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Population density, size, age, reproduction and microdistribution in the Jaera albifrons group (Isopoda)

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Specimens of species of the *Jaera albifrons* group (Isopoda) were collected from 25 stones each month over a period of one year from two different shores. The density was found to be 4–20 per m² undersurface in winter and 2500–11400 in summer. The animals usually die within one year. Females always outnumber males. Reproduction took place between April and September–November. A strong correlation between size and number of eggs was found. The egg number/brood varied from a mean of 8 up to a mean of 60. A theoretical potential productivity of a hibernating female was estimated to be 9200 descendants in the autumn. Up to 60% of the females in a sample were carrying dead eggs and young.

At one of the localities two species occurred. No evidence of differences in microdistribution was found between these. On exposed sites, however, spatial segregation between the sexes and between different size classes was found.

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Проводился ежемесячный сбор изопод из группы *Jaera albifrons* из-под 25 камней на двух различных участках побережья в течение года. Численность их составляла 4–20 экз./1 м² нижней поверхности камней – зимой и 2500–11400 экз./1 м² – летом. Животные обычно погибали в течение года. Самки по численности превосходили самцов.

Размножение происходит с апреля до сентября-ноября. Установлена строгая зависимость между размером и количеством яиц. Количество яиц в кладке в среднем от 8 до 60. Теоретическая потенциальная продуктивность зимующих самок составляет 1:9200 осенью. Примерно на 60% самок в пробах находили погибшие яйца и молодь.

В одном местообитании найдено 2 вида. Не было установлено различий в их микрораспределении. Однако, на исследованных участках обнаружена пространственная сегрегация между самцами и самками и различными размерными группами.

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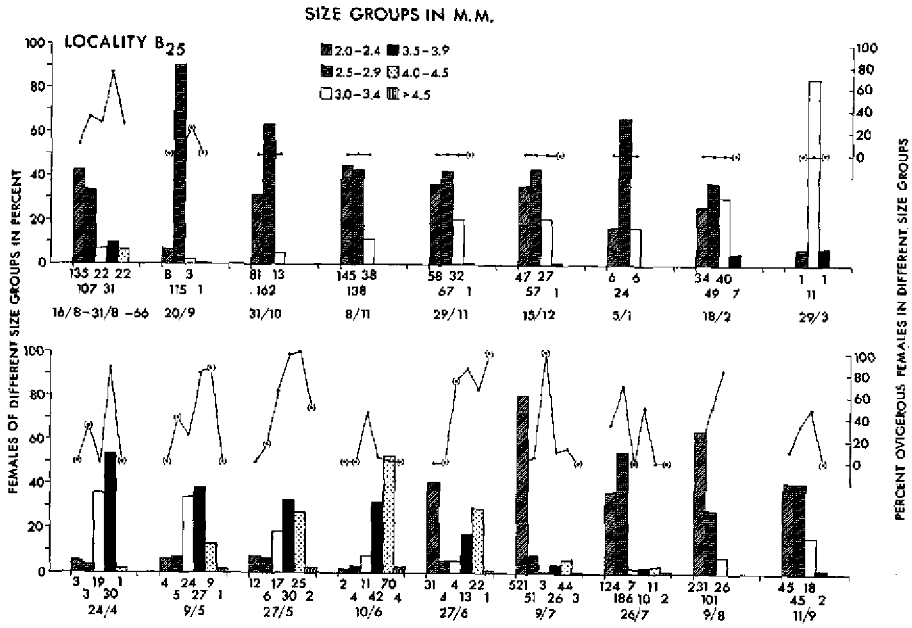

Fig. 2. Percent females (*J. ischiosetosa and J.a. syei*) of different size groups (staples), and percent ovigerous females (. – .) in these groups. Locality B_{25} August 1966 to September 1967. ( ) shows that the value is based on less than 10 females.

were found to be 31 to 47 days old. The animals, the growth of which was followed in the laboratory were all from the Swedish west coast (ca. 30‰ S).

In this investigation males longer than 1.5 mm have been classified as adults. Consequently some of the animals in the size groups should probably have been more correctly classified as juveniles. For the study of the dynamics of size in the population this error is, however, of no importance.

In 1966 all the animals in a sample from 25 stones were pooled. As the number of juveniles was often very high (up to 1250 in one sample) small males might have escaped discovery. Consequently the data on males from the summer 1966 are not quite accurate. This source of error was reduced in 1967 because the animals from each stone were then being examined separately.

In the October sample, at the end of the reproduction period, 100% of the adult females were smaller than 3.5 mm and 94.8% were 2 to 2.9 mm long (Fig. 2). During the winter the distribution of size-classes slowly changed. In March 92.3% of the females were between 3 and 3.9 mm long. The growth of these females could be followed up to, and including, July when some of them had grown to a length of more than 4.5 mm. This generation was absent from all of the following samples. The new generation appeared among the adults in the samples from April onwards ,and constituted the dominating part from July.

The results from the other shore are very similar, but differ in the occurrence of larger females (>3.5 mm) throughout most of the year. In September 1967 one female of the size group 4–4.5 mm was found. A possible reason for this difference may be the fact that the animals of different sizes seem to have a tendency of being separated at Locality B_{25} but not at Locality B_{21} (see sect. 7).

From November 1966 to September 1967 the growth of 3 mm long females of *Jaera ischiosetosa*, of some males and their descendants born in the aquarium, was measured in the laboratory. The results are given in Tab. 1. Niether these values nor those of Forsman can be said to be completely relevant for a free living Baltic *Jaera* population since both values concern animals in the laboratory. Also Forsman's animals were from the West coast. Which species they concern is not clear. However, on the basis of Forsman's (1944) estimate of

Tab. 1. The growth rate of *J. ischiosetosa* adults and their descendants in an aquarium. The salinity was 6‰ and the temperature followed more or less the nature conditions. Food consisted of detritus and diatoms growing in the aquarium. Start of the experiment November 8th 1966 when the females were 3 mm long.

	Size in mm	May 27th	July 4th	July 26th	Oct. 12th
Females	5	0	1	0	1
	4,5–5	4	17	3	0
	4–4,5	28	4	4	4
	3,5–3,9	1	0	0	3
	3–3,4	0	61	6	10
	2,5–2,9	0	102	9	34
	2–2,4	0	38	2	22
Juv.	2	400	200	48	170
Males	2,5	1	0	0	0
	2,2–2,5	0	0	1	1
	1,9–2,1	0	49	10	27
	1,6–1,8	0	75	29	49

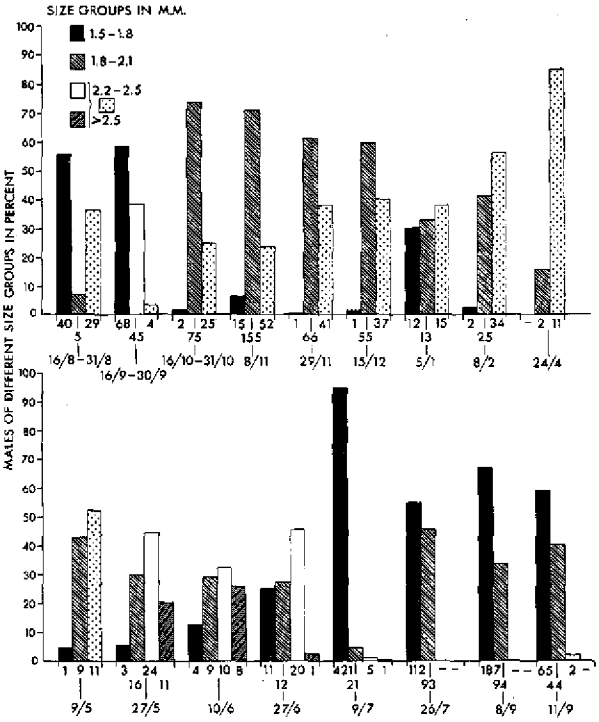

Fig. 3. Percent males (*J. ischiosetosa* and *J.a. syei*) of different size groups. Locality B_{25} August 1966 to September 1967.

2.1 mm long females being between 31 and 47 days and on the data given in Tab. 1, an idea of the age and size relationship may be obtained. The age of 3–3.5 mm long females would thus be 2 to 3 months and that of females 4–4.5 mm long, 4.5 to 5 months.

Some of the females born in the aquarium in spring reached the length of 4–4.5 mm by autumn. If a hypothetical length of a one year old female is taken as 4 mm this is consequently not too high a value. High percentages of females at least 4 mm long were found during the first part of the reproduction period but very low ones during the winter (Fig. 2). This indicates that as a rule, females born during one reproduction period die before or during the next one, at an age of up to about one year.

In April all males were more than 1.9 mm long (Fig. 3). It is not possible to say whether some of them were bigger than 2.5 mm at that time as all males bigger than 2.1 mm were put into the same group until the late May collection. The old generation could be followed up to and including June. In May and June some of the males had attained a length of >2.5 mm.

The new generation appears from May onwards. After June only males of this new generation are found. Thus the hibernating males were born during the previous reproduction period. In the next one they die at an age of about one year.

According to Forsman, males reach a length of 2.5 mm in 3 months. Thus, some of the males born at Askö early in the spring would have reached that size by July. However, of 1594 males collected at the two localities between July 1 and Sept. 11, 1967, none had attained the length of 2.5 mm. Forsman's values are perhaps not valid for free living Baltic males, or for Baltic males on the whole. Any differences in size between Baltic and North Sea adult *Jaera* have not been noticed by the author.

The proportion of juveniles in the samples varies

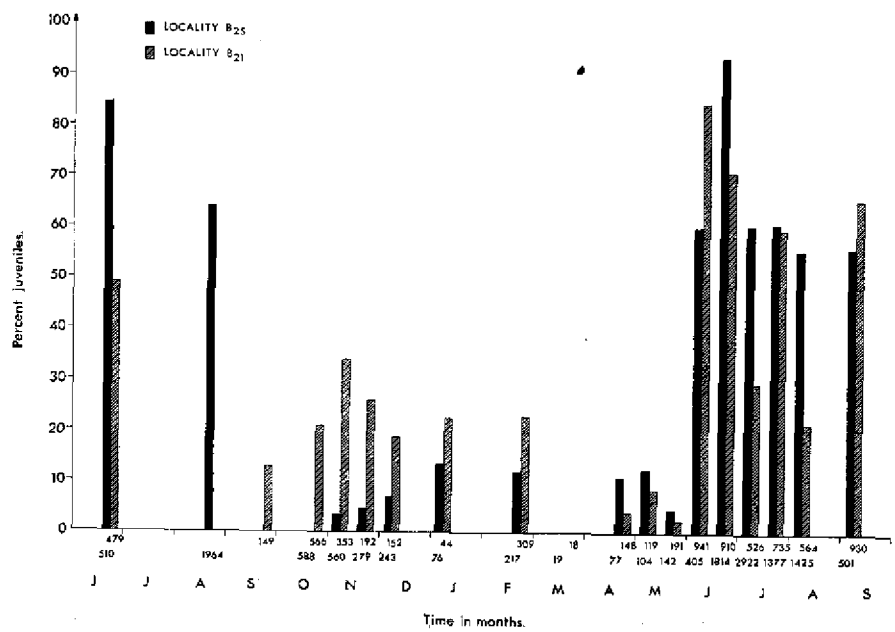

Fig. 4. Percent juveniles on Locality B_{21} (*J.a. syei*) and B_{25} (*J. ischiosetosa* and *J.a. syei*) June 1966 to September 1967.

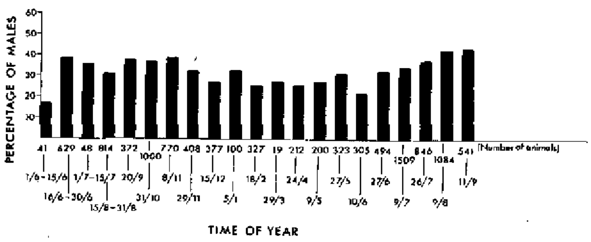

Fig. 5. Sex ratio (*J. ischiosetosa* and *J.a. syei*) June 1966 to September 1967.

during the year as a result of the restricted reproduction period. From October to May 0 to 34.8% of the animals in a collection were juveniles but during the reproduction period this proportion was as much as 94% (Fig. 4).

To sum up, the animals in the October collections were born since spring, the same year. The females were 2 to 3.9 mm long, and most of the males 1.9 to 2.1 mm. The animals starting the production of a new generation in the spring were born during the previous reproduction period. The females were between 2.5 and 3.9 mm long. Animals born during one reproduction period as a rule die during the next one, and they usually reach an age of up to one year.

Differences in maximum age between males and females are not shown by the above analyses. However, the variations in sex ratio throughout the year (see below) gave an intimation of – but did not prove – the possibility of the females having a longer life span than the males.

5. Sex ratio

The females always outnumber the males (Syei 1887, Forsman 1944, Naylor et al. 1961). A smaller number of males are being born (Naylor et al. 1961), but it is probable that males also have a shorter life span.

The percentage of males varied between 17.1% and 41.3% on one shore and between 18.9% and 50.2% on the other. The proportion of males was low in winter and spring, but increased when the new generation appeared in the samples. (Fig. 5). Thus, the males probably die first.

6. Reproduction and reproductivity

In England Naylor et al. (1961) found ovigerous females all the year round but high frequencies were concentrated during the summer. In the Kieler Bucht the oveigerous females appear in March–April (Syei 1887) and at the Swedish West coast in April–May and disappear at the end of October (Forsman 1944). During the reproduction period females produce several broods. Theoretically they may have one brood every 20th day (Forsman 1944). This interval, however, is probably dependent on temperature and consequently it varies during the reproduction period. At Askö temperature varies from 7.6 to more than 20°C. The connection between the temperature and the reproduction period is pointed out by Forsman (1944) and shown in my own experiments which will be published.

During the period investigated the last females carrying eggs or young at Askö were found in the late November sample at Locality B_{21} and in the late September one at Locality B_{25} (Fig. 6). The first ovigerous females appeared at both localities in the late April samples. (In the following "ovigerous" females also includes females with young in the brood pouches). In different size groups the number of ovigerous females differs within a sample (Fig. 2). The mean size of the ovigerous females was largest (3.5 to 3.9 mm) at the beginning of the reproduction period. From July onwards, when the young from the early spring births had started to reproduce, the mean size was, as a rule, less than 3.5 mm. As the populations during the later part of the reproduction period is much larger than during the early part, the reproduction is mainly carried out by smaller females (Fig. 2).

From May to September samples were taken at an interval of 14 days. As is seen in Fig. 6 the frequency of females with eggs and young varied during this period. The frequencies of ovigerous females were higher at Locality B_{21}. This result is discussed in another paper (Sjöberg 1969).

The number of eggs is dependent on the size of the females (Forsman 1944). For other species the number of eggs has been found to be inversely correlated with temperature and consequently also with rate of growth (Clemens 1950) as well as with population density (Eisenberg 1966). If this is relevant here, too, the number of eggs of females of the same size groups ought to be higher in spring than in autumn.

The mean number of eggs varied from ca. 60 in the largest size groups down to ca. 10 in the smallest (Tab. 2). Furthermore the number of eggs within a size group varied during the reproduction period. However, the size groups are so large that the differences received might well be due to the distribution of size within a size group. Exact values of length or narrower limits of the size groups are needed for final conclusions concerning a possible connection between number of eggs and time of reproduction period.

How many animals might originate from an hibernating female during the following reproduction period? An estimation based on the following presumptions was made.

A female gets her first eggs 1.5 months after she has left the marsupium of her mother. Every 20th day she gives birth to a new litter. Every litter contains 10 juveniles of which 50% are females. The hibernating female starts to release young in the middle of April,

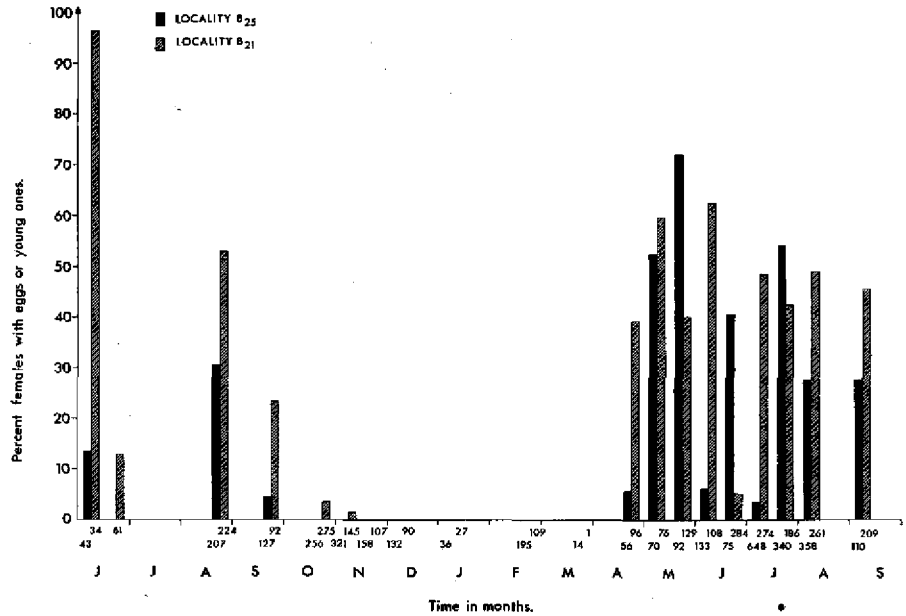

Fig. 6. Percent females carrying eggs or young in their brood pouches on two shores, Locality B_{21} (*J.a. syei*) and Locality B_{25} (*J. ischiosetosa* and *J.a. syei*), June 1966 to September 1967.

dies at the end of July and by then has had 4 litters. The females born in the middle of April the same year, however, will have 6 births during the reproduction period which is over by the middle of October. Females born between the middle of April and the end of August have successively less litters. Those born after the beginning of September do not reproduce until the following spring.

The number of descendants achieved in this way is 9200. The number is based on the number of eggs in the smallest size group and is consequently – in this respect – the lowest possible. On the other hand the majority of reproducing females belongs to the smaller size groups (see above). If the estimation instead is based on 20 eggs, a number of 170,000 descendants is obtained.

These values are purely theoretical but such values give an intimation of the potentiality of the animals to create large populations under favourable conditions. Normally predation from e.g. fish and disease keep the population density down. E.g. the relation between the density of animals received in a sample in April and in October was not 1:9200.

One important factor, controlling the density of animals may be pests. In July and August up to 60% of the ovigerous females in a collection had dead eggs and young in the marsupiums. Possibly the increase in number of infected females in the middle of the summer was due to the increased temperature. Infected males, and females not being ovigerous, were not observed.

7. Microdistribution of species, sizes and sexes

On stones at Locality B_{25} the species *J. ischiosetosa* and *J. a. syei* occur together, with *J. ischiosetosa* as the dominating species (90%). Different ecological prefer-

Tab. 2. The number of eggs or young in the brood pouches in different size groups at different part of the reproduction period. The numbers are given as means with 95% confidence intervals.

	Date / Size in mm	9/5	26–27/5	9–10/6	27–29/6	8–10/7	26/7	9/8	11/9	Significant diff. between dates
J. ischiosetosa dominating Locality B_{25}	2 –2.4					12.0 ± 3.7	9.8 ± 0.7	8.6 ± 0.8	9.2 ± 1.5	–
	2.5–2.9	21.5 ± 4.0	26 ± 5.7			20.5 ± 4.0	13.3 ± 0.9	13.9 ± 0.9	14.3 ± 1.5	x x x
	3 –3.4	21.5 ± 4.8	25.3 ± 2.7	27.3 ± 4.8	25.0 ± 5.6	27.0 ± 6.8	–	19.2 ± 2.6	18.9 ± 3.7	x x
	3.5–3.9	35.8 ± 2.9	32.5 ± 2.7	36.5 ± 10.1	36.2 ± 4.3	38.0 ± 10.1	18.0 ± 14.2			–
	4 –4.5	42.9 ± 7.7	39.6 ± 4.5	67.0 ± 21.9	43.7 ± 5.6	55.0 ± 8.9	40.0 ± 21.9			x
Locality B_{21} *J.a. syei*	2 –2.4			11.0 ± 5.1		11.6 ± 1.0	9.3 ± 0.8	9.2 ± 1.0	9.2 ± 1.1	x x
	2.5–2.9	17.0 ± 6.8	16.0 ± 3.9	15.0 ± 3.9	21.5 ± 4.8	16.7 ± 1.1	14.2 ± 1.4	14.0 ± 1.1	14.0 ± 1.1	x x
	3 –3.4	28.3 ± 3.4	23.4 ± 3.4	24.3 ± 2.5	30.4 ± 5.0	29.7 ± 6.5	17.3 ± 5.6	28.5 ± 8.0	21.8 ± 2.6	x x
	3.5–3.9	32.9 ± 3.0	31.1 ± 2.1	43.4 ± 2.6	30.0 ± 5.1	58.0 ± 10.2	44.0 ± 10.2		34.0 ± 10.2	x x x
	4 –4.5	38.9 ± 3.1	49.7 ± 5.4	58.1 ± 2.8	57.0 ± 13.2	45.8 ± 6.6	60.0 ± 13.2		50.0 ± 13.2	x x x

Tab. 3. The preportion of *J. ischiosetosa* and *J.a. syei* on stones with ≦10 males and on stones with >10 males.

Species	Amount of males on the stones with ≦10 males	>10 males	Totally
J. ischiosetosa	139	742	881
J.a. syei	22	75	97
	161	817	978

$\chi^2 = 2{,}55$ $p > 0{,}1$

ences for these species have been pointed out by several authors (Forsman 1944, 1949, 1956, Bocquet 1953, Naylor et al. 1961, 1967, Haathela 1965). On Askö any obvious ecological preferences for the species living on stones have not be found (Sjöberg 1969) except for a dominance of *J. a. syei* in deeper layers. *J. a. syei* is regarded as the more recessive species when compared with other *Jaera* species (Bocquet 1953, Naylor and Haahtela 1967). Does this condition influence the distribution of species at Locality B_{25}? Is there a tendency for the species to be separated? And, in that case, do *J. a. syei* then occur on less attractive stones than *J. ischiosetosa*?

To get an answer to these questions it was tested whether the proportions of *J. a. syei* were constant between different stones and consequently if the mixing of the species was good or not. The material available for this test was small and therefore the proportions of *J. a. syei* males on stones with less than 11 males and on stones with more than 10 males were compared. See Tab. 3. No significant differences were found ($p > 0{,}1$) and consequently no indications of the species being separated.

Are the *Jaera* of different sizes separated? To see if the detailed collections could give any information about that, the number of adult *Jaera* on each stone was divided into size groups. The size groups were 2 to 2,4 mm and >2.5 mm for the females, and 1.5 to 1.8 mm and >1.9 mm for the males. Only stones with at least 15 specimens of the studied sex were taken into consideration. The different sexes and collections were studied separately. The tests used were Chi square tests.

At Locality B_{21} there was no sign of the sizes being separated. At Locality B_{25} however significant differences in the distribution indicated a possibility of the size groups being separated.

An ocular examination of the proportions of adults and juveniles on different stones indicates a tendency for the juveniles to be joined together. This is probably dependent of the fact that a large female gives life to up to ca. 60 young at a time, and that the young might be more stationary than the adults, at least during a calm period.

The distribution of the sexes was also tested (Chi square test). A tendency for males and females to be separated was found at Locality B_{25} but not at Locality B_{21}. Perhaps the females search out more protected parts when they release their young from the marsupium.

The distribution of sizes as well as of sexes being different at Locality B_{25} but not at Locality B_{21} might be caused by e.g. the differences in species and degree of exposure on the two shores. The ability to withstand strong movement in the water might vary with age, sex and stage of an ovigerous female. Were e.g. the lower frequencies of ovigerous females in the samples from the more exposed shore (B_{25}) caused by migration to more protected parts? Perhaps the distribution of sizes and sexes would show the same difference at Locality B_{21} after a period with strong waves.

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