

Breeding and bionomics of the British members of the *Jaera albifrons* group of species (Isopoda: Asellota)

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(With 12 figures in the text)

A detailed 24 month study (1968–1970) of the breeding cycles and population structures of the four British members of the *Jaera albifrons* Leach group of species (Isopoda: Asellota) has been carried out in Milford Haven, Pembrokeshire. The species often show overlapping ecological distributions and they can only be identified on male secondary sexual characters. Sampling stations had therefore to be selected carefully to ensure that single species populations were studied. In this way virtually single-species populations of *Jaera forsmanni* Bocquet, *Jaera prae-hirsuta* Forsman, and *Jaera ischiosetosa* Forsman have been studied but the *Jaera albifrons* Leach population was somewhat mixed with *J. ischiosetosa*, particularly when the stream normally inhabited by the last species dried up in the summer. Only one hybrid was found (between *J. albifrons* and *J. ischiosetosa*) in a total of 6214 specimens collected. Gravid females were taken every month for each species with peaks of breeding occurring during spring and summer. Young were liberated throughout the year by *J. albifrons* and *J. ischiosetosa*, but with summer peaks. *J. prae-hirsuta* and *J. forsmanni* had a particularly limited summer period for the release of juveniles. *J. forsmanni* was consistently the largest species and has a restricted geographical distribution. *J. prae-hirsuta* also has a patchy distribution. The sex ratio of males to females was never 1:1 for any species. Females outnumbered males by up to 14:1, with the sex ratio varying throughout the year except in *J. prae-hirsuta* where it remained at about 1.5:1.

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Introduction

The *Jaera albifrons* group of species in Britain comprises *Jaera albifrons* Leach, *Jaera ischiosetosa* Forsman, *Jaera praehirsuta* Forsman and *Jaera forsmanni* Bocquet which are readily distinguished on the basis of male secondary sexual characters (Forsman, 1949; Bocquet, 1953). Each has fairly characteristic ecological preferences but their ranges often overlap, with little or no evidence of hybridization (Naylor & Haahtela, 1966). Some controversy still exists concerning the taxonomic status of the members of the group and in this context it seemed worthwhile to make a detailed study of their breeding biology. The present study therefore set out to look for possible differences in breeding patterns and population structure, to determine whether the previously described habitat preferences were consistently recognizable throughout a long period of time and to look for possible interbreeding between the four species. While this work was in progress Jażdżewski (1969) and Sjöberg (1969 & 1970) have reported briefly on breeding populations of two of the above species, *J. ischiosetosa* and *J. praehirsuta*, together with the form *Jaera (albifrons) syei* Bocquet in the Baltic, but other information on reproduction has been of a more general nature (Elmhirst, 1922; Evans, 1936; Forsman, 1944, 1951; Naylor & Slinn, 1958; Naylor, Slinn & Spooner, 1961; Schütz, 1963; Kuznecov, 1964; Brattegard, 1966). Present work reports on the breeding biology and seasonal population changes of *J. ischiosetosa*, *J. praehirsuta*, *J. forsmanni* and *J. albifrons* in a restricted locality in Britain where all four species occur on the same shore.

Material and methods

The species of *Jaera* used in this investigation were collected from populations at Black Tar Beach in Milford Haven, Pembrokeshire, S.W. Wales (Nelson-Smith, 1965, 1967), following the methods of Naylor & Haahtela (1966) who found that each species had fairly distinct distributions on this shore. *J. ischiosetosa* was found under stones in a small, freshwater stream which crossed the shore (station 1), *J. albifrons* was taken under stones at M.T.L. where surface water was retained at low tide (station 2), *J. praehirsuta* was collected from *Fucus serratus* L. (station 3) and *J. forsmanni* was found under stones on well-drained parts of the shore at L.W.N.T.—L.W.S.T. (station 4). Stations 1, 2 and 4 were sampled separately, one person collecting intensively for 15 min. At station 3 four large polythene bags of *F. serratus* were collected on the shore and washed free of animals in the laboratory for a total sorting time of 15 min. All specimens were transferred direct to 4% seawater formalin to kill them and avoid cannibalism in the sample jars. Following some depletion of the populations at stations 1 and 2, collections for these species from October 1969 were taken from identical microhabitats at Sandy Haven, a similar shore in the same estuary. The temperature of the water at each station was recorded every month at the time of the sample.

In the laboratory, specimens were flattened on a microscope slide, and body length (measured from the line of the antero-lateral corners of the cephalon to the posterior border of the telson) was measured to the nearest 0.01 mm using a micrometer eye-piece in a binocular microscope. Specimens were grouped as follows: (1) *Young animals*—all specimens less than 1.50 mm length including Bocquet's (1953) stages 1–4 of post embryonic development. (2) *Males*—male praeperculum fully developed and the characteristic patterns of secondary sexual features on the peraeopods (Forsman, 1949; Bocquet, 1953; Naylor, in press). (3) *Immature females*—females lacking oöstegites. (4) *Gravid females*—females with fully developed oöstegites forming brood pouches which are either empty or contain young stages. The gravid females were further staged according to the development of the young in the marsupium.

Population "purity"

An important problem arises in this study in that the four species are distinguishable only on adult male characteristics and yet their ecological ranges overlap. Sampling areas were therefore selected to give males which were predominantly of one species only and the assumption was made that the juveniles and females in the sample were also of that species. On this basis, over the whole sampling period, three of the four stations were about 90% pure for the species selected, but one was more mixed (Table I). Station 2 was more mixed than the other three, largely owing to the immigration of *J. ischioestosa* to the typical *J. albifrons* microhabitat during dry periods when the stream inhabited by the former dried up. The procedure adopted here therefore is to draw conclusions from the populations at station 1 (*J. ischioestosa*), station 3 (*J. praehirsuta*) and station 4 (*J. forsmanni*) which seem to be almost single species populations, and to interpret results from station 2 (*J. albifrons* selected) partly on the basis of the results at the other three stations.

TABLE I

The total numbers of males for each species collected at each station during the sampling period and the percentage "purity" for the selected species

Station no.	Total <i>J. ischioestosa</i>	Total <i>J. albifrons</i>	Total <i>J. praehirsuta</i>	Total <i>J. forsmanni</i>	Total males	% of selected sp.
1	330	15	3	—	348	94.82
2	102	237	15	—	354	66.94
3	—	4	540	78	622	87.45
4	—	—	14	191	205	93.14

Breeding cycles

Gravid females

In this method of analysis of breeding, the numbers of gravid females per month are expressed as a percentage of the total adult population (referred to as "gravidity"), following the method adopted by Eltringham & Hockley (1961) for *Limnoria*. The data are presented in Fig. 1 using a moving averages procedure to reduce the sampling variance. The repeated annual pattern of the results suggests that the smoothing procedure is an acceptable method of analysis. At station 1 (*J. ischioestosa*) gravidity remained around the 40% level for most of the sampling period but was higher in spring than at other times of the year, reaching 60% in the spring of the 2nd year (Fig. 1). At station 3 (*J. praehirsuta*) there was a slight increase in gravidity in spring but the main breeding period on this evidence was in the summer when almost 40% of the adult population were females in the reproductive condition, compared with low values of around 10% in winter. Females at station 4 (*J. forsmanni*) showed greater seasonal changes in gravidity, with over 60% gravid females in February/April, falling to around 20% in winter. This high spring gravidity was influenced by poor samples collected at this station during the spring when

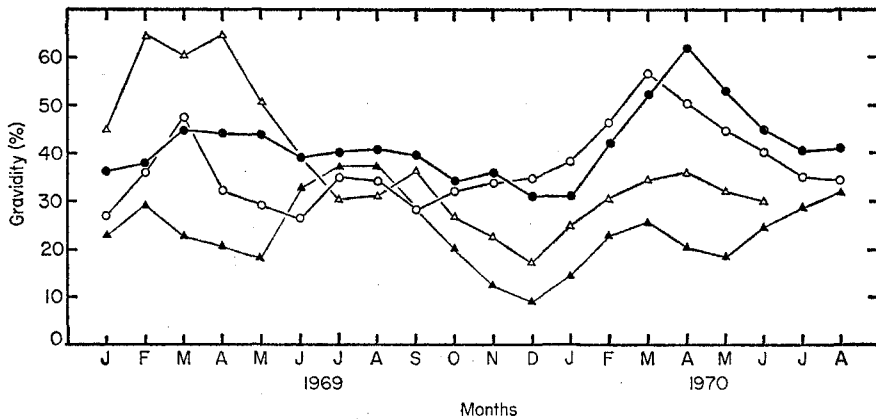


FIG. 1. Monthly changes in numbers of breeding *Jaera* females collected at each station and expressed as a percentage of the total adult sample. (Results smoothed by a moving averages procedure applied to successive batches of three monthly values.)

●, *J. ischiosetosa*; ○, *J. albifrons*; ▲, *J. praehirsuta*; △, *J. forsmani*.

out of 21 females caught, 18 were ovigerous. However, a spring peak of over 30% gravidity occurred during 1970 when the sample numbers were larger. Whereas the results at stations 1, 3 and 4 are fairly straightforward to interpret since the populations at these stations were almost species pure, station 2 samples require more detailed consideration. In these,

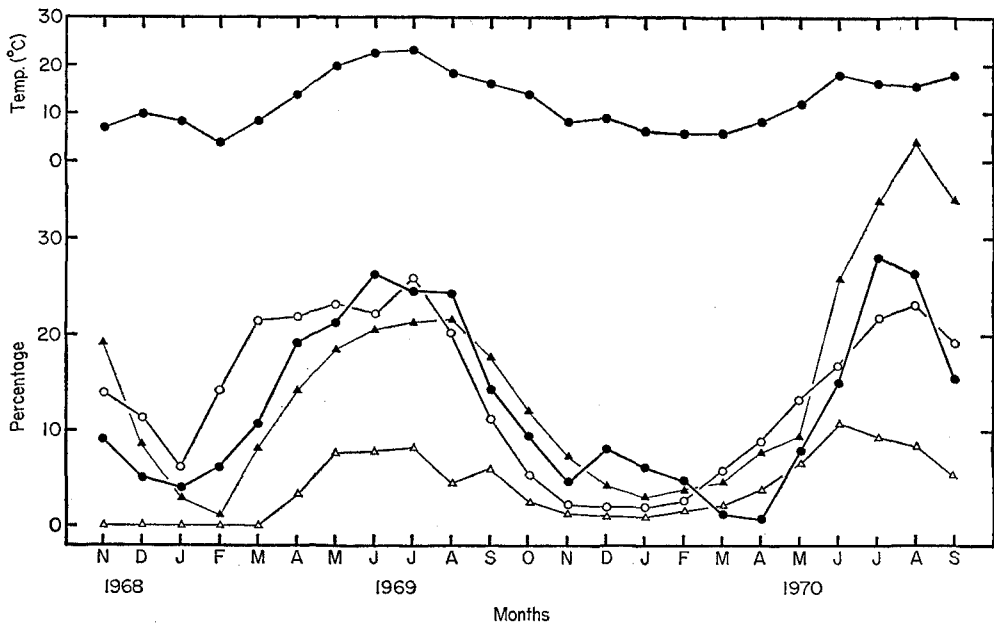


FIG. 2. Release of juveniles expressed as a percentage of the total sample per month at each station (results smoothed by a moving averages procedure applied to batches of successive three monthly values) together with mean monthly sea-water temperatures.

●, *J. ischiosetosa*; ○, *J. albifrons*; ▲, *J. praehirsuta*; △, *J. forsmani*.

the annual variation of gravidity is almost as low as in station 1 (*J. ischiosetosa*) samples. This is consistent with the finding of about 40% *J. ischiosetosa* in the station 2 samples (Table I). The station 2 pattern differs from that at station 1 in having a slightly earlier spring peak, which is presumably a feature of *J. albifrons* which comprises the remaining 60% of the sample.

Release of young

Though young animals (<1.50 mm body length) were collected throughout the year at all the stations, maximum release took place in the summer (Fig. 2). In the first year of study (1969) the majority of young were liberated at station 2 from February–August, station 1 from March–September, and stations 3 and 4 from April–September. However, in the second year (1970) station 4 (*J. forsmanni*) was the only one to retain its 1969 pattern of maximum release. The peak period for each of the other three stations was delayed until May. This delay (and consequent shortening of the release period) may have been a direct result of the lower temperatures recorded in 1970 when compared with 1969 (Fig. 2).

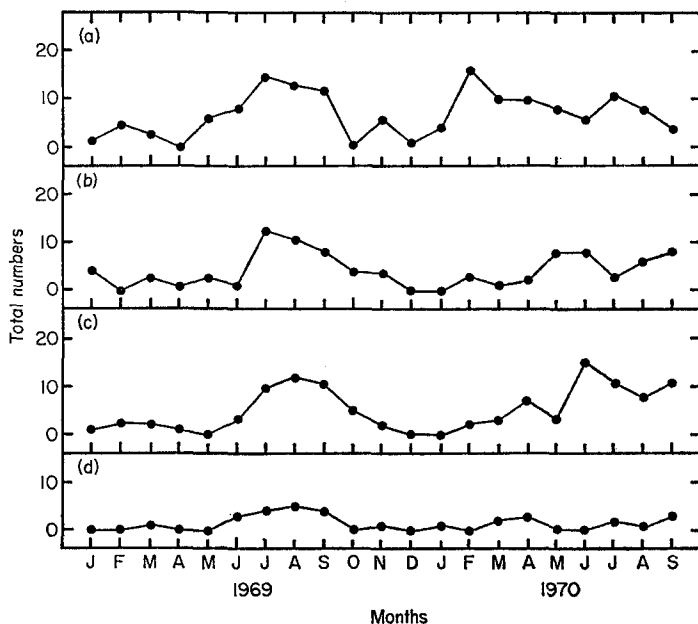


FIG. 3. Seasonal variation in the brood composition of gravid females collected at station 3 (*J. praeheirsuta*). (a) Eggs; (b) embryos (stage 2); (c), stages 3+4; (d) females with empty brood pouches.

Brood composition

The seasonal fluctuations in brood composition for *J. praeheirsuta* are shown in Fig. 3. The stages referred to are summarized in Table II. In general there is a sequential pattern in which a peak of females bearing eggs is followed by a peak for embryos and later a peak for stages 3 and 4. This pattern was not shown so clearly by the other three species studied in the investigation.

TABLE II

Showing the average size ranges for each embryological stage of development at each of the sampling stations

Stage of embryology	Character	Average size (mm)			
		Station 1	Station 2	Station 3	Station 4
1	Newly released egg with <i>egg membrane</i> , no cleavage visible, oval in shape, may have embryonic membrane inside	0.24-0.29	0.26-0.32	0.22-0.28	0.25-0.30
2	Egg membrane ruptured, cleavage visible, embryo surrounded by <i>embryonic membrane 1</i> , limb buds develop, dorsal transverse fissure present, eyes become pigmented, general comma-shape	0.28-0.33	0.29-0.35	0.25-0.33	0.27-0.33
3	Embryo straightens and ruptures 1st embryonic membrane, <i>2nd embryonic membrane</i> now surrounds the embryo and allows free movement of the appendages. No setae	0.54-0.81	0.48-0.78	0.48-0.78	0.58-0.82
4	2nd embryonic membrane lost and setae released, body similar to adult stages but lacks 7th pair of peraeopods, 7th thoracic segment small, yolk almost disappeared. Corresponds to the 1st free-living stage	0.70-0.88	0.78-0.87	0.70-0.97	0.92

Reproductive potential

Marsupial development

McMurrich (1895) and Forsman (1944) have described the embryology and marsupial stages of the "superspecies" *J. albifrons* and the latter are summarized in Table II. There were no detectable differences between equivalent marsupial stages in the four species and all the embryos in any one marsupium were at the same stage of morphological development. There was some variation in the colour of the yolk in any one brood ranging from green to brown, in contrast to the observations of Evans (1936) and Forsman (1944) who both reported a standard green colour in the yolk of the majority of the broods they examined.

Egg production

The numbers of newly-deposited eggs produced by gravid females at each station have been related to the body length of the incubating female (Fig. 4). This general correlation of egg number with female size has been reported by Evans (1936) and Jażdżewski (1969) for *J. albifrons* from other regions. There is no significant difference between the slopes of the fitted regression lines (Fig. 4) suggesting a similar increase of egg numbers with increasing body length for all species. The mean sizes and average brood numbers for each species (with eggs only) in Pembrokeshire are given in Table III. Averaging the results obtained in this investigation for *J. ischiosetosa*, *J. albifrons* and *J. praehirsuta* (which make up the populations of *J. albifrons sensu lato* used by the other authors) a figure of 20 eggs is obtained for a similar size range. All figures on brood production in Table III are therefore compared with this average figure.

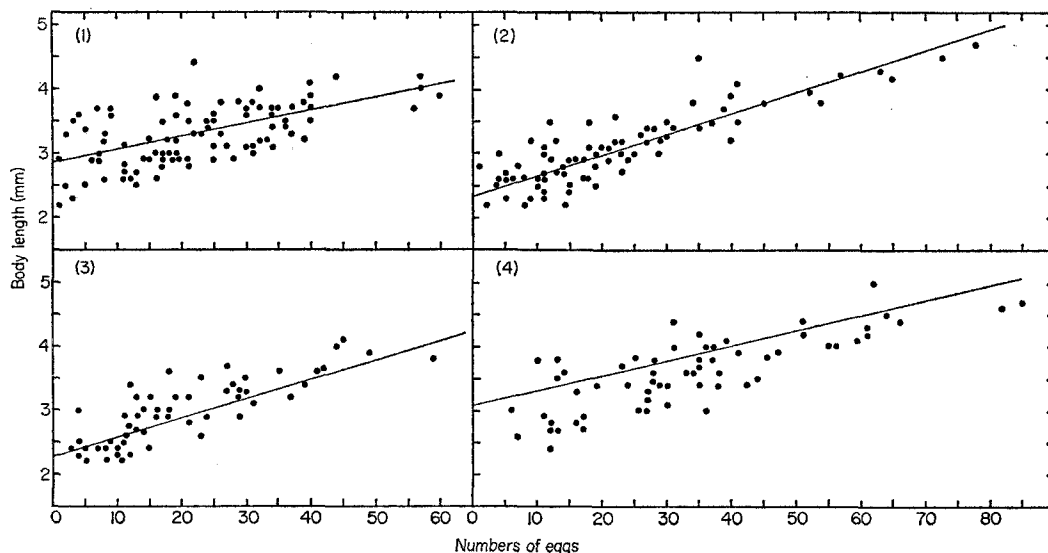


FIG. 4. Egg production plotted against total length of incubating female for the four species of *Jaera* with fitted regression lines.

(1) Station 1 (*J. ischiosetosa*); (2) station 2 (*J. albifrons*); (3) station 3 (*J. praehirsuta*); (4) station 4 (*J. forsmani*). The formulae for the regression lines are:

(1) $y = 0.02x + 2.86$, (2) $y = 0.03 + 2.36$; (3) $y = 0.03 + 2.28$, (4) $y = 0.03x + 2.8$.

TABLE III

Summary of previous information on brood numbers and breeding periods and including a comparison with the present investigation

Author	Species	Size of incubating female (mm)	Average Nos. of eggs	Breeding time	Brood production	Locality
Kuznecov (1964)	<i>J. albifrons sensu lato</i>	2.80-3.50	22-44	Jun.-Aug.	—	Barents Sea
Kuznecov (1964)	<i>J. albifrons sensu lato</i>	2.80-3.50	22-44	Jun.-Jul.	+18%	White Sea
Brattegard (1966)	<i>J. albifrons sensu lato</i>	—	—	Jun.-Sep.	—	W. Norway
Forsman (1944)	<i>J. albifrons sensu lato</i>	—	—	Mar.-Sep.	—	Sweden
Jażdżewski (1969)	<i>J. albifrons sensu lato</i>	2.80-3.50	11	Mar.-Sep.	-59%	Poland
Schütz (1963)	<i>J. albifrons sensu lato</i>	2.80-3.50	25	Apr.-Nov.	-7%	Kiel Canal
Elmhurst (1922)	<i>J. albifrons sensu lato</i>	—	—	Jan.-Sep.	—	Scotland
Naylor, Slinn & Spooner (1961)	<i>J. albifrons sensu lato</i>	—	—	Jan.-Dec.	—	S. & W. Britain
Evans (1936)	<i>J. albifrons sensu lato</i>	2.80-3.40	15	Mar.-Dec.	-44%	Aberystwyth, W. Wales
Present study	<i>J. ischiosetosa</i>	3.10	12	Jan.-Dec.		Pembrokeshire
	<i>J. albifrons</i>	3.00	21	Jan.-Dec.		
	<i>J. praehirsuta</i>	2.80	17	Jan.-Dec.		
	<i>J. forsmani</i>	3.50	18	Jan.-Dec.		

Brood mortality

The results of this investigation are shown in Fig. 5. Since the final stage [(4) Table II] is that which eventually escapes from the marsupium it was possible that some premature loss may have been induced at this stage during initial handling and preservation. However, Fig. 5 indicates that the losses between stages 3 and 4 were no greater than between the earlier stages, suggesting an average and overall brood mortality of around 50%, with little evidence of differences between species.

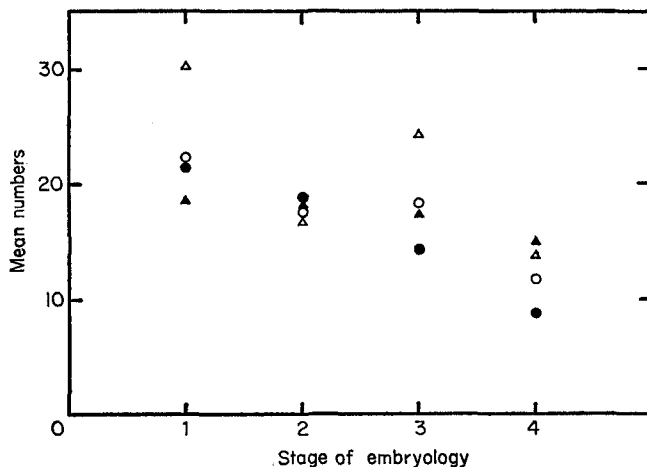


FIG. 5. Brood mortalities for each species based on average numbers for each stage counted in a single marsupium. ●, *J. ischiosetosa*; ○, *J. albifrons*; ▲, *J. praeahirsuta*; △, *J. forsmanni*.

Seasonal population changes

The population structure was very similar for each of the four stations sampled. The following description relates to station 1 (*J. ischiosetosa*), but population histograms are also included for the other two single-species populations at station 4 (*J. forsmanni*) and station 3 (*J. praeahirsuta*), and for the mixed population at station 2. With a continuous high gravidity and a ubiquitous release of young animals it is difficult to interpret life-histories, but some seasonal changes are indicated in Figs 6 and 7. In January 1969 the percentage of young animals and mature males was low, but percentages of maturing and gravid females were high (sex ratio ♂:♀ = 1:7.1). During this month the young developed and accounted for the increase in the male population by February (sex ratio 1:2.9). Thus in February there was a high percentage of males and females in a reproductive condition and this continued into March to form the peak of breeding for this station in the spring (Fig. 1). Male numbers decreased by April suggesting that some males must have died after copulation (sex ratio 1:6.1). Females concerned in this peak probably returned to a non-reproductive condition and accounted for the large specimens collected in March and April. The number of released juveniles increased during this period and formed the beginning of the peak of liberation (Fig. 2). In May the older males and females died, but the spring broods grew quickly and reproduced later in the year. Thus breeding females in autumn were smaller than spring breeding specimens (Fig. 6). The number of newly-

released young decreased gradually from August to December and the November sample contained young females which had matured from juveniles released during the summer. The results for the other three stations are shown in Figs 8 to 10. The sex ratio at station 3 (*J. praeirsuta*) was stable throughout the sampling period (Fig. 7), but the population

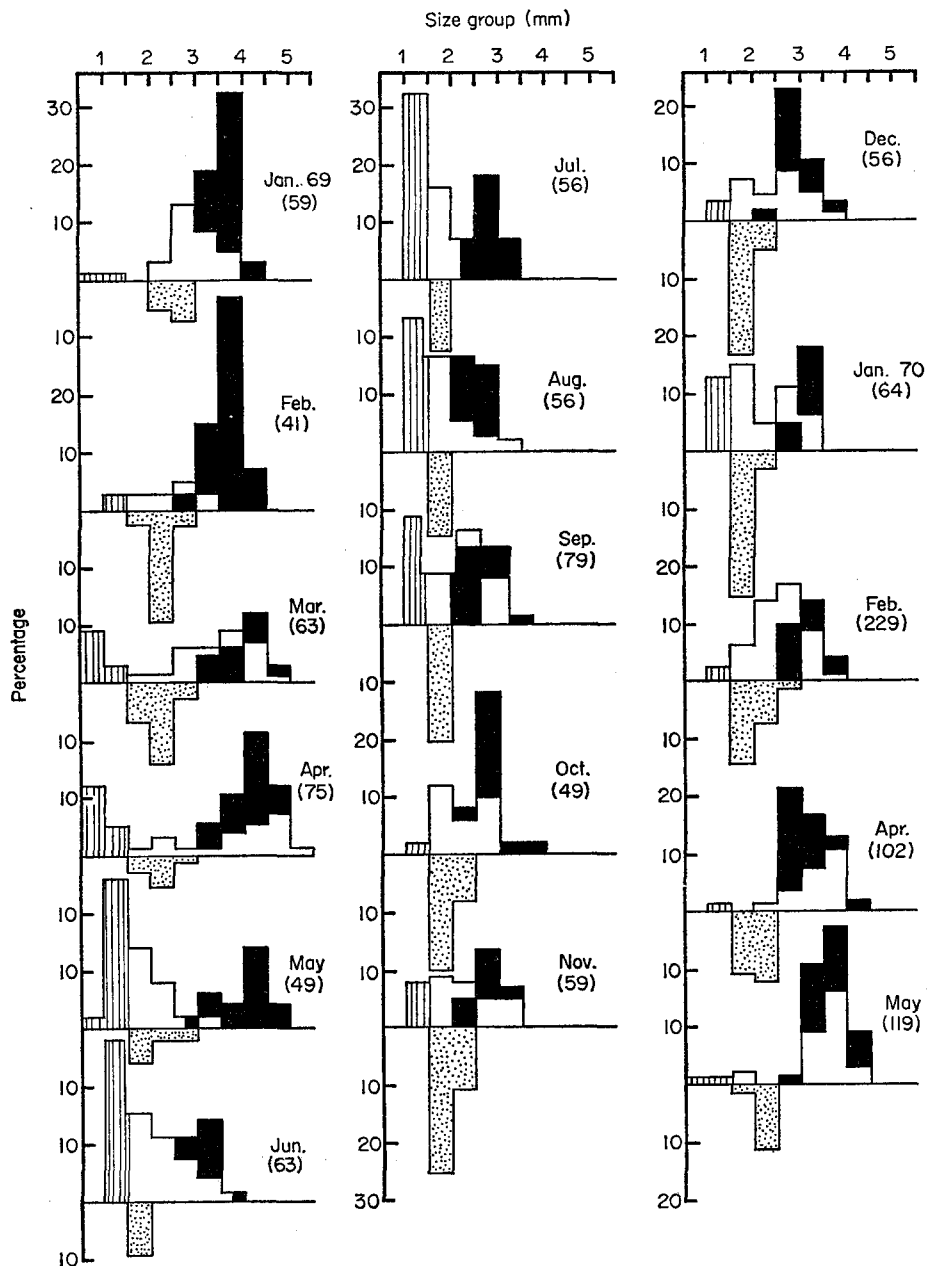


FIG. 6. Population histograms for *J. ischiosetosa*. Total sample numbers are given in brackets. Vertical shading, juveniles; open, immature females; stipple, males; solid, gravid females.

changes are otherwise similar (Fig. 8). *J. forsmanni* also had a stable sex ratio (Fig. 7) and its population changes are shown in Fig. 9. In the case of the mixed population at station 2, the numbers of males other than *J. albifrons* increased during July–October (Fig. 10). However, after this period all males caught were *J. albifrons*.

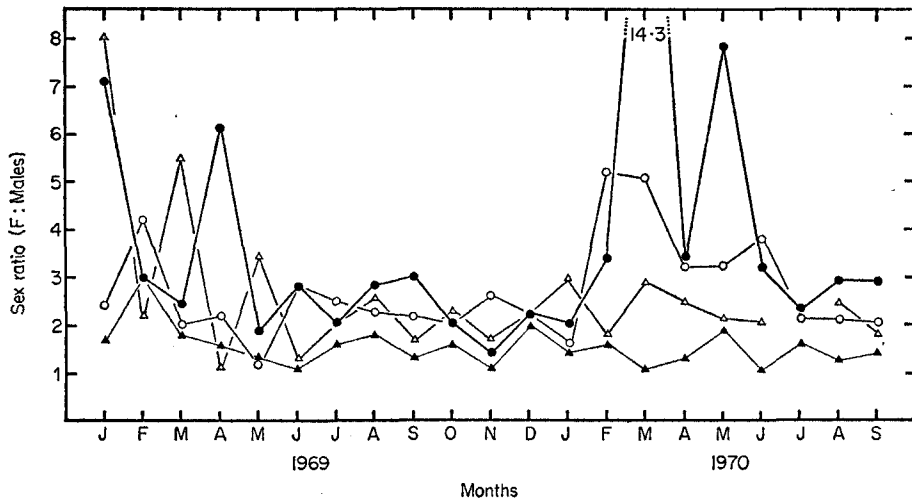


FIG. 7. Season variation in the sex ratio for each species.

●, *J. ischiosetosa*; ○, *J. albifrons*; ▲, *J. praeheirsuta*; △, *J. forsmanni*.

Seasonal size variations

The mean monthly sizes for males, females and reproductive females (with oöstegites) for the four stations are shown in Fig. 11. In general the four populations follow a similar pattern of growth.

Males

The minimum size at which *J. forsmanni* could be identified was 1.30 mm, *J. ischiosetosa* at 1.27 mm, *J. albifrons* at 1.34 mm and *J. praeheirsuta* at 1.36 mm, although the specimens were not fully developed sexually. Maximum sizes reached were *J. forsmanni*—3.52 mm, *J. praeheirsuta*—2.95 mm, *J. ischiosetosa*—2.75 mm and *J. albifrons*—2.40 mm. *J. forsmanni* not only achieves the largest individual size but also the biggest mean size for each sampling month (Fig. 11(c)). Jażdżewski (1969) was able to identify *J. (albifrons) syei* at 1.20–1.30 mm, *J. ischiosetosa* 1.40–1.50 mm, and *J. praeheirsuta* at about 1.50 mm in Poland. Maximum average sizes for all species in Pembrokeshire occurred in late winter/early spring and the smallest were recorded in the summer.

Non-reproductive females

The mean monthly sizes for the non-reproductive females varied and overlapped considerably (Fig. 11(b)), but in general those collected at station 4 were the largest. Young females were recognized at an early stage in development (1.37 mm). The largest female was collected at station 3 (7.25 mm) in May 1969. Maximum average sizes for all four

stations occurred during March/April (3.0–3.80 mm) but then declined due to the death of older females in May, the release and subsequent growth of young females into the populations during early summer, and the continual maturation of females into a gravid condition. The mean sizes increased after August due to the growth of a new generation of females which were released as juveniles in the summer.

Gravid females

Gravid females at the four stations followed a similar pattern of growth during their life-cycle (Fig. 11(a)). The smallest female found with eggs occurred at station 3 (*J.*

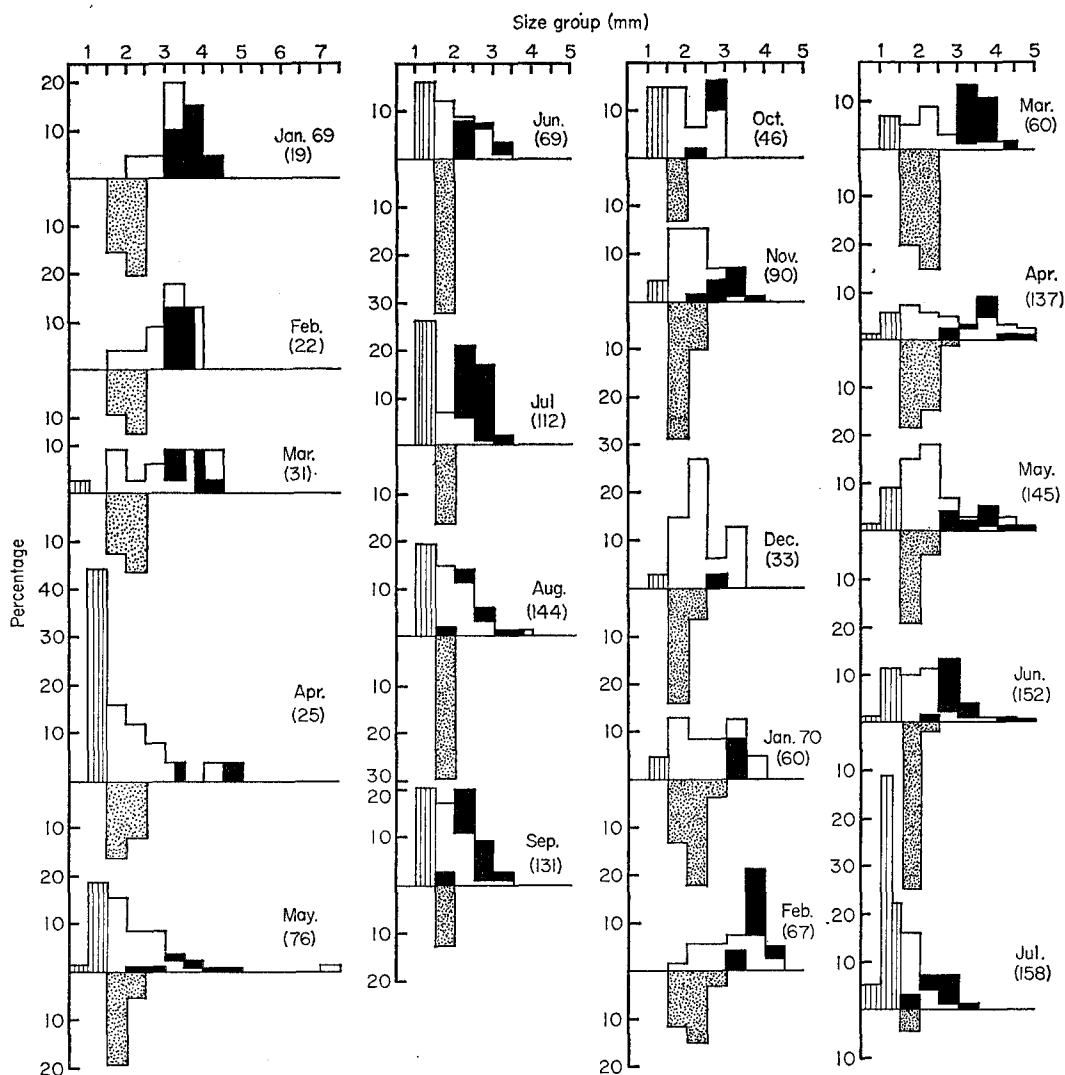


FIG. 8. Population histograms for *J. praeirsuta*. Total sample nos. are given in brackets. Vertical shading, juveniles; open, immature females; stipple, males; solid, gravid females.

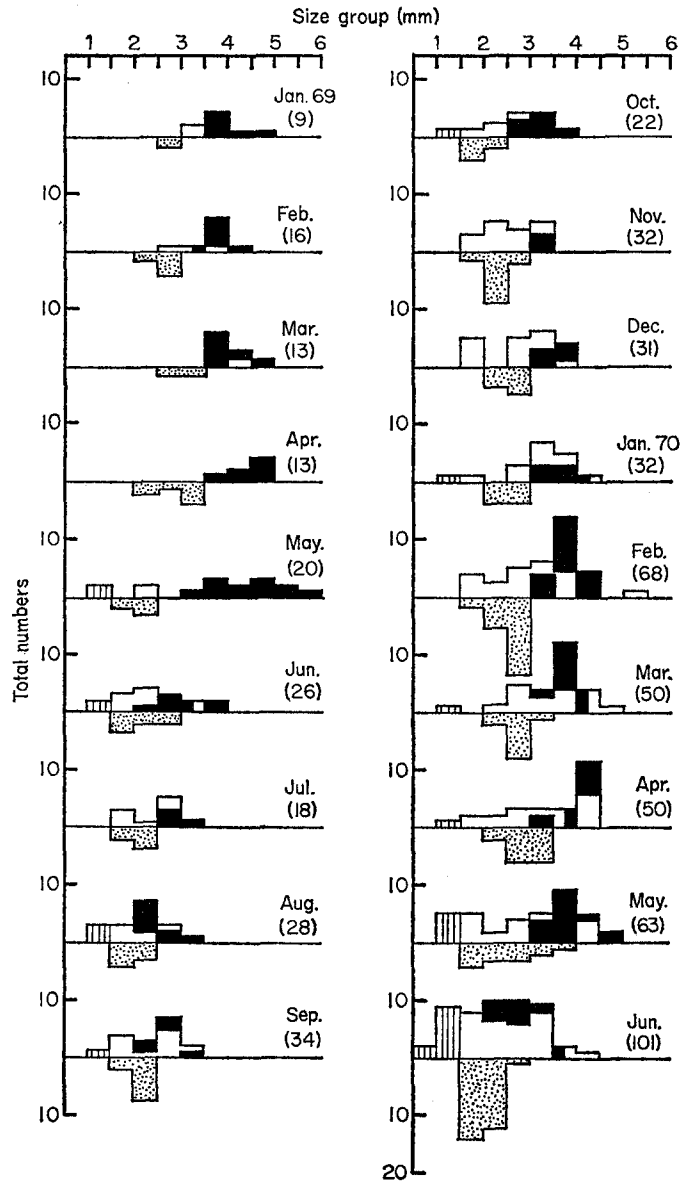


FIG. 9. Population histograms for *J. forsmanni*. Total sample nos. are given in brackets. Vertical shading, juveniles; open, immature females; stipple, males; solid, gravid females.

prae-hirsuta) and was 1.70 mm long (August 1970). Minimum sizes for gravid female *Jaeraalbifrons* from other regions include 2.0 mm at Aberystwyth (Evans, 1936) and The White Sea (Kuznecov, 1964), 2.20 mm in the Bay of Puck (Jażdżewski, 1969), and 2.50 mm in the Kiel Canal (Schütz, 1963) and the Barents Sea (Kuznecov, 1964).

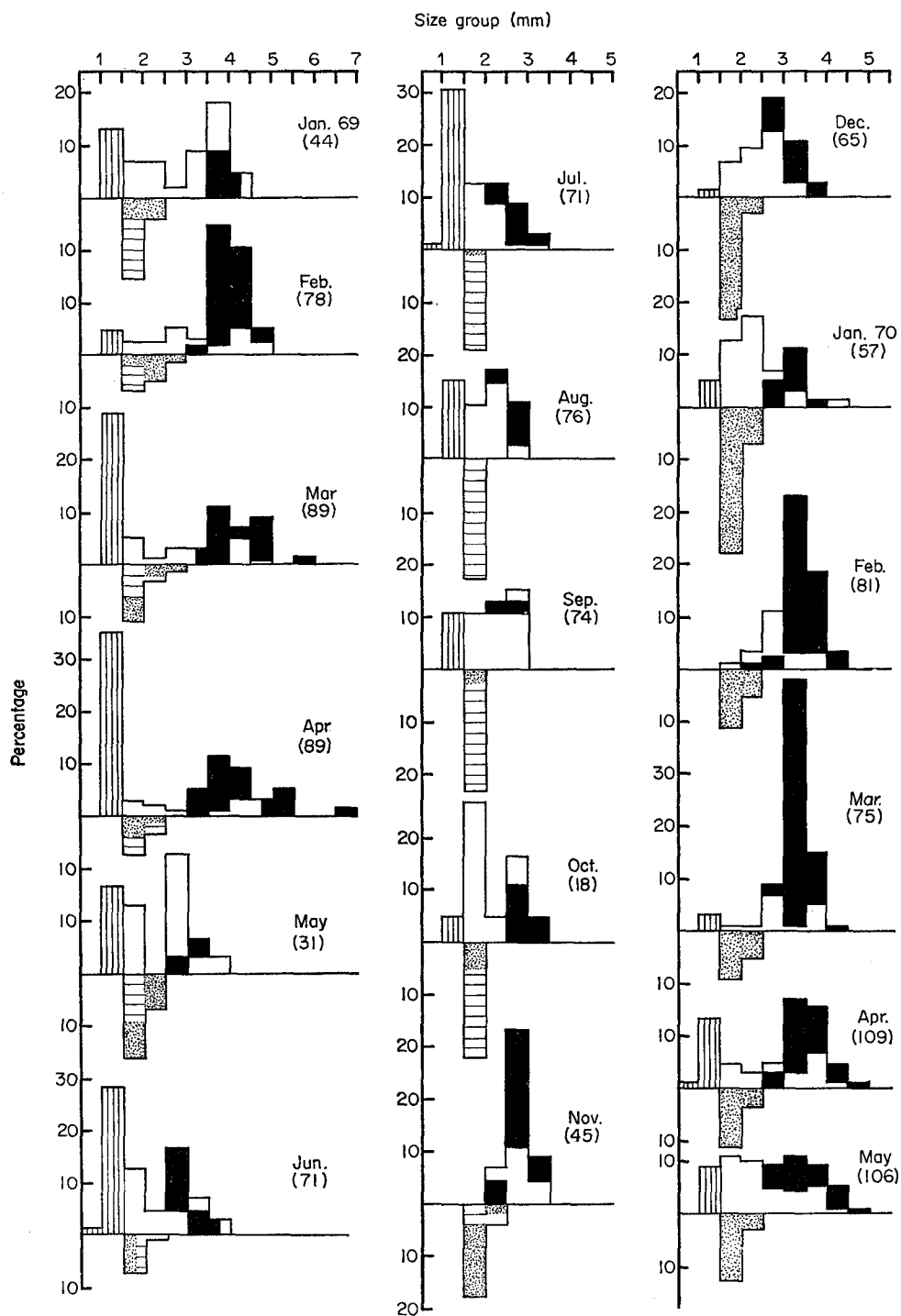


FIG. 10. Population histograms for station 2. Total sample nos. are given in brackets.

Vertical shading, juveniles; open, immature females; stipple, *J. albifrons*; horizontal shading, *J. ischiosetosa*; solid, ♀ gravid females.

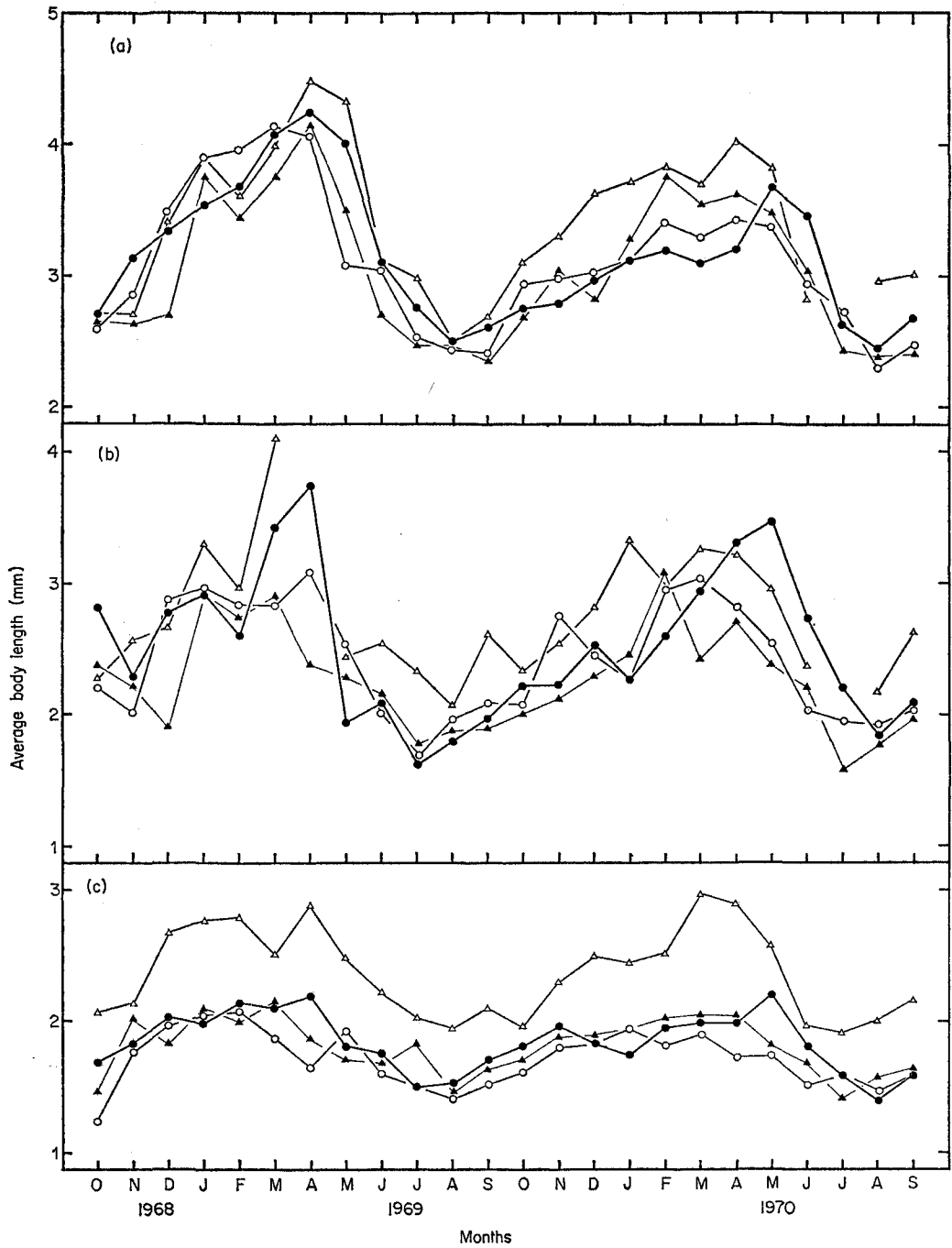


FIG. 11. Season variations in the mean sizes of (a) gravid females, (b) immature females, and (c) males for each species.

●, *J. ischiosetosa*; ○, *J. albifrons*; ▲, *J. praehirsuta*; △, *J. forsmani*.

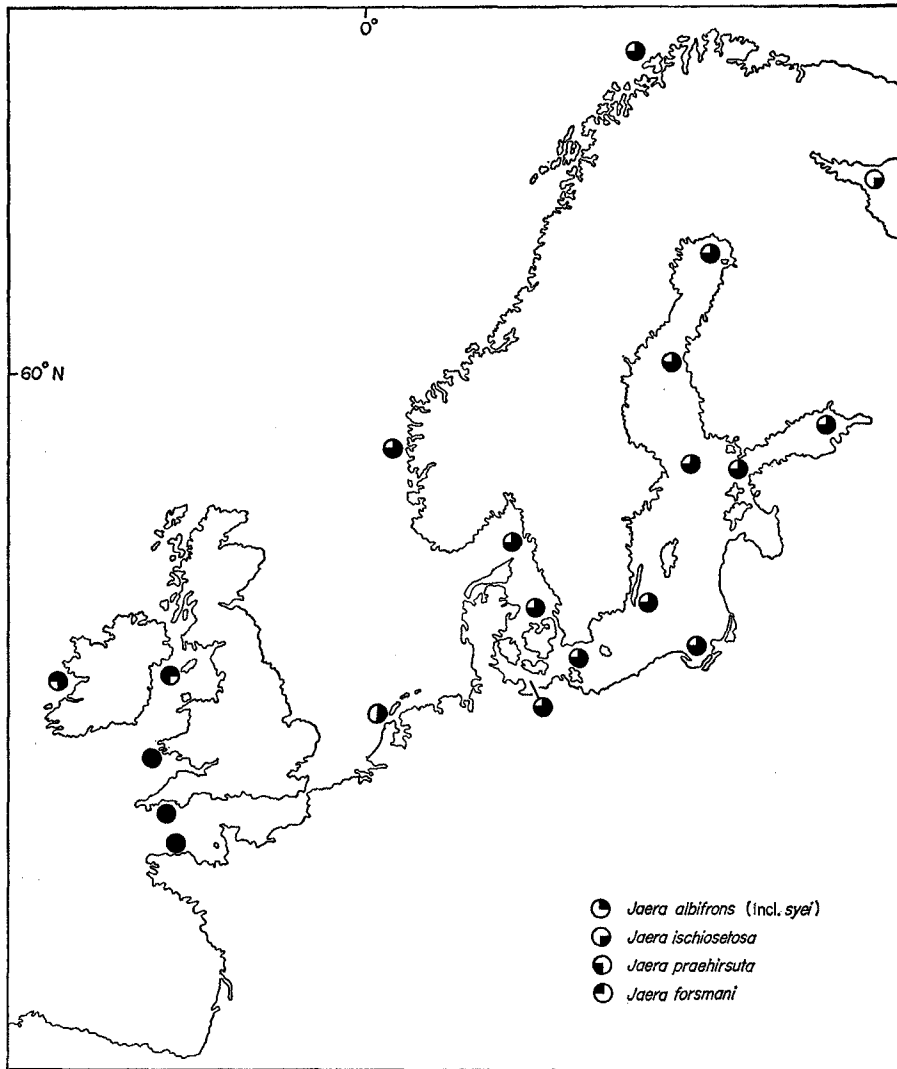


FIG. 12. Geographical distribution of the four species of *Jaera* in Northern Europe. (Based on references cited in text and additional references indicated by an asterisk in the bibliography.)

Discussion

It can be concluded from this investigation that the habitat preferences of the four species of the *Jaera albifrons* group (Naylor & Haahtela, 1966) were persistent throughout a two-year period except for some mixing of *J. ischiosetosa* with *J. albifrons* during periods of drought. Other slight mixing also occurred (Table I) but despite the overlaps there was virtually no evidence of interbreeding to produce hybrids (Bocquet, 1953). Only one hybrid, between *J. albifrons* and *J. ischiosetosa*, was obtained during the study in a total of 6214 specimens examined. The sex ratio of males to females for any species was never 1:1

(Fig. 7) supporting the earlier work of Naylor, Slinn & Spooner (1961), Brattegard (1966) and Sjöberg (1967). *J. prae-hirsuta* has the most stable sex ratio. Broadly speaking the seasonal patterns of breeding were similar in the four species, but some differences are evident in *J. forsmanni* and *J. prae-hirsuta* which showed maximum brood production in summer, a few months later than the other two species. *J. forsmanni* also proved to reach a consistently larger size than the other three species. The ecological separation of the four species is therefore enhanced by a slight difference in the breeding pattern of two of them and the growth pattern of one of them, when compared with typical *J. albifrons*.

The summer breeding of *J. forsmanni* and *J. prae-hirsuta* may relate to the fact that these species seem to extend less far north than the other two in Europe (Fig. 12). Although there is a record shown on the map for *J. prae-hirsuta* from N. Norway, this is based on the report of only a single specimen (Hussey, 1964). The absence of *J. forsmanni* in the Baltic is probably explained by its preference for high salinity localities (Naylor & Haahtela, 1966), but its absence among extensive collections in southern and northern Norway (Brattegard, 1966; Sjöberg, 1967; Hussey, 1964) may well relate to different temperature tolerances. The group as a whole also shows a restriction of the breeding period to the summer months in the northern part of the range. Thus, the breeding period is from April–November in Germany (Schütz, 1963), March–September in Sweden (Forsman, 1944) and Poland (Jazdzewski, 1969), June–September in Norway (Brattegard, 1966) and June–August in the Barents and White seas (Kuznecov, 1964). Experimental investigation of the temperature preferences and salinity tolerances remain as profitable lines of inquiry into the mechanism of ecological isolation in the group.

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* See Fig. 12.