

NOTES ON THE LIFE HISTORY OF *Bovallia gigantea* (Pfeffer) (CRUSTACEA, AMPHIPODA)

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THE establishment of laboratory facilities at Signy Island, South Orkney Islands, has led to a considerable increase in biological activity at this British Antarctic Survey scientific station (Holdgate, 1965). In 1961 a general ecological survey of the littoral and shallow-water fauna was started. Diving techniques, as well as conventional methods, have been used to obtain representative samples of the fauna. Crustacea of the Order Amphipoda have been well represented in these collections. During identification of the amphipod material it became apparent that some useful information might be obtained from a closer examination of the specimens of *Bovallia gigantea* (Pfeffer).

B. gigantea is a large and distinctive amphipod, reddish in colour, which attains a maximum length of about 50 mm. The species has been taken at many localities in Graham Land, the South Shetland Islands, the South Orkney Islands, the South Sandwich Islands and in South Georgia. It is a shallow-water species occurring on suitable substrates from low water to a depth of about 40 m. Typically, it is found associated with large algae (e.g. *Desmarestia anceps* and *Phyllogigas grandifolius*) on rock, boulder, or sand and rock bottoms.

The only reference in the literature to an ovigerous female appears to be to a specimen collected by the Swedish South Polar Expedition at Maiviken, South Georgia, on 15 May 1902 (Schellenberg, 1931).

The specimens in the present collection were obtained in all months of the year except November. (Only two collecting stations were worked in this month and both of them were on bottoms with very little algae.) It is therefore probable that the population of *Bovallia* is static and shows no local movements as do some amphipods such as the Antarctic lysianassids reported on by Hodgson (Walker, 1907).

588 specimens from 37 of the 81 stations worked have been examined. Of these, 24 were damaged and have therefore been ignored. The following observations are based on 211 males, 29 ovigerous females, 258 non-ovigerous females and 66 juveniles. Fuller details of collection and distribution will appear in a later report on the Amphipoda by the author.

The presence of 29 ovigerous females is of particular interest. These specimens were collected in February, March, April, June, July and September. Eggs from each of these females have been examined. It has been possible to assign each female to one of five arbitrary, but reasonably distinct, classes depending on the developmental condition of the eggs. These classes are:

- i. Ovum with close-packed yolk cells but no trace (in the preserved material) of any embryo.
- ii. Early embryo present in which yolk cells are partly or completely surrounded by the embryonic membranes, but in which the embryo shows little or no macroscopic structure.
- iii. Embryo in which somites and limb buds can be made out.
- iv. Late embryo in which development is almost complete and in which pigment has been laid down in the eyes.
- v. Hatching, at which stage some at least of the embryos have hatched and are free in the brood pouch. Developmental stages of eggs of ovigerous females are shown in Table I.

Despite the small sample size, it is clear that eggs are laid in late February or March, that early development is slow and that hatching occurs in late September or October. This is nearly 7 months after laying, a considerably longer period than that reported for other amphipods. However, several workers (e.g. Clemens, 1950; Hynes, 1954, 1955; Kinne, 1960) have shown that the rate of development of amphipods is more rapid at higher temperatures. Incubation in *Rivulogammarus duebeni* (Lilljeborg) takes 14 days at 18°C but 55 days at 5°C (Hynes, 1954), while the incubatory period of *Crangonyx pseudogracilis* Bousfield is 14–17 days at 15°C and 48 days at 3–5°C (Hynes (1955) as *C. gracilis*). The glacial relict *Pontoporeia*

TABLE I. DISTRIBUTION IN TIME OF THE STAGES OF DEVELOPMENT REACHED BY THE EGGS OF 29 OVIGEROUS FEMALES

| Date | Station number | Developmental stage | | | | | Total |
|--------------|----------------|---------------------|----|-----|----|---|-------|
| | | i | ii | iii | iv | v | |
| 1964 | | | | | | | |
| 15 April | 67, 68, 69 | 5 | — | — | — | — | 5 |
| 19 April | 76 | 2 | — | — | — | — | 2 |
| 29 June | 70 | — | 1 | 1 | — | — | 2 |
| 1 July | 81 | 1 | 2 | 1 | — | — | 4 |
| 14 September | 74 | — | — | — | 1 | — | 1 |
| 20 September | 75 | — | — | 1 | 1 | 1 | 3 |
| 1965 | | | | | | | |
| 26 February | 28 | 1 | — | — | — | — | 1 |
| 1 March | 20 | 2 | — | — | — | — | 2 |
| 4 March | 16, 17 | 9 | — | — | — | — | 9 |
| | | | | | | | — |
| | | | | | | | 29 |

affinis (Lindström), which breeds in December and January in Norway, has an incubation period of 3 months (Mathisen, 1953). Lower temperatures and the larger size of *B. gigantea* probably account for the prolonged incubation period.

It has been shown for a number of amphipod species that fecundity is proportional to the volume of the incubating female. Data have been given by Sexton (1928) for *Gammarus chevreuxi* (Sexton), by Hynes (1955) for *Rivulogammarus pulex* (L.) and *C. pseudogracilis*, by Cheng (1942) for *R. duebeni*, *Marinogammarus marinus* (Leach) and *Marinogammarus obtusatus* (Dahl) and by Mathisen (1953) for *P. affinis*. Jensen (1958) has concluded that "The quantity of eggs produced by a female as regards the *absolute number* is determined by the external factors, whereas the *relative number* depends on the volume of the female in such a way that the number of eggs becomes a linear function of the volume of the female."

Six specimens were selected to cover the size range of ovigerous females (animals suspected of having lost eggs were rejected). The eggs carried by each female were counted and found to be proportional to (length)³ of the respective female (Table II). *B. gigantea* therefore conforms with the pattern demonstrated by Jensen for some malacostracan species.

TABLE II. RELATION BETWEEN NUMBER OF EGGS AND LENGTH OF INCUBATING FEMALE

| Station number | Number of eggs | Length of female (mm.) |
|----------------|----------------|------------------------|
| 75 | 139 | 49 |
| 17 | 126 | 46 |
| 17 | 116 | 46 |
| 17 | 96 | 45 |
| 17 | 91 | 44 |
| 16 | 80 | 41 |

Linear dimension of eggs at stages (i) and (iv) have been measured to the nearest 0.01 mm. and their volumes calculated. Stage (i) eggs are symmetrical about the long axis, while stage (iv) eggs are symmetrical about a longitudinal vertical plane. The formula used to calculate the volume is $\frac{1}{6}\pi lw^2$ for stage (i) eggs and $\frac{1}{6}\pi ldw$ for stage (iv) eggs, where l , d and w are the length, depth and width, respectively.

21 stage (i) eggs from a 46 mm. female from station 17 had an average length of 1.531 mm. (range 1.33–1.73 mm.), and an average width of 1.153 mm. (range 1.04–1.23 mm.). The average volume of these eggs is 1.0679 mm.³ (range 0.9079–1.2879 mm.³). Corresponding results for 20 stage (iv) eggs from a 49 mm. female taken at station 75 are: length 2.060 mm. (1.97–2.17 mm.), width 1.491 mm. (1.36–1.60 mm.), depth 1.846 mm. (1.75–1.97 mm.) and volume 2.9824 mm.³ (2.6573–3.2922 mm.³). There is, therefore, a three-fold increase in volume during development.

Although the breeding biology of a number of amphipods has been investigated, little information is available on egg sizes within this Order. No figures are available for the Pontogeneiidae, but Spooner (1947) has provided data for two species of the Gammaridae, a closely related family. The results obtained from *B. gigantea* have been compared with data for *Gammarus locusta* (L.) and *Gammarus zaddachi salinus* Spooner (Table III). It can be seen from this table that the eggs of the two species of *Gammarus* are relatively larger than those of *B. gigantea*.

TABLE III. COMPARISON OF SIZE OF EGGS OF *Gammarus locusta*, *Gammarus zaddachi salinus* AND *Bovallia gigantea*

| | <i>G. locusta</i> * | <i>G. zaddachi salinus</i> * | <i>B. gigantea</i> |
|--------------------------------------|---------------------|------------------------------|--------------------|
| Average length of females (mm.) | 11.0 | 10.5 | 45.3 |
| (Average length) ³ | 1331 | 1157.625 | 92959.677 |
| Number of ovigerous females measured | 25 | 19 | 29 |

$$\frac{\text{Volume (L}^3\text{) of } \varnothing \text{ } B. gigantea}{\text{Volume (L}^3\text{) of } \varnothing \text{ } G. locusta} = \frac{92959.677}{1331} = 69.84$$

$$\frac{\text{Volume of } \varnothing \text{ } B. gigantea}{\text{Volume of } \varnothing \text{ } G. zaddachi salinus} = \frac{92959.677}{1157.625} = 80.30$$

$$\frac{\text{Volume of stage i eggs of } B. gigantea}{\text{Volume of stage i eggs of } G. locusta} = \frac{1.0679}{0.0366\dagger} = 29.18$$

$$\frac{\text{Volume of stage i eggs of } B. gigantea}{\text{Volume of stage i eggs of } G. zaddachi salinus} = \frac{1.0679}{0.0703\dagger} = 15.19$$

Therefore, eggs of *G. locusta* are relatively larger than those of *B. gigantea* by a factor of $69.84/29.18 = 2.39$, and the eggs of *G. zaddachi salinus* are relatively larger than those of *B. gigantea* by a factor of $80.30/15.19 = 5.29$.

* Data from Spooner (1947, table I).

† Based on 16 *G. locusta* and 11 *G. zaddachi salinus* in the "newly laid and early developmental stages" of Spooner (1947).

The relatively small eggs of *B. gigantea* might be expected to result in a short period of development, and a less well-developed stage at hatching, but the development period is shown to be very long. It is probable that low temperature is mainly responsible for this prolongation which is accentuated by the large size of the species.

From the information in Table I it is apparent that breeding occurs only once in each year, and that hatching is confined to a relatively short period during the early spring. With such a breeding cycle it is possible that year groups of animals may be detected.

Length-frequency histograms for each month of the year are given for 211 males (Fig. 1), 287 females including 29 carrying ova (Fig. 2) and 66 juveniles (Fig. 3), and these have been used to construct a growth curve (Fig. 4). (The apparent preponderance of specimens in February, March and April is due to the larger number of samples collected during these months than at other times of the year.)

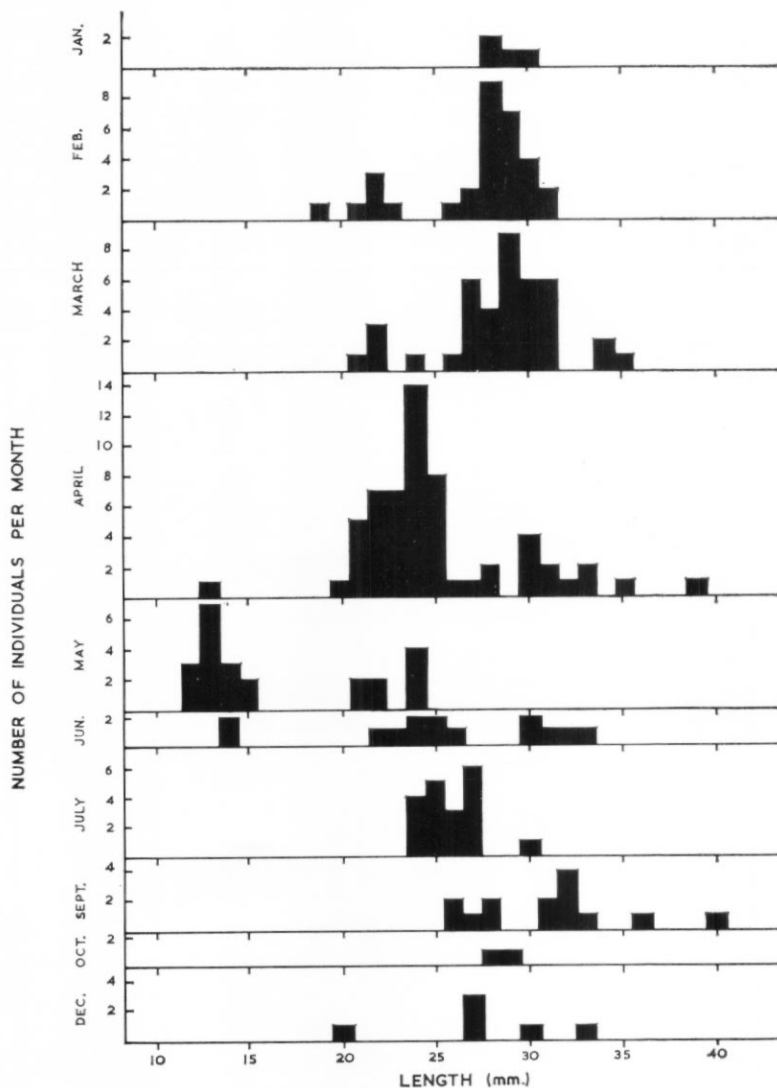


Fig. 1. Length-frequency distribution of 211 male *Bovallia gigantea* grouped by months.

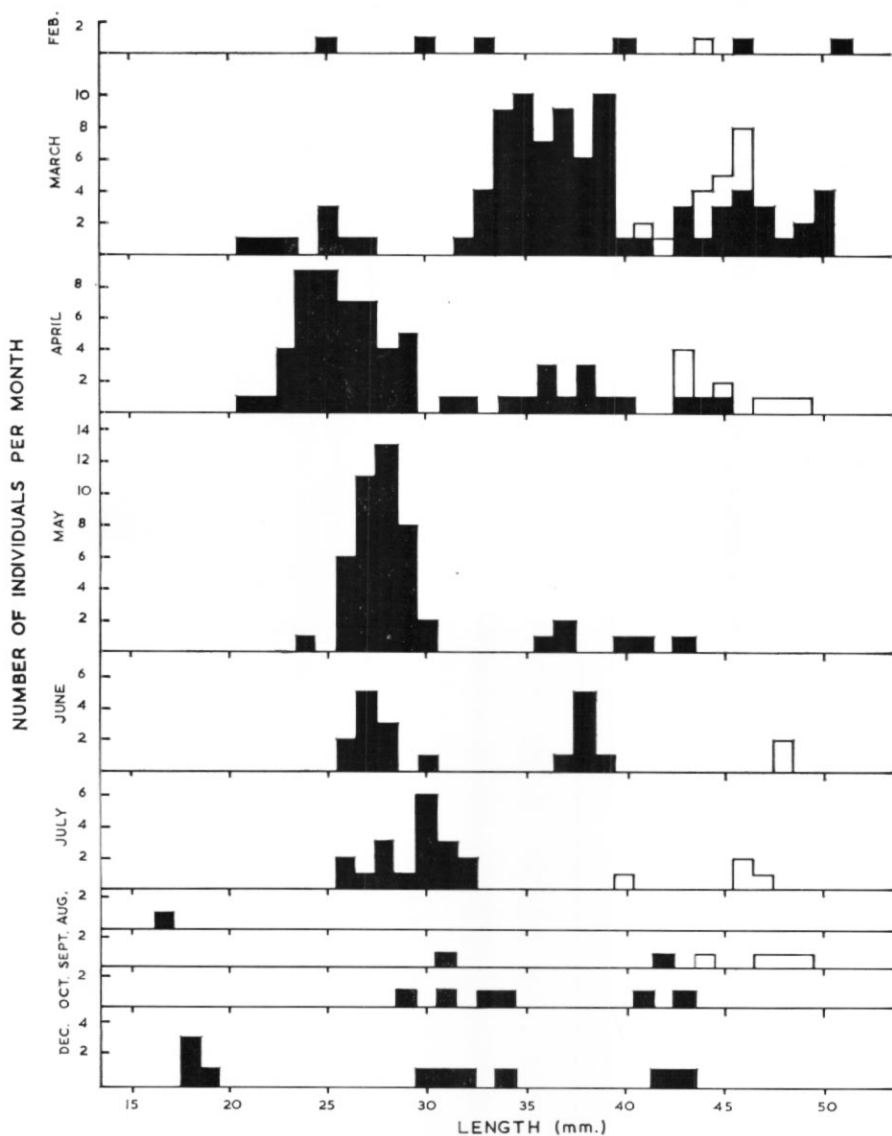


Fig. 2. Length-frequency distribution of 287 female *Bovallia gigantea* grouped by months. Unshaded areas represent ovigerous females; shaded areas represent non-ovigerous females.

The young are hatched in September or October and they reach a length of 12–14 mm. by the following May when males can be recognized by the development of rudimentary genital papillae. Females can be recognized by the presence of vestigial oostegites at a length of 17–18 mm. which is attained 1 year after hatching. During the second year, males increase in length by 10 mm. to an average of about 28 mm. Two males (lengths 30 and 31 mm.) have been found with sperm strands issuing from the genital papillae, so it is probable that males are sexually mature during the breeding season which occurs 28–29 months after they were hatched. There appears to be high mortality of males during the subsequent winter but a few probably survive, possibly breeding again at an age of 40 months, by which time a maximum length of c. 40 mm. may be attained.

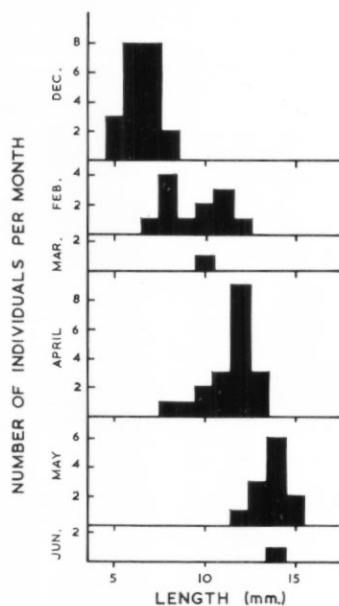


Fig. 3. Length-frequency distribution of 66 juvenile *Bovallia gigantea* grouped by months.

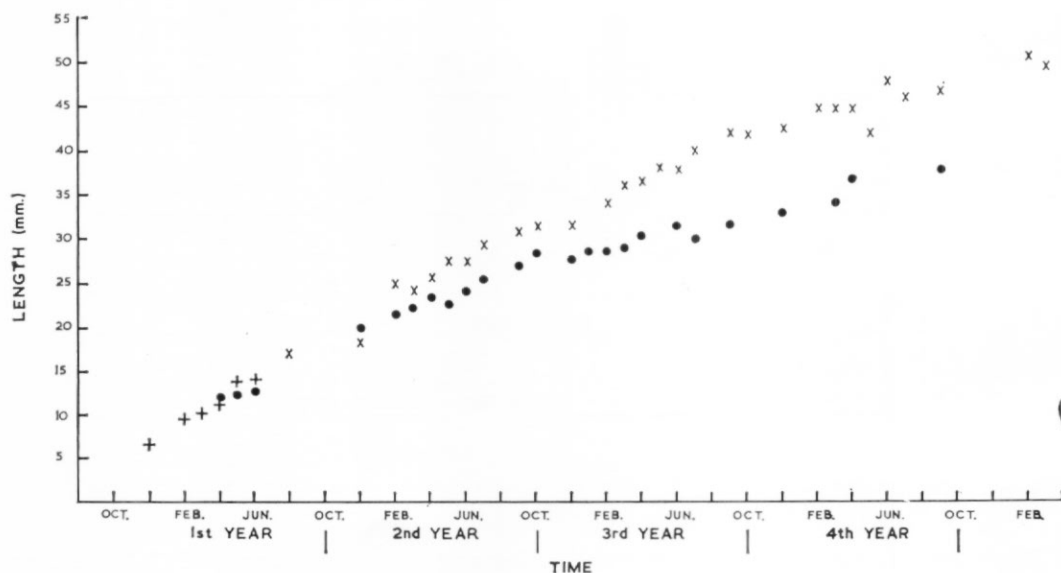


Fig. 4. Growth curve for *Bovallia gigantea*. ● = male, × = female, + = juvenile.

During the second year, the females grow faster than the males; at an age of 2 years they are about 32 mm. long, which is about 4 mm. longer than males of a similar age. A further growth increment of 10 mm. occurs during the third year. Sexual maturity is attained and eggs are produced at an age of 40–41 months. Most females die during the summer after the release of their young but, although some survive until the next breeding season, it appears unlikely that they breed a second time.

Sexton (1924) has given no figures for the increase in size at each moult in *G. chevreuxi*, but her excellent illustrations of successive moults obtained from a single female allow these length increments to be calculated (Table IV).

TABLE IV. LENGTHS AND GROWTH FACTORS AT SUCCESSIVE MOULTS OF *Gammarus chevreuxi*
(Data from Sexton (1924, pl. I-V))

| Moult number | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
|---------------------|------|------|------|------|------|------|------|------|
| Actual length (mm.) | 1.90 | 2.44 | 2.95 | 3.72 | 4.95 | 6.03 | 7.59 | 9.13 |
| Growth factor | | 1.28 | 1.21 | 1.26 | 1.33 | 1.22 | 1.26 | 1.20 |

Average growth factor; moults 1-8 = 1.25.

It can be seen that growth in *G. chevreuxi* is exponential, that is, it conforms to Brooks's Law (Fowler, 1909). The average growth factor is 1.25, which is very close to 2^{-3} (= 1.26), a factor considered significant by Przibram (1929) as it indicates a doubling of the body volume at each moult. Assuming a factor of 1.26 and a hatching length of 3.00-3.75 mm., it is possible to calculate that males become recognizable at moult 6 (12-15 mm.) and are certainly sexually mature by moult 10 (30-38 mm.). Maturity is probably attained at moult 9 (24-30 mm.). In the female, rudimentary oostegites generally appear at moult 8 (19-24 mm.) and eggs are laid after moult 11 (38-48 mm.). A few females may undergo a twelfth moult. These tentative figures are compared with data for *G. chevreuxi* in Table V. The disparity between figures for females reflects the differences in length relative to the male in the two species. In *Bovallia*, females reach a greater length than males (50 mm. as opposed to 40 mm.), while in *G. chevreuxi* the reverse is true; males reach about 14.5 mm. while females attain only 9 mm. (Sexton, 1928).

TABLE V. COMPARISON OF MOULT STAGES AND MATURITY IN *Bovallia gigantea*
AND *Gammarus chevreuxi**

| Stage | Moult | |
|------------------------------------|--------------------|---------------------|
| | <i>B. gigantea</i> | <i>G. chevreuxi</i> |
| Male distinguishable | 6 | 6 |
| Male mature | 9 | 8 |
| Female with rudimentary oostegites | 8 | 5 |
| Female mature | 11 | 8 |

* Data for *G. chevreuxi* from Sexton (1924).

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