THE LARVAL DEVELOPMENT AND POPULATION DYNAMICS OF *DEROCHEILOCARIS ALGOENSIS* (CRUSTACEA, MYSTACOCARIDA)

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ABSTRACT

Seven larval stages of *Derocheilocaris algoensis* have been described and appear to be identical with those of *D. typica* from North America. This stresses the remarkable conservativeness of this subclass of Crustacea. The population biology of *D. algoensis* has been studied over 16 months and reproduction has been found to continue throughout the year but to exhibit some distinct peaks. Growth from egg to reproductively active adult appears to take approximately 60 days. The total life-span is approximately eight months, of which the latter six are spent in reproductive activity.

INTRODUCTION

Derocheilocaris algoensis McLachlan & Grindley, 1974, first discovered on Kings Beach, Port Elizabeth, in 1973, has since been found to be abundant at the HW level on this beach. Because of its accessibility and easy identification it suggested itself for a population study. It has since become evident that *D. algoensis* is actually the second most important meiofauna species on this beach (McLachlan in press) and therefore a good starting point for a series of population studies. Description of the larval stages was, however, a necessary precursor to a detailed population study.

Larval stages of *D. remanei* Delamare & Chappius have been described by Delamare Deboutteville (1954) and those of *D. typica* Pennak & Zinn have been described by Hessler & Sanders (1966). *D. remanei* has 10 preadult stages of which the first is a nauplius while *D. typica* has seven larval or preadult stages of which the first is a metanauplius. As mystacocarids are notoriously conservative (Hessler 1972) it was felt that it would be interesting to see how *D. algoensis* differed from these two patterns. Further, Delamare Deboutteville (1960) found reproduction in *D. remanei* to continue throughout the year, while Hall & Hessler (1971) found seasonal reproduction confined to Spring and Summer in *D. typica.* As in other aspects of meiofauna work, comparative data for the southern hemisphere is lacking and, further, there is a general paucity of seasonal studies (Hessler 1971). This study is an attempt to obtain such data.

This work on *D. algoensis* was started towards the end of 1973 and had the following aims in mind:

(1) to collect and describe the larval stages and compare them with those of *D. delamarei* and *D. typica*;

(2) to study the population dynamics of *D. algoensis* by a program of regular sampling at a preselected site. From this it was hoped to be able to estimate growth rates, life spans and reproductive patterns.

The population work was started in January 1974 and ended in April 1975.

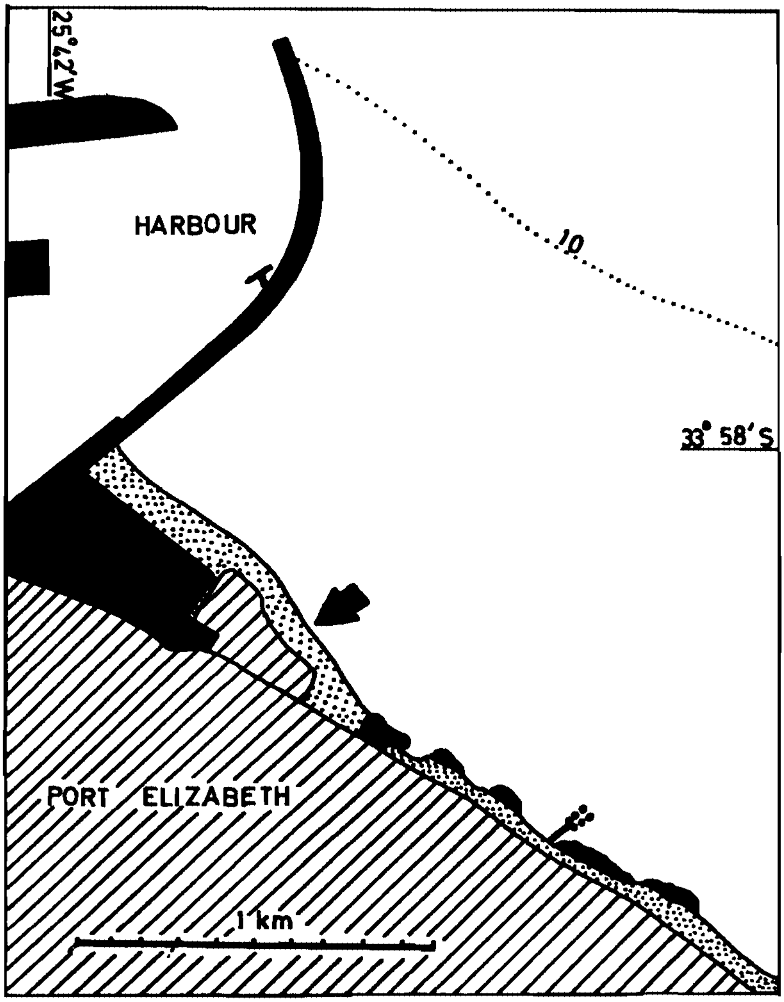


FIGURE 1

Map showing the sampling locality for *D. algoensis* on Kings Beach (marked by arrow). Black areas denote rocks and harbour areas, stippled area denotes beach. Depth contour in m.

METHODS

Larval Stages

All specimens for this study were collected at the HW level on Kings Beach (Figure 1) at depths of 0–90 cm in the sand. Samples were extracted by means of an Oostenbrink (1960) extractor as modified by Furstenberg (personal communication) and stained overnight in 0,1 % rose bengal. Mystacocarids were removed and mounted in 5 % formalin in sea water on semi-permanent wax-ring slides. The larval stages were examined using interference microscopy. Lengths were measured from the anterior tip of the cephalon to the tip of the supra-anal process on undistorted specimens. Specimens were measured through the body lying on their sides or lying flat using a camera lucida and slide micrometer.

Twenty specimens of each larval stage were measured as well as 20 gravid females and 20 non-gravid adults. These two sets of adults were measured because Hessler & Sanders (1966) found two adult stages in *D. typica*, the one larger than the other. It was thought that if this was the case gravid females would belong mainly to the larger group and other adults would include at least a fair number of the smaller group. Gravid is used here in the sense of reproductively active in that the thoraco-abdomen of adult females is filled with a white opaque substance which is thought to represent reproductive tissue (Hall & Hessler 1971)

Population Dynamics

For the population study collections were made approximately every three weeks from the beginning of January 1974. On each occasion a surface area of approximately 40 cm^2 was sampled to a depth of 90 cm. Usually 200–300 mystacocarids were obtained in this manner and mounted on slides. All of these were identified to larval stage; the first 40 adults were sexed to obtain a sex ratio and the first 25 adults were measured to obtain an idea of the relative proportions of the two adult stages in the population. The percentage of gravid females was also noted on each occasion.

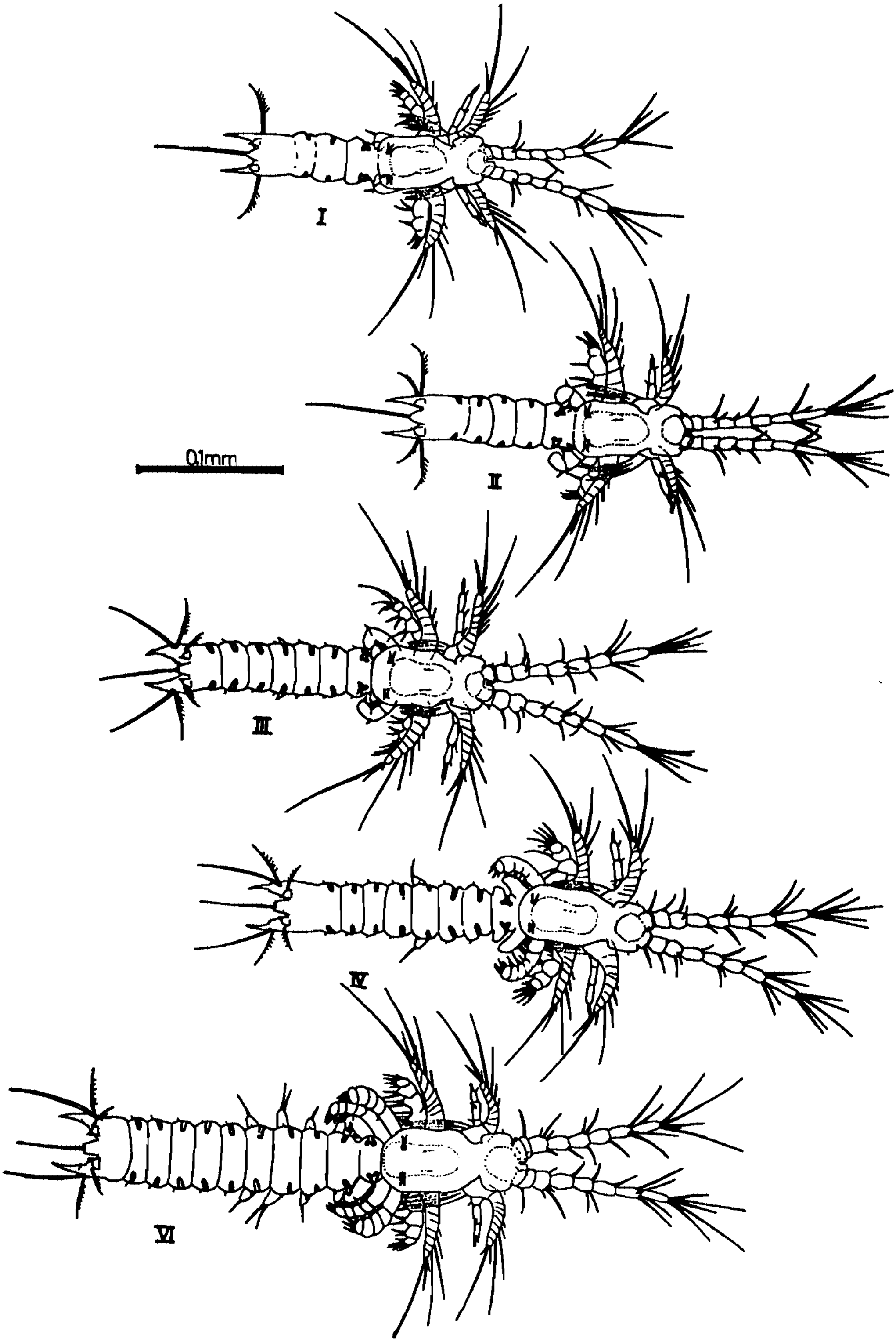
RESULTS

Larval Stages

Seven larval stages have been recognized and appear to be identical to those described by Hessler & Sanders (1966) for *D. typica* from the North Atlantic. Stages I, II, III, IV and VI are illustrated in Figure 2 and the lengths of all stages are given in Figure 3. Despite careful examination no differences other than size have been found between the larvae of *D. algoensis* and *D. typica* and what follows is a brief description of the distinguishing characteristics of each larval stage. (For description of adult see McLachlan & Grindley 1974.)

Stage 1. A metanauplius with four post-cephalic segments; one lateral seta on each furcal claw; first maxilla rudimentary; first and second antennae and mandible more or less well developed; mean length 0,17 ± 0,012 mm.

Stage 2. Six post-cephalic segments; two setae on each furcal claw; first maxilla still rudimentary; mean length 0,20 ± 0,010 mm.


I
0.1mm
II
III
IV
VI

Stage 3. Eight post-cephalic segments; three setae on each furcal claw as in adult; first maxilla better developed; second maxilla a rudimentary bump; mean length 0,22 $\pm$ 0,014 mm.

Stage 4. Ten post-cephalic segments; first maxilla approximately fully developed; second maxilla a rudimentary lobe; maxilliped a rudimentary bump; mean length 0,25 $\pm$ 0,014 mm.

Stage 5. Eleven post-cephalic segments (the adult number); second maxilla almost fully developed; maxilliped a rudimentary lobe; mean length 0,27 $\pm$ 0,022 mm.

Stage 6. Second maxilla basically as in adult; maxilliped almost fully developed; second antenna still with a naupliar process; mean length 0,30 $\pm$ 0,021 mm.

Stage 7. All appendages essentially as in adult; second antenna has lost its naupliar process but segment 2 of the endopod is not yet subdivided; mean length 0,32 $\pm$ 0,025 mm.

Stage 8. Adult. Segment 2 of the endopod of the second antenna divided into two; length measurements show two adult size groups with means of approximately 0,34 $\pm$ 0,041 mm and 0,38 $\pm$ 0,023 mm length. Males have three medial hooks on the fourth thoraco-abdominal limb while females have no hooks but three terminal setae as opposed to two.

The only notable difference between the larval stages of *D. algoensis* and *D. typica* is one of size. Where *D. algoensis* grows from 0,17 mm to approximately 0,40 mm, *D. typica* grows from approximately 0,23 mm to 0,62 mm. The first stage of *D. remanei*, however, measures only 0,15 mm, but is a nauplius and not a metanauplius and is followed by nine other larval stages as opposed to six. The largest male specimen of *D. algoensis* measured 0,45 mm as opposed to 0,69 mm in *D. typica*.

It was also noticeable that the earlier larval stages were confined to the shallower substrate layers. Thus 90 per cent of the Stage 1–3 specimens were recorded between 15 cm and 45 cm depth while 99 per cent of the other stages, including adults, occurred between 15 cm and 90 cm depth, with a mean at 48 cm.

Population Dynamics

The temperature range recorded at the sampling station during this study is shown in Figure 4. This shows only the morning temperature range recorded at depths of 30 cm and 90 cm in the sand. Surface temperatures vary a lot more than this and the range of temperatures found on the surface at HW was 5,0–33,5°C. However, as more than 90 per cent of these animals occur between 30 cm and 90 cm in the sand, and the temperature range decreases rapidly beneath the surface, the range shown in Figure 4 can be said to be a good reflection of the temperatures that the bulk of the *D. algoensis* population must experience.

The population composition at each time of sampling is shown in Figure 5 in histogram form. Figure 6 shows the proportions of adults and larvae in the population as well as the variations in adult lengths recorded during the study period. The horizontal line at 0,36 mm in Figure 6 represents an arbitrary division of the adults into two size groups. It can be seen

FIGURE 2

Larval stages 1, 2, 3, 4 and 6 of *D. algoensis*. Stages 5 and 7 are not figured.

that in February – May and October – December 1974 the smaller size group dominated. Proportions of larvae and adults fluctuated throughout the year but there was one period of very high larval numbers (January – April 1974). This peak did not reappear in 1975. Figure 7 shows the numbers of *D. algoensis* recorded as well as the sex ratios and percentage of adult females which were gravid during the sampling period.

It can be seen that the total numbers of *D. algoensis* recorded fluctuated widely and this is obviously indicative of a patchy distribution which is well known for mystacocarids (Hessler 1971). In fact, it was found that samples taken close to each other often showed very wide variations in the numbers of mystacocarids they contained. Sex ratios showed some surprising fluctuations, the most noticeable being in April 1974 when there were 17 females and one male recorded. This is, however, probably due to sampling error as only 18 adults were obtained in this sample which was made up of 91 per cent larvae. Other than for a value of seven in February 1975 the ratio generally remained between 0,7 and 2,0 females per male. The proportion of adult females showing reproductive activity was consistently high, only dropping below 60 per cent during the period of high larval numbers in January – April 1974. The period from August to October 1974 witnessed more than 80 per cent of the adult females reproductively active. This corresponded to the end of the May – September period dominated by adults of the larger size group.

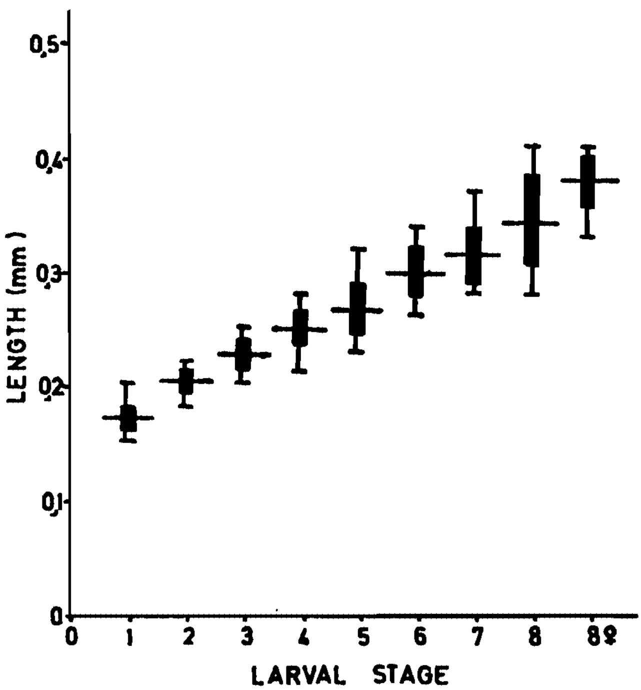


FIGURE 3

Lengths of larval stages of *D. algoensis* showing means, standard deviations and ranges.

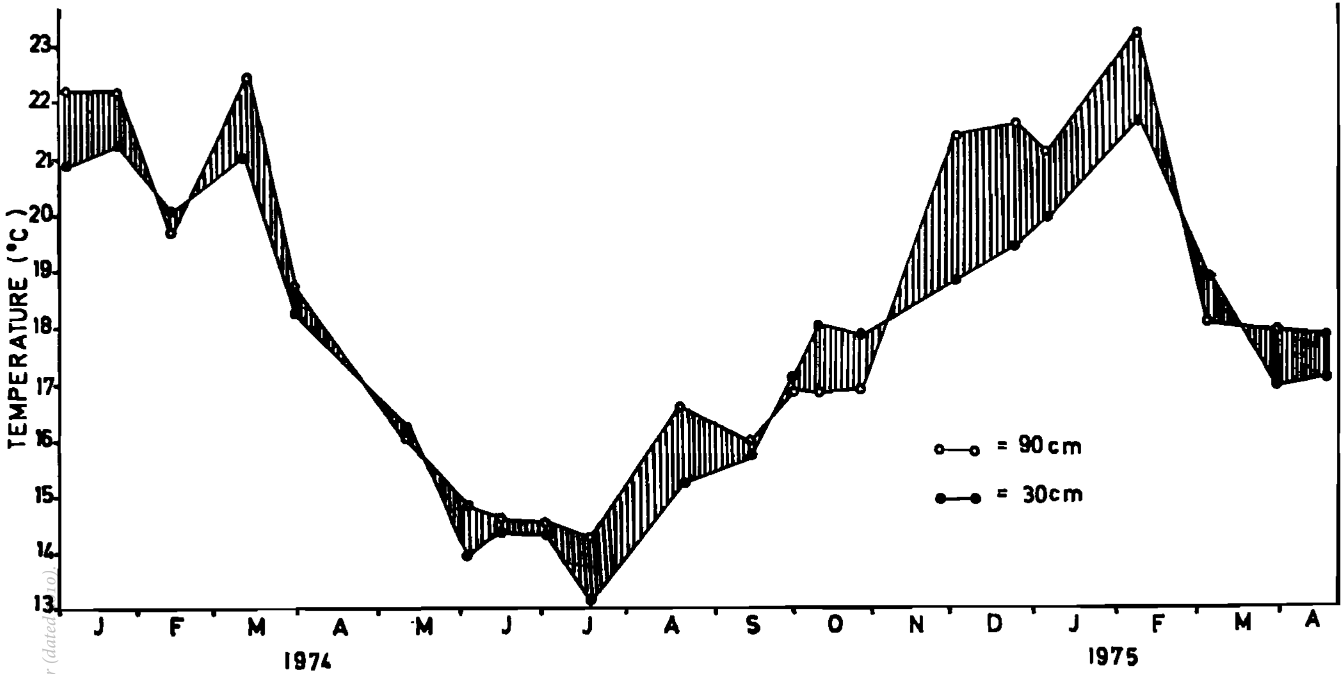


FIGURE 4

Morning temperatures recorded at the sampling locality at depths of 30 cm and 90 cm in the sand.

DISCUSSION

The close similarity between the larval stages of *D. algoensis* on the southern African coast and those of *D. typica* on the north-eastern American coast is remarkable. This may be taken as another clear indication of the extreme conservativeness found in the Mystacocarida (Hessler 1972). The most surprising aspect, however, is that *D. remanei*, which also occurs on the African continent, has quite different larvae (Delamare Deboutteville 1954). Hessler (1972)

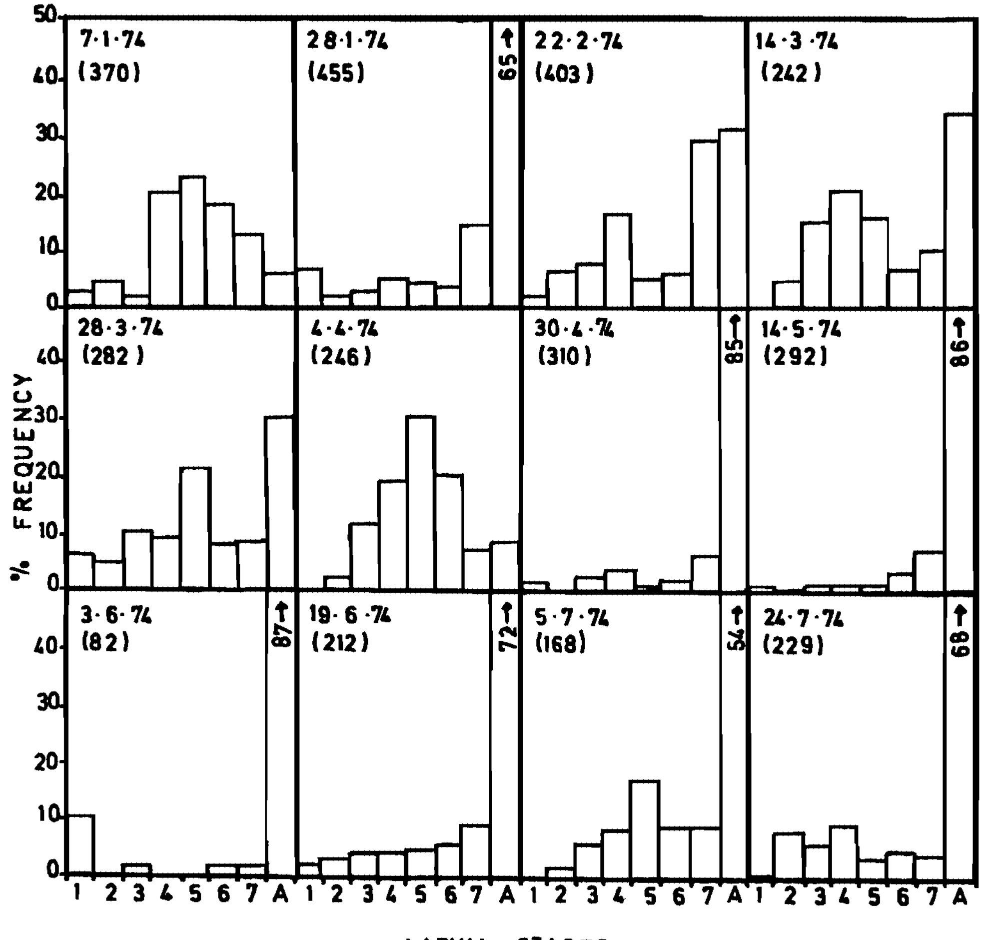


FIGURE 5

Population compositions of *D. algoensis* on Kings Beach. Included are dates of sampling and the number of animals examined.

states that 'Mystacocarids are totally benthonic in habit, both as adults and larvae, and therefore the Atlantic Ocean represents an unbridgeable separation'. How does it occur then that species on opposite sides of the Atlantic and the equator resemble each other more closely than species occurring on beaches of the same continent?

Although not studied in detail, larval stages of *D. delamarei* collected during this study

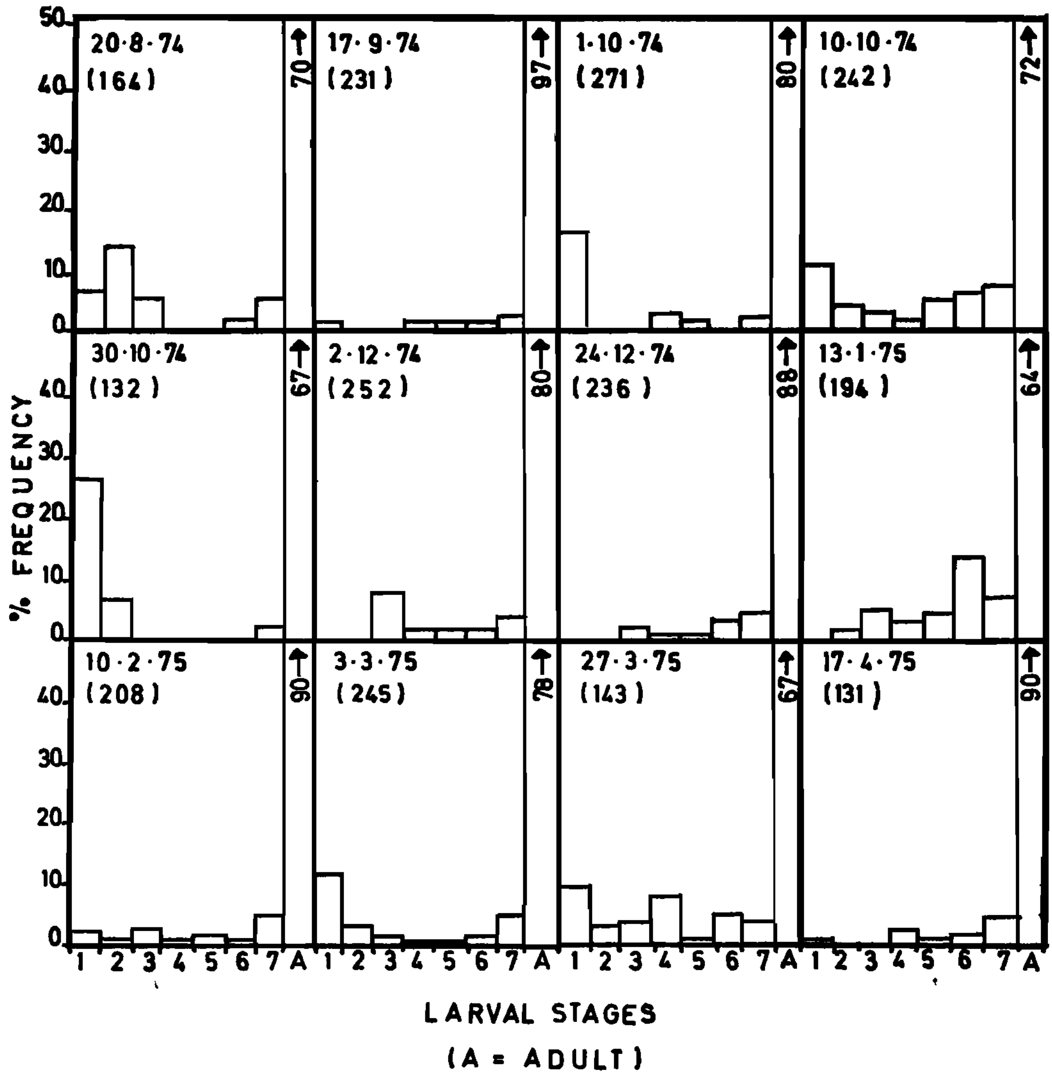


FIGURE 5
Continued.

also appear identical to those of *D. typica* and are extremely difficult to distinguish from the larvae of *D. algoensis*. In view of mystacocarid conservativeness, however, it may be expected that the larval stages of all species, except *D. remanei*, are basically the same as those of *D. typica*. The reason for the apparent aberrance of *D. remanei* is unknown. *D. algoensis* is separated geographically from *D. remanei* by at least two species, *D. delamarei* and *D. angolensis* (Hessler 1972). As *D. delamarei* has larvae that appear to be identical to those of *D. algoensis* a study of the larvae of *D. angolensis* would be most worthwhile.

As found by Hall & Hessler (1971) for *D. typica*, *D. algoensis* appears to have two adult size groups. These had mean lengths of 0,34 mm and 0,38 mm in Figure 3 but, owing to a certain amount of mixture, the smaller group probably has a lower mean size and the larger group a larger mean size. Inspection of the adult lengths in Figure 6 suggests that the actual mean lengths for these two groups lie at approximately 0,33 mm and 0,39 mm. It may thus be concluded that after reaching the adult stage these animals still undergo one moult to a larger size. Size increases between the different larval stages are regular, which suggests a regular growth rate.

The most prominent feature of the population study is the continued reproduction throughout the year in *D. algoensis*. Larvae generally averaged 30 per cent of the population but distinct fluctuations did occur (Figure 6). The most pronounced fluctuation occurred in the Summer and Autumn (January to April) of 1974 when the population was dominated by larvae. This was not repeated in 1975 and may therefore be considered not to be a normal fluctuation. From the adult length curve in Figure 6 it appears that many of the 'old' adults died during the Summer and Autumn of 1974 to be replaced by large numbers of maturing larvae present at that time. By May most of these had moulted to the larger adult size group which was the dominant size group until September. In September these 'old' adults appear to have died out and were replaced again by smaller adults which had been recruited from the larvae.

This dying of 'old' or large adults and acquisition of smaller adults is no doubt going on all the time. However, because of the exceptionally high proportion of larvae from January to April 1974, the fate of this group dominated the adult length graph until the group appeared to have died out in September. From this it may be concluded that the life span of *D. algoensis* is approximately eight months (*i.e.* from Stage 1 larvae in December 1973 – February 1974 to adults that died from August to October 1974). The curve in Figure 7 showing the percentage of adult females which were reproductively active supports this conclusion. A relatively low proportion of the adult females were gravid during the period of high larval numbers early in 1974. This proportion steadily increased until May as these females became active. After this the proportion of gravid females dropped, presumably owing to a further influx of younger adults, and then continued to increase again until September. In September, when the adult length graph indicates the dying off of 'older' adults the percentage of gravid females also falls sharply. It does not, however, fall as low as January/February 1974, as some adults still remain from the June to August period of fairly high larval numbers (see lower graph in Figure 5). From this point onwards the percentage of females which are reproductively active shows regular fluctuations which correspond to earlier fluctuations in the larval recruitment.

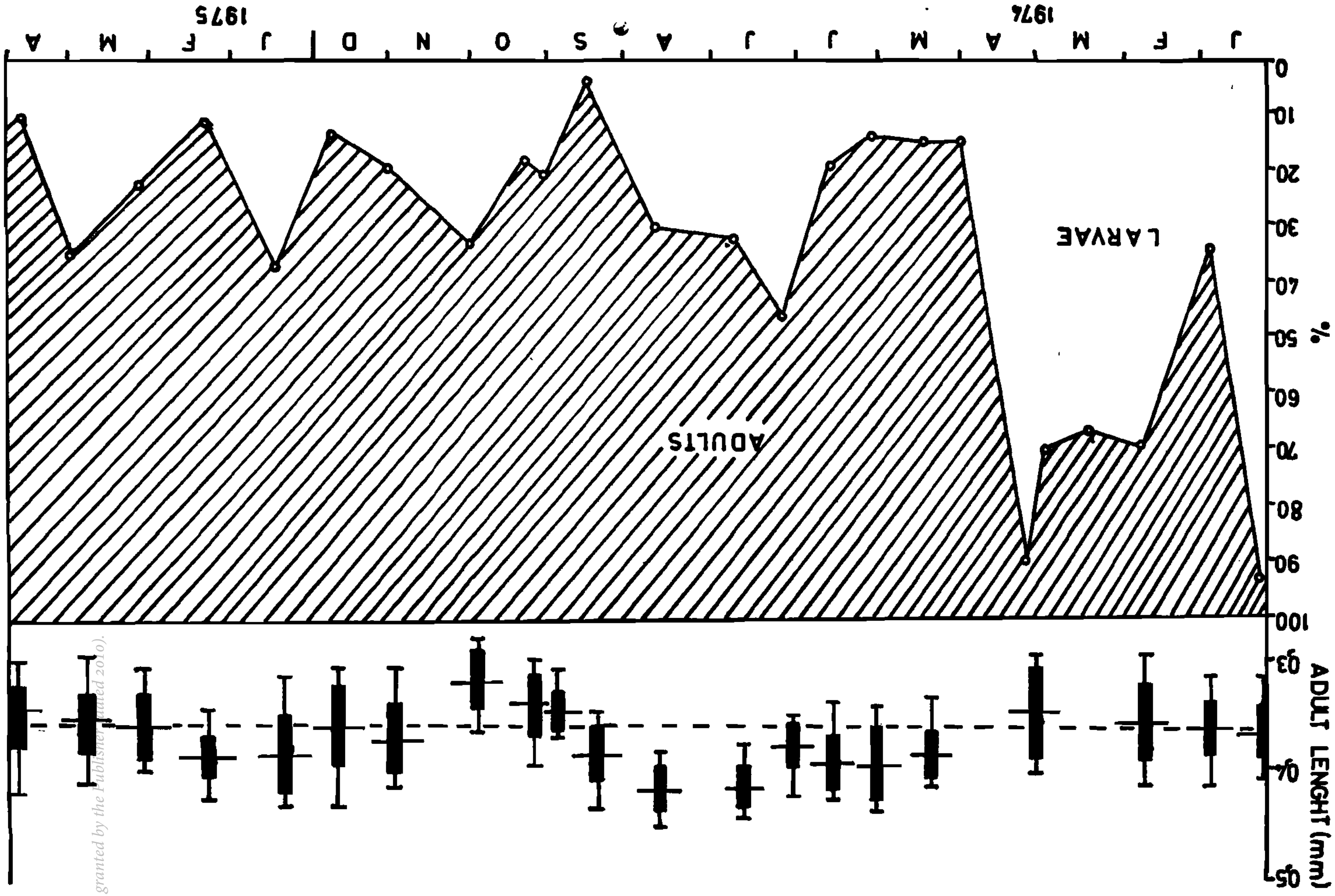


FIGURE 6
Proportions of adults and larvae in the population (below), and adult lengths of the *D. algoensis* (above). Length plots show means, standard deviations and ranges recorded at each time of sampling.

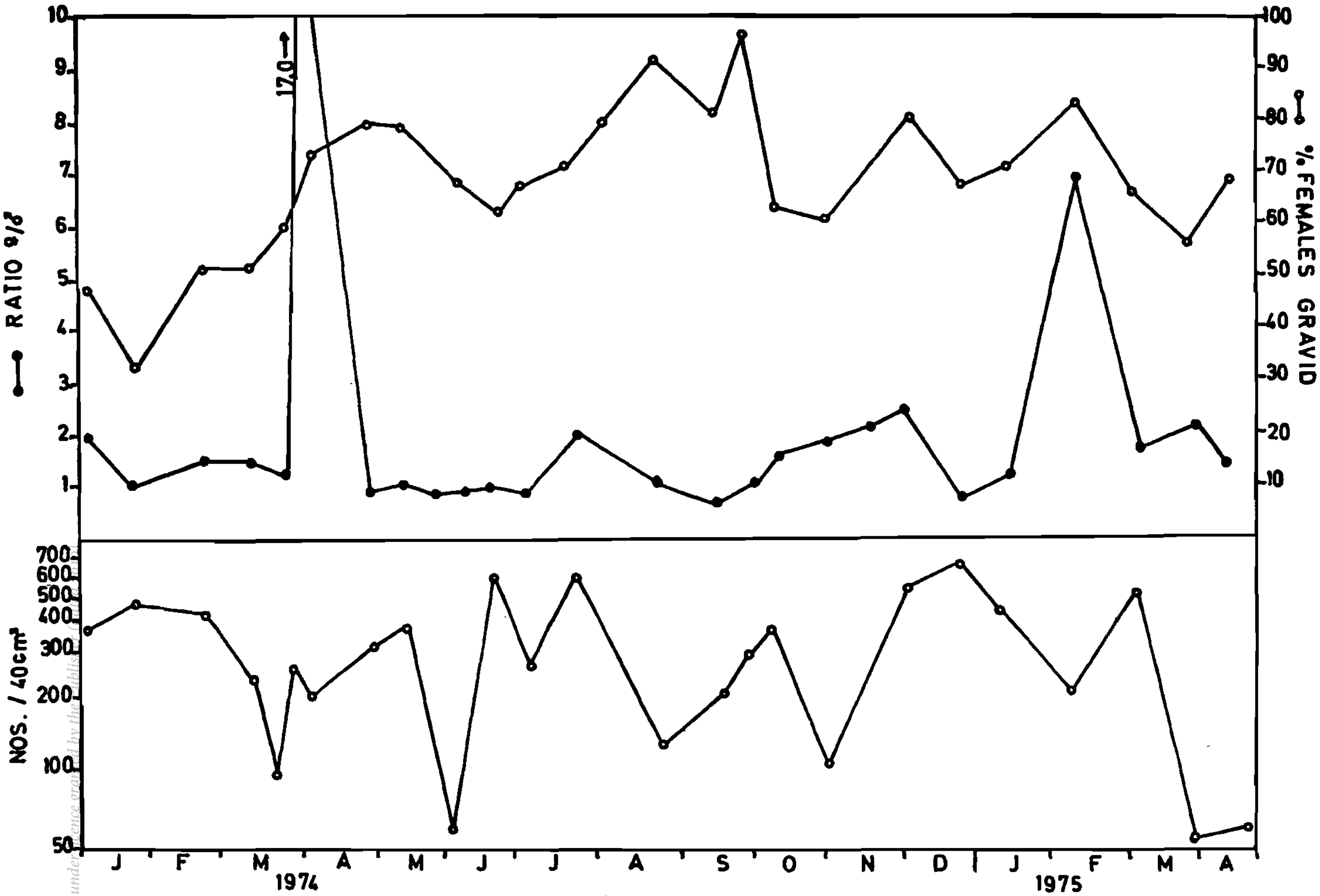


FIGURE 7

Total numbers of *D. algoensis* recorded during the study period (below), and sex ratios and percentage of the adult females which were gravid (above).

By noting the time lags between fluctuations in the proportions of gravid females and fluctuations in the proportions of larvae it is possible to estimate the growth rate from larva to reproductively active adult. Taking four modes of high larval numbers as being (1) early April, (2) late July, (3) the end of October 1974 and (4) the middle of January 1975 (Figure 6), the corresponding modes of high percentages of gravid females occur during (*a*) early May, (*b*) late August, (*c*) the beginning of December 1974 and (*d*) mid-February 1975 (Figure 7). As the larvae tend to appear in batches over a period of one to a few weeks at a time it is not always easy to pinpoint peaks. However, a reasonable estimate of the growth rate can be derived from the time lags between the above-mentioned sets of modes in the following manner.

First it must be assumed that growth is linear, *i.e.* that the time taken to moult from one larval stage to the next is constant (seasonal differences are ignored here). It is also assumed that the same time is taken to change from egg to Stage 1 larva and from inactive Stage 8 adult to reproductively active Stage 8 adult. In other words, from egg to reproductively active adult (assuming no sex differences) occurs in nine equally spaced steps. The number of such 'steps' involved in each of the above sets of modes can be estimated by determining the dominant larval stage making up each peak in larval numbers. Dividing the time lags by the estimated number of growth 'steps' in each case gives values of 7,5; 7,6; 4,3 and 6,7 days per 'step'. The mean, 6,5 days per 'step', results in a 59 day growth period from egg to reproductively active adult. This may be approximated to 60 days or two months. It would therefore appear that *Derocheilocaris algoensis* on Kings Beach has an approximate life span of eight months of which the first two are spent in growth and the latter six in reproductive activity.

Sex ratios (Figure 7) showed wide fluctuations but were mostly in the range of 1–2 females per male. This differs from *D. typica* where males outnumbered females (Hall & Hessler 1971). *Derocheilocaris algoensis* also differs from *D. typica* (Hall & Hessler 1971) in not having seasonal reproduction; in taking approximately 47 days to develop from Stage 1 larvae to Stage 8 adults, as opposed to 40 days; and in having a life span of approximately eight months as opposed to a maximum of one year.

ACKNOWLEDGEMENTS

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