# MEASURES OF BIOMASS, MOULTING BEHAVIOUR AND THE PATTERN OF EARLY GROWTH IN *Chorismus antarcticus* (Pfeffer)

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ABSTRACT. The circum-Antarctic benthic hippolytid decapod *Chorismus antarcticus* (Pfeffer) was sampled at approximately monthly intervals throughout 1972 at King Edward Cove, South Georgia. Fresh weight, dry weight and ash weight interrelationships were examined with particular reference to the techniques used and the results were compared with those for other decapods. Moulting, as indicated by an elevated water content, was found to occur more frequently in the warmer summer months and in the younger stages. Estimates of water uptake and loss of mineral ash at ecdysis are given. An estimated growth curve for the first 15 months of post-larval life showed a marked seasonal pattern of relatively rapid growth in summer and slow growth in winter. Comparison with published data indicated that relative growth during this period was less than in any temperate water caridean decapod so far studied.

*Chorismus antarcticus*, a benthic prawn of the family Hippolytidae, was first described from South Georgia by Pfeffer (1887) as *Hippolyte antarctica*.† It has a circum-polar distribution in Antarctic waters and, unusual in a benthic organism, also extends across the Antarctic Convergence to the Straits of Magellan (Holthuis, 1952; Garth and others, 1967). It has been reported from depths of 15–915 m. (Zarenkov, 1970) and at South Georgia it is common on suitable substrates from the sub-littoral across the continental shelf (Maxwell, 1972). The pelagic larva and the early post-larva have been described by Gurney (1937). The only other species in the genus is the similar *Chorismus tuberculatus*, described by Bate (1888) from specimens collected by H.M.S. *Challenger* at Marion Island in the sub-Antarctic.

The biology of *C. antarcticus* is of interest as this is one of only two widely distributed and common natantian decapods found in the Antarctic, a region which, in comparison with the Arctic and temperate waters, is notable for the virtual absence of decapod crustaceans (Yaldwyn, 1965; Zarenkov, 1970).

The biology of *Notocrangon antarcticus*, the other common Antarctic caridean, has been described in detail by Makarov (1970) and Zarenkov (1970).

The present paper is intended to provide well-defined base-line values for the biomass parameters necessary as a basis for subsequent biochemical analysis. The paper is collaborative with no senior author; the sampling procedure and biological interpretation are described and discussed by A.C., the numerical and biomathematical aspects of the study are the responsibility of K.H.L.

## MATERIALS AND METHODS

The prevailing population of *C. antarcticus* at King Edward Cove, South Georgia (lat. 54°17'S., long. 36°30'W.), was sampled at approximately monthly intervals throughout 1972–73 using a 0·5 m. Agassiz trawl. Sampling was limited to areas relatively free of kelp (*Macrocystis pyrifera*) and soft mud, as these areas tended to produce damaged prawns unsuitable for biochemical work.

15 min. trawls were made along one of the sampling transects (Fig. 1) at the fastest speed compatible with efficient trawling. Prawns were placed immediately in clean sea-water for transport to the laboratory, where they were kept in aerated sea-water until required for analysis. Measurements of fresh weight, dry weight, ash weight and carapace length were made on individual specimens. In some months the catch of very small prawns was high and a number

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† Nomenclatural changes in decapods have been frequent; synonyms and taxonomic authorities are given in the Appendix.
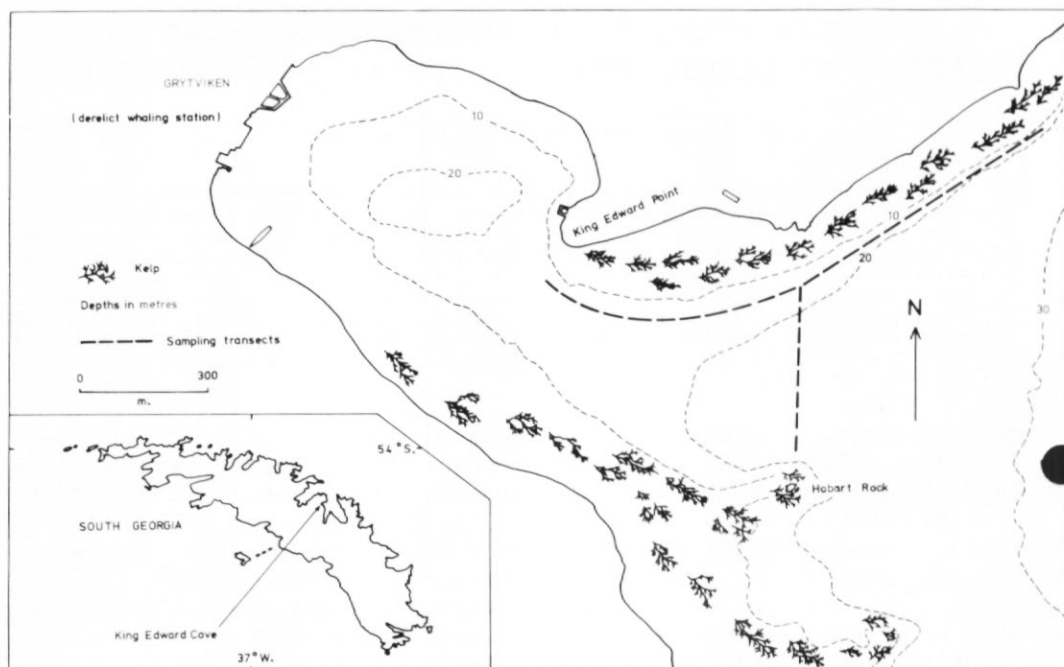
Fig. 1. King Edward Cove, Cumberland East Bay, South Georgia, showing the location of the sampling transects.

of these tended to die before their fresh weights could be measured. Since the water content of a prawn may change after death, dry weight only was measured in these prawns.

Fresh weight was measured after rapid but gentle blotting on a filter paper; the smooth folded edge of another filter paper was used to remove sea-water trapped by surface tension among the bases of the appendages. For comparative purposes, one sample was washed briefly (less than 2 sec.) in distilled water before blotting and weighing. Eggs were removed from ovigerous (berried) females by gentle coaxing with a spatula, rapidly counted and analysed separately.

Dry weight was measured after drying for 48 hr. in an oven at $60°$ C. Although small prawns had reached a steady dry weight after 12–24 hr., up to 48 hr. drying was necessary for the large specimens.

Ash weight was measured after ignition for 12 hr. in a muffle furnace at either $550°$ or $800°$ C. After both drying and ashing, specimens were allowed to cool in a desiccator, over fresh silica gel or anhydrous $P_2O_5$. Drying and ashing at $550°$ C were carried out on numbered microscope slides which were checked for changes in weight. Ignition at $800°$ C was carried out in vitreosil crucibles which were also checked for changes in weight. Weight changes in prawns during weighing were monitored and found to be negligible. All weighings were made to the nearest $0·2$ mg.

Carapace length was measured to the nearest $0·1$ mm. with vernier calipers. Measurements were taken from the rear of the eye socket to the rear edge of the carapace in the mid-dorsal line.

Though the actual sampling effort was comparable from month to month, there is no direct way of assessing from the sample data whether the sampled catch was proportional to the prevailing population. Each monthly sample provided sufficient material for the biochemical

analyses but the number of prawns collected varied from 30 to 212. Newly metamorphosed post-larvae were found to be associated with the benthic algae and the sampling procedure is thus likely to have been biassed against the very early post-larvae.

## RESULTS AND DISCUSSION

### Fresh weight and dry weight

#### The measurement of fresh weight

The problem of obtaining accurate and reproducible values for the fresh weight and dry weight of bulk plankton samples was thoroughly investigated by Lovegrove (1966). A major difficulty in the measurement of fresh weight is that the internal water of a marine animal is in a state of dynamic equilibrium with the surrounding sea-water and the permeability of the outer surface can allow rapid loss of this internal water when the animal is exposed to air during weighing. This problem is particularly acute for small animals where the surface area: volume ratio is high and Weiser (1960), working with interstitial meiofauna, went so far as to dismiss fresh weight as a meaningful parameter at all.

In crustaceans the presence of a chitinous exoskeleton generally reduces the rate of evaporation of water from the body fluids, although Bogorov (*in* Lovegrove, 1966) reported losses of up to 39 per cent of the fresh weight from specimens of the euphausiid *Thysanoessa inermis* and the amphipod *Themisto abyssorum* during 10 min. exposure to air, and recommended that fresh weights should be measured within 3 min. of removing the animals from sea-water. Control runs were made for *C. antarcticus* and it was found that blotting excess sea-water from a specimen, measuring the carapace length and weighing could be performed in less than 1 min., and that no significant loss of weight occurred within 1–1½ min. exposure to air except in the very smallest prawns.

A second source of error in fresh-weight determinations of marine animals is the trapping of sea-water among the appendages. Many methods have been used to remove this sea-water and techniques suggested have included draining (Clarke and Bishop, 1948), straightforward blotting (Krey, 1958), washing with fresh water (Orr, 1934; Nakai, 1955; Lovegrove, 1966) and rapid washing with alcohol (Bogorov, 1934).

Blotting can cause significant damage to bulk samples of small delicate organisms (Clarke and Bishop, 1948); Orr (1934) even recorded rupturing of the oil sac of stage V *Calanus finmarchicus*, with consequent loss of much organic material, by merely transferring the copepods from one container to another. Nevertheless, gentle blotting proved excellent for even the smallest *C. antarcticus*. The rounded edge of a folded filter paper was found to be a rapid and effective method of removing the remaining sea-water trapped by surface tension among the pleopods and thoracic appendages.

Several workers have used washing to remove adhering sea-water. Washing can, however, also remove significant amounts of internal salts and organic material. Clarke and Bishop (1948) washed bulk zooplankton samples consisting largely of copepods by pouring distilled water over the sample and squeezing. This procedure removed 65 per cent of the chloride and 55 per cent of the magnesium from the sample, probably by rapid osmotic removal from internal body fluids as well as mechanical damage.

Examination of dried unwashed *C. antarcticus* revealed no encrusting salt crystals, and a comparison of results obtained from samples of washed and unwashed prawns collected at the same time of year revealed no marked differences. The regression relationships between dry weight and fresh weight, and between ash weight and dry weight were comparable for washed and unwashed prawns (Figs. 2 and 3), and the hypothesis of the equality of the regression parameters was not rejected by the standard significance testing procedure.

The fresh weights, dry weights and ash weights of the *C. antarcticus* specimens in the present
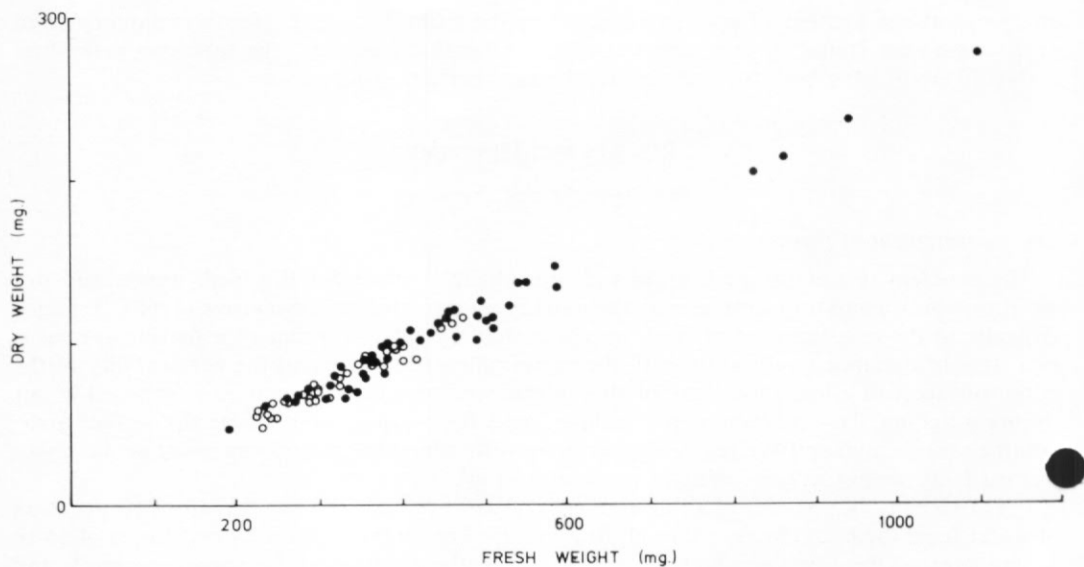
Fig. 2. Linear regression of dry weight on fresh weight for *Chorismus antarcticus;* South Georgia.
● Unwashed prawns, February 1972.
  Dry weight ∼ 0·244 fresh weight.
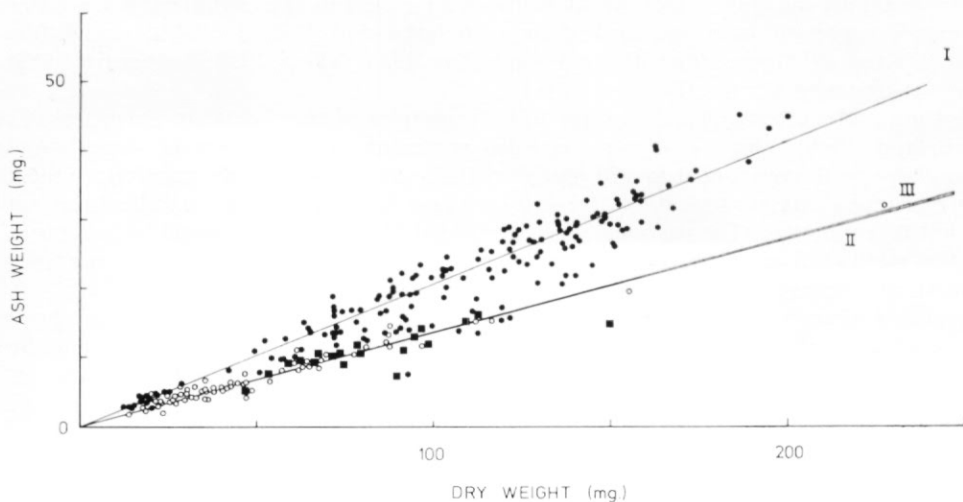○ Washed prawns, February, 1973.
  Dry weight ∼ 0·237 fresh weight.



Fig. 3. Linear regression of ash weight on dry weight for *Chorismus antarcticus;* South Georgia, 1972–73.
● Unwashed prawns, ashed at 550° C, line I.
  Ash weight ∼ 0·2057 dry weight.
○ Unwashed prawns, ashed at 800° C, line II.
  Ash weight ∼ 0·1353 dry weight.
■ Washed prawns, ashed at 800° C, line III.
  Ash weight ∼ 0·1367 dry weight.

study were based on unwashed samples, but the results and relationships obtained are unlikely to be much different from those that might have been obtained using washed specimens.

### Fresh weight/dry weight relationship and moulting behaviour

It is not possible to assess directly the pattern of moulting behaviour in *C. antarcticus*, since individual specimens were not examined to determine moult stage. The process of moulting does, however, result in an increased water content immediately after ecdysis. This will affect the relationship between fresh weight and dry weight in the population, and thus a planned analysis of the weight measurements obtained should yield an understanding of certain features of the pattern of moulting behaviour.

Moulting in *C. antarcticus* is likely to be influenced by factors such as season and the age of the individual. The first analysis of the weight measurements was therefore a broad examination of the effects of these two factors on the relationship between fresh weight and dry weight in the sampled prawns.

The data for each month were divided into two weight groups, 0–50 mg. dry weight and over 50 mg. dry weight. This grouping was based on a study of the weight distributions of the month-ly samples and it approximately divided the sampled prawns into young specimens (under 1 yr. old from the date of metamorphosis) and older specimens (see Table V). Separately, for each month and for each of the two weight groups, the regression relationship of dry weight on fresh weight was examined, using the elementary model $y_i = \beta x_i + z_i$, where $y_i$ and $x_i$ denote respectively the dry- and fresh-weight observations and $z_i$ is the associated error term. This simple model was found to be remarkably adequate. Thus, in 19 out of 22 analyses, the model accounted for more than 90 per cent of the total observed variation in the dependent variable, and in 14 of these the actual variation explained was from 95 to 99 per cent. For the remaining three sets of data, the model accounted for 64, 68 and 84 per cent of the total observed variation, but the scatter diagrams showed that the model was nevertheless appropriate and that the apparent poor performance was due to the small observed range of the independent variable.

The estimate, $\hat{\beta}$, of $\beta$ varied from one set of data to the next. Fig. 4 shows, separately for the two weight groups, the values of $(1-\hat{\beta})$, the estimate of the proportionate water content, and their 95 per cent confidence limits plotted against the sampling dates. The younger prawns had a significantly higher water content and the prawns in both weight groups displayed a similar seasonally fluctuating pattern of low water content during the winter months of May–August, and high water content during the summer months of December–March. This is interpreted as indicating an increased rate of moulting in summer compared with winter, and in young prawns compared with older prawns. Superimposed on this cyclical trend was a large upward movement in the water content of both young and older prawns in October.

The size of the prawns changed with time, and so, in the above interpretation of Fig. 4, it is possible that the seasonal effect and the effect of growth masked each other. The data for each month were therefore divided into a number of narrower weight classes; the estimates of the proportionate water content for the prawns in these weight groups are shown in Fig. 5. This clearly supports the earlier interpretation of Fig. 4 and confirms that prawns of all size groups showed an increased water content in October.

A comparison of Figs. 4 and 5 with the estimated growth curve (Fig. 10) shows that a high growth rate and increased moulting activity (as indicated by an elevated water content) both occurred in the relatively warmer summer months (cf. Fig. 6). It is of interest that at the time of the observed increase in water content of the prawns in October, the estimated growth curve indicated a decline in the mean dry weight of the prawns. While a second recruitment of post-larvae in October would also lead to a decreased mean dry weight and an increased population water content, the available evidence of the life history makes a second recruitment in October unlikely (cf. p. 76). Furthermore, recruitment of post-larvae in October cannot explain the increase in water content in prawns of all sizes.
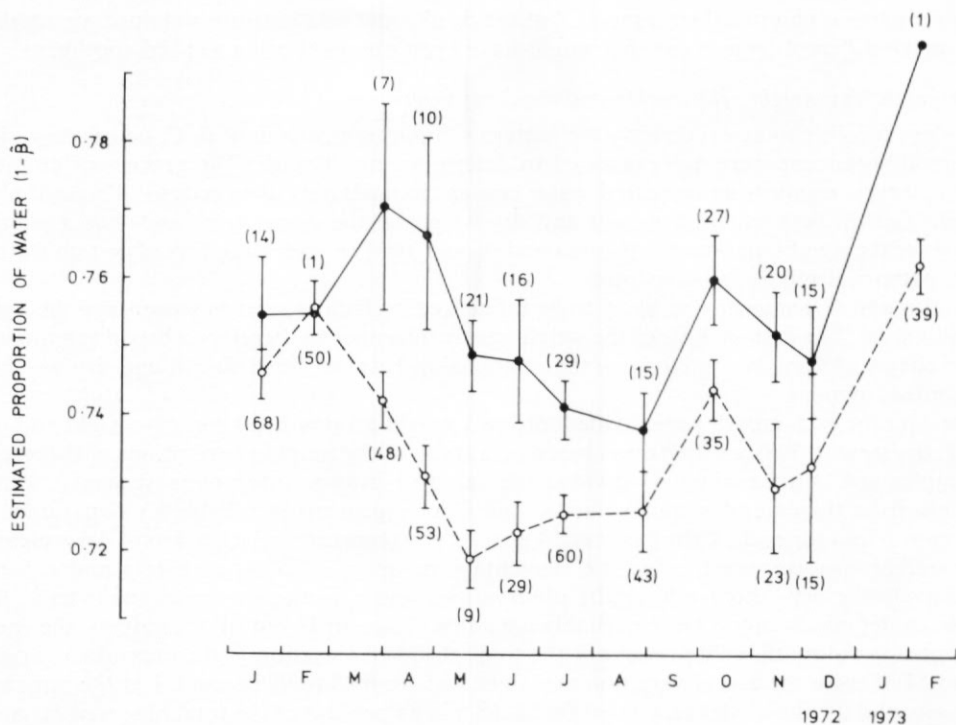
Fig. 4. Seasonal changes in the water content of *Chorismus antarcticus;* South Georgia, 1972–73. Data are presented as means with estimated 95 per cent confidence intervals; sample size in brackets.
●————● Prawns under 50 mg. dry weight.
○— — — ○ Prawns over 50 mg. dry weight.

A conjectural explanation is that, although growth and moulting are associated, the immediate effect of ecdysis is a decrease in the dry weight of the individual. It may therefore be possible for the observed mean dry weight of a population of prawns to decline temporarily if a large number of individuals were to moult almost simultaneously. It may therefore be that, following a period of low growth and moulting activity during winter, the prawn population showed an enhanced and almost synchronous moulting in the spring month of October, resulting in an elevated water content in the prawns and contributed to the reduction in the observed mean dry weight of the population.

An alternative approach for analysing the weight data is to calculate the percentage dry weight/fresh weight for each individual prawn and examine the frequency distribution of these values. Table I shows the observed frequencies of the percentage dry-weight values of the prawns in the two weight groups for each month. An examination of this table indicates, as would be expected, a similar pattern to that shown by Figs. 4 and 5. Thus, for both weight groups the percentage dry-weight values were relatively low in the warmer months (January–April) and relatively high in the colder months (June–August). Also, for each month the smaller of the two size groups showed relatively lower percentage dry-weight values. Although individual prawns were not systematically examined for moult stage, all those prawns with very high water contents (i.e. >80 per cent) had obviously just moulted, having a very soft exoskeleton when fresh and a wrinkled appearance when dried.

It is thus likely that the observed differences in water content were due mainly to the differences in moulting behaviour between the younger and older prawns, and between summer
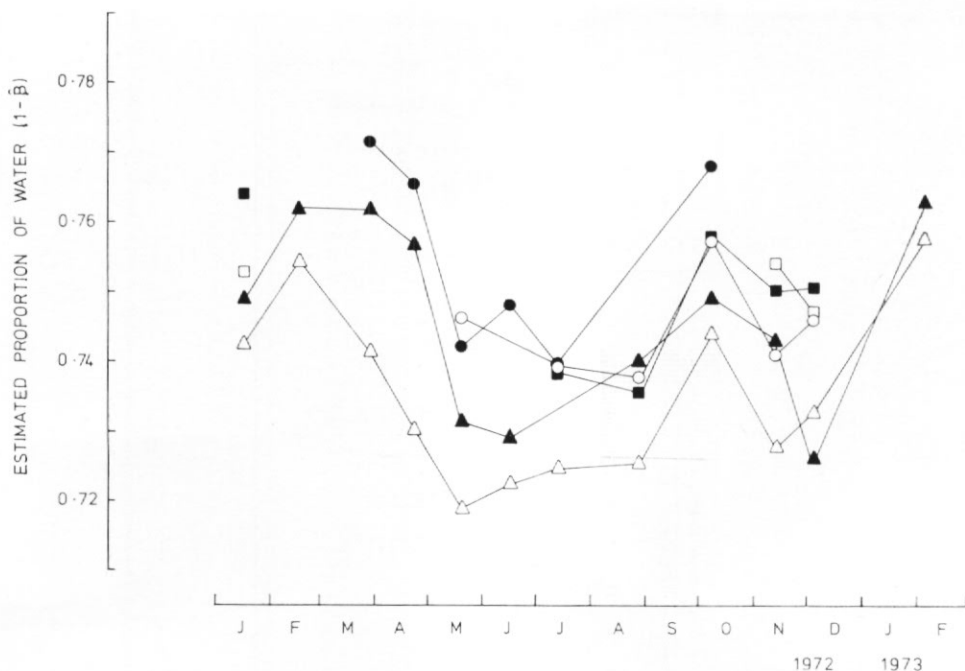
Fig. 5. Seasonal changes in the mean water content of *Chorismus antarcticus;* South Georgia, 1972–73.
- ● 10–20 mg. dry weight.
- ○ 20–30 mg. dry weight.
- ■ 30–40 mg. dry weight.
- □ 40–50 mg. dry weight.
- ▲ 50–100 mg. dry weight.
- △ >100 mg. dry weight.

and winter. The alternative possibility that the water content of *C. antarcticus* fluctuated with external water temperature must, however, also be considered. Though there is no direct information on the ability of *C. antarcticus* to regulate its water content, Spaargaren (1971) found that at normal salinities, the shrimp *Crangon crangon* was able to regulate its internal water content within the temperature range 15–21° C. In addition, a study of the prawns *Palaemon serratus* and *Lysmata seticaudata* included comparisons of the water content of whole prawns at 4° and 22° C and at different salinities (Spaargaren, 1972). These comparisons showed no firm correlation between environmental temperature and internal water content. In three of the seven comparisons given in Spaargaren's table II, the observed water content was lower at the high temperature. Two of the seven comparisons indicated statistically significant differences in water content at the different temperatures, and one of these showed a significantly lower water content at 22° C. In the case of *C. antarcticus*, the observed annual temperature variation at South Georgia was over a fairly narrow range of −0·3° to +3·5° C (Fig. 6) and the observed water content of the prawns was consistently higher at the warmer temperature. The estimated growth rates were also higher in these months. It is normal for growth in crustaceans to be associated with warmer water temperatures, and for increased moulting activity to be associated with this increased growth rate. The observed pattern of fluctuation in the water content of *C. antarcticus* is therefore interpreted as indicative of moulting behaviour rather than a physical temperature-related phenomenon.

A decrease in the proportion of recently moulted shrimps with increasing size was noted by Allen (1960) with samples of *Crangon allmanni* from Northumberland. A relatively high rate of

TABLE I. FREQUENCIES OF PERCENTAGE DRY-WEIGHT VALUES FOR *Chorismus antarcticus;* SOUTH GEORGIA, 1972–73

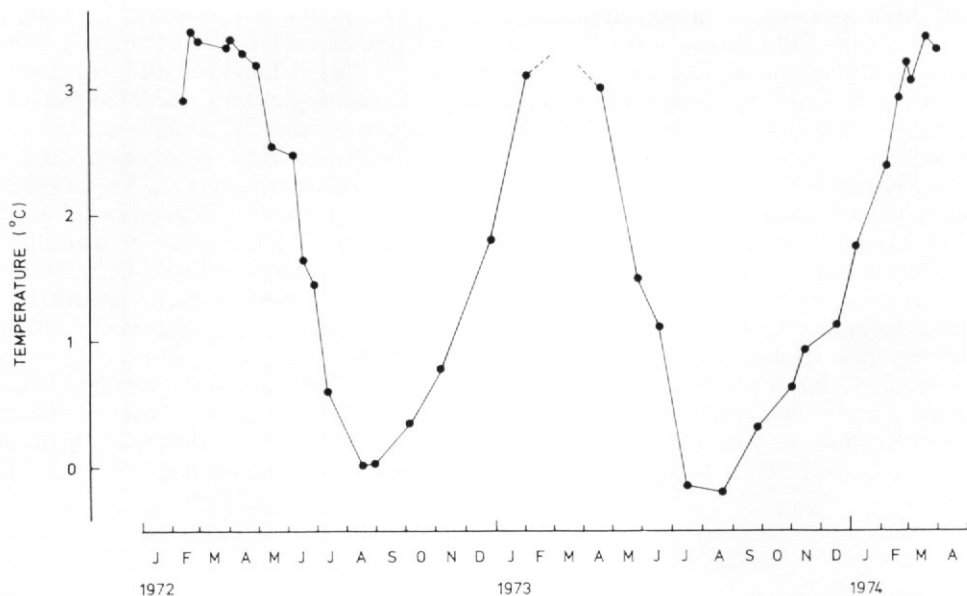| Percentage dry weight | 0–50 mg. dry-weight class | | | | | | | | | | | | | | >50 mg. dry-weight class | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | J | F | M | A | M | J | J | A | S | O | N | D | J | F | J | F | M | A | M | J | J | A | S | O | N | D | J | F |
| 17–18 | | | | | | | | | 1 | | | | | | | | | | | | | | | | | | | |
| 18–19 | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
| 19–20 | | | 1 | | | | | | | | | | | | 1 | 1 | | | | | | | | | | | | |
| 20–21 | | | 3 | | | | | | 1 | | | | | 1 | 1 | 2 | | | | | | | 2 | | | | | 1 |
| 21–22 | 1 | | 1 | | | | | | 1 | 1 | | | | | 1 | 4 | 2 | | | | | | | | | | | 4 |
| 22–23 | 1 | | 1 | | | 2 | | | 1 | 1 | 1 | | | | 1 | 6 | 3 | 1 | | | 2 | | | | 2 | | | 5 |
| 23–24 | 3 | | 4 | 2 | 1 | 2 | 2 | 1 | 5 | 1 | 4 | | | | 2 | 7 | 3 | 4 | | | 2 | 1 | | | 2 | 2 | | 8 |
| 24–25 | 2 | 1 | 1 | 2 | 4 | 1 | 3 | 1 | 7 | 3 | 1 | | | | 14 | 10 | 9 | 2 | | 1 | 2 | 2 | | 7 | 1 | 2 | | 16 |
| 25–26 | 6 | | | 2 | 9 | 6 | 7 | 4 | 6 | 9 | 3 | | | | 21 | 17 | 11 | 6 | | 1 | 11 | 5 | 15 | 9 | 2 | | | 5 |
| 26–27 | 1 | | | | 5 | 3 | 12 | 5 | 4 | 5 | 4 | | | | 22 | 3 | 15 | 9 | 2 | 12 | 12 | 8 | 7 | 4 | 1 | | | |
| 27–28 | | | | | 1 | 1 | 5 | 4 | 1 | | 2 | | | | 5 | | 4 | 17 | 3 | 9 | 22 | 18 | 4 | 5 | 3 | | | |
| 28–29 | | | | | 1 | 1 | | | | | | | | | | | 1 | 12 | 4 | 5 | 9 | 5 | | | 1 | | | 4 |
| 29–30 | | | | | | | | | | | | | | | | | | | 2 | | 1 | | 2 | | | 2 | | |
| 30–31 | | | | | | | | | | | | | | | | | | | | | | | | | | 1 | | 1 |

Fig. 6. Water temperature at 10–15 m. depth, near Hobart Rock, King Edward Cove, South Georgia, 1972–73. (Data from Grantham, 1973; Tappin, 1974; Berry, 1975.)

moulting in the younger stages has also been recorded in the prawns *Palaemonetes varians* (Jeffries, 1964) and *Caridina weberi* (Nagabhushanam and Chinnayya, 1972), the lobsters *Panulirus argus* (Travis, 1954) and *Homarus americanus* (Herrick, 1911) and the crabs *Pachygrapsus crassipes* (Hiatt, 1948) and *Callinectes sapidus* (Churchill, 1917–18). In many cases this increased rate of moulting is associated with an increased relative growth rate (measured variously as length, breadth, fresh weight or dry weight) and this is probably general among decapods.

Similarly, seasonal variations in the proportion of recently moulted specimens in samples were found with *Crangon allmanni* and *Pandalus montagui* by Allen (1960, 1963). Increased moulting in summer has also been recorded in the prawns *Palaemon serratus* (Drach, 1944), *Palaemon xiphias* (Scheer, 1960), *Palaemonetes varians* (Jeffries, 1964), *Penaeus japonicus* (Choe, 1971) and *Caridina weberi* (Nagabhushanam and Chinnayya, 1972). This increase in moulting during summer is usually ascribed to the effect of the rise in water temperature, which is often much greater than the 3–4° C rise recorded at South Georgia. Lloyd and Yonge (1947) found a range of intermoult periods of 13–30 days in summer for *Crangon crangon* of total lengths 30–40 mm. from the Severn estuary; this increased to 60–70 days in winter. However, in the warmer waters around Monaco the summer range was only 10–12 days (Nouvel-Van Rysselberge, 1937). In *Alpheus armillatus*, Darby (1938) found no relationship between moulting and water temperature but a careful examination by Hess (1941) showed that the moulting of this shallow-water snapping shrimp was apparently governed by the temperature of the water in the tidal pools in which it lives, this temperature in turn being affected primarily by the day-time air temperature. Moulting thus took place solely by day when the water temperature had increased above 29° C; there was, however, no mention of any seasonal variation. An increased rate of growth in summer has been described for the Australasian *Metapenaeus bennettae* (Dall, 1958) and the American *Penaeus setiferus* (Linder and Anderson, 1956) but the probable associated increase in moulting was not mentioned.

Seasonal variations in the moulting rate of crabs have long been known and these too have

usually been ascribed to the direct influence of environmental temperature. In Maryland, U.S.A., the soft-crab industry which depended on the annual exploitation of recently moulted blue crabs, *Callinectes sapidus*, ceased from October to May (Churchill, 1917–18). Decrease of moulting in winter has also been recorded in *Cyclograpsus punctatus* (Broekhuysen, 1941) and *Pachygrapsus crassipes* (Hiatt, 1948), which was found to cease moulting in the laboratory when the water temperature fell below 14 °C. Roberts (1957), investigating oxygen uptake, kept *P. crassipes* at $8 \cdot 5$ °C in order to halt moulting altogether. Broekhuysen (1936) considered that *Carcinus maenas* moulted only twice a year when sexually mature, moults occurring only between May and September with males moulting on average 2 months earlier than females. The moulting rate of juvenile *C. maenas* is, however, influenced markedly by temperature (Klein Breteler, 1975). In *Cancer pagurus* the length of the moulting period is different in northern waters from the warmer waters off south-west England, where the moulting period can be greatly extended (Williamson, 1900; Bennett, 1974).

The lobsters, *Panulirus argus* and *Homarus americanus*, also both show strongly seasonal moulting patterns with moulting largely during summer, the moulting peak in *Homarus* occurring at different times in different areas (Herrick, 1911; Travis, 1954). The pattern of moulting in *C. antarcticus*, as indicated by population water content, is thus typical of decapods in general.

### Mature females

Table II shows the observed percentage dry-weight frequencies for those prawns which were either ovigerous or had a fresh weight of over 1,200 mg. Since *C. antarcticus* is a protandrous

TABLE II. FREQUENCIES OF PERCENTAGE DRY-WEIGHT VALUES FOR OVIGEROUS AND MATURE (FRESH WEIGHT >1,200 mg.) FEMALE *Chorismus antarcticus*; SOUTH GEORGIA, 1972

| Percentage dry weight | Ovigerous period | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | J | F | M | A | M | J | J | A | S | O | N | D |
| 22–23 | | | | | | | | | | 1 | | |
| 23–24 | | | | | | | | | | | | |
| 24–25 | | 1(1) | | | | | | | | 1(1) | 1 | 2 |
| 25–26 | | | 1 | | | | | | | 4(1) | | 2 |
| 26–27 | | | 1(1) | | | | | | | 1(1) | | |
| 27–28 | | | | | 2(2) | 1(1) | 3(1) | 2 | | 1(1) | | 1 |
| 28–29 | | | 1 | | 4(4) | | 4(2) | 2(1) | | | | |
| 29–30 | | | | | | | 1 | 1(1) | | | | 1 |
| 30–31 | | | | | | | | | | | 1 | 1 |

Unbracketed figures: total number of females; figures in brackets: number of ovigerous females.

hermaphrodite (Yaldwyn, 1966; Maxwell, 1977), this group will have included only mature or ovigerous females. In calculating the percentage dry-weight values for ovigerous females, egg weights were excluded. Only a few females were observed each month; none was found moulting and the percentage dry-weight values were generally higher than for younger specimens. The spring month of October showed relatively lower percentage dry-weight values, supporting the earlier data (Fig. 5).

Female prawns and shrimps tend to moult only twice during the later stages of sexual

maturation: once prior to the onset of ovary maturation and once prior to spawning (Lloyd and Yonge, 1947). In *C. antarcticus* with an increased reproductive span characteristic of polar marine invertebrates (Thorson, 1950; Maxwell, 1977), these together with a post-ovigerous moult may result in as few as three moults per year in mature females.

### Total water content

Because of the large natural variation in total water content apparent from Figs. 4 and 5, and Table I, it is difficult to give a single value for the water content of a prawn for comparison with other species. A representative value has been estimated separately for prawns less than 50 mg. dry weight and greater than 50 mg. dry weight. Since moulting is thought to be reduced during the winter months of May–August, the water contents of the prawns sampled during these months approximate to the intermoult water content. It can be seen from Fig. 4 that the estimates of water content for these months ranged from $0 \cdot 738$ to $0 \cdot 749$ in younger prawns and from $0 \cdot 719$ to $0 \cdot 726$ in the older ones; water content in the younger prawns was thus $\sim 2$ per cent higher than in the older ones. For each size group a single overall estimate was derived by pooling the data for the 4 winter months and calculating an overall regression of dry weight on fresh weight. The resultant calculated mean water contents with standard errors obtained for the two weight groups are compared with data for other decapods in Table III.

Although *C. antarcticus* falls in the centre of the data for shrimps and prawns, it must be noted that many other determinations were based on small samples with no allowance for possible disturbances caused by moulting activity. The water contents of crabs and lobsters are generally lower due to their relatively thicker exoskeletons.

### Water uptake at ecdysis

If $F$ and $D$ denote the fresh and dry weights of a pre-moult prawn, $F'$ and $D'$ the fresh and dry weights of the same individual immediately after ecdysis (when water content is at a maximum), and $f$ and $d$ are the fresh and dry weights of the cast exoskeleton, then the water contents of the pre-moult and post-moult prawns and of the cast exoskeleton are respectively: $W = F - D$, $W' = F' - D'$ and $w = f - d$. The water uptake at ecdysis is then $W' + w - W$.

The estimation of the water uptake at ecdysis by *C. antarcticus* involved a number of assumptions and approximations based on limited information. It was assumed that the four individuals thought to have just moulted (cf. p. 66) had water contents close to the maximum reached during ecdysis, i.e. the observed weight measurements provided values of $F'$, $D'$ and hence $W'$. A small number of prawns maintained alive in the laboratory provided values for the post-moult prawn dry weight and the dry weight of the corresponding cast exoskeleton for two individuals. These were $310 \cdot 3$, $41 \cdot 19$ and $35 \cdot 5$, $5 \cdot 25$ mg. respectively for each prawn, suggesting the approximation $d \sim 0 \cdot 14 \, D'$ (i.e. at ecdysis the dry weight lost in the exoskeleton is approximately 14 per cent of the dry weight of the post-moult prawn) and hence $D (= D' + d) \sim 1 \cdot 14 \, D'$. Further, assuming that the water content of the cast exoskelton is 70 per cent of its fresh weight (mean of two determinations for *Palaemon serratus*; data from Panikkar (1941)) gave the approximation $w \sim 2 \cdot 33 \, d \sim 0 \cdot 326 \, D'$. Finally, the fresh- and dry-weight data for the winter months May–August (when moulting was thought to be reduced) were pooled to derive regression relationships for estimating the fresh weight of a pre-moult prawn, given its dry weight. Separate relationships were calculated for prawns of dry weight over and under 50 mg. dry weight. These were used to estimate the pre-moult fresh weights ($F$) of the four freshly moulted individuals, and hence also their pre-moult water contents, $W$. Using $W'$ and the estimates of $W$ and $w$, the water uptake at ecdysis was estimated for these four individuals.

Previous estimates for other species of decapod have involved measurement and expression of the water uptake at ecdysis in a variety of ways. In Table IV the results for *C. antarcticus* are compared with these other determinations, expressing both water uptake as a percentage

TABLE III. INTERMOULT WATER CONTENT OF DECAPOD CRUSTACEA ADAPTED TO NORMAL TEMPERATURE AND SALINITY

| Species | Water content (per cent fresh weight) (mean ± std error) | (n) | Reference |
|---|---|---|---|
| NATANTIA | | | |
| *Lysmata seticaudata* | 69·3 ±0·29 | (6) | Spaargaren, 1972 |
| *Sicyonia carinata* | 70·2 ±0·36 | (6) | Spaargaren, 1972 |
| *Palaemon serratus* | 71·0 ±2·6 | (6) | Spaargaren, 1972 |
| | 72·7 | (1) | Panikkar, 1941 |
| *Pontocaris cataphracta* | 72·8 ±0·33 | (6) | Spaargaren, 1972 |
| *Chorismus antarcticus* | | | |
| 0–50 mg. dry weight | 74·28±0·13 | (81) | This paper |
| >50 mg. dry weight | 72·33±0·11 | (141) | This paper |
| *Crangon allmanni* | 74·9 ±0·71 | (5) | Grimm, 1965 |
| *Crangon crangon* | 74–75 | | Spaargaren, 1971 |
| | 75·8 ±0·82 | (5) | Grimm, 1965 |
| *Penaeus indicus* | 75·5 | | Greshov (*in* Vinogradov, 1953) |
| *Notocrangon antarcticus* | 78·7 | (3) | This paper |
| *Penaeus brasiliensis* | 80·0 | | Nilson and Coulson (*in* Vinogradov, 1953) |
| | | | |
| REPTANTIA | | | |
| *Xantho incisus* | 57·2 | (4) | Drach, 1939 |
| *Cancer pagurus* | 62·2 | (7) | Drach, 1939 |
| *Callinectes sapidus* | 62–67 | | Haefner, 1964 |
| *Carcinus maenas* | 65·3 | (8) | Drach, 1939 |
| | 65·4 | (5) | Robertson, 1960 |
| *Hemigrapsus oregonensis* | 66·6 (♂) | | } Olmstead and Baumberger, 1923 |
| | 68·7 (♀) | | |
| *Uca pugilator* | 67·9 | | Guyselman, 1953 |
| *Pachygrapsus crassipes* | 68·8 (♂) | | } Olmstead and Baumberger, 1923 |
| | 64·7 (♀) | | |
| *Maja squinado* | 69·2 | (4) | Drach, 1939 |
| *Macropipius vernalis* | 69·3 | (5) | Drach, 1939 |

TABLE IV. Uptake of water at ecdysis in decapod Crustacea

| Species | Intermoult fresh weight | n | Percentage water uptake — Intermoult fresh weight (mean ± std error) | Post-moult water — Intermoult water (mean ± std error) | Reference |
|---|---|---|---|---|---|
| **CARIDEA** | | | | | |
| *Chorismus antarcticus* | 333·3 mg. | 1 | 33·25 | 1·35 | This paper |
| | 304·9 mg. | 1 | 34·32 | 1·36 | This paper |
| | 74·8 mg. | 1 | 39·70 | 1·43 | This paper |
| | 52·1 mg. | 1 | 23·83 | 1·22 | This paper |
| *Palaemon serratus* | 1,135·5 mg. | 1 | 25·06 | 1·30 | Panikkar, 1941. Re-calculated from original data to take into account loss of dry weight and water in cast exoskeleton |
| **MACRURA** | | | | | |
| *Homarus gammarus* | 158 g. | 1 | 46·61 | 1·70 | Lowndes and Panikkar, 1941 |
| *Panulirus argus* | 519–669 g. | 6 | 18·8 ± 0·013 | 1·27 ± 0·02 | Travis, 1954 |
| **BRACHYURA** | | | | | |
| *Carcinus maenas* | 16–68 g. | 8 | 66·3 ± 7·03 | 2·01 | Robertson, 1960 |
| *Uca pugilator* | 1·54–1·96 g. | 3 | 42·9 ± 5·54 | 1·63 ± 0·08 | Guyselman, 1953 |
| *Pachygrapsus crassipes* | | 22 | 33·9 | | Olmstead and Baumberger, 1923; Baumberger and Olmstead, 1928 |
| *Hemigrapsus oregonensis* | | 19 | 44·9 | | Olmstead and Baumberger, 1923; Baumberger and Olmstead, 1928 |
| *Maja squinado* | 48–292 g. | 27 | 124·9 ± 3·71 | 2·82 ± 0·05 | Drach, 1939 |
| *Cancer pagurus* | 5–118 g. | 22 | 94·2 ± 2·49 | 2·51 ± 0·04 | Drach, 1939 |
| *Xantho incisus* | 3–24 g. | 7 | 18·8 ± 0·013 | 1·91 ± 0·11 | Drach, 1939 |

of the pre-moult fresh weight, and also immediate post-moult water content as a fraction of the intermoult water content. Most previous determinations have been for crabs and, although there is much variation, these are consistently higher than the values for *C. antarcticus*.

## Mineral ash content

### The effect of the ashing temperature

A wide variety of ignition temperatures has been used in determining the ash content of biological material, ranging from 500° C (Raymont and others, 1969) to 1300° C (Giese, 1966). Measurements made at different temperatures are, however, unlikely to be comparable. Grove and others (1961) investigated the loss of specific minerals from blood and serum samples ashed at various temperatures. They found that within 24 hr. at 450–500° C losses of $Na^+$ and $K^+$ were insignificant and that most of the carbon was burnt. By about 700–900° C up to 90 per cent of the $K^+$, and 40–70 per cent of the $Na^+$ had been volatilized. Paine (1964) found that above 600° C there was a steady loss of $CaCO_3$ by decomposition to CaO, and that at 825° C decomposition was complete. Since $Na^+$, $K^+$ and $CaCO_3$ are all major constituents of crustacean tissue (Clarke and Wheeler, 1922; Vinogradov, 1953; Kobyakov and Saprykin, 1973), ashing at 1000° C will lead to low results. The commonly used ashing temperature of 800° C will also yield low results and in addition the data may show increased variability caused by incomplete volatilization of certain fractions.

Additional difficulties with organisms containing large amounts of $CaCO_3$ or silica include the retention of relatively large amounts of crystal lattice water at conventional "drying" temperatures and its subsequent loss during ignition (Paine, 1964; Dayton and others, 1974). This water content can be allowed for if the proportion of $CaCO_3$ or silica in the ash is known and both drying and ashing are carefully controlled. Guyselman (1953) attempted to circumvent this problem by determining $CaCO_3$ content separately and then ashing at 1150° C.

During bomb calorimetry, temperatures can rise in excess of 1000° C and hence measurement of ash as the residue after firing will also lead to low results, with the added complication of heat exchange during decomposition of the mineral salts possibly affecting the calorimetry results (Paine, 1964).

In order to estimate the losses at higher ashing temperatures, prawns were ashed at both 550° and 800° C, and the regression relationships of the ash weight on dry weight examined. Simple straight-line relationships through the origin were found to be adequate; these are shown in Fig. 3. The estimates of the slopes of lines I and II in Fig. 3 show that the additional loss of ash by increasing the ashing temperature from 550° to 800° C is about 34 per cent of the ash content at 550 °C. This volatilized fraction is presumably largely $Na^+$, $K^+$ and $CO_2$ from $CaCO_3$.

The different ashing temperatures used by various authors make a comparison of result difficult. The data for *C. antarcticus* ashed at 550° C are, however, typical of small decapods ashed at about this temperature (see, for example, Raymont and others, 1969).

### The effect of moulting

The mineral constituents of decapods are known to undergo fluctuations with environmental salinity (Haefner, 1964; Spaargaren, 1971, 1972), season (Colvocoresses and others, 1974) and the moult cycle (Robertson, 1960; Haefner, 1964; Hagerman, 1973). At ecdysis, casting of the exoskeleton results in the loss of a substantial amount of mineral ash, although this may be offset to a slight extent by resorption from the old cuticle prior to moulting (Travis, 1954; Robertson, 1960), intake of sea water during ecdysis and subsequent eating of the cast exoskeleton.

The percentage loss of ash at ecdysis is 100 $(m/M)$, where $m$ and $M$ are the ash contents of the cast exoskeleton and pre-moult prawn, respectively. This percentage loss of ash (at the ashing

temperature of 550° C) was estimated for *C. antarcticus* to be about 29 per cent as follows.

The ash and dry weights of 59 prawns collected during June and July (when moulting activity was thought to be low) were used to obtain the regression relationship $M \sim 0 \cdot 2242D$, the simple model accounting for 99 per cent of the observed total variation in $M$. The dry weight and ash weight of eight cast exoskeletons were obtained from prawns maintained alive in the laboratory. These data provided the relationship $m \sim 0 \cdot 5308d$, the model accounting for 82 per cent of the observed total variation in $m$. Finally, using the earlier established relationships $D = D' + d$ and $d \sim 0 \cdot 14D'$,

$$d \sim 0 \cdot 1228D$$

and hence $\qquad m \sim 0 \cdot 0652D,$

so that the estimated loss of ash at ecdysis, $100 \ (m/M)$, is of the order $100(0 \cdot 0652/0 \cdot 2242) \sim$ 29 per cent. Much of this loss is presumably $CaCO_3$ from the cuticle and it is of interest that this loss at ecdysis is similar in magnitude to the 34 per cent loss of $Na^+$, $K^+$ and $CO_2$ from $CaCO_3$ on increasing the ashing temperature from 550° to 800° C.

The actual loss to the prawn may be even higher, since in some decapods the calcium resorbed from the old cuticle is excreted rather than stored (Travis, 1955). Dall (1965), however, could detect no resorption from the cuticle prior to ecdysis in *Metapenaeus bennettae*. In the wild these losses may be offset by subsequent eating of the cast exoskeleton which has been recorded in *Palaemon longirostris* (Gurney, 1923), *Crangon crangon* (Lloyd and Yonge, 1947) and *Palaemonetes varians* (Jeffries, 1964).

### Individual moulting behaviour

Moulting was never actually observed in *C. antarcticus* but several aspects of the moulting process were noted. Moulting invariably took place at night in those prawns which moulted in the laboratory, and where possible the prawns appeared to select relatively secluded areas. The old exoskeleton separated between the cephalothorax and the first abdominal segment and one prawn found dead in the act of moulting had withdrawn the cephalothorax from the old exoskeleton before the abdomen. In these features *C. antarcticus* is consistent with the moulting process as described for *Palaemon longirostris* (Gurney, 1923), *Palaemon elegans* (Höglund, 1943), *Crangon crangon* (Lloyd and Yonge, 1947) and *Palaemonetes varians* (Jeffries, 1964). In *P. elegans* moulting also occurs by day, and in the tropical intertidal *Alpheus armillatus* it takes place entirely by day with a peak at 12.00–13.00 hr. in July (Darby, 1938; Hess, 1941). The retreat into a secluded area is probably an adaptation to avoid contact with predators during the very vulnerable immediately post-ecdysial stage, when it may even be eaten by other members of the same species (Gurney, 1923; Jeffries, 1964). On one occasion, newly moulted prawn was found partially eaten by other *C. antarcticus*. It is possible that this was aberrant behaviour induced by captivity, although Jeffries (1964) recovered similarly attacked *P. varians* in trawl samples, so cannibalism may also occur in the wild. On two occasions, prawns which had moulted in aquaria were seen to be eating their cast exoskeletons; as with cannibalism, it is difficult to know whether such behaviour is a normal occurrence in the wild.

### Growth curve

*Estimated growth curve for the early months of post-larval existence*

There is no method of accurately assessing the age of an individual prawn or shrimp. The growth curve for *C. antarcticus* cannot therefore be estimated directly from the sample data. A well-known method for constructing a growth curve applicable to those species where recruitment of the new offspring to the population occurs within a small time interval is based on the location of the weight-class peaks. A peak in the weight-class distribution is caused by

the relatively sudden influx of young into the sampled population, and the location of this peak can be followed through time in successive samples. Lakhani and Satchell (1970) used this method to obtain the growth curve of the common earthworm, *Lumbricus terrestris*. The background theory has been covered by Skellam (1967a, b).

The ovigerous period for female *C. antarcticus* lasts from the onset of the berried condition with spawning in January/February, over winter until October (Maxwell, 1977; cf. Table II). It is likely that the eggs hatch about October. Larval development is thought to last until late January/early February when metamorphosis to the first post-larval stage occurs at a carapace length of about 3 mm. (measurement taken from fig. 99 in Gurney (1937)). Gurney reported larval *C. antarcticus* in the plankton around South Georgia from November to early January, and early post-larvae in February and March (with an isolated record in July). Three small post-larvae of dry weights 5·5, 7·9 and 9·1 mg., respectively, were caught during the early sampling months. Assuming these to have recently metamorphosed, this suggests a dry weight at metamorphosis of 7·5 mg. If the carapace length at metamorphosis of 3 mm., taken from Gurney (1937), is converted to dry weight using a previously derived relationship, an estimated dry weight at metamorphosis of ∼ 8 mg. is obtained, agreeing with the estimate from the sample data. The 10–20 mg. dry-weight post-larvae were first caught in March. This observation, coupled with Gurney's report of larvae in early January and post-larvae in February and March, fixes the period of peak metamorphosis as late January/early February. As a working hypothesis, the date of metamorphosis was presumed to be 31 January, at a mean dry weight of 7·5 mg.

The sampling procedure was thought likely to be biassed against the very early post-larvae (cf. p. 63), and in the present data (Table V) the newly metamorphosed post-larvae may have been highly under-represented. Thus, the observed high frequencies in the dry-weight class 10–20 mg. were not matched by even a single recorded high frequency in the lowest dry-weight class, 0–10 mg. This relative paucity of the very young post-larvae in the sampled catch is also shown in Fig. 7, based on all the observations in Table V. The discrepancy in the observed frequencies of the earlier weight classes was too large to have been due simply to the early slow growth of the prawns (Fig. 10).

A second feature of Table V is that the observed frequencies of the larger prawns in different months were erratic. Thus, larger prawns were absent in May and September but present in relatively large numbers in adjacent months. There is no clear explanation for this. While it is possible to have large fluctuations in the sample data if the prawns are in aggregations on the sea bed, it is also possible that the larger prawns may make short-term migrations into deeper water away from the shallow-water sampling area.

Table V also shows that the weight-class distributions could be followed without much difficulty untill about 15 months after metamorphosis. By this time (April) the modal dry weight of the post-larvae was ∼ 140 mg. (Fig. 10). During the following few winter months the data were sparse and difficult to interpret, although there was no indication of any marked further growth. For this reason, all prawns of > 200 mg. dry weight were pooled.

The pattern of growth in *C. antarcticus* was estimated from the progress of the modal peaks in the monthly weight-class distributions. To reduce sampling error, the observed cumulative weight distributions were smoothed (Fig. 8). The modal weight value, M, was obtained from the smoothed weight-class distributions (Fig. 9) derived from the smoothed cumulative curves, using the elementary formula:

$$M = l + \left( \frac{d_1}{d_1 + d_2} \right) h,$$

where $l$ is the lower limit of the modal weight class,

TABLE V. DRY WEIGHTS OF ALL SAMPLED *Chorismus antarcticus;* SOUTH GEORGIA, 1972-73

| Dry weight (mg.) | J | F | M | A | M | J | J | A | S | O | N | D | J | F | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0–10 | 1 | | 1 | 1 | | | 1 | | | 2 | 1 | | | | 7 |
| 10–20 | | | 6 | 9 | 15 | 16 | 56 | 33 | 33 | 50 | 15 | 4 | | | 237 |
| 20–30 | 1 | | | | 4 | | 39 | 99 | 49 | 36 | 63 | 28 | 5 | | 324 |
| 30–40 | 3 | | | | | | 1 | 21 | 12 | 8 | 55 | 33 | 13 | | 146 |
| 40–50 | 9 | 1 | | | 2 | | 2 | | 2 | 2 | 21 | 19 | 9 | 1 | 68 |
| 50–60 | 7 | | | | | 1 | 4 | 2 | | 2 | 6 | 11 | 2 | 5 | 40 |
| 60–70 | 9 | 6 | | | 2 | 2 | 6 | 2 | 1 | 2 | 11 | 3 | 1 | 11 | 56 |
| 70–80 | 8 | 6 | 1 | 2 | 1 | 3 | 6 | 8 | | 1 | 3 | 1 | 2 | 8 | 50 |
| 80–90 | 14 | 7 | 2 | | | 3 | 9 | 8 | | 3 | 2 | 2 | | 6 | 56 |
| 90–100 | 10 | 5 | 3 | 2 | | 3 | 5 | 6 | | 2 | 1 | 3 | | 6 | 46 |
| 100–110 | 7 | 7 | 4 | 1 | | 1 | 4 | 3 | | 3 | 2 | | 1 | 1 | 34 |
| 110–120 | 7 | 8 | 5 | 3 | | 1 | | 3 | | 2 | 5 | 4 | | 2 | 40 |
| 120–130 | 4 | 2 | 8 | 9 | | 1 | 5 | 3 | | | | | 1 | 3 | 33 |
| 130–140 | 1 | 3 | 6 | 11 | | | 2 | 4 | | | | | | | 28 |
| 140–150 | 1 | 1 | 4 | 11 | | 3 | 1 | 3 | | | 1 | 2 | | | 27 |
| 150–160 | | | 6 | 10 | | 2 | | 1 | | 1 | 1 | | 1 | | 22 |
| 160–170 | | | 3 | 1 | | 3 | 3 | 2 | | 1 | 1 | 1 | 1 | | 16 |
| 170–180 | | | 1 | 1 | | 1 | 2 | | | 1 | | | | | 6 |
| 180–190 | | | 2 | 1 | | 1 | | 2 | | | | 1 | | | 7 |
| 190–200 | | | | | | | 2 | | | 2 | | | | | 4 |
| >200 | | 5 | 3 | 1 | 6 | 4 | 11 | 12 | | 20 | 8 | 8 | 10 | | 85 |
| TOTAL | 82 | 51 | 55 | 63 | 30 | 45 | 159 | 212 | 97 | 138 | 196 | 120 | 46 | 40 | 1,332 |

Detailed dry-weight data for the pooled >200 mg. dry-weight class are available on request from one of the authors (A.C.).
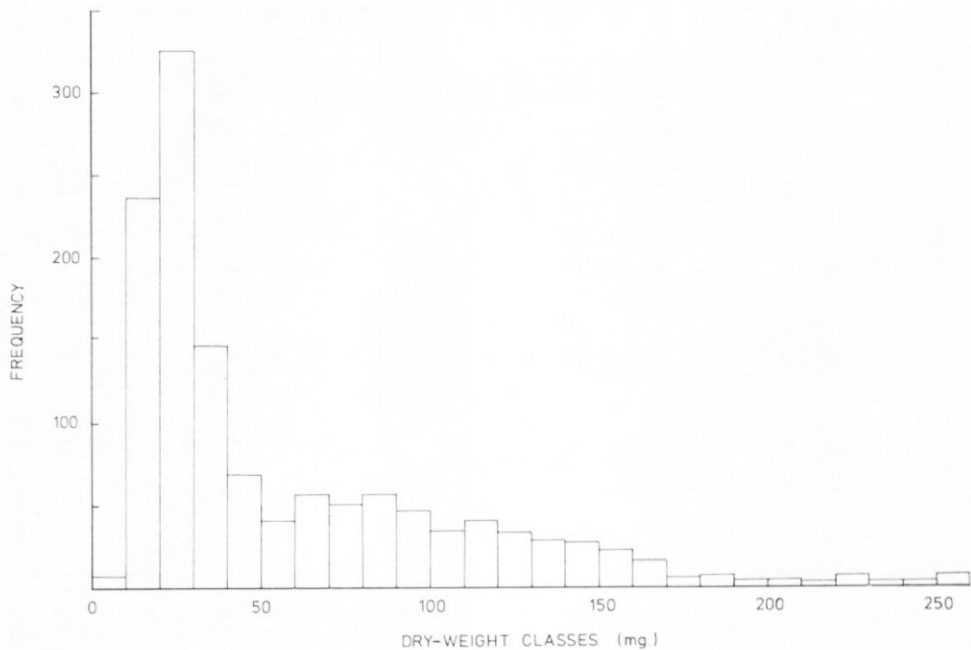
Fig. 7. Weight-class frequencies of *Chorismus antarcticus* (truncated); South Georgia, 1972–73.
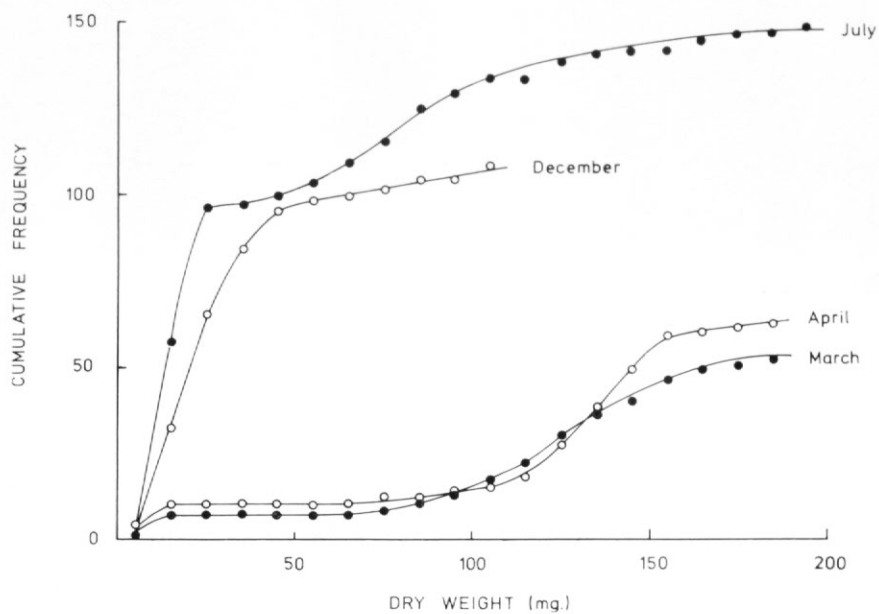


Fig. 8. Smoothed cumulative weight distributions of *Chorismus antarcticus* from four monthly samples (truncated); South Georgia, 1972–73.
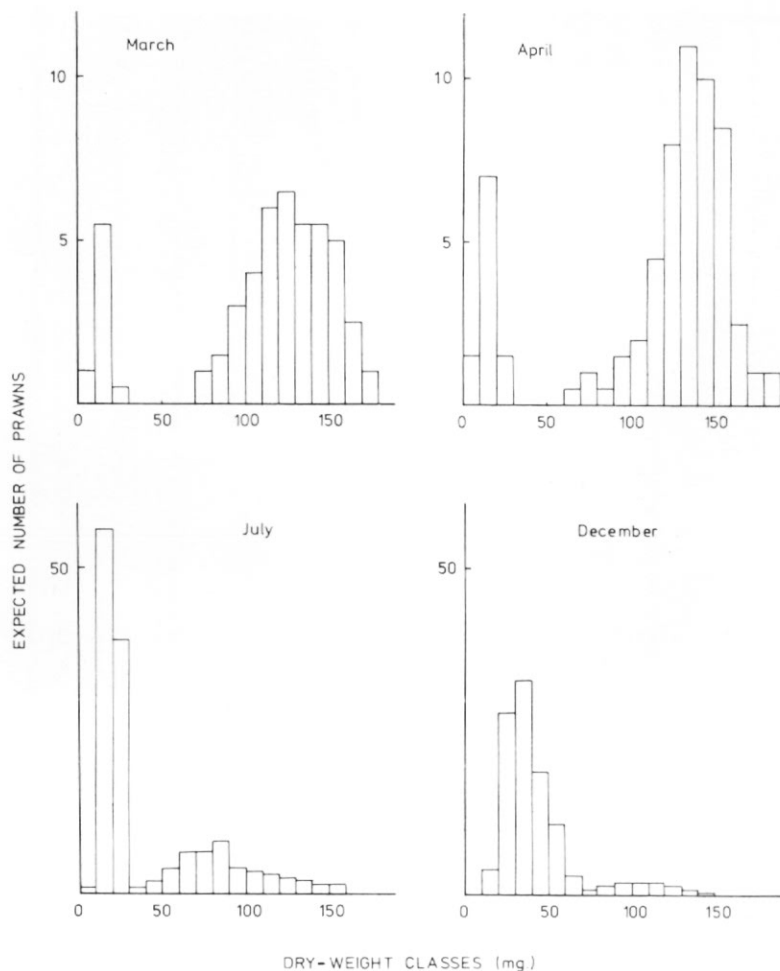
Fig. 9. Smoothed weight distributions of *Chorismus antarcticus* from four monthly samples (truncated); South Georgia, 1972–73.

$d_1$ is the difference between the frequencies of the modal weight class and the preceding weight class,

$d_2$ is the difference between the frequencies of the modal weight class and the following weight class,

and $h$ is the interval width for the weight classes.

These modal values were then plotted against sampling data to obtain the growth curve (Fig. 10). To illustrate changes in relative growth rate, the data were also plotted on a logarithmic scale (Fig. 11).

These growth curves indicated an initial high rate of growth, with a relative growth rate of $\sim 4 \cdot 04$ mg. /mg. per annum, up to about the end of March. The relative growth rate over the colder winter months was less, of the order of $0 \cdot 7$ mg./mg. per annum. After this period of very slow growth, the relative growth rate increased again to $\sim 3 \cdot 9$ mg./mg. per annum. The estimate of the initial growth rate is obviously dependent on the estimated date of peak metamor-

6
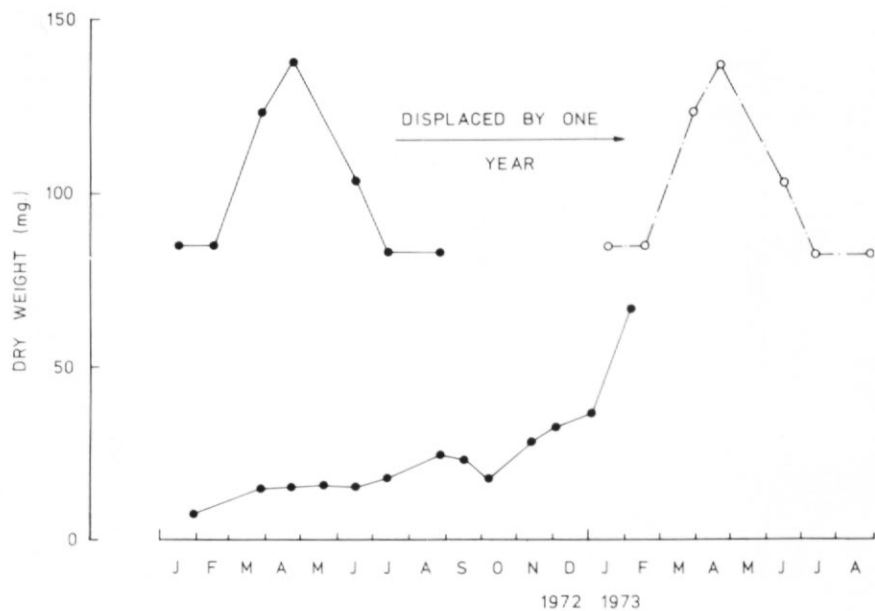
Fig. 10. An estimated growth curve for early post-larval life in *Chorismus antarcticus;* South Georgia, 1972–73.
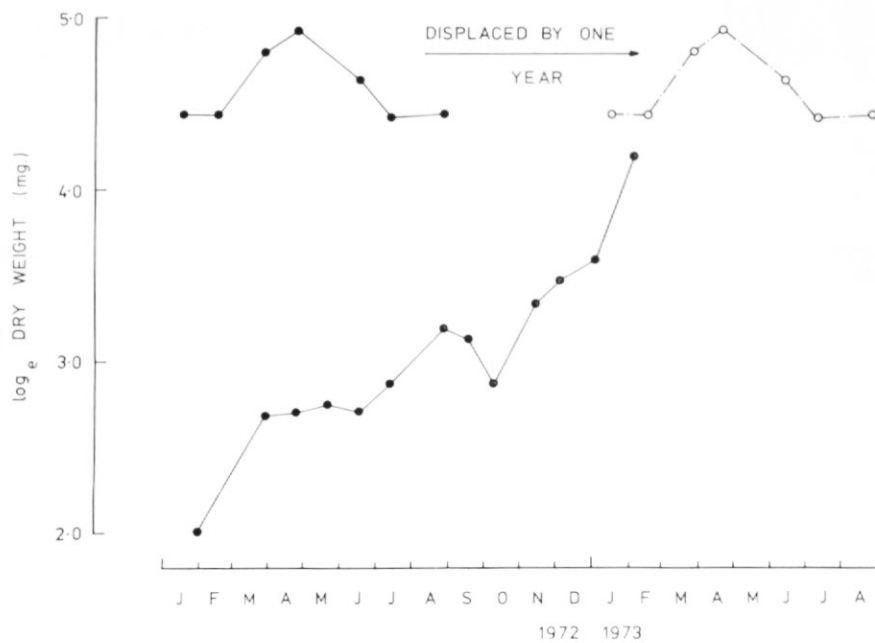


Fig. 11. The logarithmic transformation of the estimated pattern of early growth in *Chorismus antarcticus;* South Georgia, 1972–73.

phosis and the estimated mean dry weight at metamorphosis. The picture of an initial high relative growth rate in the newly metamorphosed post-larval prawns obtained with the working hypothesis of peak metamorphosis on 31 January at a mean dry weight of 75 mg. is, however, consistent with the rapid moulting rate indicated by Figs. 4 and 5. The relative growth rates obtained are approximately equivalent to dry-weight gains of 4, 1 and 18 mg./month during the first post-larval summer, winter and following summer, respectively.

A striking feature of the estimated growth curve was the apparent substantial decrease in the weight of the prawns during the second post-larval winter (Fig. 10). Crustacea in captivity have been recorded as losing weight with each successive moult when the food supply ceases (Lasker, 1966), and hence the observed decrease in weight might possibly reflect a severe shortage of food. There was, however, no corresponding decrease in weight in the first winter prawns at the same time of year, and there is no indication from the cycle of lipid storage that *C. antarcticus* undergoes a severe shortage of food (Clarke, 1977).

An apparent decrease in weight of the second winter prawns could also result if there were a migration away from the sampling area of the larger prawns. A migration of sexually mature individuals to spawning grounds separate from the juvenile area is a well-established feature of the biology of many prawn and shrimp species (e.g. *Spirontocaris lilljeborgii* (Pike, 1954), *Palaemon squilla* (Jensen, 1958) and *Pandalus montagui* (Mistakidis, 1957; Allen, 1963)); seasonal migrations to deeper water associated with feeding are also known (cf. Allen, 1966). Dissection of prawns collected in January and February 1973 (when spawning is believed to occur) showed that male prawns with well-developed testes and vasa deferentia occurred over a range of dry weights down to ∼ 120 mg. The hypothesis that the larger prawns may migrate away from the shallow-water sampling area is supported by the observation that prawns of dry weight >120 mg. were caught much less frequently after April (Table V). The general scarcity of ovigerous females may also indicate a tendency for mature prawns to migrate to deeper water.

### Comparison of growth in C. antarcticus with other Caridea

For comparison with other published work on decapod growth, the modal dry-weight values plotted in Fig. 10 were converted to estimated carapace lengths using the allometric relationship between observed carapace length and dry weight for a sample of 179 prawns derived by the standard least-squares linear regression technique after logarithmic transformation of the variables. A simple straight line through the origin model accounted for 98 per cent of the total observed variation in the logarithms of carapace length and the estimate of the variance about the regression line was very small (0·003), hence any bias due to the use of sample estimates of the regression parameters to estimate carapace length was negligible (Mountford and Bunce, 1973). Where published data were presented as total lengths, these were converted to estimated carapace lengths using either the author's published relationship or a transforming factor derived from accurate published diagrams.

Comparison of absolute growth rates between different species is complicated by the differing sizes of the various species at the point of metamorphosis to the first post-larval stage. For this reason, the growth data for all species were expressed relative to the carapace length at metamorphosis (Fig. 12). The comparative pattern was, however, similar if the untransformed original data were plotted. Published growth data which start several months after metamorphosis, or where the date of metamorphosis is unclear (for example, fishery data for commercially exploited species which become catchable only after a certain minimum size has been reached) have not been plotted.

The results in Fig. 12 show that relative growth in *C. antarcticus* at South Georgia is slower during the first 15 months of post-larval life than that of any temperate-water prawn or shrimp so far studied, and considerably slower than that of some warm-water species (see, for example, the growth rates quoted in appendix table I in Forster and Wickins (1972)).
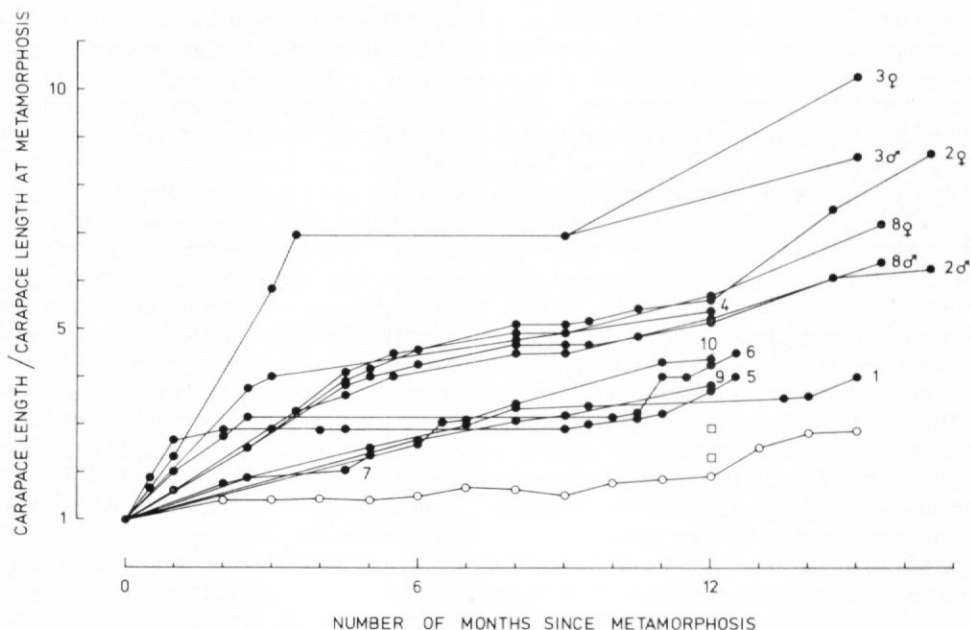
Fig. 12. Comparison of early growth in *Chorismus antarcticus* from South Georgia with published data for
     temperate-water Caridea.
     ● Growth curves from published data:
       1. *Crangon allmanni* (Allen, 1960).
       2. *Spirontocaris lilljeborgii* (Pike, 1954).
       3. *Palaemon serratus* (Forster, 1951*a*, 1959).
       4. *Palaemon elegans* at Plymouth (Forster, 1951*b*)
       5. *Palaemon elegans* at Kristineberg, Sweden (Höglund, 1943).
       6. *Palaemon squilla* (Jensen, 1958).
       7. *Pandalus montagui* (Allen, 1963).
       8. *Pandalus bonnieri* (Pike, 1952).
       9. *Pandalus borealis* from Northumberland (Allen, 1959).
      10. *Pandalus borealis* from Oslo (Rasmussen, 1953).
     □ *Pandalus borealis* from Jan Mayen and Spitsbergen (Rasmussen, 1953).
     ○ *Chorismus antarcticus* at South Georgia (this paper).

The only forms showing comparably slow growth are the Jan Mayen and Spitsbergen
populations of the deep-sea prawn *Pandalus borealis*. This widely distributed circum-boreal
species has been extensively studied and found both to grow more slowly and to take longer
to reach sexual maturity in the colder-water Arctic populations ($<0°$ to $+3°$ C) than in the
warmer waters (a mean of $7°$ to $8°$ C) of the Skagerak and off the Northumberland coast
(Rasmussen, 1953; Allen, 1959). The growth rates of *P. borealis* in the Strait of Georgia and
the Gulf of Maine are similar to those in Norway but, although these are fast growth rates
for this species, they are exceeded by three of the four sympatric species of pandalid shrimp
in the Strait of Georgia (Butler, 1964; Haynes and Wigley, 1969). These differences may be
related to the different feeding habits of the shrimps.

A comparison of the growth of *Palaemon elegans* at Plymouth and Kristineberg, Sweden,
showed a slightly greater overall growth rate at Plymouth (Höglund, 1943; Forster, 1951*b*).
Whereas growth at Plymouth appeared to be continuous, in Sweden growth was virtually non-
existent in winter and very rapid in summer. This may be related to the greater seasonal varia-
tion in water temperature at Kristineberg ($-2°$ to $+20°$ C) than at Plymouth ($8-15°$ C) rather
than to absolute temperature differences. It would, however, appear from the differing patterns

of migration in the two populations that food availability, itself intimately related to temperature, is also an important factor (Allen, 1966).

The annual variation in water temperature at South Georgia, where *C. antarcticus* shows a strongly seasonal pattern of growth, is only $-0 \cdot 3°$ to $+3 \cdot 5°$ C (Fig. 6). In contrast, Price (1962) found that the sand shrimp *Crangon septemspinosa* in the Delaware Bay area appeared to grow continuously throughout the year despite a seasonal variation in temperature of 0–26° C. Farther north at Rhode Island, Wilcox and Jeffries (1973) found a much slower growth rate which varied both with size and seasonal temperature: for a shrimp of total length 30–38 mm., growth increments were $1 \cdot 13$–$1 \cdot 25$ mm./week at 20° C and $0 \cdot 25$–$0 \cdot 38$ mm./week at 0° C compared with an overall mean of 4 mm./week in the Delaware Bay area, the southern limit of distribution for this largely cold-water species. Once again, differences in feeding may underlie these differences in growth rate. Although growth rates free from temperature effects are the exception rather than the rule (Wilcox and Jeffries, 1973), it is clear that the influence of temperature on growth is neither simple nor necessarily dominant; food and feeding behaviour are also important factors and a coherent picture of decapod growth has yet to be formulated.

In this context, it would be of interest to examine the pattern of growth in *C. antarcticus* from both the warmer waters north of the Antarctic Convergence, and also from the true Antarctic waters around Antarctica, where seasonal variations in the very low water temperature are almost non-existent.

The exact relationship between environmental temperature and growth in *C. antarcticus* is thus, as yet, unclear; furthermore, a seasonal fluctuation in the availability of food could also be affecting the growth pattern. *C. antarcticus* appears to be a typical decapod scavenger and, although the marked cycle of productivity characteristic of the polar environment is largely a feature of the plankton, such seasonal food availability also affects the benthos, albeit muted in comparison with the plankton. *C. antarcticus* can, however, be found with a full gut at all times of the year and an examination of the pattern of lipid storage revealed no marked summer synthesis of an overwintering lipid store such as is shown by some polar planktonic forms (Littlepage, 1964; Clarke, 1977). It is thus possible that there is a seasonal fluctuation in the availability of food for *C. antarcticus* at South Georgia sufficient to induce a seasonal pattern of growth, but not sufficient to necessitate the production of an overwintering lipid store.

Although the calculated value of the relative growth rate during the first post-larval summer (0– group) is sensitive to the estimated date of peak metamorphosis, it is of interest that the relative growth rates in summer for 0– and 1– group prawns were comparable. *C. antarcticus* is presumably growing as fast as possible (although conjectural reasons for evolving a reduced growth rate in polar waters have been discussed by Dunbar (1968)) and, although explanation of the seasonal pattern of growth may be relatively straightforward, the reason for the overall very slow growth rate, when some polar ectotherms can apparently grow relatively rapidly, is unclear.

Slow growth has been observed in a wide variety of Arctic and Antarctic ectotherms and has long been considered an inevitable consequence of adaptation to the polar environment. Some polar ectotherms appear to have metabolic rates (as measured by oxygen consumption) elevated above the level predicted by the extrapolation to polar temperatures of the metabolic rates of related warmer-water forms. This elevated metabolic rate, together with the apparently associated slow growth due to relatively less of the energy intake being available for growth, forms the classical concept of metabolic cold adaptation (Scholander and others, 1953).

Some polar animals, including crustaceans, molluscs and sponges, have been found to exhibit relatively rapid growth rates (Dayton and others, 1974; White, 1975); others have been found to have oxygen-consumption rates below that accepted as classically cold adapted. These features may be related and in turn associated with endemism, and the whole concept

of cold adaptation (*sensu* Scholander and others, 1953) has recently come under review (Holeton, 1974; White, 1975; Everson, 1977).

Recent data on the growth rates of a number of polar marine invertebrates have indicated that, although Antarctic ectotherms can exhibit a range of growth rates (Antarctic molluscs, for example, show a wide spectrum of growth rates), examined overall, the growth rates of polar marine invertebrates are nevertheless distinctly slower than those of related warmer-water forms. It may be that these slower growth rates are due to a simple slowing down of metabolic rates caused by the cold water temperatures, rather than to a partitioning of energy intake with relatively less energy going to growth in colder waters suggested by the classical hypothesis of metabolic cold adaptation (cf. Everson, 1977).

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## APPENDIX

TAXONOMIC AUTHORITIES AND SYNONYMS OF DECAPOD NOMENCLATURE USED IN THIS PAPER

| *Nomenclature used in this paper* | *Synonyms used in literature referred to in this paper* |
|---|---|
| DECAPODA | |
| NATANTIA | |
| CARIDEA | |
| Atyidae | |
| *Caridina weberi* de Man, 1892 | |
| Alpheidae | |
| *Alpheus armillatus* H. Milne Edwards, 1837 | *Crangon armillatus* |
| Crangonidae | |
| *Crangon allmanni* Kinahan, 1857 | |
| *Crangon crangon* (Linnaeus, 1758) | *Crangon vulgaris* |
| *Crangon septemspinosa* Say, 1818 | |
| *Notocrangon antarcticus* (Pfeffer, 1887) | *Crangon antarcticus* |
| *Pontocaris cataphracta* (Olivi, 1792) | *Pontocaris cataphractus* |
| Hippolytidae | |
| *Chorismus antarcticus* (Pfeffer, 1887) | *Hippolyte antarctica* |
| *Chorismus tuberculatus,* Bate, 1888 | |
| *Lysmata seticaudata* (Risso, 1816) | |
| *Spirontocaris lilljeborgii* (Danielssen, 1859) | |
| Palaemonidae | |
| *Palaemon elegans* (Rathke, 1837) | *Leander squilla* |
| *Palaemon longirostris* H. Milne Edwards, 1837 | *Leander longirostris* |
| *Palaemon serratus* (Pennant, 1777) | *Leander serratus* |
| *Palaemon squilla* (Linnaeus, 1758) | *Leander adspersus,    Palaemon adspersus* |
| *Palaemon xiphias* Risso, 1826 | *Leander xiphias* |
| *Palaemonetes varians* (Leach, 1814) | |
| Pandalidae | |
| *Pandalus bonnieri* Caullery, 1896 | |
| *Pandalus borealis,* Krøyer, 1838 | |
| *Pandalus montagui* Leach, 1814 | |
| Penaeidae | |
| *Metapenaeus bennettae* (Racek and Dall, 1965) | *Metapenaeus mastersii* |
| *Penaeus brasiliensis* Latreille, 1817 | |
| *Penaeus indicus* H. Milne Edwards, 1837 | |
| *Penaeus japonicus* Bate, 1888 | |
| *Penaeus setiferus* (Linnaeus, 1761) | |
| *Sicyonia carinata* (Brunnich, 1768) | |
| REPTANTIA | |
| MACRURA | |
| Nephropsidae | |
| *Homarus americanus* H. Milne Edwards, 1837 | |

| | |
|---|---|
| *Homarus gammarus* (Linnaeus, 1758) | *Homarus vulgaris* |
| Palinuridae | |
| *Panilirus argus* (Latreille, 1804) | |
| BRACHYURA | |
| Cancridae | |
| *Cancer pagurus* Linnaeus, 1758 | |
| Grapsidae | |
| *Cyclograpsus punctatus* H. Milne Edwards, 1837 | |
| *Hemigrapsus oregonensis* (Dana, 1851) | |
| *Pachygrapsus crassipes* Randall, 1893 | |
| Majidae | |
| *Maja squinado* (Herbst, 1788) | *Maia squinado* |
| Ocypodidae | |
| *Uca pugilator* (Bosc, (1801 or 1802)) | |
| Portunidae | |
| *Callinectes sapidus* Rathbun, 1896 | |
| *Carcinus maenas* (Linnaeus, 1758) | *Carcinides maenas* |
| *Macropipus vernalis* | |
| Xanthidae | |
| *Xantho incisus* (Leach, 1814) | *Xantho floridus* |