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Life History Patterns of Two Coexisting Isopods (*Ligidium japonicum* and *Ligidium koreanum*) in a *Cryptomeria japonica* Plantation of Southwestern Japan

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Abstract Population dynamics and life histories of two coexisting species of *Ligidium* (Crustacea, Isopoda) were studied in the Sanbe Experimental Forest of Shimane University from May 1991 to April 1993. The study stand was a plantation of *Cryptomeria japonica* of about forty-years-old located on the middle of the northwestern slope of Mt. Sanbe. Changes in density of the two species were found to be very different. Density of *Ligidium* japonicum was relatively stable (29～63 m^{-2}), but that of *Ligidium koreanum* showed much fluctuation with regular pattern (10～97 m^{-2}). The patterns of life histories of the two species were also very different. Pregnant females of *Ligidium japonicum* and *Ligidium koreanum* were sampled from late June to early August in 1991 and up to late August in 1992, and from late April to early June in 1991 and up to late June in 1992, respectively. Newly hatched animals of *Ligidium japonicum* and *Ligidium koreanum* appeared first in early August and in late June of both the years. Young *Ligidium japonicum* scarcely grew in the birth year, and began to grow after overwintering and bred in the next June, while young *Ligidium koreanum* grew more rapidly in the birth year and began to breed in the next April, soon after overwintering. After breeding, all the adults of the two species died and a generation overlap was not observed at all. The natality of *Ligidium koreanum* was higher than that of *Ligidium japonicum* (693～839 m^{-2} and 256～499 m^{-2}, respectively). Mortality in both the species was very high initially and after breeding, but were very low during winter. Mortality in the growth stage of *Ligidium koreanum* was higher than that of *Ligidium japonicum.*

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Introduction

Terrestrial isopods are very common in warm temperate forests in Japan and some species of them are sympatric. Population dynamics and life histories of coexisting species were examined by SAITO (1965) of *Armadillidium vulgare* (LATREILLE), *Porcellio scaber* LATREILLE and *Ligidium japonicum* VERHOEFF, by KATO (1976) of *Ligidium japonicum* and *Ligidium* sp., by TSUKAMOTO (1977) of *Ligidium japonicum* and *Ligidium paulum* NUNOMURA, and by WATANABE (1980) of *Sphaerillo dorsalis* (IWAMOTO), *Porcellio* sp. and *Trichoniscus* sp.. Two ecological studies on sympatric members of the genus *Ligidium* have been conducted by KATO (1976) and TSUKAMOTO (1977). However, differences in population dynamics and life histories of *L. japonicum* and *Ligidium koreanum* FLASAROVA in the same habitat have not yet been reported. *L. japonicum* is a common species from Hokkaido District, Honshu District and Shikoku District in Japan, while L. koreanum has been reported mainly from Kyushu District in Japan (NUNOMURA, 1983). But *L. koreanum* was found in a plantation of *Cryptomeria japonica* D. DON in the Sanbe Experimental Forest of Shimane University for the first time other than the Kyushu District. This is the eastern limit of distribution of this species (NUNOMURA, personal communication).

L. japonicum and *L. koreanum* coexist in this study site, and populations and life histories of these two species were examined from May 1991 to April 1993. In this paper, different patterns of population dynamics, growth and breeding of the two species are discussed.

Study Site

The present study was carried out at the Sanbe Experimental Forest of Shimane University (35° 10′ N, 132° 40′ E). The study site is located on the northwestern slope of Mt. Sanbe situated 400m above sea level. The study stand of *Cryptomeria japonica* was about 40 years old, with density of 1250 stems/ha, mean height of 16.4 m, mean diameter at 1.3 m above ground of 22.9 cm. The soil type is $Bl_{D(d)}$ (Andisol).

Methods

A sampling plot (10 m × 35 m) was set up in the middle part of the northwestern slope. Twenty-eight samples were taken randomly each month from May 1991 to April 1993, except during the snowy season from December to February. When a sampling could not be finished in a day, the rest of the samples were taken within six days. A cylindrical sampler ($170.2 cm^2$) was inserted into the ground to a depth of 5 cm, and a block of forest litter and soil was collected along with the animals, and then isopods were sucked by an aspirator from the sample soils spread on a tray. During the study period, 2.45% area of the plot was sampled.

The animals collected were brought back to the laboratory and fresh weights of individuals were measured immediately using an electric balance. After weighing, the animals were preserved in 70% ethanol. Species and sex of animals were determined under a microscope with a micrometer eyepiece. The sex of the individuals less than 2.0 mg in body weight could not be determined. When pregnant females were found, body lengths of the individuals were measured and the number of young and embryos in the brood pouch were counted.

To measure precipitation and air temperature, two data loggers (Squirrel Meter/Loggers, Grant, Co., UK) were set in an open area and in a plantation of *C. japonica* near the study stand.

Results

Climate in study site

Precipitation and air temperature measured by data loggers are shown in Table 1. Annual precipitation from May 1991 to April 1992 was 2472.5 mm and the total precipitation during the study period was 3565.0 mm. The maximum mean air temperature was 23.2℃ in August 1992 and the minimum mean air temperature was 2.1℃ in February 1992.

Population density

Changes in population densities of the two species during the period of study are shown in Fig. 1. The detailed data are shown in Appendix 1. During the study period, the density of *L. japonicum* was relatively stable. The maximum density was 63 m^{-2} on 25, 26 June 1992 and the minimum density was 29 m^{-2} on 4, 6 August 1991 and on 29 August, 2 September 1991. The density scarcely decreased between December to February.

The seasonal changes in the density of *L. koreanum* indicated the same pattern both in 1991 and 1992. The density suddenly increased in June, remained constant until September and then decreased gradually until May, but the number of individuals scarcely decreased during winter. The highest density was observed during the season from late June to August (about 90 m^{-2}) and the lowest density in May (10～20 m^{-2}). The seasonal changes in the density of the two species were quite different, inconspicuous in *L. japonicum* and conspicuous in *L. koreanum*.

Table 1. Precipitation and mean air temperature from May 1991 to November 1992.

Month	Temperature(℃)	Precipitation (mm)
May 1991	14.7	53.5
Jun.	19.6	349.5
Jul.	22.3	495.0
Aug.	21.8	122.5
Sep.	19.6	260.5
Oct.	13.2	124.5
Nov.	8.3	123.0
Dec.	6.8	164.0
Jan. 1992	3.0	191.0
Feb.	2.1	186.5
Mar.	5.1	244.5
Apr.	10.8	158.0
May	13.4	198.0
Jun.	17.2	102.0
Jul.	19.9	120.5
Aug.	23.2	252.0
Sep.	18.7	142.0
Oct.	13.0	91.0
Nov.	9.2	187.0

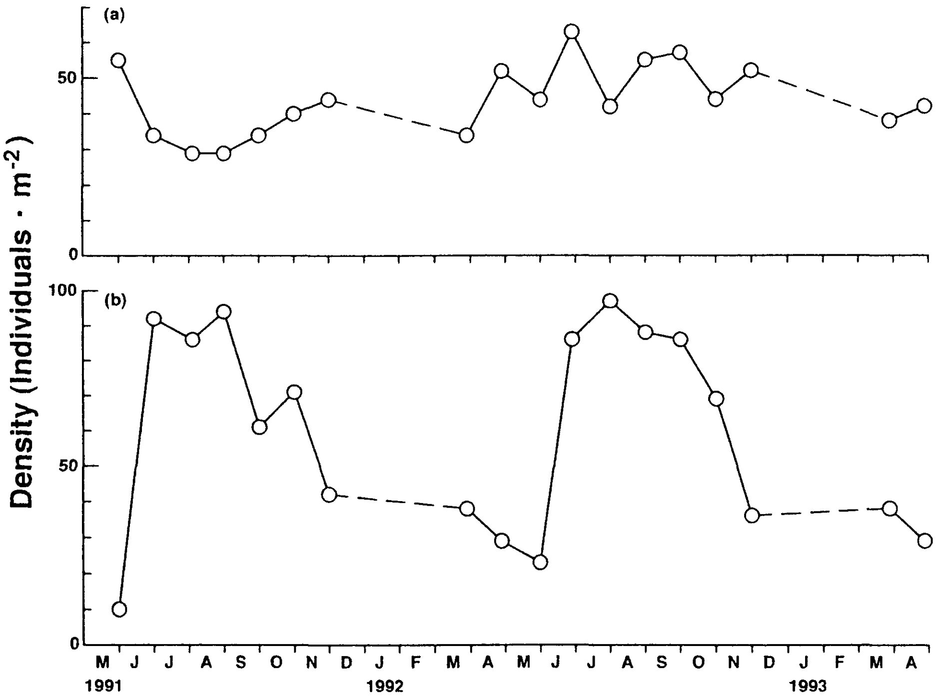

Fig. 1. Seasonal change in population density of *Ligidium japonicum* (a) and *Ligidium koreanum* (b) during the study period.

About the other isopods except the genus *Ligidium*, *Porcellionicles pruinosus* BRANDT and *Sphaerillo russioi* (ARCANGELI) were observed during the study period. Mean densities given with standard error of *P. pruinosus* and *S. russioi* were $6.4 \pm 0.8\ m^{-2}$ (min.-max.; 0～17 m^{-2}) and $14.7 \pm 2.8\ m^{-2}$ (min.-max.; 2～48 m^{-2})

Size structure and growth pattern

The frequency distributions of size classes (fresh weight) for *L. japonicum* and *L. koreanum* are shown in Fig. 2 and Fig. 3, respectively. The number in each size class is shown as a percentage of the total number sampled. The *L. koreanum* young larger than 2.0 mg sampled before late August was regarded as unknown sex, because the sex of this species could not be determined until late September.

In the population of *L. japonicum*, the newly hatched young ones were sampled first in early August both in 1991 and 1992. Two cohorts could be recognized in early August, but animals hatched the previous year disappeared before long and a new cohort mostly occupied the population in September, thus generations did not overlap. A cohort which appeared in early August 1991 was observed for about fourteen months until the next late September. Adults were no more observed after 29 August, 2 September in 1991 and after 30 October in 1992. Life span seemed to change a little yearly, because disappearing time of adults was different between 1991 and 1992.

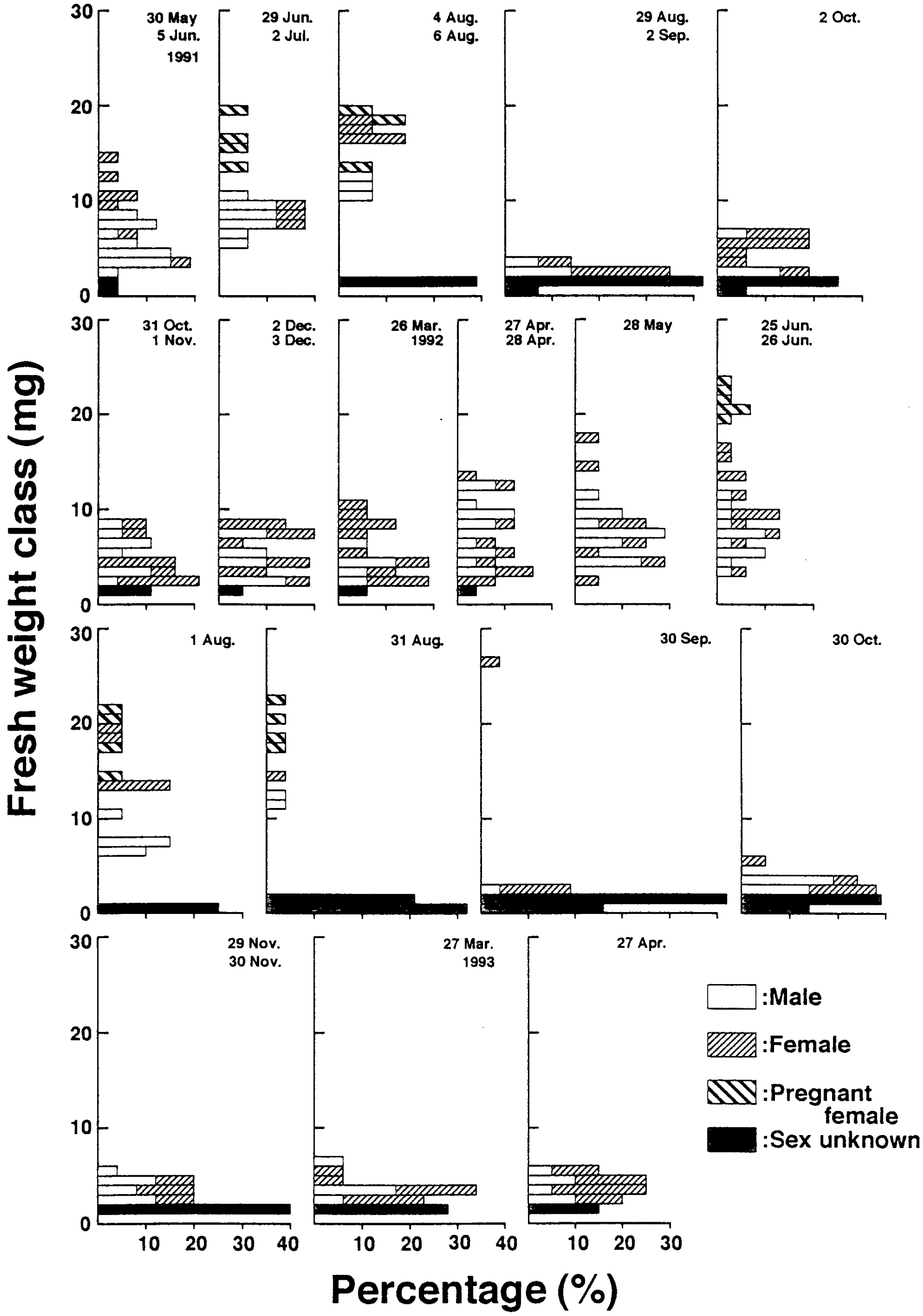

Fig. 2. Size class distribution of *Ligidium japonicum* in percentages on the monthly sampling dates. Size classes are given as fresh body weight.

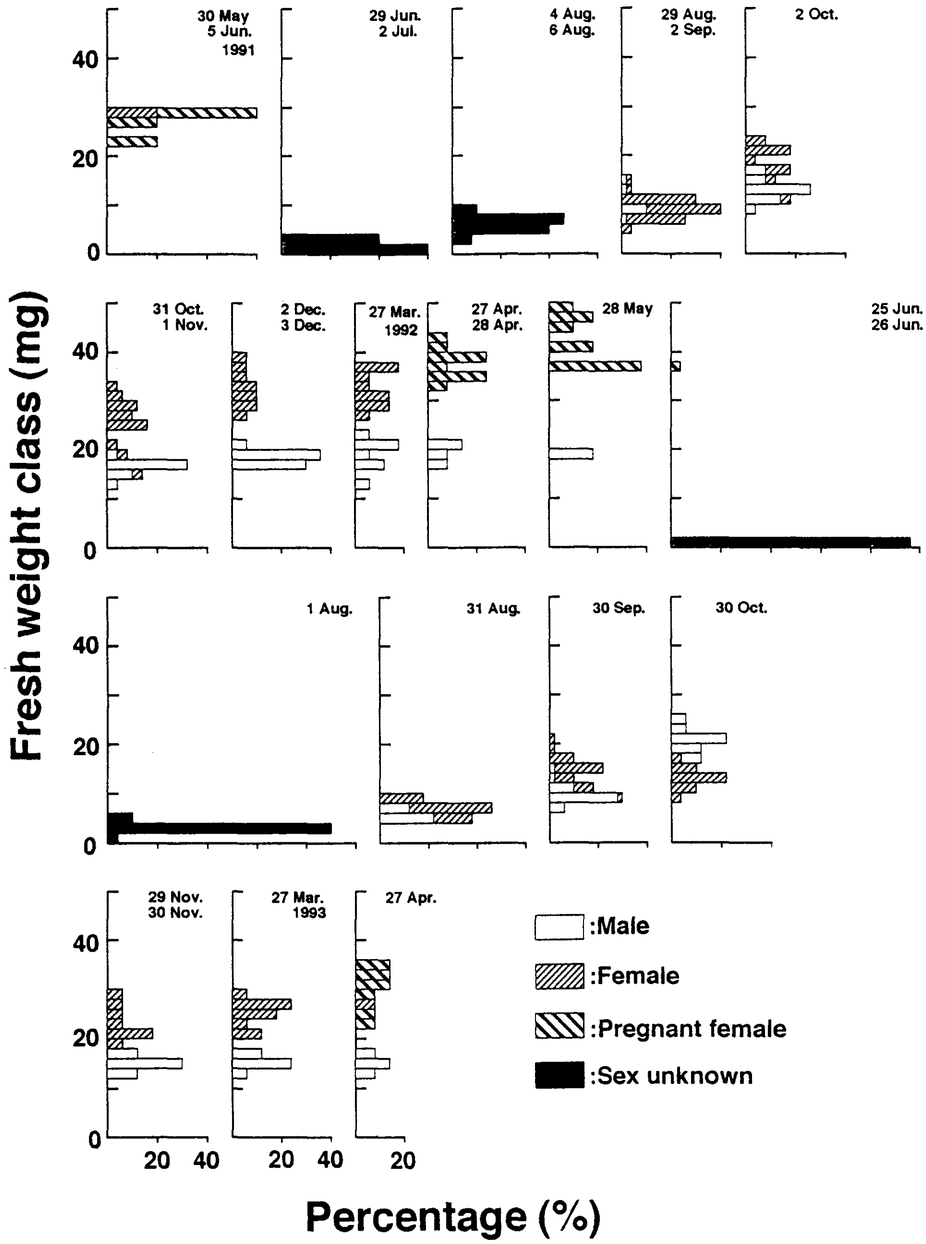

Fig. 3. Size class distribution of Ligidium koreanum in percentages on the monthly sampling dates. Size classes are given as fresh body weight.

In the population of *L. koreanum*, recruitment of young animals and decrease of adults were observed in late June of both 1991 and 1992, generations not overlapping. Weight difference between males and females was apparent from late September. Females grew larger than males and the size distribution was bimodal by sex in March just before the breeding season. Life span of a cohort born in 1991 was about twelve months and two months shorter than that of *L. japonicum*. There was one month difference in the disappearing time of adults between 1991 and 1992. It can be considered that the life span changes annually as in *L. japonicum*.

The mean growth curves calculated for the two species from the field data are shown in Fig. 4. Mean fresh weights of the two species are shown in detail in Appendix 2. *L. japonicum* grew little in the birth year and rapidly from the next May. In contrast to this, *L. koreanum* showed a rapid growth in the birth year and began to breed soon after the overwintering. Mean body weight of the two species did not increase at all during winter. Mean body weight of *L. japonicum* adults were much smaller than that of *L. koreanum*. In each species, mean body weight of a cohort which was born in 1991 was much larger in same month than that in 1992, thus yearly changes of body size was observed.

The relative growth rates of the two species are shown in Fig. 5. The growth rate was calculated by the following formula: growth rate$=W_t/W_{t-1}$, where W_t, W_{t-1} are mean body weights at the present time, and at the previous sampling time. The highest growth rate of each

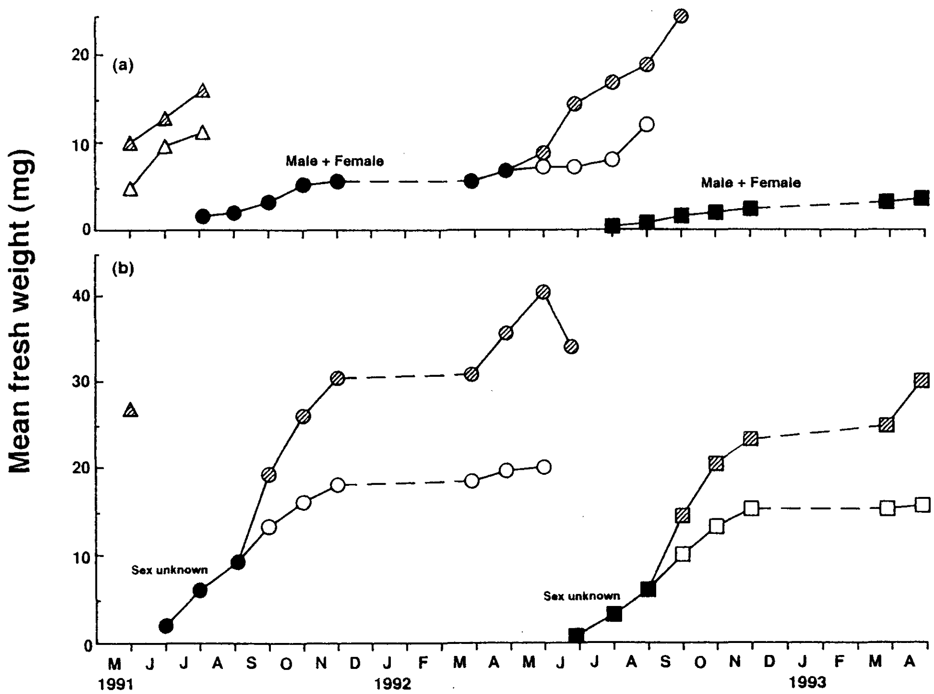

Fig. 4. Growth curves of yearly cohorts of *Ligidium japonicum* (a) and *Ligidium koreanum* (b). Cohort considered born in 1990, cohort born in 1991 and cohort born in 1992 are shown by symbols, △, ○ and □, respectively. Refer to Fig. 2 for the patterns inside the symbols.

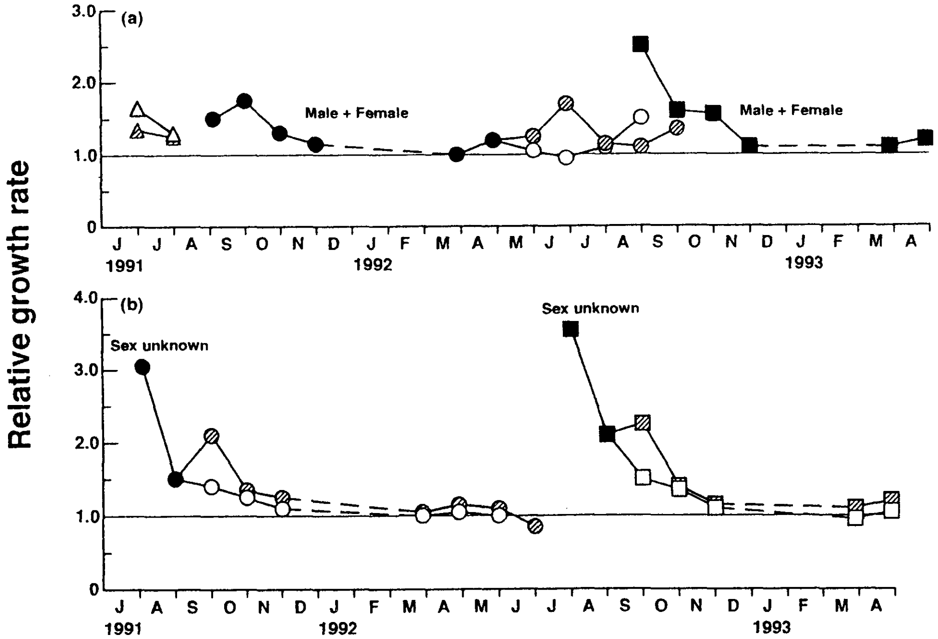

Fig. 5. Relative growth rates of *Ligidium japonicum* (a) and *Ligidium koreanum* (b). Refer to Fig. 4 for the symbols.

cohort was observed in initial stages of both the species: 1.76 in late September 1991 and 2.50 in late August 1992 for *L. japonicum*, and 3.05 in late June 1991 and 3.56 in late June 1992 for *L. koreanum*. In *L. koreanum*, the growth rate of females in late September both in 1991 and 1992 was much higher than that of males, which caused a bimodal in size distribution by sex shown in Fig. 3.

Breeding biology and natality

L. japonicum females with brood pouches were observed from late June to early August in 1991 and from late June to late August in 1992 (Fig. 2). Pregnant females of *L. koreanum* were sampled first in late April in both years and observed until late May in 1991 and until late June in 1992 (Fig. 3). Pregnant females of each species appeared at almost the same time every year, but disappeared at different time. About breeding times, it is considered that cohorts of the two species bred once during their life spans.

In *L. japonicum*, the number of eggs were not clearly related to the body length of the females (Fig. 6a). But the correlations between the number of eggs and body length of the females in *L. koreanum* both in 1992 and 1993 were very positive (Fig. 6b). The number of eggs of *L. koreanum* in 30 May 1991 were not determined.

The estimates of the natality of the two species are shown in Table 2. The development time was needed for the calculation of natality, but the length of pregnancy of the two species were not investigated.

Except in August 1992, the pregnancy rate of *L. japonicum* was low and the breeding

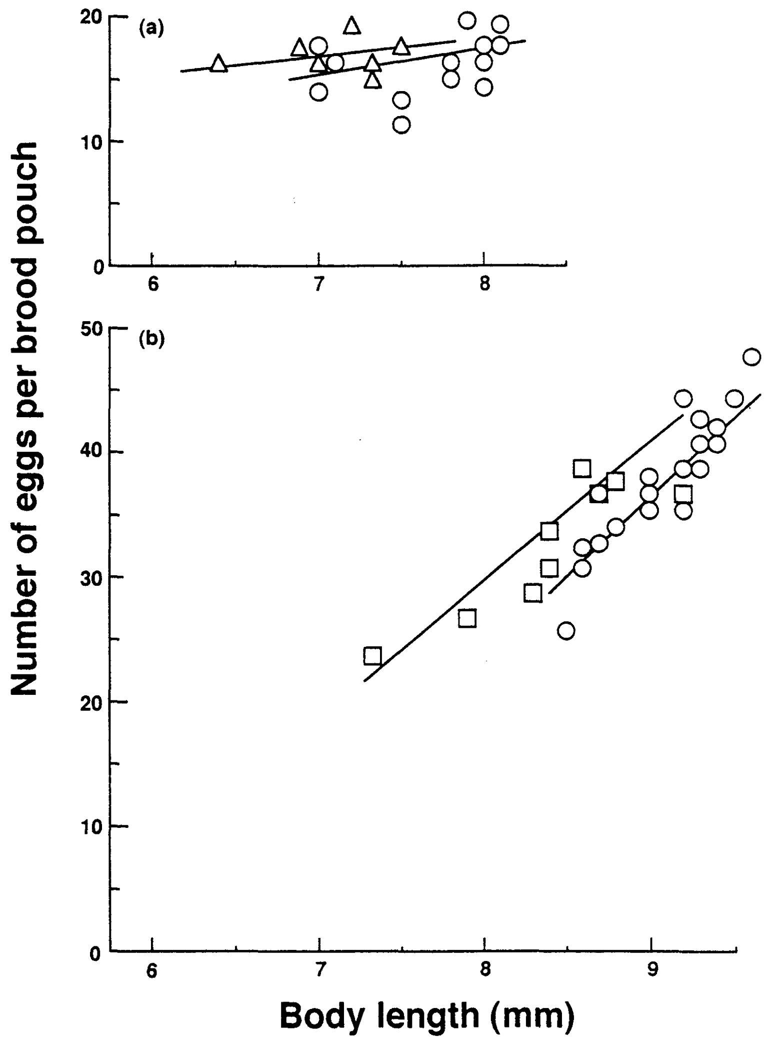

Fig. 6. Regressions of the number of eggs per brood pouch on female body length of *Ligidium japonicum* (a); 1991(△; $Y=0.45X+14.36$, $n=7$, $R^2=0.02$), 1992 (○; $Y=1.94X+1.78$, $n=13$, $R^2=0.12$) and *Ligidium koreanum* (b); 1992 (○; $Y=14.49X-93.25$, $n=20$, $R^2=0.82$), 1993 (□; $Y=9.27X-45.01$, $n=9$, $R^2=0.78$) .

period was not synchronized (Table 2). Consequently, it was assumed that the development time of this species was shorter than the sampling interval. Because of the shorter development time, the number of pregnant females at each sampling date during the period was multiplied by the fecundity of the same sampling date and summed to become natality per breeding period.

In contrast with *L. japonicum*, the pregnancy rate in *L. koreanum* was nearly 100% during

Table 2. Natalities estimated of *Ligidium japonicum* and *Ligidium koreanum* during the period of study.

		Sampling date	No. of females	No. of pregnant females	Pregnancy rate (%)	Mean body length of prgnant females (mm)	Fecundity (Eggs per female)	Estimated number of youngs (/m²)
Ligidium japoicum	1991	29 Jun., 2 Jul	7	4	57.1	7.1	17	143
		4 Aug., 6 Aug	7	3	42.9	7.1	18	113
								Total 256
	1992	25, 26 Jun.	17	6	35.3	7.9	17	214
		1 Aug.	9	4	44.4	7.3	18	151
		31 Aug.	5	4	80.0	7.5	16	134
								Total 499
Ligidium koreanum	1991	30 May	5	4	80.0	8.9		
	1992	27, 28 Apr.	10	10	100.0	9.2	40	839
		28 May	9	9	100.0	9.0	37	
		25, 26 Jun.	1	1	100.0	9.0	37	
	1993	27 Apr.	10	9	90.0	9.0	33	693

the breeding period and the occurrence of pregnant females was highly synchronized (Table 2), therefore this species was assumed to have a longer development time than the sampling interval. Natality was obtained by multiplying the highest density during the breeding period by the fecundity of the sampling date.

In this study, the brood mortality was not determined. SAITO (1969) calculated the natality by defining the brood mortality as 0% and this value was also adopted in the calculation of natality in the present study.

Fecundity of *L. japonicum*, shown in Table 2, was calculated using the mean number of eggs, because the R^2 of regression calculated for *L. japonicum* was very low, while that of *L. koreanum* was calculated using the formula in Fig. 6(b). The estimated natality of *L. japonicum* was 256 m^{-2} in 1991 and 499 m^{-2} in 1992, and that of *L. koreanum* was 839 m^{-2} in 1992 and 693 m^{-2} in 1993.

Mortality and life table

The age specific survivals of each cohort in the two species throughout the study period are shown in Fig. 7. The natalities were plotted at the sampling date when pregnant females were not observed at all.

In both the species, the number of individuals decreased suddenly during the term from the months in which the natalities were plotted to the next sampling time. The mortality of the term was 86.7% in 1991 an 91.2% in 1992 for *L. japonicum*, and 88.4% in 1992 for *L. koreanum*. This indicated that the mortality of newly hatched young was very high.

Number of individuals became 0 m^{-2} from late June when pregnant females appeared (refer to Fig. 2) to after a few months in *L. japonicum* and from late May when pregnant females appeared (refer to Fig. 3) to after one or two months in *L. koreanum*. This indicated that the mortality of adults after breeding was 100% in both the species.

The life tables of the two species are shown in Table 3. Since many more individuals of *L. japonicum* were collected in the breeding stage than in the growth stage, d_x became negative. e_x in growth stage were 2.35 in *L. japonicum* and 0.83 in *L. koreanum*. Difference of e_x in growth stage between the two species was much larger than 0.88 and 0.64 in the initial stage, and 0.50 and 0.50 in the breeding stage.

Discussion

Population dynamics

Differences in density between the two species were explained by higher natality of *L. koreanum* than that of *L. japonicum*. Natality was calculated by multiplying the density of pregnant females by the fecundity per brood pouch. The density of pregnant females were almost same between the two species, but *L. koreanum* females had about twice as much as fecudity than *L. japonicum*, and difference in fecudity was caused by that pregnant females of *L. koreanum* were much larger than those of *L. japonicum*.

About the density of *L. japonicum* in other papers in each different study site, it is stated that density of adults was 209 m^{-2} in early August 1962 and 1963 by SAITO (1965), density was 47～142 m^{-2} from March to December 1972 by KATO (1976) and mean density was 119 m^{-2} in ridge plot and 127 m^{-2} in bottom from June to November 1974 by TSUKAMOTO (1977), and these densities which have been reported are much higher than the densities in the present study. It seems that the overlapping generations which have been reported in the all other

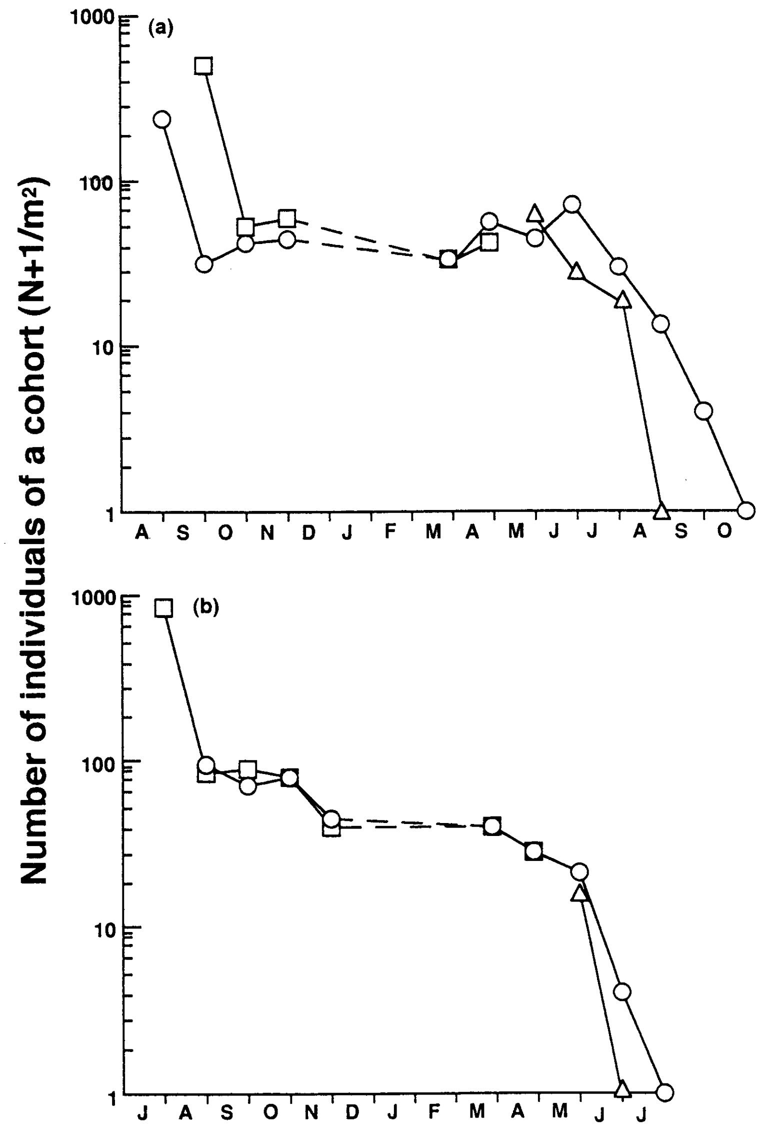

Fig. 7. Survivorship curves of *Ligidium japonicum* (a) and *Ligidium koreanum* (b); cohort considered to be born in 1990 (△), cohort born in 1991 (○), 1992(□).

studies except the present study was one of the factors for the higher densities of the previous study. In the case of overlapping generations in the population, density of pregnant females is raised because 2-year age animal also breed, and the population had the high natality (SAITO, 1965•1969).

Patterns of seasonal change in density differed between the two species. In *L. koreanum*

Table 3. Life tables of *Ligidium japonicum and Ligidium koreanum*. Initial stage: interval between natality plot and the next plot in Fig. 8. Growth stage: interval between next plot after natality and plot just before pregnant females were found in Fig. 8. Breeding stage:interval that pregnant females were found.

	Life stage(X)	Number estimated entering life stage(N_x)	Number surviving at start of life stage per 1000(l_x)	Number dying within life stage(d_x)	Life stage specific mortality(q_x)	Mean expectation of further life(e_x)
Ligidium japoicum	Initial stage	256	1000	867	867	0.88
	Growth stage	34	133	−113	−849	2.35
	Breeding stage	63	246	246	1000	0.50
	stage after breeding (A cohort born in 1991)	0	0	0	1000	
Ligidium koreanum	Initial stage	839	1000	895	895	0.64
	Growth stage (A cohort born in 1992)	88	105	70	667	0.83
	Breeding stage	29	35	35	1000	0.50
	stage after breeding (A cohort born in 1991)	0	0	0	1000	

increase in number was larger and more rapid in contrast to *L. japonicum*. This large and rapid increase in number was caused by highly synchronous recruitment, associated with the synchronized appearance of pregnant females in this specie. The breeding period of *L. japonicum* did not synchronize and this is consistent with the other reports (SAITO 1965, 1969). Differences in breeding pattern between the above-mentioned two species may be related to the different growth patterns. Young of *L. koreanum* newly hatched in June grew within the year to the suitable size for breeding and started to breed simultaneously soon after the overwintering, while young of *L. japonicum* hatched about one month later than *L. koreanum* scarcely grew in their birth year and began to grow again after winter and the breeding started in June as individuals gained breeding size. I think that the start of breeding of *L. koreanum* was restrained by low air temperature or short photoperiod in winter, but it is not apparent for *L. japonicum* that the environmental factor promoting the start of breeding.

Life history

In this study, the longevity of both the species was about one year and they are thought to breed only once a year. The other studies noted that a few individuals of *L. japonicum* lived for two years and bred again (SAITO 1965, KATO 1976).

In *Armadillidium vulgare*, the life span and the breeding schedule were affected by predation, winter temperature, photoperiod, rainfall and food supply (Sutton *et al.*, 1984). In the present study, it was not possible to determine which factors affected most strongly the life span and the breeding schedule.

Survivorship curves which have been reported for *Armadillidium vulgare* by PARIS and PITELKA (1962) and for *L. japonicum* by SAITO (1965) coincide with type II of the survivorship curves given by DEEVEY (1947). But the present study survivorship curves of the two species did not coincide with any of the three basic types given by DEEVEY, because of mortality in the growth much lower stage than those of the other stages.

I found that breeding periods of the two species were different. In some studies, it is cosidered that difference in life history patterns among some related species in the same habitat is available against resource partitioning as a mechanism of coexisting (BENKE & BENKE 1975, SOTA 1985). There was no clear evidence for resource partitioning in the present, but I also think that the difference of breeding period between *L. japonicum* and *L. koreanum* may be related to segregation for food, allowing their coexistence.

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摘　要

安藤義範（島根大学農学部森林環境学講座　〒690　島根県松江市西川津町1060）：西南日本のスギ人工林において共存する等脚目２種（ニホンヒメフナムシとチョウセンヒメフナムシ）の生活史パターン.

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島根大学三瓶演習林スギ植林地において共存するヒメフナムシ属の2種，ニホンヒメフ ナムシとチョウセンヒメフナムシの個体群動態と生活史について調査を行った。2種の個 体群密度とその変化には大きな違いがみられた。すなわち，ニホンヒメフナムシの個体群 密度は1 m^2 当り29～63個体であり，密度変化が小さかったのに対して，チョウセンヒメフ ナムシの個体群密度は1 m^2 当り10～97個体であり，密度変化が大きかった。生活史につい ても2種間で違いがみられた。繁殖期は，ニホンヒメフナムシで6月から1991年は8月ま で，1992年は9月まで，チョウセンヒメフナムシで4月から1991年は6月まで，1992年は 7月までであった。8月に出現したニホンヒメフナムシの幼体は生まれた年にはあまり成 長せず，越冬後，再び成長を始め，6月に繁殖を開始した。6月に出現したチョウセンヒ メフナムシの幼体は生まれた年に繁殖が可能なサイズまで成長し，越冬後，すぐに繁殖を 開始した。2種ともに世代の重複が観察されなかったことから，寿命は約1年と考えられる。ニホンヒメフナムシの出生率（256～499 m^{-2}）はチョウセンヒメフナムシの出生率（693～839 m^{-2}）より低かった。2種ともに初期死亡率，繁殖終了後の死亡率が非常に高 かったが，冬期の死亡率は非常に低かった。成長期の死亡率は，チョウセンヒメフナムシ の方がニホンヒメフナムシより高かった。

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Appendix 1. Number of individuals of *Ligidium japonicum* and *Ligidium koreanum* collected and detailed density (N/m^2) estimates at each sampling date.

Sampling date		*Ligidium japonicum*			*Ligidium koreanum*		
		Animals collected	Means±S.E.	N/m^2	Animals collected	Means±S.E.	N/m^2
1991	30 May, 5 Jun.	26	0.93±0.20	55	5	0.18±0.07	10
	29 Jun., 2 Jul.	16	0.57±0.16	34	44	1.57±0.37	92
	4 Aug., 6 Aug.	14	0.50±0.13	29	41	1.46±0.35	86
	29 Aug., 2 Sep.	14	0.50±0.17	29	45	1.60±0.31	94
	2 Oct.	16	0.57±0.15	34	29	1.04±0.20	61
	31 Oct., 1 Nov.	19	0.68±0.15	40	34	1.21±0.24	71
	2 Dec., 3 Dec.	21	0.75±0.23	44	20	0.71±0.15	42
1992	26 Mar.	16	0.57±0.12	34	18	0.64±0.16	38
	27 Apr., 28 Apr.	25	0.89±0.22	52	14	0.50±0.14	29
	28 May	21	0.75±0.19	44	11	0.39±0.20	23
	25 Jun., 26 Jun.	30	1.07±0.18	63	41	1.46±0.43	86
	1 Aug.	20	0.71±0.14	42	46	1.64±0.35	97
	31 Aug.	26	0.93±0.20	55	42	1.50±0.29	88
	30 Sep.	27	0.96±0.22	57	41	1.46±0.28	86
	30 Oct.	21	0.75±0.18	44	33	1.18±0.18	69
	29 Nov., 30 Nov.	25	0.89±0.19	52	17	0.61±0.13	36
1993	27 Mar.	18	0.64±0.19	38	18	0.64±0.12	38
	27 Apr.	20	0.71±0.19	42	14	0.50±0.11	29

Appendix 2. Mean fresh weights (mg) of each cohort of Ligidium japonicum and Ligidium koreanum collected at each sampling date. Mean fresh weight is given with standard error.

Sampling date		*Ligidium japonicum*			*Ligidium koreanum*		
		Male+Female	Male	Female	Sex unknown	Male	Female
1991	30 May, 5 Jun.		5.5±0.4	9.8±1.2			27.4±0.8
	29 Jun., 2 Jul.		9.1±0.9	13.0±1.6	2.0±0.1		
	4 Aug., 6 Aug.	1.4±0.2	11.8±0.5	17.3±0.7	6.1±0.2		
	29 Aug., 2 Sep.	2.1±0.2			9.2±0.3		
	2 Oct.	3.7±0.5				13.1±0.5	19.4±0.9
	31 Oct., 1 Nov.	4.7±0.5				16.4±0.3	26.4±1.0
	2 Dec., 3 Dec.	5.3±0.5				18.3±0.4	32.4±1.0
1992	26 Mar.	5.4±0.7				18.8±1.0	32.8±1.1
	27 Apr., 28 Apr.	7.0±0.7				19.8±0.8	37.8±0.9
	28 May		7.4±0.6	8.7±1.7		20.0±0.1	42.3±1.6
	25 Jun., 26 Jun.		7.1±0.6	14.8±1.4	0.9±0.0		36.2±0.0
	1 Aug.	0.4±0.0	8.0±0.5	16.8±1.0	3.2±0.1		
	31 Aug.	1.0±0.1	12.0±0.4	18.7±1.3	6.7±0.2		
	30 Sep.	1.6±0.1				9.9±0.4	15.0±0.6
	30 Oct.	2.5±0.3				13.3±0.5	20.2±0.5
	29 Nov., 30 Nov.	2.8±0.3				15.1±0.5	23.1±1.1
1993	27 Mar.	3.0±0.3				15.0±0.4	25.2±0.6
	27 Apr.	3.5±0.3				15.4±0.7	30.1±1.3