ON THE FECUNDITY OF SOME GAMMARIDS

By C. Cheng, B.Sc.

From the Department of Zoology of the University College of North Wales, Bangor

(Text-figs. 1, 2)

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INTRODUCTION

There is available comparatively little information regarding the fecundity of gammarids. Sexton (1913, 1928) makes some remarks upon the reproductive capacity of *Gammarus chevreuxi*, *G. pulex* and *G. locusta*. Recently she and Spooner (1940) have made an exhaustive taxonomic study of the marine littoral forms, and include brief records of the size of the broods in each species. The present investigation was undertaken with the object of making a statistical study of the fecundity of several species with special reference to the relation between the body weight and fecundity.

The great profusion of marine fauna, particularly of littoral species, on the north coast of Wales is well known (Jackson, 1940). The number of species of *Gammarus* and *Marinogammarus* previously recorded as occurring here is seven, namely, *G. pulex*, *G. locusta*, *G. zaddachi*, *G. duebeni*, *G. chevreuxi*, *M. marinus* and *M. obtusatus*.

In this investigation, the specimens were collected mainly from the upper part of the intertidal zone at the following two places along the Bangor coast of the Menai Straits: (1) the shore on either side of the pier at Bangor, (2) the stream (Gorad-y-Gyt) flowing towards the Straits. Altogether a total of fourteen samples was obtained, nine from the former and five from the latter. The dates of collection are as follows:

Shore collection	Stream collection
Sample I: 27 Nov. 1940	Sample X: 16 Nov. 1940
,, II: 11 Dec. 1940 ,, III: 28 Jan. 1941	" XI: 20 Nov. 1940 " XII: 22 Nov. 1940
" III: 28 Jan. 1941 " IV: 10 Feb. 1941	" XIII: 9 Dec. 1940
" V: 6 Mar. 1941	" XIV: 7 Mar. 1941
,, VI: 19 Mar. 1941	
" VII: 19 May 1941 "VIII: 20 May 1941	
" IX: 29 May 1941	

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An examination of the material reveals the occurrence of six species¹ as shown in Table I.

TABLE I	
Habitat	Abundance
	very abundant abundant
33 33	rare
", brackish water	abundant very abundant
33	very rare
	Habitat marine " " brackish water

It will be seen that M. marinus and G. duebeni dominate the shore and the stream respectively. Not infrequently the former was also encountered in the stream collection. The conclusion that these two species can be found in association has been noted by Beadle & Cragg (1940). It is noteworthy that the distribution of M. obtusatus appears to be very restricted in this region, occurring only in a particular area where there is sewage discharge. M. stoerensis is usually found in company with M. obtusatus, but on one occasion a female was obtained from the stream area. It shows that M. stoerensis, though a marine species, prefers to inhabit a place with freshwater influx as already noticed by Sexton & Spooner (1940). All these species are found to be widely distributed in this country, especially M. marinus and G. duebeni (see Crawford, 1937; Sexton & Spooner, 1940, etc.).

I wish to express my thanks to Prof. Brambell for advice and criticism. My thanks are also due to Mr Cragg for having placed at my disposal a list of species recorded by him and for his kind help in various ways.

BODY WEIGHT AND FECUNDITY DATA

Owing to the extremely small numbers of females which were obtained, M. *finmarchicus* and G. *chevreuxi* are excluded from this investigation. The mean values of the body weight² and the fecundity of other species, together with the standard deviations, are shown in Table II.

It will be seen that the mean and the standard deviation of the body weight vary with the species, being highest in *M. marinus* and lowest in *M. stoerensis*. The former is nearly nine times as heavy as the latter.

As regards mean fecundity, the species fall into the following order: M. stoerensis > M. marinus > G. duebeni > M. obtusatus, the difference between the first and the last being fifteen eggs per brood.

By comparing these two sets of data, it may be seen that the size of a species bears no relation whatever to the reproductive capacity, as shown plainly in *M. stoerensis*. Although it is the smallest species, its mean fecundity is

¹ Their identification has been confirmed by Mrs Sexton to whom my thanks are due.

² Before weighing, the eggs were taken out of the brood pouch and counted. The animals were then drained thoroughly by means of blotting paper for a certain time depending on the size of the animal.

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greater than that of the others. Sexton (1928) obtained the same result from her investigation into the reproduction of various species of *Gammarus*, stating: 'The number of young in a brood varies with the species, but the size of the species is no gauge of either the size or the number of young. *G. chevreuxi* is



Fig. 1. Percentage frequency distribution of fecundity of various species.

a small species compared with G. *pulex*, yet it produces up to 63 young in a brood, whilst the highest record for G. *pulex* is only 28.'

A comparatively small difference exists in the maximum fecundity of the four species examined; the maximum is highest in *M. marinus* with forty eggs per brood and lowest in *M. obtusatus* with only twenty-three eggs per brood.

TABLE II

	Number	-	Body weight (m	g.)	Fecundity (no. of eggs per brood)				
Species	of	Range	Mean	Standard deviation	Range	Mean	Standard deviation		
M. marinus	128	19-63	37·71±0·91*	10.3 ±0.64*	11-40	21.68±0.53	6.02 ± 0.38		
M. obtusatus	42	10-30	18.17 ± 0.64	4·18±0·46	6-23	12.02 ± 0.63	4.09 ± 0.45		
M. stoerensis	21	3-6	4.52 ± 0.16	0.75±0.11	12-37	27·I ± I·32	6.04 ± 0.93		
G. duebeni	254	7-27	15·29±0·21	3·34±0·15	5-36	18.13 ± 0.42	6.63 ± 0.29		

* Standard errors.

TABLE III

Species		G. duebeni		M. obt	usatus	M. marinus			
Sample no.	X-XII	XIII	XIV	I–II	VII-VIII	III-IV	V-VI	VII-IX	
Date	16–22 Nov.	9 Dec.	7 Mar.	27 Nov. and 11 Dec.	19–20 May	28 Jan. and 10 Feb.	6–19 Mar.	19–29 May	
No. of animals	30	102	122	22	20	15	73	40	
Mean fecundity	13.7±1.01	15±0.45	21.8 ± 0.57	10 ± 0.64	14·2±0·9	19.9 ± 1.2	22·3±0·71	20·9±0·97	
Standard devia- tion	5·53±0·71	4·58±0·32	6·36±0·41	2·99±0·45	2·99±0·45	4·64±0·85	6·03±0·5	6·12±0·68	

The largest broods recorded by Sexton & Spooner (1940) for *M. marinus* and *M. obtusatus* number fifty and twelve respectively.

The percentage frequency distribution of fecundity in the various species is represented by histograms in Fig. 1. It will be seen that the modal class is by no means the same in the four species, being 9–10 in M. obtusatus, 18 in G. duebeni, 21 in M. marinus and 32 in M. stoerensis. This diagram provides a clear picture of the reproductive potentiality of each species.

As already mentioned in the introduction, the collecting period extended from 27 November to 29 May for the 'shore' samples and from 16 November to 7 March for the 'stream' samples. In order to show whether there exists any seasonal variation in the fecundity of various species, another figure (Fig. 2) has been drawn in which each month is represented by a separate histogram. It is evident that the fecundity does vary with season, being generally higher in the spring than in the winter months, as is also shown clearly in Table III. The phenomenon is best displayed in *G. duebeni* in which the modal class for each month is apparently different, being 9 for November, 18 for December, and 23 for March.

That the mean fecundity is on the whole higher in the spring than in the winter is not unexpected, because in the former period external conditions, such as temperature and food, are obviously more congenial. It is found in *Daphnia* that the size of a brood produced by a female in the laboratory can be increased by both higher temperature (up to a certain limit) (Berg, 1931) and rich food (Ingle, 1933). The increase in fecundity in the spring has no connexion with the age of the animal, because an analysis of the material reveals that a female of the same weight generally produces less eggs per brood in the winter. It is unfortunate that the collecting period does not extend beyond May, so that no comparison can be made between the mean fecundity of various months of the year. Such an investigation has been carried out in other animals. Berg (1931), studying the productivity of *Daphnia* in nature throughout the whole year, finds that the maximum fecundity occurs in May.

Practically nothing is known regarding the breeding of these species in nature except in G. *chevreuxi*, which has been found to breed all the year round (Mrs Sexton, private communication). In the present investigation pregnant females of M. *marinus*, M. *obtusatus* and G. *duebeni* were present in all the samples collected, showing that these species are capable of breeding in the winter as well as in the spring.

RELATION BETWEEN BODY WEIGHT AND FECUNDITY

The species used in this investigation are M. marinus, M. obtusatus and G. duebeni, because the number of females obtained is relatively larger in these species. Their body weight and fecundity data are shown in Table IV. It will be seen that although there appears to be a great variation in the fecundity of certain body-weight classes, particularly so in G. duebeni, the general tendency



Fig. 2. Monthly percentage frequency distribution of fecundity of various species.

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TABLE IV

60		Λ	1. ob	tusat	tus				1	И. <i>т</i>	arinu	\$					G.	dueb	eni	
eggs	36-40										I		I	2	<u>``</u>	1.		2		.`
fe	31-35										I	3	3	I	I		2	10		
°.(p	26-30					I		I		3	3	Ĩ	I	2	I		5	14	4	
0 0	21-25				I	I	I	4	7	IO	IO	8	I	2		2	22	16	6	I
(no. of brood)	16-20		I	4	I	2	4	13	7	5	5	2				3	41	23	3	I
r th	11-15	3	IO	4			2	9	6	2	I					2	42	20	3	
pe	6-10	9	9													4	18	8		
n	I-5																2			
Fecundity per h		-15	-20	-25	-30	-20	-25	-30	-35	-40	-45	-50	-55	-60	-65	-IO	-15	-20	-25	-30
		ġ	-9I	21.	26	16	21.	26	31.	36	41·	46	51.	56	61.	0	II	16	21	26
							F	Body	weig	ht (n	1g.)									

is towards an increase in fecundity with an increase in body weight. Sexton (1928) obtained the same result from her experimental investigation into the reproduction of G. *chevreuxi*, stating 'the number of young in a brood increases as the female grows'. A comparison of these three tables reveals that the trend is most marked in M. *obtusatus* and least in G. *duebeni*. In the latter the positive correlation between the body weight and the fecundity does not appear to hold for the heavier groups exceeding 20 mg. in body weight. These larger females are found to be present in all the samples collected. No such tendency to reduction in fecundity of older individuals is discernible in the other two species, probably due to lack of sufficient material, especially in M. *obtusatus*.

The relation between fecundity and body weight in the three species is measured statistically by estimating the value of the correlation coefficient. The result is shown in Table V.

TABLE V

	No. of	Correlation	Test of sign	ificance of r
Species	animals	(r)	t	Þ
M. marinus	128	+0.668	7.524	<0.01
M. obtusatus	42	+0.713	4.566	<0.01
G. duebeni	254	+0.383	5.494	<0.01

It is noteworthy that the correlation coefficient of M. obtusatus is nearly twice as high as that of G. duebeni. It is expected because, in the latter, the positive correlation between the body weight and the fecundity appears to break down after the 19 mg. body-weight class. The observed correlations are definitely significant because p is less than 0.01.

The relation between body weight and fecundity has been studied in other animals by several investigators (Wynne-Edwards, 1929; Gregory, 1932; Stone, 1938). Their result shows that fecundity bears an almost linear relationship to the body weight of the animal studied. The same holds true of the relation between body length and fecundity (Allen, 1895; Stone, 1938; Hickling,

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1940). All these investigators agree that the productivity increases as the animal grows. The present investigation reveals, however, that the linear relation between the body weight and the fecundity does not hold for the higher body-weight groups and that fecundity reaches a maximum at a certain body weight or age, as seen in the case of *G. duebeni*. This finding is substantiated by the outcome of the breeding experiments. In *G. chevreuxi*, it is found that after reaching its maximum, the size of broods produced by a female becomes greatly reduced towards the end of the reproductive period (Sexton, 1928). In *Daphnia*, the reproductive capacity drops to a low level after attaining its peak at about the 12th-14th instar (Ingle, Wood & Banta, 1937; Banta, 1939). It thus leads to the conclusion that the correlation between body weight and fecundity is positive at first and then becomes negative after the latter has reached its maximum at a certain age.

SUMMARY

1. The number of species found in this investigation is six, of which four are marine and two brackish water.

2. The mean value of the body weight and the fecundity varies with the species. The size of a species bears no relation whatever to the reproductive capacity.

3. The fecundity is subject to seasonal variation, being generally higher in the spring than in the winter months.

4. In general, a positive correlation exists between body weight and fecundity of the individuals of each species. This rule does not, however, apply to *Gammarus duebeni*, in which the fecundity appears to fall after reaching its maximum at the 19 mg. body-weight class.

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