

ASPECTS OF THE BIOLOGY OF THE ANTARCTIC AMPHIPOD *Bovallia gigantea* Pfeffer AT SIGNY ISLAND, SOUTH ORKNEY ISLANDS

By D. G. BONE

ABSTRACT. Aspects of the biology and ecology of *Bovallia gigantea* Pfeffer have been investigated, some for the first time and others to confirm earlier work. Studies of habitat and food supply indicate that shelter plays a large part in determining distribution. Gut contents show that *B. gigantea* is a predator/omnivore. Food supply is found to have a greater effect on growth rate than temperature and it is thought to be partly responsible for the long marsupial development time, advantage being taken of a summer maximum to provide food for young and developing oocytes. It is shown that growth rates vary between year groups but the causes are not evident. Growth factors are discussed and a possible regime is suggested. Gonad histology shows that males can breed for the first time at age 18 months and females at 40–42 months. The number of broods is not finite, oostegite morphology providing further evidence for the thesis that more than one brood can be produced. Predation upon, and parasitism of, the species is discussed.

THE biology of the weed-dwelling amphipod *Bovallia gigantea* was the subject of two papers by Thurston (1968, 1970). They were based on the examination of about 600 specimens from Signy Island, and many of the conclusions were somewhat tentative. The present paper, based on the examination of more than 2,500 specimens from the same locality, confirms and amends his results and also extends knowledge of the species. These specimens were collected between March 1967 and January 1969.

A monograph on the amphipods of the South Orkney Islands (Thurston, in press) has given an idea of the abundance of *B. gigantea* relative to the other, basically weed-dwelling, amphipods. Unfortunately, at the present time no strictly quantitative work has been carried out in this habitat.

SAMPLING METHODS AND STATIONS

Monthly samples of *B. gigantea* (hereafter referred to as "*Bovallia*") were collected by means of a 60 cm. by 30 cm. Agassiz trawl fitted with a nylon net of 15 mesh/cm. This was worked from a 12 or 16 ft. [3·6 or 4·9 m.] outboard-powered boat during periods of open water and through ice when necessary. The method used to trawl under ice was as follows: two holes about 1 m.² and 30–40 m. apart were cut, using a petrol-driven chain saw, and connected by parallel cuts 15–20 cm. apart. The ice between these cuts was broken up and removed with the aid of two steel hooks. The net was dropped in at one end hole and towed up to the other by hand, the rope passing along the slot. If necessary, different ground could be covered by cutting slots from the end holes at right-angles to the connecting slot, lowering the trawl to the bottom at the end of one of these and then returning to the original slot before commencing to haul.

The very uneven nature of the ground trawled and the unlikelihood of being able to cover the same ground twice, particularly when working from a boat, prevented accurately repeatable quantitative sampling. Short of diving, however, trawling was the best available method of collecting.

The monthly samples were nearly all collected from one site—a rock shelf on the south side of Cam Rock in Borge Bay, Signy Island (Fig. 1). This is a relatively isolated outcrop, rising from a gently sloping sea bed of sand and gravel, to a height of about 0·5 m. above E.H.W.S.T., a vertical distance of 10–12 m. The lower slopes of this rock form a stable substrate for beds of *Desmarestia* and *Phyllogigas*. Most of the trawling was carried out over these algal communities which are typical of those fringing the coast and offshore islands in this depth of water (Price and Redfearn, 1968). The area was chosen as a sampling site because of its accessibility and the relatively easy trawling ground that it offered. When sampling at Cam Rock was not possible, the nearest site offering the same conditions was used. Shore and shallow-water collecting was carried out at Elephant Flats and around Drying Point (Fig. 1).

The body-length measurements used by Thurston are not directly comparable with the present ones; he measured his specimens from the tip of the rostrum to the tip of the telson.

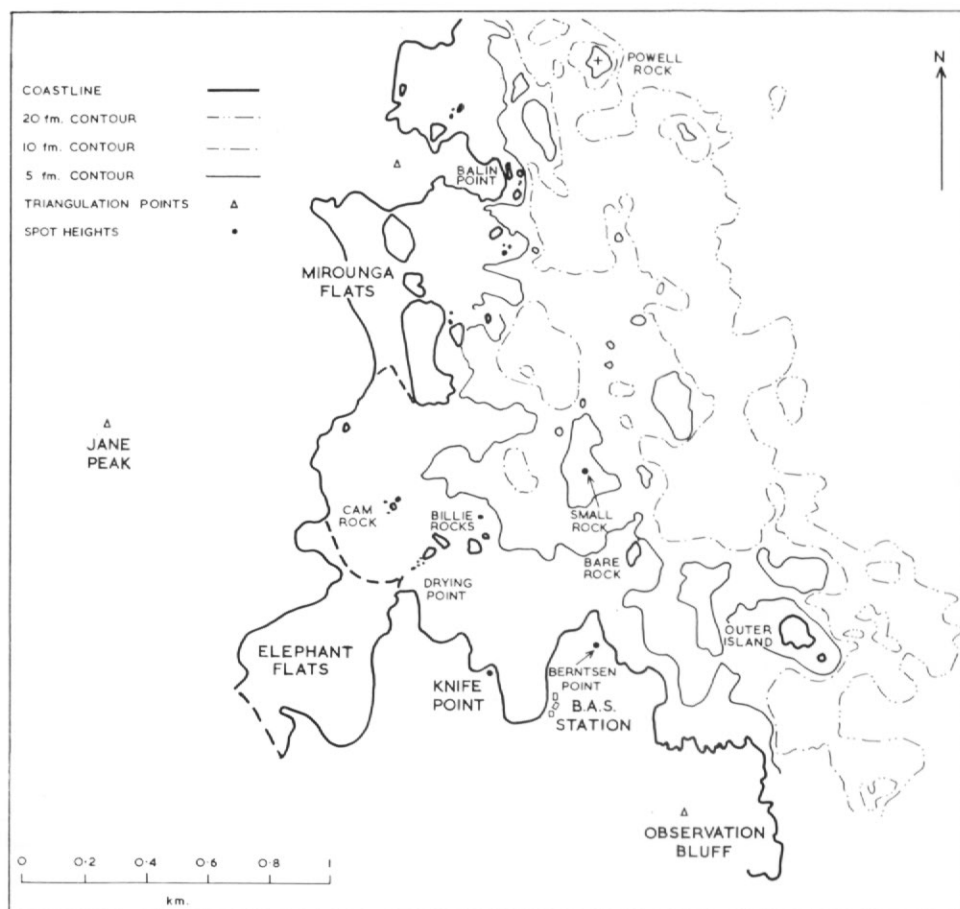


Fig. 1. Map of Borge Bay, Signy Island, showing sampling sites.

Animals used in the present study were measured from the tip of the rostrum to the base of the telson, the former measurement being on average 1.09 times the latter. The base of the telson was used as it provides a more stable datum, the telson being liable to damage, and it was an easier measurement to make.

BATHYMETRIC DISTRIBUTION

Data used to determine the bathymetric distribution were obtained from three sources:

- i. Collections made during the present investigation.
- ii. Examination of general trawl samples made at a series of stations from 6 to 37 m. by M. G. White and I. Everson.
- iii. Examination of fish (*Notothenia neglecta*) stomach contents collected by I. Everson.

The results are probably valid as this species does not often move very far in search of food (personal communication from I. Everson). These data indicate that *Bovallia* occurs from the lower littoral to a depth of 30 m. The bulk of the population is between E.L.W.S.T. and 15–17 m., with a maximum density around 12 m.

It is possible that the species occurs below 30 m. but a number of trawls made in 40 m. or more have not yielded a single specimen.

HABITAT

Previous work by Thurston (1968, 1970, in press) has described the typical habitat of *Bovallia* as the algal associations dominated by *Desmarestia* and *Phyllogigas*. The present work suggests that the highest concentrations do occur there but a number of observations indicate that the picture is not a simple one.

Hand collections, and inspections, made during the summer period in the area of Drying Point showed that *Bovallia* could be found in the lower littoral and immediately sub-littoral zones. In this area the shore consists of a stable pavement of boulders embedded in a matrix of sand and gravel, overlain by a number of smaller loose boulders with spaces beneath and between them. In this zone macro-algae are restricted to a few *Adenocystis utricularis*.

A collection of the empty shells of the mollusc *Laternula* sp. made by divers in approximately 10 m. was found to contain a number of *Bovallia*.

In late November and early December, a marked reduction in catching rate was apparent for trawls made over the *Desmarestia*/*Phyllogigas* beds. During winter these beds form relatively discrete communities but in November and December there is a rapid growth of *Adenocystis utricularis* in areas which were previously bare rock. Possibly, these annual algae provide a large area of additional shelter for the amphipods, resulting in dispersion and a lower population density. Such dispersal would result in smaller trawl catches. Post-breeding mortality can be eliminated as a factor in this reduction because the smaller catches are not confined to adult classes.

In samples taken from the major weed beds around Cam Rock it was noticeable that whenever a quantity of the red algae, such as *Geogiella confuens*, forming the underflora of the algal beds, was brought up then catches of *Bovallia* were high. This is an indication that this amphipod inhabits the underflora of the algal beds rather than the plants of *Desmarestia* (or *Phyllogigas*) themselves. Further supporting evidence is that a number of *Desmarestia* plants collected by divers, who enclosed them in a nylon mesh bag *in situ*, yielded very few specimens.

PHYSICAL ASPECTS OF THE ENVIRONMENT

The physical aspects of the marine environment around Signy Island have been the subject of continuous studies for a number of years and the data so far available are being analysed (personal communication from M. G. White).

Temperature and salinity

For the present study, temperature and salinity were recorded regularly at the Cam Rock site, 18 measurements being made between September 1967 and June 1969. The temperatures were taken close to the bottom in 8–10 m. of water using protected reversing thermometers. Fig. 2 shows the annual temperature cycle taken from these records. For months when more than one reading is available the mean values are plotted.

The curve is typical of the temperature regime as measured over a longer period at other stations in the vicinity (Everson and White, 1969; Everson, 1970; personal communication from M. G. White). The characteristic features are that it shows a narrow range, rapid cooling taking place from February to June, followed by a prolonged warming.

Water samples for salinity measurements were obtained with N.I.O. pattern water-sampling bottles, which also carried the thermometers. The salinity was measured by use of a hydrometer and reference to Knudsen's (1959) tables. Very little variation was found to occur, and 15 readings made between September 1967 and October 1968 gave a mean salinity of 33.44‰ (range 33.08–33.85‰).

Ice regime

It seems unlikely that ice has a very marked direct effect on habitats similar to those around Cam Rock.

Severe physical disruption may be caused occasionally by large pieces of ice (bergy bits and growlers) (Armstrong and Roberts, 1956) grounding in the area, but this does not occur sufficiently often in any one place to change the habitat greatly.

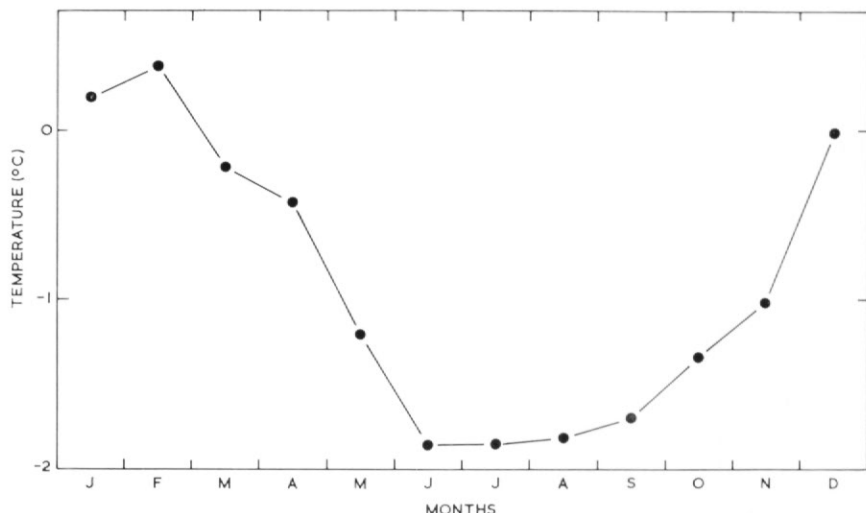


Fig. 2. Monthly temperature cycle of the sea at Cam Rock for the period September 1967–June 1969.

Anchor ice has a marked effect in McMurdo Sound (Dayton and others, 1969). But the formation of this is not as great at Signy Island as it appears to be at McMurdo Sound; and no damage has been observed that can be directly related to this ice form. Specimens of *Bovallia* have been observed to inhabit ice-platelet clusters without coming to any harm.

Ice cover, that is fast and pack ice, in the Borge Bay area is very variable in thickness, duration and permanence. In most years fast ice is present from late May until early October; during this period the ice may break out and re-freeze a number of times. Exceptionally, ice cover will continue virtually uninterrupted from May to December. After the fast ice has broken out there is a period of 3 months or so during which pack ice can be expected in the area, although rarely for more than 2 or 3 days without interruption.

The ice thickness does not often exceed 0.5 m. including the surface snow cover; but thicknesses up to 1 m. may occur and, if pack ice is present, it may contain floes of 2 m. or more.

Away from the shore the effect of ice cover on the *Bovallia* population is a secondary one, due to the reduction of algal growth consequent on the reduction in available light. Ice also damps down wave action with the result that the only water movements are tidal ones.

Thus animals living in this area will have their environment further stabilized by the presence of ice rather than disrupted by it.

Shore and shallow-water environment

Populations of *Bovallia* inhabiting the littoral and immediately sub-littoral zones experience a less stable environment. During spring and summer when the terrestrial snow cover is melting, quantities of fresh water run into the sea. This water, which may also be of a higher temperature than sea-water, does not mix readily with it. During periods of heavy melt-water run-off, a surface layer of water having very low salinity has been known to form extensively in Borge Bay. These changes are felt most strongly by animals inhabiting the shore.

Further changes may be brought about more directly by weather. In shallow water, strong sunlight shining on dark rocks raises the water temperature by 2–4° C, temperatures up to 4° C having been recorded in the vicinity of Drying Point. Similarly, very cold winds will rapidly cool the shallow waters and form ice on the shore. Tides will ensure that exposure to these "extreme" conditions is of short duration only.

Owing to the great difficulty of sampling, it is not possible to say what happens to animals inhabiting the shore zone while sea ice is present. During ice formation the entire shore and shallow water may be clogged with ice and are therefore very inhospitable. When the sea ice reaches its mature form, the floating ice is connected to the solid "ice foot" by a series of blocks

which either float up or tilt with each tide. Observations made at times of ice break-up and by divers suggest that the shallow sub-littoral zone remains relatively undisturbed. Anchor ice may form extensively in this area.

FOOD SUPPLY AND GUT CONTENTS

In order to facilitate a study of the food supply available to *Bovallia*, the trawl catches, after removal of the *B. gigantea* specimens, were passed through a sieve. The fraction which passed through an aperture of 2.0 mm. but not through one of 0.5 mm. was retained. These samples which consisted almost entirely of crustaceans were prepared for microscopic examination. The method used was staining in lignin pink in alcohol, followed by dehydration and mounting in D.P.X. Examination of these preparations by dark field and transmitted light illumination allowed both the gut contents and the whole animals to be recognized without difficulty.

A clear pattern was evident in the samples; the September ones consisted almost entirely of copepods and small species of amphipod. These appear to have been feeding largely on diatoms but the volume of food that they contained was small and many did not appear to contain anything.

During October–November there is an increase in the proportion of copepods, closely followed by the appearance of many newly released amphipods and isopods, which by December form a very prominent part of the sample. During this period all the crustaceans are feeding heavily on diatoms.

In the April sample there is a sharp division between the juvenile amphipods, which have now reached a length of 5–6 mm., and the more permanent members of the group, the copepods and small species of amphipod, which remain in the 1–2 mm. class. The April sample also showed a marked change by the juvenile amphipods towards an animal diet, recognizable by fragments of crustacean exoskeleton. Also, in some cases, copepod eggs were recorded in the gut of these specimens.

GUT CONTENTS OF *B. gigantea*

The gut contents of over 100 individuals were examined; they represent all months of the year and cover the full size range of animals. The technique used was similar to that described above.

The volume of plant and animal material present was estimated; excluding plant material in the gut of other crustaceans eaten by *Bovallia*, the material examined showed that over the year 70 per cent of the food taken was of animal origin and 30 per cent of plant origin.

As with the amphipods mentioned above, the animal material was recognizable as pieces of the integument of small crustaceans. Although no specific identifications were attempted, it is apparent that much of the material was from copepods, including the occasional egg mass. Some material from small amphipods was present.

The plant material consisted mainly of diatoms but there were a few pieces of cellular plant material. Plant material was present to some extent in each month of the year but, as expected, there was much more present during the summer months than during the winter. In eight cases between November and February the guts contained plant material and virtually nothing else.

It is of interest that newly hatched specimens of *Bovallia* collected in October contained as much as 90 per cent of animal material, which seemed to consist largely of copepod remains. The proportion of animal material in the newly released specimens diminished through November and December until the January sample contained little apart from diatom frustules. By March they had returned to an animal diet.

In spite of the fact that a large amount of decaying vegetable matter (macro-algae, moss and lichen) is available during the autumn (February–May) it does not seem to form an important part of the diet. This suggests that *Bovallia* has a strong preference for fresh live food rather than any form of detritus, a supposition further strengthened by observations of the animals' mode of feeding. Specimens kept in a tank took up positions where the abdomen and most of the thorax was hidden, but with the antennae arrayed as in Fig. 3. From time to time the antennae swept the water, moving downwards and inwards. When a suspension of small



Fig. 3. Feeding/resting posture of *B. gigantea*.

crustaceans was dropped into the water in such a way that they drifted over a specimen, it engaged in a short period of feverish activity, the antennae being swept rapidly and repeatedly through the cloud of crustaceans, any captured specimens being combed off by the gnathopods.

DEVELOPMENT WITHIN THE MARSUPIUM

Eggs or juveniles from the marsupium of 45 ovigerous female *Bovallia* were used to study development within the marsupium. As it was not possible to work on the material at the time of collection and because many features are not very clear in the preserved material, no attempt is made to describe the development in detail. The main purpose of the study was to establish the time taken to complete development.

The developing embryos have been divided into six arbitrary classes to aid description and timing. These classes, which fit the present material better than Thurston's, are defined below:

1. Initial holoblastic division has taken place, and some unequal division along the line of the embryo.
2. Limb buds and somites visible.
3. Limbs identifiable and eyes present.
4. Development almost complete and pigment laid down in eyes.
5. Egg membranes broken and juveniles free in brood pouch but with yolk still present in the thoracic/abdominal cavity.
6. Yolk gone except for remains in gut.

Fig. 4 shows the distribution of these stages by months. The occurrence of stage 6 specimens agrees well with the appearance of newly emerged specimens in trawl samples. The first free-living specimens were captured on 12 September in both 1967 and 1968 but the bulk of them do not appear until late October.

Fig. 4 indicates a maximum development time of about 8 months and a possible minimum of about 6 months, the average evidently being close to 7 months as suggested by Thurston. The period over which development is taking place in the marsupium clearly extends from January to November.

GROWTH AND DEVELOPMENT AFTER RELEASE

Male *Bovallia* have been found to develop genital papillae in the fourth or fifth month after release, when they have reached a length of 8–9 mm., which is slightly earlier than reported by Thurston. The females are not positively identifiable until the oostegites appear; this happens when they reach a length of 16–18 mm. about 14–17 months after hatching.

The smallest free-living specimens captured were 4.5 mm. long, but observation on the broods of three ovigerous females kept in captivity showed that young emerged at 3.5 mm. and very shortly afterwards moulted to 4.5 mm. The figure of 3.5 mm. corresponds to the length of the most advanced young removed from the brood pouch of a freshly caught ovigerous female. When plotted as histograms of frequency against body length, most of the monthly samples separate easily into year classes. The growth curves in Fig. 5 are derived from a plot of 3 month running averages of mean body length of year classes. Parts of the development of five separate years' hatches are shown but ovigerous females and males longer than 26 mm. have been excluded.

The fact that hatching can take place over a 3 month period, combined with the long period of growth (around 42 months in the case of females), is probably responsible for the wide variation in the size of animals in any one nominal age group (see Fig. 8), and this leads to some overlapping. In males, this overlapping is increased by the marked reduction in growth rate which occurs about 20 months after hatching.

It can be seen from Fig. 5 that both sexes grow at about the same rate until a length of 17–20 mm. is reached (at age 16–18 months). From this point on the males grow at a slower rate than the females.

Males continue to grow for a further 12–14 months, by which time they have reached a length of 25–26 mm. After this there is a very marked decline in their number and they are no longer identifiable as a year group. The largest male recorded was 31 mm. long.

Females continue to grow steadily until a length of 29–40 mm. is reached (at age 38–42 months). At this point, variation in size is very great. There is a further increase in size when the females moult to the mature condition, ovigerous specimens being 32–45 mm. long.

Data are given below which suggest that there is little or no increase in length after females reach maturity, irrespective of the number of further moults undergone.

RATE OF GROWTH

From Fig. 5 it can be seen that the growth rate is not constant but varies during the year. There is also variation in growth rate between different year classes.

Seasonal variation

All year groups show a seasonal variation in growth, the rate beginning to show an increase during September or October and reaching a maximum during the period January–April. This is followed by a tailing off in growth rate during the June–September winter period.

Variations in the amount of growth achieved from year to year

It can be seen from Fig. 5 that there is some variation in the mean length of year classes reaching the same nominal age. Table I defines some of these variations and gives their level of significance.

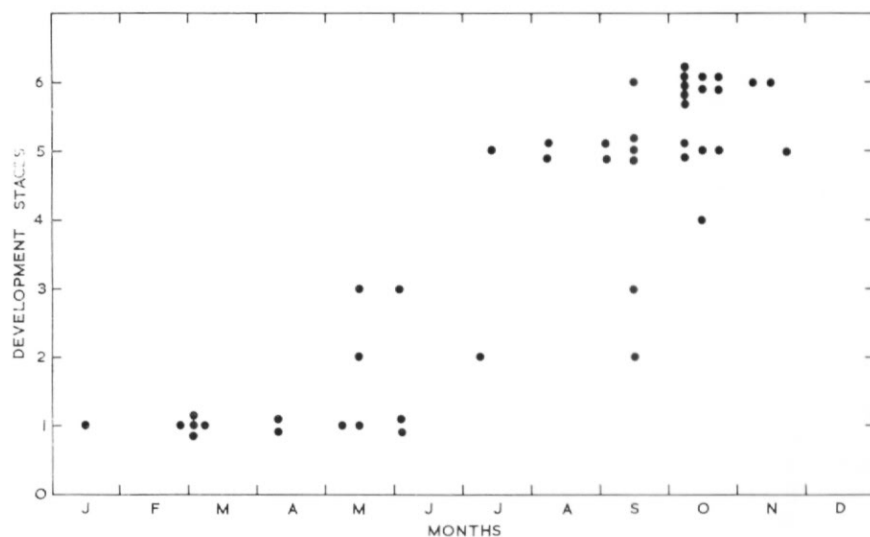


Fig. 4. Distribution of marsupial development stages by months.

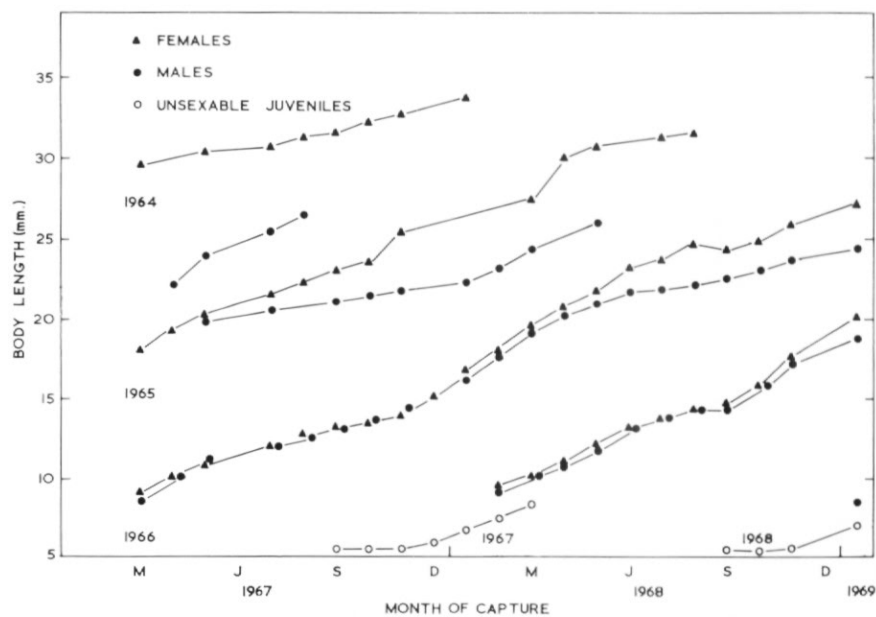


Fig. 5. Part of the growth curve for 5 years' hatches of *B. gigantea*. Points plotted are a 3 month running average of monthly means of year groups.

TABLE I

	\bar{x} (mm.)	<i>Difference</i>	<i>n</i>	<i>t</i>
<i>Growth achieved in 2 years</i>				
Males 1965 hatch	21.42	0.98	113	3.2018
Males 1966 hatch	22.40			
Females 1965 hatch	23.0192	1.0	85	2.8184
Females 1966 hatch	24.0192			
<i>Growth achieved in 12-14 months</i>				
Males 1966 hatch	13.55	2.35	175	8.2106
Males 1967 hatch	15.9			
Females 1966 hatch	13.39	3.87	167	9.2253
Females 1967 hatch	17.26			

GROWTH FACTOR

Attempts to find out how much *Bovallia* increases in size at each moult, i.e. to establish a growth factor, met considerable difficulty. Results from an experiment in which length was measured before and after moult were inconclusive and no really satisfactory method of determining the instar could be found. A few instars were separated, for females, by plotting oostegite length against body length (Fig. 6). Groups 3 and 4 are clearly separated and a division can be demonstrated to exist between groups 1 and 2. However, it is unlikely that group 2 is a completely accurate representation of a single instar, and group 1 almost certainly consists of two or more instars. Furthermore, "group 4" which is composed of morphologically mature females possibly contains three or more instars; this is, however, a slightly different case, as will be shown below. The mean body length of animals forming group 3 is larger than that of group

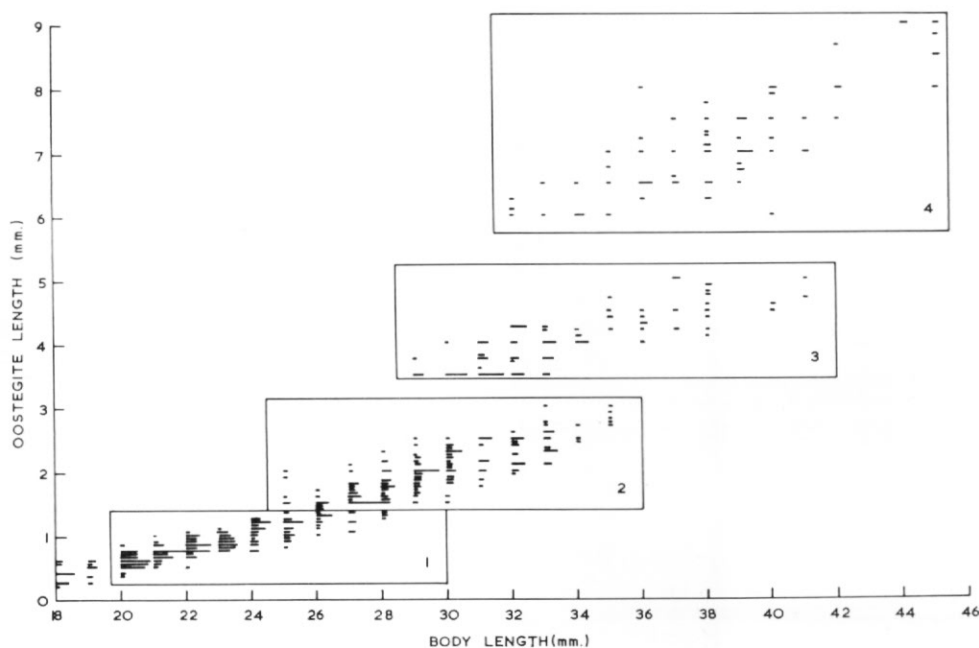


Fig. 6. Plot of oostegite length against body length. Rectangles enclose instars or groups of instars.

2 by a factor of 1.14; similarly, the mean length of group 4 specimens is larger than that of group 3 by 1.145. The increase between groups 1 and 2 is much greater at 1.313.

It has been shown by Kurata (1962) and others that there is frequently a reduction in growth factor in crustaceans when they reach maturity. A number of considerations point to this being the case in *Bovallia*. It even seems likely that the reduction in growth factor is total, and that after maturity is reached there is negligible increase in length irrespective of the number of moults undergone.

Evidence is given below (see section on fecundity) that *Bovallia* is almost certainly capable of carrying more than one brood, and an "interbrood" condition has been recognized. This means that group 4 will consist of females which are carrying their first brood, some which are carrying their second brood and some in the interbrood condition. Fig. 7 shows the size-

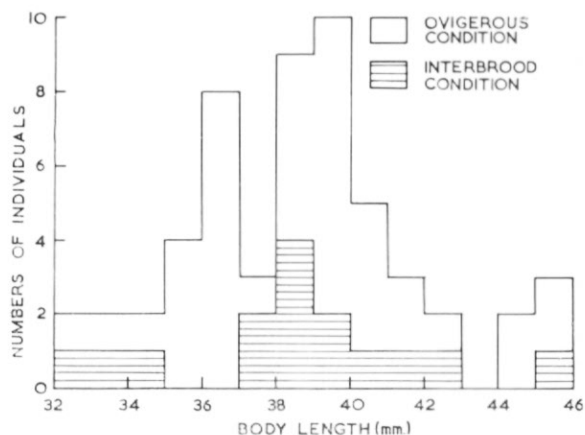


Fig. 7. Size-frequency distribution of ovigerous and interbrood (cross-hatched) *B. gigantea*.

frequency distributions of both the ovigerous specimens and those in the interbrood condition. There is no significant difference between these two populations ($P = 0.20$). Also, if the greatest body lengths recorded in group 3 (the pre-ovigerous group) are multiplied by 1.145, they give rise directly to the greatest lengths of group 4; there is no need for an intermediate length increase. There is similar matching of the least values in each group. These two facts lend considerable weight to the thesis that there is negligible length increase after maturity is reached.

Further pointers to a changing growth factor with approaching maturity are that extrapolation back from the mean length of group 2 (29.35 mm.), dividing by the factor of 1.14, indicates a group with a mean length of 25.6 mm., which almost corresponds to the division between groups 1 and 2. Also, the factor of 1.313 obtained for this "moult" would seem to be too large; but extrapolation back from group 2 using the factor 1.26 of Przibram (1929) as suggested by Thurston gives quite a good fit. Groups of 23.29, 18.48 and 14.67 mm. mean length are indicated and a total of nine instars back to hatching length. This would make a total of 12 moults to reach maturity.

The whole growth situation is summarized in Fig. 8.

REPRODUCTION

Development of testes

The paired testes lie along the anterior/posterior axis of the animal in the thoracic cavity immediately below the heart, and anterior to the seminal vesicles, which are connected to the genital papillae by short vasa deferentia.

Examination of the testes (sectioned and stained in haematoxylin and eosin) shows that they appear to be mature in the breeding season which occurs 14-17 months after hatching.

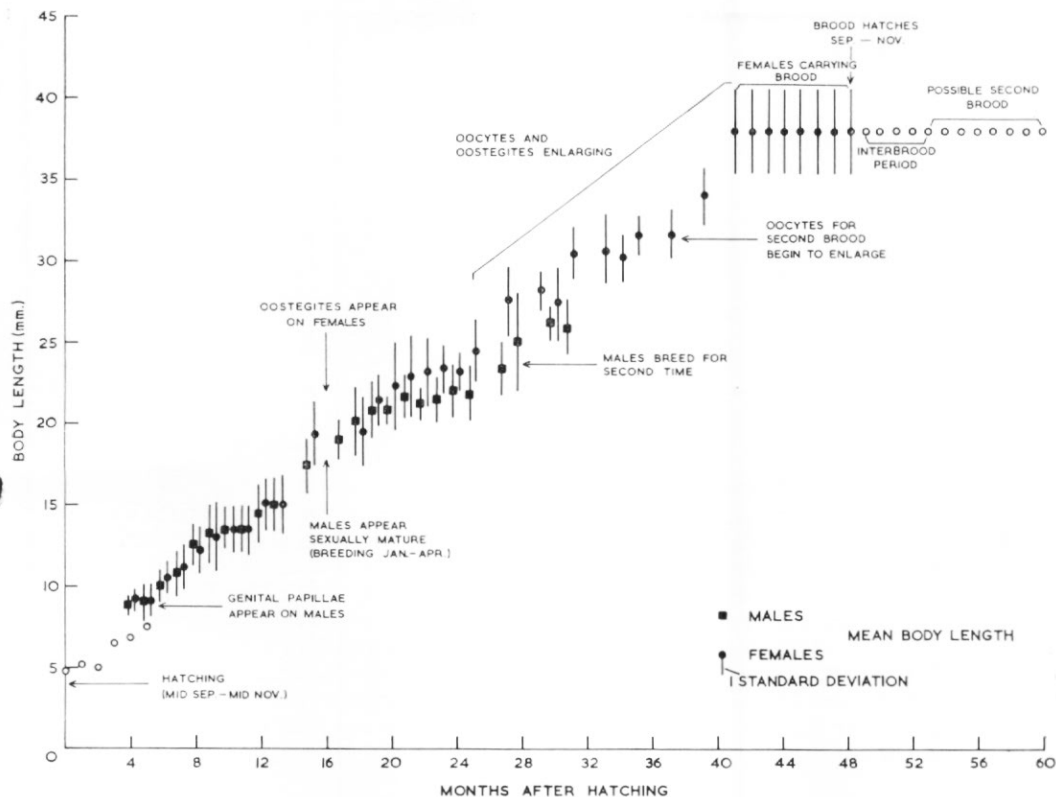


Fig. 8. Constructed overall growth curve for *B. gigantea*. Vertical lines represent one standard deviation either side of the mean.

Specimens selected at random from the 9–11 month old group in August had mature or maturing sperms in their gonads. The seminal vesicles enlarge and the sperm become more densely packed up to the January–March breeding season.

Although there was a slight decline in the amount of sperm present after the breeding season, all males examined which were 14–17 months or more old had apparently mature sperm in their seminal vesicles, irrespective of time of year. There is no morphological difference between the sperm of these 14–17 month old specimens and those of 26–29 month old animals.

Examination of the testes shows that they are not both in the same state of development at any one time in the same animal, although the seminal vesicles simultaneously contain mature sperm. This is difficult to explain as no direct connection appears to exist between right and left testes or seminal vesicles.

Development of the ovaries

For this study, sections or whole mounts of the ovaries from 40 specimens were examined; these were taken from animals ranging in size from 25 to 45 mm. and they came from each month of the year except February, June and December. The ovaries are paired and lie in a similar position to the testes, and consist of discrete oögonia which vary in size; the smallest lies along the mid-line and the largest away from it (Fig. 9). During the later stages of development it is obvious that only a portion of the oögonia present mature during one season. It appears that the number of oögonia is not definitive. Thus females which are carrying a brood can be found with enlarging oocytes in their ovaries, and these may represent a potential second and perhaps third brood.

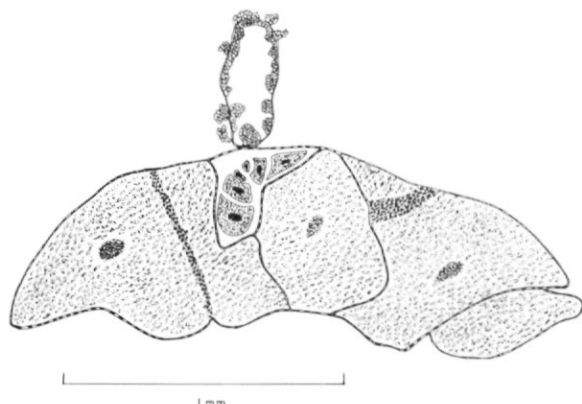


Fig. 9. Transverse section of ovary from an ovigerous female *B. gigantea* of body length 41 mm. captured in July.

Of the above 40 specimens, 12 were selected for measurement of oocyte size. These were taken from four periods of the year: January, March/April, July/August and October. A "mean cell diameter" was found by measuring the greatest and least diameters of each cell and averaging them. Only cells sectioned through the nucleus were used. The 265 measurements obtained were plotted on histograms which showed year classes of cells. The mean diameters of cells in these year classes were used to plot the curve (Fig. 10). This shows that the remarkable time of 16 months is required for oocytes to grow from $40\text{--}50\text{ }\mu\text{m}$. to the $1,000\text{--}1,400\text{ }\mu\text{m}$. attained before laying. Examination of the gonads and the occurrence of females with newly deposited eggs in the brood pouch shows that the majority of eggs mature and are laid during January–March. A few are not laid until April.

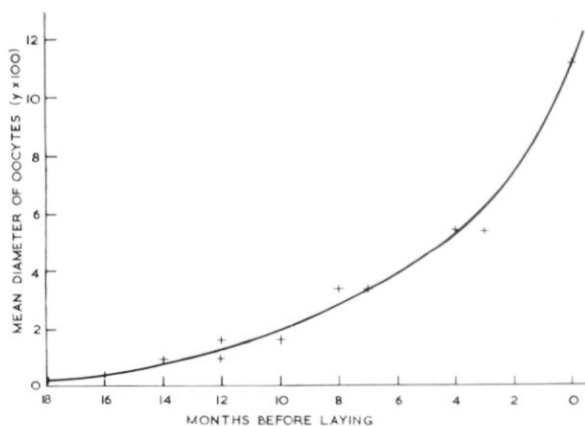


Fig. 10. Oocyte development in terms of mean cell diameter against months prior to laying.

Reproductive behaviour

Copulation was never observed in *Bovallia*, neither was pre-copulative pairing, either in specimens held in tanks or in freshly captured ones. It is therefore thought that pre-copulative pairing does not occur, a fact that may be linked with the unusual sex ratios shown in Table II.

TABLE II. SEX RATIOS

Overall, males/females	1 : 1.17
1 year old males/females	1 : 1.09
2 year old males/females	1 : 0.80
8, 9, 10 month males/17, 18, 19 month females	1 : 0.28
Mature males/mature females	1 : 0.18

FECUNDITY

In order to determine the relationship between egg number and body length, 80 ovigerous female *Bovallia* were examined. Specimens suspected of having lost eggs were not used.

A plot of egg numbers against body length is given in Fig. 11. The line which was fitted by regression analysis ($y = 96.644 + 4.727x$) indicates that egg number is not proportional to (body length)³ as suggested by Thurston.

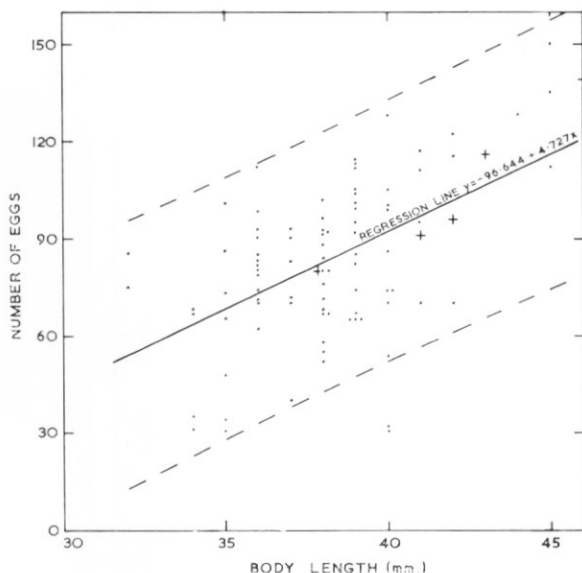


Fig. 11. Regression of egg numbers on body length, with upper and lower 95 per cent confidence limits (dashed lines). Crosses denote data of Thurston (1968, 1970) with length corrections made.

Number of broods

Evidence from the gonads, given above, suggests that production of more than one brood is, at least potentially, the normal state of affairs. This is further supported by the study of the oostegites, three forms of which are found (Fig. 12). Type 1, the "smooth" or unspined form, is that which is found on the immature non-ovigerous specimens. Type 2 is the fully spined form that is found in ovigerous specimens and type 3 a partially spined form that occurs in the summer period only.

The relationship of these three forms is made clear by the presence of a number of oostegites in which the form that they will take during the next instar can be clearly seen during the present one. These are as follows:

- 14 type 1 which will moult to type 2;
- 5 type 2 which will moult to type 3;
- 6 type 3 which will moult to type 2.

From this it is fairly clear that the type 3 partially spined condition is the form taken by the oostegite during the interbrood period, and it can be reasoned that the female will breed again if circumstances allow.

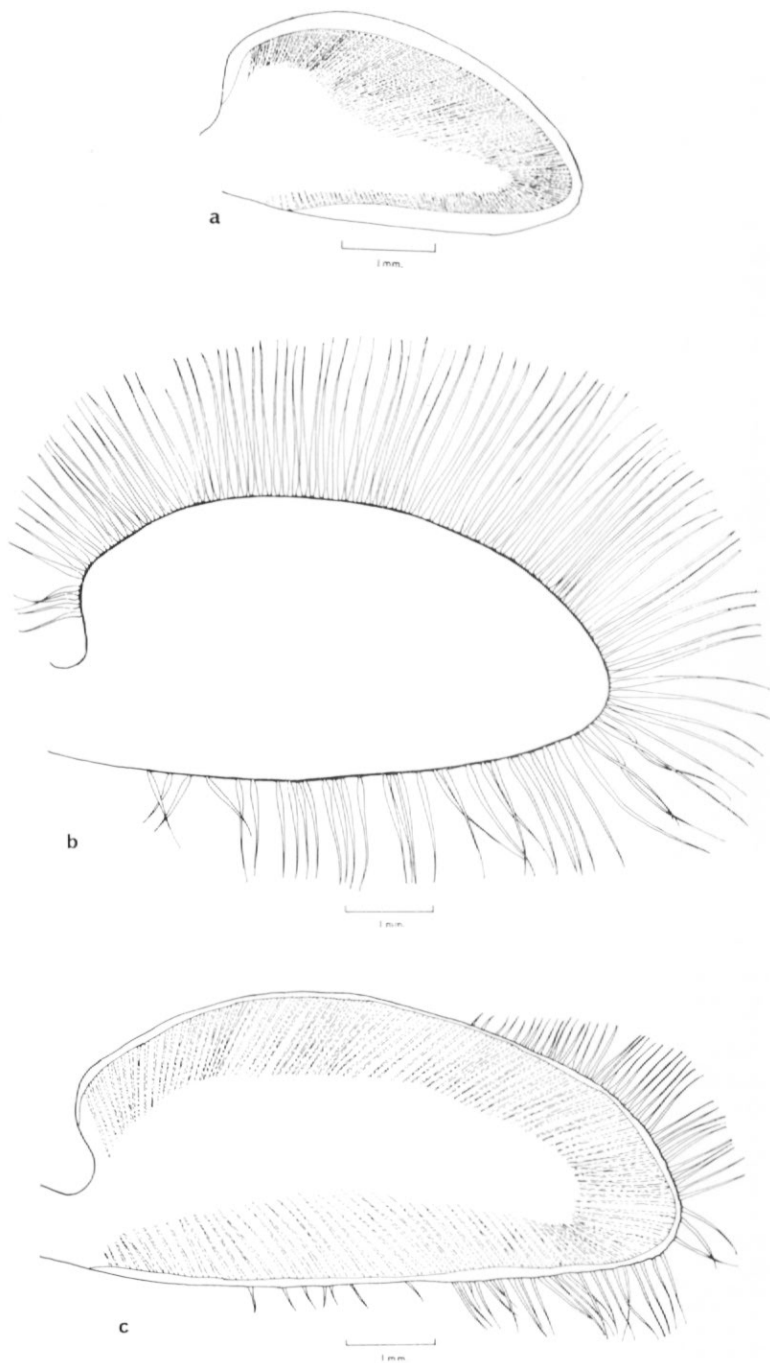


Fig. 12. Forms of oostegite from *B. gigantea*.

a. "Type 1" unspined form.

b. "Type 2" fully spined form from ovigerous specimens.

c. "Type 3" partially spined form found in the summer period only.

Mortality during development

Most amphipods investigated show a loss or mortality during development in the brood pouch. Owing to the wide variation in length of animals in this relatively small sample, it was not possible to investigate this point with animals of one length only. Fig. 13 is a plot of egg/young numbers per individual, by months, ignoring variation due to length. (There is a decline of about 1 mm. in mean length of ovigerous specimens in the latter part of the development period.)

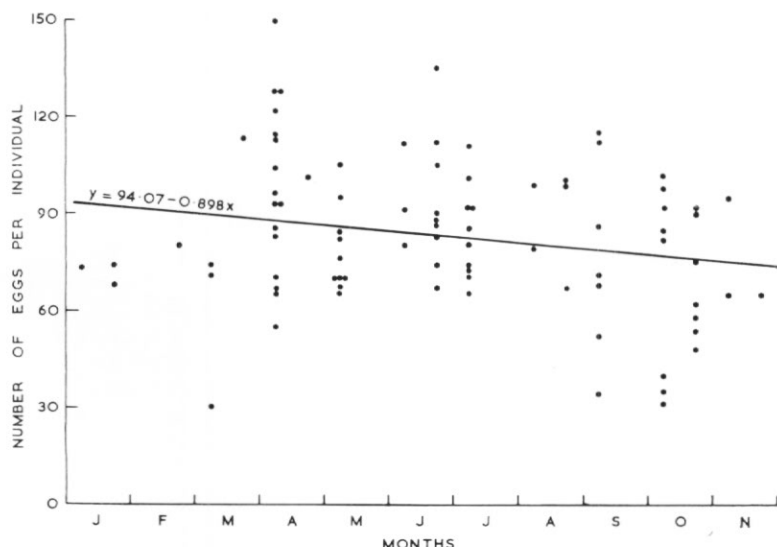


Fig. 13. Plot of egg/larvae numbers by months with fitted regression line ($r = 0.2050$, $m = 86$).

PREDATION AND PARASITES

Predation

The degree to which fish, e.g. *Notothenia neglecta*, prey upon *Bovallia* is obscure; 19 out of 35 fish stomachs collected by I. Everson contained one or more *Bovallia* but of 68 examined by the author only eight contained them. This difference is difficult to account for as sampling methods, stations and times of year were substantially the same. There were rarely more than four to five specimens in any one fish but it was noticeable that they were usually above 25 mm. body length. When kept in captivity together, the large isopod *Glyptonotus antarcticus* captured and ate specimens of *Bovallia* and it is probable that it does so in the field.

Antarctic terns feeding around Drying Point at low tide have been observed to take large *Bovallia* and another large and distinctive amphipod, *Paraceradocus mersi*.

Parasites

A number of parasites was found in *Bovallia* but none has been identified to species. During the course of dissection, four out of 150 specimens were found to contain a juvenile stage of an acanthocephalid worm. All of a small sample of specimens examined in the fresh state were found to contain gregarine gut parasites.

A high proportion of ovigerous females examined had ostracods inhabiting their brood pouches. These do not appear to be harmful and should probably be considered as commensal.

DISCUSSION

It would seem that both shelter and food supply play a part in determining the distribution of *Bovallia*. As abundant shelter is known to exist below 30 m., it is reasonable to conclude that food is ultimately responsible for limiting the species' bathymetric range. (Unfortunately no

data are available on the composition of necto-benthos below 30 m.) Shelter probably plays a greater part in determining distribution within the range. The animals which were found on the shore itself probably have little significance; it is likely that they were individuals trapped there by the falling tide. Similarly, there is probably little significance in the presence of *Bovallia* in the shallow sub-littoral during periods of environmental stress. It illustrates that the animal is tolerant of greater changes in temperature and salinity than are met with by the bulk of the population, but little more.

From the study of gut contents and feeding methods, *Bovallia* can be classed as a predator/omnivore. Enequist (1949) stated that detritus-feeding amphipods frequently contain some animal remains such as crustacean exoskeletons. The mode of feeding and absence of sand or mud in the gut makes such a diet unlikely in the case of *Bovallia*.

The very long marsupial development time described by Thurston (1968, 1970) and confirmed here is highly advantageous, for the females with maturing ovaries have the benefit of the summer food supply for laying down yolk, and the juveniles emerge just as a suitable food supply is available to them. This would suggest that in the case of *Bovallia* the very long development time that undoubtedly occurs in cold waters has undergone adaptation to span two seasons. Barnard (1959) considered a period of 6 months as likely for the development of *Gammarus wilkitzkii*, a pelagic amphipod found in the Arctic Ocean and of a size approaching that of *Bovallia*. Dunbar (1946, 1957) hinted at a development time running into several months for *Parathemisto libellula*, another pelagic arctic amphipod. The former releases its young at a time when available food is increasing but the case is not so clear cut for *P. libellula*.

The growth data obtained from this study do not differ markedly from those presented by Thurston. However, the growth-rate variations brought to light are interesting. The seasonal increase in growth rate coincides with both a rise in temperature and a great increase in available food. A few experiments carried out by the author to determine the effect of temperature on metabolism (oxygen consumption) cast doubt on the likelihood of such a small rise in temperature affecting the growth rate. It is considered that increased food supply is probably responsible for this rise.

Table I shows some of the variations in growth achieved within a given time to be very highly significant. Unfortunately, insufficient ecological data are available to establish the cause of these variations. They may have been brought about by differences in hatching date or different growth rates, but the fact that growth rate seems to be largely dependent on food supply would suggest that changing food availability is the primary cause of the variation. These changes in food supply must be caused by changes in primary production of some similar basic property of the environment.

The growth factors are based on very little evidence and it is unlikely that they give a true picture. However, it is felt that the pattern outlined fits the evidence better than the single overall factor tentatively suggested by Thurston. Although this factor was worked out on the population of females, it is unlikely that the males differ greatly, except that the total number of instars is less. The instar of mean length c. 18.5 mm. might well be the one in which the oostegites make their appearance in the females. Another point that should be borne in mind is that there may be a seasonal change in growth factor. For instance, the transition between groups 1 and 2 is made during the summer "fast" growing period; it is possible that the growth factor is larger during the favourable growing period than it is during the unfavourable one. Seasonal variations in adult size have been noted in various copepods (Deevey, 1960).

The unusually long time taken for the gonads to develop is not surprising when considered in the light of the longevity and growth rate of the animal itself.

The appearance of the ovaries would suggest that the number of broods that a female is capable of producing is not strictly limited. It is probable that the limiting factor is the mortality rate. Fish (and terns) certainly take larger specimens most frequently and there is probably some mortality at the moult which occurs when the young are released from the brood pouch. However, the branchiae and oostegites of the present material show little or none of the degeneration described by Thurston (1970). In the absence of any evidence to the contrary, it must be assumed that any broods subsequent to the first one are approximately the same size. The regression line in Fig. 13 shows a downward trend throughout development but a visual examination of the data shows that there is a rather marked decline in brood numbers during the

last 3 months. This decline was not accounted for by the change in the mean length of animals collected during these months, which would only cause a reduction of five or six in the brood number. This reduction in numbers could be due either to an actual mortality or to active specimens escaping from the brood pouch. There is a small increase in size of larvae in the brood pouch but there is no evidence to show whether or not this is due to a moult, as occurs in *Marinogammarus marinus* (Vlasblom, 1969), or stretching of the integument.

The sex ratios (Table II) show an interesting and unusual pattern. The overall sex ratio is a rather meaningless statistic owing to the disparity in breeding age. When animals of equal age are compared, the numbers are nearly equal, but when maturity stages are compared there are many more males than females. Even if sampling error exaggerates the difference, it must nonetheless be substantial. This very unusual situation is obviously brought about in part by the longer time taken for females to mature, but it may be aggravated by predators, such as fish, tending to take large specimens rather than small ones. There could be a link between this situation and the absence of pre-copulatory pairing. An excess of males would increase the chances of male and female meeting during the (possibly short) period during which the female is receptive.

The regression line in Fig. 11 does not confirm Thurston's (1968) postulate that egg number is proportional to (body length)³, although the six points selected by him could have this relationship. His six points are plotted in Fig. 11 and fall well within the distribution of the present data.

It is not surprising that an amphipod which forms a conspicuous part of the diet of notothenid fish should be a vector for acanthocephalids which are common in the gut of these fish. Ökland (1969) reported finding acanthocephalid larvae in five *Gammarus lacustris*. The occurrence of gregarines (in the gut) is not unusual for arthropods and has been reported in the arctic pelagic amphipod *Themisto libellula* (Dunbar, 1946).

Barnard (1959) noted the presence of ostracods in the brood pouch of *Gammarus wilkitzkii*.

ACKNOWLEDGEMENTS

I am particularly indebted to M. G. White and P. K. Bregazzi for much help and encouragement both in the Antarctic and this country, and Dr. I. Everson for allowing me to use his collection of fish stomach contents. I should also like to thank K. H. Lakhani for help with statistical problems, Dr. E. Naylor and Dr. R. M. Laws for reading and criticizing the manuscript, and finally the many companions on Signy Island who gave valuable assistance with field work.

MS. received 28 January 1971

REFERENCES

- ARMSTRONG, T. and B. ROBERTS. 1956. Illustrated ice glossary. *Polar Rec.*, **8**, No. 52, 4-12.
- BARNARD, J. L. 1959. Epipelagic and under ice amphipods of the central Arctic Basin. (In BUSHNELL, V. C., ed. *Scientific studies at Fletcher's ice island, T-3, 1952-1955*. Bedford, Mass., Geophysics Research Directorate, U.S. Air Force Cambridge Research Center, **1**, 115-52.)
- DAYTON, P. K., ROBILIARD, G. A. and A. L. DEVRIES. 1969. Anchor ice formation in McMurdo Sound, Antarctica, and its biological effects. *Science, N.Y.*, **163**, No. 3864, 273-74.
- DEEVEY, G. B. 1960. Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. *Bull. Bingham oceanogr. Coll.*, **17**, No. 2, 54-85.
- DUNBAR, M. J. 1946. On *Themisto libellula* in Baffin Island coastal waters. *J. Fish. Res. Bd Can.*, **6**, No. 6, 419-34.
- . 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt. *Can. J. Zool.*, **35**, No. 6, 797-819.
- ENEQUIST, P. 1949. Studies on the soft bottom amphipods of the Skagerak. *Zool. Bidr. Upps.*, **28**, 297-492.
- EVERSON, I. 1970. The population dynamics and energy budget of *Notothenia neglecta* Nybelin at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 23, 25-50.
- and M. G. WHITE. 1969. Antarctic marine biological research methods involving diving. *Rep. Underwat. Ass.*, **4**, 91-95.
- KNUDSEN, M. ed. 1959. *Hydrographical tables*. Copenhagen, Tutein and Koch.
- KURATA, H. 1962. Studies on the age and growth of Crustacea. *Bull. Hokkaido reg. Fish. Res. Lab.*, No. 24, 1-115.

- ÖKLAND, K. A. 1969. On the distribution and ecology of *Gammarus lacustris* (G. O. Sars) in Norway, with notes on its morphology and biology. *Nytt Mag. Zool.*, **17**, No. 1, 111-52.
- PRICE, J. H. and REDFEARN. 1968. The marine ecology of Signy Island, South Orkney Islands. (In *Symposium on Antarctic oceanography. Santiago, Chile, 13-16 September 1966*. Cambridge, Scott Polar Research Institute, 163-64.)
- PRZIBRAM, H. 1929. Quanta in biology. *Proc. R. Soc. Edinb.*, **49**, No. 18, 224-31.
- THURSTON, M. H. 1968. Notes on the life history of *Bovallia gigantea* (Pfeffer) (Crustacea, Amphipoda). *British Antarctic Survey Bulletin*, No. 16, 57-64.
- . 1970. Growth in *Bovallia gigantea* Pfeffer (Crustacea : Amphipoda). (In HOLDGATE, M. W., ed. *Antarctic ecology*. London, Academic Press, 269-78.)
- . In press. The Crustacea Amphipoda of Signy Island, South Orkney Islands. *British Antarctic Survey Scientific Reports*, No. 71.
- VLASBLOM, A. G. 1969. A study of a population of *Marinogammarus marinus* (Leach) in the Oosterschelde. *Neth. Jnl Sea Res.*, **4**, No. 3, 317-38.