. However, in *C. monoceros,* the juveniles after emerging from the brood pouch clung onto the mother's body and grew there for about 15-20 days. In *C. scaura,* the maternal behavior was similar to that of *C. monoceros*, however, the mother-juvenile relationship of the species was found to be lesser than that of *C. monoceros* and the maternal care period was up to 10 days. In *C. decipiens,* the juveniles emerged from brood pouch stayed around their mother and grew up there for about 30 days. In each maternal care species, the mother defended her juveniles from other epiphytic animals. In the 8 species of which reproductive characteristics were examined, 3 maternal care species produced larger number of smaller eggs than 5 non-maternal care species. Moreover, 2 non-maternal care species produced larger eggs than 3 maternal care species. There seems to present a major paradox in the reproductive characteristics. The reason for the paradox in maternal care could be explained by the difference in the microhabitat utilization.

Caprellids are the amphipods well adapted to cling to the substrata such as hydroids and algae, and the females of caprellids release their progenies as juveniles. Thus, the caprellids living on *S. patens* thalli have to face the problem,

i.e., even the very small newly-born juveniles will have to live on the seaweed thalli. The 8 *Caprella* species examined in this study were classified into three groups according to the means of microhabitat utilization by which they solved the above mentioned problem. The grouping based on microhabitat utilization corresponded to the difference in reproductive characteristics. The females in Group A produced smaller number of larger juveniles which were large enough to cling onto the seaweed thalli. The juveniles dispersed onto the seaweed substratum immediately after the emergence from the mother's brood pouch. In Group B, female caprellids produced larger number of smaller juveniles, and the juveniles experienced maternal care until becoming large enough to crawl on the seaweed substratum. In Group C, females produced smaller number of smaller juveniles. The newly-born juveniles immediately detached their mother and hid in the epiphytic secondary habitats such as hydroids. Hydroid branches were thin enough for the juveniles to cling onto and are supposed to work as refuges for them. Mean size-specific reproductive effort (R/W) of the examined species was 0.3-0.5 and not significantly different among the species. However, only in *C. monoceros*, R/W was smaller than that of other species. It appears to be due to the excess reproductive investment this species make for the cling-type maternal care. The difference in the way of distribution of the limited reproductive energy to each egg appear to closely related to their life style such as microhabitat utilization.

Comparing the life history characteristics between the 2 maternal care species: *C. monoceros* and *C. decipiens* and 2 non-maternal care species: *C. danilevskii* and *C. tsugarensis*, life-time fecundity of maternal care species was apparently larger than that of the non-maternal care species. Moreover, the 2 maternally cared species constituted the most dominant species on the *S. patens* thalli. And the other maternally cared species *C. scaura* was the most dominant species in the algal undergrowth.

The population increase of the caprellids on *S. patens* thalli, except that of *C. monoceros*, were well synchronized with the space expansion of the *S. patens* community. Sudden drop in the population density of the species was with the thinning of the plants. The caprellid population fluctuation was found to be independent of the predatory fish abundance. Thus, the major factor affecting the epiphytic caprellid population density seems to be the availability of habitat space. On the other hand, the population of *C. monoceros* reached a maximum in May-June: the decaying season of plants, and moved onto the algal undergrowth to sustain the population until August. It appears that *C. monoceros* is not much affected by the substrate availability owing to their cling-type maternal care behavior. Moreover, *C. monoceros* seems to succeed in the habitat temporally segregated with other dominant species.

While *C. monoceros* and *C. scaura* used both *S. patens* and algal undergrowth as their habitat, most species occurred in the *S. patens* bed specialized to use the *S. patens* thalli. The population fluctuations of the caprellids occurred on algal undergrowth were independent of the algal biomass. The population fluctuations of caprellids both on *S. patens* thalli and on algal undergrowth implies the presence of population ceiling, namely the carrying capacity of epiphytic caprellid populations. Large number of caprellids of many species coexisted in the *S. patens* bed through habitat segregations. Microhabitat segregation was achieved by using epiphytic secondary habitats and by the employment of maternal care behavior. Vertical habitat segregation of the caprellids between *Sargassum* thalli and algal undergrowth was the result of specialized habitat utilization. Temporal habitat segregation was also observed between *C. monoceros* and other caprellids.

In situ rearing experiments showed that all 4 species: *C. danilevskii, C. decipiens, C. monoceros and C. tsugarensis* had the generation time 40-70 days and the life span less than 110 days. Life-time egg production by one female was found to be between 130-150 in *C. danilevskii* and *C. tsugarensis*, and between

330-360 in *C. decipiens* and *C. monoceros*. Comparing the life history characteristics between caprellids and gammarids, both the life span and generation time of caprellids are apparently shorter than those of gammarids. Moreover, the reproductive effort of caprellids is generally larger than that of the gammarids. It appears that caprellids make maximum reproductive investment within their short life time. Taking account of the life style on the ephemeral habitats such as *Sargassum* seaweed and the life history characteristics mentioned above, the caprellids on *S. patens* thalli is considered as rather opportunistic among the amphipod crustaceans.

Part I. Introduction

Sessile marine benthic communities are broadly organized in one of three distinct manners, pertaining respectively to rocky littoral and shallow sublittoral communities, cryptic reef communities, and macroalgal epifauna communities (see Seed, 1985). Among these communities, macroalgal epifaunal community has a conspicuous characteristic which is considered to be significantly different from that of other communities. In the sublittoral communities, in general, habitat space is provided by the natural disturbances. On the other hand, for the macroalgal epifaunal animals, the space to attach and grow is also supplied by the plant growth. The habitat expansion by the plant growth provides a channel of escape from competitive dominance in epifaunal community (see Seed, 1985). However, the dynamics of this algal population can also have a great impact on the epifauna communities. In particular, large macroalgae such as *Sargassum* seaweed which show drastic seasonal fluctuations, the epifaunal animals also will have to find some way out to maintain their populations from the complete extinction. Plant-animal interaction among the epifaunal population and macroalgae is one of the fascinating topic in the sublittoral ecology.

Till date, numerous studies have been made on the seagrass epifauna (see Kikuchi, 1977, 1980; Pollard, 1984) and kelp associated fauna (see Moore, 1985). However, the studies on the epifauna of *Sargassum* beds are relatively few (see Edgar and Moore, 1986; Mukai, 1990). It may be due to the underwater sampling and the large number of species associated with.

In general, *Sargassum* seaweed communities show drastic seasonal fluctuations. At peak the season, *Sargassum* seaweeds constitute a huge seaweed forest, however, immediately after the reproductive season the plant bodies settle down and decay or carried away by the water current. To be more precise, *Sargassum* seaweeds and their algal undergrowth such as red algae constitute a *Sargassum* bed. It is rather different environment compared to the neighboring

ones. Water movement damps down in the *Sargassum* bed (Toda, 1989), and temperature and pH in the seaweed forest are different from the outside environment (Komatsu et al., 1982; Komatsu, 1985; Komatsu and Kawai, 1987). *Sargassum* seaweeds provide a large habitat for the epiphytic animals and give shelter and food to fish and various invertebrates (Fuse, 1962). Moreover, the drifting *Sargassum* seaweeds make a characteristic 'drift seaweed community' (Hirosaki, 1964; Arimoto, 1979; Kingsford and Choat, 1985; Ito et al., 1988), and the stranded seaweeds constitute a unique terrestrial community along the shoreline.

Most of the studies on epiphytic animals in the *Sargassum* bed focused on the community composition and its spatio/temporal variation and organizing factors, such as grazing activity (Norton and Benson, 1983; Duffy, 1990; Edgar, 1983b), physical factors (Tararam and Wakabara, 1981; Edgar, 1983c; Wakabara et al., 1983; Takeuchi et al., 1987; Russo, 1990) and predation (Edgar, 1983a,b; Holmlund et al., 1990). In some of these studies which have investigated the seasonal trend of epiphytic fauna, identification of the animals was made up to higher taxonomic order such as Order or Family (Fuse, 1962; Mukai, 1971; Kito, 1975; Tsukidate and Takamori, 1978). Few studies have focused on the epiphytic species populations of *Sargassum*. The groups of species of which the population studies have been made so far include the gammarid amphipods (Edgar, 1983d; Russo, 1989), caprellid amphipods (Imada and Kikuchi, 1984; Aoki, 1988), gastropods (Mukai, 1976), copepods and nematodes (Kito, 1977, 1982). However, epiphytic animals in these studies all appeared to have only short reproductive cycles and life span. Thus, the attempts of analyzing life history characteristics in some studies have resulted in inconclusive. Moreover, it was difficult to evaluate the density of epiphytic animals due to the complex and temporal variation in the three-dimensional structure of the *Sargassum* plants (Edgar, 1983a; Russo, 1990).

Present study was carried out in a *Sargassum patens* bed in Tomioka, Amakusa Shimoshima Island. This seaweed bed was large consisted of *S. patens*, some algal undergrowth and relatively small quantity of other macroalgae. Thus the structure of this seaweed community was relatively simple and homogeneous. Caprellid amphipods were selected as a representative epifauna of the *S. patens* bed. Caprellids are the amphipods well adapted to the epiphytic life (Dahl, 1977) and constituted one of the major component of *Sargassum* bed communities in Amakusa (Imada et al., 1981; Edgar, 1991). Though the size of substrate plants is closely related to the size of animals living there (Edgar, 1983a), it is really difficult to know how the animals use the habitat space. However, in case of caprellids, the exact habitat utilization can be understood easily, since they usually cling onto the substratum with their pereopods. They do not swim actively, but usually crawl on the substratum. Moreover, many of them even show morphological adaptation to their habitat substrata (Caine, 1978; Vader, 1983; Aoki and Kikuchi, 1990a). Thus, they are believed to respond sensitively and easily to the changes of the host plant, and seem to be as the good material for studying the plant-animal interaction in the *S. patens* bed. In this study, special attention has been paid to the structural and qualitative changes of the *S. patens* community as the dynamic space for the epiphytic caprellids.

In temperate regions, caprellids have short generation time, rapid reproductive cycles, and short longevity (Caine, 1979b; Takeuchi and Hirano, 1988; Sakaguchi, 1989). Since, the females directly release their juveniles from the brood pouches, by doing the rearing experiment, it is easy to follow the whole life history of caprellids. In this context, I have conducted rearing experiments both at in situ and in laboratory condition.

The reproductive ecology of the caprellids in the *S. patens* bed include maternal care behavior (Aoki and Kikuchi, 1991). Though parental care is a central topic in the recent behavioral ecology (Trivers, 1985; Krebs and Davies, 1987; Clutton-Brock, 1991), surprisingly few studies have been made on the

parental care in marine invertebrates (see Clutton-Brock, 1991). The maternal care behavior of caprellids seems to be closely related to the microhabitat utilization, reproductive characteristics and population dynamics. Hence, the present study was carried out to establish a link between the behavioral ecology and other ecological characteristics of caprellids.

The ecological studies so far been made on caprellids were as follows: feeding ecology (Costa, 1960; Saunders, 1966; Keith, 1969; Caine, 1974, 1976, 1977, 1979a), community ecology (Caine, 1980, 1983, 1989b; 1991b; Hirayama and Kikuchi, 1980), morphological adaptation (Caine, 1978; Bynum, 1980; Caine, 1989a; Takeuchi et al., 1987; Vader, 1983; Aoki and Kikuchi, 1990a), habitat preference (Round et al., 1961; Keith, 1971; Hirayama and Kikuchi, 1980; Imada et al., 1981; Takeuchi et al., 1987), reproductive behavior (Lewbel, 1978; Lim and Alexander, 1986; Aoki and Kikuchi, 1991; Caine, 1991a; Conlan, 1991) and rearing methodology (Takeuchi and Hirano, 1988; Sakaguchi, 1989, 1990; Aoki, 1991b; Takeuchi and Hirano, 1991). The population structures of caprellids in temperate regions were examined by some researchers (Bynum, 1978; Lewbel, 1978; Imada and Kikuchi, 1984; Aoki, 1988). However, attempts to know the life history characteristics of the field population so far resulted in incompleteness. This is because the size structure analysis of caprellid populations in temperate regions showed that they had overlapping generations. In this study, the life history and population dynamics of caprellids were examined with specific intention to find out the different aspects of reproductive ecology.

The Part II of this thesis describe the study area, and in the Part III, the caprellid fauna in the *S. patens* bed is reexamined from the taxonomic point of view. This is believed to give the basic information necessary for the following studies. In the Part IV, the details of maternal care behavior are explained, and in the Part V, microhabitat utilization by the caprellids on the *S. patens* thalli is described. In Part VI, the reproductive characteristics of the caprellids are

described with the help of the results obtained from the rearing experiments and field samplings, with special reference to the maternal care behavior. In the Part VII, the seasonal trend of the field populations in the *S. patens* bed is described in relation to the reproductive characteristics. The general discussion for these ecological studies of caprellids in the *Sargassum* is included in the Part VIII.

Part II. Study Area

Routine field samplings and occasional sample collections were carried out in a *Sargassum patens* bed locating on the east coast of Tomioka Peninsula, the northwest corner of Amakusa Shimoshima Island (32° 32'N, 130° 02'E), West Kyushu (Fig. II-1). The *S. patens* bed consists of *Sargassum patens* over 85% in dry weight all through the year (Fig. VII-4).

The *S. patens* bed is located in the midst of a dense *Sargassum* bed. In the early spring, four species of *Sargassum* seaweeds form a dense bed, which extends for a distance of about 400m parallel to the shoreline and about 150m offshore on a boulder bottom. These four species make distinctive zonations along the shore. *Sargassum thunbergii* forms a narrow band along the lower edge of the littoral zone. The mixed zone of *S. patens* and *S. hemiphyllum* and the *S. patens* zone present offshore side of the *S. thunbergii* zone. *S. horneri* belt presents at the outermost margin of the bed (see Imada et al., 1981).

The depth at the study area was 2-4m and the *S. patens* plants grow on the large rocks on the sand bottom (Fig. VII-3). During the routine sampling period, October 1985 to December 1988, maximum water temperature at the bottom of the study area was 28.0 °C and minimum was 13.5 °C (Fig. II-2). The surface water temperature in Tomioka Bay varied 10.6 °C to 29.2 °C from 1985 to 1991 (Fig. II-3).

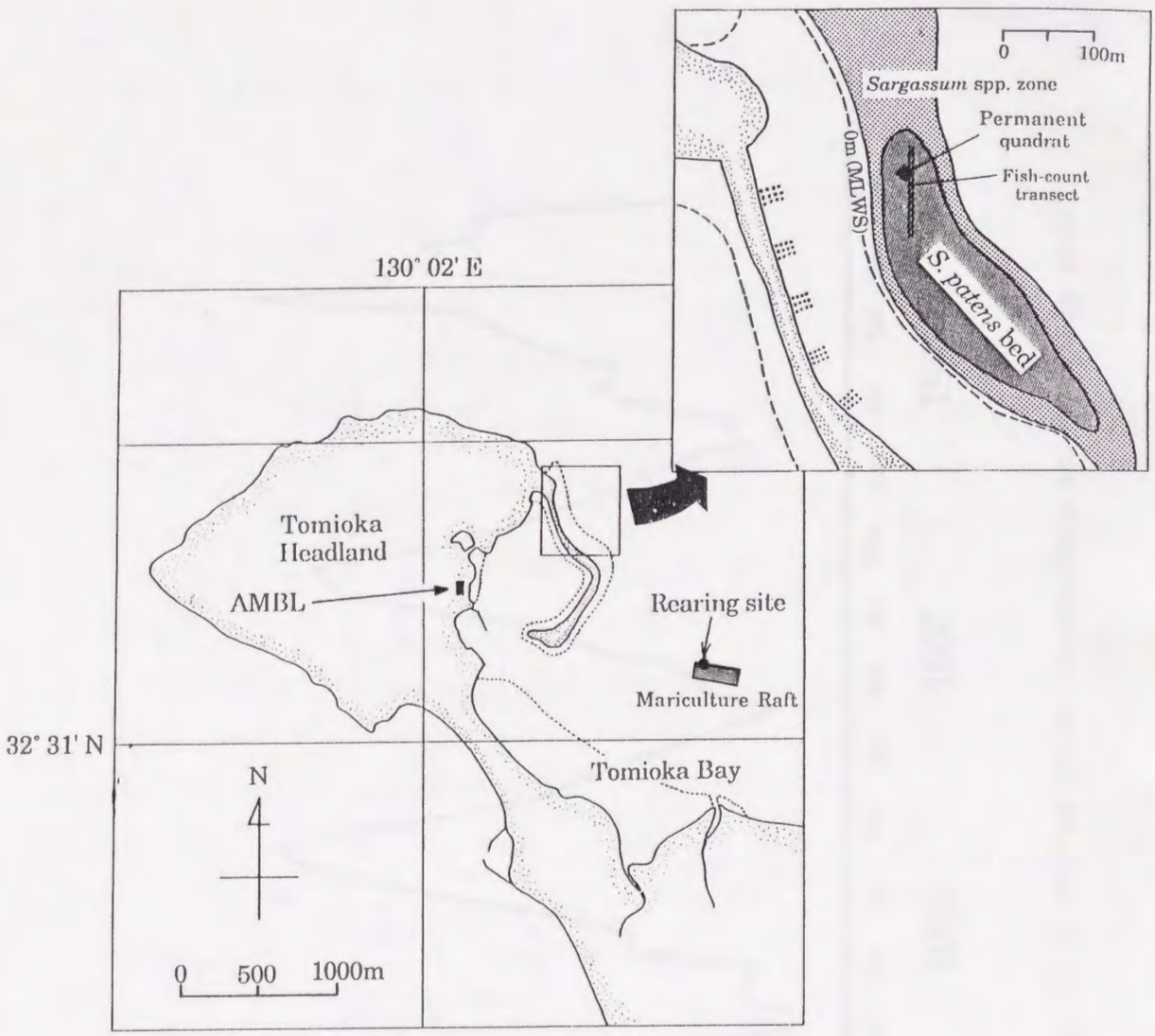


Fig. II-1. Map of the study area. AMBL: Amakusa Marine Biological Laboratory.

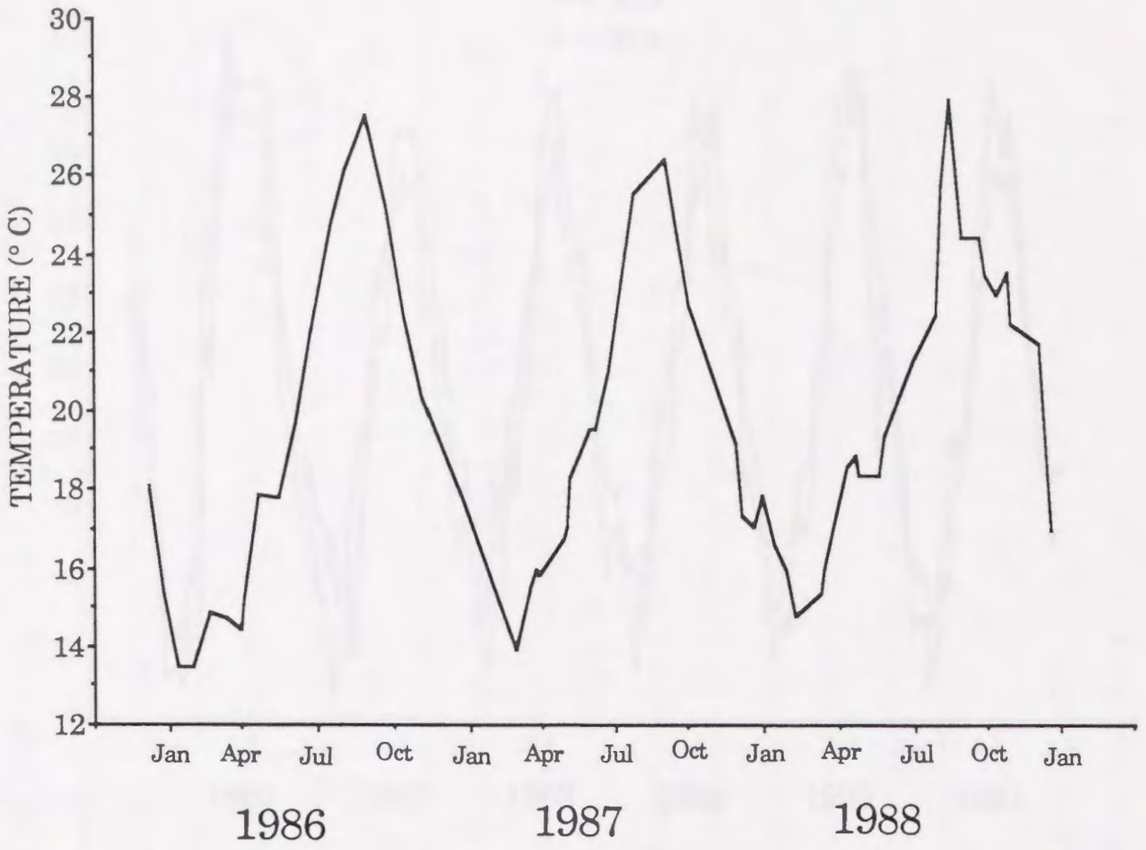


Fig. II-2. Bottom water temperature at the study area.

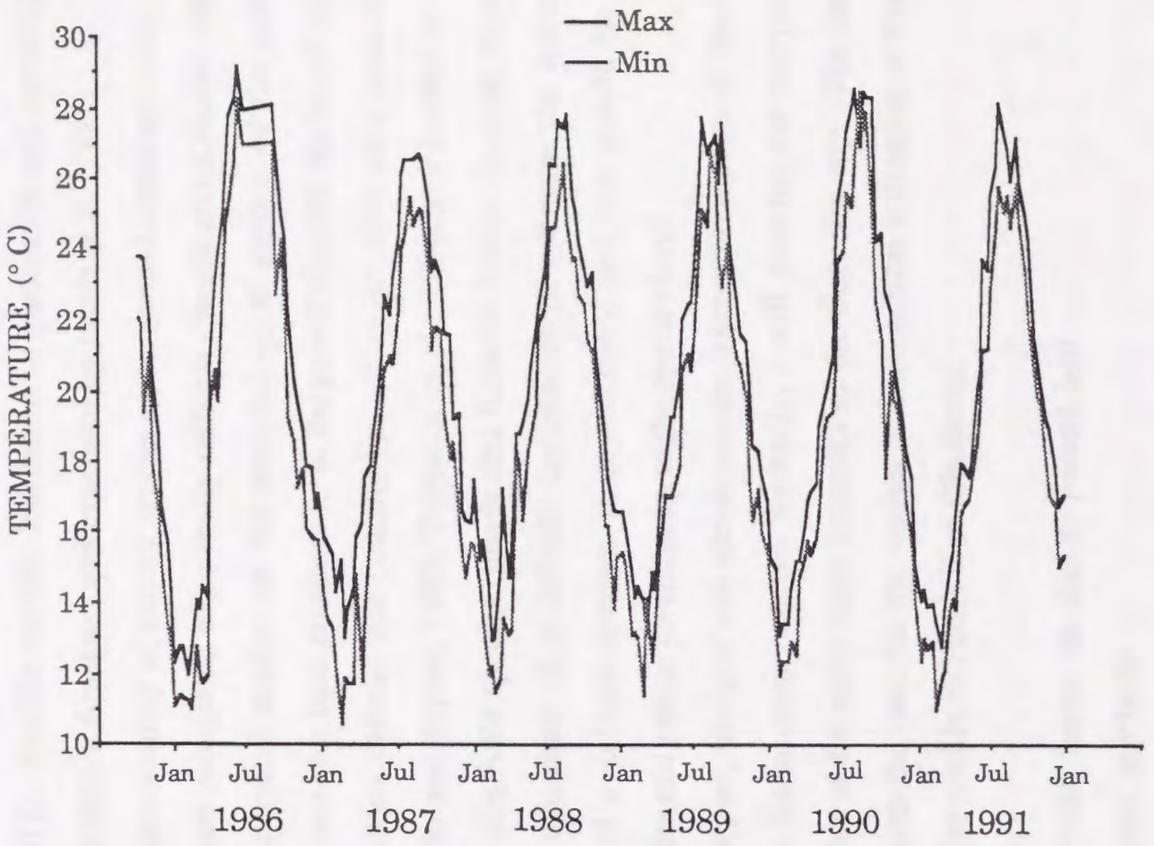


Fig. II-3. Maximum and minimum water temperature at the surface of Tomioka Bay.

Part III. Systematics

III-1. Introduction

Taxonomic aspects of caprellid amphipods in the *Sargassum* bed in Amakusa have been studied earlier by Utinomi (1947, 1964) and Arimoto and Kikuchi (1977). And the vertical distribution of gammarids and caprellids on the *Sargassum* plants in Amakusa was examined by Imada et al. (1981).

The identification of various species of the genus *Caprella* in early juvenile stage has been considered to be really difficult (Imada and Kikuchi, 1984), and hence, comparative studies on the morphological aspects of the early stage juveniles have never been conducted. In the past ecological studies of caprellids, juveniles under a definite size (usually limited by the sieve size) were neglected (e.g. Costello and Myers, 1989; Takeuchi et al., 1990b) or treated as just the juveniles of *Caprella* species (Imada and Kikuchi, 1984). In order to study the population dynamics of a definite species, or to examine the microhabitat utilization of a definite species, it is necessary that one should be able to distinguish the early stage juveniles up to the species level.

In this part, firstly, I will reexamine the taxonomic aspects of the caprellid fauna in the *Sargassum* patens. Secondly, I will mention the morphological characteristics of the early stage juveniles of the *Caprella* spp. The taxonomic study will form the base for the studies of microhabitat utilization in Part V and the population studies in Part VII of this thesis.

III-2. Caprellid fauna in the *S. patens* bed

Materials and methods

Caprellids examined for taxonomic aspects were collected from the *Sargassum patens* bed by SCUBA diving. Immediately after the collections, the specimens were fixed in filtered 10% formalin (neutralized by hexamine).

Nineteen species belonging to 4 genera of caprellids were recorded from the *S. patens* thalli and from the undergrowing algal turf on the rocks in the

S.patens bed (Table III-1). Caprellids on the *S. patens* thalli include the ones which utilize thalli as the primary substrata and also the ones inhabiting the epiphytic hydroids on the thalli of *S. patens* (see Figs. V-1, 2; Table V-1).

Among the caprellids recorded previously from the *Sargassum* beds at Tomioka (Utinomi, 1947, 1964; Arimoto and Kikuchi, 1977; Imada et al., 1981), only female individuals of the species *Caprella bidentata* occurred and they were found together with the males and females of *Caprella monoceros*. These two species share most of the morphological characteristics, differing only in the presence of dorsal spines on the pereonites 3-4 in *C. bidentata* which is absent in *C. monoceros*. *Caprella bidentata* was originally described based on only the female specimens (Utinomi, 1947). Aoki and Kikuchi (1990b) carried out an in situ rearing experiment to find out whether the *C. bidentata* is a spinous variant of *C. monoceros*. A clutch of juveniles of *C. monoceros* exhibited two types of body spination, one as typical *C. monoceros* and the other as *C. bidentata*. The experimental result showed that the *C. bidentata* is a morphological variant of the female *C. monoceros*. This also explains the overlapping geographical distribution of the species as shown by Arimoto (1973, 1976) and the lack of description of males in *C. bidentata*.

During the study, I found an unusual amphipod of the genus *Caprella* that occurs only on erect branching hydroids. This species belongs to the *Caprella acutifrons* group (see Mayer 1890, 1903) and displays some unique characters which appear as the morphological adaptations to the life on the hydroid substratum. The literature review showed that, it represented a new species, and hence was described as a new species *Caprella glabra* Aoki, 1991 (see Aoki, 1991a). The characteristic pereopods 5-7 of *C. glabra* appear to be well adapted to grasp thin branches of hydroids. Moreover, the antenna 2 of the species sparsely bear the short setae. Most of the known species of *Caprella* possess the antenna 2 with dense swimming setae. The species of the genus *Caprella* feed primarily by filtering or by scraping (Caine 1974, 1977, 1979a). The sparse

Table III-1. Caprellid fauna in the *Sargassum patens* bed.

Species	*S. patens*	Main habitat undergrowth
1. *Caprella brevirostris* Mayer, 1903		o
2. *C. californica* Stimpson, 1856		o
3. *C. danilevskii* Czerniavskii, 1868	S	
4. *C. decipiens* Mayer, 1890	S	
5. *C. equilibra* Say, 1818		o
6. *C. glabra* Aoki, 1991	H	
7. *C. kominatoensis* Takeuchi, 1986		o
8. *C. monoceros* Mayer, 1890	S	
9. *C. okadai* arimoto, 1930	S	
10. *C. penantis* Leach, 1814	H-S	
11. *C. polyacantha* Utinomi, 1947	S ?	
12. *C. scaura* Templeton, 1836	S	o
13. *C. simia* Mayer, 1903		o
14. *C. tsugarensis* Utinomi, 1947	S	
15. *C. verrucosa* Boeck, 1871	H-S	
16. *Hemiaegina minuta* Mayer, 1890	H	
17. *Metaprotella sandalensis* Mayer, 1898	S	
18. *Paracaprella crassa* Mayer, 1903	H	
19. *paracaprella* sp.	H	

H: hydroid as substratum; S: *Sargassum* thalli as substratum

short swimming setae of *C. glabra* suggest that filter feeding is unlikely and the primary mode of feeding may be different from that of most species of the genus *Caprella.*

Two forms of *Caprella verrucosa* have been described so far: one is the stout form and the other is the slender form (Laubitz, 1972; Arimoto, 1976). However, from the *Sargassum patens* bed, only the slender type of the species could be collected. No intermediate type of specimen between the two forms was observed. Also, there seems to be no apparent evidence for separating them as individual species. Hence, in this study, the slender type of the species is described as the species *Caprella verrucosa.*

In *C. scaura,* seven forms have been recorded by Mayer (1890, 1903) and Utinomi (1947). McCain (1968) recognized them as intraspecific variations. In Japan, Arimoto (1976) retained three subspecies, diceros, hamata and typica, which are distinguished by the dorsal spination of pereonites 2 to 4. However, these 3 subspecies were recorded in Tomioka and they seem to occur sympatrically, so they were treated as intraspecific variations of *C. scaura* according to Mayr's definition (Mayr, 1957, 1969).

III-3. Identification of the juvenile caprellids

Materials and methods

For the identifications of *Caprella* juveniles, morphological characteristics of the newly-born juveniles of the 9 species: *Caprella danilevskii, C. decipiens, C. glabra, C. monoceros, C. okadai, C. penantis, C. scaura, C. tsugarensis* and *C. verrucosa,* were examined. Adult females just before releasing the juveniles were identified underwater by its whitish color of brood pouches. Seaweeds were disturbed underwater to let the caprellids swim away from the seaweed branches and adult females just before releasing juveniles, identified as mentioned above, were collected one by one. The individuals were put in the glass bottles underwater, brought back to lab and kept in the indoor rearing

system (see Fig. IV-3). The juveniles were fixed immediately after the emergence from mother's brood pouch. Only those juveniles emerged within 24 hours after the collection were examined. Morphological characteristics such as length of antennae and length of pereopods were examined for at least 6 individuals (produced by different females). Body lengths of 12-60 juveniles, produced by 6 different females (2-10 juveniles produced per female), were measured for each species.

Results

Among the 15 species of caprellids belonging to the genus *Caprella* occurred in the *S. patens* bed, I disregarded the following 4 species from the juvenile morphological analysis such as: *C. brevirostris, C. californica, C. equilibra and C. polyacantha.* They were quite few in number (less than 0.1 % of total specimens: see Appendix Table 2), and the morphological characteristics of the newly-born juveniles of the 4 species were quite similar to those of their adults. Hence, it was easy to distinguish among them. Small number of *C. simia* and *C. kominatoensis* occurred on the S. patens thalli and algal undergrowth on the rocks (see Appendix Table 2). The juveniles of *C. simia* have elongated and slender pereonite 5 looking like the one of their adult, so it was easy to identify the species from the others. The juveniles of *C. kominatoensis* which have 2-3 flagellar articles of antenna 1 (supposed to be 1st-2nd instars) resembles to those of *C. decipiens.* The juveniles larger than these sizes were distinguishable by the morphological differences of pereopods 5-7. However, the number of distinguishable *C. kominatoensis* individuals occurred on the Sargassum thalli and algal undergrowth were rather fewer than those of *C. decipiens* (see Appendix Tables, 2,4). The juveniles of these two species which fell under the size mentioned above were divided proportionately to the number of distinguishable larger individuals collected from the same substratum. Then they were counted separately.

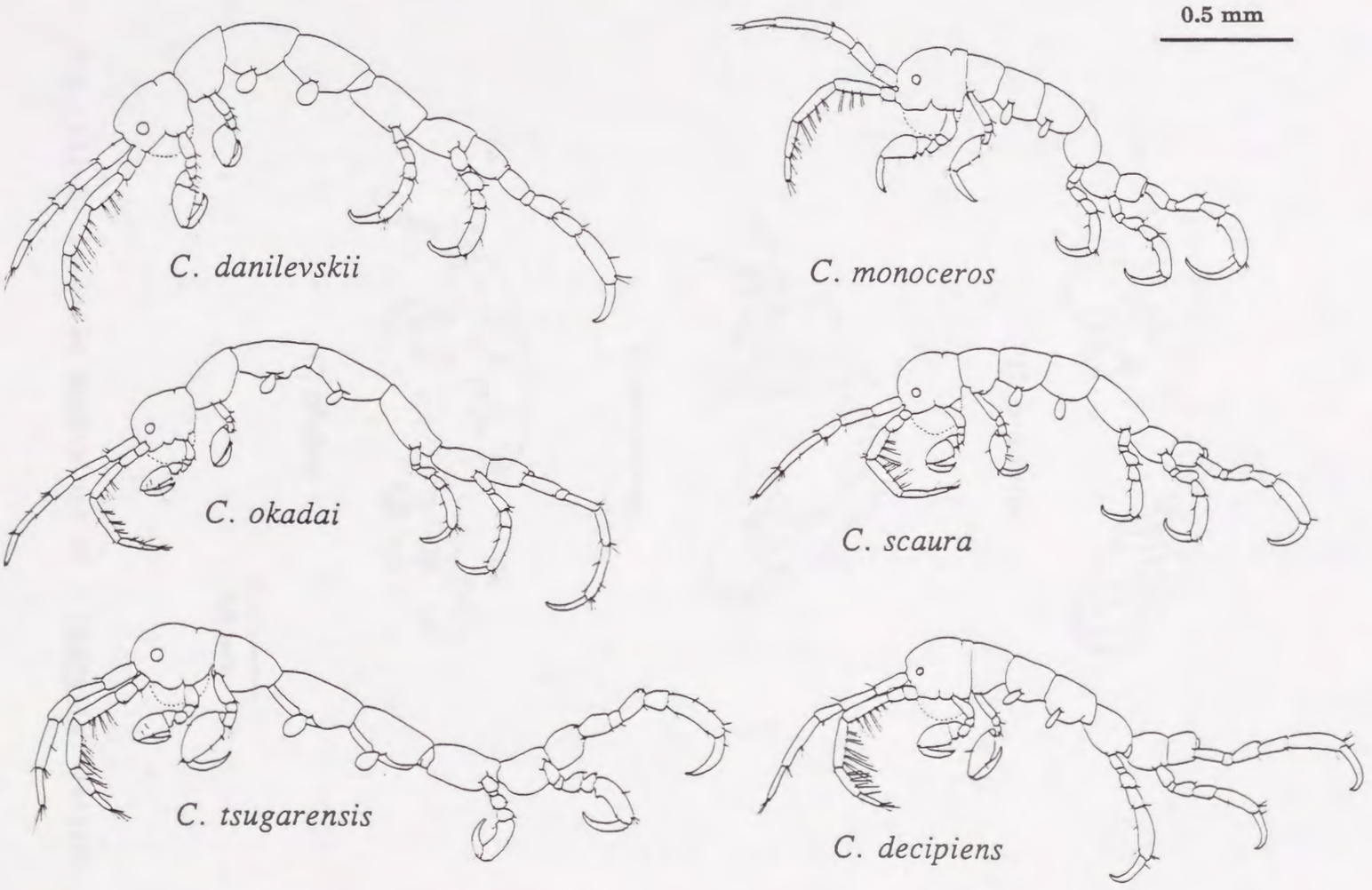


Fig. III-1. Juvenile morphology of 6 Caprella species.

C. penantis

C. verrucosa

C. glabra

0.5 mm

Fig. III-2. Juvenile morphology of 3 Caprella species.

Table III-2. Measurements of the body parts (Mean & S.E.; lengths in mm) of the newly-born juveniles in the 9 caprellids of the genus Caprella. A1: Antenna 1; A2: antenna 2; G1p: propodus of gnathopod 1; G2p: propodus of gnathopod 2; P5: pereopod 5; P6: pereopod 6; P7: pereopod 7.

Species (No. examined)	Body length	Antenna		Gnathopod		Pereopod	
C. monoceros	1.10 (0.043)	A1	0.59 (0.030)	G1p	0.12 (0.004)	P5	0.43 (0.025)
(6)		A2	0.65 (0.036)	G2p	0.14 (0.007)	P6	0.48 (0.021)
		A1/A2	0.92 (0.014)	G2p/G1p	1.15 (0.057)	P7	0.59 (0.026)
			A1 < A2 ***		G1p < G2p ***		
C. scaura	1.17 (0.036)	A1	0.62 (0.035)	G1p	0.12 (0.006)	P5	0.44 (0.018)
(6)		A2	0.59 (0.022)	G2p	0.14 (0.007)	P6	0.50 (0.040)
		A1/A2	1.06 (0.027)	G2p/G1p	1.19 (0.064)	P7	0.58 (0.030)
			A1 > A2 **		G1p < G2p ***		
C. decipiens	1.29 (0.042)	A1	0.74 (0.030)	G1p	0.15 (0.004)	P5	0.56 (0.017)
(6)		A2	0.73 (0.023)	G2p	0.18 (0.013)	P6	0.63 (0.026)
		A1/A2	1.01 (0.025)	G2p/G1p	1.21 (0.069)	P7	0.73 (0.021)
			A1 = A2 NS		G1p < G2p ***		

*** P < 0.001, ** 0.001 < P < 0.01, NS not significant (Student's paired t-test, one-tailed)

Table III-2. Continued.

Species (No. examined)	Body length	Antenna		Gnathopod		Pereopod	
C. danilevskii	1.73 (0.062)	A1	0.72 (0.034)	G1p	0.16 (0.012)	P5	0.49 (0.031)
(6)		A2	0.73 (0.028)	G2p	0.16 (0.011)	P6	0.53 (0.030)
		A1/A2	0.99 (0.047)	G2p/G1p	1.00 (0.092)	P7	0.71 (0.058)
		A1 = A2 NS		G1p < G2p NS			
C. tsugarensis	1.67 (0.083)	A1	0.70 (0.047)	G1p	0.15 (0.009)	P5	0.47 (0.039)
(6)		A2	0.67 (0.042)	G2p	0.20 (0.016)	P6	0.53 (0.050)
		A1/A2	1.04 (0.023)	G2p/G1p	1.33 (0.090)	P7	0.73 (0.053)
		A1 > A2 **		G1p < G2p ***			
C. okadai	1.75 (0.018)	A1	0.66 (0.012)	G1p	0.13 (0.006)	P5	0.46 (0.026)
(5)		A2	0.60 (0.024)	G2p	0.16 (0.006)	P6	0.53 (0.017)
		A1/A2	1.09 (0.054)	G2p/G1p	1.23 (0.084)	P7	0.77 (0.015)
		A1 > A2 **		G1p < G2p **			

Table III-2. Continued.

Species (No. examined)	Body length	Antenna		Gnathopod		Pereopod	
C. penantis	1.09 (0.055)	A1	0.46 (0.027)	G1p	0.12 (0.006)	P5	0.39 (0.018)
(6)		A2	0.44 (0.031)	G2p	0.14 (0.012)	P6	0.43 (0.029)
		A1/A2	1.04 (0.015)	G2p/G1p	1.22 (0.121)	P7	0.51 (0.027)
			A1 > A2 ***		G1p < G2p **		
C. verrucosa	1.29 (0.131)	A1	0.34 (0.024)	G1p	0.11 (0.011)	P5	0.34 (0.025)
(6)		A2	0.38 (0.024)	G2p	0.14 (0.015)	P6	0.38 (0.019)
		A1/A2	0.89 (0.056)	G2p/G1p	1.30 (0.088)	P7	0.46 (0.025)
			A1 < A2 **		G1p < G2p ***		
C. glabra	1.26 (0.038)	A1	0.40 (0.043)	G1p	0.12 (0.011)	P5	0.37 (0.018)
(6)		A2	0.35 (0.020)	G2p	0.15 (0.008)	P6	0.41 (0.024)
		A1/A2	1.14 (0.067)	G2p/G1p	1.26 (0.081)	P7	0.47 (0.011)
			A1 > A2 **		G1p < G2p ***		

Therefore, in this study, morphological characteristics of the newly-born juveniles of the 9 dominant *Caprella* species were examined. Examination of the juveniles of each species revealed that it is possible to identify the juveniles up to the species level. Specific characteristics for identification were the body length, length and proportions of antennae 1,2, length and proportion of gnathopods 1,2, and the lengths of pereopods 5-7 (Figs. III-1,2; Figs. IV-11,12; Table III-2). Common characteristics of the 9 newly-born juvenile were the 2-segmented flagellar articles of antenna 1.

Based on the size data of the different body parts of the juveniles (Table III-2; Figs. IV-11,12), key to the species for the 9 caprellid species was constructed.

Key to species for the newly-born juveniles of the 9 common caprellids in the *S. patens* bed

1. Body length larger than 1.5mm ---------- **2**

Body length smaller than 1.5mm ---------- **4**

2. Propodus of gnathopod 2 larger than that of gnathopod 1 ---------- **3**

Propodus of gnathopod 2 nearly equals to that of gnathopod 1 ---------- ***C. danilevskii***

3. Pereopod 7 slender ---------- ***C. okadai***

Pereopod 7 not slender ---------- ***C. tsugarensis***

4. Length of antenna 1 longer than 0.5mm ---------- **5**

Length of antenna 1 shorter than 0.5mm ---------- **7**

5. Antenna 2 setose ---------- **6**

Antenna 2 not setose ---------- ***C. glabra***

6. Dorsal surface of body smooth ---------- ***C. penantis***

Dorsal surface of the body with humps ---------- ***C. verrucosa***

7. Length of antenna 1 longer than

that of antenna 2 ---------- ***C. scaura***

Length of antenna 1 shorter than

that of antenna 2 ---------- ***C. monoceros***

Length of antenna 1 nearly equals

to that of antenna 2,

pereopods 5-7 slender ---------- ***C. decipiens***

Besides the above stated characteristics, the shape of head and the shape of grasping margin of the pereopods 5-7 propodi (Figs. IV-13,14,15) were the useful morphological characters for species identification.

III-4. Discussion

Importance of rearing experiments in the caprellid taxonomy

The rearing experiments of Aoki and Kikuchi (1990b) disclosed that, *C. bidentata* is a morphological variant of the female *C. monoceros*. We have also demonstrated that the body spination can not always be a useful taxonomic character for identification, as in the case of *C. monoceros*.

Both age variation and sexual dimorphism are widely known in caprellids. For example, females are always more spinose than males in *Caprella scaura* and *Caprella californica* (see McCain, 1968; Arimoto, 1976). In *Pseudoprotella phasma* (see Harrison, 1940) and *Caprella scaura* (see Arimoto, 1976) the body spines become larger and sharper as the juveniles mature. As well as variation

with age and sex, some caprellid species show broad intraspecific morphological variations whereas others appear to be highly invariable. In *Aeginella spinosa* (see Laubitz, 1972) and *Metaprotella sandalensis* (Aoki, unpublished), for example, body spination appears to be quite constant. However, in *Aeginina longicornis* and *Caprella unica*, the degree of body spination varies from almost smooth to quite spiny (McCain, 1968; Laubitz, 1972). The non-spiny form of *C. unica* was thought to be a separate species, namely *C. grahami* (see Wigley and Shave, 1966). *C. septentrionalis* exhibits a wide variety of body spination. Several of these forms were treated as variants of one species at one time and distinct species or subspecies at other times (McCain, 1968; McCain and Steinberg, 1970; Laubitz, 1972). On the contrary, continuity of morphological variation has been used as the evidence of synonymy, as in the case of *C. unica* and *C. septentrionalis* (see McCain, 1968; Laubitz, 1972).

As we have seen in the above examples, it is often difficult to decide the validity of a specific morphological character, in particular when we identify the closely related species. According to the Mayr's biological species concept (Mayr, 1957, 1969), subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species. Thus, the subspecies are normally allopatric. However, the information about the migration or actual genetic exchange between the local populations of a definite species is often lacking. In such an occasion, a rearing experiment is useful. To date, no experimental methods have been employed to solve the taxonomic problems within the Caprellidea, except the work of Aoki and Kikuchi (1990b). In temperate region, caprellids have more than one generation in a period of one year, and in each generation they reproduce many times (Bynum, 1978; Hughes, 1978; Caine, 1979b; Imada and Kikuchi,1984). This is because of the short and rapid growth and maturation (Takeuchi and Hirano, 1988; Aoki and Kikuchi, 1990b; Sakaguchi, 1990; Takeuchi and Hirano, 1991). Moreover, since juveniles

of caprellids emerge directly from the brood pouch of the female, it is easy to obtain a clutch of newly hatched juveniles for rearing experiment. Thus, caprellids appear to be a good experimental organism for short-period rearing experiments. As demonstrated in Aoki and Kikuchi (1990b), the *in situ* rearing method of caprellids is an excellent technique for solving the problems in taxonomy. I do believe that this technique can be applied to other marine invertebrates, to gather valuable taxonomic information.such rearing experiments.

Juvenile morphology

Identification of the early stage juveniles is considered as a prerequisite to know the microdistribution of a species or to study the population trends of certain species. To date, the morphological characteristics of the caprellid juveniles have not been studied.

When we consider the phylogenetic relationship among the caprellid species, the wide morphological variations of the adult caprellids often confuse us. The comparative morphological studies of the juveniles could give us much valuable implications for phylogenetic studies of caprellids.

Part IV. Maternal care behavior

IV-1. Introduction

Maternal care is one of the central topics in the behavioral ecology and the reproductive ecology. However little is known about the maternal care in marine invertebrates (see Clutton-Brock, 1991).

In crustaceans, maternal care of juveniles has been known and studied in decapods such as crayfish (Little, 1975; Hazlett, 1983) and bromeliad crab (Diesel, 1989). However, in the smaller crustaceans, only few studies have so far been carried out on the maternal care behavior.

In caprellid crustaceans, the adult female lays eggs in her brood pouch and the eggs hatch in the mother's brood pouch and become juveniles. In most of the caprellids, the juveniles emerge from the brood pouch immediately and disperse onto the substratum. On the other hand, only two reports are available about the maternal care behavior of the caprellids for the juveniles after emerging from the brood pouch. In *Caprella scaura* Templeton, 1836 (*C. scaura typica* Mayer, 1890) and in *Pseudoprotella phasma* (Montagu, 1804), juveniles emerged from the brood pouch cling onto their mother for a certain period and in the former, the mother takes care of her juveniles during that period (Harrison, 1940; Lim and Alexander, 1986). However, these are the short behavioral descriptions and the ecological significance of this behavior has not been examined until now.

Among the caprellids found in the *Sargassum patens* bed, another "juvenile-cling type" maternal care was observed in *Caprella monoceros.* In addition, a new type of maternal care behavior was observed in *Caprella decipiens.* Preliminary report on the behavior of the two species have already been published (Aoki and Kikuchi, 1991; Fig. IV-1). In this study, I have examined in detail the ecological characteristics of the maternal care behavior of caprellids in the *S. patens* bed. That will be explained under the following headings such as: 1) Laboratory observation of the maternal care behavior, 2) Maternal care behavior of caprellids in the field, 3) *In situ* rearing experiment

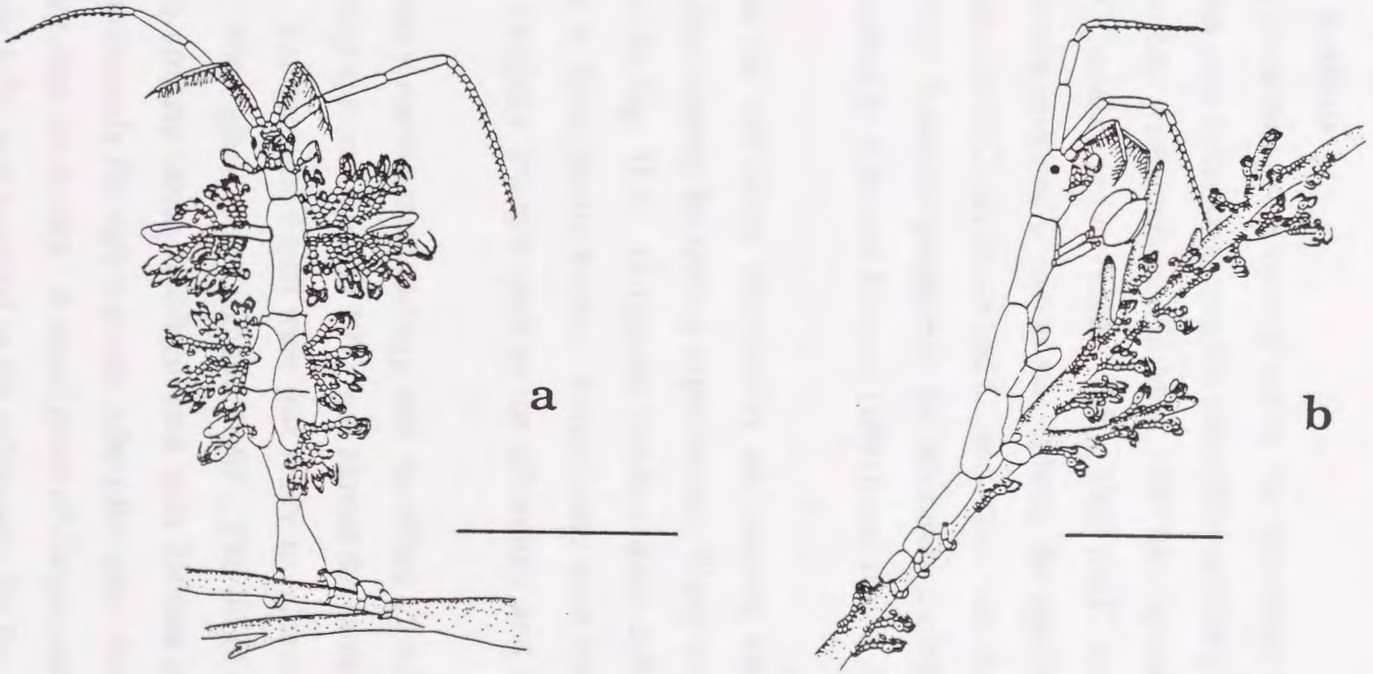


Fig. IV-1. Maternal care behavior of caprellids. a: Caprella monoceros; b: Caprella decipiens (from Aoki & Kikuchi, 1991).

conducted for understanding the ecological significance, 4) The morphological specialization of the newly-born juveniles of the maternal care species.

IV-2. Laboratory observation

Materials and methods

Rearing experiments were carried out in the laboratory to examine the degree of maternal care behavior among the caprellids collected in the *S. patens* bed. The experiments were conducted in May, 1989 for *Caprella decipiens, C. monoceros and C. scaura;* and in February-May, 1991 for *C. glabra, C. okadai, C. penantis, C. tsugarensis and C. verrucosa.* Among the species examined, the maternal care behavior of *C. decipiens* and *C. monoceros* was described in Aoki and Kikuchi (1991). Water temperature in the laboratory during the experiment in 1989 was described in Aoki and Kikuchi (1991), and that in 1991 was shown in Fig. IV-2.

Individuals for laboratory observation and rearing experiments were collected just before starting the rearing experiments. Water temperature at the field was shown in Fig. II-2. Ovigerous females were collected from the seaweed and put in 50ml plastic bottles. Immediately after the collection, the caprellids were carefully brought back to the laboratory and kept in running seawater tanks.

The laboratory rearing methodology was described in Aoki and Kikuchi (1991). The rearing system I used in 1991 was almost the same as that of 1989 (see Fig. IV-3). The females which were just ready to release juveniles were kept in separate 140ml glass bottles (height: 9cm) . The lid of each bottle was provided with an opening (area: 7cm^2) covered with 250mm mesh. Seawater was supplied continuously through a plastic tube (diameter: 4mm) from a tank placed 8cm higher than the bottles. A small piece of *Sargassum patens* branch (wet weight: about 1-2g) was supplied as the substratum for the animals in each bottle except for *C. scaura,* for which a piece of the red algae *Gelidium amansii*

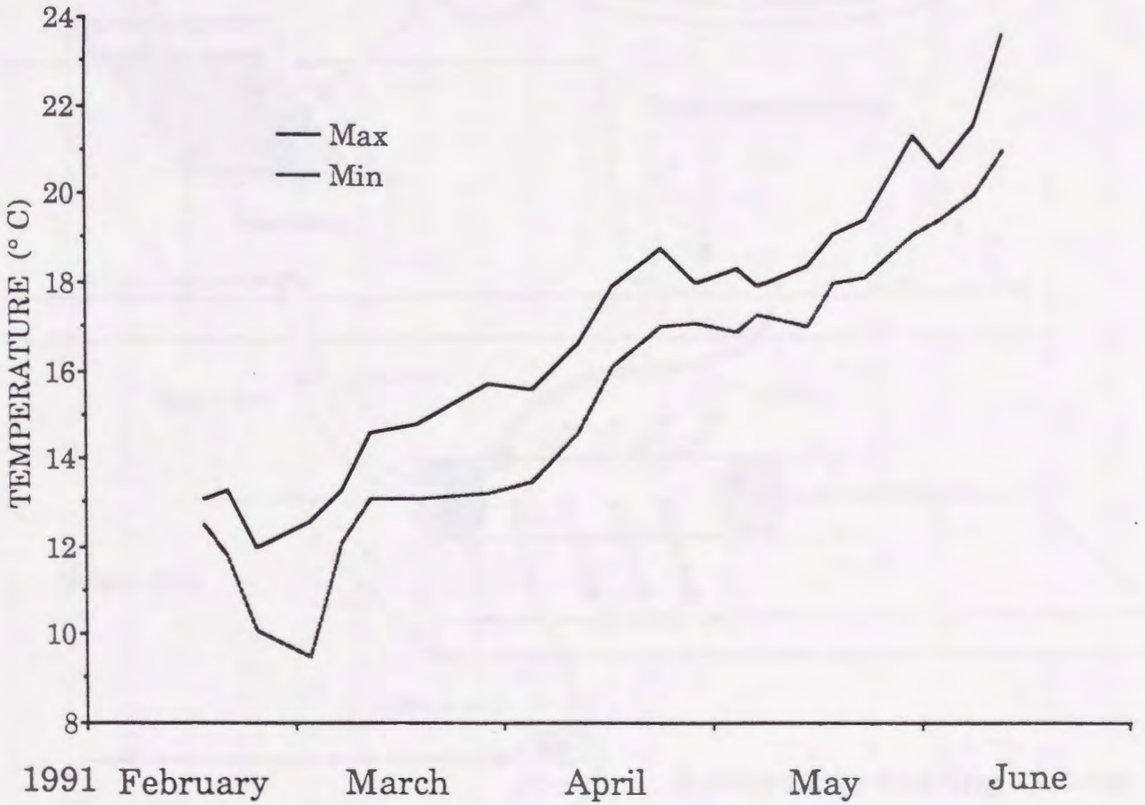


Fig. IV-2. Maximum and minimum temperature of the running seawater used for the rearing experiment.

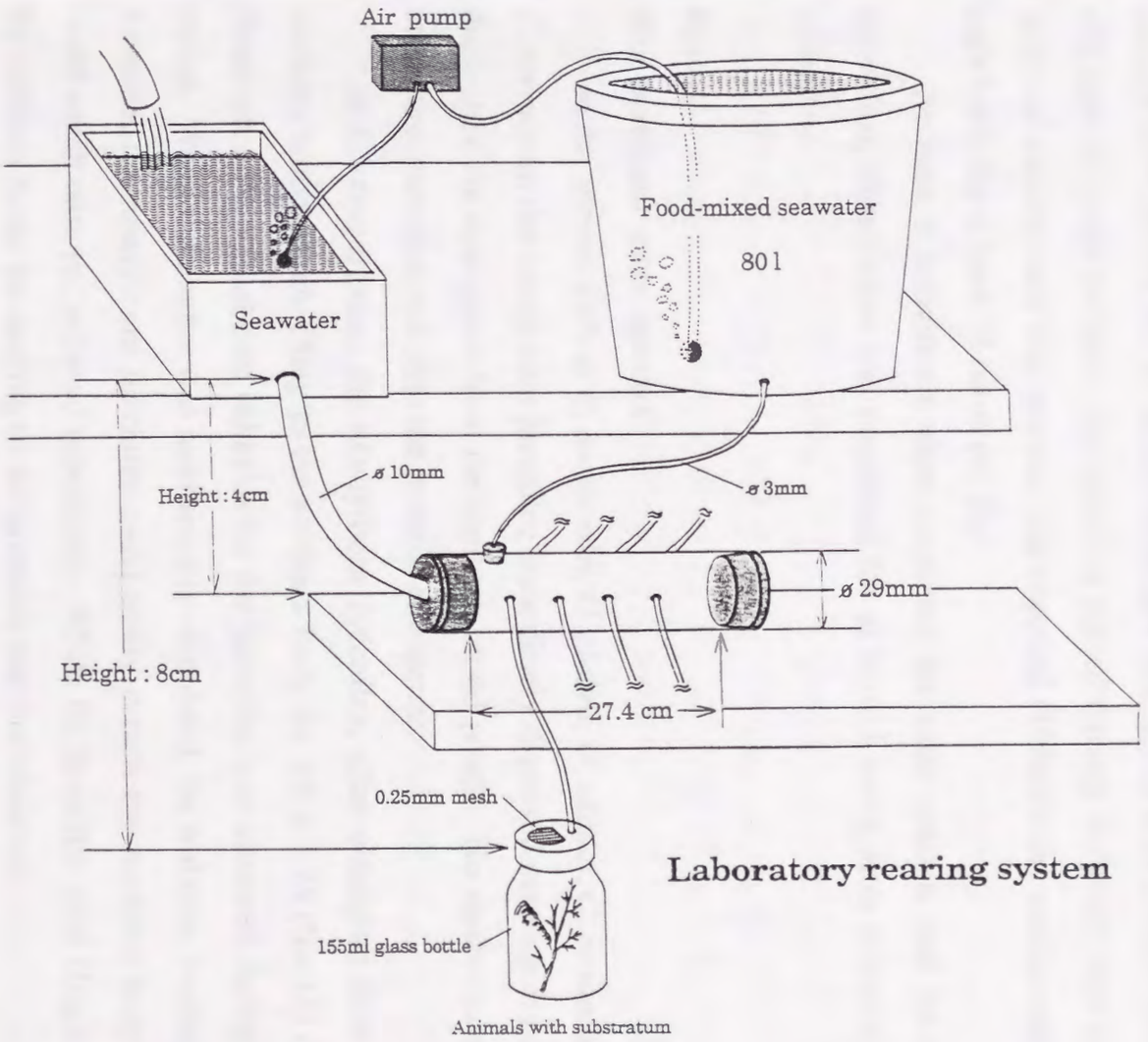


Fig. IV-3. Diagrammatic representation of the laboratory rearing system.

was supplied as the substratum. Each individual was observed at least once a day. The substratum was replaced once in every 3-5 days and the bottle and the lid were cleaned every day. Natural diatoms and detritus were supplied as food. Diatoms and detritus settled on fresh *Sargassum patens* (about 500g by wet weight) were shaken out in the seawater tank and sieved with 250mm mesh to eliminate the large particles. The particles passed through the mesh were mixed in 6-l of seawater and this mixture was supplied (100ml/hour) continuously to each bottle for at least 12 hours per day.

At least 6 individuals were examined for each species, and for each individual, observation was continued for at least 1 week after releasing the juveniles.

Results

Non-maternal care species

In the species such as *C. danilevskii, C. glabra, C. okadai, C. penantis* and *C. verrucosa,* the newly-born juveniles immediately dispersed onto the *S. patens* thalli after the emergence from the mother's brood pouch. No mother-juvenile interaction was observed after the juvenile emergence.

In *C. tsugarensis*, the newly-born juveniles, after emerging from the mother's brood pouch, clung to the mother's body for 2.8 $\pm$ 1.75 (N= 18) days. However, no maternal care behavior for the juveniles was observed during this period. When the mother was mechanically stimulated, for instance, touched by a needle, the newly-born juveniles could easily detach the mother's body and could attach onto the seaweed substratum. While the juveniles were clinging to the mother's body, the molting of the juveniles was not observed.

Maternal care species

In *C. monoceros*, the newly-born juveniles have clung to the mother's body for 16.3 ± 3.5 (N=3) days. During this period, the juveniles molted at least 4 times. The mothers did not molt while carrying the juveniles, and the juveniles were defended and often groomed by their mother. The newly-born juveniles could not detach the mother's body, even though the mother was on the very thin substratum such as hydroid stems. The details of the behavior was described in Aoki and Kikuchi (1991).

In *C. decipiens*, the newly-born juveniles immediately moved onto the seaweed substratum where their mother was clinging onto. The juveniles stayed within about 3cm of their mother and grew up there for 32.5 ± 3.1 (N=4) days. During this period, the mother defended the juveniles on the seaweed. When they were disturbed by stopping the water flow or shaking their substrata, the mother picked up the juveniles and moved to another place in the same way as done by *C. monoceros*. The mother of *C. decipiens* molted 7.2 ± 2.8 days (n=4) after the release of juveniles, even while the juveniles stayed around her. This behavior in detail was described in Aoki and Kikuchi (1991).

The maternal care behavior of *C. scaura* was observed for a period of 1 week. The newly-born juveniles of this species often detached from the mother's body and moved to the red algal substratum, however, they always stayed on or around their mother and never dispersed during the observation period (1 week).

IV-3. Field samplings

Materials and methods

Field samplings were carried out in order to examine the natural activities of the 3 maternal care species. *C. tsugarensis* was also sampled in order to ascertain the nature of maternal care-like behavior under the natural field condition. While the maternally cared colonies of *C. decipiens, C.monoceros* and *C. scaura* were collected from the *S. patens* bed in April, 1991, the females of *C.*

tsugarensis with the newly-born juveniles on her body were collected in February, 1991. The *S. patens* branch with 1 female and her juveniles were gently cut out and put in the 50cc plastic bottles separately. These individuals were taken back to the laboratory and were fixed immediately. For each colony, the number, the body lengths and the number of flagellar articles in the antenna 1 of the juveniles, and the body length of the mother were recorded.

Results

Data of the above aspects are shown in Tables IV-1-4.

Each maternal care colony of *C. monoceros* apparently contained one cohort of juveniles (see Aoki and Kikuchi, 1991). In *C. monoceros,* the maternal care colony consisted of about 50-100 juveniles which were smaller than 5mm and having less than 12 flagellar articles on the antenna 1 (Table IV-1). Referring to the growth data of the *in situ* rearing experiments (mentioned in the Part VI; Figs. VI-5, 21), the juveniles need about 15-20 days to reach 5 mm of the body length. Thus the maternal care period of the species in the natural condition is supposed to be about 15-20 days. The result matches very well to the one obtained in the laboratory experiment.

In *C. scaura*, the colony consisted of about 20-60 juveniles which were smaller than 4 mm in body size and having less than 10 flagellar articles onantenna 1 (Table IV-2). I did not carry out the in situ rearing experiments for this species. Hence, referring to the report of Sakaguchi (1989), under 20 °C, the juveniles need 10.7 days to reach the 5th instar stage, which is about 5mm in body length and having 7-11 flagellar articles on antenna 1. Thus the maternal care of this species in the natural condition is supposed to be about 10 days.

Each colony of *C. decipiens* contained about 200-500 juveniles and some of them seem to be consisted of more than one cohort (Table IV-3), and hence, the size structure of each colony was examined. The length of second pereonite was measured for each individual. The size histograms of 8 colonies were shown in

Table IV-1. Maternal care aggregations of *C. monoceros* collected from the *S. patens* bed on April 5, 1991. Body length of juvenile is in Mean [S.E.]. Number in parenthesis represents the number of replicates. FA: flagellar articles of antenna 1.

	Body length of mother (mm)	Number of Juveniles	Body length of Juveniles (mm)	Number of FA
A	13.21	83	3.21 [0.53] (10)	6 - 9
B	14.85	72	4.60 [0.74] (10)	8 -12
C	13.66	98	2.48 [0.13] (10)	6
D	13.09	55	3.69 [0.62] (10)	9 -12
E	12.96	53	3.64 [0.16] (10)	9 -10
F	14.36	67	3.78 [0.20] (10)	8 - 9
G	15.26	103	3.80 [0.34] (10)	9 -10
H	12.05	64	3.63 [0.20] (10)	8 - 9

Table IV-2. Maternal care aggregations of *C. scaura* collected from the *S. patens* bed. The body length of juvenile is in Mean [S.E.]. Number in parenthesis represents the number of replicates. FA: flagellar articles of antenna 1.

Date of collection	Colony	Body length of mother (mm)	Number of Juveniles	Body length of Juveniles (mm)	Number of FA
April 5	A	10.34	19<	1.36 [0.25] (10)	2 - 3
April 5	B	9.43	64	1.14 [0.05] (5)	2
April 20	C	8.72	24	1.20 [0.08] (10)	2
April 21	D	10.44	12<	2.48 [0.31] (12)	6 - 9
April 22	E	11.49	44	4.07 [0.64] (12)	7 -10

Table IV-3. Maternal care colonies of *C. decipiens* collected from the *S. patens* bed. FA: flagellar articles of antenna 1.

Date of collection	Colony	Body length of mother (mm)	Number of Juveniles	Number of FA
April 1	A	15.98	336	2 - 3
April 20	B	16.46	256	2 - 9
April 20	C	16.58	355	2 - 9
April 21	D	17.08	346	2 - 3
April 21	E	17.71	260	5 -10
April 22	F	19.02	393	5 - 8
April 22	G	18.43	240	2 - 8
April 22	H	18.46	539	2 - 9

Table IV-4. *C. tsugarensis* juveniles being carried by their mother, collected in the *S. patens* bed on February 27, 1991. Body length of juvenile is in Mean [S.E.]. Number in parenthesis represents the number of replicates. FA: flagellar articles of antenna 1.

Colony	Body length of mother (mm)	Number of Juveniles	Body length of Juveniles (mm)	Number of FA
A	10.07	46	1.76 [0.09] (6)	2
B	11.85	32	1.79 [0.09] (6)	2
C	11.63	23	1.70 [0.03] (6)	2
D	9.88	26	1.71 [0.06] (6)	2
E	9.82	20	1.66 [0.05] (6)	2

Fig. IV-4. The number of cohorts in each colony appeared to be: 1 in colonies A,D; 2 in colonies B,C,E; 1-2 in colony G; 2-3 in colonies F,H. The maximum size of the juveniles as the pereonite 2 length was smaller than 1 mm (= about 7 mm in body length). No matured females were found among the juveniles in the colony. According to the *in situ* rearing experiment results given in Part VI, the juveniles required about 30 days to reach 1mm in pereonite 2 length (Fig. IV-5). Also from the results, it was possible to estimate the interval of juvenile releasings by a female by measuring the distance between the peaks of each cohort in the size histogram (Fig. IV-5). According to the field data of colonies B, C and E, each of which appeared to contain 2 cohorts of individuals, the juvenile releasing interval was about 15 days. On the other hand, in colonies F, G and H, which appeared to contain more than two cohorts, the overlapping of n-cohorts was so large that the peak of each cohort could not be detected. In these colonies, the juvenile releasing interval must be shorter than 15 days.

In *C. tsugarensis*, the juveniles that were clinging to the mother's body were always the newly-born juveniles having 2 flagellar articles on antenna 1. Thus, the juveniles of this species detach the mother's body and disperse onto the *S. patens* thalli before the first molting.

IV-4. *In situ* rearing experiments

Materials and methods

To examine the role of mother in the maternal care behavior, an *in situ* rearing experiment was conducted. The method of the experiment was described in Aoki (1991) (see Fig. IV-6). The plastic basket containing the containers for the experimental organisms were suspended at 3.5m below the water surface at the mouth of Tomioka Bay, which is about 1km away from the *S. patens* bed. The variations of water temperature at the rearing site were shown in Fig. IV-7.

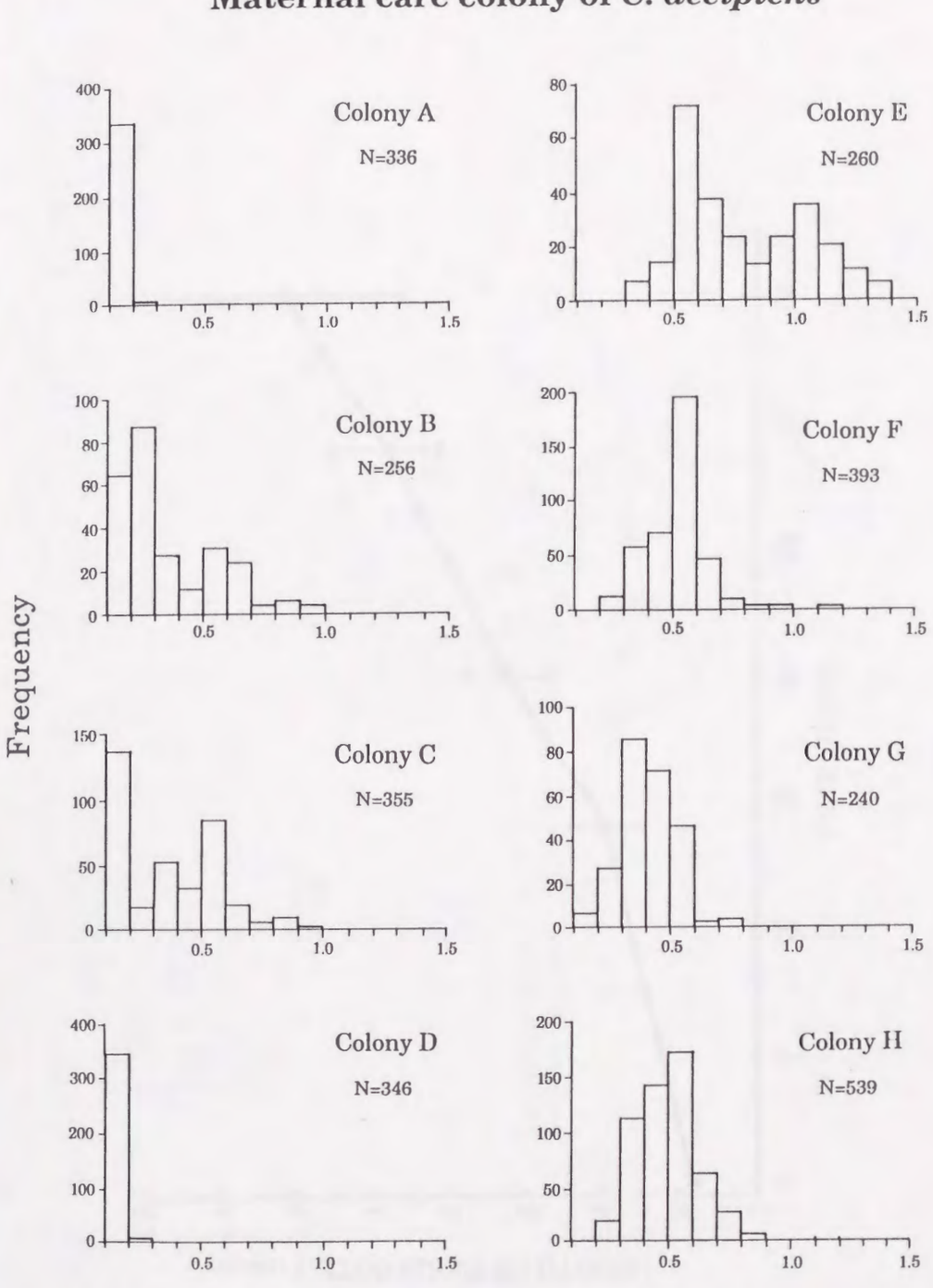


Fig. IV-4. Juvenile size distribution in the maternal care colonies of Caprella decipiens.

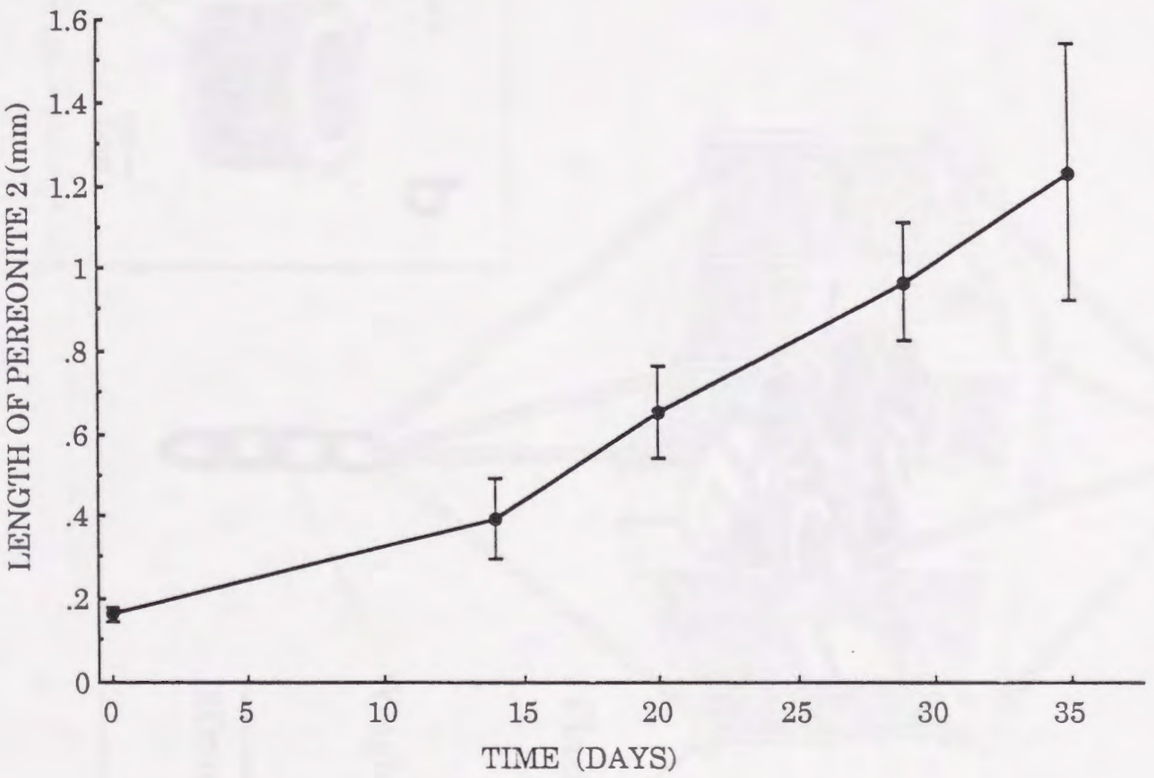


Fig. IV-5. Growth of pereonite 2 in length of Caprella decipiens reared at the in situ condition.

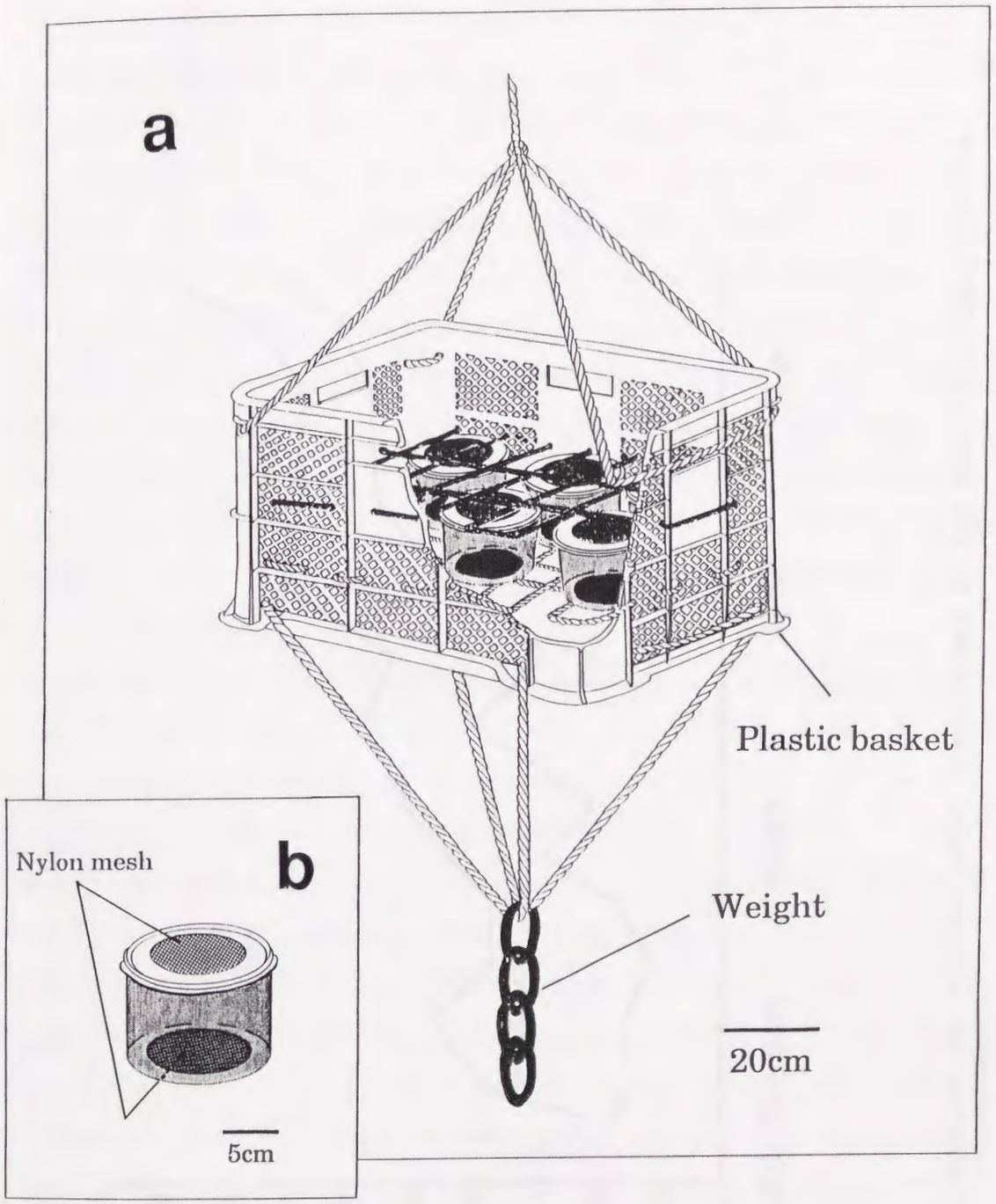


Fig. IV-6. In situ rearing system for caprellids (from Aoki, 1991b).

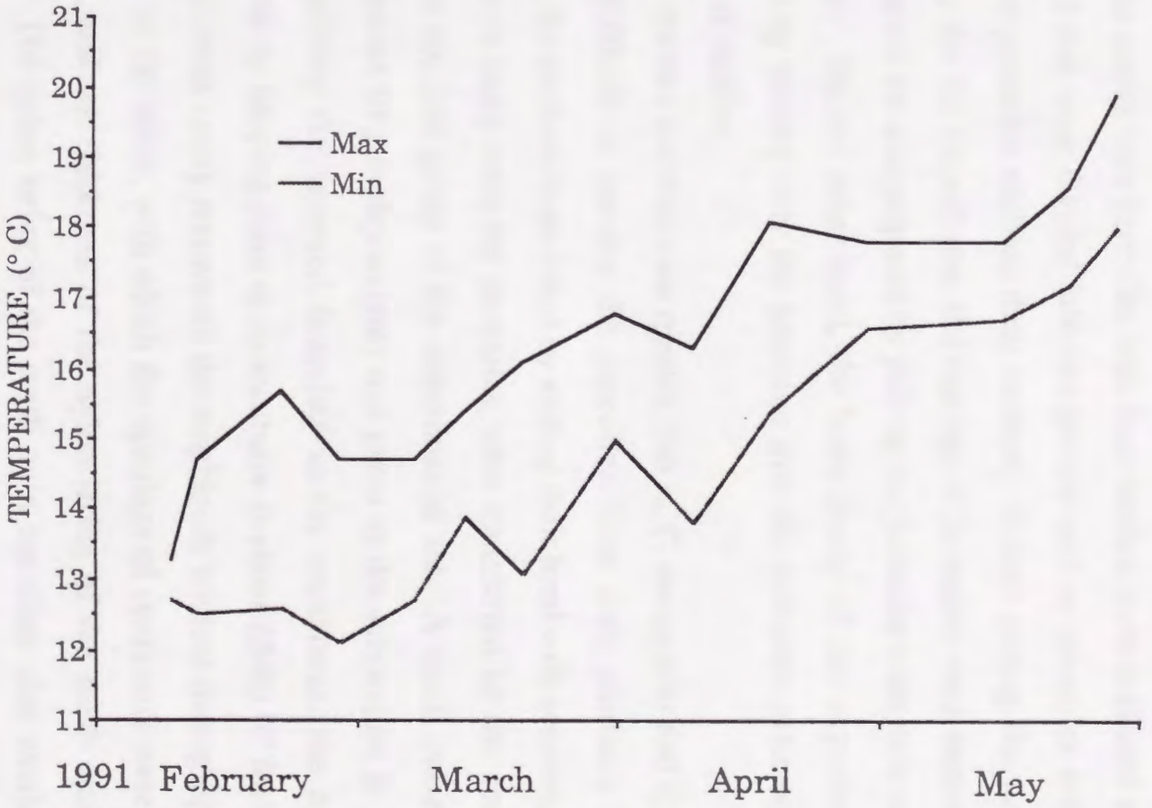


Fig. IV-7. Maximum and minimum water temperature at the site of in situ rearing experiments.

The experiments were conducted to study the difference of the survivorship and the growth of the juveniles under the natural condition, with or without the mother. The experiments were carried out in February-March, 1991 for *C. decipiens* and *C. monoceros*, and in March-April, 1991 for *C. danilevskii, C. scaura* and *C. tsugarensis*. Experimental period extended for 29-30 days.

The newly-born juveniles with their mother were collected as described in Part III-3 and were divided into two groups such as juveniles with mother, and the other juveniles without their mother. Before setting the juveniles in the container for the experiment, the number of juveniles were recorded. The first experimental set was prepared by putting the juveniles with their mother into the container. On the other hand, the latter group of the experimental set was prepared by putting only the juveniles into the container after separating them from their mother.

In the two maternal care species, that is, *C. monoceros* and *C. scaura*, since it was difficult to remove the juveniles from their mother's body without damage, the mothers were killed by cutting their head with scissors, and the piece of mother's body with the juveniles were transferred to the container. This served as the 2nd group of the experimental set. A small piece of *S. patens* branch (about 10 g in dry weight) was given as the substratum in all containers. Before adding the seaweed branches in the containers, the branches were defaunated by keeping them in an incubator at about 25-30 °C for 2 hours. This treatment could easily remove all the amphipods without damaging the seaweed. The size of the mesh, with which the openings of containers were covered, was 0.25mm, and the thickness of the nylon string of the mesh was 0.14 ± 0.02 (N=14). The nylon string of the mesh on a container also would work as the clinging substratum for the animals.

After 29-30 days, all animals were retrieved from the rearing site. The number, the body length and the body dry weight (kept at 60 °C for 24 hours) of the survived juveniles were recorded for each species.

Results

The results of the 1-month rearing experiment for 5 species were given in Figs. IV-8,9,10 and Table IV-5. The survival rate was higher and the growth was better for the juveniles with mother in *C.monoceros*. On the other hand, in *C. scaura*, only the growth was better in the juveniles with maternal care. In *C. tsugarensis*, the survival rate was higher and the growth was better in the male juveniles without maternal care. In *C. danilevskii* and in *C. decipiens*, no significant difference was observed between the juveniles with mother and without mother.

IV-5. Morphological adaptation of the juveniles

Materials and methods

Morphological characteristics of pereopod 7 often reflect the adaptation to habitat in caprellids. Thus the morphology of pereopod 7 of the newly-born juveniles and of their mother was examined for 6 species, viz., *C. danilevskii, C. decipiens, C. monoceros, C. okadai, C. scaura* and *C. tsugarensis*. The specimens examined were obtained by the same method as described in Part III-3. The data of the morphological characteristics of the newly-born juveniles were given in the Table III-2.

Results

Three maternal care species appear to show the morphological specialization for the maternal care behavior.

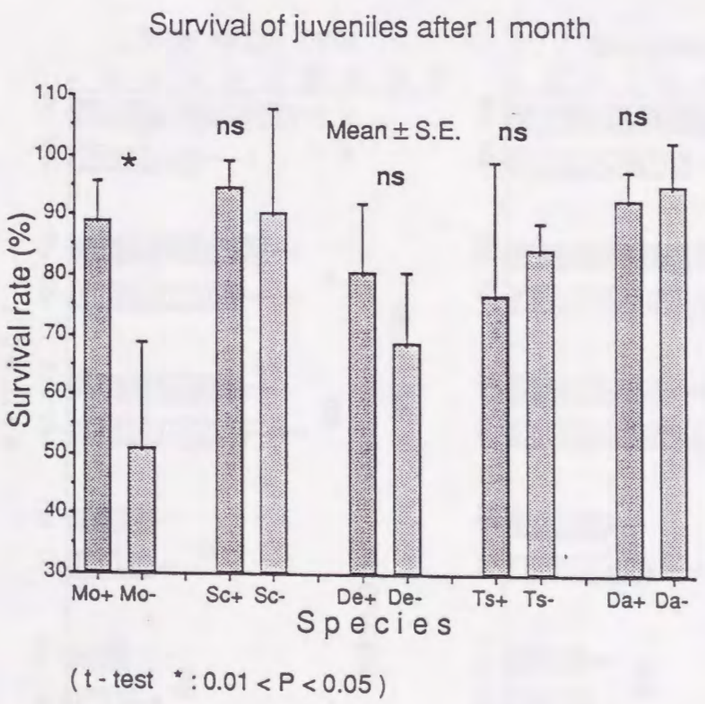


Fig. IV-8. Survival rate of the caprellid juveniles reared in situ for a period of 1 month. DA: Caprella danilevskii; DE: C. decipiens; MO: C. monoceros; SC: C. scaura; TS: C. tsugarensis; +: juveniles with mother; -: juveniles without mother.

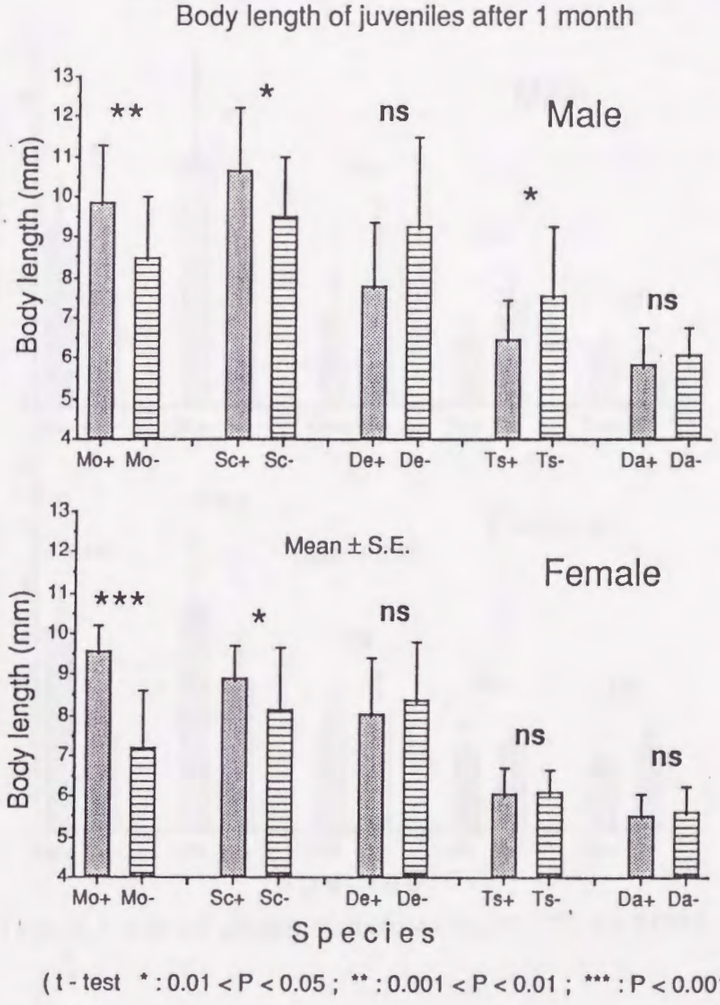


Fig. IV-9. Body length of the caprellid juveniles reared in situ for a period of 1 month (refer Fig. IV-8 for the explanation of the abbreviations).

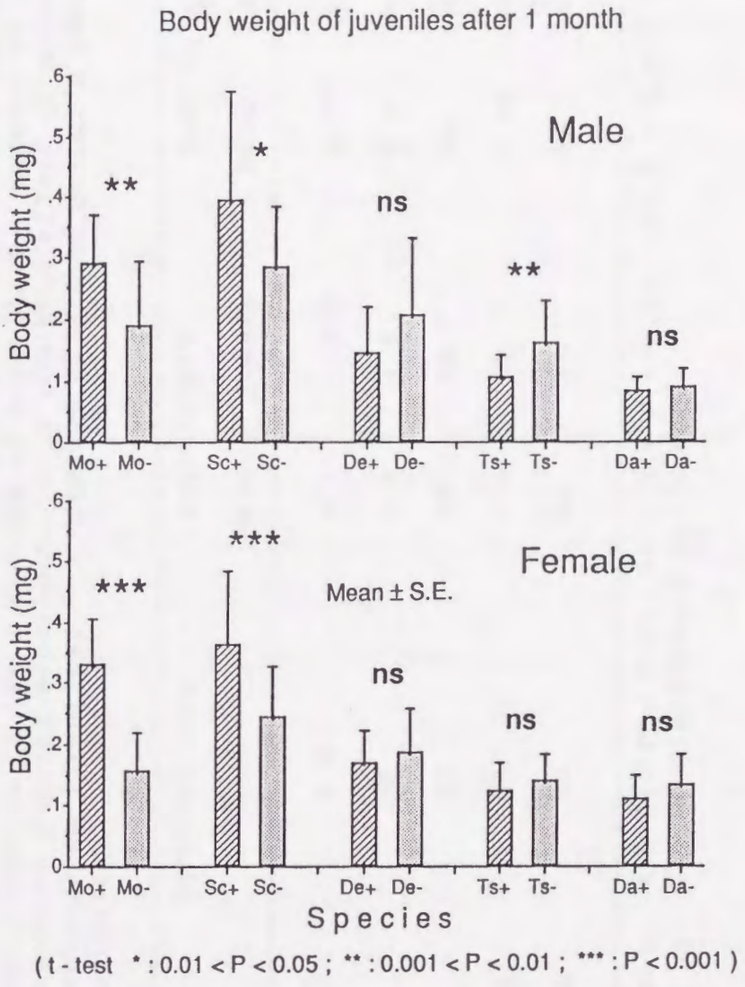


Fig. IV-10. Body weight of the caprellid juveniles reared in situ for a period of 1 month (refer Fig. IV-8 for the explanation of the abbreviations).

Table IV-5. Effect of the presence of mother presence on the early stage juveniles measured as the survival rate, body length and weight of the juveniles in the 5 species of caprellids. Summary of the one-month rearing experiment. + : positive effect of mother's presence on juveniles, - : negative effect of mother's presence on juveniles.

Species	Survival rate	Body length		Body weight	
		Male	Female	Male	Female
C. monoceros	+ *	+ **	+ ***	+ **	+ ***
C. scaura	NS	+ *	+ *	+ *	+ ***
C. decipiens	NS	NS	NS	NS	NS
C. tsugarensis	NS	- *	NS	- **	NS
C. danilevskii	NS	NS	NS	NS	NS

Student's t-test: * $0.01 < P < 0.05$, ** $0.01 < P < 0.01$, *** $P < 0.001$
NS: no significant difference

Among the species examined, the newly-born juveniles of *C. decipiens* had the longest pereopods 5 and 6 and a very long pereopod 7, though the body length was relatively small (Figs. IV-11, 12). It appears to be an adaptation for clinging to the *S. patens* branch immediately after the emergence from their mother's brood pouch. The newly-born juveniles of *C. monoceros* and *C. scaura* have unique characteristics in pereopods 7. The shape of the pereopod 7 of the juveniles are basically the same as those of the adults in other species (Fig. IV-13). However, in the above two species, the shapes of the pereopods 7 are apparently different from those of the adults. Propodus of pereopod 7 have deeply concaved grasping margin and the dactylus is slender and long (Fig. IV-14). The characteristic is more peculiar in *C. monoceros* than in *C. scaura*. The pereopod 7 seems to be the adaptation for clinging onto the thin part of mother's body. The shape of the pereopod 7 of the *C. monoceros* juvenile shows a drastic change as it grow up, by quickly turning to the shape which is similar to the adult pereopod (Fig. IV-15). The morphological change seems to be in accordance with the substrate shift of the juveniles, that is from the mother's body to the seaweed thalli.

IV-6. Discussion

Characteristics of the maternal care species

Caprella monoceros

The one-month rearing experiment showed that, in *C. monoceros*, the absence of the mother affected the survival and growth of the juveniles. Moreover, the pereopods of the juveniles seemed to be specialized for clinging onto the mother's body. The newly-born juveniles of the species never detached themselves from the mother's body until they reached the size enough for moving to the seaweed substratum. It is supposed that the size of the newly-born juveniles is too small to move onto the *S. patens* thalli, thus the mother of the species serves them by providing her body as the primary substratum for

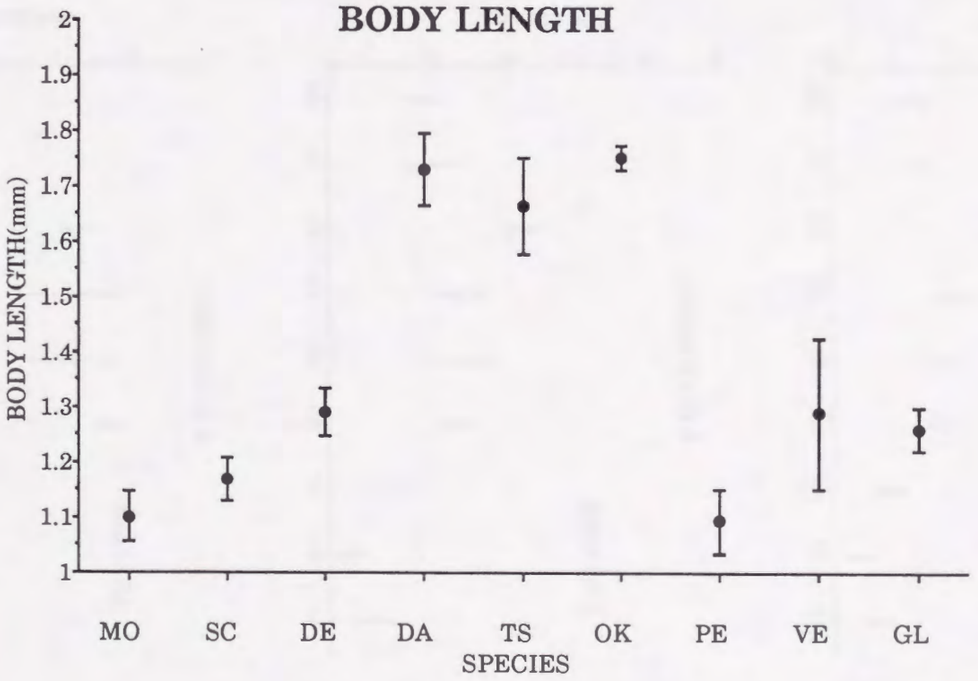


Fig. IV-11. Body length (mean and S.E.) of the first instar juveniles of 9 Caprella species. DA: Caprella danilevskii; DE: C. decipiens; GL: C. glabra; MO: C. monoceros; PE: C. penantis; SC: C. scaura; TS: C. tsugarensis; CV: C. verrucosa.

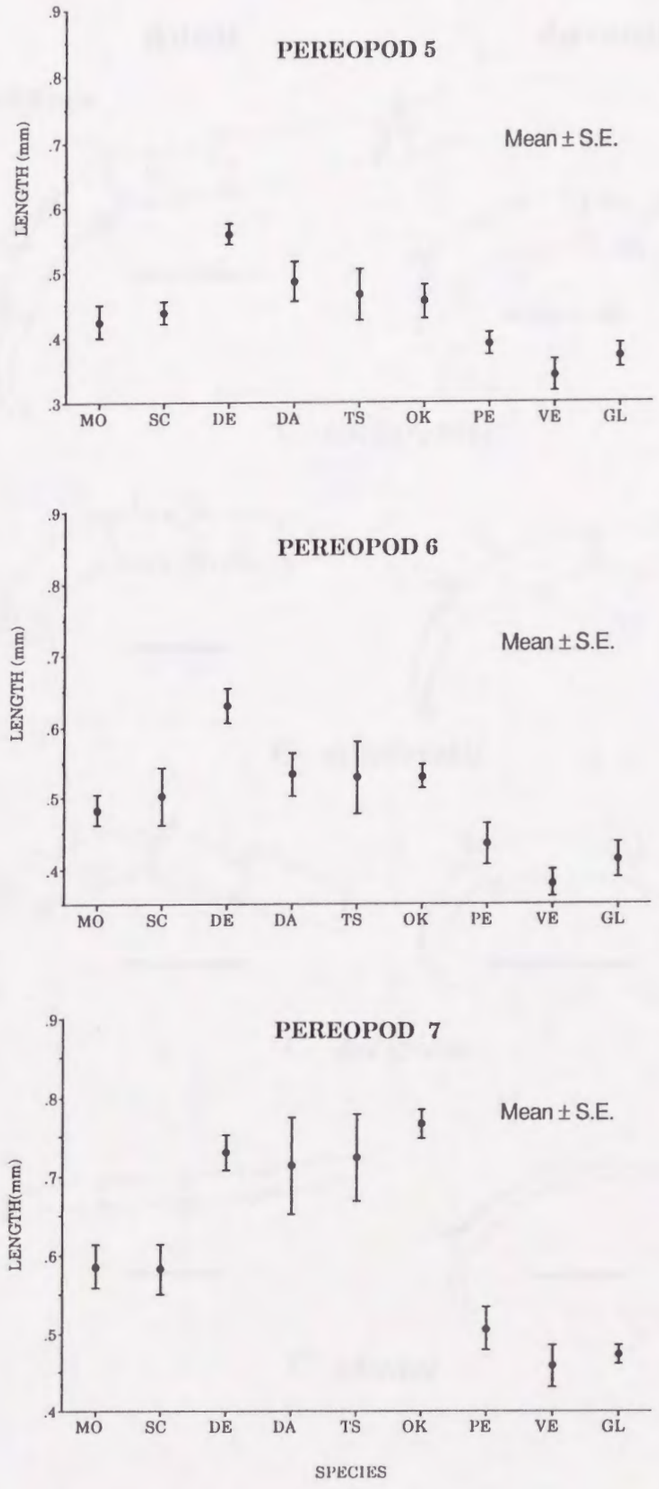


Fig. IV-12. Length (mean and S.E.) of pereopods 5-7 of the first instar juveniles of 9 Caprella species (abbreviations as in Fig. IV-11).

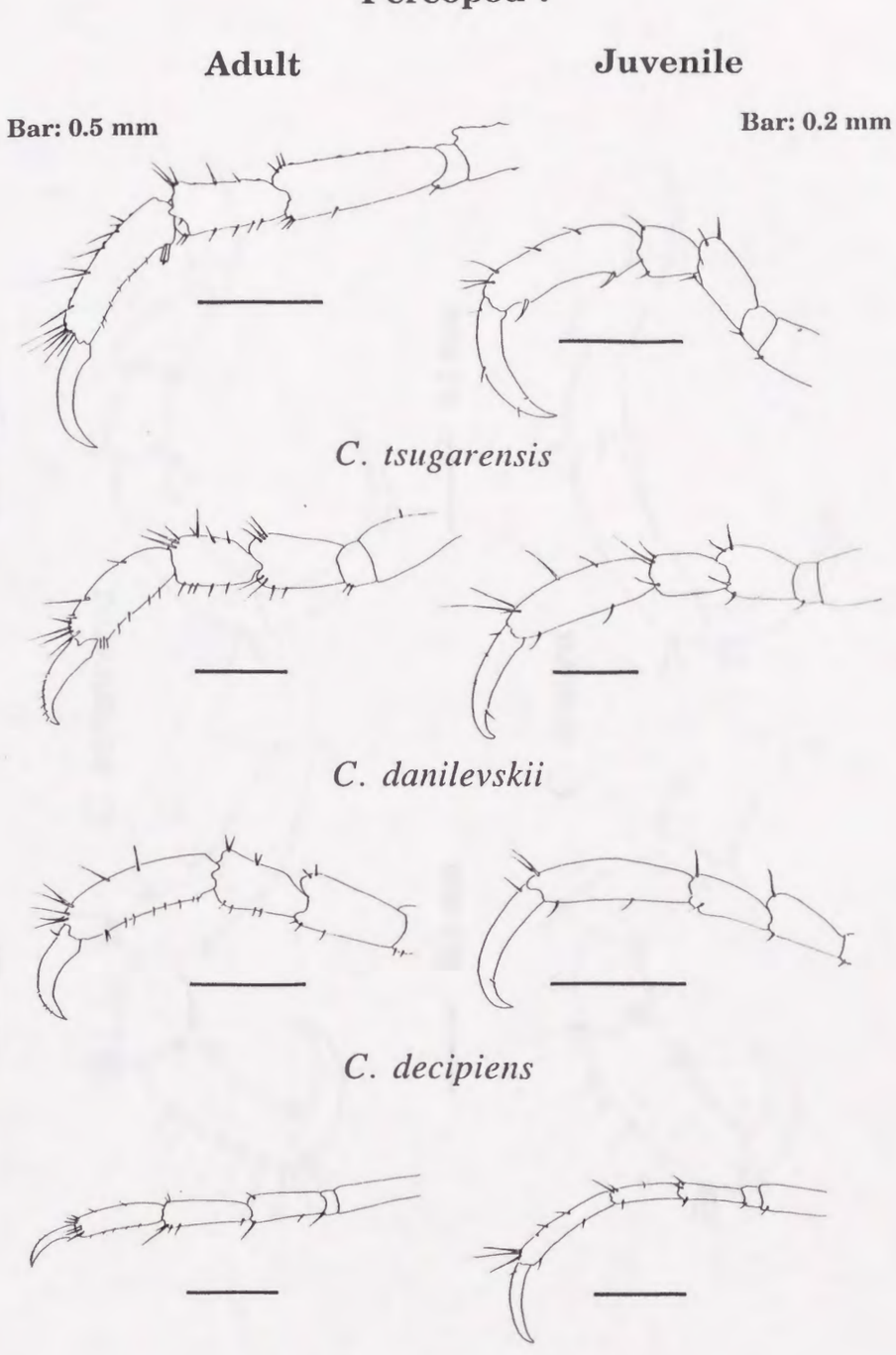


Fig. IV-13. Morphology of the pereopod 7 of adult female and first instar juvenile in 4 Caprella species.

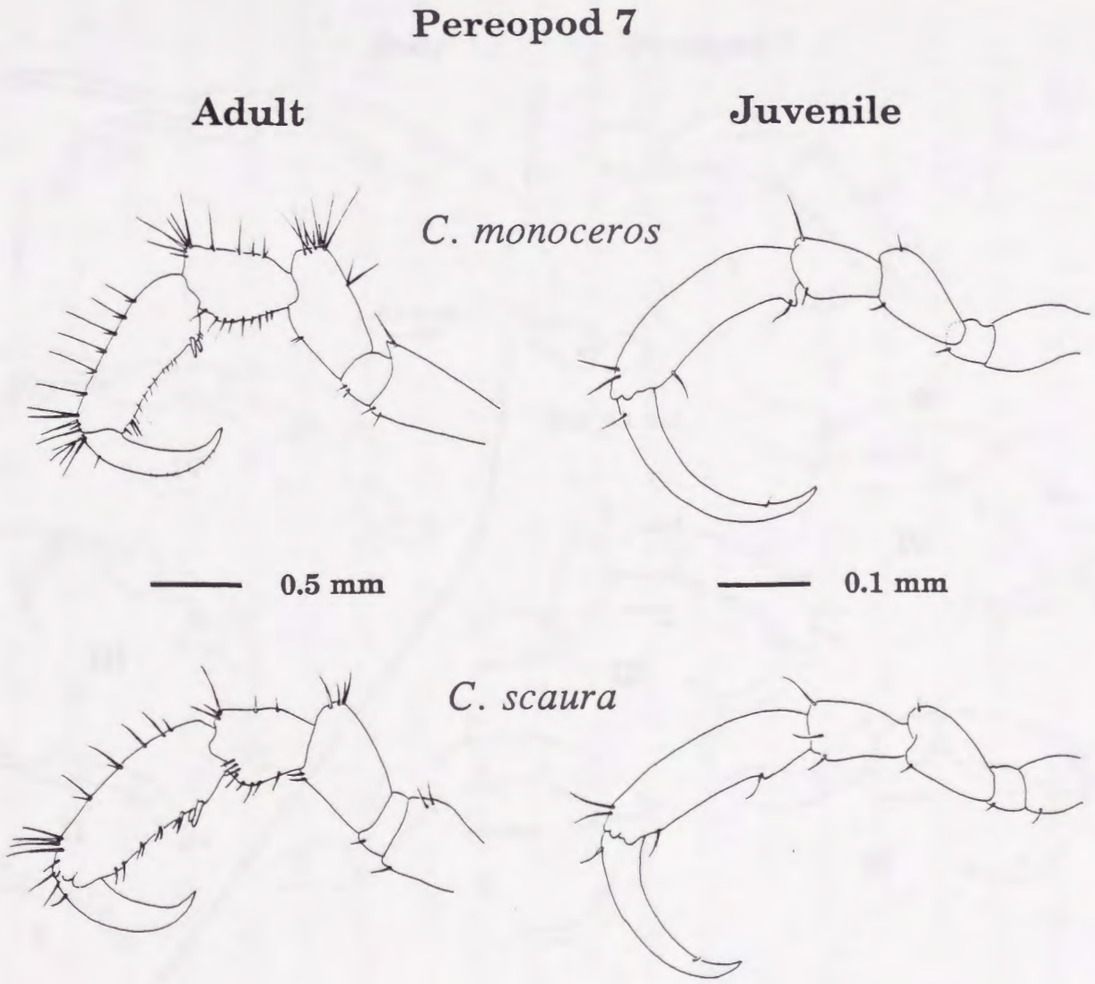


Fig. IV-14. Morphology of the pereopod 7 of adult female and first instar juvenile in 2 maternal care Caprella species.

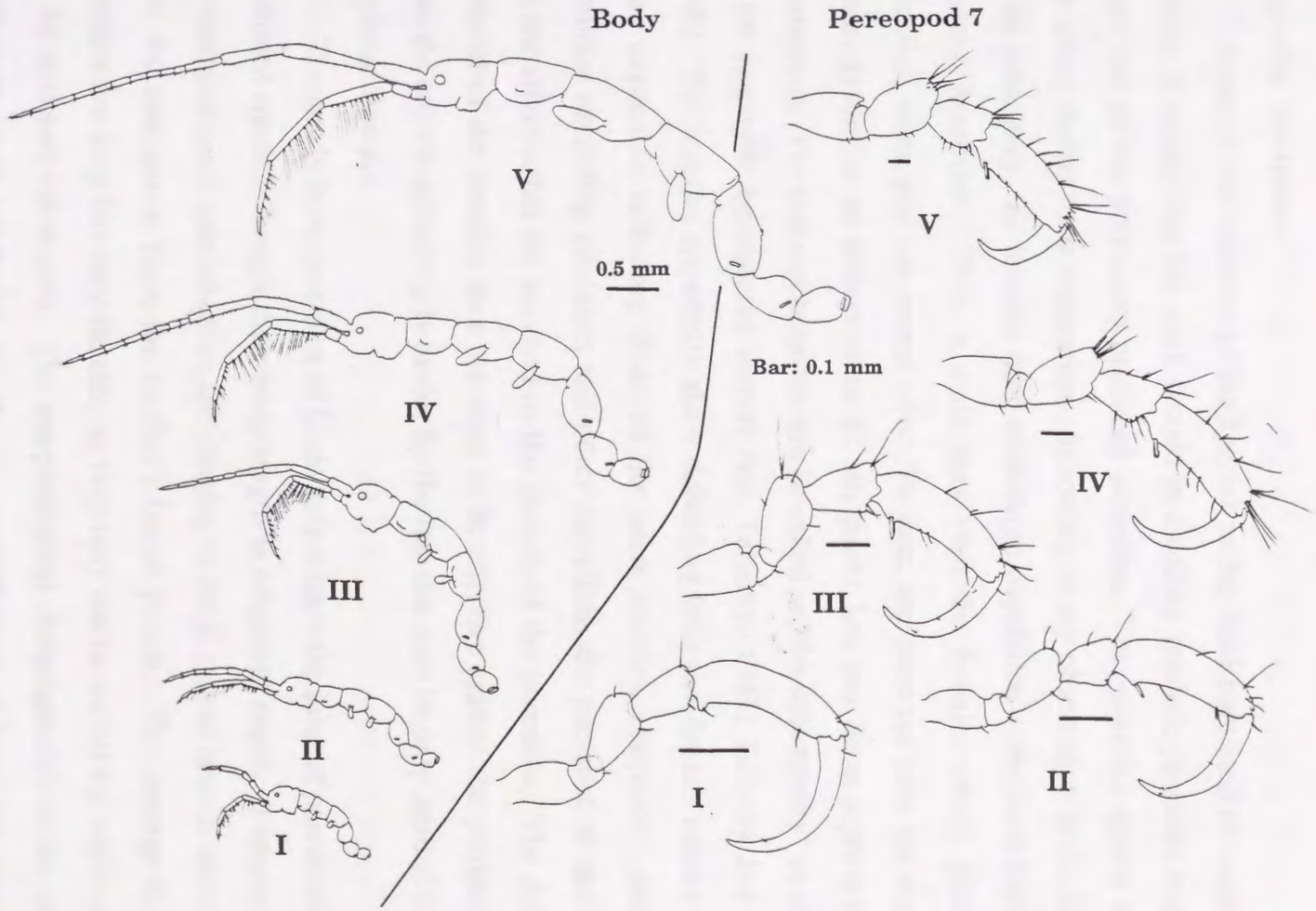


Fig. IV-15. Morphological changes in the juveniles of Caprella monoceros with growth.

attachment and growth. *C. monoceros* appears to be a species well specialized for the life on *Sargassum* thalli.

Caprella decipiens

Some of the colonies of the species in the field consisted of more than 1 cohort. It means that the adult female in a colony produce juveniles before the dispersion of the previously produced juveniles. The juveniles appear to leave the colony before their maturation. According to my observation in the field and in the laboratory, the females need to undergo copulation every time before they produce juveniles. Thus, a male may visit the female, which guards her juveniles, when she can accept him. To date, the maternal care for the multi-cohort juveniles as observed in *C. decipiens* has not been reported in the crustaceans. The colonial behavior can be called as "the subsociality" as observed in the epiphytic hemipteran insects (see Tallamy, 1984; Tallamy and Wood, 1986). The females apparently show defending behavior for her colony against other caprellids including those of the same species. However, under the condition excluding predators and other caprellids, the presence of the mother did not affect either the survival or the growth of the juveniles. The defending behavior of the females does not seem to be effective against the predatory fish. Thus the colony-defending behavior by the females may be only against the other epiphytic animals.

The newly-born juveniles of *C. decipiens* have the longest pereopods in the examined species, though their body length is relatively small. It appears to be the morphological specialization for clinging to the *S. patens* branch immediately after the emergence from the mother's brood pouch. The pereopods of the juveniles are long but very slender, so they may not be useful for rapid crawling on the seaweed substratum. The morphological characteristics of the juveniles seem to be as an adaptation for staying in the colony of juveniles guarded by their mother.

Caprella scaura

In *C. scaura,* the presence of the mother was effective for the growth of the juveniles, though not effective for the survivorship. Main habitats of the species are highly-branched turf red algae such as *Gelidium amansii.* Moreover, the newly-born juveniles could detach their mother and cling to the substratum. Thus, the mother's body seems to be not as much important as the juveniles' primary substratum in *C. scaura* than in *C. monoceros.* This explains the high survivorship of the species even under the absence of the mother. The morphological specialization of pereopods for clinging to the mother's body in the newly-born juveniles is less peculiar in *C. scaura* than in *C. monoceros.*

All these factors clearly explain that why *C. scaura* prefer to inhabit on the undergrowth turf algae than the *Sargassum* thalli.

Phylogenetic relation of *C. monoceros* and *C. scaura*

Behavioral and morphological similarities were present in *C. monoceros* and *C. scaura.* The clinging behavior of the juveniles and the care for them by their mother in *C. monoceros* is quite similar to that in *C. scaura* (Lim and Alexander, 1986; Aoki and Kikuchi, 1991). The arrangement of the dorsal spines of the *bidentata* type females of *C. monoceros* is quite similar to that of the *C. scaura* females (Arimoto, 1976; Aoki and Kikuchi, 1990b). Moreover, the morphological characteristics of the newly-born juveniles of *C. monoceros* and *C. scaura* resemble each other, though they look quite different from the other 7 species examined (see Table III-2; Figs. III-1, 2; Figs. IV-13, 14).

Considering the morphology of pereopods, early stage juveniles of *C. monoceros* is much adapted to cling to their mother's body than those of *C. scaura.* Moreover, according to the results of *in situ* survival experiment, the presence of mother is more necessary to the early stage juveniles in *C. monoceros* than in *C. decipiens.* Therefore, the maternal care behavior appears

to be more developed in *C. monoceros* than in *C. scaura*, hence making *C. monoceros* to dominate on the *S. patens* thalli, which have broader leaves than those of red algae.

Caprella monoceros is endemic to Japan and its adjacent waters (McCain and Steinberg, 1970; Aoki and Kikuchi, 1990b). On the other hand, *Caprella scaura* distributes widely over the world (McCain and Steinberg, 1970; Arimoto, 1976). Taking account of the geographical distribution of the two species, *C. monoceros* seems to be derived from the original species of *C. scaura* or from *C.scaura* itself. Habitat segregation or any geographical or reproductive segregation should have worked on the speciation of *C. monoceros*.

Dependence on substratum of *C. decipiens* and *C. monoceros*

Both *C. decipiens* and *C. monoceros* are the species dominated on *S. patens* thalli. They appear to be well adapted to the life on the *S. patens* thalli. However, the mode of adaptation on the seaweed thalli is quite different between the 2 species. In *C. monoceros*, the early stage juveniles are carried by their mother, thus the juveniles do not have to use the seaweed substratum. On the other hand, in *C. decipiens*, the newly-born juveniles have to use the *Sargassum* thalli as their primary substratum, and the size of a colony consisting more than 1 cohort of juveniles is very large. Thus, the mother of *C. decipiens* can hardly move her whole colony to other places, though the mother can manage to move a part of juveniles in the colony in case of emergency (Aoki and Kikuchi, 1991).

From the above mentioned factors, it is concluded that *C. decipiens* is more dependent on using seaweed substratum in its life history than in *C. monoceros*.

Mother-juvenile communication

The three maternal care species share some common behavioral characteristics. First, the juveniles stay around their mother after the emergence from the brood pouch, while the juveniles of the caprellids with no maternal care

disperse immediately after the emergence. Second, the mother gathers her juveniles and carries them away to another place in case of emergency, which is the common behavior in *C. decipiens, C. monoceros* and *C. scaura*. Considering the above two behavioral characteristics, it is believed that there should be some communication between a mother and her juveniles in the maternally cared caprellids. In Crustacea, the chemical communication while the maternal behavior has been reported in crayfish (Little, 1975, 1976). In Amphipoda, a female sex pheromone and a male chemo-sensory antennal receptor for sensing the female pheromone has been reported (Dahl et al., 1970).

Phylogenetic implications of maternal care in caprellids

The development of amphipods in the brood pouch can be divided into two periods: 1) from ovulation to hatching (the embryonic period), and 2) from hatching to emergence from the brood pouch (the juvenile period) (Borowsky, 1980). The former is the period of maternal care for eggs and the latter is for the juveniles. Moreover, the maternal behavior observed in caprellids are the maternal care for juveniles in "the period after the emergence from brood pouch" (the post-emergence period) (Aoki and Kikuchi, 1991).

In other amphipod crustaceans, besides caprellids, some reports have been made on the mother-juvenile interactions in the post-emergence period. However, most of them are short descriptions as a part of the ecological studies and have not viewed in detail from the behavioral aspects. Therefore, in the following section, I reviewed the information on the mother-juvenile interactions of amphipods in the post-emergence period.

In Gammaridea, the behavior in which juveniles emerge from the brood pouch and return to the brood pouch has been known in *Neohaustorius schmitzi* (see Croker, 1968), in *Eulimnogammarus (Marinogammarus) obtusatus* and *E. finmarchicus* (see Sheader and Chia, 1970) and in *Gammarus palustris* (see Borowsky, 1980). Furthermore, in *Dulichia rhabdoplastis* and *Dyopedos*

monacanthus, the mother constructs a mast-like structure as her territory and stays there with her juveniles for a certain period. In particular, in *D. monacanthus*, the mother on the mast defends her juveniles against other animals (McCloskey, 1970; Mattson and Cedhagen, 1989). It is generally accepted that caprellids have evolved from podocerid-like ancestors in Gammaridea in the process of adapting to the 'clinging to the substratum' type life style (McCain, 1970; Laubitz, 1976). It is noticeable that the maternal behavior which is quite similar to the one in caprellids was observed among the podocerids (Mattson and Cedhagen, 1989), the ancestral amphipods of caprellids.

In Hyperiidea, the maternal society has been known in *Phronima sedentaria* (Laval, 1980). The newly-born juveniles (up to 600) of *P. sedentaria* grasp the wall of the host barrel and arrange themselves in a compact cluster. In the cluster the juveniles always show a spatial organization. When the mother is removed, the whole group of juveniles passes on to the outer surface of the barrel where they can not feed. Usually, the passage of the juveniles on to the outer surface of the barrel is prevented by their mother. She forces the juveniles back in the middle of the barrel by combing them inwards with the tip of the gnathopods. Moreover, the mother brings prey to the juveniles (see the review by Laval, 1980).

In other peracarid crustaceans, the formation of monogamous social colony has been reported in *Hemilepistus reaumuri*, an oniscoid isopod (Linsenmair and Linsenmair, 1971; Linsenmair, 1972).

From the above reported observation, one general tendency appear to present in the mother-juvenile interaction during the post emergence period. The mother-juvenile interaction seem to be well developed in the animals which have smaller mobility and living in a limited and unstable habitat.

Laval (1980) noted in his review, "Phronimids make a nest from a living host, an habit closer to that of parasitoid insects which lay their eggs on or inside a host." There is a good possibility that the mother-juvenile interaction in the

post-emergence period is widely present among other peracarid crustaceans. They could have subsocialities or possibly socialities which are as equivalent to those in terrestrial insects.

Part V. Microhabitat utilization

V-1. Introduction

To date, Caine (1979b) described the microhabitat utilization of caprellids on seagrass leaves. Morphological adaptations of caprellids to the microhabitats such as hydroids were reported by Caine (1978), Vader (1983) and Aoki and Kikuchi (1990a). In Aoki and Kikuchi (1990a), we studied the morphological adaptation of caprellids inhabiting a hydroid *Plumularia setacea*, an epiphytic secondary habitat on *S. patens* thalli. However, in these studies, microhabitat utilization by juvenile caprellids and the actual utilization of epiphytic microhabitats through the life history of caprellids were not examined.

V-2. Field samplings

Materials and methods

To examine the microhabitat utilization of the caprellids in the *Sargassum patens* bed, "microhabitat samplings" were conducted by SCUBA diving. Firstly, on April 9, 1988, caprellid fauna on two species of epiphytic hydroid: *Thecocarpus nigra* and *Plumularia setacea* were examined. Six colonies of *T. nigra* and 5 colonies of *P. setacea* were collected. They were brought back to the lab, fixed with neutralized formalin, sorted and counted. Secondly, on April 21, 1991, to compare the fauna on the different microhabitats, the caprellids directly attaching to the seaweed substrata and the caprellids inhabiting epiphytic hydroid *Aglaophenia suensoni* were collected separately. Eight pieces of *Sargassum patens* without hydroids on their surface were cut out from the middle height of the different plants (length of the main stem: 30cm each), and gently put each piece of seaweed in the 450cc glass bottle respectively. Eight colonies of *Aglaophenia suensoni* on the *S. patens* were cut out from different plants and put each colony in separate 450cc glass bottles. These specimens were taken back to the laboratory immediately after the collection, and observed under the binocular

microscope to know the exact locations to where the juveniles were clinging to. All of them were fixed with neutralized formalin after the observation, sorted and counted. To compare the thickness of the substrata where the juveniles were clinging to, the thicknesses of hydroid branches, tips of the *S. patens* branches and appendages of the female *C. monoceros* were measured. Substrate seaweeds and hydroids were dried and weighed. Total dry weight of 8 substrate seaweed samples was 21.17 g (105 °C, 24hrs.), and total dry weight of 8 substrate hydroids was 153.5 mg (60 °C, 24 hours). When it was needed, 100um mesh was used for sieving animals. While the 100um mesh sieve was used, all caprellids including the newly-born juveniles of all species were retained. The caprellid fauna on the epiphytic hydroids and that on *Sargassum* thalli were compared. In particular, the utilizations of microhabitats by the newly-born juveniles, which have two-segmented flagellar articles on antenna 1, were noted.

Results

Interspecific difference of the microhabitat utilization

Unique caprellid fauna were present on the epiphytic hydroids, and not found on the *S. patens* thalli. *Hemiaegina minuta* and *Paracaprella crassa* were found only on *Plumularia setacea* (see Fig. V-1). *Caprella glabra* were found on *Aglaophenia suensoni* and on *Thecocarpus nigla* (see Fig. V-1; Table V-1).

With respect to the microhabitat utilization by the newly-born juveniles, an interspecific difference could be detected (Table V-1). The newly-born juveniles of *C. penantis* and *C. verrucosa* were found only on the hydroids and not found on the *S. patens* thalli, even though the larger individuals could be observed on the thalli. On the other hand, the newly-born juveniles of *C. danilevskii, C. tsugarensis* and *C. okadai* were clinging to the *S. patens* thalli and rarely occurred on the hydroids. The early stage juveniles of *Caprella monoceros* were clinging to their mother and never found on other substrata, as mentioned in the Part IV.

Caprellids on epiphytic hydroids

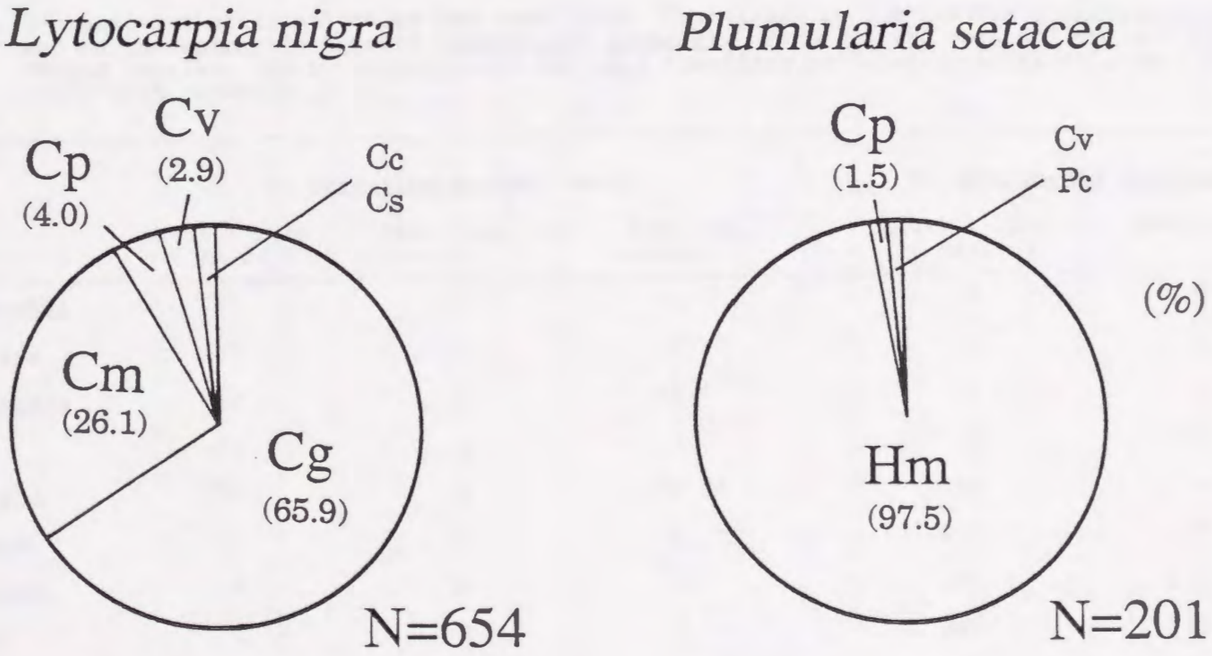


Fig. V-1. Caprellid fauna on epiphytic hydroids on Sargassum patens (proportion in %). Cc: Caprella californica; Cg: C. glabra; Cm: C. monoceros; Cp: C. penantis; Cs: C. scaura; Cv: C. verrucosa; Hm: Hemiaegina minuta.

Table V-1. Microhabitat utilizations by the caprellids. Caprellids on the seaweed Sargassum patens thalli and on the epiphytic hydroid Aglaophenia suensoni. Both seaweed data and hydroid data are from 8 samples. FA-x: individualds having x flagellar articles on antenna 1, FA-2 is the newly-born juvenile.

Species	On Sargassum patens thalli			On Aglaophenia suensoni	
	Adult + Juvs. (FA-2<)	FA-2 juvs. on thalli	Juvs. on mother	Adult + Juvs. (FA-2<)	FA-2 juvs.
C. danilevskii	20	4	0	0	0
C. decipiens	37	0	0	0	0
C. tsugarensis	19	3	89 *	0	0
C. okadai	11	4	0	0	0
C. monoceros	176	0	27 **	144	0
C. penantis	1	0	0	218	93
C. verrucosa	7	0	0	337	219
C. glabra	0	0	0	468	49
C. californica	0	0	0	3	0

*: FA-2 juvs on mother; ** : FA 6 > juvs on mother

The thickness of the hydroid stem and branches were apparently thinner than that of *S. patens* branches. The thickness of the appendages of the female *C. monoceros*, to where the juveniles were clinging, were nearly the same as that of the hydroids (Table V-2).

The size of newly-born juveniles

The juveniles of non-maternal care species living on hydroids were small (1.0-1.3mm in body length), though the juveniles clinging to the *S. patens* thalli were larger (1.6-1.8mm in body length)(see Table III-2; Fig. IV-11). The juveniles of three maternal care species were smaller in size and showed morphological adaptations in their pereopods for clinging to their habitat substratum (Table III-2; Fig. IV-11; Figs. IV-13, 14).

V-3. Discussion

With respect to the interspecific difference of habitat utilization and the maternal care behavior of some species, the ways of microhabitat utilization by caprellids can be classified into 4 types (Fig. V-2).

A) Both adults and juveniles use *S. patens* thalli as their substrata. Non-maternal care species. Large Juveniles (BL: 1.6-1.8mm) after emergence from the mother's brood pouch immediately disperse onto the *S. patens* thalli.

B) Smaller juveniles (BL: 1.0-1.3mm) stay on or around their mother under the maternal care. They disperse when they reach the size to crawl on the *S. patens* thalli.

C-1) Smaller juveniles (BL: 1.0-1.3mm) use epiphytic hydroids as their substrata. They can move to the seaweed thalli as they grow up. Non-maternal care species.

C-2) Both small juveniles (BL: 1.0-1.3mm) and adults use epiphytic secondary habitats, and never found on the *S. patens* thalli. Non-maternal care species.

Table V-2. Size of the clinging substrata where the juveniles were found attached to. Mean [S.E.] (mm) of diameters. Number in parenthesis represents the number examined (Data of A and B are from Aoki and Kikuchi, 1991).

A. Size of the body parts of C. monoceros adult females where the juveniles were found attached to; Gl: Gill; Gn: Gnathopod; Pd: Pereopod; Pn: Pereonite; ND: no data available.

Pereonites of Mother		Appendages / Gills of Mother	
Pn 2	0.55 [0.10] (4)	Gn 2	0.18 [0.02] (4)
Pn 3	0.61 [0.08] (4)	Gl 3	0.18 [0.03] (4)
Pn 4	ND	Gl 4	0.18 [0.02] (4)
Pn 5	0.61 [0.09] (4)	Pd 5	0.24 [0.03] (4)
Pn 6	0.50 [0.05] (4)	Pd 6	0.24 [0.03] (4)
Pn 7	0.44 [0.04] (4)	Pd 7	0.25 [0.03] (4)

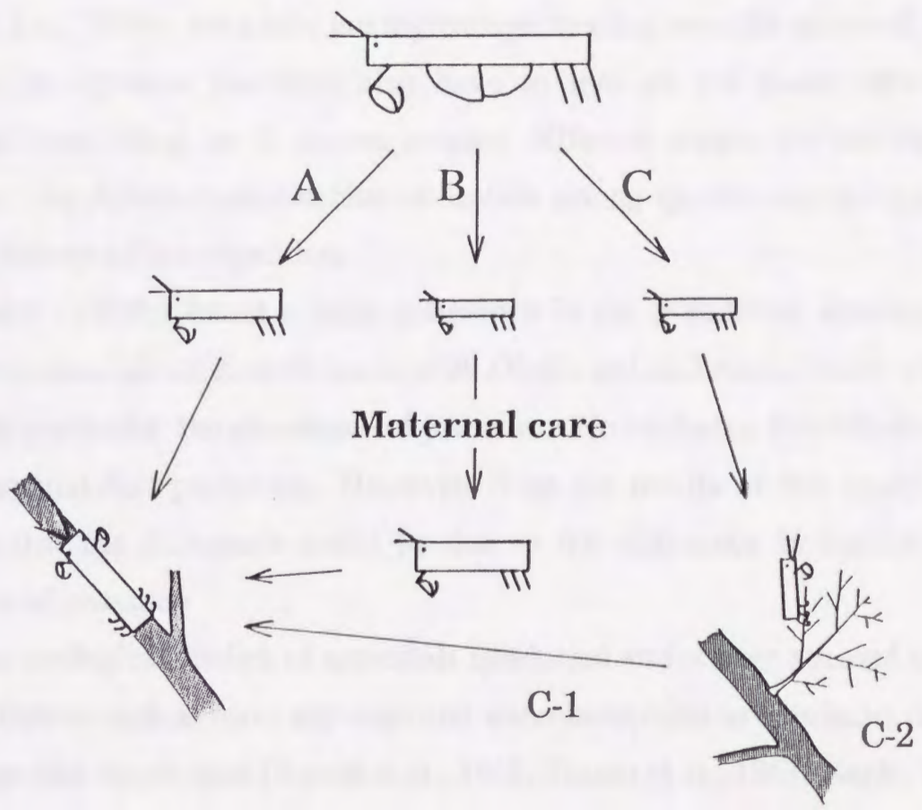
B. Size of the seaweed branch where the C. monoceros juveniles were clinging onto.

Branch	0.93 [0.18] (11)

C. Size of the stem and branch of Aglaophenia suensoni.

Stem	Hydrotheca on Branch	
	Thickest part	Thinnest part
0.20 [0.02] (8)	0.23 [0.03] (8)	0.12 [0.01] (8)

Microhabitat utilization of caprellids



Group	A	B	C-1	C-2
Habitat (Juv. → Adult)	S→S	[Care]→S	H→S	H→H
Species	*C. danilevskii* *C. okadai* *C. tsugarensis*	*C. decipiens* *C. monoceros* *C. scaura*	*C. penantis* *C. verrucosa*	*C. glabra*

Fig. V-2. Schematic representation of the microhabitat utilization by Caprella species. S: Sargassum patens thalli; H: epiphytic hydroids on S. patens

The point is that, the species bearing larger juveniles release the juveniles directly onto the seaweed thalli, though the species bearing smaller juveniles have to use the epiphytic secondary habitat or have to experience the mother's care. The caprellids living on the large seaweed such as *S. patens* have to face the problem, i.e., "While the adults are big enough to cling onto the seaweed thalli, even the newly-born juveniles also have to live on the same substrata." Caprellids coexisting on *S. patens* employ different means for solving the problem. The different microhabitat utilization among species may mitigate the possible interspecific competition.

Caine (1979b) found a large difference in the population structures of *Caprella laeviuscula* on *Zostera* leaves with *Obelia* and on *Zostera* leaves without *Obelia,* in particular the abundance of juveniles. He attributed this difference to the differential fish predation. However, from the results of this study, it is believed that the difference could be due to the difference in microhabitat utilization of juveniles.

The ecological studies of caprellids conducted so far have stressed on the physical factors such as wave exposure and water movement as regulating factors of the caprellid distribution (Round et al., 1961; Sloane et al., 1961; Nagle, 1968; Hirayama and Kikuchi, 1980; Takeuchi et al, 1987). However, the size and morphology of the juvenile caprellids apparently limit their habitat preferences. Taking account of the life style of caprellids largely depending on the substratum and their low swimming capacity, the morphological characteristics of the early stage juveniles appear to be the one of the important limiting factors of the caprellid distribution.

Part VI. Growth and reproduction

VI-1. Introduction

So far, numerous studies have been made on the life history and the reproductive ecology of gammarid amphipods (see reviews of Morino, 1978; Nelson, 1980; Van Dolah, 1980; Wildish, 1982; Fenwick, 1985; Dauvin, 1989; Sainte-Marie, 1991). Many of the gammarids have relatively long generation time and have limited reproductive seasons, thus the overlapping of generations is little. Therefore, in the most of the ecological studies of gammarids, field populations were examined by the size structure analysis. In order to support the field data, laboratory rearing (Cooper, 1965; Morgan and Woodhead, 1984; Kusano et al., 1987; Naylor et al., 1988; Kusano, 1989; Kamihira, 1990a) and *in situ* rearing (Hiwatari and Kajiwara, 1984) experiments have been conducted. *In situ* rearing have also been used for the species which have overlapping generations such as some species of *Corophium* (Birklund, 1977; Omori and Tanaka, 1984).

On the other hand, in caprellid amphipods, reproductive characteristics (Bynum, 1978; Lewbel, 1978; Costello and Myers, 1989; Sakaguchi, 1990; Takeuchi and Hirano, 1991; Vassilenko, 1991) and reproductive behaviors (Lewbel, 1978; Lim and Alexander, 1986; Aoki and Kikuchi, 1991; Caine, 1991a) only have been studied. Though some attempts have been made to know the life history characteristics of the field population of caprellids, the results of most of the studies were inconclusive (Bynum, 1978; Imada and Kikuchi, 1984; Aoki, 1988). Only the studies of *Caprella septentrionalis* in White Sea (Heptner, 1963) and *Pseudoprotella phasma* inhabiting a hydroid (Hughes, 1978) have succeeded in cohort analysis of field populations. In the temperate regions, caprellids of the genus *Caprella* reproduce all through the year with short generation period, thus the cohort analysis of their field populations seems to be almost impossible (Bynum, 1978; Lewbel, 1978; Imada and Kikuchi, 1984; Aoki,

1988). Rearing experiments appear to be useful to know the life history of field populations of caprellids. However, the actual food utilization of most of the caprellids in the field are still unknown. Though some attempts of long term rearings of caprellids in the laboratory have been made (Sakaguchi, 1989; Takeuchi and Hirano, 1991), it is difficult to apply the laboratory data to the field populations. As has been shown in the studies of deposit feeding gammarid, *Corophium* (Birklund, 1977; Omori and Tanaka, 1984), *in situ* rearing experiments are quite useful for the field populations which have overlapping generations. The *in situ* rearing method of caprellids have already been reported (Aoki and Kikuchi, 1990b; Aoki, 1991b). While the laboratory rearings of caprellids need much maintenance effort even for one species, the *in situ* rearing method in Aoki (1991b) makes it possible to rear many species at a time with little maintenance effort. Using this *in situ* rearing experiment, the individuals of plural species can be reared simultaneously, and reliable comparative data on reproductive characteristics of the species can be obtained.

In Part VI of this thesis, the growth and reproductive characteristics of caprellids were investigated. Both laboratory rearing and *in situ* field rearing experiments have been conducted. At the same time, field samplings have also been conducted in order to obtain the data on the reproductive traits of field populations. The relation between the maternal care behavior, microhabitat utilization, and the life history characteristics of each caprellid were revealed by the results of the rearing experiments and the field population investigations.

VI-2. Laboratory experiments

Materials and methods

Laboratory rearing experiments of female caprellids were conducted in order to know their brooding cycles. The increase in the number of antenna 1 flagellar articles per one molt was also examined, which was to know the validity of the character as an indicator of moltings.

Four species of caprellids, *Caprella danilevskii, C. decipiens, C. monoceros* and *C. tsugarensis* were selected for the rearing experiment. They consisted of 2 maternal care species and 2 non-maternal care species. The rearing method and the rearing condition were described in Part IV-2 (see Figs. IV-2, IV-3). Adult males and ovigerous females which were just ready to release juveniles were collected underwater following the method described in Part III-3. One female and 1-3 males were put in the 155cc glass bottle. About 10 replicates were provided for each species. During February-June, 1991, the animals in each bottle were examined everyday, and moltings, ovulations and juvenile release of females were recorded. Every time the mother of non-maternal care species released her juveniles, the juveniles were removed. The juveniles produced by the maternal care species were removed as soon as they detach from their mother's body. When a female molted, old exoskeleton was retrieved and the number of antenna 1 flagellar articles were counted.

Results

Brooding cycle

The results of the examination of brooding cycles: the interval between a juvenile release and the next one (J-J interval), between a juvenile release and the following molting (J-M interval), and between a molting and the following juvenile release (M-J interval) of 4 species were in shown in Figs. VI-1-4 and in Table VI-1. In all the species examined, ovulations of females followed moltings within 1 day.

Caprella danilevskii

Seven females released juveniles at least 3 times, the maximal one released juveniles 10 times during 10 weeks (Fig. VI-1; Table VI-1). The brooding cycle of this species was the shortest among the 4 species examined, and also it got shortened as temperature became higher. Molting, copulation and ovulation

occurred within 0-3 days after the releasing of juveniles except for one example in early March (6 days).

The mean J-J interval was 11 days in March, 8.36 days in April and 7.71 days in May. The mean J-M interval in days was 2.44 in March, 1.59 in April and 0.83 in May. The mean M-J interval was 9.50 days in March, 7.09 days in April and 6.75 days in May.

Caprella decipiens

Ten females released juveniles at least twice, the maximal one released juveniles 5 times during 11 weeks (Fig. VI-2; Table VI-1).

The mean J-J interval was 12.00 days in March-April and 12.86 days in May-June. The mean J-M interval was 2.83 days in March-April and 5.6 days in May-June. The mean M-J interval was 9.20 days in March-April and 7.80 days in May-June.

Caprella monoceros

Ten females released juveniles at least twice, the maximal one released 4 times during 13 weeks (Fig. VI-3; Table VI-1). The brooding cycle of this species was the longest among the 4 species examined, though it got shortened according to the temperature increase. The female, which released juveniles, needed 10-29 days for the next molting and ovulation.

The mean J-J interval was 30.83 days in March-April and 18.00 days in May-June. The mean J-M interval was 21.5 days in March-April and 13.8 days in May-June. The mean M-J interval was 8.83 days in March-April and 6.33 days in May-June.

Caprella tsugarensis

Nine females released juveniles at least twice, some of them released juveniles 3 times (Fig. VI-4; Table VI-1).

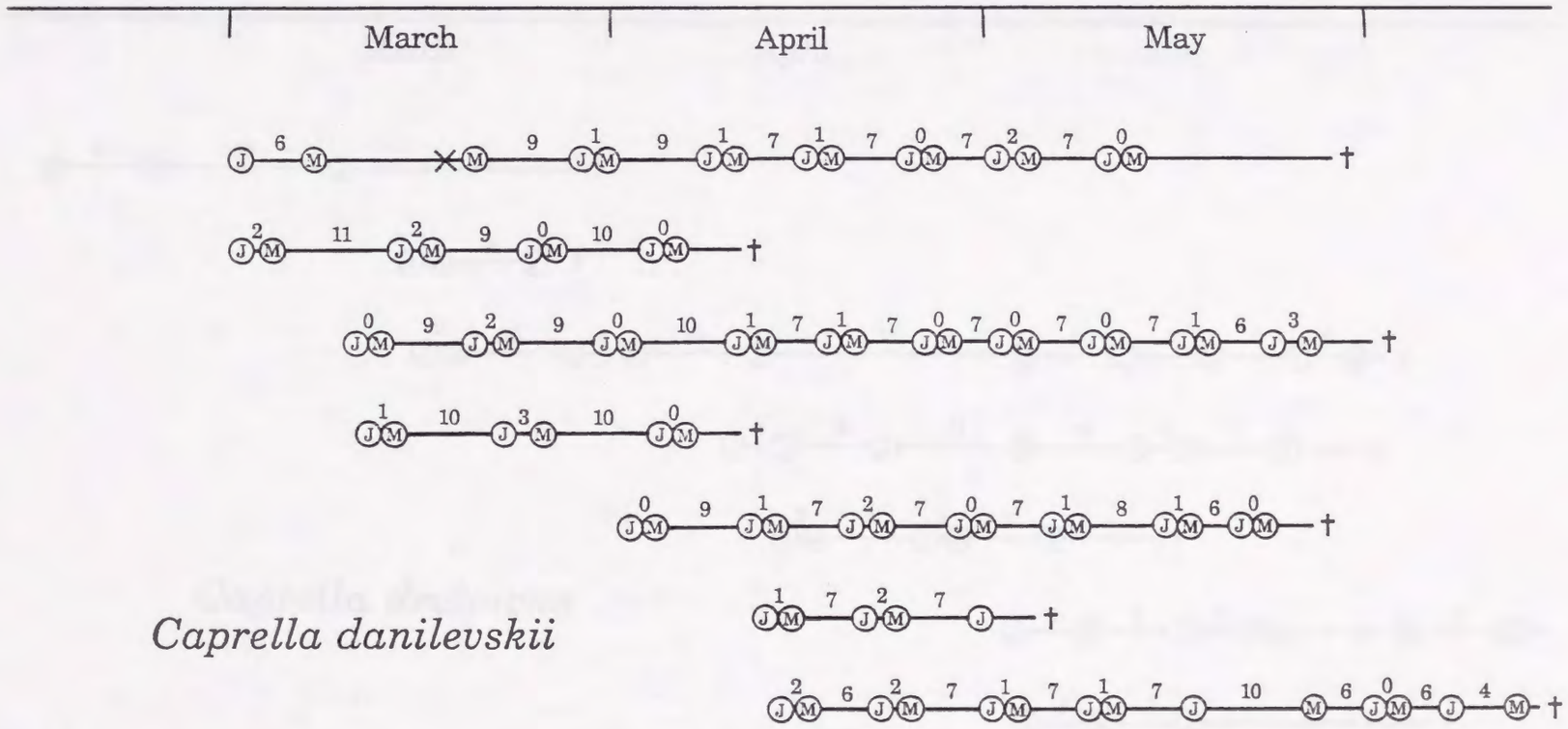


Fig. VI-1. Brooding cycle of Caprella danilevskii reared in the laboratory. Numerals are the intervals in days.

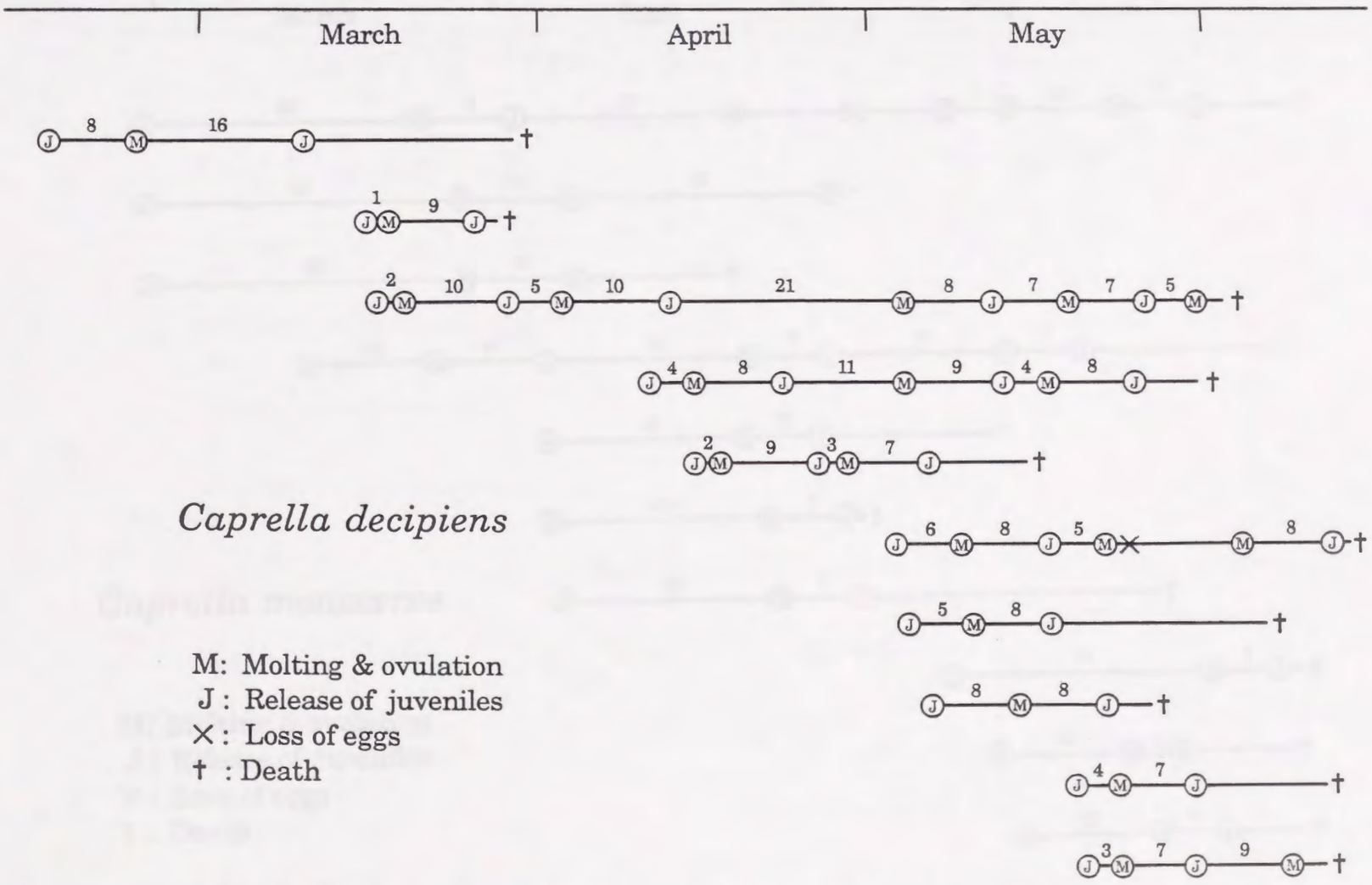
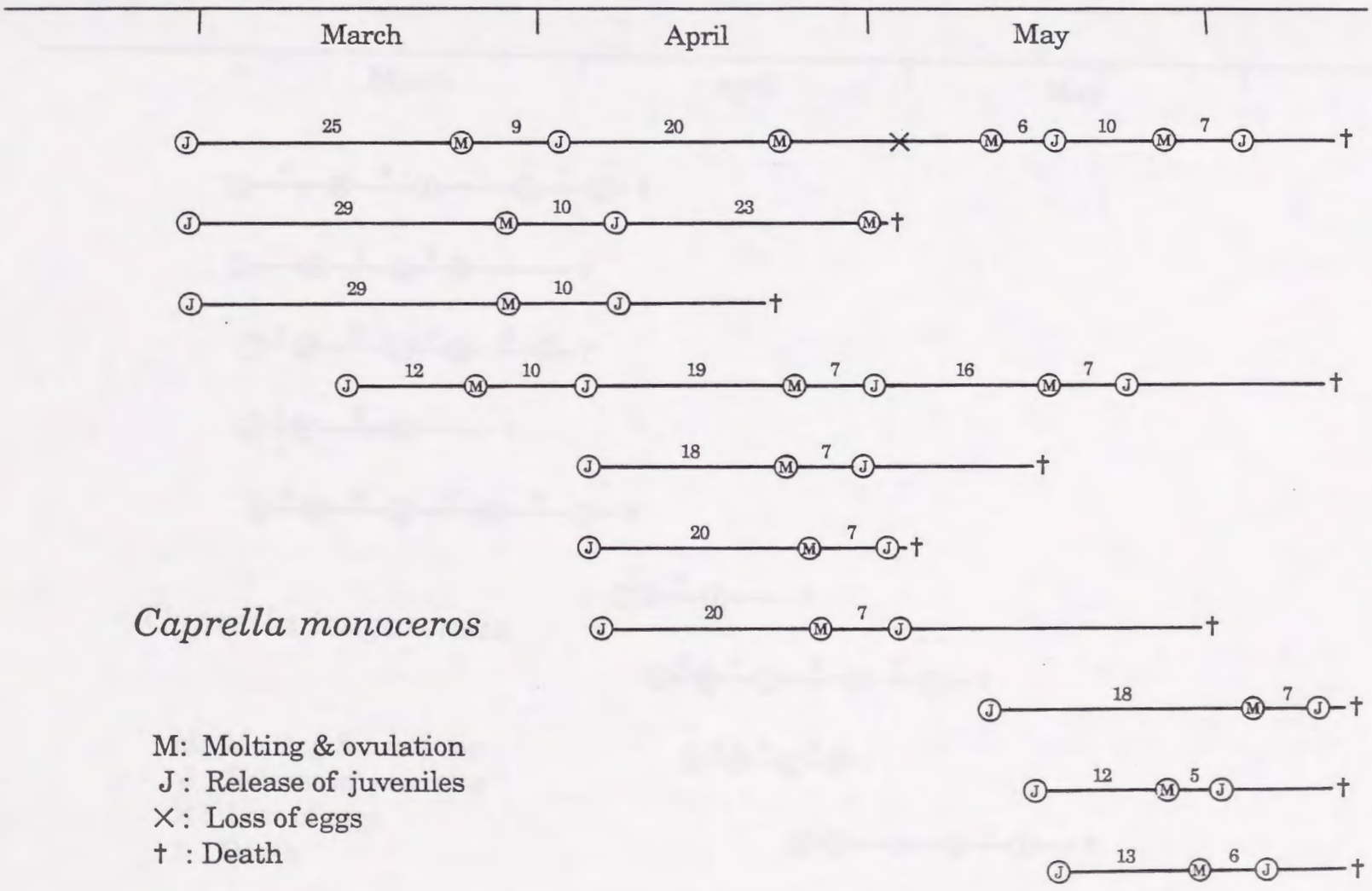


Fig. VI-2. Brooding cycle of Caprella decipiens reared in the laboratory. Numerals are the intervals in days.



Caprella monoceros

Fig. VI-3. Brooding cycle of Caprella monoceros reared in the laboratory. Numerals are the intervals in days.

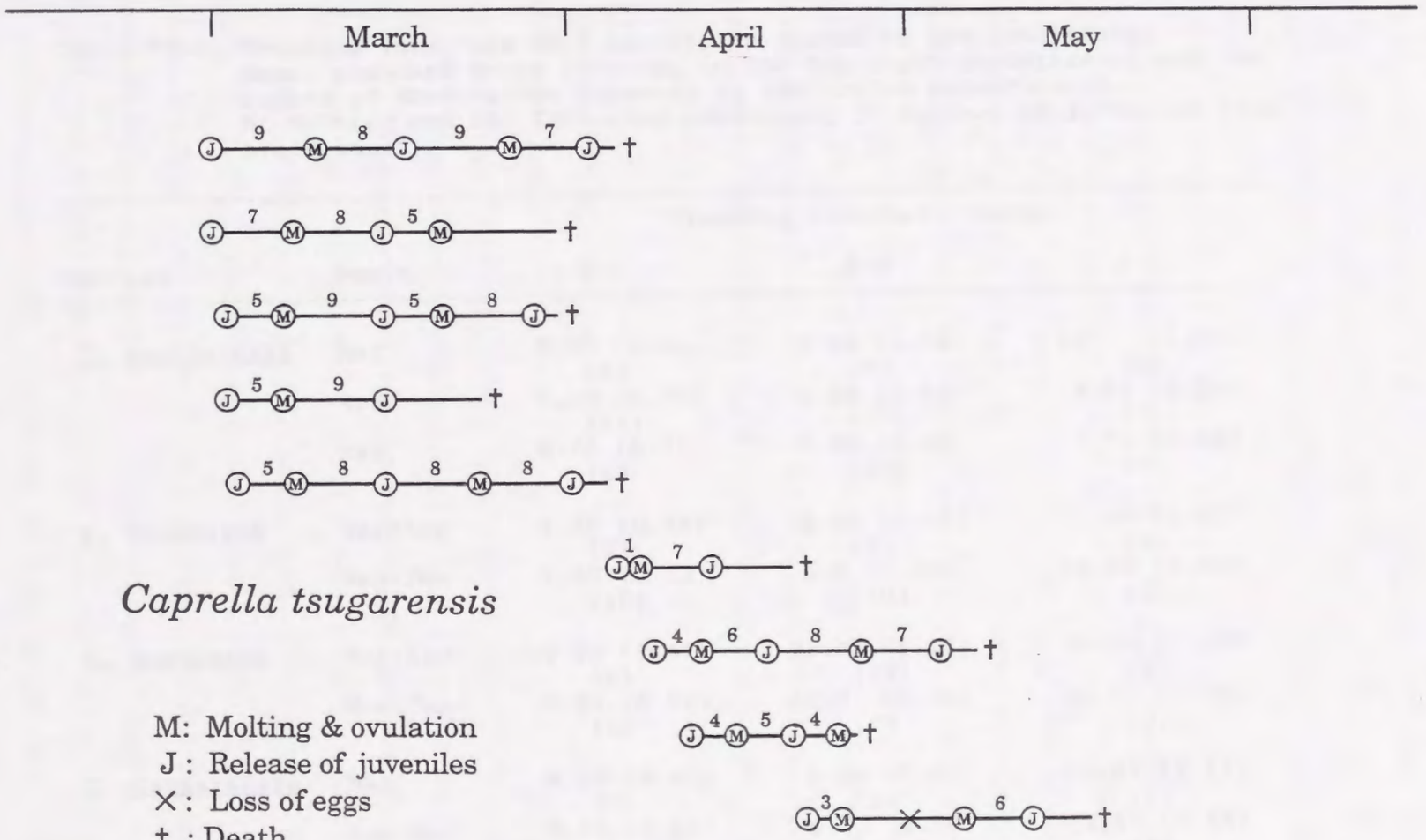


Fig. VI-4. Brooding cycle of Caprella tsugarensis reared in the laboratory. Numerals are the intervals in days.

Table VI-1. Breeding intervals of 4 caprellids reared in the laboratory. Mean, standard error (numeral in the top right parenthesis) and the number of observation (numeral in the bottom parenthesis). M: Molting and the following ovulation; J: Release of juveniles from brood pouch.

Species	Month	Breeding intervals (days) M-J	J-M	J-J
C. danilevskii	Mar	9.50 (0.84) (6)	2.44 (2.74) (9)	11 (1.41) (5)
	Apr	7.09 (0.70) (11)	1.59 (3.54) (17)	8.36 (0.50) (11)
	May	6.75 (0.71) (8)	0.83 (0.94) (12)	7.71 (0.95) (7)
C. decipiens	Mar-Apr	9.20 (0.84) (5)	2.83 (1.47) (6)	12.00 (1.87) (5)
	May-Jun	7.80 (0.63) (10)	5.6 (1.90) (10)	12.86 (2.04) (7)
C. monoceros	Mar-Apr	8.83 (1.47) (6)	21.50 (5.19) (10)	30.83 (7.47) (6)
	May-Jun	6.33 (0.82) (6)	13.8 (3.19) (5)	18.00 (6.29) (5)
C .tsugarensis	Mar	8.29 (0.49) (7)	6.44 (1.81) (9)	14.57 (1.51) (7)
	Apr-May	6.20 (0.84) (5)	3.33 (2.58) (6)	10.50 (3.11) (4)

The mean J-J interval was 14.57 days in March and 10.50 days in April-May. The mean J-M interval was 6.44 days in March and 3.33 days in April-May. The mean M-J interval was 8.29 days in March, 6.20 days in April-May.

Increase of antenna 1 flagellar articles

Increase of antenna 1 flagellar articles was shown in Table VI-2. Antenna 1 of many caprellids have fused segments at the base of the flagellar articles (see Sakaguchi, 1989; Takeuchi and Hirano, 1991). The number of fused segments in my observations were given in the Table VI-2. On the antenna 1 of the adult females of *C. decipiens, C. monoceros* and *C. tsugarensis,* one flagellar article (or one fused article in one example) was added at a molt. Therefore, in these three species, the number of the articles was used as the indicator of moltings. In *C. danilevskii*, no particular pattern of article increment was observed. According to the results of the experiment, the fused articles will be counted as 1 article in the following studies.

VI-3. *In situ* rearing experiments

Materials and methods

In situ rearing experiments were conducted in February-May, 1991. Materials for the experiments were the same 4 species as in the laboratory rearing experiments. The purpose of the rearing experiment was to know the growth, actual brooding cycle and longevity of the 4 species under the same field condition. The rearing method was described in Aoki (1991b) (Fig. IV-6). The juveniles for the rearings were obtained by the method described in Part III-3. In the non-maternal care species, each clutch of juveniles was put in the plastic container with a piece of defaunated *S. patens* branch (about 10g in dry weight). On the other hand, in the maternal care species, each clutch of juveniles was put in the container along with their mother and the substrate seaweed. After the maternal care period, the mothers were removed from the containers underwater.

Table VI-2. Change in numbers of flagellar articles of the first antenna in the female caprellids of 4 species reared in laboratoty. Numeral in parenthesis is the number of basal fused articles.

C. danilevskii

Individual No.	No. of articles
1	(2) 9 - (3) 9
2	(1)10 - (2)10 - (2)10
3	(2) 9 - (2)10 - (2)10 - (2)10 - (2)10
4	(2) 9 - (1)10 - (1)10 - (2)11
5	(2)10 - (2)10 - (2)11
6	(2) 8 - (2) 9 - (2) 9

C. monoceros

Individual No.	No. of articles
1	(3)16 - (3)17
2	(2)18 - (2)19
3	(3)18 - (3)19
4	(3)20 - (3)21
5	(3)18 - (3)19
6	(3)21 - (3)22

C. decipiens

Individual No.	No. of articles
1	(3)12 - (3)13
2	(3)13 - (3)14
3	(2)15 - (3)15
4	(3)14 - (3)15 - (3)16
5	(3)15 - (3)16
6	(2)14 - (2)15
7	(2)14 - (2)15

C. tsugarensis

Individual No.	No. of articles
1	(2)11 - (2)12
2	(2) 9 - (2)10
3	(2)10 - (2)11

Six clutches of juveniles for each species were set in the underwater *in situ* rearing system. Each container containing animals was cleaned off at least once in a week.

After 20-30 days from the onset of the experiment, the *in situ* periodical samplings of juveniles from the containers were started. For each species, at least 8 juveniles from 4-6 containers were collected underwater once a week to know the average growth of the juveniles. At each sampling time, the specimens brought back to the laboratory were fixed, and the body length and the number of antenna 1 flagellar articles were examined. Besides the regular samplings, the condition of the organisms, in particular the growth stage of females, in each container was also checked and the outer surface of the containers was cleaned off once in 2 days.

Just before the maturation of females, all caprellids were brought back to the laboratory with keeping in seawater of the field temperature. In the laboratory, living caprellids were sorted under binocular microscope and one premature female and 2-3 males from the container of the same clutch were put in a different container with substrate seaweed. During the period of the laboratory treatment, the animals not under observation were kept in the running seawater aquaria. About 10 animals out of the remained animals after the above treatment were kept in their original container as stock. Then all the containers were taken back to the underwater rearing system. Six sets of the containers containing a female and 2-3 males were prepared for each species. All the treatments were carried out within 24 hours. During the experimental period, in case the males in the containers died, new males were supplied from the stock containers which I mentioned above, to keep the density and composition of each container the same.

After the maturation of the females, the animals were examined in the laboratory at an interval of 12-14 days. Besides the laboratory observations, *in situ* observations were also made to know the condition of the females, at least

once in 2-3 days. At the time of laboratory observation, the containers containing 1 female with 2-3 males were brought back to the laboratory with keeping in the seawater of the field temperature. The body length and the number of antenna 1 flagellar articles of the living animals were examined under the microscope, and they were taken back to the underwater rearing system within 24 hours. The animals under examination were always kept wet on the cotton which was damped in the seawater maintaining the field temperature. The observations of the field animals were continued until when all the females and males, which completed terminal molts, died off. The animals in the terminal stage could be easily identified, because the body surface of the animals which had not been molted for a long time were covered with microfauna and microflora such as hydroids and microalgae (see Pipe, 1982; Sakaguchi, 1989).

Results

Growth and brooding cycle

Caprella danilevskii

Maximum longevity of the species was up to about 110 days both in males and in females. Females matured when they attained about 7mm in body length about 50 days after their demarsupiations. After the maturation, females kept growing at a constant ratio and reached 8.5mm (Fig. VI-5). At any observation time, ovigerous females could be found. They seemed to be molting, growing and brooding continuously during their reproductive period (about 55 days). Only in *C. danilevskii* among the 4 species studied, the juvenile releasing intervals were shorter than the intervals in the laboratory observations. Therefore, the brooding cycles of this species at the in situ rearing condition were estimated from both the field rearing data and the laboratory rearing data. The juvenile releasing intervals observed in the laboratory rearings were 8.36 days in April and 7.71 days in May (Fig. VI-1; Table VI-1). Hence it is assumed that the

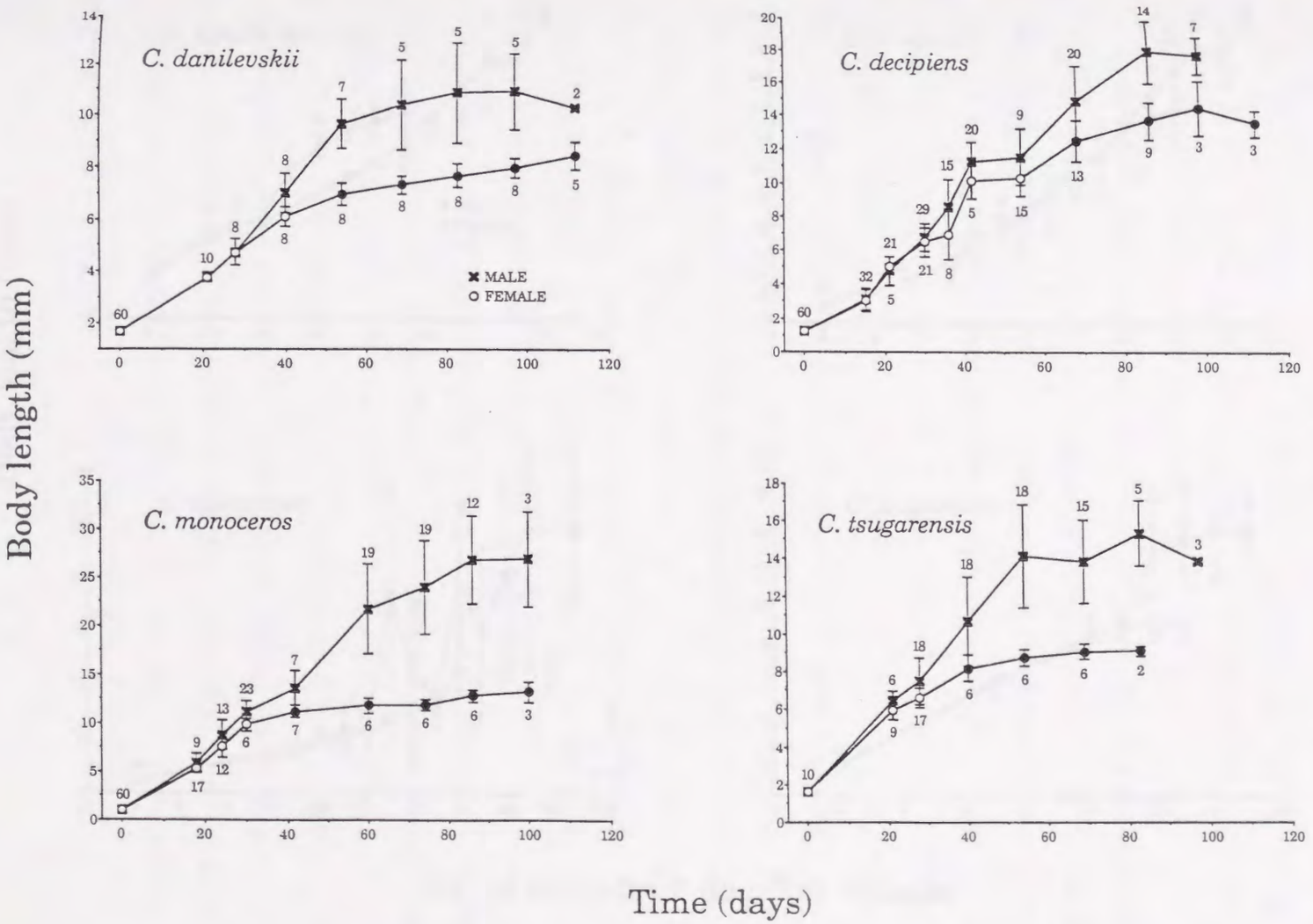


Fig. VI-5. Growth in body length (Mean & S.E.) of four Caprella species reared at the in situ condition. Small numerals in the figure represent the number of individuals examined; solid circles show the occurrence of ovigerous female.

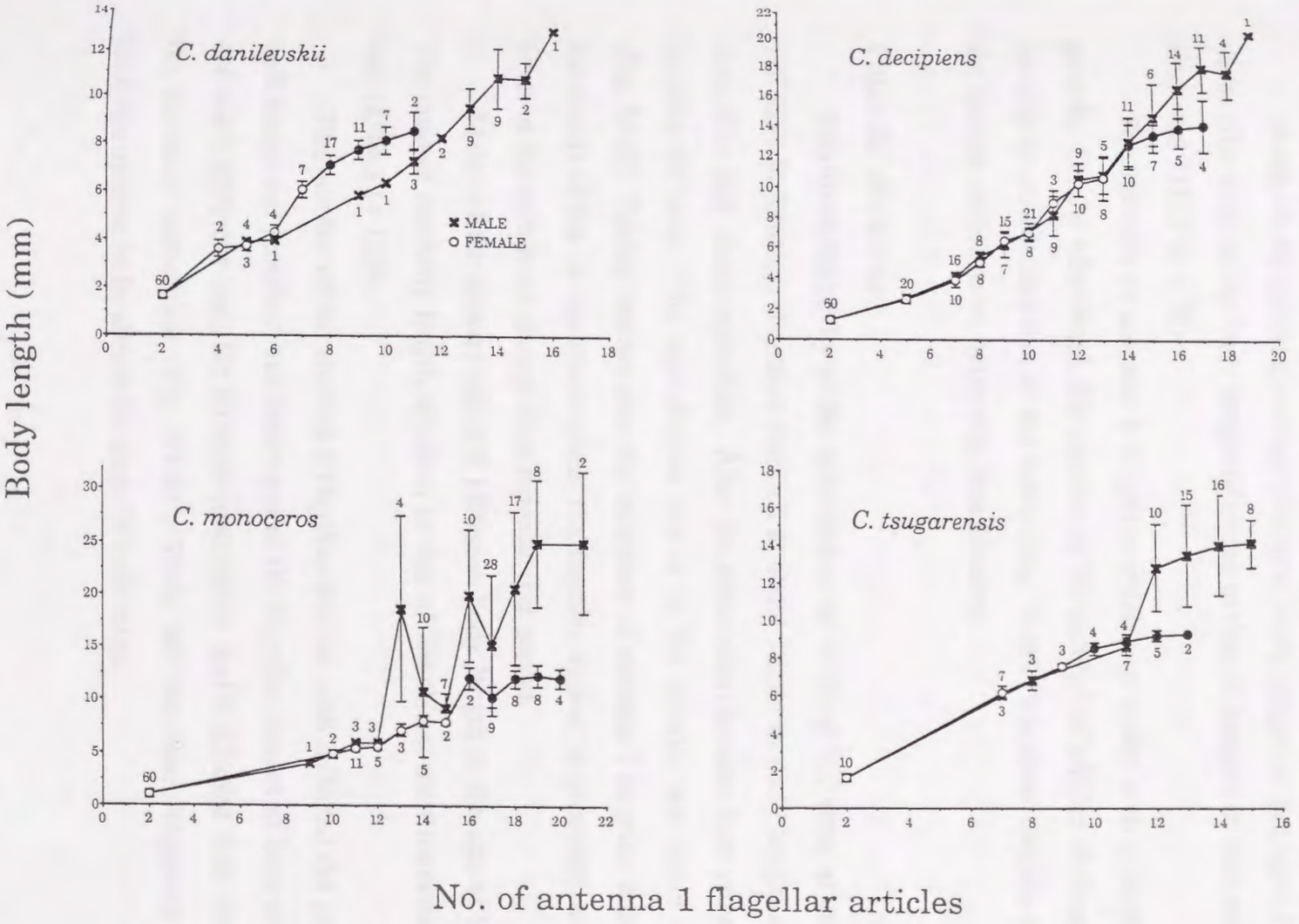


Fig. VI-6. Relationship between the number of flagellar articles in the antenna 1 and the body length (Mean & S.E.) in four Caprella species reared at the in situ condition. Small numerals in the figure represent the number of individuals examined; solid circles show the occurrence of ovigerous female.

females of the species released juveniles 7 times at the maximum during their reproductive periods.

Males of the species reached 10mm in body length at the age of 90-100 days. The ratio of the body length of males to that of females at their maximum sizes was 11/8.5 (= 1.29).

The number of antenna 1 flagellar articles of males well reflected their growth. On the other hand, the increase of the number of articles of females was noticeably slower than that of the males (Fig. VI-6). It is clear that the males of the species molted more frequently than females.

Caprella decipiens

Maximum longevity of the species was up to about 100 days in males and 110 days in females. Females matured at about 12mm in body length about 70 days after their demarsupiations. After the maturation, females kept growing and reached 14.5mm. The reproductive period of the females was about 40 days (Fig. VI-5). Taking into account the increment of antenna 1 flagellar articles and the results of the *in situ* observation, the females appear to produce juveniles 4 times at the maximum during their reproductive period.

Males of the species reached 18mm in body length at the age of 90 days. The ratio of the body length of males to that of females at their maximum sizes was 18/14.5 (= 1.24).

The number of the antenna 1 flagellar articles well reflected the growth in both males and females. The increment of the flagellar articles of both sexes was not much different until the females' maturation, and it differed little even after the females' maturation (Fig. VI-6). Thus, the life-time frequency of the moltings appears to be almost the same in both sexes.

Caprella monoceros

Maximum longevity of the species was up to about 100 days both in males and females. Females matured at about 11mm in body length about 40 days after their demarsupiations. The reproductive period of the females was about 60 days (Fig. VI-5). According to the results of the laboratory observations and periodical *in situ* observations, matured females molted and produced juveniles 4 times at the maximum and reached 13mm in body length.

Males of the species grew markedly larger than females and finally reached about 27mm in body length. The ratio of the body length of males to that of females at their maximum sizes was 27/13 (= 2.08).

The number of flagellar articles of antenna 1 show conspicuously wide variations among the individuals particularly in males, and hence it can not be considered as a useful indicator of growth in this species (Fig. VI-6).

Caprella tsugarensis

Maximum longevity of the species was up to about 100 days in males and 80 days in females. Females matured at about 8mm in body length about 40 days after their demarsupiations. The reproductive period of the females was about 40 days (Fig. VI-5). According to the results of the laboratory observations and periodical in situ observations, matured females molted and produced juveniles 4 times at the maximum and reached 9mm in body length.

Males of the species reached about 15mm in body length. The ratio of the body length of males to that of females at their maximum sizes was 15/9 (= 1.67).

The number of flagellar articles of antenna 1 of males varied widely after it reached 12. The maximum number of the flagellar articles is larger in males than in females, thus the males of the species appear to molt more frequently than females (Fig. VI-6).

VI-4. Field samplings

Materials and methods

In order to know the fecundity, the number of eggs and juveniles produced were examined. In April, 1991, ovigerous females and the females which were ready to release juveniles were collected by the method described in Part III-3 and in Part IV-3.

The ovigerous females, taken back to the laboratory were fixed and kept in 10% neutralized formalin for more than one month before the examinations. For each female, the body length, the number of eggs and the developmental stage of eggs were recorded. The description of egg stages followed the ones in Kamihira (1990c). As for the egg number, only the data of the early stage eggs (Stages I-III in Kamihira, 1990c; Stages I-II in Sheader and Chia, 1970) were used for the data analysis. Furthermore, egg sizes and egg weights were examined for each species.

Preliminary examination of the eggs of *C. monoceros* showed that the egg sizes would change in the process of egg development (Fig. VI-7). Thus egg sizes and egg weights were examined for 60 eggs (10 eggs each from 6 different females) in the Stage III. For the egg size data, the long axis and the short axis of the eggs were measured and egg volume was calculated by the following equation:

$$\text{Egg volume} = 4/3\ \pi\ a\ b^2 \quad (a: \text{long axis}/2,\ b: \text{short axis}/2)$$

Egg weights were obtained from more than 200 eggs (at least 50 eggs each from 4-10 females) for each species. Eggs were kept in 60°C for more than 24 hours and weighed.

Newly-born juveniles with their mother were obtained by the method described in the Part III-3. For each female with juveniles, the body length of the mother and the number of released juveniles were recorded. Moreover, the body lengths and the body weights of 60 (10 each from 6 different mothers) juveniles were examined.

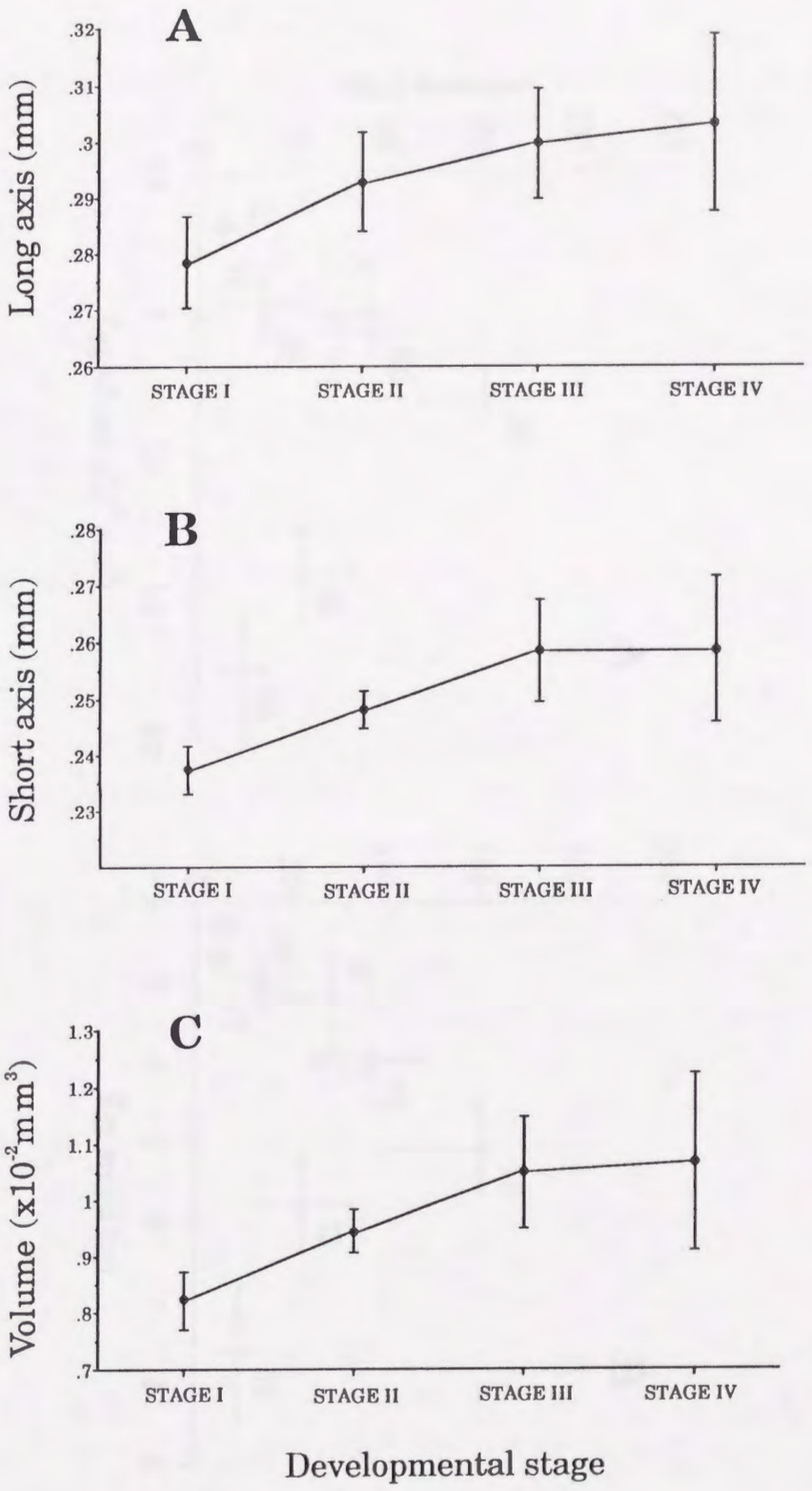


Fig. VI-7. Egg size of Caprella monoceros at each developmental stage. A: long axis of eggs; B: short axis of eggs; C: volume of eggs.

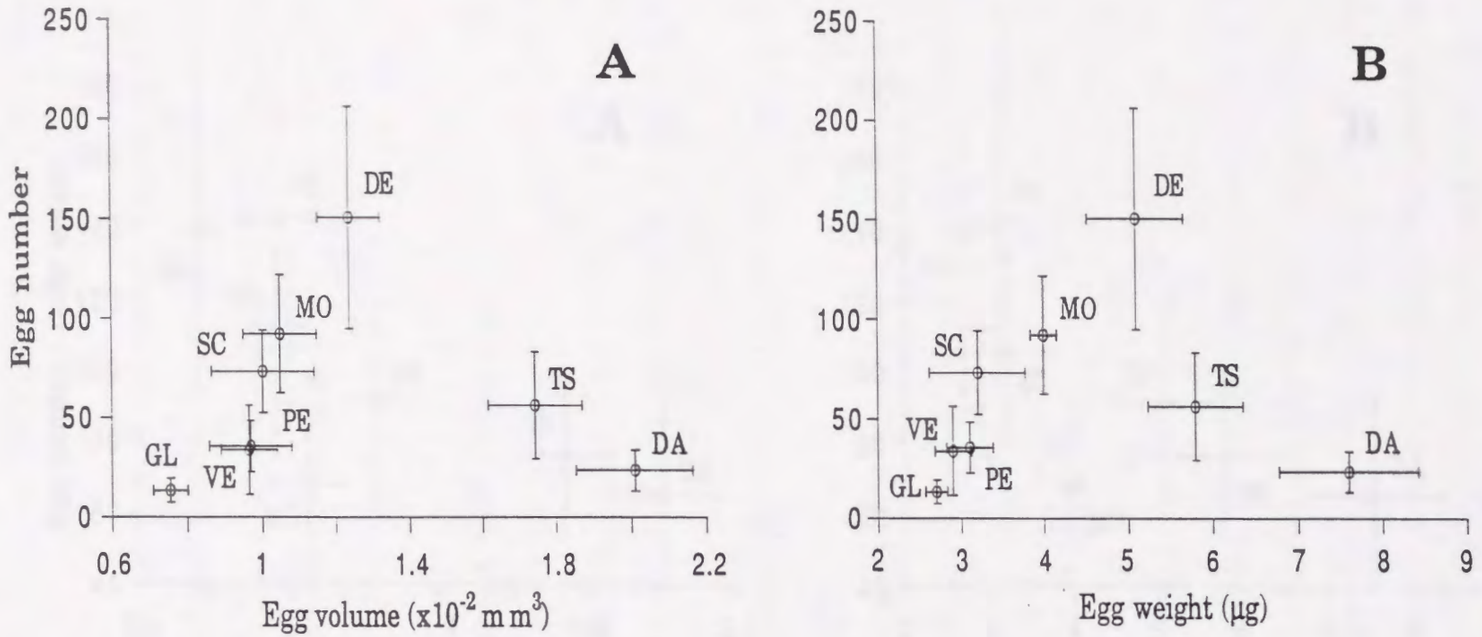


Fig. VI-8. Egg number in relation to egg volume (A) and egg weight (B) in 8 Caprella species. DA: Caprella danilevskii; DE: C. decipiens; GL: C. glabra; MO: C. monoceros; PE: C. penantis; SC: C. scaura; TS: C. tsugarensis; CV: C. verrucosa.

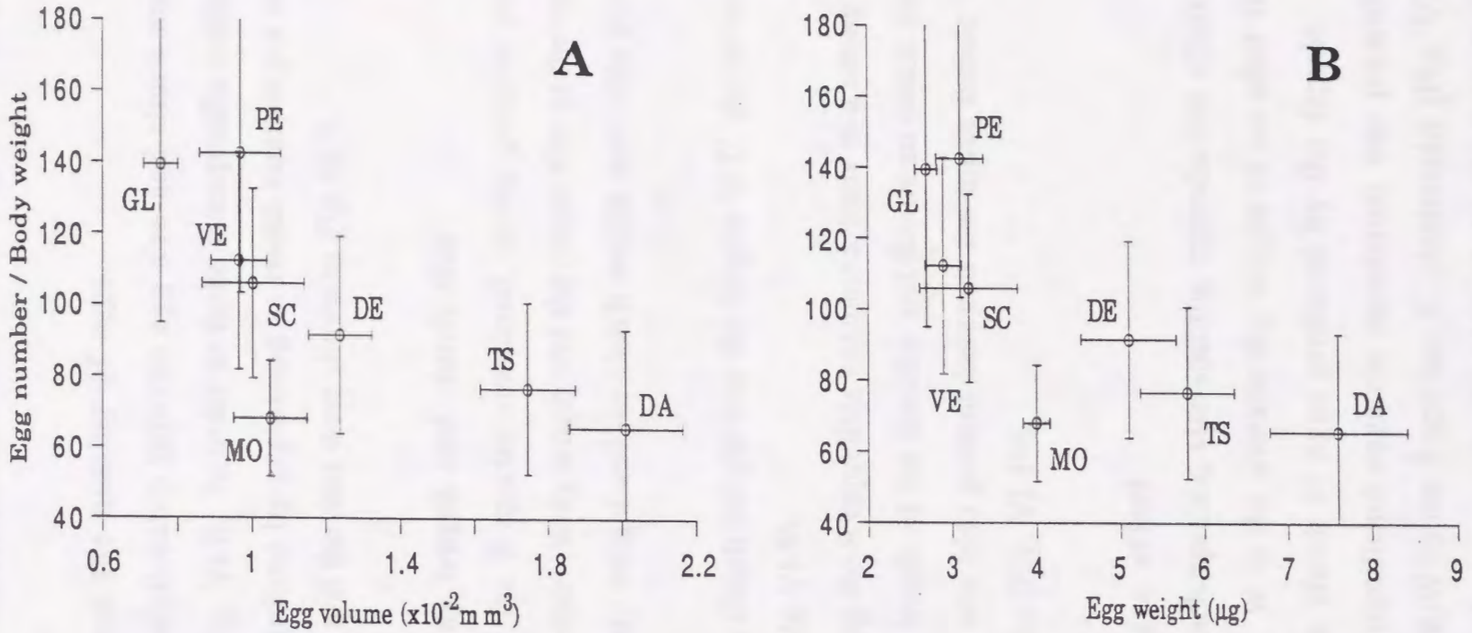


Fig. VI-9. Standardized egg number in relation to egg volume (A) and egg weight (B) in 8 Caprella species (abbreviations as in Fig. VI-8).

Results

Reproductive characteristics of the 8 species were summarized in Table VI-3.

The size and the number of eggs

The relationship between egg size and clutch number of 8 species was shown in Fig. VI-8. In order to make interspecific comparison, clutch size data were standardized by expressing as clutch number per mother's body weight (g dry weight) and the data were shown in Fig VI-9.

Female body length and clutch size

In all the 8 species examined, strong positive correlation was observed between mothers' body length and the clutch size or the number of juveniles. The mother's body weight and the clutch weight were also positively correlated (Figs. VI-10-17).

Mean clutch weight was the largest in *C. decipiens* and the smallest in *C. glabra* (Table VI-3).

Among the 8 caprellids examined, there is a strong correlation between the mean body length of the females and the mean clutch size (Fig. VI-18). Strong correlation was also present between the mean female body weight and mean clutch weight (Fig. VI-19).

Reproductive effort

For each species, size-specific reproductive effort of females (R/W) was calculated. W is the somatic dry weight of an adult female and R is the dry weight of a clutch of eggs produced by the female. Among the 8 species examined, significant negative correlation was present between female body length and R/W in the 3 species: *C. danilevskii* (Fig. VI-10C; df=37, R=-0.43, $P<0.01$), *C. decipiens* (Fig. VI-11C; df=42, R=-0.37, $P<0.05$) and *C. monoceros*

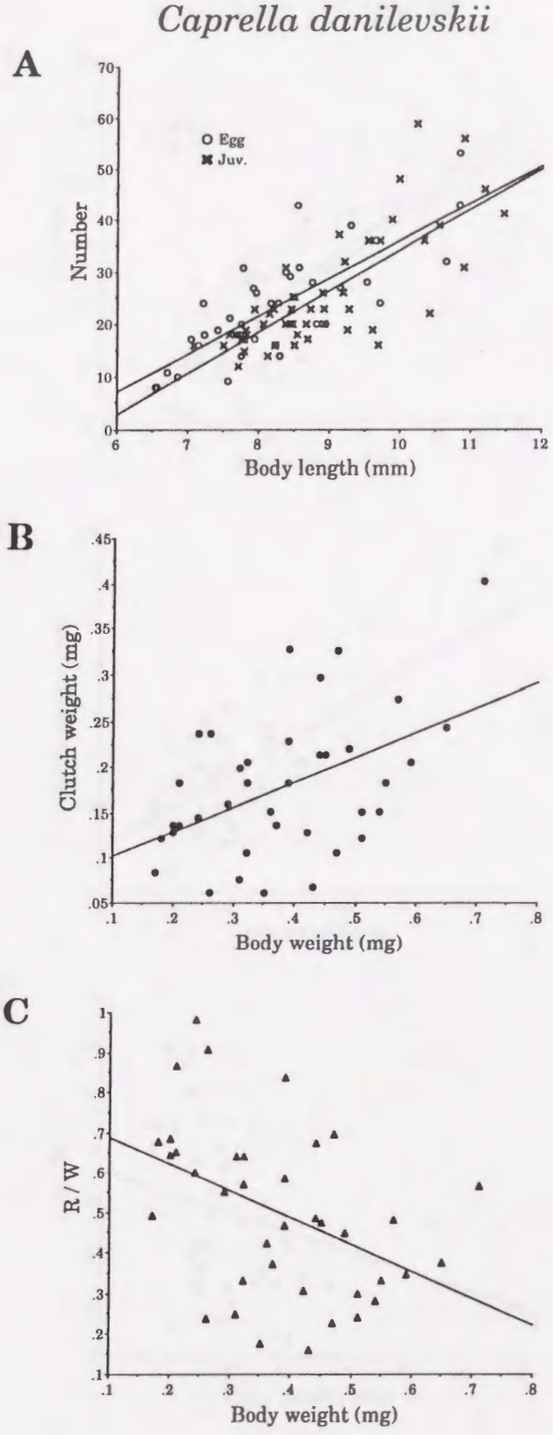


Fig. VI-10. Caprella danilevskii. A: Egg number and juvenile number (y) against female body length (x). Eggs: y=7.25x-36.26 (r=0.79, df=37, P < 0.001), Juvs.: y=7.85x-44.39 (r=0.76, df=49, P < 0.001); B: Clutch weight (y) against female body weight (x). y=0.27x+0.07 (r=0.48, df=37, P < 0.01); C: R/W (y) against female body weight (x). y=-0.66x+0.75 (r=-0.43, df=37, P < 0.01).

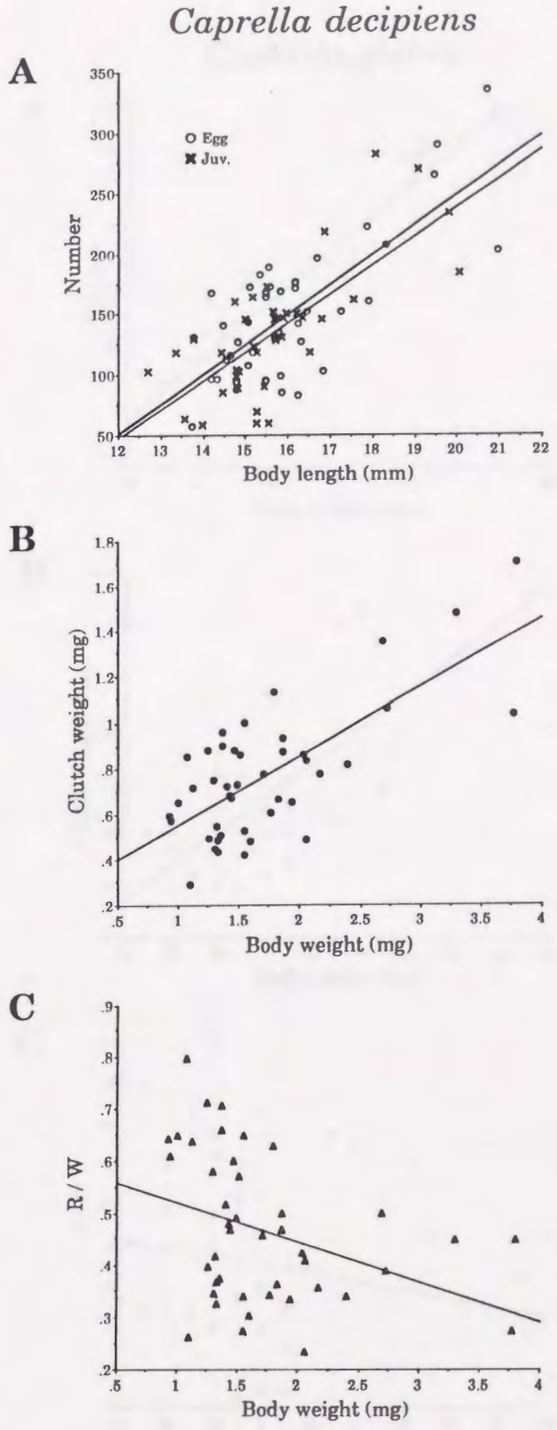


Fig. VI-11. Caprella decipiens. A: Egg number and juvenile number (y) against female body length (x). Eggs: y=24.62x-243.98 (r=0.75, df=42, P < 0.001), Juvs.: y=23.77x-237.35 (r=0.73, df=36, P < 0.001); B: Clutch weight (y) against female body weight (x). y=0.30x+0.25 (r=0.71, df=42, P < 0.001); C: R/W (y) against female body weight (x). y=-0.077x+0.60 (r=-0.37, df=42, P < 0.05).

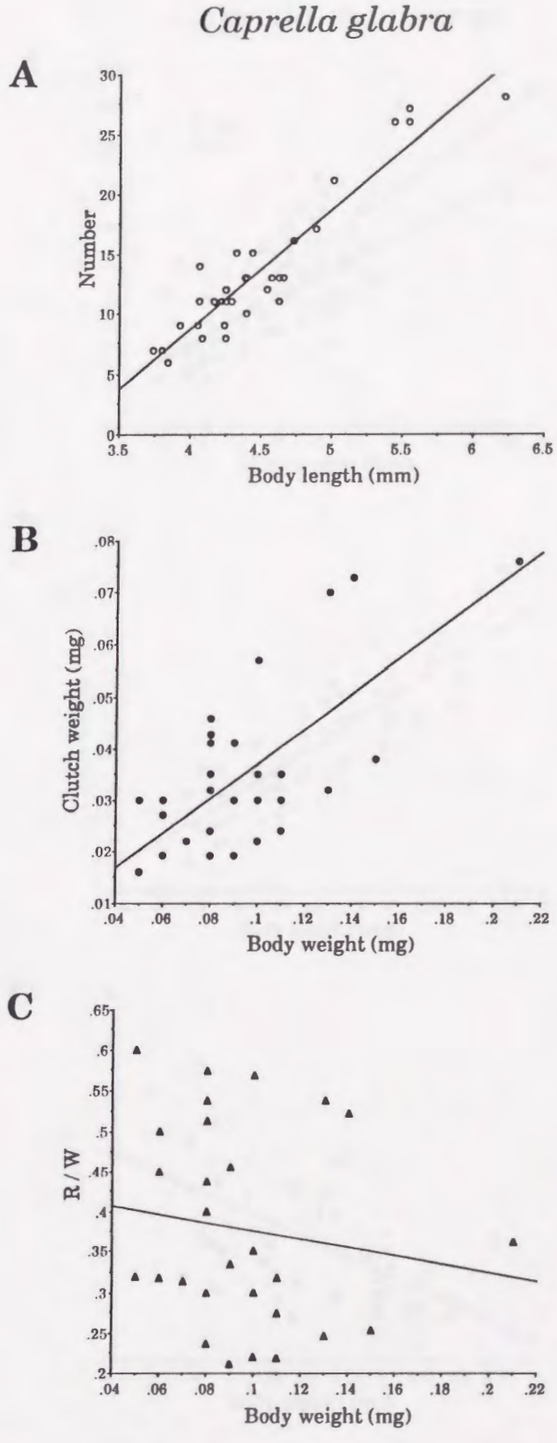


Fig. VI-12. Caprella glabra. A: Egg number(y) against female body length (x). y=9.95x-31.07 (r=0.94, df=32, P < 0.001); B: Clutch weight (y) against female body weight (x). y=0.34x+0.003 (r=0.68, df=32, P < 0.001); C: R/W (y) against female body weight (x). y=-0.52x+0.43 (r=-0.14, df=32, P > 0.1).

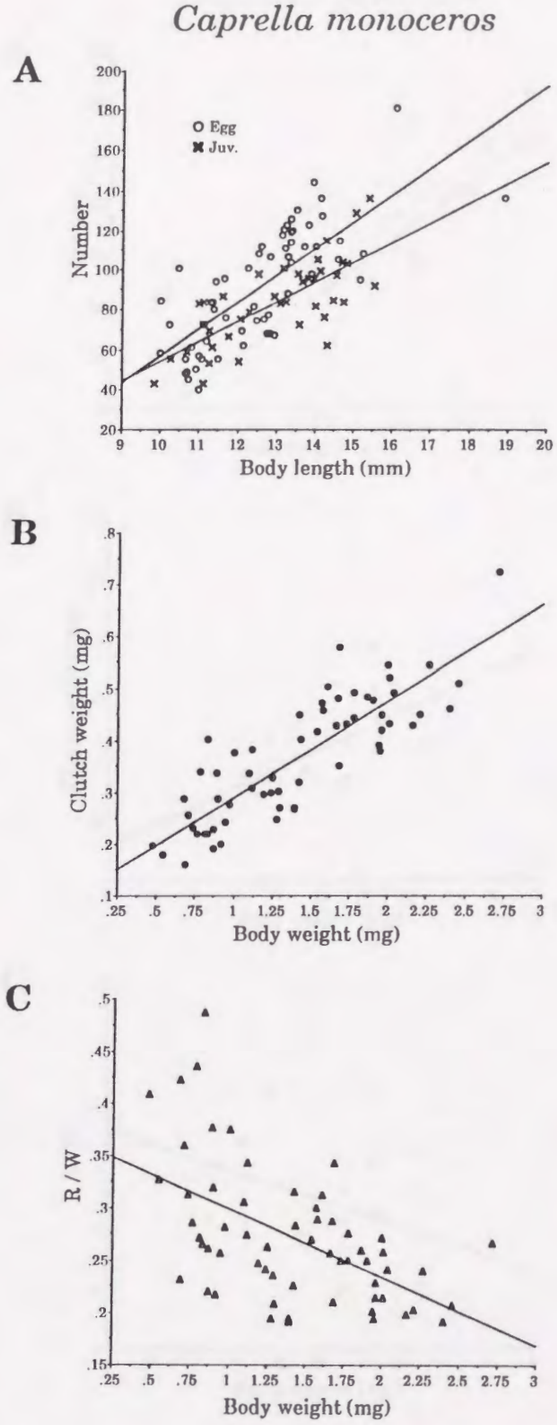


Fig. VI-13. Caprella monoceros. A: Egg number and juvenile number (y) against female body length (x). Eggs: y=13.48x-77.74 (r=0.75, df=59, P < 0.001), Juvs.: y=9.97x-45.83 (r=0.74, df=38, P < 0.001); B: Clutch weight (y) against female body weight (x). y=0.18x+0.11 (r=0.84, df=59, P < 0.001); C: R/W (y) against female body weight (x). y=-0.066x+0.37 (r=-0.54, df=59, P < 0.001).

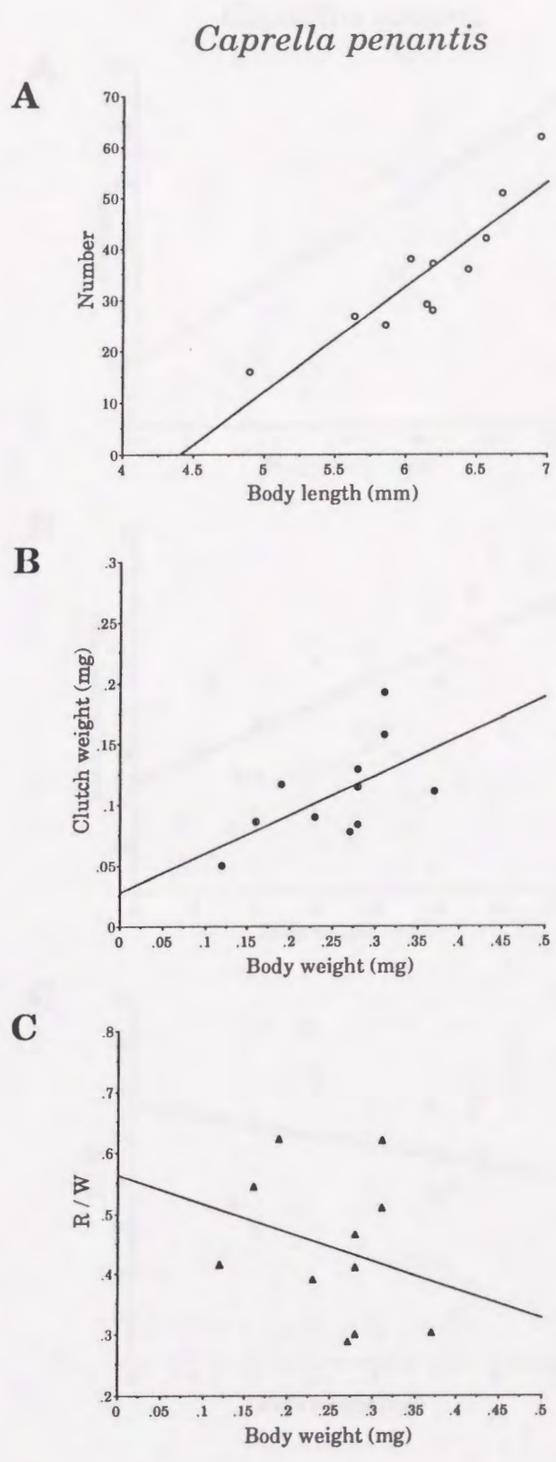


Fig. VI-14. Caprella penantis. A: Egg number (y) against female body length (x). y=20.48x-90.28 (r=0.89, df=10, P < 0.001); B: Clutch weight (y) against female body weight (x). y=0.32x+0.03 (r=0.59, df=10, 0.05 < P < 0.1); C: R/W (y) against female body weight (x). y=-0.47x+0.56 (r=-0.29, df=10, P > 0.1).

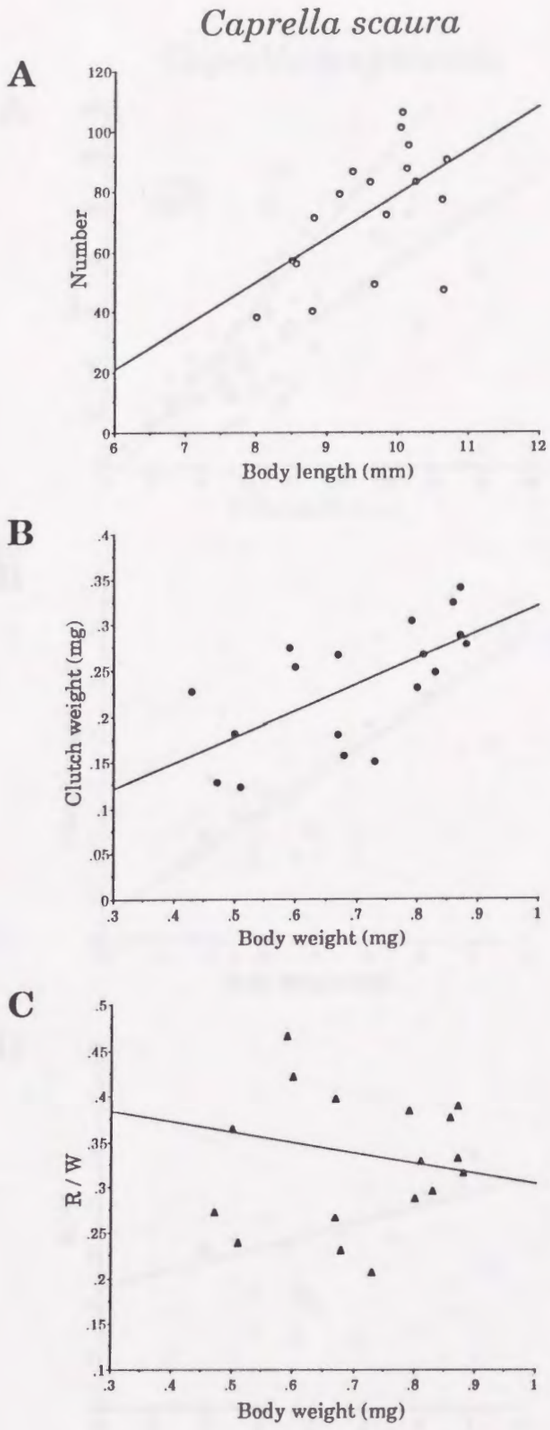


Fig. VI-15. Caprella scaura. A: Egg number (y) against female body length (x). y=14.45x-65.66 (r=0.56, df=17, P < 0.05); B: Clutch weight (y) against female body weight (x). y=0.29x+0.03 (r=0.65, df=17, P < 0.005); C: R/W (y) against female body weight (x). y=-0.11x+0.42 (r=-0.20, df=17, P > 0.1).

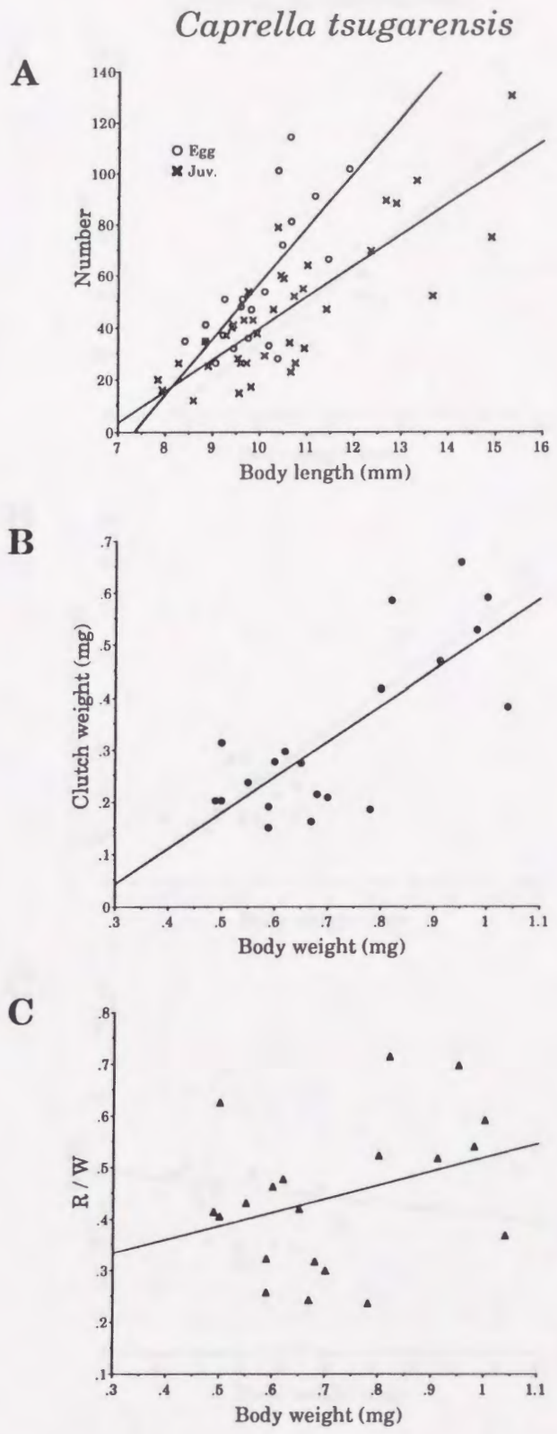


Fig. VI-16. Caprella tsugarensis. A: Egg number and juvenile number (y) against female body length (x). Eggs: y=21.58x-158.71 (r=0.72, df=20, $P < 0.001$), Juvs.: y=12.09x-81.12 (r=0.81, df=37, $P < 0.001$); B: Clutch weight (y) against female body weight (x). y=0.68x-0.16 (r=0.76, df=20, $P < 0.001$); C: R/W (y) against female body weight (x). y=0.27x+0.25 (r=0.33, df=20, $P > 0.1$).

Caprella verrucosa

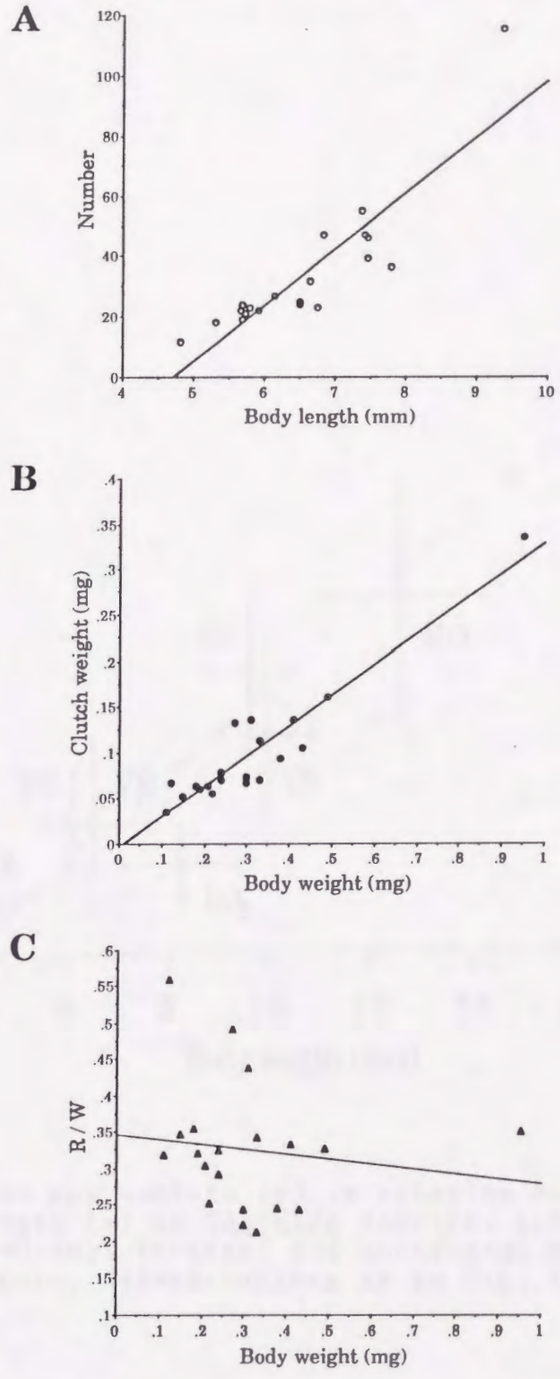


Fig. VI-17. Caprella verrucosa. A: Egg number (y) against female body length (x). y=18.60x-87.82 (r=0.88, df=19, $P < 0.001$); B: Clutch weight (y) against female body weight (x). y=0.33x-0.004 (r=0.93, df=19, $P < 0.001$); C: R/W (y) against female body weight (x). y=-0.068x+0.35 (r=-0.14, df=19, $P > 0.1$).

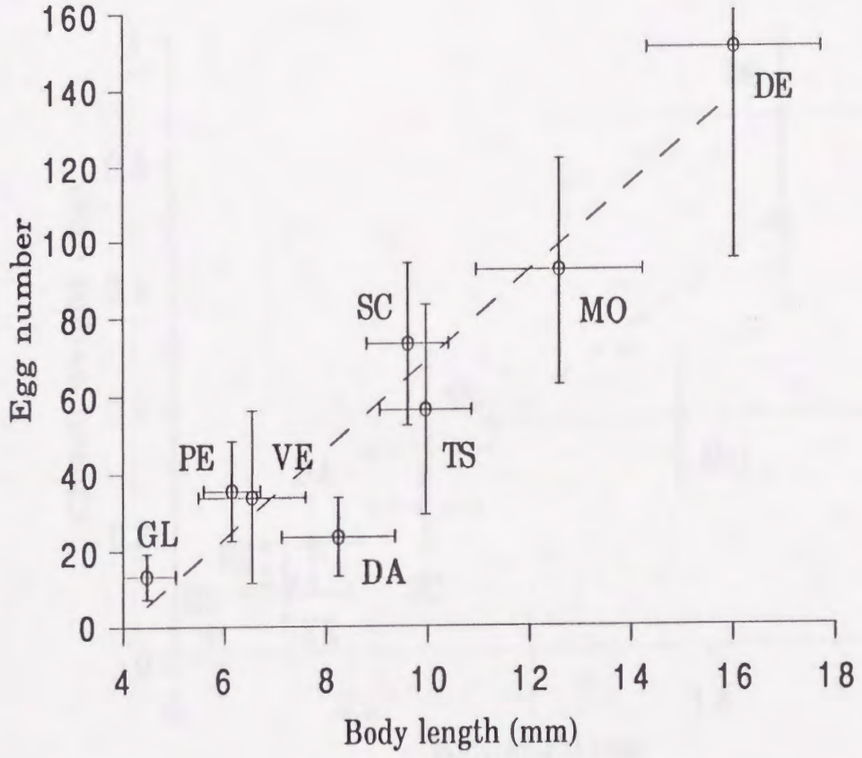


Fig. VI-18. Mean egg numbers (y) in relation to mean female body length (x) in Caprella species. y=11.46x-45.64 (r=0.96). Vertical and horizontal bars are standard errors. Abbreviations as in Fig. VI-8.

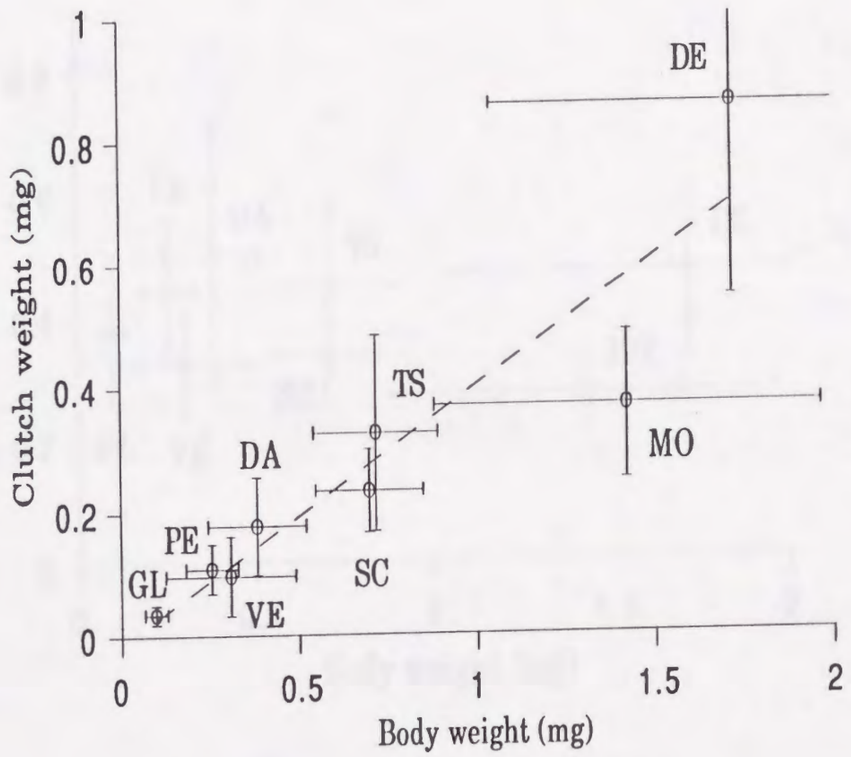


Fig. VI-19. Mean clutch weight (y) in relation to mean female body length (x) in Caprella species. y=0.413x-0.012 (r=0.91). Vertical and horizontal bars are standard errors. Abbreviations as in Fig. VI-8.

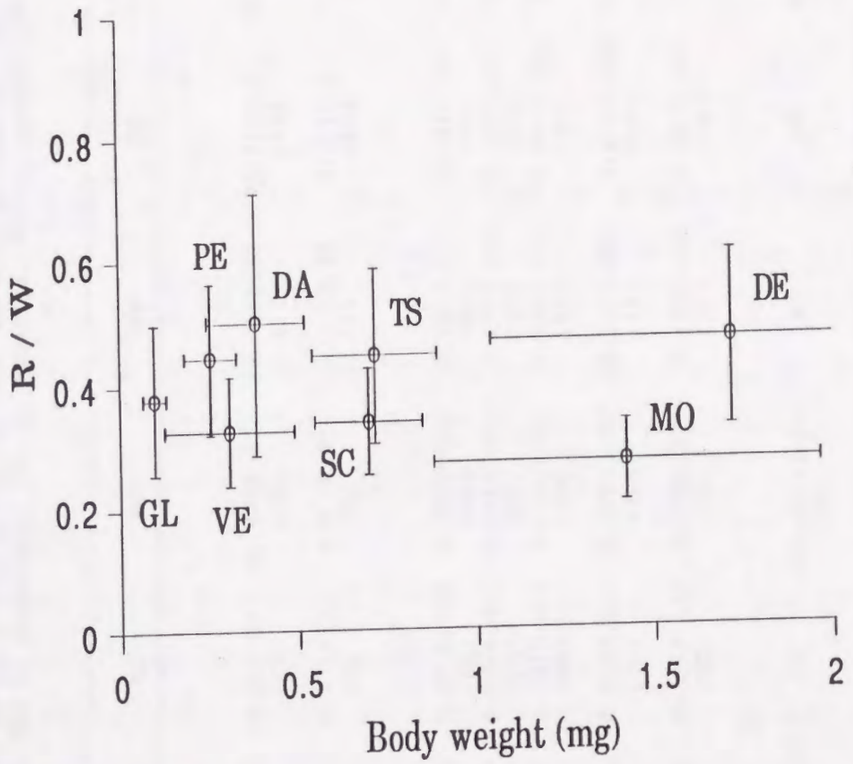


Fig. VI-20. Mean R/W value in relation to female body weight in Caprella species. Vertical and horizontal bars are standard errors. Abbreviations as in Fig. VI-8.

Table VI-3. Summary of the reproductive characteristics in 8 species of caprellids. Mean (S.E.); Numeral in bottom parenthesis represents the number of materials examined. ND: no data available. DA: Caprella danilevskii; DE: C. decipiens; GL: C. glabra; MO: C. monoceros; PE: C. penantis; SC: C. scaura; TS: C. tsugarensis; VE: C. verrucosa.

	DA	DE	GL	MO	PE	SC	TS	VE
[Egg]								
Number	23.5(10.3) (38)	150.7(55.8) (43)	13.3(6.0) (33)	92.1(29.6) (60)	35.6(12.9) (11)	73.2(20.8) (18)	56.2(27.0) (21)	33.9(22.4) (20)
Weight (ug)	7.6 (0.8) (6)*	5.1 (0.6) (7)	2.7 (0.1) (4)	4.0 (0.2) (5)	3.1 (0.3) (4)	3.2 (0.6) (10)	5.8 (0.6) (10)	2.9 (0.2) (4)
Size								
Long axis (mm)	0.37(0.01) (60)	0.31(0.01) (60)	0.27(0.01) (60)	0.30(0.01) (60)	0.29(0.01) (60)	0.29(0.02) (60)	0.36(0.01) (60)	0.30(0.01) (60)
Short axis (mm)	0.32(0.01) (60)	0.28(0.01) (60)	0.23(0.01) (60)	0.26(0.01) (60)	0.25(0.01) (60)	0.26(0.01) (60)	0.31(0.01) (60)	0.25(0.01) (60)
volume (x10-2mm3)	2.01(0.15) (60)	1.24(0.09) (60)	0.76(0.05) (60)	1.05(0.10) (60)	0.97(0.11) (60)	1.00(0.14) (60)	1.74(0.13) (60)	0.97(0.08) (60)
Clutch weight (mg)	0.18(0.06) (38)	0.86(0.33) (43)	0.04(0.02) (33)	0.37(0.16) (60)	0.11(0.05) (11)	0.23(0.12) (18)	0.33(0.16) (21)	0.10(0.04) (20)
R / W	0.50(0.21) (38)	0.47(0.14) (43)	0.38(0.12) (33)	0.27(0.07) (60)	0.44(0.12) (11)	0.34(0.09) (18)	0.45(0.14) (21)	0.33(0.09) (20)
[Juvenile]								
Number	25.46(10.94) (50)	135.39(52.17) (39)	ND	83.62(21.24) (39)	ND	ND	46.05(26.04) (38)	ND
Body length (mm)	1.73(0.06) (60)	1.29(0.04) (60)	1.26(0.04) (60)	1.10(0.04) (60)	1.09(0.06) (60)	1.17(0.04) (60)	1.17(0.04) (60)	1.29(0.13) (60)
Body weight (ug)	11.5 (0.8) (60)	6.4 (0.90) (60)	ND	3.6 (0.44) (60)	ND	4.7 (0.87) (60)	8.4 (1.40) (60)	ND

* number of broods examined

(Fig. VI-13C; df=59, R=-0.54, P<0.001). No significant correlation was observed in the other 5 species.

Mean reproductive effort was 0.3-0.5 and there was no significant difference among the species except in *C. monoceros*. In *C. monoceros*, it was significantly smaller than in other species (Fig. VI-20; Table VI-3).

Life-time fecundity

On the basis of the growth data obtained from the in situ rearing experiments and the regression equations from the relationship between clutch size and female body length, the life-time fecundity of 4 species was calculated (Table VI-4). Mean body length of the females at each growth stage was calculated from the growth data obtained in the *in situ* rearing experiments. Only in *C. danilevskii*, though a female was estimated to produce eggs 7 times in her life time, only 4 growth stages of females could be recorded in the *in situ* rearing (see Part VI-3).

Thus the female body size of 3 missing stages were estimated by calculating the mean of the two continuous growth stage data obtained by the *in situ* rearing. In *C. danilevskii*, the fecundity was 145.0 (1.10mg in dry weight), which was very close to that of *C. tsugarensis:* 138.0 (0.80mg in dry weight). Total egg number of *C. decipiens* was 354.6 (1.81mg in dry weight), which was very close to that of *C. monoceros:* 341.7 (1.37mg in dry weight).

Total number of the juveniles followed the same trend as that of the eggs. In all species, juvenile number was apparently smaller than the egg number. It is clear that some of the eggs in the mother's brood pouch were lost or died before reaching the juvenile stage.

Table VI-4. Estimated lifetime fecundity of 4 caprellids reared under *in situ* condition. FBL: female body length.

C. danilevskii

Brood	FBL (mm)	Egg No./Brood	Juv. No./Brood	Egg-Juv. Survival(%)
1	7.09	15.1	11.3	74.7
2	---	(17.4)*	(13.7)	
3	7.71	19.6	16.2	82.4
4	---	(21.1)	(17.8)	
5	8.12	22.6	19.4	85.8
6	---	(23.9)	(20.9)	
7	8.49	25.3	22.3	88.3
Total no.		145.0	121.6	
Total weight (mg)		1.10		

* Concerning the data in parenthesis, see detail in text

C. decipiens

Brood	FBL (mm)	Egg No./Brood	Juv. No./Brood	Egg-Juv. Survival(%)
1	12.76	70.3	65.9	93.8
2	13.42	86.5	81.6	94.3
3	13.87	97.6	92.3	94.6
4	13.98	100.3	94.9	94.6
Total no.		354.6	334.7	
Total weight (mg)		1.81		

Table VI-4. Continued.

C. monoceros

Brood	FBL (mm)	Egg No./Brood	Juv. No./Brood	Egg-Juv. Survival(%)
1	11.21	73.4	66.0	89.8
2	11.88	82.5	72.7	88.1
3	12.80	94.9	81.8	86.2
4	13.25	100.9	86.3	
Total no.		341.7	306.8	
Total weight (mg)		1.37		

C. tsugarensis

Brood	FBL (mm)	Egg No./Brood	Juv. No./Brood	Egg-Juv. Survival(%)
1	8.49	24.5	21.5	87.8
2	8.89	33.2	26.4	79.6
3	9.19	39.6	30.0	75.7
4	9.24	40.7	30.6	75.2
Total no.		138.0	108.5	
Total weight (mg)		0.80		

VI-5. Discussion

Reproductive characteristics of 8 species

Eight species examined can be grouped into three groups, namely, Group A, B and C based on the following data:

a) egg volume-egg number relationship (Fig. VI-8A, Table VI-3)
b) egg weight-egg number relationship (Fig. VI-8B, Table VI-3)
c) the body size of juveniles (Table III-3, Fig. IV-11, Table VI-3)
d) the body weight of juveniles (Table VI-3)

The grouping of the species based on the reproductive characteristics well coincided with the classification according to the difference in microhabitat utilization (Fig. V-2). Thus, the difference of life history characteristics of the epiphytic caprellids appear to be closely related to their habitat utilization.

Group A

Group A includes *C. danilevskii* and *C. tsugarensis*. The clutch size of this species group was small (ca 20-60) and the size of eggs (ca 1.7-2.0mm3 in volume; ca 5-8ug in weight) and juveniles (ca 1.6-1.7mm in body length; ca 8-12ug in weight) were large (Fig. VI-8; Table VI-3).

Standardized data showed that the females of these species produce less number of large eggs per body weight (Fig. VI-9). According to my observation and the body length data (Table III-3, Fig. IV-11), *Caprella okadai* should also be included in this group, although no data on egg is available for the species. The species in this group were non-maternal care species.

The life-time fecundity of *C. danilevskii* was almost the same as that of *C. tsugarensis*. However, the reproductive trends were entirely different among the 2 species. *C. danilevskii* matured later (at ca. 50 days) and produced less number (ca 15-25) of eggs more frequently (7 times at the most) than *C. tsugarensis*. On

the other hand, *C. tsugarensis* matured earlier (at ca. 40 days), and produced ca. 24-40 eggs 4 times at the most (Fig. VI-21).

The laboratory rearing of *C. danilevskii* was reported in Takeuchi and Hirano (1991). According to that, the females of *C. danilevskii* kept under 20 °C, produced 69.0 offsprings. The generation period was 25.9 days and the longevity was 40-50 days at the maximum (except 1 female which lived for ca 70 days). I conducted the *in situ* rearing experiments under the condition of water temperature ranging between 12-20 °C in the water temperature. The results of the experiments were rather different from those reported in Takeuchi and Hirano (1991). Temperature could be one of the major factor making the difference in the results, and food should be the other important factor. The caprellids in the genus *Caprella* are basically filter-feeders or scrapers (Caine, 1974, 1977). However, they often catch and eat small crustaceans such as copepods, and moreover, the food may vary among the species (Keith, 1969; Caine, 1979a; Aoki pers. observ.). The caprellids reared at the *in situ* condition can choose to feed on various natural food, which was smaller than the mesh size of rearing containers (250 um). On the other hand, in the rearing experiment in Takeuchi and Hirano (1991), only diatoms of one species were supplied as food, which could make the reproductive characteristics rather different from those of the natural condition.

Group B

Group B includes *C. decipiens, C. monoceros* and *C. scaura.* The clutch size of the species group was large (ca 70-150) and the egg size was medium (ca 1.0-1.2mm3 in volume; ca 3-5ug in weight). The size of juveniles was small (ca 1.0-1.3mm in body length; ca 3-6ug in weight)(Fig. VI-8; Table VI-3). Standardized data showed that the females of the species group produced medium number of medium size eggs per body weight. In particular, *C. monoceros*

produced rather lesser number of eggs than the others (Fig. VI-9). It is noticeable that the 3 species in this group are maternal care species.

The life-time fecundity of *C. decipiens* and *C. monoceros* is almost the same and both the species produced eggs 4 times at the most. However, the way of producing juveniles was quite different among the 2 species. In *C.decipiens,* females matured late (at 70 days) and produced eggs within an interval of 12-13 days. On the other hand, *C. monoceros* matured earlier (at age 40 days) than *C. decipiens* and produced eggs in longer intervals (18 days) (Fig. VI-21). It appears that the difference of the reproductive traits reflects the difference in maternal care behavior in these two species. In *C. decipiens,* the mother in a colony can molt even though the juveniles she produced are staying around her. On the other hand, in *C. monoceros,* the mother carrying juveniles does not molt, supposed to be due to the presence of the juveniles on her body. Thus the brooding cycle is longer than the mother's juvenile carrying period (Aoki and Kikuchi, 1991).

C. monoceros and *C. scaura* appear to be phylogenetically close to each other (see Part IV-6). Also they have similar reproductive characteristics (Figs. VI-8, 9), though the adult body size is smaller in *C. scaura* than in *C. monoceros.* In *C. monoceros,* however, size-specific reproductive effort and size-specific clutch number are apparently smaller than other species (Fig. VI-9; Fig. VI-20; Table VI-3). This may be due to the larger energy investment for more advanced cling-type maternal care in *C. monoceros.*

Group C

Group C includes *C. glabra, C. penantis* and *C. verrucosa.* The clutch size of the species group (ca 10-40), the egg size (ca 0.7-1.0mm3 in volume; ca 2-3ug in weight) and the juvenile size (ca 1.0-1.3mm in body length) were small (Fig. VI-8; Table VI-3). Standardized data showed that the females of the species

group produced rather large number of small eggs per body weight. All of them were non-maternal care species.

The 3 species in the Group C all belong to *C. acutifrons* group, thus, they are phylogenetically close to each other (see Part II). Their body size is smaller than that of the other species, thus the clutch size and the weight were small (Figs. VI-18, 19). However, size-specific clutch number was apparently larger than the other species (Fig. VI-9). Moreover, reproductive effort was not affected by the female body size. The data on their life-time fecundity is lacking, but it was observed that their brooding cycles were very short. Thus, it appears that they have high reproductive potential. In *Sargassum patens* bed, the juveniles of the 3 species occurred only on epiphytic hydroids on the seaweed (see Part V). The utilization of epiphytic hydroids as shelter allowed them to escape from predatory fishes (Caine, 1979b). It appears that they can maintain their population by the production of a small clutch of small eggs because of the utilization of epiphytic hydroid habitat and their high reproductive potential.

Life span and generation time

The longevity of the 4 species reared at the *in situ* condition was up to 110 days and the generation time was 40-70 days. Whereas, Takeuchi and Hirano (1991) reported that the longevity of the caprellids they reared in the laboratory at 20°C was about 2 months and their generation time was 20-30 days. Sakaguchi (1989, 1990) reported that the life span of *C. scaura* reared in the laboratory at 20°C was up to 5 months and the generation time was 20-30 days. Present study and all these reports suggest that the life span of *Caprella* is up to 4-5 months and the generation time is shorter than 70 days. Comparing these life history characteristics of caprellids with those of the gammarid amphipods, it is clear that both the life span and the generation time of the caprellids are apparently shorter than those of the gammarids (Sainte-Marie, 1991). Taking into account the life history characteristics and the life style depending on ephemeral habitats,

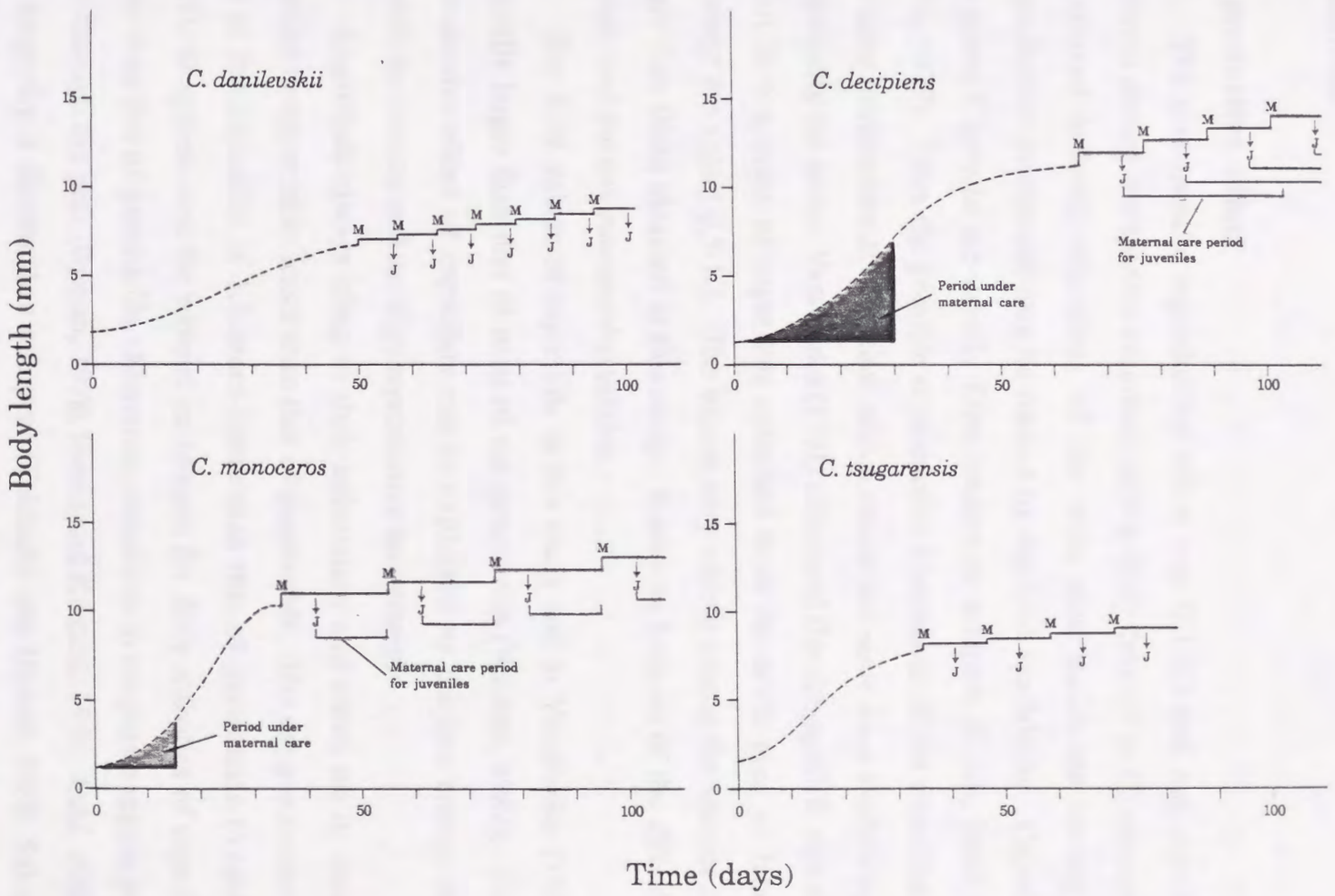


Fig. VI-21. Diagrammatic representation of the growth of 4 Caprella species reared in situ condition. M: molting and following ovulation; J: release of juveniles.

caprellids appear to be rather opportunistic members among the amphipod crustaceans.

Reproductive effort

The size-specific reproductive effort was 0.3-0.5 and not significantly different among the species examined in this study (except in *C. monoceros* as mentioned before), regardless of the wide size variations among them. Reproductive investment may be limited by the food availability. Caprellids in the genus *Caprella* are usually filter-feeders or scrapers (Keith, 1969; Caine, 1974, 1977). Thus the possible reproductive investment of the caprellids under the same environmental condition, which means the same food availability, may be basically the same. Vassilenko (1991) calculated the size-specific reproductive effort in 6 species of caprellids collected from the north area of Japan and obtained the value: 0.5-1.3. The values vary widely among the species and are larger than those obtained in this study. It may be because of the difference in habitats and the environmental condition.

The R/W values of caprellids in this study and in Vassilenko (1991) are generally larger than that of most of the gammarids (Wildish, 1982). The high reproductive effort of caprellids can be explained by the low energy cost for somatic investment and the high reproductive investment.

Caprellids always cling to their substratum and crawl on it, thus their mobility is appreciably lesser than that of gammarids. The oxygen consumption rate of the caprellids is 1.5 times lower than that of gammarids (Vassilenko, 1985). It appears that the somatic investment for daily activities of caprellids is lower than that of gammarids. Moreover, caprellids in temperate region produce eggs through the year (Bynum, 1978; Imada and Kikuchi, 1984; Aoki, 1988) and the longevity is shorter than one year (Takeuchi and Hirano, 1988; Sakaguchi, 1989; this study). It means that caprellids in temperate regions reproduce all the

time possible. They seem to make maximum investment in reproduction in their life.

Reproductive strategies in relation to maternal care behavior

As I mentioned in the Part V-3, the caprellids living on *S. patens* thalli have to face a problem: "Adult caprellids are big enough to live on the *S. patens* thalli, and also, the small newly-born juveniles are forced to live on the thalli." In order to solve the problem, they employed 3 strategies (Fig. V-2).

First, the strategy of the Group A species: adult females produce the juveniles which are large enough to cling onto the seaweed thalli. In this case, the number of juveniles produced is small, because the energy investment for reproduction is limited.

Second, the strategy of the Group C species: adult females produce small juveniles. It is difficult for them to cling onto the substrate seaweed, and hence they cling onto the epiphytic hydroids and grow in that shelter. The juveniles on the hydroid bush can avoid fish predation, thus the clutch number is small.

Third, the strategy of the Group B species: adult females produce small juveniles. The juveniles have rather low mobility or cannot cling onto the substrate seaweed, thus they stay around or stay on the mother and grow up under the maternal care. In this case, the maternal care colony on the seaweed thalli are exposed to the fish predation; thus the number of juveniles in a colony should be big enough to compensate the loss of other sacrificed colonies. The mother's body size hence should be large enough to carry or defend the large number of juveniles.

In *C. decipiens* and *C. monoceros*, which are maternal care species, the juveniles under maternal care can not leave the colony until they reach a definite size. Moreover, the body size of the adult females of these species is larger than that of the non-maternal care species. Ito (1989) showed that larger caprellids tend to sink faster than smaller caprellids. In *C. monoceros*, swimming seems to

be difficult for the female carrying her juveniles. Thus, in these species, the mobility and the dispersion ability of both adult females and the juveniles in the early stages are apparently limited. In particular, in *C. decipiens,* the female defending her juveniles cannot leave her colony. Thus, the ability of dispersion by swimming in these species may be limited. On the other hand, *C. penantis* and *C. equilibra*, which are non-maternal care species, have been collected from the water column as plankton (Williams and Bynum, 1972). These species are distributed all over the world. They appear to migrate by swimming. Therefore, it appears that the mobility and dispersion ability of non-maternal care species are greater than those of maternal care species. The limited geographical distribution of *C. monoceros* and *C. decipiens* can be explained by the limited dispersion ability. Both of the maternal care species are endemic to Japan and adjacent waters, which may be due to their low dispersion ability. These species have been found on the drifting seaweed (Hirosaki, 1964; Arimoto, 1979; Ito et al., 1988). The drifting seaweed can move along the current up to 1200km along the coast (Yoshida, 1963). The maternal care species thus can utilize the drifting seaweed as substratum for their short distance dispersion.

Maternal care paradox in the caprellids in *S. patens* bed

It is generally accepted that the animals which show maternal care behavior produce small number of large progenies. However, among the caprellids living on the *S. patens* thalli, the females of maternal care species produce larger number of smaller eggs or smaller juveniles. "The maternal care paradox" can be explained by the following two essential factors that is specific to the caprellids on the seaweed thalli.

The first point is the fish predation. It is generally believed that larger animals have better chance of survival, because most animals which have maternal care behavior are not prey animals (see Clutton-Brock, 1991). However, on the seaweed substratum, size selective predation by fish worked on the larger

caprellids (Caine, 1989b; Edgar and Aoki, in preparation). Thus, the large juveniles should disperse immediately after the demarsupiation to decrease the chance to be sacrificed by fish. In maternal care caprellids, the whole colony consisted of small juveniles and mother have the chance to be eaten up by fish. The colony size therefore should be large enough to compensate the lost juveniles in other sacrificed colonies. Thus, here, I would like to call the maternal care observed in caprellids as "Coward's maternal care", which is the maternal care by prey animals.

The second point is the food resource. Caprellids in the genus *Caprella* can feed by filter-feeding (Keith, 1969; Caine, 1974; 1977). The mother in a colony carry or defend the juveniles, but, she has no need to feed them. Therefore, food resource cannot be a limiting factor for the number of caprellids in a colony.