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Seasonal Traits of Reproduction in a Gnathiid Isopod *Elaphognathia cornigera* (Nunomura, 1992)

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ABSTRACT—Field studies on the reproductive traits of a population of a gnathiid isopod *Elaphognathia cornigera* (Nunomura) were conducted at a rocky intertidal shore on the Izu Peninsula, southern Japan. Fortnightly surveys for two years showed some peculiar seasonal trends in the female reproductive characteristics. While adult males and juveniles of the species occurred throughout the year, semelparous adult females occurred only from spring to autumn. Based on the occurrence patterns of the females in six different reproductive stages, there seemed to be four generations in 1994 and three in 1995. Though the reproductive investment of a female showed no significant variation through each year, there were marked seasonal variations in the female broods. Female body size and brood size became the largest in early summer, but egg size reached its maximum in autumn. Maximum food availability (high density of gobies) in spring and the unfavorable environmental conditions in winter were thought to be the major controlling factors of the size and number of female broods.

INTRODUCTION

Gnathiidae is a family of Isopoda, which shows the biphasic life cycle. Although the juveniles are temporary ectoparasites of fishes (Monod, 1926), sexually dimorphic adults, having very different morphology from the juveniles, are non-feeding and the females are semelparous (Mouchet, 1928; Stoll, 1962; Upton 1987; Wägele, 1988; Klitgaard, 1991; Tanaka and Aoki, 1998). Adult gnathiids are generally found on substrata such as muddy bottom, sponges and dead corals (Monod, 1926; Holdich and Harrison, 1980). Since different stages of larvae frequently appeared from benthic habitats together with adults, larval gnathiids are believed to utilize the habitats as resting and molting places after their ectoparasitism on the host in each larval stage (Mouchet, 1928; Stoll, 1962; Upton 1987; Wägele, 1988; Klitgaard, 1991; Tanaka and Aoki, 1998). Most of gnathiids, however, are found in very low densities and it has been difficult to conduct intensive field surveys on the gnathiid populations except for *Paragnathia formica* (Hesse), previously studied in France (Amanieu, 1963) and England (Upton, 1987).

The aberrant life history displayed by Gnathiidae has attracted much interest from researchers after Hesse (1864) described the metamorphosis from larval gnathiids to adult males. The life cycle with three larval and one adult stages has been described for five species of Gnathiidae (Mouchet,

1928; Stoll, 1962; Wägele, 1988; Klitgaard, 1991; Tanaka and Aoki, 1998). A harem forming phenomenon by males has been found repeatedly for *Paragnathia formica*, *Caecognathia calva* (Vanhöffen) and *C. abyssorum* (Sars) (Monod, 1926; Upton, 1987; Wägele 1988; Klitgaard, 1991). However, further investigations, particularly population studies, are still restricted to the Afro-European species *P. formica*.

At a rocky intertidal shore on the Izu Peninsula, southern Japan, a high density population of gnathiids, present throughout the year, was found in a demosponge *Halichondria okadai* (Kadota) (Tanaka and Aoki, 1998). Although the gnathiid was formerly described as *Gnathia* sp. in Tanaka and Aoki (1998), it was identified as *Elaphognathia cornigera* (Nunomura) through a close comparison with the holotype of *E. cornigera*. The species was discovered in the demosponge, *Haliclona permolis* (Bowerbank), at Kyushu, Japan at first and described as *Gnathia cornigera* by Nunomura (1992). However, the species was moved to the genus *Elaphognathia* according to the review and reexamination of gnathiidean genera by Cohen and Poore (1994).

Based on the analysis of larval size structures, *Elaphognathia cornigera* was supposed to grow up to adults shuttling three times between the fish host and benthic habitat (see Tanaka and Aoki, 1998). Moreover, laboratory rearing experiments showed the semelparity of the species (Tanaka, unpublished). These characteristics are common in the other gnathiids so far studied (Mouchet, 1928; Stoll, 1962; Wägele, 1988; Klitgaard, 1991).

Although the basic life history pattern and harem-forming behaviors of males are known in gnathiids, the reproductive

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characteristics of females are poorly known. Moreover, the ecological studies on gnathiids have so far been conducted only in the Atlantic Ocean (Amanieu, 1963; Upton, 1987) and there has been no study in the Pacific Ocean. In this paper, we describe the seasonal traits of reproduction of *Elaphognathia cornigera*, in particular, through the examination of female reproductive characteristics, based on the

intensive long-term field studies.

MATERIALS AND METHODS

Field sampling

Sampling was conducted periodically at an intertidal rocky shore in the innermost part of Oura Bay located in the southern end of the Izu Peninsula, Japan (34°40' N, 138°57' E). The shore is composed

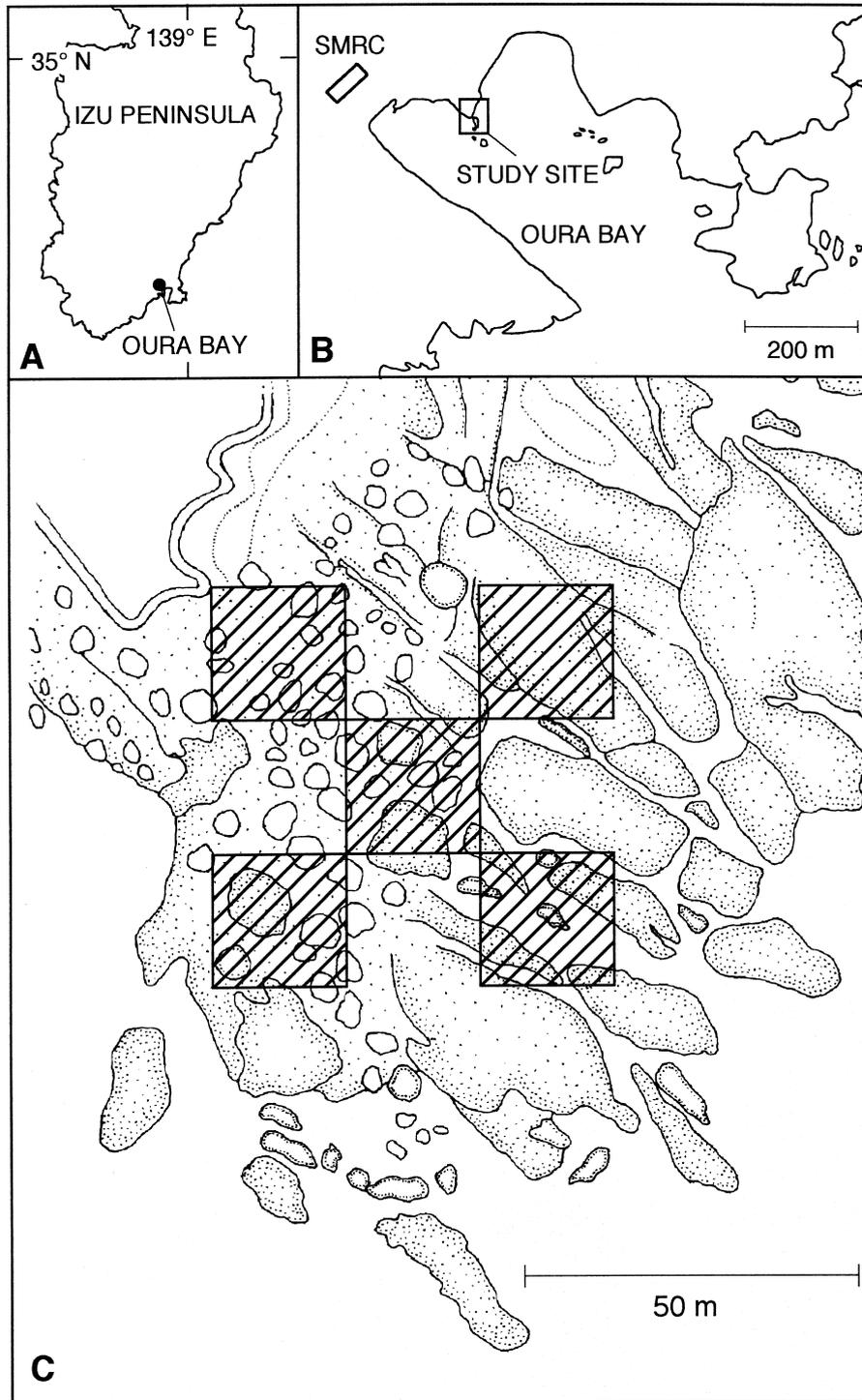


Fig. 1. Study area. A: Izu Peninsula, B: Oura Bay, C: Study site. SMRC: Shimoda Marine Research Center, University of Tsukuba. Samplings were conducted in the quadrats indicated by hatched areas.

of many flat rocks divided by grooves and channels. *Halichondria okadai* is the most dominant sponge within the shore and is abundant in tide pools and rocky crevices in the eulittoral zone (per. obs.) Daily surface water temperatures of Oura Bay were measured by personnel at Shimoda Marine Research Center, University of Tsukuba throughout the investigation. Semimonthly averages of the daily data were calculated.

Five permanent quadrats of 20 m × 20 m were set on the study area (Fig. 1). During the lowest water of every spring tide from April 1994 to March 1996, samples of gnathiids in the sponge colonies were collected. Five pieces of *Halichondria okadai* were collected from the different colonies in each of five quadrats in April 1994. However, after May 1994, the sample number was changed to eight for more accurate analysis of the population of *Elaphognathia cornigera*. Each sponge sample was taken by a 2-cm diameter corer. When it was difficult to use the corer due to the projections of rocks, equivalently sized pieces of the sponge tissue were picked by hand. Samples were taken back to the laboratory and then fixed in neutralized 10% formalin in seawater. The sponge samples were carefully dissected under a binocular microscope and all infauna including gnathiids were sorted out. Individuals of *E. cornigera* were classified into larvae, adult males and adult females by their morphological characteristics. After removal of the infauna, each sample of sponge tissue was dried at 80°C for over 48 hr to constant weight for the measurement of dry weight.

Measurement of female reproductive traits

Females of *Elaphognathia cornigera* were classified into six phases according to the developmental stages of embryos carried in the brood pouch (Fig. 2). In order to exclude the egg size variation due to the developmental stage of eggs, numbers and sizes were measured only for the eggs carried by phase II females. Both the long axis and short axis of all eggs brooded by phase II females were measured. The volume of eggs was calculated using the formula for the volume of an ellipsoid:

$$V = \pi LS^2/6$$

Where V, L and S are egg volume, long axis and short axis, respectively.

Lengths of all segments, namely, the cephalon, six pereonites, five pleonites and pleotelson, were measured for ninety-nine females which were collected in May and June 1994. The combined length of all segments of each female body length (BL) was regressed by the combined length from the third to sixth pereonites (PL) and the following equation was obtained.

$$BL = 0.69 + 1.29 PL \quad (r^2 = 0.76, p < 0.001, n = 99)$$

Body lengths of phase II females used for data analysis were estimated from this equation.

Statistical analysis

To examine the seasonal variation in female reproduction, the brood size (BS), mean egg volume within a brood (EV), total brood volume (BV = BS × EV) and female body length (BL), were each pooled within each month, because phase II females were relatively few per sampling time. BV divided by BL³ was calculated as an index of reproductive investment of females. Regression analysis was used to compare BS and BL across months. The BS, EV, BL and BV / BL³ data within a month was tested for normality within Kolmogorov-Smirnov test. Two-way ANOVA's could not be used due to missing data for April 1994. Consequently, one-way ANOVA's were used to compare each of BS, EV, BL and BV / BL³ between months and between years pooling months. Interactions were checked for graphically.



1 mm

Fig. 2. Reproductive phases of females classified by the developmental stages of embryos in their brood pouch. I. Before ovulation. Although eggs in the ovary are visible in the dorsal part of female gnathiid, the brood pouch is empty. II. Just after ovulation. Clear and oval eggs are filled in the brood pouch. III. Females carrying embryos with eyes in irregular shape. Embryos have no remarkable body segments. IV. Females carrying embryos with distinguishable cephalon, thorax and abdomen. V. Females carrying fully developed larvae moving in the brood pouch. VI. Females already released larvae. The brood pouch is empty.

RESULTS

Seasonal changes in *E. cornigera* population

Seasonal fluctuations in the density of *Elaphognathia cornigera* (number of individuals per gram sponge dry weight) are shown in Figure 3. In 1994, the density of larvae abruptly increased in June and a remarkable increase of adults of both sexes occurred in July. After that, the total density reached 79.4 in August and was kept rather constant with minor fluctuations until October. Females decreased from November and were completely absent by early January. The female emergence period was almost consistent with the period when high water temperature above 18°C was recorded. Males and larvae overwintered and subsisted until the following May with

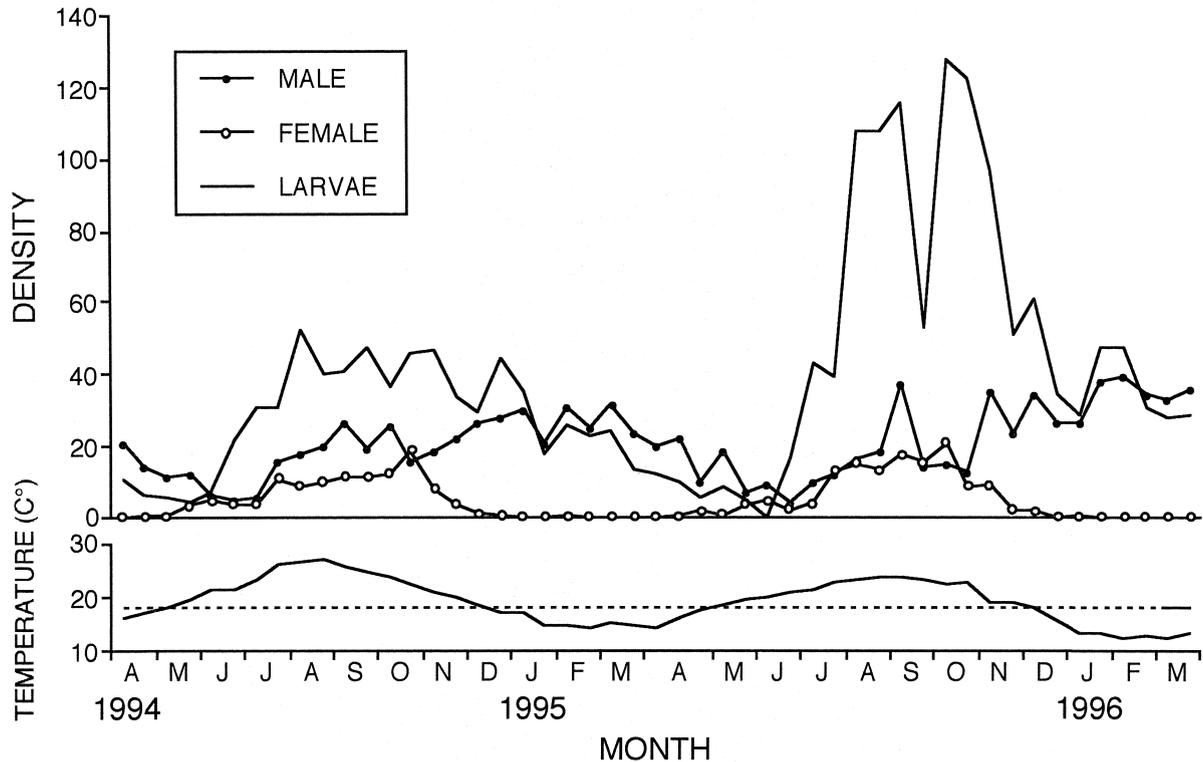


Fig. 3. Upper: Seasonal fluctuations in the density of *Elaphognathia cornigera* males, females and larvae. Density is in number of animals per gram of dried sponge. Lower: Surface water temperature of Oura Bay. Broken line indicates the 18°C line.

a slight decrease in densities. Although the pattern of changes in the second year was basically the same as that of the first year, females emerged earlier and the density of gnathiids changed more drastically (maximum and minimum of total density were 171.0 in September and 15.7 in May respectively) owing to a much higher density of larvae in the second year.

The pattern of seasonal changes in abundance of females in each reproductive phase was basically the same in each year (Fig. 4). Of the females that started to appear in spring, younger phase I and II individuals were dominant (100% in early May 1994, 84.6% in late April 1995). Females in later phases, particularly phase VI individuals (females with empty brood pouches), appeared two weeks later. After that, all six phases of females were observed in most months until October. From October to December, females in phase I and II decreased in abundance and then disappeared and those in later phases became dominant. Finally, females completely disappeared by late January. Curves of the changes in abundance of individuals in each phase were apparently polymodal, indicating four peaks in phases II, IV and V in 1994 and three peaks in phases III and IV in 1995. The intervals between the peaks were 1.5 to 2 months in each year.

Female body length, brood size and egg size

Phase II females were obtained from May to November 1994 and from April to November 1995 (Fig. 5). Although the slope, intercept and regression coefficient of the regression

equation between female body length and brood size varied among months, positive relationships were obtained in several months (May, June, September, October 1994 and July–October 1995) in which the equations were statistically significant (Table 1).

Although each of female body size, brood size, egg volume and brood volume per body length cubed as the reproductive investment of females were significantly different among years (Table 2), the pattern of seasonal changes in these reproductive variables was almost the same in each year (Fig. 5). Body length of the females increased from spring, reached a peak in summer and then gradually decreased (Fig. 5A). Brood size rose from spring to summer and returned to a low level during autumn (Fig. 5B). Although the general trend of seasonal fluctuations in brood size was similar to that of female body length, the seasonal fluctuation in egg size differed markedly (Fig. 5C). Eggs were relatively small from spring to summer but then egg volume increased and reached a maximum in late autumn (Fig. 5C). As a result, reproductive investment of females to eggs as brood volume per female body length cubed (BV/BL^3) increased from spring to summer, decreased from summer to autumn and rose again in late autumn (Fig. 5D).

While female body length, brood size and clutch volume were significantly different between months in both in 1994 and 1995, no significant difference was observed for the reproductive investment of females as BV/BL^3 (Table 3).

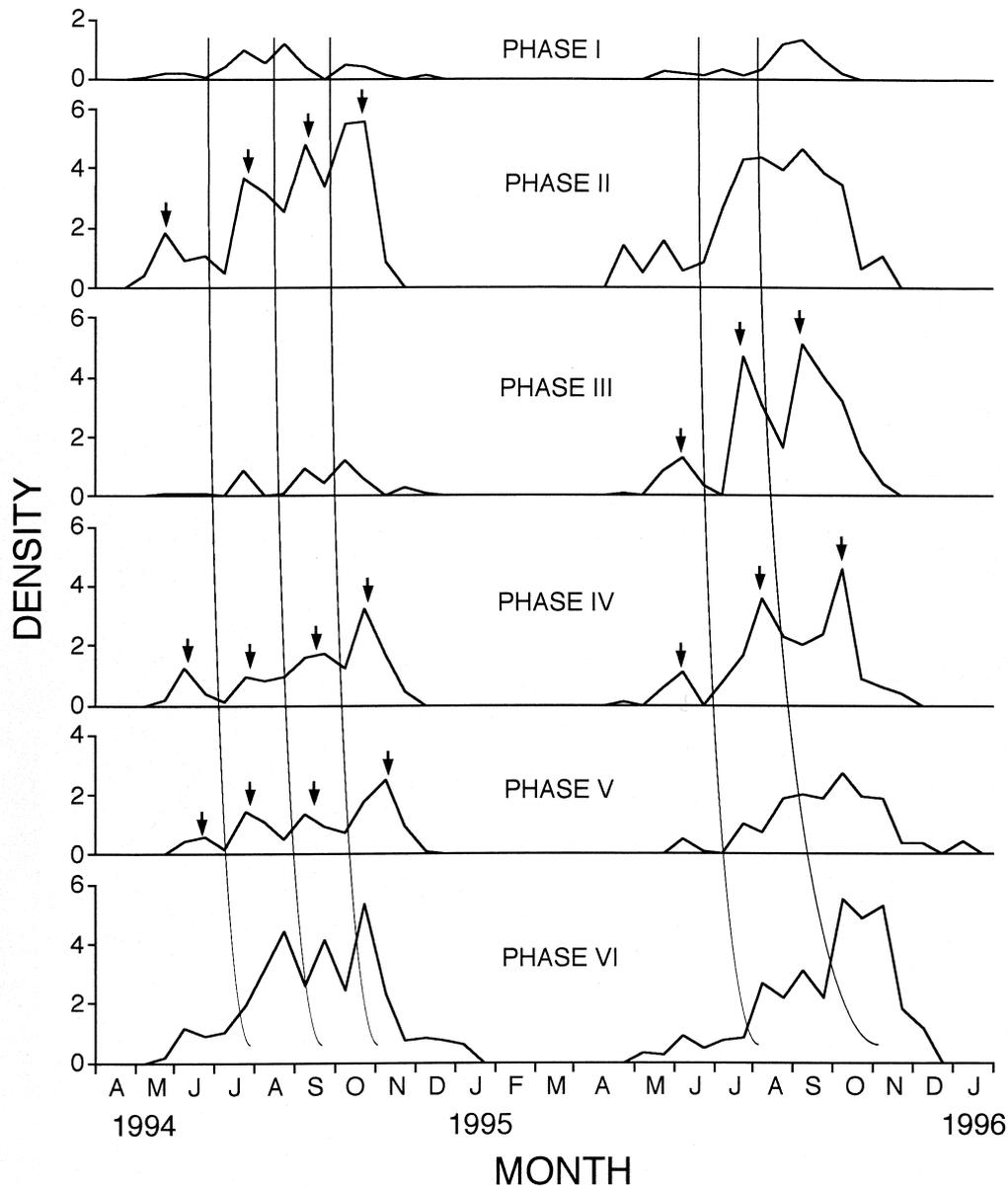


Fig. 4. Seasonal emergence patterns of females of *Elaphognathia cornigera* in each reproductive phases. Density is in number of animals per gram of dried sponge. Emergence patterns appear to have 4 peaks in 1994 and 3 peaks in 1995, indicated by arrows.

DISCUSSION

Differential occurrence patterns between sexes

For *Elaphognathia cornigera* in this study, a difference in the emergence period of adults among sexes was apparent. Absence of females in winter indicates that no maturation of the gnathiid occurs in the season. This may be due to the developmental halt of larvae by low temperature as known in *Paragnathia formica* both in the laboratory (Stoll, 1962) and in the field (Upton, 1987). Since simultaneous increases of adult males and females of *E. cornigera* in early summer (July 1994 and June-July 1995) suggest that both sexes of individuals matured synchronously, the subsistence of males and absence of females during colder months are considered to be caused not by the difference in maturation timing between sexes, but

by the longer longevity of males than that of semelparous females. The shorter life span of females than males was also reported in *P. formica* (Upton, 1987). Overwintering males of *E. cornigera* are likely to contribute to the reproduction from the following spring.

Generation number and generation time

Based on the comparison among occurrence patterns of *Elaphognathia cornigera* females in different reproductive phases, especially the number of peaks in the patterns, there seemed to be four generations in 1994 and three in 1995. Time lag between the first emergence of Phase I females and the abrupt increase of larvae in July implies that the incubation period of eggs in *E. cornigera* is approximately a half month. The estimation is also supported by the first appear-

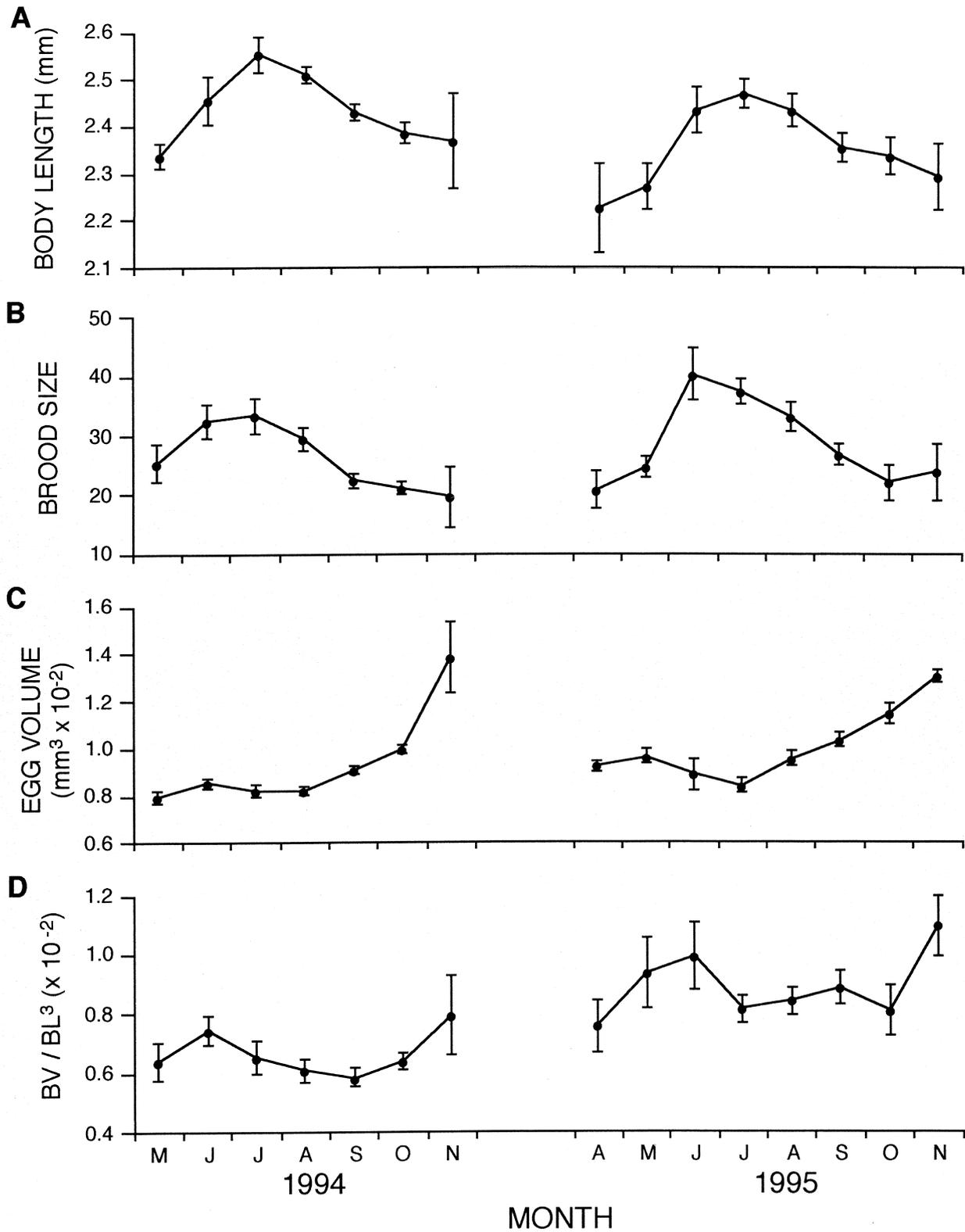


Fig. 5. Seasonal changes in reproductive variables of *Elaphognathia cornigera* in 1994 and 1995. Means and standard errors (vertical bars) are shown. **A:** body length of females, **B:** brood size, **C:** mean egg volume within one brood, **D:** brood volume per body length cubed (BV/BL^3).

Table 1. Results of monthly linear regression analysis between body length and brood size of female of *Elaphognathia cornigera*. NS: not significant.

Year	Month	N	Slope	Intercept	r ²	P
1994	May	17	98.1	-203.1	0.585	<0.01
	Jun.	13	37.7	-59.9	0.406	<0.05
	Jul.	24	26.3	-33.4	0.112	NS
	Aug.	35	32.2	-50.7	0.091	NS
	Sep.	56	27.7	-44.8	0.164	<0.05
	Oct.	49	22.1	-31.5	0.195	<0.05
	Nov.	5	24.3	-37.2	0.266	NS
1995	Apr.	7	24.6	-33.9	0.493	NS
	May	8	-1.3	27.9	0.01	NS
	Jun.	8	10.3	15.4	0.012	NS
	Jul.	37	43.9	-70.9	0.362	<0.01
	Aug.	16	42.2	-71.9	0.278	<0.05
	Sep.	21	28.0	-38.5	0.206	<0.05
	Oct.	12	46.0	-83.4	0.439	<0.05
	Nov.	3	61.6	-117.5	0.845	NS

Table 2. Results of one-way ANOVA's on reproductive variables of female *Elaphognathia cornigera* comparing years pooling months. BL: body length; BS: brood size; EV: egg volume; BV/BL³: brood volume per body length cubed.

df	Variables	F	P
1	BL	6.06	<0.05
1	BS	14.8	<0.001
1	EV	10.8	<0.005
	BV/BL ³	62.5	<0.001

Table 3. Results of one-way ANOVA's on reproductive variables of female *Elaphognathia cornigera* comparing between months. BL: body length; BS: brood size; EV: egg volume; BV/BL³: brood volume per body length cubed; NS: not significant.

Year	df	Variables	F	P
1994	6	BL	6.18	<0.001
	6	BS	6.47	<0.001
	6	EV	23.19	<0.001
	6	BV/BL ³	1.54	NS
1995	7	BL	2.74	<0.05
	7	BS	4.75	<0.001
	7	EV	6.80	<0.001
	7	BV/BL ³	0.86	NS

ance of Phase VI females with empty brood pouches after a half month from the beginning of the breeding season. Judging from the period from the first appearance of the newly born larvae until the increase in adult densities, the larval period of *E. cornigera* is estimated to be about one and a half months. Therefore, the generation time of female *E. cornigera* at the study site may be about two months including a half month spent in the mother's brood pouch and one and a half months as larvae. It is clear that the longevity of the female *E. cornigera* is shorter than that of females of *P. formica* which have annual life cycle (see Upton, 1987).

Water temperature is a dominant factor affecting the growth rate of gnathiids. Stoll (1962) showed that the higher

water temperature caused shorter molting intervals in *Paragnathia formica*. Females of *P. formica* in a southern French population matured several months earlier than those in a British population due to the warmer environmental conditions in France (Upton, 1987). The life span of male *P. formica* is about two years (Upton, 1987). In contrast, in the Antarctic region, the males of *Caecognathia calva* could live over several years after maturation (Wägele, 1988). Therefore, the shorter generation time and the larger number of generations in a year in *Elaphognathia cornigera* may be attributed to the warm conditions of the study area. It is also possible that fewer generations of *E. cornigera* in 1995 is due to the lower water temperature during the breeding season than in 1994.

Seasonal changes in the female body size

Body size is apparently a major limiting factor in the reproductive investment of female *Elaphognathia cornigera*, because the reproductive output per female size, which is represented as brood volume per body length cubed, was not significantly different among the samples collected in the different seasons. Females will not have to save energy for the future reproduction or somatic growth, because of the semelparity. The body size considered to express the amount of accumulated energy should directly affect the total reproductive investment of a female.

In most crustaceans, lower temperature causes larger body size by prolonging intermolt period and the accumulation of biomass between molts (see Hartnoll, 1982). For instance, an isopod *Paracerceis sculpta* (Holmes) showed a negative correlation between ambient temperature and the size of all adult morphotypes (Shuster and Guthrie, 1999). Since larger females of *Elaphognathia cornigera* in summer were regarded to be born in spring when water temperature was relatively low, they seem to follow the assumption. However, individuals collected in spring can not be explained by the temperature effect. The size of the *E. cornigera* females maturing in spring is expected to be the largest, because they are assumed to overwinter during their larval period. But, these overwintering females were actually smaller than those sampled in other seasons. This may be attributed to the energy loss for overwintering. Thus, ambient water temperature is not considered as the single factor controlling female body size in *E. cornigera*.

Apart from physical factors, biological factors such as food availability or predation can affect the size of individuals in a population. Food availability is the most plausible explanation for the seasonal changes in female body size in *Elaphognathia cornigera*. At our study site, an intertidal goby *Chasmichthys dolichognathus* (Hilgendorf), regarded as the main host of the ectoparasitic *E. cornigera*, was most abundant in spring and was less common from summer to autumn (Tanaka, unpublished data). The goby is known to have an annual life cycle with the breeding period in spring (Sasaki and Hattori, 1969). Larger female gnathiids in summer may be attributed to the high availability of the host during their larval period in spring.

On the contrary, smaller females in spring may be due to the scarce food availability (low abundance of gobies) from autumn to winter in their larval period. Besides food availability, size-selective predation may also change the size distribution of the prey. At the Great Barrier Reef, Australia, a cleaner fish *Labroides dimidiatus* feeds mainly on larval gnathiids and the fish prefer the larger prey (Grutter, 1994, 1997). Though there is no data about the fish predation of *E. cornigera*, it is possible that such size-selective predation by visual predators caused seasonal changes in the size distribution of the female gnathiids. More detailed field surveys and laboratory experiments, however, are needed to elucidate the biological factors which potentially affect the female body size in *E. cornigera*.

Trade-off between egg number and size

In *Elaphognathia cornigera*, as in most other isopods, there were positive relationships between female body size and the brood size within a month, but the relationships varied among months. Females produced a large number of smaller eggs in spring, and fewer larger eggs in autumn (Fig. 6). The upper limit of total reproductive output was constrained by female body size, thus the trade-off between the quality and the quantity of eggs was evident. Increase of egg size may be explained as an adaptation to unfavorable environment to reduce the early mortality of offspring (Brody and Lawlor, 1984; Kusano and Kusano, 1988; Bell and Fish, 1996). In the terrestrial isopod *Armadillidium vulgare* (Latreille), the birth size increased when the mother faced food shortages (Brody and Lawlor, 1984). Kusano and Kusano (1988) showed that egg size of the freshwater amphipod *Jesogammarus spinopalpus* Morino was positively related to the seasonal changes in water temperature. For *J. spinopalpus*, as water temperature became higher, the early mortality of juveniles rose (Kusano *et al.* 1987) together with the egg size (Kusano and Kusano, 1988). Thus, the larger egg size of *E. cornigera* in autumn is potentially an adaptation for increasing the survival rate of juveniles against the low host availability or the subsequent colder season. On the other hand, greater quantity of eggs, with favorable conditions in spring, would contribute to the rapid recovery of the population size after overwintering.

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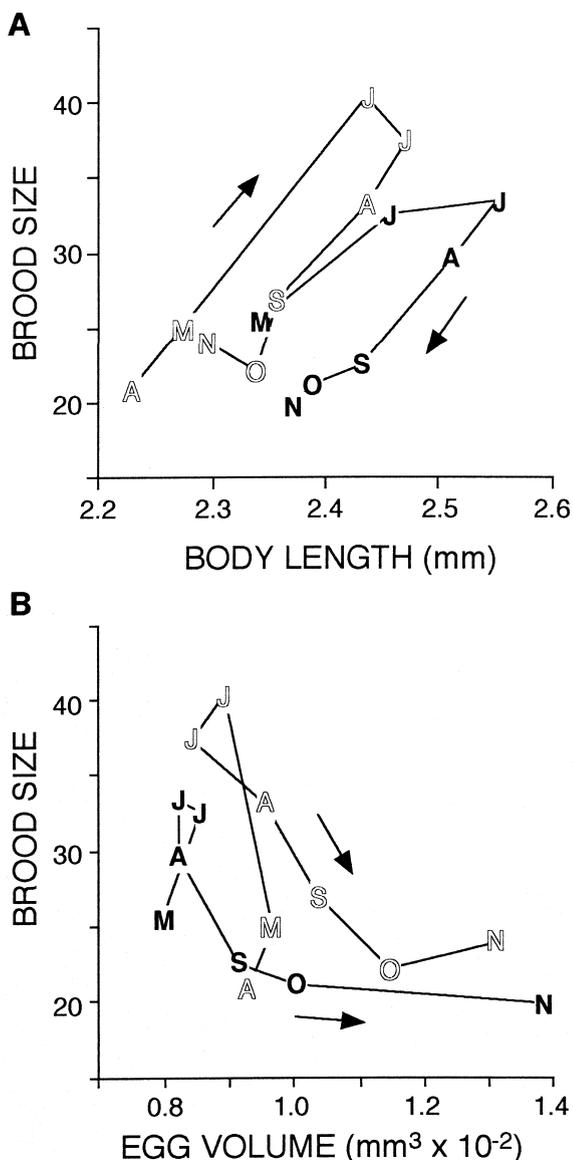


Fig. 6. Relationships among reproductive variables. Monthly average of brood size is plotted versus body length (A) and egg volume (B). Initial letters of months are presented in bold characters for 1994 and in outline characters for 1995.

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