

BREEDING BIOLOGY AND SEASONAL POPULATION CHANGES OF *JAERA NORDMANNI* *NORDICA* LEMERCIER [ISOPODA, ASELOTOTA]

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(Text-figs. 1-5)

An extensive, 20 months, quantitative and qualitative sampling of a population of *Jaera nordmanni nordica* Lemercier (Crustacea, Isopoda, Asellota) has been carried out in Castletown Estuary, Isle of Man. The species is able to reproduce successfully in conditions of fluctuating salinity and strong water flow. Breeding, expressed in terms of females in a reproductive condition, was limited during the period from November to March, but high numbers of gravid females occurred in the other months with a peak in May. Juvenile specimens were collected each month except April with a peak in summer. The sex ratio fluctuated seasonally, although it was stable in May and June at the times of high reproductive activity. *J. nordmanni nordica* has a higher egg production and a lower rate of brood mortality than *Jaera albifrons* Leach *sensu lato*. These results are discussed in relation to the competition between these two closely related forms.

INTRODUCTION

Jaera nordmanni (Rathke) occurs abundantly beneath stones and algae in freshwater streams (McCartan & Slinn, 1953), brackish water pools (Naylor & Slinn, 1958), and estuaries (Naylor, Slinn & Spooner, 1961; Harvey, Jones & Naylor, 1973). The species is widely distributed and ranges from the Black and Mediterranean Seas south to the Azores, and north to the west coast of Scotland (Naylor, 1972). Three forms of *J. nordmanni* have been described (Lemercier, 1958, 1960) of which only *Jaera nordmanni nordica* Lemercier has been recorded in Britain (Naylor, 1972; Jones & Fordy, 1973). The two other forms, *Jaera nordmanni nordmanni* Lemercier and *Jaera nordmanni massiliensis* Lemercier, have a more southerly distribution (Naylor, 1972), and can be separated from *J. nordmanni nordica* by differences in male sex characters (Lemercier, 1958, 1960; Jones & Fordy, 1973). Apart from some eco-physiological work (Naylor *et al.* 1961; Harvey *et al.* 1973) and a recent study with a scanning electron microscope (Jones & Fordy, 1973), little is known of the biology of *J. nordmanni*. The present paper reports on the breeding biology and seasonal population fluctuations of *Jaera nordmanni nordica*, and compares the results with a similar study on the members of the *Jaera albifrons* Leach group of species (Jones & Naylor, 1971) which are closely related to and often in competition with *J. nordmanni*.

MATERIALS AND METHODS

Monthly samples of *Jaera* were collected from Castletown Estuary, Isle of Man, from June 1972 to January 1974 following the sampling methods outlined for *J. albifrons* by Jones & Naylor (1971). The isopods were taken from the underside of stones in a region of strong water flow, and stored

in 5% sea-water formalin. In the laboratory, specimens were flattened on a microscope slide and body length (measured from the anterior edge 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 into the following classes: (1) Juveniles – all specimens less than 1.50 mm (Renault, 1958). (2) Males – male praepereculum fully developed and secondary sex characters present on the pereopods (Lemercier, 1958, 1960; Naylor, 1972; Jones & Fordy, 1973) as described for *J. albifrons* (Jones & Fordy, 1971). (3) Immature females – females lacking oostegites. (4) Gravid females – females with fully developed oostegites forming brood pouches which are either empty or contain developing young. The contents of each marsupium were removed, counted, measured and staged according to their morphological development (following the stages described for *J. albifrons* by Forsman, 1944; Jones & Naylor, 1971; Steele & Steele, 1972).

Salinity and temperature fluctuations during tidal cycles were measured at the collection site using a National Institute of Oceanography salinity-temperature bridge (Jones, 1972a).

RESULTS

Study area

A description of Castletown Estuary has been given by Bruce, Colman & Jones (1963) and collections of *Jaera* were taken at the limit of the influence of neap tides below a small weir. Salinity and temperature records from the bottom of the stream at that site

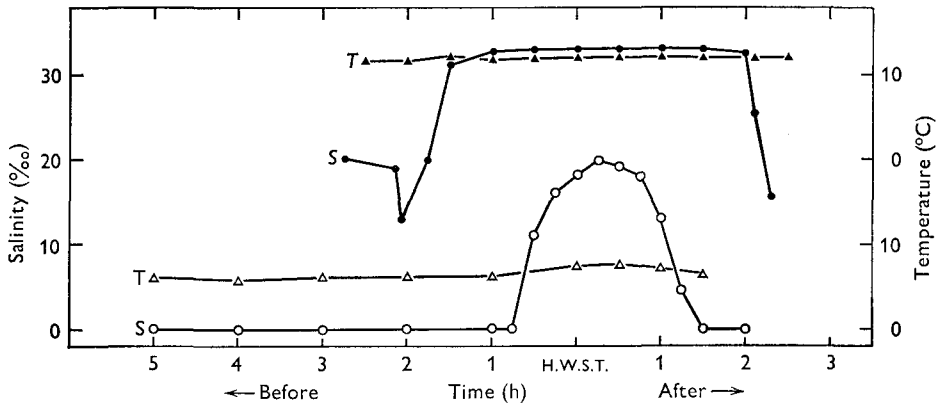


Fig. 1. Salinity (*S*) and temperature (*T*) fluctuations at the collection site. (Open symbols, spring tide/wet period; closed symbols, spring tide/dry period.)

are shown in Fig. 1. The recordings were taken for spring tides during a dry period (26 October 1972) and after heavy rainfall (12 December 1972), and show that although temperature did not fluctuate over the tidal cycle, there were extreme differences in the salinity values. After heavy rainfall, salinity was very low for most of the tidal cycle but rose quickly to 20‰ soon after the expected time of high water. During the dry period, salinity did not fall below 10‰ and was above 30‰ several hours before and after the expected time of high water (Fig. 1). These results illustrate that *J. nordmanni* has to tolerate a range of salinities from fresh water to almost full strength sea water, and also the times of immersion in each of the extremes of this range fluctuate depending on the quantity of freshwater flow into the estuary.

Breeding cycle

The reproductive period has been expressed in terms of the numbers of gravid females (gravidity) and juveniles collected each month. Both sets of data are presented in Fig. 2 and have been treated with a moving averages procedure to reduce sampling variance. The repeated annual pattern of the results suggests that the smoothing procedure is an acceptable method of analysis (Jones & Naylor, 1971).

Gravid females. In this method of expressing breeding the numbers of gravid females are plotted as a percentage of the total adult female population (females with a body length greater than 1.50 mm) (Harvey, 1969; Smaldon, 1972). The results indicate a

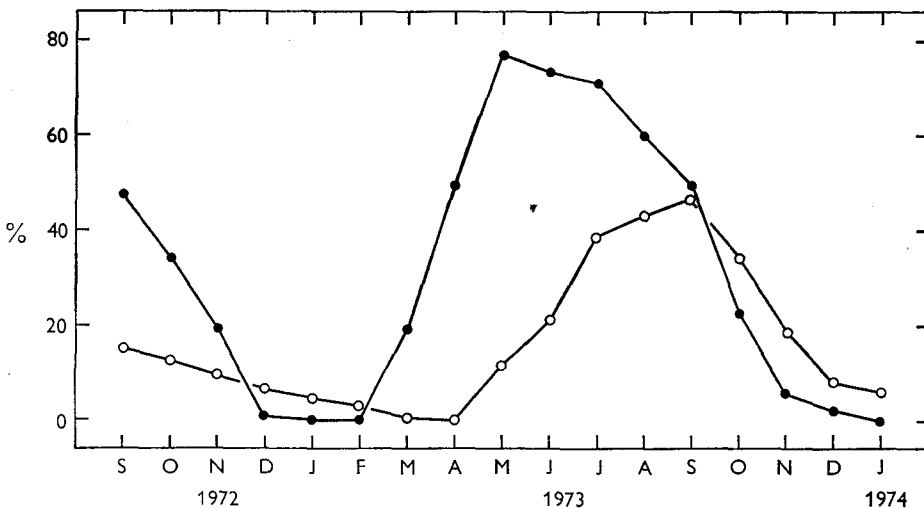


Fig. 2. Percentage numbers of gravid females (closed circles) and juveniles (open circles) collected each month. (Results smoothed by a moving averages procedure applied to successive batches of three monthly values.)

period of intensive reproductive activity from April to September when over 45% of the females collected were gravid. Gravidity increased to over 70% in May, June and July with a peak of 76% in May. Gravidity declined after this period and limited numbers of gravid females occurred in November and December. Females with brood pouches were absent from the January and February collections but reappeared, in small numbers, during March (Fig. 2).

Release of young. Juveniles are expressed as a percentage of the total number of specimens collected each month. Young individuals were present in all the samples except April, although they only occurred in large numbers from June to October. During this period, a peak of liberation was reached in August and September when over 40% of the population were juveniles. Numbers of young then steadily declined forming less than 10% of the population from November to April, but started to increase again in May following the earlier high numbers of gravid females.

Brood biology

Seasonal variation in brood composition. The monthly fluctuations in the ratios of gravid females with each stage of marsupial development are shown in Table 1 together with females with empty brood pouches. All the stages within a single marsupium were at the

TABLE 1. SEASONAL VARIATION IN BROOD COMPOSITION

Date of collection	Total nos. of gravid ♀♀	Marsupium contents				Empty
		S1	S2	S3	S4	
6. vi. 1972	12	4	—	6	2	—
6. vii. 1972	23	6	4	7	6	—
7. viii. 1972	23	10	10	2	1	—
6. ix. 1972	41	10	8	22	1	—
4. x. 1972	41	8	12	16	5	—
2. xi. 1972	2	—	1	—	—	1
4. xii. 1972	—	—	—	—	—	—
3. i. 1973	—	—	—	—	—	—
6. ii. 1973	—	—	—	—	—	—
1. iii. 1973	1	1	—	—	—	—
6. iv. 1973	68	59	8	1	—	—
7. v. 1973	153	1	7	101	22	22
5. vi. 1973	137	20	27	54	10	26
4. vii. 1973	65	15	25	19	3	3
5. viii. 1973	87	3	10	44	24	6
11. ix. 1973	45	4	9	11	14	7
10. x. 1973	6	1	2	2	—	1
16. xi. 1973	—	—	—	—	—	—
8. xii. 1973	2	1*	—	1	—	—
7. i. 1974	—	—	—	—	—	—

* Malformed brood contents probably not capable of further development.

same stage of morphological development as is the general rule for isopods (Green, 1965; Jones, 1970; Jones & Naylor, 1971), though exceptions have been recorded (Howes, 1939; Kjennerud, 1950; Eltringham & Hockley, 1961; Holdich, 1968; Venkatakrishnan & Balakrishnan, 1973). Gravid females were rarely collected from November to March, but there was a high level of reproductive activity in April when the majority of gravid females collected had eggs (stage 1 young) in the brood chambers. There was also some indication, during this month, of earlier breeding by the presence of a few females with stage 2 embryos, and one with stage 3 young in the marsupium. By May, the majority of females had broods of stage 3 young, although females with stage 4 young and empty brood pouches were also common. A second peak for females with eggs occurred in June, followed by a peak of females with stage 2 embryos in July, and stage 3 young in August. Again, females with other stages of brood development were collected during this month suggesting females are being continuously recruited to the reproductive condition, and each gravid female is capable of several different broods within a single breeding season. Females with stage 4 young and empty brood pouches were never found in high numbers which may reflect the short duration of these stages.

Brood numbers, mean sizes and brood mortality. The information on average brood numbers, mean sizes for each development stage, and the percentage brood mortality for the whole of the sampling period is given in Table 2. There is a linear relationship

between the length of the incubating female and the number of eggs in the brood chamber ($y = 11.28x - 17.6$), as reported for other peracarid crustaceans (Jones, 1970; Jones & Naylor, 1971; Mauchline, 1973). Therefore, to remove the biasing effect of length of gravid females from the discussion of brood numbers they have been grouped into the size classes shown in Table 2. There is a reduction in brood numbers, for each female size

TABLE 2. MEAN BROOD NUMBERS, SIZE OF EACH STAGE OF DEVELOPMENT AND PERCENTAGE BROOD MORTALITY IN RELATION TO LENGTH OF INCUBATING FEMALE

Size range of gravid ♀♀ (mm)	Brood stage	Nos. of broods examined	Length of stage (mm)		Nos. of stages/brood		% Brood mortality
			Mean	S.D.	Mean	S.D.	
1.51-2.0	1	9	0.27	0.03	6	1.0	26.7 (10)
	2	10	0.30	0.02	5.1	1.1	
	3	12	0.57	0.06	5.4	1.4	
	4	5	0.67	0.02	4.4	4.4	
2.01-2.5	1	45	0.25	0.01	9.5	3.0	15.8 (12.6)
	2	43	0.29	0.03	7.4	2.1	
	3	68	0.59	0.06	8.3	2.0	
	4	10	0.70	0.06	8.0	2.1	
2.51-3.0	1	53	0.25	0.02	15	4.3	26.0 (16)
	2	29	0.28	0.02	14.8	4.0	
	3	117	0.59	0.06	12.6	3.0	
	4	25	0.76	0.05	11.1	3.3	
3.01-3.5	1	13	0.25	0.01	21.9	5.7	37.4 (0.4)
	2	18	0.29	0.01	18.6	3.4	
	3	31	0.59	0.08	21.8	5.9	
	4	9	0.78	0.15	13.7	6.8	
3.51-4.0	1	1	0.22	—	28	—	— (1.4)
	2	1	0.32	—	24	—	
	3	3	0.6	0.03	27.6	2.5	
	4	—	—	—	—	—	

class, as marsupial development proceeds from stage 1 to stage 4. The mean percentage brood mortality is 26.5% with a range of 15.8-37.4%. This is lower than the brood mortality reported for the isopods *Dynamene bidentata* (Adams) (36%, Holdich, 1968) and *Jaera albifrons* Leach *sensu lato* (50%, Jones & Naylor, 1971), but higher than the 10% reported for many species of mysids (Mauchline, 1973). As stage 4 young are capable of locomotion within the brood chamber some premature release may be influencing these figures. The results of Holdich (1968) confirm that the decrease in number of young in the brood chamber is highly significant between the non-motile and motile stages ($P < 0.001$). If brood mortality for *J. nordmanni nordica* is assessed on the non-motile stages an average figure of 8% is achieved with a range of 0.4-16% (Table 2, figures given in parentheses).

The results of the measurements of the various stages of development show that the embryos increase in size until hatching, with a dramatic size increase between stages 2 and 3 when the embryo straightens. The size of the embryo is not related to the length of the incubating females and the sizes reported here, for each development stage, are similar to those recorded for *Jaera albifrons* (Jones & Naylor, 1971).

Seasonal population changes

The length-frequency histograms for *Jaera nordmanni nordica* for the collecting period are shown in Fig. 3, and the seasonal variation in the sex ratio in Fig. 4. In January and February there was a complete absence of breeding females in the population, the sex ratio of males to one female declined to less than 1:1, and limited numbers of juveniles were collected. The number of females increased during March (sex ratio, 1:0.68), and

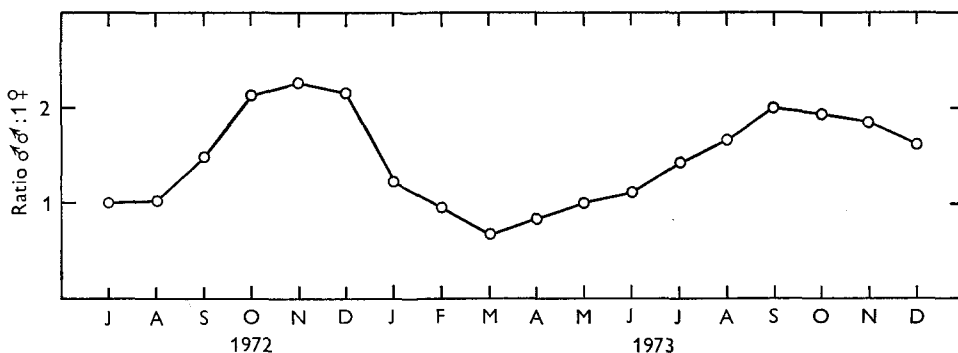


Fig. 4. Seasonal variation in the sex ratio. (Results smoothed as in Fig. 2.)

the first indication of breeding occurred although juveniles were rare. During April and May the numbers of females in a reproductive condition increased rapidly, the sex ratio became stable, and only one juvenile was collected. The high number of gravid females continued in the population from June to September. During this time the number of juvenile specimens increased rapidly forming over 40% of the population in August and September, and the sex ratio of males to one female increased to 1:2. From September to December the number of gravid females and juveniles declined, the large specimens died, and the sex ratio remained at its high level with males outnumbering females by 2:1.

Seasonal size variations

The mean lengths of males, females and gravid females in each monthly sample are shown in Fig. 5, treated with a moving averages procedure (Jones & Naylor, 1971). The results confirm that male *Jaera nordmanni* are consistently larger than females (Naylor *et al.* 1961), and although the mean lengths of gravid females in October and November of the first year of study were larger than the corresponding lengths for males, the pattern was not repeated in the following year. Both males and females have a similar growth pattern with large specimens occurring during April–June, and smaller ones in October–December. It is difficult to follow the growth pattern for gravid females as they were absent from the population during certain months of the year, and it is likely that a continuous recruitment of females into the gravid condition occurs in the breeding period. However, the graph shows that the females which formed the May peak of reproduction were in the size range 2.5–3.0 mm, and those breeding at the end of the

breeding period were between 1.5 and 2.0 mm. This suggests that the summer peak was made up of mature females probably breeding for a second time, whereas the late breeding females were young forms breeding for the first time.

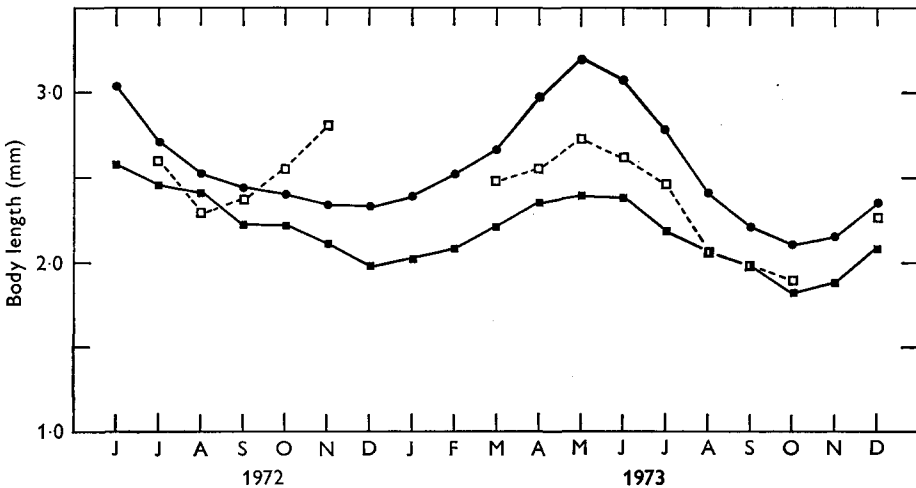


Fig. 5. Seasonal variations in the mean sizes of *J. nordmanni nordica*. (Males, closed circles; females, closed squares; gravid females, open squares. Results smoothed as in Fig. 2.)

DISCUSSION

The results of this investigation show *Jaera nordmanni nordica* to be a very common species in Castletown Estuary throughout the year, although it has limited breeding in the winter months of the year. Naylor *et al.* (1961) collected *J. nordmanni* from brackish water pools at Scarlett Point, Isle of Man, and found ovigerous females whenever samples were taken (January, February, April, June and November) with a peak of breeding in the spring and summer. The lack of gravid females in Castletown Estuary therefore seems likely to be directly related to the specific conditions occurring there in the winter when compared with the pools. The main difference seems to be the increase in freshwater flow into the estuary, and the related consequences of this, as the salinity and temperature ranges in the pools (Naylor & Slinn, 1958) are similar to the ones recorded in the present study (Fig. 1). A comparative study of the breeding of the same species in estuarine and non-estuarine conditions would seem very worthwhile in the light of these results.

Two methods of expressing reproduction have been used in this study (Fig. 2) and it appears that the presence of gravid females in the samples is a more reliable indication of breeding than the presence of juveniles for two main reasons. First, gravid females are large (Figs. 3 and 5) and consequently not overlooked during collecting, whereas juveniles are less than 1.50 mm and difficult to collect. Secondly, *J. nordmanni*, which in the Irish Sea is nearing the northern limit of its range (Naylor, 1972), is a low latitude species and low temperature delays maturation of juveniles of such species leading to the presence of immature specimens throughout the year (Harvey, 1968, 1969; Jones, 1970).

Jaera nordmanni does not have the chromosomal complications observed in *J. albifrons* (Staiger & Bocquet, 1956; Naylor *et al.* 1961) indicating that sex determination is normal. However, the sex ratio does fluctuate seasonally (Fig. 4) and the average sex ratio, for the whole of the sampling period, was 1:1.26 (2001♀♀: 2520♂♂).

Ecological studies show that *Jaera nordmanni* penetrates farther into estuaries and freshwater streams than the members of the *J. albifrons* group (McCartan & Slinn, 1953; Naylor *et al.* 1961; Naylor & Haahtela, 1966; Jones & Naylor, 1971; Harvey *et al.* 1973), and this has been attributed to the greater ability of the former species to survive in dilute saline when compared with the latter (Naylor *et al.* 1961). Both species are euryhaline (Naylor & Slinn, 1958; Naylor *et al.* 1961; Jones, 1972*a, b*; Harvey *et al.* 1973; Forbes, 1974), and one member of the *J. albifrons* group, *J. ischiosetosa* Forsman (which has not been recorded on the Isle of Man), can tolerate distilled water for as long as *J. nordmanni nordica* (Jones, 1972*a*; Harvey *et al.* 1973). However, the work cited has tested survival under stable conditions of salinity and it would be worthwhile to examine the tolerance of adult and juvenile forms, of each species, under a fluctuating salinity régime for differences which might explain their ecological separation.

Feeding is not a factor involved in the isolation of *Jaera nordmanni nordica* and *J. ischiosetosa* as their mouthparts are identical (Jones, 1972*c*; Jones & Fordy, 1973). Also, the high rate of egg production and low brood mortality of *J. nordmanni nordica* is compensated by the continuous high level of reproduction shown by *J. ischiosetosa* (Jones & Naylor, 1971), suggesting that differences in reproductive potential are not involved in competition. However, both the present study and that of *J. albifrons* (Jones & Naylor, 1971) recorded breeding at the optimum part of the ecological range for each species. It would be interesting to compare the reproductive potential of each species at the extremes of their ecological distributions and in areas of mixing, as an assessment of competition.

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