J. mar. biol. Ass. U.K. (1961) 41, 817–828
Printed in Great Britain

OBSERVATIONS ON THE BRITISH SPECIES OF *JAERA* (ISOPODA:ASELLOTA)

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(Text-figs. 1–4)

Two species of *Jaera* (Isopoda: Asellota) are recognized in Britain, namely *J. albifrons* Leach [= *J. marina* Bate & Westwood = *Oniscus marinus* Fabricius *nec* Linné] and *J. nordmanni* (Rathke) (see Bate & Westwood, 1868; Tattersall, 1906). Both species are found beneath stones and amongst algae in estuaries, in brackish pools and in or near freshwater streams running over the shore. In Britain the two have often been confused, particularly since Sars (1898) wrongly suggested that *J. nordmanni* described by Bate & Westwood (1868) might really be the male of *J. albifrons*. In addition, until very recently (Lemercier, 1960), little seems to have been written about the relative ecological distribution of the two species (see Kesselyak, 1938), though Stebbing (1876) suggested that near Torquay *J. nordmanni* occupied a higher zone on the beach than *J. albifrons*.

Though unrecorded in the revised edition of the *Plymouth Marine Fauna* (Marine Biological Association, 1957), *J. nordmanni* was found to be present in the district, as soon as it was looked for in the right places. Records by one of us (G.M.S.) are included in the Appendix (Table 2).

At present we aim to clarify some of the specific differences between *J. albifrons* and *J. nordmanni*, and also to compare the ecological distribution of the two species. General faunistic surveys of two restricted localities (McCartan & Slinn, 1953; Naylor & Slinn, 1958) have suggested that when the two species occur together, *J. nordmanni* extends farther into fresh water than *J. albifrons*. Present work on material from many localities in the British Isles confirms this view.

SUBSPECIATION

Forsman (1949) and Bocquet (1953) have recently made extensive studies on *J. albifrons* for which they have described five European subspecies (*albifrons*, *praehirsuta*, *forsmani*, *ischiosetosa*, *syei*). The subspecies are recognizable in males only, on the basis of secondary sexual characters, and each is reported to have a characteristic habitat range. In Britain we have recognized all five subspecies, but observations suggest that the habitat preferences of the various subspecies in Britain are not so clearly defined as those described on the continent of Europe by Bocquet (1953, 1954), nor are they so clearly zoned according to tidal levels on the shore as is claimed in Europe. In addition, in Britain, the typical subspecies varies towards, and merges into, the condition of *syei*, particularly in the more brackish habitats. The separate identity of *syei* may therefore be in doubt, but the other four subspecies appear to retain their complete identity even when the populations mix. Intermediates, identifiable as hybrids from Bocquet's experiments, are quite rare.

Subspeciation has also been described in *J. nordmanni* by Lemercier (1960). Of the three subspecies which she has described, *J. nordmanni nordica* Lemercier is regarded as the only form found north of latitude 45° N., and so is likely to be the only one occurring in Britain. At present, though the subspecies of *J. albifrons* have been recognized, it is not possible to generalize about subspecific habitats. We propose, therefore, to deal mainly with the 'superspecies' *J. albifrons* and *J. nordmanni* and hope to discuss the subspecies problem in Britain at a later date.

IDENTIFICATION

The main characters separating *J. nordmanni* and *J. albifrons* are illustrated in Fig. 1. The body of *J. nordmanni* is more flattened and more widely oval in shape than that of *J. albifrons*. Furthermore, in the former species the sides of the head, thorax and abdomen are more setose, and the eyes are set more medially on the head. The male operculum, which lies ventrally, anterior to the pleopods, is narrow and pointed in *J. nordmanni*, whilst that of *J. albifrons* is T-shaped (Fig. 2).

A striking difference which has not apparently been reported, except in an unpublished thesis[1], concerns the size of adult males and females. When specimens are found in 'precopula' the male of *J. nordmanni* is almost invariably larger than the female, whereas in *J. albifrons* the male is smaller than the female. The mean lengths of ten randomly taken males and ovigerous females of each species from the Isle of Man and from Wales were as follows: *J. albifrons* ♂♂ 1·7 mm, ♀♀ 3·3 mm; *J. nordmanni* ♂♂ 3·3 mm, ♀♀ 2·8 mm.

The same feature was noted in all the South Devon collections. In the Broadsands sample of *J. nordmanni* taken on 3 May 1958 the five largest males were 4·6–4·2 mm body length (2·5–2·1 mm broad), while the largest females were only 3·7–3·2 mm long (1·8–1·6 mm broad), indicating an average length ratio (male to female) of about 5:4.

[1] On *Jaera marina* (Fabricius) and *Jaera nordmanni* (Rathke). G. Evans, M.Sc. Thesis, Univ. Coll., Aberystwyth.

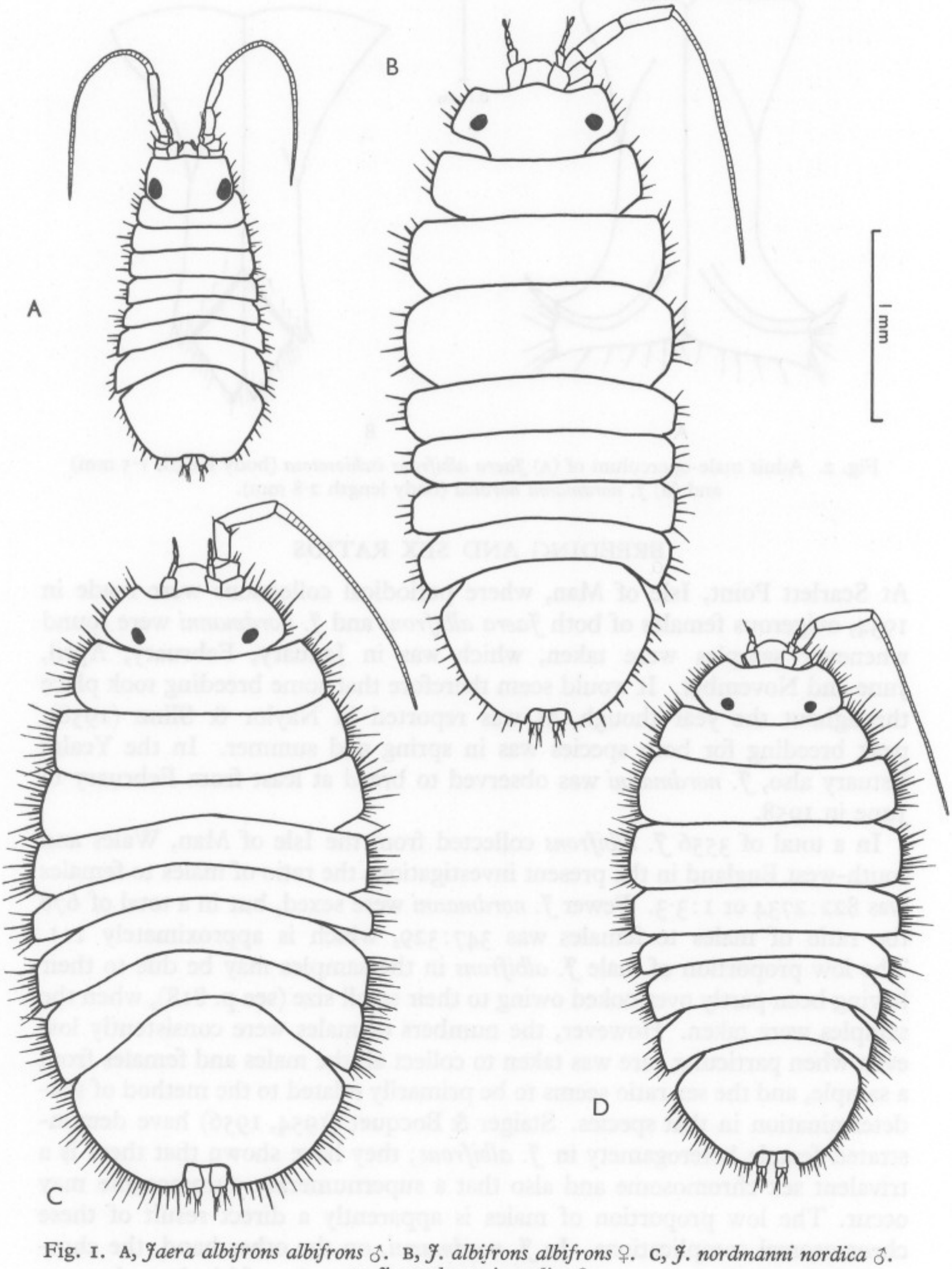

Fig. 1. A, *Jaera albifrons albifrons* ♂. B, *J. albifrons albifrons* ♀. C, *J. nordmanni nordica* ♂. D, *J. nordmanni nordica* ♀.

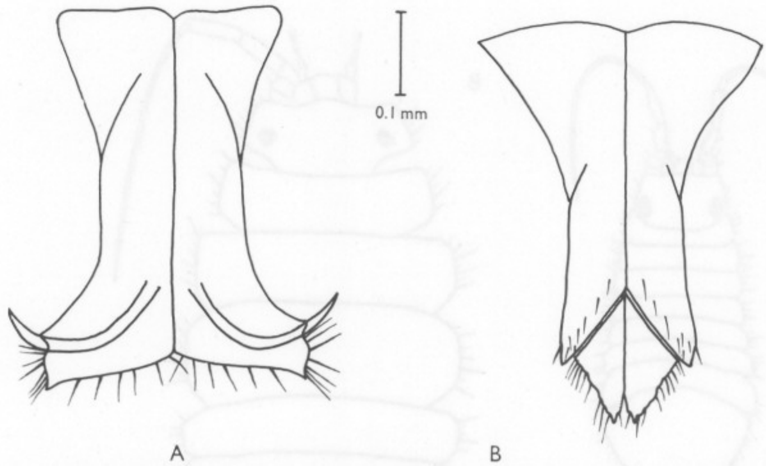

Fig. 2. Adult male operculum of (A) *Jaera albifrons ischiosetosa* (body length 1·5 mm) and (B) *J. nordmanni nordica* (body length 2·8 mm).

BREEDING AND SEX RATIOS

At Scarlett Point, Isle of Man, where periodical collections were made in 1954, ovigerous females of both *Jaera albifrons* and *J. nordmanni* were found whenever samples were taken, which was in January, February, April, June and November. It would seem therefore that some breeding took place throughout the year though, as was reported in Naylor & Slinn (1958), peak breeding for both species was in spring and summer. In the Yealm Estuary also, *J. nordmanni* was observed to breed at least from February to June in 1958.

In a total of 3556 *J. albifrons* collected from the Isle of Man, Wales and south-west England in the present investigations the ratio of males to females was 822:2734 or 1:3·3. Fewer *J. nordmanni* were sexed, but in a total of 676 the ratio of males to females was 347:329, which is approximately 1:1. The low proportion of male *J. albifrons* in the samples may be due to their having been partly overlooked owing to their small size (see p. 818), when the samples were taken. However, the numbers of males were consistently low even when particular care was taken to collect all the males and females from a sample, and the sex ratio seems to be primarily related to the method of sex-determination in that species. Staiger & Bocquet (1954, 1956) have demonstrated female heterogamety in *J. albifrons*; they have shown that there is a trivalent sex chromosome and also that a supernumerary chromosome may occur. The low proportion of males is apparently a direct result of these chromosomal complications. In *J. nordmanni*, on the other hand, the chromosomal complement seems to be constant at 24 pairs of bivalent chromosomes, and the species shows none of the chromosomal complications observed in *J. albifrons* (Staiger & Bocquet, 1956). It thus seems likely that the method of sex-determination is normal in *J. nordmanni*, which would account for the approximate 1:1 ratio of males to females observed in the present investigations.

ECOLOGICAL DISTRIBUTION

Collections from under stones

At several localities in the British Isles where fresh water flows over the intertidal zone, specimens of *Jaera* were collected from under stones. Ten-minute collections were made at several tidal levels in each locality and the results of the more detailed of these surveys are given in Fig. 3. Tidal levels were determined with the use of surveying equipment in the harbours at Castletown and Ramsey, and also on the shores at Spaldrick and Poyll Vaaish, all in the Isle of Man. At Ramsey, Ordnance Datum was related to Chart Datum using the constant given in the *Admiralty Tide Tables* (1959). For the other localities in the Isle of Man the approximate data given by Southward (1953) have been used to make this conversion. In the streams on the shores at Llansantffraid, Ilfracombe, Newton Creek and Portwrinkle the tidal levels were roughly estimated from the water level on a calm day and from the zonation of algae. At all localities in Fig. 3 the relative positions of the tidal levels have been standardized for comparison.

Apart from the localities mentioned in Fig. 3 and Table 2 (p. 826) collections have been made in other parts of the Isle of Man, Wales and in the Plymouth area. Collections have also been examined from Cullercoats (Northumberland), Carnalea (Co. Down), Dublin, Jersey (Channel Islands) and Wrabness (Essex). All results confirm the general pattern illustrated in Fig. 3 in which it can be seen that *J. nordmanni* occurs from just below M.H.W.S. to M.T.L., usually being most abundant rather below M.H.W.N. *J. albifrons*, on the other hand, is not often found above M.H.W.N. and its numbers increase below that level as the numbers of *J. nordmanni* decline. Unlike *J. nordmanni* it is found down to about M.L.W.S.

Away from the influence of fresh water on the open shore the numbers of both species decline considerably. On the other hand, both species may extend relatively farther upstream on wave-beaten shores, depending upon the amount of sea water which is forced inland. At Scarlett Point in the Isle of Man both species occur in pools above M.H.W.S., with *J. albifrons* being restricted to the seaward end of the pools and *J. nordmanni* penetrating farther into fresh water (Naylor & Slinn, 1958). Owing to the indented nature of the coastline and the direction of the prevailing wind at Scarlett Point surf and spray periodically reach the pools. Similarly, on an indented coastline at Carnalea, Co. Down, *J. nordmanni* was found to extend some 2 ft. above M.H.W.S. (McCartan & Slinn, 1953). In an extreme case in the present investigation *J. nordmanni* was found beneath stones in a small stream on a

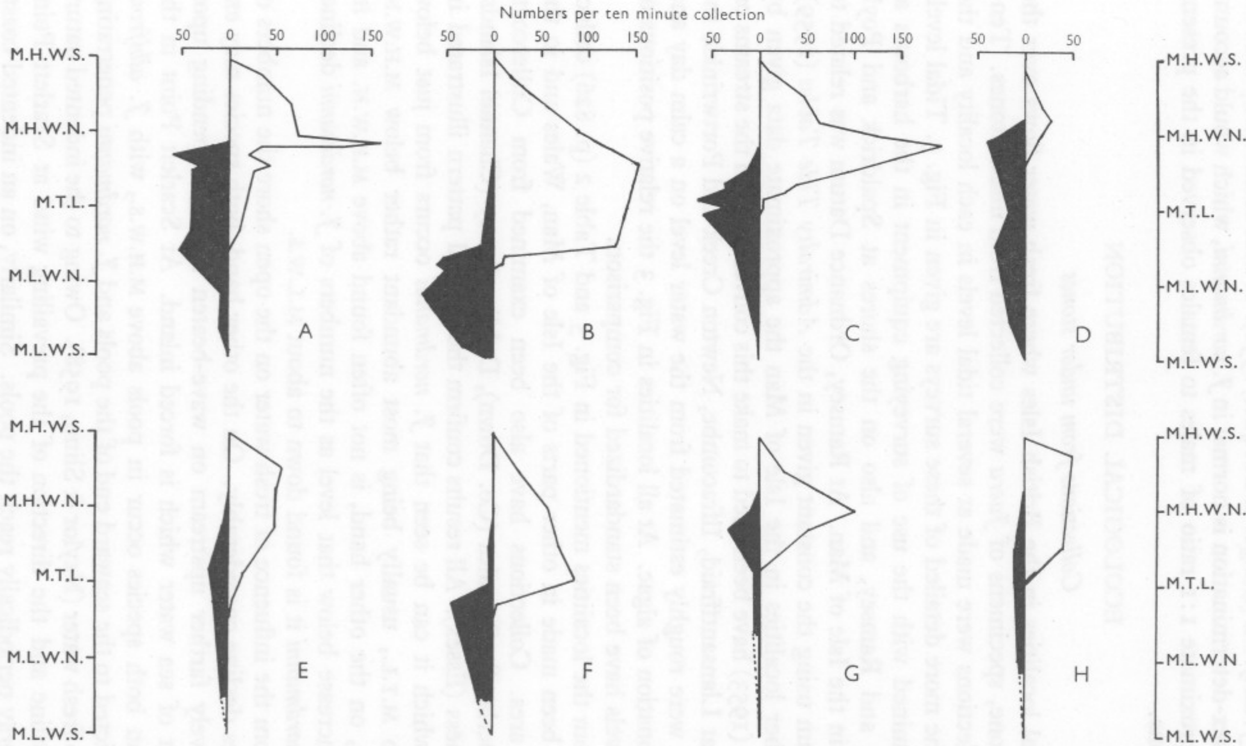

Fig. 3. Total numbers of *Jaera albifrons* and *J. nordmanni* in 10 min. collections beneath stones at various levels from M.L.W.S. to M.H.W.S. in sheltered estuaries at (A) Ramsey and (B) Castletown, Isle of Man, and in streams running over the shore at (C) Poyll Vaaish and (D) Spaldrick, Isle of Man, (E) Ilfracombe, north Devon, (F) Newton Ferrers Creek, south Devon, (G) Portwrinkle, east Cornwall, (H) Llansantffraidd, Cardiganshire. ●, *Jaera albifrons*; ○, *J. nordmanni*.

cliff face in the Calf of Man at a point approximately 150 ft. above sea level. The cliffs in that area face the prevailing south-westerly winds and spray would often reach the cliff tops.

Jaera was found to be most common under stones where the substrate was firm and consisted of gravel or muddy gravel. On rocky substrates, such as at Spaldrick (Fig. 3), *Jaera* was less abundant. In that locality stones were not embedded in the substrate and either provided insufficient shelter or were too unstable. Specimens were rare or absent from shingle banks and under stones in streams running over clean sand. In the last two types of habitat the substrate is presumably too unstable for populations of *Jaera* to become established.

Collections from amongst algae

Besides occurring beneath stones *Jaera* may often be found amongst algae which grow in or near streams which run over the shore and in estuaries. They are particularly abundant amongst algae in very sheltered estuaries but are much less common on algae than under stones on coasts exposed to only moderate wave action. On the moderately wave-beaten shore at Spaldrick (Fig. 3), a fairly sheltered part of Port Erin Bay, *Jaera* was virtually absent amongst algae. It was not found amongst *Fucus serratus* L. or *Fucus vesiculosus* L. and only single specimens could be found amongst *Ascophyllum nodosum* (L.) Le Jol and *Polysiphonia* sp. *Jaera* was more common amongst algae at Poyll Vaaish than at Spaldrick. Poyll Vaaish has about the same degree of exposure to wave action and wind as Spaldrick but the volume of fresh water flowing over the shore is considerably greater. Above M.L.W.N. at Poyll Vaaish small numbers of *J. albifrons* were found amongst *Fucus serratus*, *Gigartina stellata* (Stackh.) Batt and *Ascophyllum nodosum* at the edges of the stream. *Fucus ceranoides* L. in the stream contained considerable numbers of *J. albifrons* and, above M.T.L., a few specimens of *J. nordmanni*. Higher up, between M.T.L. and M.H.W.N., small numbers of *J. nordmanni* were found amongst *Enteromorpha* sp.

The two estuarine harbours investigated in the Isle of Man provided particularly sheltered conditions and *Jaera* was quite abundant amongst algae collected there. At Ramsey (see Fig. 4) *Fucus ceranoides* was examined from the level of M.L.W.N. to about M.H.W.N. where the weed became sparse and stunted. On this alga *J. albifrons* was common, being most abundant around M.T.L.; a few *J. nordmanni* were found between M.H.W.N. and M.T.L. At Castletown, *J. albifrons* was abundant on *Fucus ceranoides* from about M.T.L. almost up to M.H.W.N. In addition, at about M.H.W.N. the *F. ceranoides*, though sparse, contained fair numbers of *J. nordmanni*. In the Castletown estuary *J. albifrons* also occurred sparingly amongst *Enteromorpha* spp. between M.L.W.N. and M.H.W.N., and abundantly amongst *Ascophyllum* and *Polysiphonia* up to about M.H.W.N.

To compare the ecological distribution of the two species of *Jaera* where their ranges overlapped collections were made amongst *Fucus ceranoides* and under stones in the estuaries at Ramsey and Castletown, at a number of levels between M.L.W.N. and M.H.W.N. From these results it is not possible to make quantitative comparisons between the total numbers of *Jaera* under

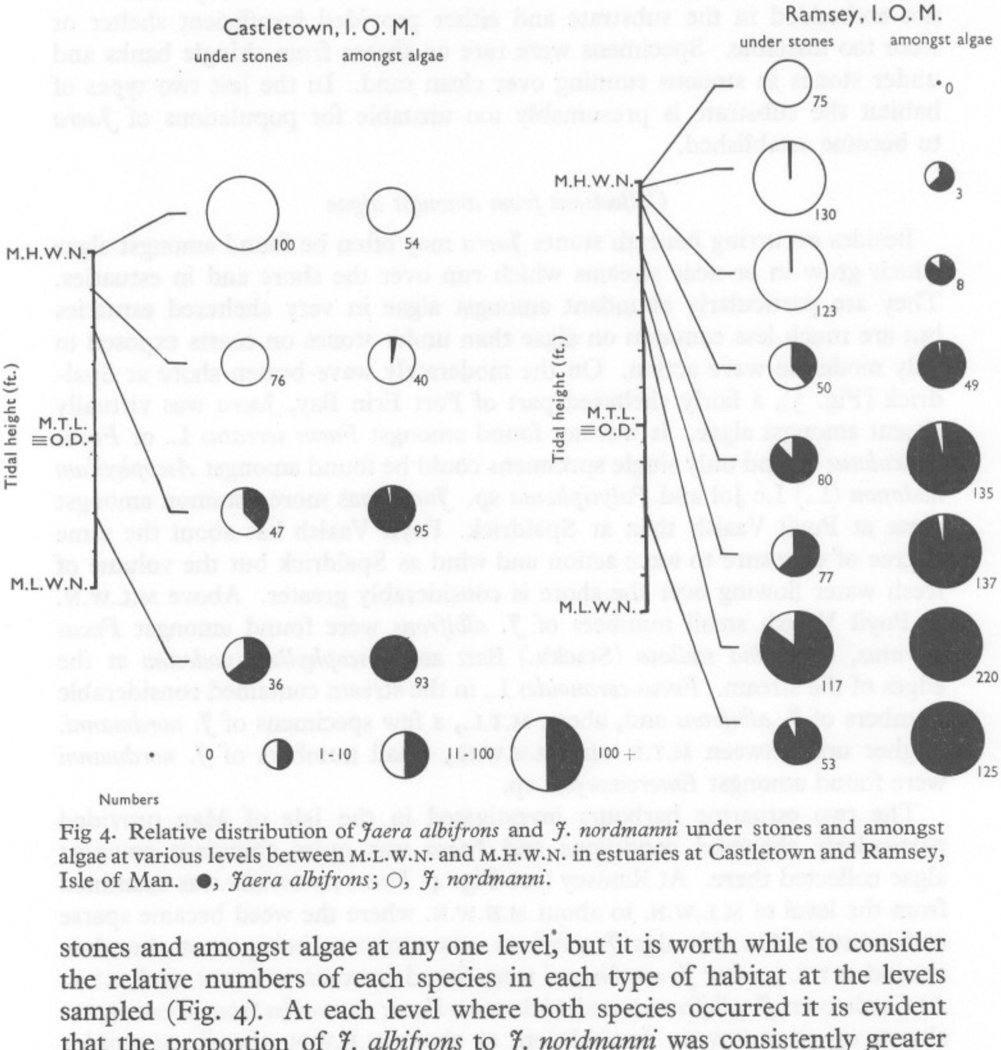

Fig 4. Relative distribution of *Jaera albifrons* and *J. nordmanni* under stones and amongst algae at various levels between M.L.W.N. and M.H.W.N. in estuaries at Castletown and Ramsey, Isle of Man. ●, *Jaera albifrons*; ○, *J. nordmanni*.

stones and amongst algae at any one level, but it is worth while to consider the relative numbers of each species in each type of habitat at the levels sampled (Fig. 4). At each level where both species occurred it is evident that the proportion of *J. albifrons* to *J. nordmanni* was consistently greater amongst algae than under stones. Conversely the proportion of *J. nordmanni* to *J. albifrons* was greater under stones than amongst algae. The significance of these results is discussed below (p. 826).

TOLERANCE OF REDUCED SALINITY

Preliminary work suggested that *J. nordmanni* was more tolerant of reduced salinities than *J. albifrons* (Naylor & Slinn, 1958) and those experiments have been confirmed and extended in the present work. In the present experiments specimens of both species of *Jaera* were kept in water of various salinities from 0 to 34‰, as far as possible under conditions of constant temperature, and the results of these experiments are combined in Table 1. It is clear that in water of salinity 3·4‰ and above, both species survived equally well for periods up to 4 days. *J. nordmanni* however, survived much better than *J. albifrons* in salinities below 3·4‰. In distilled water both species normally survived for only a few hours, but again *J. nordmanni* survived longer than *J. albifrons*.

TABLE 1. PERCENTAGE SURVIVAL OF *JAERA NORDMANNI* AND *J. ALBIFRONS* DURING SUCCESSIVE DAYS IN WATER OF VARIOUS SALINITIES

Total numbers alive at the start of each experiment in parentheses.

Time in days	*J. nordmanni*. Salinity (‰)				
	34	3·4	0·34	0·034	Distilled
1	100 (30)	96 (44)	80 (49)	68 (79)	6 (50)
2	100	91	82	66	—
3	100	86	65	53	—
4	100	82	47	50	—

Time in days	*J. albifrons*. Salinity (‰)				
	34	3·4	0·34	0·034	Distilled
1	100 (30)	95 (57)	58 (40)	49 (70)	3 (60)
2	95	88	33	37	—
3	95	87	27	—	—
4	95	78	17	—	—

DISCUSSION

It is clear that both British species of *Jaera* are euryhaline and are most commonly found where fresh water flows between tide-marks. The pattern of distribution, with *J. albifrons* occurring in the more marine part of the range and *J. nordmanni* penetrating farther into fresh water, persists throughout the year in localities which have been visited regularly (see also Naylor & Slinn, 1958). Experiments in which specimens were kept in water of reduced salinity show that *J. nordmanni* is more tolerant of very low salinities than *J. albifrons*. This clearly suggests that the former species might be physiologically better able to withstand the extreme variations in salinity which prevail in the more estuarine conditions where it is most abundant. Yet the results in Table 1 indicate that the two species tolerate equally well salinities of from 3·4‰ to 34‰. It would seem therefore that *J. nordmanni* is restricted to the more estuarine conditions by competition with the less euryhaline species *J. albifrons* (Naylor & Slinn, 1958).

Despite the fact that both species occur beneath stones and amongst algae it is evident that when the two species occur together in sheltered harbours the proportion of *J. albifrons* to *J. nordmanni* is greater amongst *Fucus ceranoides* and *Ascophyllum nodosum* than it is under stones at the same tidal level. On the other hand, *J. nordmanni* is relatively more abundant beneath stones, though admittedly algae are normally sparse at the upper limits of its distribution. This difference in habitat exhibited by the two species is not, however, generally applicable in a wider range of habitats. In slightly more wave-beaten situations, particularly where only a small volume of fresh water flows over the intertidal zone and where *Fucus ceranoides* is absent, then both species are rare amongst algae, even amongst *Ascophyllum* (p. 823). Also, in pools at Scarlett Point in the Isle of Man both species were found to be more abundant amongst algae than under stones when a choice of habitat was available (Naylor & Slinn, 1958). In that case it was possibly due to the *Jaera* seeking algae to avoid the more stagnant conditions beneath stones. When there is sufficient fresh water to immerse the algae and when the environment beneath stones is sufficiently well oxygenated, as is apparently so in the estuaries at Ramsey and Castletown, then mutual competition between the two species of *Jaera* is perhaps responsible for their ecological separation.

Such differences in the ecological distribution of the same species, and often of the same subspecies, made it difficult to generalize about subspecific habitats in the present investigation. As indicated earlier the habitat preferences of the subspecies of *J. albifrons* in Britain are not so clearly defined, nor so clearly zoned according to tidal level, as they are in Europe (p. 818). Finally, in Europe, *J. albifrons albifrons* Forsman is reported from beneath stones whilst *J. albifrons praehirsuta* Forsman is said to be particularly abundant amongst algae in the same localities (Forsman, 1949; Bocquet, 1953, 1954). In Britain, a similar separation of the two subspecies occurs near Plymouth. At Castletown, in the Isle of Man, however, both these subspecies occurred together amongst algae and under stones at several levels which were sampled. When more data are available it is hoped to discuss the subspecies problem in greater detail.

One of us (E.N.) is grateful to Dr F. S. Russell, F.R.S., for the provision of laboratory facilities at the Marine Laboratory, Plymouth, and to Mr J. S. Colman for facilities at the Marine Biological Station, Port Erin. Miss Winifred Chapman assisted with field work in the Isle of Man and Dr R. Howells kindly drew our attention to the unpublished M.Sc. Thesis of Miss G. Evans. Finally, we would like to thank the following people who have sent material: Dr H. O. Bull (Cullercoats), Miss M. Duhig (Dublin), Dr M. George (Dale Fort), Mr A. J. Hopson (Flatford Mill) and Mr R. F. le Sueur (Jersey).

SUMMARY

Brief descriptive notes, with comments on subspeciation, breeding and sex-ratios, are given for *Jaera albifrons* and *J. nordmanni* in Britain. The ecological distribution of each species is described. Both species occur amongst algae and under stones in estuaries, brackish pools and in freshwater streams running over the intertidal zone. *J. nordmanni* normally occurs from just below M.H.W.S. to about M.T.L., usually being most abundant just below M.H.W.N. *J. albifrons* is rarely found above M.H.W.N. and it extends down to about M.L.W.S. Experiments show that *J. nordmanni* survives better than *J. albifrons* in water of reduced salinity.

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APPENDIX

TABLE 2. *JAERA NORDMANNI* (RATHKE): OCCURRENCES IN THE PLYMOUTH AREA (G. M. S.)

Locality	Date	Tidal zone	Stones or weeds	*Jaera nordmanni* ♂	*Jaera nordmanni* ♀	*Jaera nordmanni* total	*Jaera albifrons* total	Fauna notes
Plymouth Sound: Jennycliff Bay (close to freshwater stream over shore)	4. iii. 58	Upper shore (*Fucus vesiculosus*)	S	4	0	4	31	*Procerodes ulvae*, *Protodrilus*, *Enchytraeus*, *Marinogammarus stoerensis*
		Middle shore (*Ascophyllum*)	S	1	0	1	111	*Marinogammarus stoerensis*
Heybrook Bay, opposite Renny Rocks (no stream, at most irregular freshwater seepage)	21. v. 58	H.W.N.	S	39	43	82	55	*Monodonta* common
Renny Rocks, rock pool (salinity 17·6 ‰)	21. v. 58	Pool in splash zone	S	11	5	16	0	Large *Procerodes ulvae*, *Gammarus duebeni*, *Ligia*
Yealm Estuary, south shore, freshwater stream over shore	22. iii. 58	H.W.S. (*Enteromorpha*)	S	12	12	24	0	*Gammarus duebeni* common, *G. zaddachi*
		H.W.N. to M.T.L.	S	36	26	62	34	*Procerodes ulvae*, *Marinogammarus stoerensis*
		Below M.T.L.	S	0	0	0	10	*Melita palmata*
Yealm Estuary, Cofflete Creek: Bridge at extreme head	25. ii. 58	River channel, running fresh	W	7	7	14	0	*Asellus aquaticus*, *Potamopyrgus jenkinsi*, *Gammarus zaddachi*
50 yards down from bridge, small freshwater trickle over shore	25. ii. 58 13. iii. 58	*ca.* H.W.N.	S	9	4	13	0	—
300 yards from bridge	25. ii. 58	Upper shore	S	4	3	7	115	—
300 yards from bridge	25. ii. 58	Upper shore (*Fucus ceranoides*)	W	0	0	0	0	—
Aune Estuary, station B4	8. vi. 58	Mid to upper shore	S	1	1	2	0	*Marinogammarus marinus*, *Gammarus salinus*, *G. zaddachi*
Aune Estuary, Station B6	8. vi. 58	River channel	W	2	0	2	0	*Gammarus zaddachi*
Torbay: Broadsands Marsh:								
Stream inside sea bank	3. v. 58	Stream channel	S+W	72	47	119	0	*Gammarus zaddachi*, *Melita pellucida*
Sandy shore where the stream flows over it	3. v. 58	M.T.L.	S	47	39	86	0	—
Sandy shore where the stream flows over it	3. v. 58	Below M.T.L.	S	0	0	0	0	—