# BIOLOGY AND ECOLOGICAL ENERGETICS OF THE SUPRALITTORAL ISOPOD *LIGIA DILATATA*

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# CHAPTER 1

## INTRODUCTION

Modern developments in ecology have emphasised the importance of energy and energy flow in biological systems. The interest in ecological energetics stems from work published by Lindeman (1942) who described an ecosystem in terms of energy flow between interrelated trophic levels. Perhaps the best known examples of whole ecosystem studies are those of Odum (1957) and Teal (1957) who overcame the difficulties involved in investigations based on the trophic-dynamic approach by choosing a convenient unit of habitat, categorising trophic levels within this unit according to species composition and assuming a steady state system (Phillipson, 1975). Many workers have adopted another approach based on the conviction that a complex system, even if it can be easily distinguished by habitat boundaries, should be divided into a large number of fairly simple component units (such as single species populations) rather than a few relatively complex parts (such as trophic levels). This belief has given rise to work on populations of single species of animals, and detailed studies of food consumption, assimilation, respiration and growth of all life stages of individual populations have been carried out.

It is believed that studies on individual species populations are important to gain a full understanding of ecosystem dynamics and that data gained from these studies can be incorporated into complex but meaningful models.

This approach was adopted in a study of the complex kelp bed ecosystem off the west coast of South Africa initiated in 1975. Pilot studies indicated which plant and animal species should receive particular attention and several workers engaged in detailed studies of population dynamics and ecological energetics (Greenwood, 1974; Muir, 1977; Shafir, 1978; Dieckmann, 1978; Griffiths and King, 1978). A feature of the kelp bed system is that large masses of plant material are exported due to the heavy wave action experienced (Field _et_ _al_., 1977; Velimirov _et_ _al_., 1977). Attempts have been made to trace the fate of the kelp which is exported to adjacent beaches. A study by Muir (1977) showed the importance of kelp debris for the sandy beach amphipod _Talorchestia_ _capensis_. The present study concerns the population dynamics and energetics of the supralittoral rocky shore kelp-eating isopod _Ligia_ _dilatata_ Brandt.

Apart from the fact that populations of _L_. _dilatata_ consume large masses of kelp every year and are thus active agents in breaking kelp into particulate matter in the upper intertidal zone and in recycling nutrients, there are a number of factors which make the animal interesting in its own right. The habitat in which the isopods live represents a combination of marine and terrestrial conditions. This extremely harsh environment is inhabited by few animals, either terrestrial which in the course of their evolution have moved seaward, or marine which have evolved towards the land (Carefoot, 1973a). Thus Ligia may be said to represent a transitional stage in the evolution of the land habit in isopod crustaceans.

The genus Ligia has featured in a number of physiological studies particularly with regard to osmoregulation (Parry, 1953; Todd, 1963). Nicholls (1931a, b) published some results on growth and feeding of L. oceanica in Britain and Jöns (1965) described population structure and feeding of the same species in the Baltic. There have been no comprehensive studies of the biology and energetics of the genus apart from Carefoot (1973a, b) and Newell et al. (1976) who looked at the effects of various factors on the metabolism of L. oceanica.

This study was designed to investigate some aspects of the biology of L. dilatata and to gain quantitative estimates of the population dynamics and energetics of the species.

# CHAPTER 2

## METHODS

### 2.1 The Study Area

The study site is a west-facing stretch of rock at Kommetjie, Cape Peninsula (34° 8'S, 18° 18'E) approximately 80m in length with an extensive offshore kelp bed (Fig. 2.1). Kommetjie was one of the sites studied in a survey of South African kelp beds (Field *et al.*, in press). Although detailed investigations into the kelp bed community dynamics are being conducted mainly at another site on the Cape Peninsula - Oudekraal - particular requirements made it necessary to locate some studies at other locations (e.g. Muir, 1977). Kommetjie was an ideal site to study a population of *L. dilatata*.

Populations of *L. dilatata* on South African rocky shores are associated with kelp debris which is broken from the kelp beds by wave action and is subsequently cast up on the rocks (Day, 1974). The site chosen for the present study thus had to have a sufficiently large input of kelp at all times of the year to support an isopod population. The population had to be spatially isolated from other

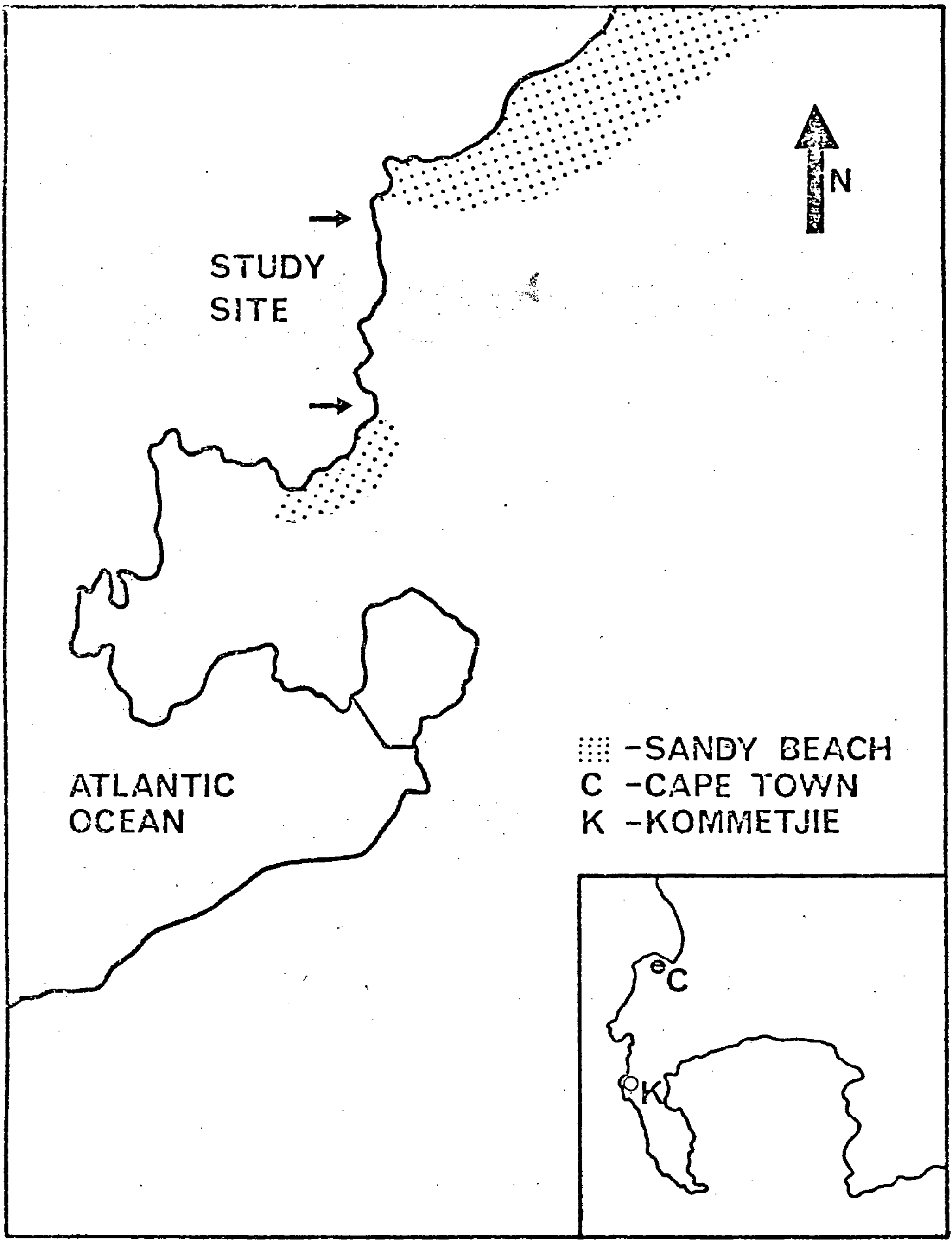


Fig. 2.1

Map of the Study Area

populations of *L. dilatata* in order to exclude immigration and emigration, and it had to be large enough for a programme of monthly sampling not to disturb the population structure significantly. The area chosen fulfilled all these requirements. It is bordered on either side by a sandy beach. Observations confirmed that *L. dilatata* do not migrate over large distances of sand thus excluding immigration and emigration. The coastline is exposed to strong south-westerly swells which cause heavy water surges resulting in large amounts of kelp being broken free from the substratum. This debris is either swept out to sea or cast up on adjacent beaches although some of it may be consumed by debris feeders such as the sea urchin *Parechinus angulosus* within the kelp bed.

## 2.2 Temperature

Temperature profiles were obtained for the four seasons of the year. Temperature was recorded using a mercury thermometer and readings correct to one decimal place were taken every two hours for 26 hours. Ambient temperature and temperature in 10 kelp debris patches containing specimens of *L. dilatata* were taken. The mean of the 10 readings from stranded kelp was calculated and a temperature profile of the kelp debris habitat was plotted.

## 2.3 Kelp Input

Monthly estimates of standing stock of kelp debris at the study site were obtained by determining the wet mass of all kelp plants found in a 5m strip at right angles to the shoreline. The location of this strip was randomly chosen by asking a person not involved in the research project to call a number between 1 and 80 (the length of the stretch of rocks in metres). This number was paced from the beginning of the rocks and represented the mid-point of the 5m corridor. The same strip was cleared of kelp once every month for 17 months. The mass of the three kelp species *Ecklonia maxima*, *Laminaria pallida* and *Macrocystis angustifolia* were measured separately.

## 2.4 Population Dynamics

### Field Methods

The sampling period extended from May 1976 to December 1977. Each month three samples of isopods were obtained from rock crevices at Kommetjie. It was not possible to sample crevices randomly since factors such as accessibility and size of crevices had to be taken into account. Attempts to sample crevices at different heights above HWS were not always successful because at times there were no animals in high shore crevices. Crevices of similar size were sampled each month and on several occasions identical crevices were used. Samples were collected at high tide at which time the population of *L. dilatata* is concentrated into a narrow strip above the high water mark. *L. dilatata* is an extremely fast moving animal and scuttles for shelter at the slightest disturbance. In order to sample the population quantitatively a sticky glue, made by mixing flour and water, was spread around the crevices to be sampled. This prevented animals escaping while they were being removed from crevices and placed in plastic bags. All samples were preserved in formalin immediately to prevent cannibalism during the journey to the laboratory. The areas of the crevices sampled were estimated using a tape measure by splitting total area up into simple geometric shapes. Monthly samples were related to the total area inhabited by *L. dilatata* at Kommetjie by measuring the area colonised by the population in a 5m strip of beach every month. From this density per m of beach was calculated.

## Laboratory Methods

In the laboratory samples were washed and the isopods removed. All animals were sized using a binocular microscope with a 0,1mm scale. Lengths were measured dorsally from the anterior border of the cephalon to the tip of the telson, and the animals were sorted into 2mm size classes. Male *L. dilatata* have easily recognisable sexual characters :

- a paired penis on the ventral side of the seventh thoracic segment, and
- a pair of copulatory styles arising at the base of the inner margin of the superior lobe of the second pair of pleopods.

All animals over 10mm in length were sexed and all smaller isopods regarded as juveniles. The reproductive state of females was noted. The number of eggs or embryos in the brood pouch of 42 specimens was counted to obtain an estimate of fecundity. Females were selected randomly using the last digit of numbers in a telephone directory.

Attempts were made to maintain live animals in the laboratory for two reasons :

- to carry out short term experiments (e.g. feeding, respiration) which were completed within several hours to a few days of collection, and
- for long term experiments such as growth and the measurement of moulting rates.

Although short experiments were generally started on the day of collection it was sometimes necessary to hold animals for a few days. This was done in plastic containers. A wad of cotton wool soaked in sea water on the bottom of the container maintained a high humidity in the holding chamber. In this way animals survived for several days without apparent ill effects. No method for holding animals in the laboratory was successful for more than 35 days. This was surprising since Hatchett (1947) and Wieser (1965) have raised terrestrial isopods with little difficulty and Ligia oceanica in Europe was held in the laboratory for a number of months (Nicholls, 1931a; Jöns, 1965). Similar difficulties have been reported only by Hayes (1969) who was unable to keep the sandy beach isopod Tylos punctatus alive in laboratory cultures for periods longer than a few days.

A number of methods were tried and several variations introduced without any success. Specimens of L. dilatata started showing negative effects after two to three weeks at which time mortality became very high. Best results were achieved in a holding chamber whose bottom was covered in very moist cotton wool (sea water) and which contained a number of stones removed from the natural environment. Animals were transferred to new chambers every three days to prevent fouling of the chamber and they were also presented with new rations of food at these times. Using this method the isopods survived slightly longer than three weeks.

## Data Processing

The three samples obtained each month were pooled and a size-frequency histogram with a class interval of 2mm was constructed for each month. Harding (1949) introduced a graphical method for resolving frequency distributions of a population into their component age groups assuming that each cohort is normally distributed. This method, with improvements introduced by Cassie (1954), was used to plot cumulative percentage curves for each of the 20 months of observations. Fig. 2.2 shows the graph for May 1976. The mean, standard deviation and theoretical limits of each cohort in the distribution can be estimated from the graph and these monthly statistics may then be used to obtain estimates of growth and mortality rates for the cohorts. This method is to some extent subjective, especially when the cohorts are not easily discernible and consequently the point of inflection on the probability graph is not clearly defined.

Another method for estimating the parameters of the frequency distributions was also employed. This is used in a computer program called NORMSEP (Hasselblad, 1966) and has the same assumptions as the method of Harding and Cassie. The method is statistically superior and it employs a $\chi^2$ test for goodness of fit of the calculated versus the

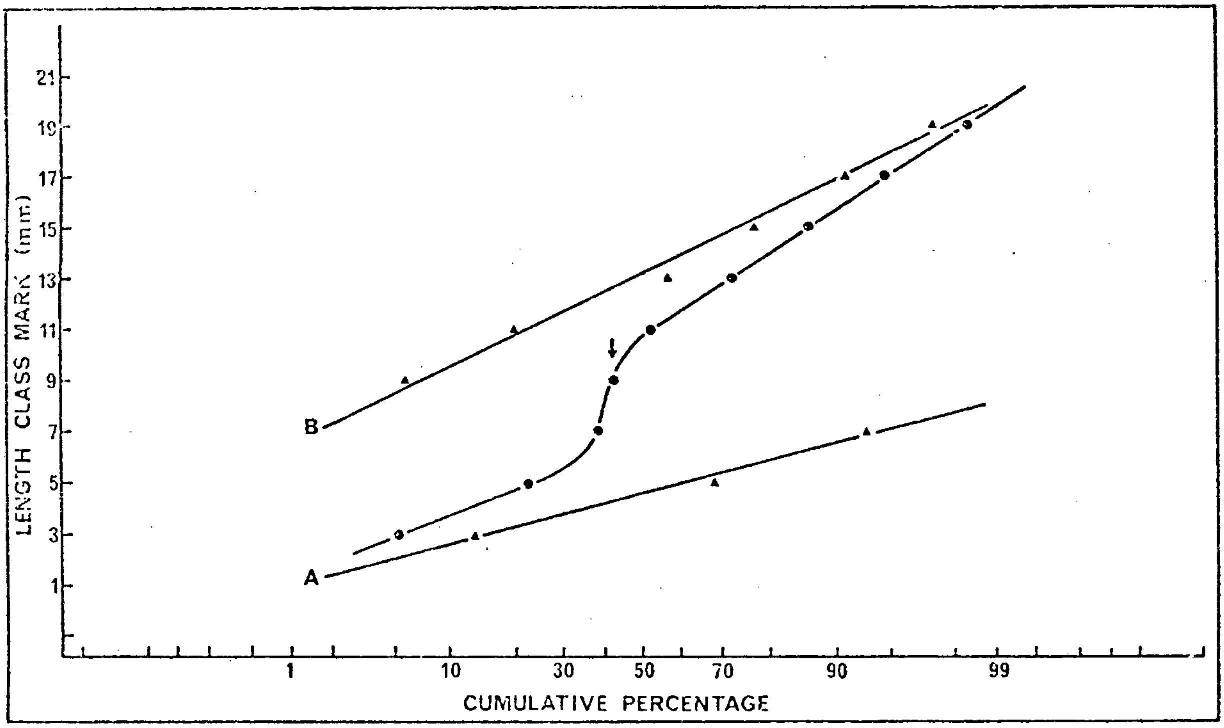


Fig. 2.2

Cumulative size frequency curve for the May 1976 sample plotted on probability paper.

Lines marked A and B indicate the normally distributed cohorts making up the population on that date. The arrow indicates the point of inflection.

observed distribution. The histograms and superimposed curves were generated on the Calcomp plotter of a UNIVAC 1100/80 computer using a program called NHIST written by M. Ripp of the School of Environmental Studies at the University of Cape Town.

## 2.5 Experimental

All experiments were carried out on freshly collected specimens and were started within three hours of sampling.

### Calorific Values

Calorific values for the different size classes of the *L. dilatata* population and for *Macrocystis angustifolia* were measured in a Gallenkamp ballistic bomb calorimeter; all other calorific values were obtained in a Phillipson microbomb calorimeter. Samples were oven dried at 60°C for 72h, then ground in a mill and returned to the oven for another 24h before combusting in the bomb. Replicates of samples were burnt in a muffle furnace for three hours at 500°C to measure the percentage of inorganic material in the samples.

## Length-Mass Relationships

Between 30 and 51 isopods were subsampled on four occasions to obtain seasonal relationships between length, wet mass, dry mass and ash-free dry mass. The animals were chosen to cover the whole size range and all developmental stages. Samples were oven dried at 60°C for 72h to measure dry mass and burned in a muffle furnace at 500°C for three hours to obtain ash-free dry mass. All length-mass curves were fitted using the method of least-squares and plotted on log-log scales.

## Food Preference, Feeding and Faeces Production

Feeding chambers were constructed from Perspex tubing (75mm diameter). Each vertical chamber consisted of an upper and a lower compartment separated by 1mm nylon mesh through which faeces could drop. Animals were separated into groups of 10 individuals each, the composition with respect to size and sex representing a cross section of the population. Experimental isopods were starved for 24h and then left to feed for 36h on freshly collected kelp. In each experiment one kelp species was placed in the upper compartment of a feeding chamber containing animals; three control chambers contained only food to allow for evaporation loss. At the end of each experiment kelp was weighed to measure the amount eaten.

In another experiment five groups of 10 isopods each (each group consistent in its size composition) were placed in experimental chambers with equal weights of four potential food species. After 36h the reduction in mass of the food was measured and corrected for natural evaporation. A gravimetric technique outlined by Klekowski and Duncan (1975) was applied to estimate consumption and egestion rates of L. dilatata. Isopods, starved for 48h, were put into feeding chambers. Each chamber contained 5 - 10 animals of the same size class and all size classes were represented in the experiment. Sufficient food was provided to exclude competition. The animals were left to feed for 48h under conditions of natural light and ambient temperature. At the end of the experiment kelp remaining in the chambers was weighed and corrected for natural water loss. The mass of food consumed by each size class was calculated. The experimental isopods were left in the chambers until they had voided their guts and all faeces were collected and weighed. The fact that faeces did not drop through the nylon mesh into the lower chamber as had been expected did not pose a problem since faecal pellets were easily collected quantitatively using forceps.

## Respiration

On four occasions between May 1976 and June 1977 isopods were collected from the shore and taken to the laboratory for respiration experiments. This was done the day after the seasonal temperature recordings outlined in Section 2.2 had been completed. The isopods were acclimated overnight (10 - 15 hours) to the estimated mean temperature of their kelp debris habitat to allow their possibly elevated metabolic rate due to handling and temperature fluctuations (Newell and Pye, 1974) to return to normal before starting the experiment. The experimental vessels of the Gilson respirometer contained 0,2ml 10% KOH in their central wells with a small strip of filter paper to enlarge the surface for $CO_2$ absorption. The animals tended to remain motionless for most of the duration of the experiment on another strip of filter paper moistened with sea water.

For the first two experiments readings were taken every 30 minutes for at least 24 h in order to detect diurnal fluctuations in metabolism as reported by Marsh and Branch (1979) and Shafir (1978). When it became evident that the animals exhibited no diurnal rhythms respiration experiments were reduced to four hours duration. A total of fifteen individuals were used in each experiment. At the end of the run the animals were measured in order to obtain their ash-free dry weights. A standard-temperature-and-pressure (S.T.P.) correction was applied to all readings.

# CHAPTER 3

# RESULTS AND DISCUSSION

## 3.1 Biology of Ligia dilatata

### Habitat and Temperature Regime

Recorded air temperature at Kommetjie during the study period fluctuated between 23,6°C at midday in January 1977 and 10,0°C at night in August 1976. Temperature in cast up kelp debris did not rise above 17,5°C (April 1977) and the lowest record was 11,3°C in August 1976 (Fig. 3.1).

The fact that the isopods live among kelp debris has several advantages. The animals are in constant contact with their food source. They seldom have to undertake foraging journeys exposing themselves to predation. Due to the high water content of the kelp they are protected from dessiccation and, as is demonstrated by the measurements of air temperature compared with temperature among kelp debris, the isopods are subjected to a significantly buffered temperature regime experiencing an annual temperature range in their habitat of less than half the range recorded for air temperature (Fig. 3.1). Although all the factors

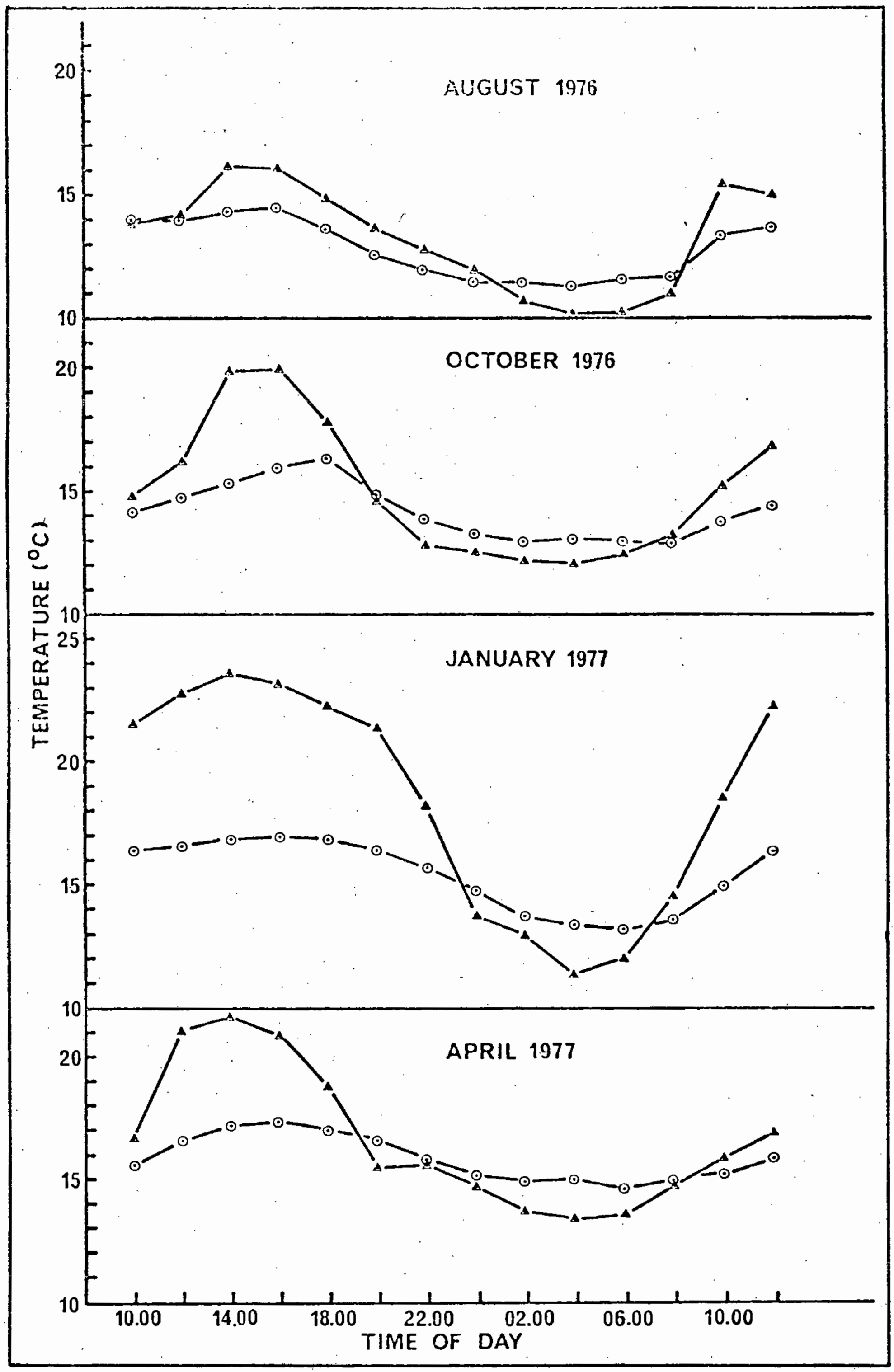


Fig. 3.1

Air temperatures ( ▲ ) and temperatures in stranded kelp debris ( ⊙ ) measured at four times of the year. Measurements were made at 2 hourly intervals for 26 hours.

mentioned above work together in determining choice of habitat by *L. dilatata*, from the point of view of energetics the fact that the animals live in a fairly constant temperature regime is particularly significant.

## Kelp Input

Standing stock figures for kelp debris cast onto the shore are presented in Fig. 3.2. The wet mass of kelp present per running metre of beach varied between 1,9kg in summer (Dec. 1976) and 35,0kg in winter (June 1977).

## Feeding and Food Preference

The fact that kelp detritus serves as a habitat for the isopod population at Kommetjie makes direct observations of feeding behaviour difficult but animals were repeatedly observed feeding on *E. maxima*. Other workers (Nicholls, 1931b; Carefoot, 1973a) state that *Ligia* is a nocturnal feeder. Observations showed that large numbers of *L. dilatata* emerged from their crevices at night, but only a small proportion of these animals were observed feeding. The reason for this is unknown.

Field observations showed that the isopods do not attack kelp plants as soon as they are cast up. Tagged plants

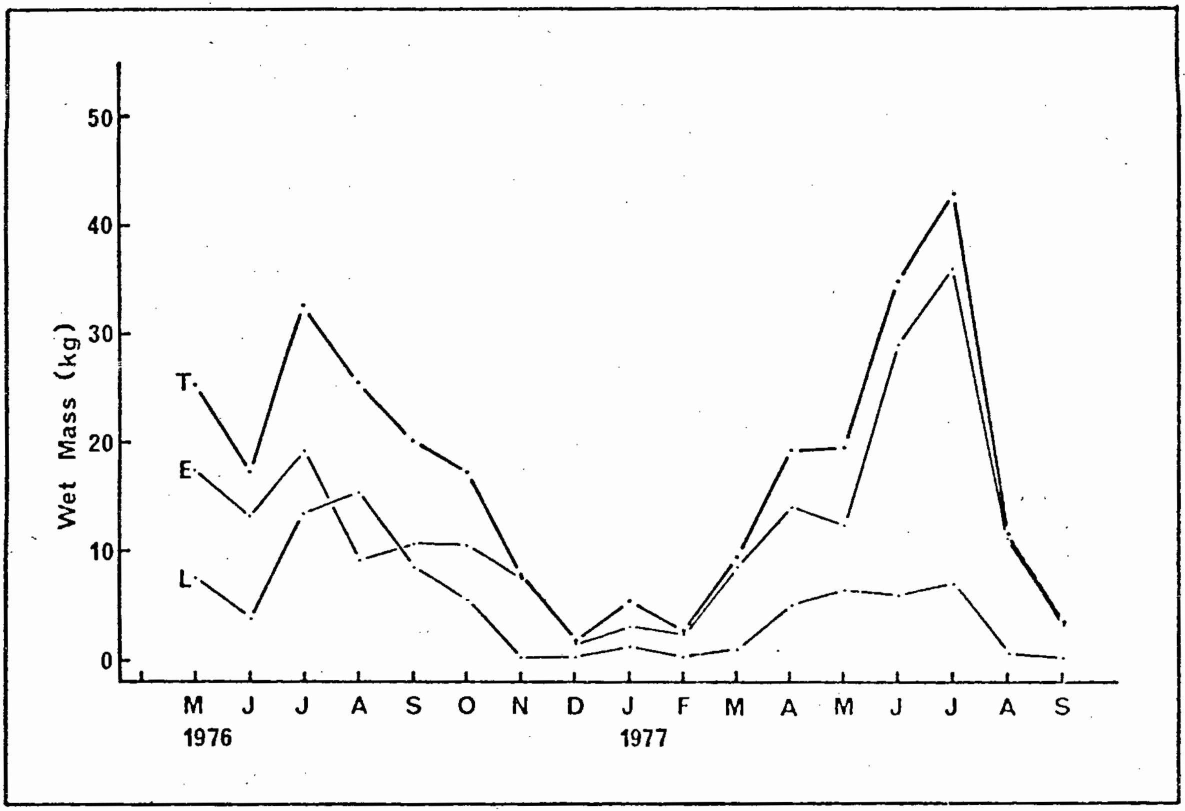


Fig. 3.2

Standing stock of kelp debris present on the beach in a 1 m corridor from HWS to LWS weighed at monthly intervals.

T = total wet mass of kelp debris consisting of three species : Ecklonia maxima (E), Laminaria pallida (L) and Macrocystis angustifolia (not plotted separately since it made up only 0 - 0,8% of monthly total mass).

showed signs of having been eaten only after they had been on the beach for 72 hours.

Contrary to the isopod *Cirolana imposita* (Shafir, 1978) *L. dilatata* were not observed consuming their exuvia and occasionally large amounts of exuvia were found on the beach.

Table 3.1 presents the results of the first food preference experiment. This indicates the food preference : *E. maxima*, *L. pallida*, *G. radula*, *M. angustifolia*, the mass of *E. maxima* consumed amounting to more than twice that of the other algae together.

| Food Species | Mass Consumed (g) by 10 animals in 24 h | Calorific Value kJ. $g^{-1}$ wet mass |
|---|---|---|
| *E. maxima* | 1,3876 | 1,95 |
| *L. pallida* | 0,4382 | 1,36 |
| *G. radula* | 0,4019 | 2,49 |
| *M. angustifolia* | 0,3371 | 1,83 |

Table 3.1

Food preference determined by presenting one of four potential food species to 10 isopods. One experiment was conducted for each food species.

A choice chamber experiment confirmed the above results.

Isopods presented with all four potential food species consumed nearly six times as much *E. maxima* as all other food species together (Table 3.2). One way analysis of variance (Zar, 1974) showed that significantly more *E. maxima* was consumed than other algae (F = 41,3 P 0,0005).

| Food Species | Mass of Food Consumed (g.24h$^{-1}$) by 10 Isopods Experiment Number | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | Mean | S.D. | Preference |
| *E. maxima* | 2,3097 | 1,2501 | 1,4378 | 1,9210 | 1,5798 | 1,6997 | 0,4202 | 1 |
| *L. pallida* | - | 0,5031 | 0,8103 | - | - | 0,2627 | 0,3757 | 2 |
| *M. angustifolia* | - | - | 0,0018 | - | 0,0365 | 0,0077 | 0,0161 | 4 |
| *G. radula* | - | 0,0030 | 0,0471 | 0,0257 | - | 0,0152 | 0,0208 | 3 |

Table 3.2

Food preference determined by offering four potential food species simultaneously to five groups of 10 isopods.

A number of authors have reported on aspects of feeding in the Ligiidae. Carefoot (1973a) states that *L. pallasii* may undertake foraging expeditions of up to 50m while Nicholls (1931b) observed that *L. oceanica* emerges from crevices at night to feed voraciously in the *Fucus* zone. *L. oceanica* was found to consume mainly *Fucus spp.* but *Laminaria*, another brown alga, and fine epiphytic algae were also eaten (Nicholls, 1931b; Jöns, 1965). Carefoot (1973a) found that in the field *L. pallasii* consumed mainly diatoms and the green algae *Enteromorpha* and *Cladophora* but laboratory experiments revealed that the animals preferred the brown alga *Nereocystis* and the green alga *Ulva* though these were inaccessible in their natural habitat.

It would appear that brown algae constitute a preferred food source for *Ligia* in other parts of the world but *L. oceanica* is opportunistic in its feeding habits, frequently resorting to scavenging on cast up plant and animal matter and occasionally to predation on the amphipod *Orchestia* or other *Ligia* (Nicholls, 1931b; Jöns, 1965).

From the point of view of energetics *G. radula* would seem to be the most suitable food species for *L. dilatata* since it has both the highest calorific value and the lowest percentage of inorganic matter (Table 3.3).

| Food Species | Calorific Value kJ.g$^{-1}$ dry mass | S.D. | Calorific Value kJ.g$^{-1}$ wet mass | % Ash | n |
|---|---|---|---|---|---|
| *E. maxima*(1) | | | | | |
| 1° frond | 12,79 | 1,11 | 1,94 | 38 | 20 |
| 2° frond | 13,13 | 0,83 | 1,95 | 47 | 20 |
| Stipe | 9,48 | 1,26 | 1,10 | 41 | 20 |
| Holdfast | 11,83 | 1,10 | 2,21 | 36 | 20 |
| *L. pallida*(2) | | | | | |
| Frond | 11,06 | 1,27 | 1,36 | 30 | 35 |
| Stipe | 8,76 | 1,50 | 0,90 | | 35 |
| Holdfast | 7,84 | 2,28 | 1,29 | | 35 |
| *G. radula*(3) | 12,30 | 0,86 | 2,49 | 25 | 10 |
| *M. angustifolia* | 10,17 | 1,09 | 1,83 | 28 | 10 |

Table 3.3

Calorific values and percentage inorganic matter for four potential food species of *Ligia dilatata*.

(1) from Field *et al.*, 1978

(2) from Dieckmann, 1978

(3) from McQuaid, in prep.

Calorific values of potential food items are an obvious and easily determined measure of their value to an animal, and a number of workers have used them in their considerations of food preference in animals (Emlen, 1966; Paine and Vadas, 1969). However, this approach appears too simplistic and other characteristics of the food bearing on the nutritional needs of the animal, the ease with which potential foods may be found, manipulated and digested, the palatability or taste of the food source and the relative proportions of indigestible material must all enter into considerations of why an animal eats a particular food.

The present study indicates that there is no correlation between calorific value and food preference (Table 3.3). Following Paine and Vadas (1969) it would appear that as far as L. dilatata is concerned availability constitutes a major factor in determining the isopods' preference for E. maxima. Certainly the amount of G. radula washed ashore at Kommetjie could not sustain the large population of Ligia. However, the experiments indicate that the preference is also a real one, for, contrary to findings by Carefoot (1973a), who discovered that L. pallasii in the laboratory preferred algae that were unavailable in the field, L. dilatata shows preference for E. maxima over other algae in the laboratory as well. Thus preference of the isopods for E. maxima is likely to be related to factors other than solely energy content and availability.

It is not known why L. dilatata prefers plant material that has been aged for several days. Several workers have found feeding on plant matter to be related to microflora growing on it. Tenore (1975) showed that consumption of eelgrass detritus by the polychaete Capitella capitata increases with increasing age of the detritus and attributed this to the increasing micro-heterotrophic community on the material. Adams and Angelovic (1970) found that various species of estuarine invertebrates were capable of assimilating $^{14}C$ from bacteria inhabiting detrital particles and Kofoed (1975) showed that assimilation of grass detritus by the gastropod Hydrobia ventrosa is dependent on the bacterial component. It is possible that a similar situation exists in the feeding of L. dilatata and that the isopods are utilising the bacteria growing on the ageing kelp as an additional source of food. This aspect was not pursued in the present study but deserves further attention.

## Reproduction

Development in L. dilatata is typical of the Peracaridan crustaceans (Jones, 1970; Naylor, 1972; Johnson, 1974; Shafir, 1978). Females brood their young in external brood pouches formed by overlapping oostegites which extend medially from the bases of the first five pairs of pereiopods. These structures are developed during a special reproductive moult which immediately precedes copulation and fertilisation of the eggs. Some time before the ovigerous moult the female is held under the body of the male in a pre-copula. The greater size of the male, particularly its greater width, allows for easy accommodation of the female below the body of the male without seriously impeding the animals' ability to move about. Pairs of L. dilatata in pre-copula were often observed covering considerable distances in their natural habitat. The advantage of this behaviour is that the male isopod is at hand when the female undergoes her ovigerous moult and copulation can take place immediately afterwards. Copulation was not observed in the present study.

The eggs are carried by the female in the marsupium where they hatch. The embryos undergo their development in the brood pouch until they are released by the female. This was observed both in the field and in the laboratory. The female flexes the abdomen upwards forcing the last pair of oostegites apart. The young isopods then move out through the opening thus formed. Females release their young onto moist rock surfaces and the whole process was observed to take between 5 and 25 minutes in specimens that were observed in the laboratory. This is in marked contrast to the 30 days required by females of Cirolana imposita to void their brood pouches (Shafir, 1978).

Breeding of isopods generally takes place in spring and summer (several authors, in Carefoot, 1973b). Usually females breed for the first time at one year of age in the summer following their release from the brood pouch.

Continuous recruitment has been reported in some species of isopods notably those of the Jaera albifrons group (Jones and Naylor, 1971) and in Excirolana braziliensis (Dexter, 1977), Cirolana harfordi (Johnson, 1974) and Cirolana imposita (Shafir, 1978) though the latter was found to have a distinct reduction of reproductive activity during summer which in that study was the time of year when environmental temperatures were lowest.

Geographical distribution certainly has some bearing on the reproductive cycle of isopods. Jaera ischiosetosa in Newfoundland breeds in May-August (Steele and Steele, 1972) in contrast to Jaera albifrons in Britain. Paris and Pitelka (1962) report that Armadillidium vulgare in California breeds at one year of age while the same species in England takes two years to reach sexual maturity (Heeley, 1941). Ligia oceanica is reported by Nicholls (1931a) to breed all year with a peak of activity in spring, whereas L. pallasii breeds in May-July (Carefoot, 1973b). The present study shows that L. dilatata follows the usual isopod pattern breeding in spring, summer and autumn. Females produce their first brood at approximately 11 months and the possibility exists that they may enter a second breeding period the following year.

## Sex Ratio

Out of a total of 5653 sexed isopods collected during the course of this study, males represented 48,81% of the total. This represents a sex ratio of males to females of 1 : 1,05. A test on the raw data showed this to be not significantly different from a 1 : 1 ratio ($\chi^2 = 3,22$; $P > 0,1$).

Analysis of the various size classes of the population showed no significant difference in the number of males and females in the 10 - 12mm size class. This presumably reflects a 1 : 1 sex ratio in juvenile animals for which no data are available since they cannot be sexed. In the size classes between 12mm and 16mm males were in the majority and no females were discovered that were larger than 21,35mm, the largest male being 25,35mm long.

Sex ratios vary a great deal among isopods. Some species have a preponderance of males while in others females are more abundant (Hatchett, 1947; Paris and Pitelka, 1962; Holdich, 1968; Jones and Naylor, 1971; Steele and Steele, 1972; Johnson, 1974; Sheader, 1977; Shafir, 1978). To date no explanation for the imbalance has been proposed. Some species, for example, Armadillidium vulgare, produce broods of only one sex (Howard, 1939) and Collinge (1947) reports that high temperatures resulted in female broods in laboratory populations of *Oniscus asellus* and *A. vulgare*. Workers tend to attribute the imbalance in sex ratios to early mortality of males. However, Holdich (1968) found that though the male : female ratio in *Dynamene bidentata* was 1 : 9 in its feeding habitat the ratio in the spatially separate breeding habitat was 1 : 4. He accounted for this apparent increase in the number of males by showing that males survive for two breeding seasons while females die after only one.

The problem is made more complex by observations that there are more males than females in some populations. Paris and Pitelka (1962) attributed this to relatively high mortality of females during their reproductive moults. High mortality after the second maternal moult was also found in *Cylisticus convexus* (Hatchett, 1947). A further potential source of mortality for female isopods may be related to differential survival of sexes in varying humidity conditions. Carefoot (1973b) found that males of *L. pallasii* survived twice as long as females in dry air. This he attributed to the greater width of the tergites in male isopods offering additional protective shielding of bunched animals thus reducing desiccation. The last observation is particularly relevant to *L. dilatata* but applies only to large animals where the difference in width between the sexes becomes substantial. It is in the large size classes that male *L. dilatata* outnumber females.

## Fecundity

Fecundity is described equally well by two linear regression lines. A graph of number of eggs in the brood pouch against length of the female shows a scatter of data points around the linear regression

$$N = 1{,}9L - 3{,}7 \qquad (r = 0{,}41)$$

where $N$ = number of eggs or embryos in a brood pouch
and $L$ = length of female in mm (Fig. 3.3).

The correlation coefficient is significant ($N = 42$, $P < 0{,}01$) (Zar, 1974). A graph of number of eggs or embryos in the brood pouch against cube length of females is described by the equation

$$N = 0{,}002 \, . \, L^3 + 17{,}63 \qquad (r = 0{,}41)$$

where $N$ = number of eggs or embryos in a brood pouch
and $L^3$ = cube length of female in mm.

Again the correlation coefficient is significant ($P < 0{,}01$).

Little evidence was found for mortality during marsupial development. Only in a few cases were underdeveloped eggs found among eggs of later stages of development or among embryos. It is possible that unfertilised eggs or underdeveloped eggs may be expelled from the brood pouch although the mechanism for this is unknown.

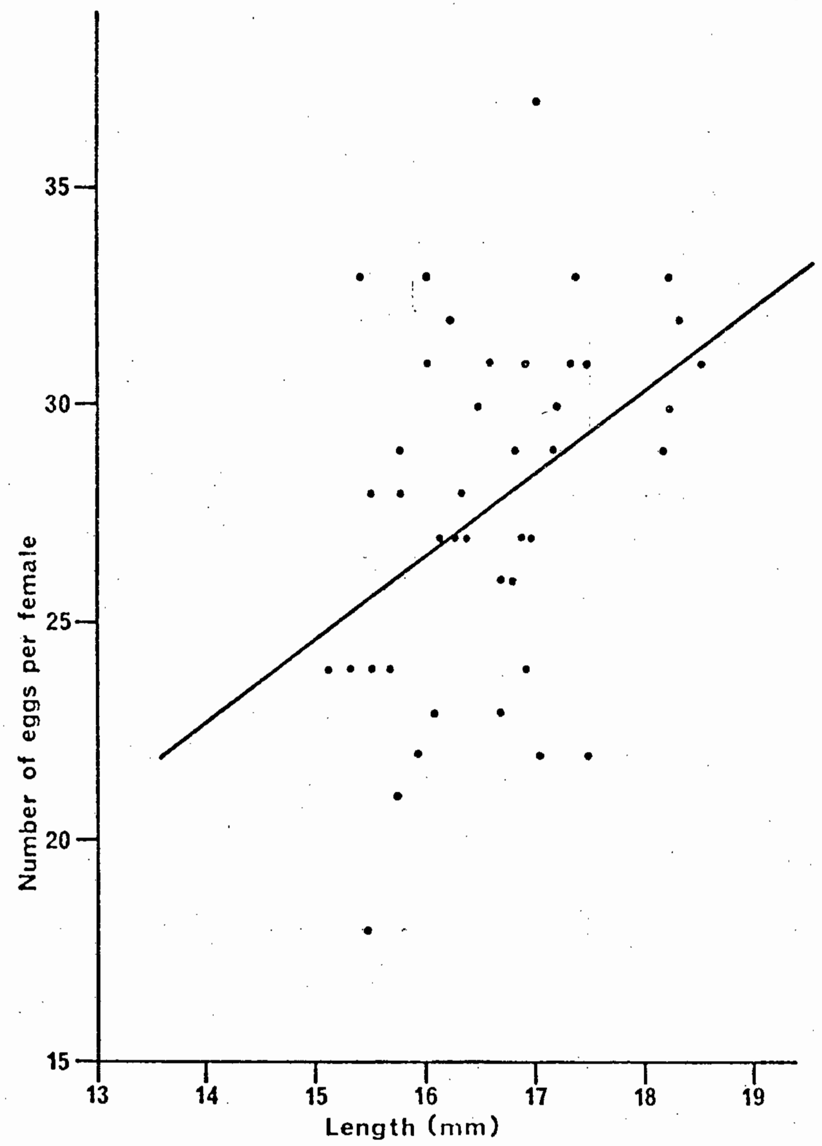


Fig. 3.3

Fecundity of *Ligia dilatata*

N = 1,9 L - 3,7 (r = 0,41; n = 42)

In the Peracarida various relationships have been reported between the number of eggs carried by females and their body length. Jensen and Schütz (in Johnson, 1974) found that fecundity increases with the cube length of females while various authors working specifically on isopods report that the relationship for these animals is a linear one (Holdich, 1968; Jones, 1970; Jones and Naylor, 1971; Johnson, 1974; Shafir, 1978). Carefoot (1973b), working on L. pallasii reports that there was "no straightforward correlation between size of female and the number of young in the brood pouch" but that a graph of these parameters resembled an inverted U-shaped curve. The present study agrees well with the typical fecundity pattern exhibited by isopods and reported in the literature (Holdich, 1968; Jones, 1970; Jones and Naylor, 1971; Johnson, 1974; Shafir, 1978).

The fact that little marsupial mortality was observed also agrees with reports in the literature. Carefoot (1973b) found that over 95% of the eggs of L. pallasii developed into young isopods demonstrating very low mortality in the brood pouch of an isopod which is ecologically equivalent to L. dilatata. Mortality during development of embryos of the isopod Cirolana imposita was likewise found to be small (Shafir, 1978).

## 3.2 Population Structure and Dynamics

### Population Dynamics and Reproductive Cycle

The population of L. dilatata showed a bimodal distribution during most of the study period (Fig. 3.4). Only at the start of a new recruitment period (October 1976 and October, November 1977) did a third cohort appear. Although the population showed recruitment for 8 months of the year the two component cohorts remained distinctly separate. Only towards the end of their lifespan did the few remaining members of a cohort tend to merge in size with the largest animals of the younger cohort. At this stage the larger cohort represented only 1,60% of the population in 1976 and only 2,75% in 1977.

At the start of the sampling period in May 1976 the population consisted of two cohorts marked A and B in Fig. 3.4 and with mean body lengths of 13,6mm and 5,2mm respectively. In the course of the next 20 months two new cohorts were observed, one (C) entered the population in October 1976 and the other (D) appeared in October 1977. Both cohort C and D entered the population with mean body lengths of 3,0mm. Ovigerous females or newly hatched isopods were present in the population from September 1976 to April 1977 and from September 1977 until the end of the

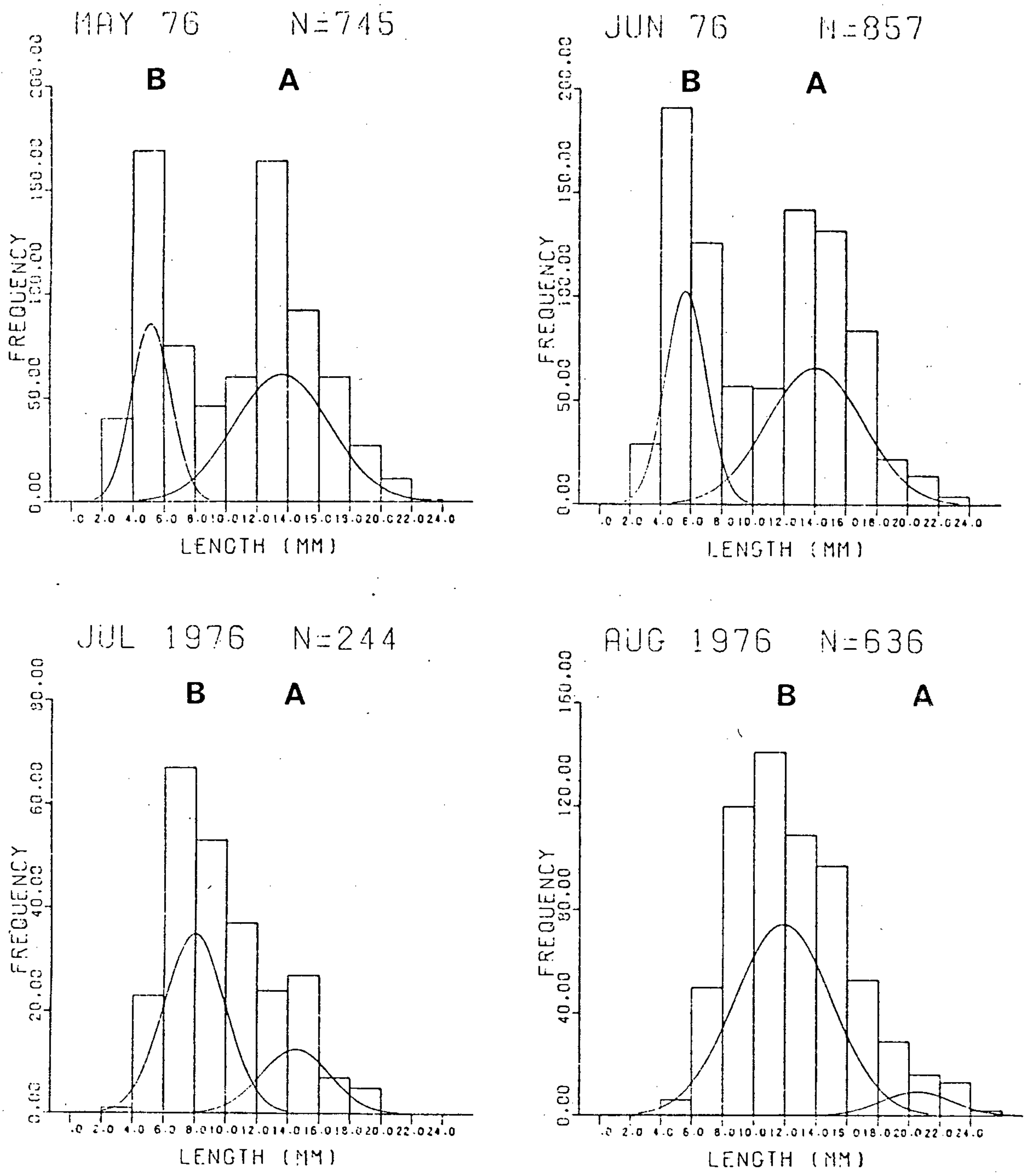


Fig. 3.4

Size frequency histograms and component normal curves plotted from the data generated by the polymodal analysis program NORMSEP. The cohorts are identified by the letters A to D.

N = number of animals in monthly samples.

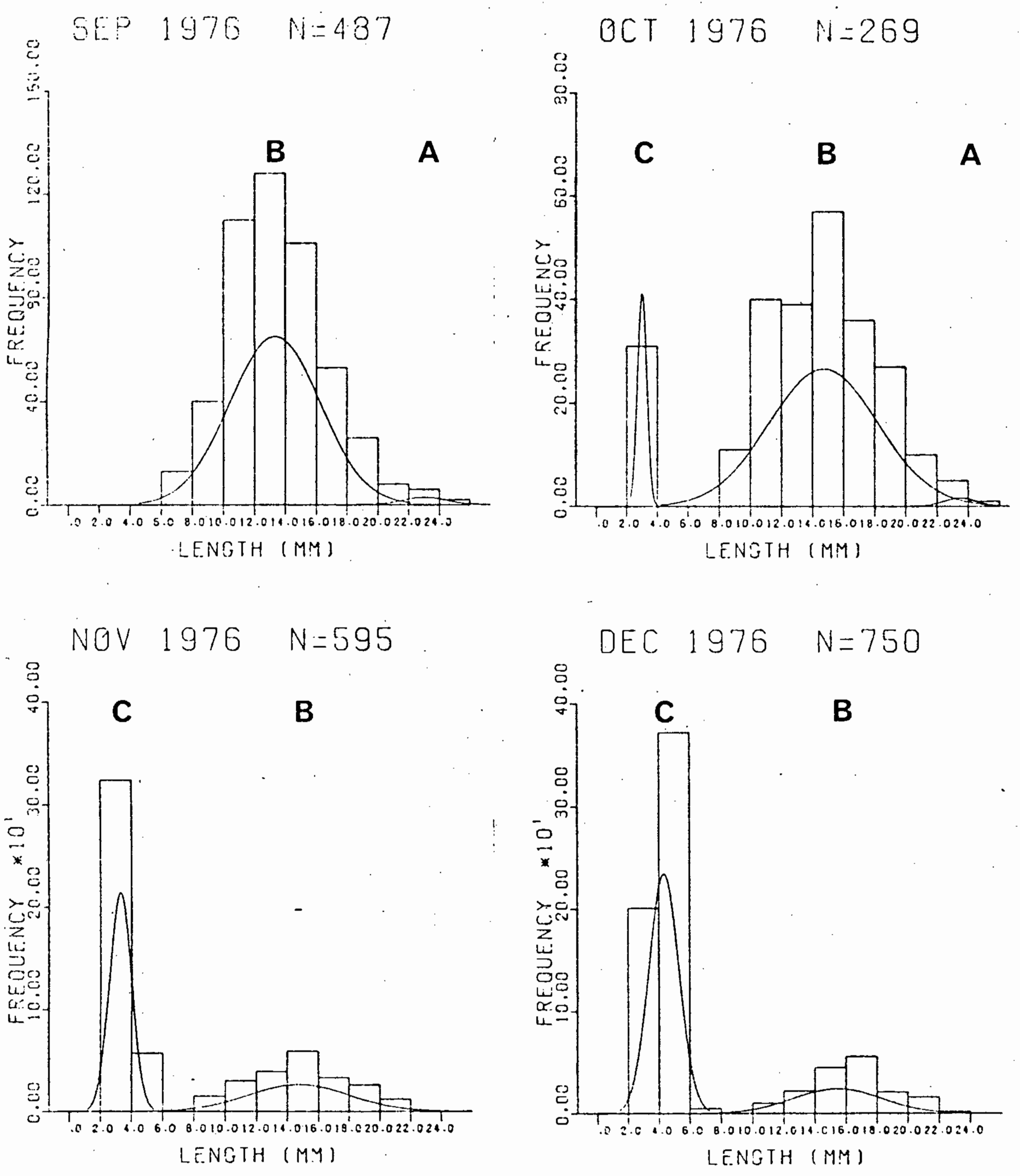
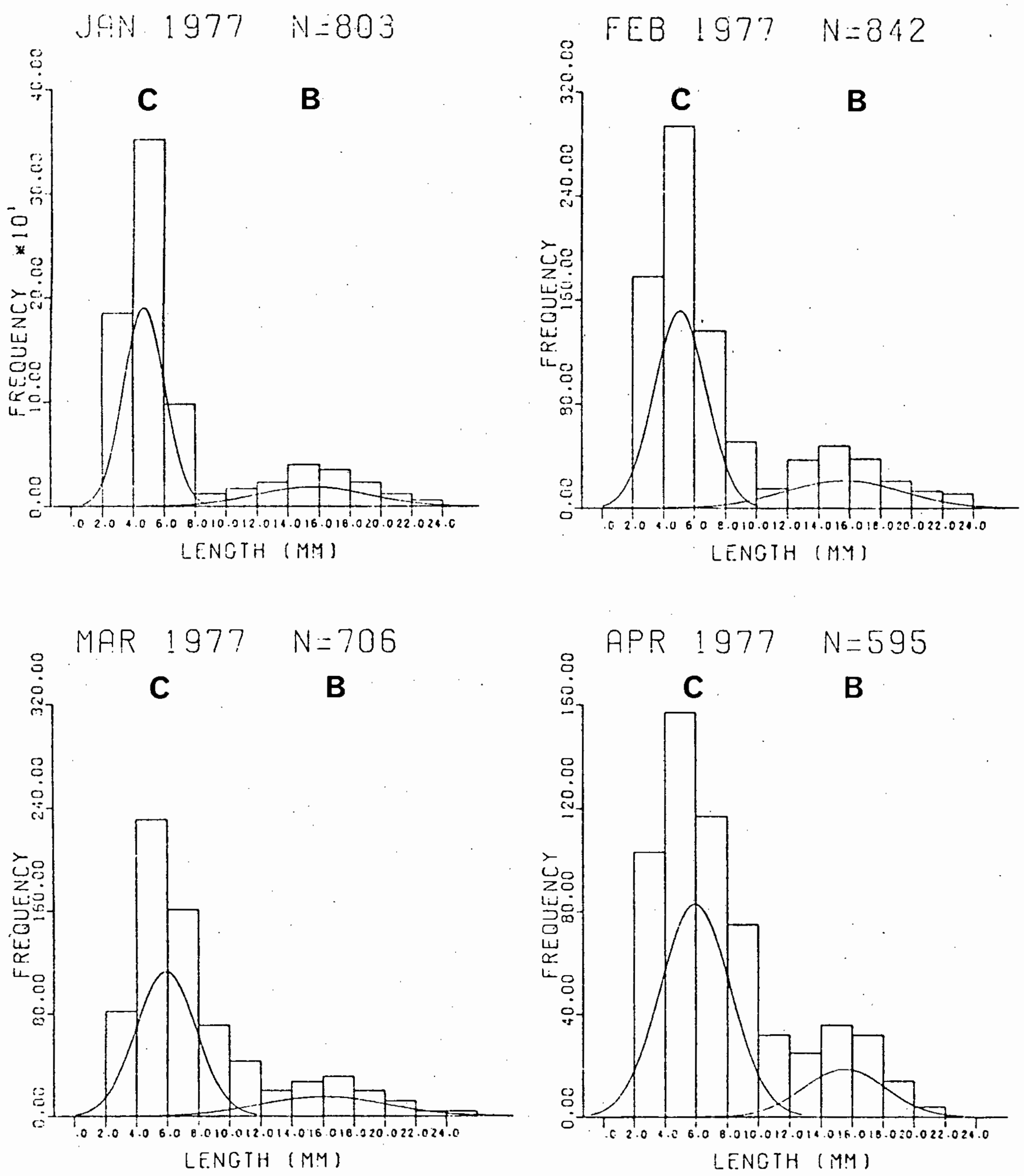


Fig. 3.4 (continued)



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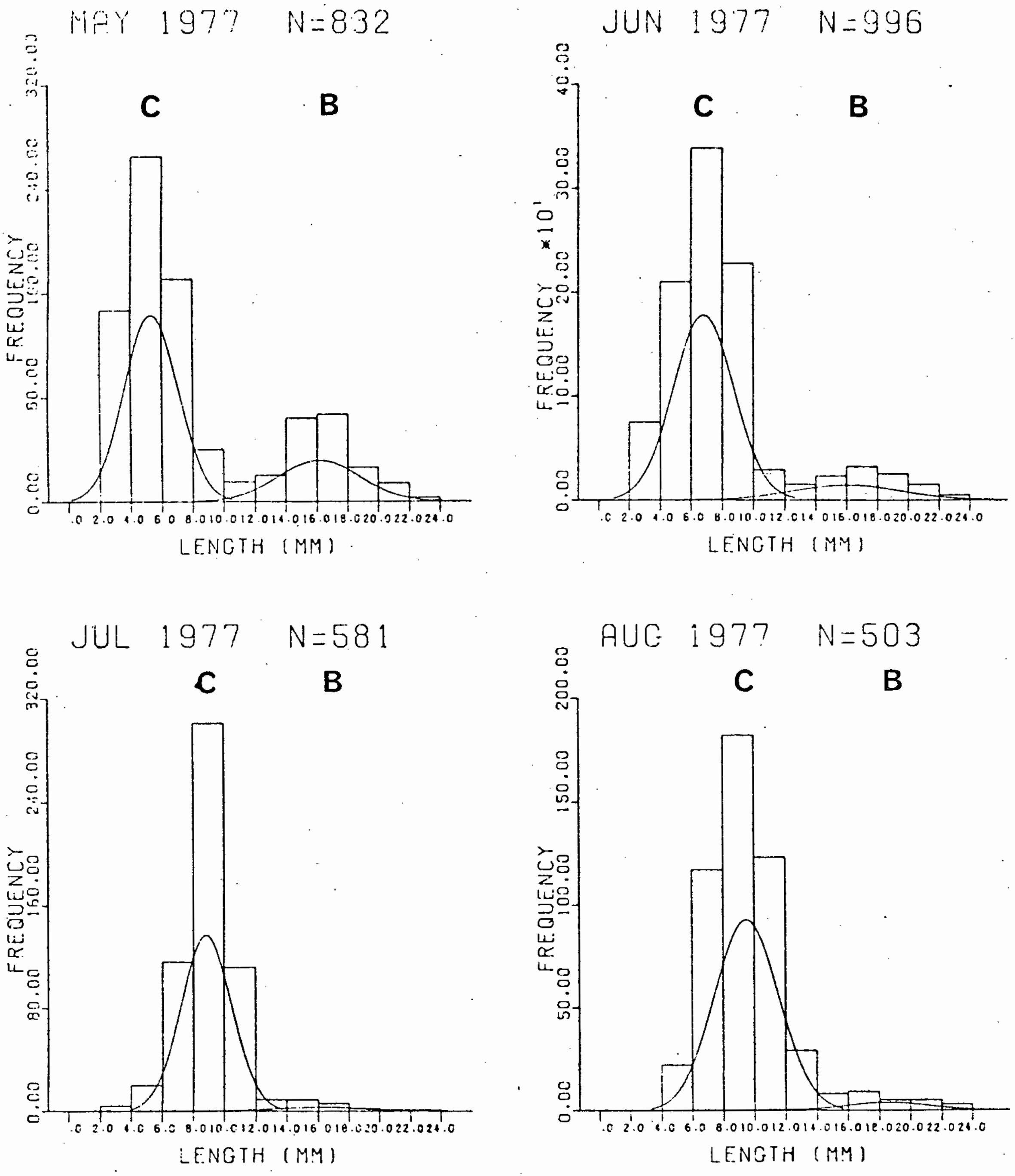

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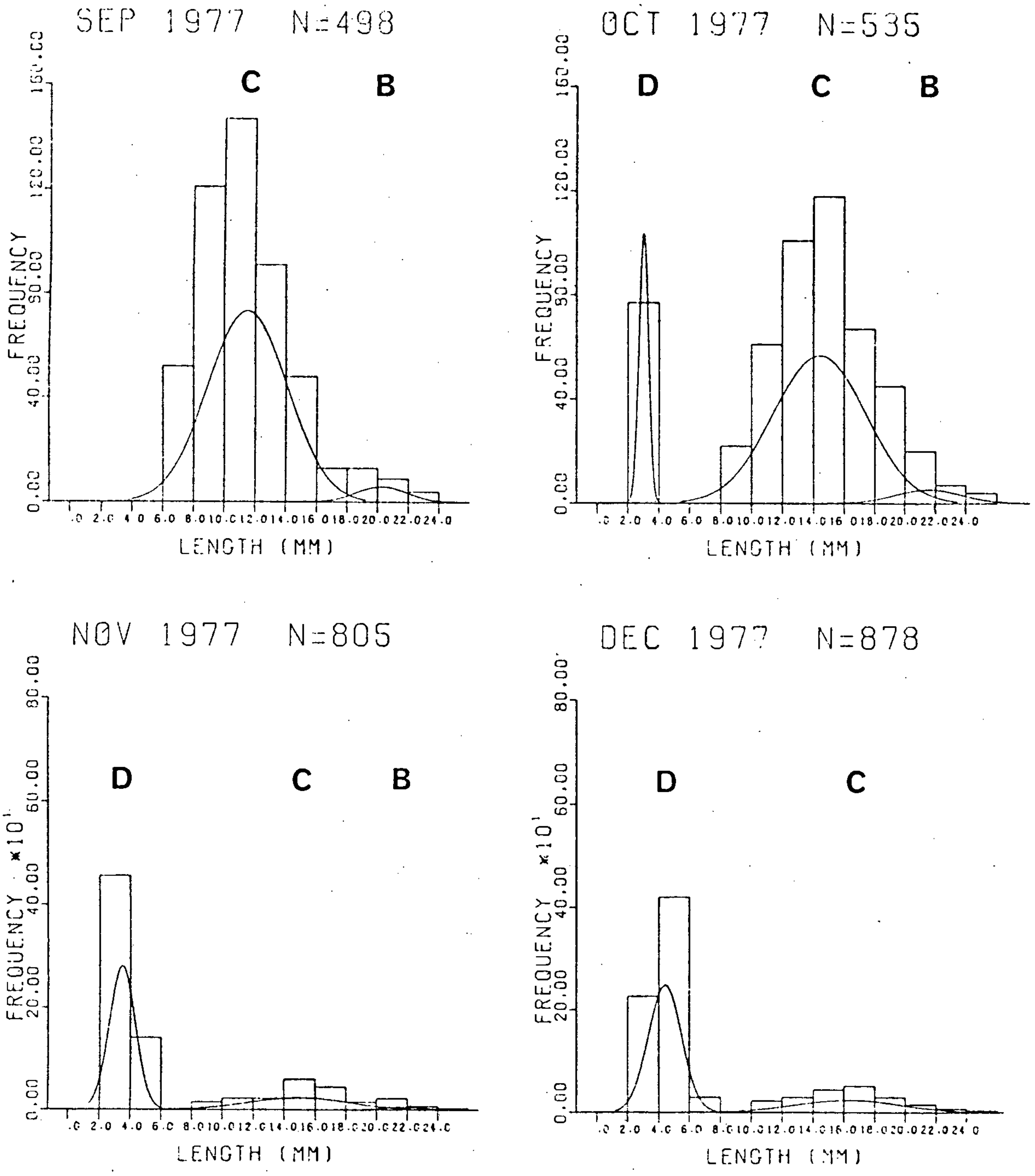

Fig. 3.4 (continued)

sampling period in December 1977. There was no evidence of females carrying winter broods as reported for *L. pallasii* by Carefoot (1973b). Due to the lack of success in keeping specimens of *L. dilatata* in the laboratory for any length of time, no direct observations on the duration of marsupial development were possible. Since the bulk of reproductive females in the population in October 1976 were animals from cohort B and a new cohort appeared in that month, this age group (cohort C in Fig. 3.4) represented largely the offspring of cohort B. In October 1977 most reproductive females were animals of cohort C, thus the new cohort (D) represents largely the offspring of cohort C. The cohorts which were encountered in the first sample in May 1976 died out in the course of the study period. Cohort A was last identified in October 1976 having reached a mean body length of 23,5mm and cohort B was last identified in November 1977 at 21,8mm mean body length (Fig. 3.4). In October 1976 cohorts A and B had mean lengths of 14,7mm and 23,5mm respectively; in October 1977 cohorts B and C had mean lengths of 14,3mm and 21,5mm respectively. These data point to a remarkable constancy of population structure for corresponding periods in successive years, something which had previously been recorded in other isopods by Johnson (1974) and Shafir (1978).

The ovigerous females encountered in the population in

September 1977 were animals that were either 23 months old and going into their second breeding season or 11 months old from the cohort which entered the population the previous October. It was not possible to estimate how many females actually survived until the second breeding season but the number is likely to be very small. During the study period the mean lengths of the two-year-old cohorts in September were 23,0mm (1976) and 20,2mm (1977) and the percentage of the total population was 2,1 and 5,0 respectively. The maximum size of females encountered during the whole period was 21,4mm whereas the largest male measured was 25,4mm long. From this it seems likely that the 2 year old cohorts in September consisted mainly of males and that few, if any, females survived until the second breeding season.

Newly released isopods first appeared in the population in the second half of October in both years of study (Fig. 3.4). Since ovigerous females were first observed early the previous month, marsupial development in L. dilatata is estimated to take about 5 - 6 weeks under temperature conditions experienced during the study period. This is in good agreement with Nicholls (1931a) reporting a summer incubation period of 40 days for L. oceanica and Carefoot (1973b) stating that marsupial development of L. pallasii takes 3 - 4 weeks at 20°C in the laboratory.

## Density

The study population shows large fluctuations in density at the study site (Fig. 3.5). The smallest number of animals per running metre of beach was recorded immediately prior to the onset of recruitment ($1161.m^{-1}$ in September and $1191.m^{-1}$ in October 1977). A peak in numbers was reached in December 1976 with 4334 animals per metre.

## Growth and Ageing

No growth data are available from laboratory experiments since the isopods did not survive for any length of time outside their natural habitat. Growth estimates were made from the size-frequency distributions of successive months by following the mean length of each cohort obtained from the NORMSEP analysis (this section) for the entire sampling period. These data were used to compile composite growth curves for each cohort of the population for the duration of the sampling period. L. dilatata showed a distinct growth pattern (Fig. 3.6). The animals hatched at 3,0mm starting in October (cohorts C and D) and there followed a period of slow growth (0,3mm per month average increment) which lasted throughout the summer and autumn until cohort C had reached a mean body length of 5,3mm in May 1977. The growth rate increased over the

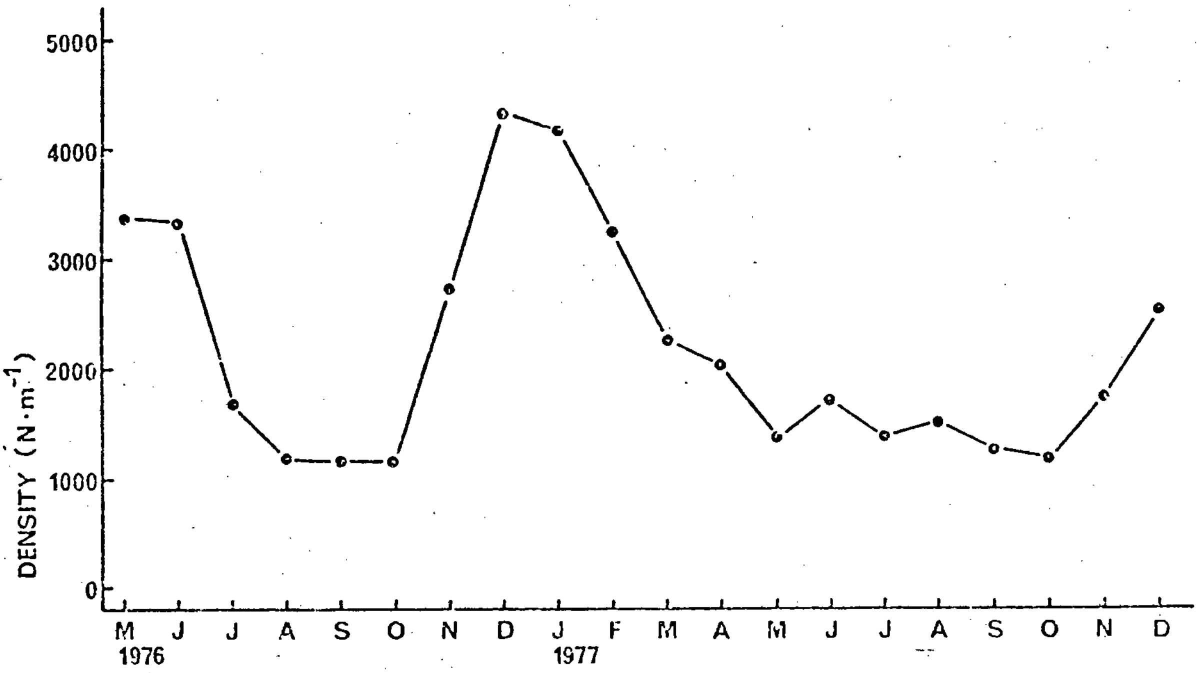

Fig. 3.5

Density (number of animals per running metre of beach) of Ligia dilatata at Kommetjie during the study period.

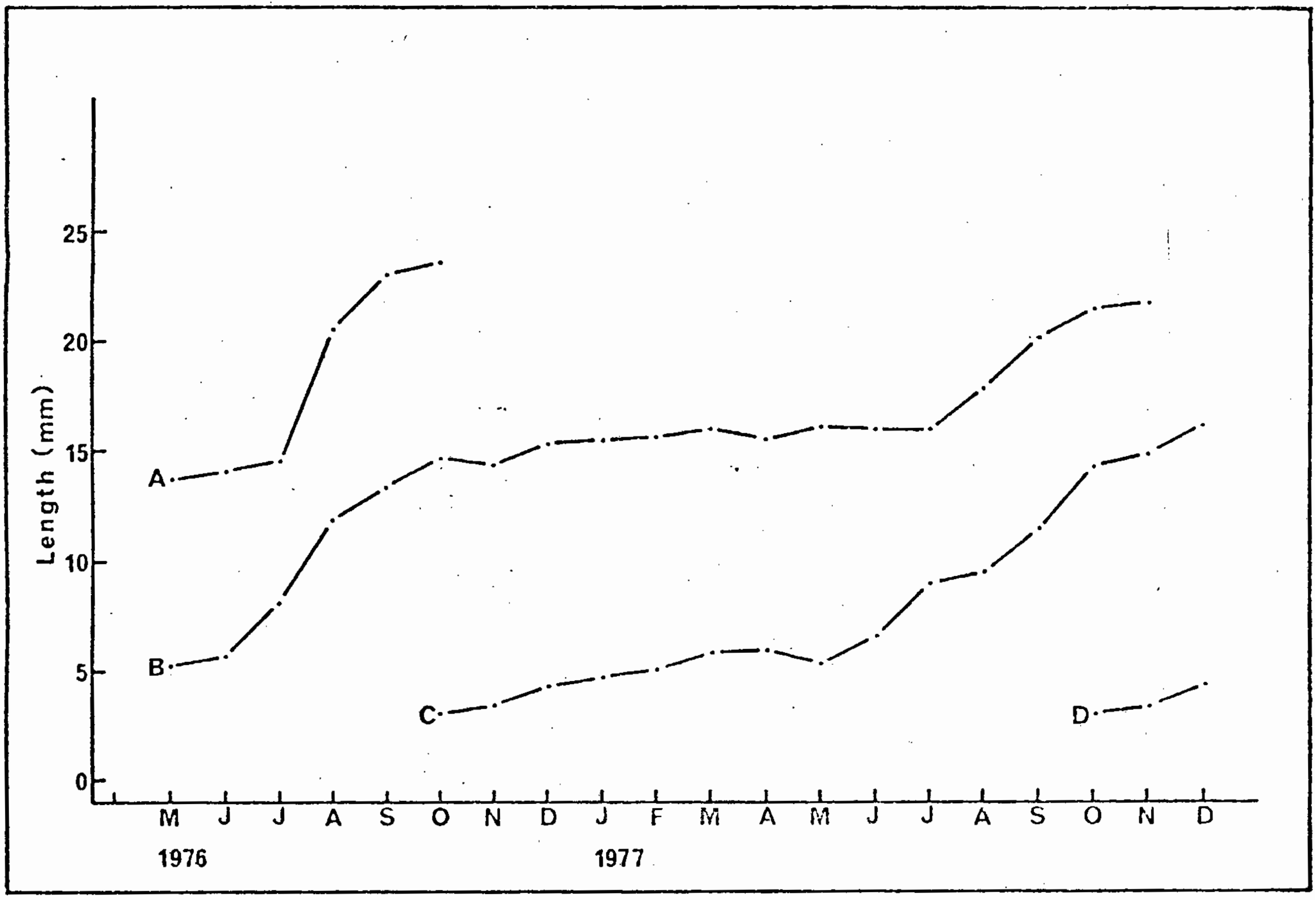

Fig. 3.6

Composite growth curves of the cohorts (A - D) of the *Ligia dilatata* population constructed from Fig. 3.4.

winter months and cohort C animals grew from 5,3mm in May to 14,3mm in October at a rate of 1,8mm per month. This period coincided with the time of reduced reproductive activity when there were no ovigerous females in the population. From October to May the growth rate of animals entering their second year of life (cohort B) was also greatly reduced and they grew from 14,7mm in October to 16,1mm in May the following year at a rate of 0,2mm per month. This too was followed by a period of rapid growth during the winter months; animals in cohort B grew from 16,1mm in May to 21,5mm in October (an average increment of 1,11mm per month).

A Ford-Walford graph was constructed to quantify mean growth rate of the population (Ricker, 1968) using data from cohorts B and C. Initial length ($l_t$) was plotted against length one year later ($l_{t+1}$). This time interval was chosen in order to compensate for the rather irregular growth pattern of *L. dilatata*, since shorter (e.g. monthly) intervals distorted the graph because of the long slow-growth phase. In order to obtain sufficient data points, overlapping time intervals were used; thus for cohort B, May 1976 was plotted against May 1977, June 1976 against June 1977 and so on. The same procedure was applied to cohort C. The resulting linear regression is described by the equation :

$$l_{t+1} = l_t(1 - e^{-k}) + L_\infty \cdot e^{-k}$$ (Ricker, 1968)

where $l_t$ = length of the animal at time t

$l_{t+1}$ = length of the animal one year later

$e$ = base of natural logarithms

$L_\infty$ = maximum length reached

$k$ = a measure for the rate at which length approaches L

The data from cohorts B and C yielded the regression (Fig. 3.7)

$$l_{t+1} = 0{,}5\ l_t + 13{,}7$$ ($r = 0{,}94$; $n = 10$)

The theoretical maximum length of 26,3mm obtained from the intercept of the regression line with the $45^\circ$ line agrees satisfactorily with the maximum observed length of 25,4mm measured in October 1976.

From studies of growth patterns and reproductive biology (this section) it is possible to estimate the ages of individuals in a population at different stages of their life cycles. The breeding period for *L. dilatata* extended from October to May during which [illegible] young isopods were being produced continually. Taking into account the results presented above, cohort A, when first sampled in May 1976 had a maximum age of 19 months and was the result of the October 1974 to May 1975 breeding

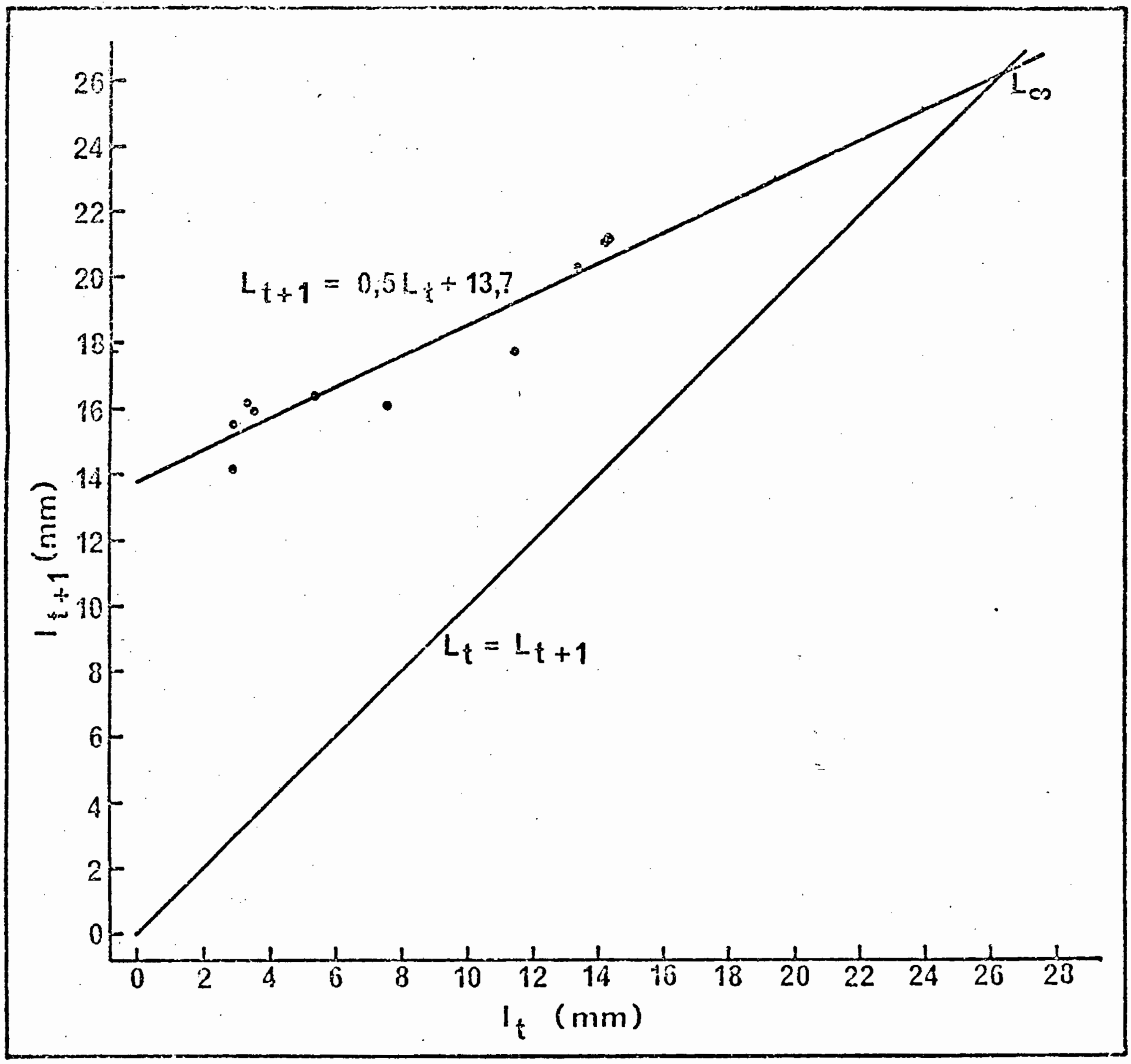

Fig. 3.7

Ford-Walford growth curve for the *Ligia dilatata* population. Initial length ($l_t$) was plotted against length one year later ($l_{t+1}$).

The intercept with the 45° line gives the theoretical maximum length ($L_\infty$).

season. Cohort B resulted from the 1975/76 breeding season and was 8 months old when first sampled. Cohorts C and D entered the population during the study period and represent the 1976/77 and 1977/78 recruitments. At the end of the study period cohorts A and B had died at 24 and 25 months respectively, cohort C had reached the age of 14 months and cohort D was 2 months old.

Growth of isopods is affected by a number of factors, one of the dominant ones being seasonal fluctuations in environmental temperature (Jones, 1970; Jones, 1974; Jones and Naylor, 1971; Sheader, 1977). The general pattern is one of breeding in spring and summer (Carefoot, 1973b), rapid growth during the early phases of life and slower growth during winter, occasionally ceasing altogether (Jones, 1970; Sheader, 1977). The isopod population under investigation in this study did not conform to the reported pattern. Growth fell into two distinct phases : a slow growth phase which lasted over summer from October to May and which coincided with the breeding period of the animals, and a phase of rapid growth in winter between May and October during which the population showed no breeding activity.

Growth could not be measured in the laboratory and growth rates are based on increments of cohort means from field data only. However, the cohorts were always easily identified and there is every reason to have confidence in the monthly estimates of mean cohort length and hence the growth rates.

In the 8 months after juveniles first appeared in the population there was constant recruitment. This may have led to an underestimate of juvenile growth rates because newly hatched animals were constantly entering the population thus tending to reduce the cohort mean size. On the other hand growth in adult cohorts during the same period was also slow. Although this may be explained by the fact that the animals were channelling a portion of the assimilated energy into reproduction, it does indicate that the slow growth rate of juveniles observed during the spring, summer and autumn months is likely to be a real phenomenon.

A further point to consider in this context is that the studies by Jones (1970), Jones (1974), Jones and Naylor (1971), Carefoot (1973b) and Sheader (1977) were carried out in climates where differences in environmental temperature between summer and winter are considerable. *L. dilatata*, because of the peculiarity of its habitat, is largely sheltered from extremes of temperature (see Section 3,1) and the total temperature range experienced by the animals during the study period was estimated to be only 6,2$^{o}$C.

Another factor that may significantly influence growth rates of animals is food preference and availability. Greenwood (1974) reports a significant increase in the growth rate of Parechinus angulosus after the juvenile animals are believed to have switched from a detrital feeding phase to the typical urchin grazing phase. From Section 3.1 it is clear that the amount of food available to the L. dilatata population varied greatly throughout the year. Very large amounts of kelp were deposited on the beach during the winter months while the mass of kelp available as potential food source was reduced in summer (Fig. 3.2). Growth patterns coincided with this variation in kelp deposition and when much food was available in winter, growth rates were high. It may safely be assumed that this condition led not only to somatic growth but that towards the end of this period some of the available food energy was channelled into reproductive tissues since ovigerous females appeared in the population in early spring.

It therefore appears that in the case of L. dilatata temperature plays only a minor role in determining growth patterns and that food availability has a far more important effect on the field population.

## Survivorship and Mortality

Survivorship estimates were obtained by plotting the decrease in density (i.e. numbers/running metre) against time.

The proportions of the cohorts in the population every month were obtained from the component normal curves calculated by the NORMSEP program (Fig. 3.4). These were multiplied by the density each month to obtain numbers of each cohort per metre of beach.

Survivorship regressions (Table 3.4) were derived by plotting the logarithm of numbers against time for each cohort after recruitment had ceased. Mortality of cohort B falls into two distinct phases (Fig. 3.8) which were estimated by eye and linear regressions were then calculated for each phase separately. This indicates that the mortality rate was not constant but varied at different stages of the life cycle. Equation $B_1$ describes survivorship of cohort B between the months of May and December 1976 and covers the time when the animals did not reproduce and the beginning of their first reproductive season. Equation $B_2$ describes survivorship of cohort B for the rest of the reproductive season and the following non-reproductive phase before the cohort disappeared in

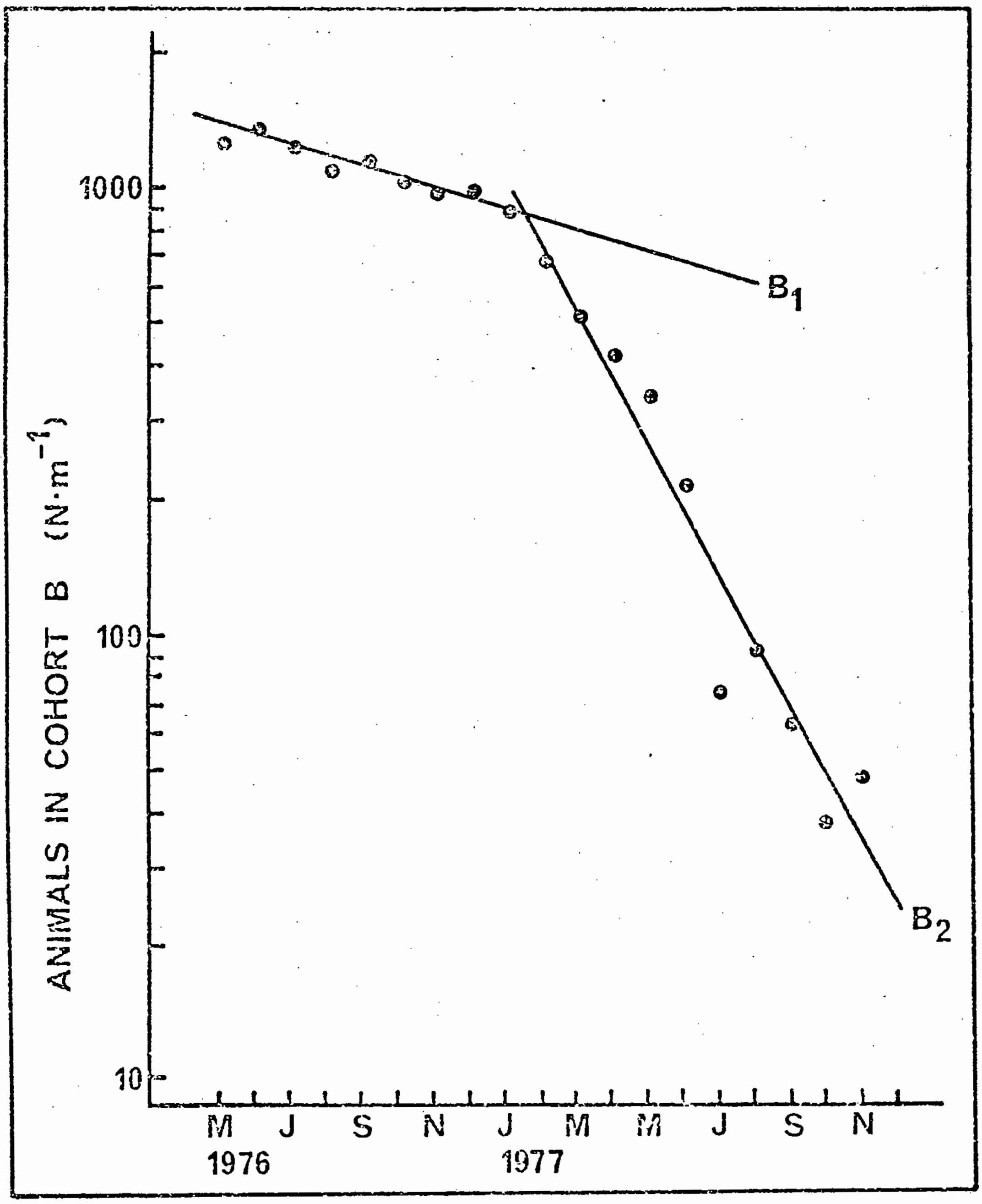

Fig. 3.8

Survivorship regression lines for the two mortality phases of cohort B.

November 1977. Cohort A consisted of large animals near the end of their lifespan. This stage of the life cycle corresponde to that of the animals in cohort $B_2$. The animals of cohort C were at the same stage of their life cycle as cohort $B_1$. A t-test comparing the slopes of the various regression lines showed no significant difference between the survivorship regressions for cohorts A and $B_2$ ($t = 1{,}27$; $P < 0{,}05$) or between C and $B_1$ ($t = 0{,}13$; $P < 0{,}05$). The regressions $B_1$ and $B_2$ had significantly different slopes ($t = 7{,}66$; $P < 0{,}05$) (Zar, 1974).

| Cohort | Equation | n | $r^2$ |
|---|---|---|---|
| A | $\log_{10}N = 4{,}00 - 0{,}48t$ | 6 | 0,97 |
| $B_1$ | $\log_{10}N = 3{,}13 - 0{,}02t$ | 8 | 0,91 |
| $B_2$ | $\log_{10}N = 3{,}14 - 0{,}15t$ | 11 | 0,97 |
| C | $\log_{10}N = 3{,}25 - 0{,}06t$ | 8 | 0,72 |

Table 3.4

Regression equations showing the decrease in numbers (N) of each cohort with time (t) in months per metre of beach.

There are many reports in the literature showing mortality patterns to be a function of age for a variety of organisms (Hughes, 1970; Sameoto, 1973; Greenwood, 1974; Johnson, 1974).

The data show that once recruitment ceased, mortality of L. dilatata stayed at a relatively low level throughout the winter and during the early reproductive phase. A mean monthly death rate of 2,4% was recorded for cohort B for the months May to December 1976. Mortality then increased significantly and over the next eleven months all the animals in the cohort died (mean monthly mortality : 9,1%).

## 3.3 Ecological Energetics

### Calorific Values

Calorific values and ash content of all material examined are shown in Table 3.5 (overleaf).

In the L. dilatata population percentage ash content rose with increase in body length. This relationship is described by the linear regression

$$A = 0{,}13L + 15{,}48 \qquad (r^2 = 0{,}93; \quad n = 12)$$

where A = percentage ash

and L = body length of the animal

Eggs and embryos had a relatively high calorific value. It dropped in newly hatched juveniles to a body length of 6 - 8 mm, then rose steadily. The highest value was recorded for animals between 20 and 22 mm in length (based

| Material | Calorific Value ($kJ.g^{-1}$) |  |  |  | % Ash | S.D. | n |
|---|---|---|---|---|---|---|---|
|  | D.M. | S.D. | AFDM | S.D. |  |  |  |
| Ligia population |  |  |  |  |  |  |  |
| Mixed | 18,39 | 1,01 | 22,29 | 1,39 | 17,42 | 2,87 | 26 |
| 2- 4 mm | 22,36 | 0,64 | 26,49 | 0,77 | 15,60 | 0,28 | 10 |
| 4- 6 mm | 21,60 | 0,80 | 25,71 | 0,99 | 15,99 | 0,22 | 10 |
| 6- 8 mm | 21,04 | 0,39 | 25,26 | 0,48 | 16,71 | 0,15 | 10 |
| 8-10 mm | 21,76 | 0,96 | 26,22 | 1,13 | 17,01 | 0,16 | 10 |
| 10-12 mm | 21,09 | 0,52 | 25,45 | 0,66 | 17,11 | 0,28 | 10 |
| 12-14 mm | 21,81 | 0,70 | 26,27 | 0,84 | 16,98 | 0,23 | 10 |
| 14-16 mm | 20,69 | 0,60 | 24,98 | 0,74 | 17,17 | 0,28 | 10 |
| 16-18 mm | 23,24 | 0,44 | 28,14 | 0,57 | 17,41 | 0,37 | 10 |
| 18-20 mm | 24,15 | 0,32 | 29,36 | 0,35 | 17,75 | 0,29 | 10 |
| 20-22 mm | 24,92 | 0,43 | 30,37 | 0,60 | 18,29 | 0,40 | 10 |
| 22-24 mm | 22,65 | 0,48 | 27,71 | 0,53 | 18,27 | 0,59 | 10 |
| 24-26 mm | 22,53 | 0,32 | 27,79 | 0,50 | 18,93 | 0,54 | 10 |
| Eggs and embryos | 26,48 | 0,61 | 28,59 | 0,61 | 7,07 | 2,22 | 10 |
| Faeces | 9,86 | 0,76 | 11,15 | 0,93 | 11,40 | 0,70 | 10 |
| Exuvia |  |  | 10,23 |  | 56,50 |  | 3 |
| Food |  |  |  |  |  |  |  |
| *Ecklonia maxima* | 13,13 | 0,83 |  |  | 47,00 |  | 20 |

Table 3.5

Calorific values and ash content for *Ligia dilatata* and *Ecklonia maxima*.

on ash-free dry mass) after which the value dropped off again for larger animals.

The calorific value for the mixed population of Ligia is a mean value based on the natural size distribution and incorporating seasonal variations as well as changes in physiological and reproductive state.

## Length-Mass Relationship

Graphs of log length against log mass in L. dilatata are linear (Figs 3.9 and 3.10). Owing to changes in the physiological state of the animals at different times of the year and at different stages of their life cycle, relationships of length to mass may not be constant for the population. In order to reflect these changes length-mass regressions were calculated periodically. Table 3.6 shows the seasonal regression equations (see overleaf).

A t-test for difference between regression coefficients (Zar, 1974) showed that the slopes of lines 2, 3 and 4 did not differ significantly at the 5% level. The slope of regression line 1 was significantly different from that of all other regressions.

The October, January and May data were pooled and the resulting regression is described by

| No. | Date | Regression Equation<br>log AFDM = a logL + b | n | $r^2$ |
|---|---|---|---|---|
| 1 | August 1976 | $\log AFDM = 3{,}10 \log L + 3{,}05.10^{-6}$ | 42 | 0,96 |
| 2 | October 1976 | $\log AFDM = 2{,}52 \log L + 2{,}49.10^{-5}$ | 40 | 0,98 |
| 3 | January 1977 | $\log AFDM = 2{,}60 \log L + 2{,}75.10^{-5}$ | 25 | 0,99 |
| 4 | May 1977 | $\log AFDM = 2{,}57 \log L + 2{,}49.10^{-5}$ | 42 | 0,99 |

Table 3.6

Seasonal length - ash-free dry mass regression equations for *Ligia dilatata*.

AFDM = ash-free dry mass of animal (g)
L = body length (mm)

$$\log AFDM = 2{,}51 \log L + 2{,}75.10^{-5} \qquad (r^2 = 0{,}98;\ n = 107)$$

where AFDM = ash-free dry mass in grams
and L = body length in mm.

This curve (Fig. 3.9) differed significantly from the winter length - ash-free dry mass regression (Fig. 3.10) at the 5% level (Zar, 1974). These results confirm that seasonal physiological differences exist in the *L. dilatata* population which is reflected in the two distinct growth phases discussed in Section 3.2.

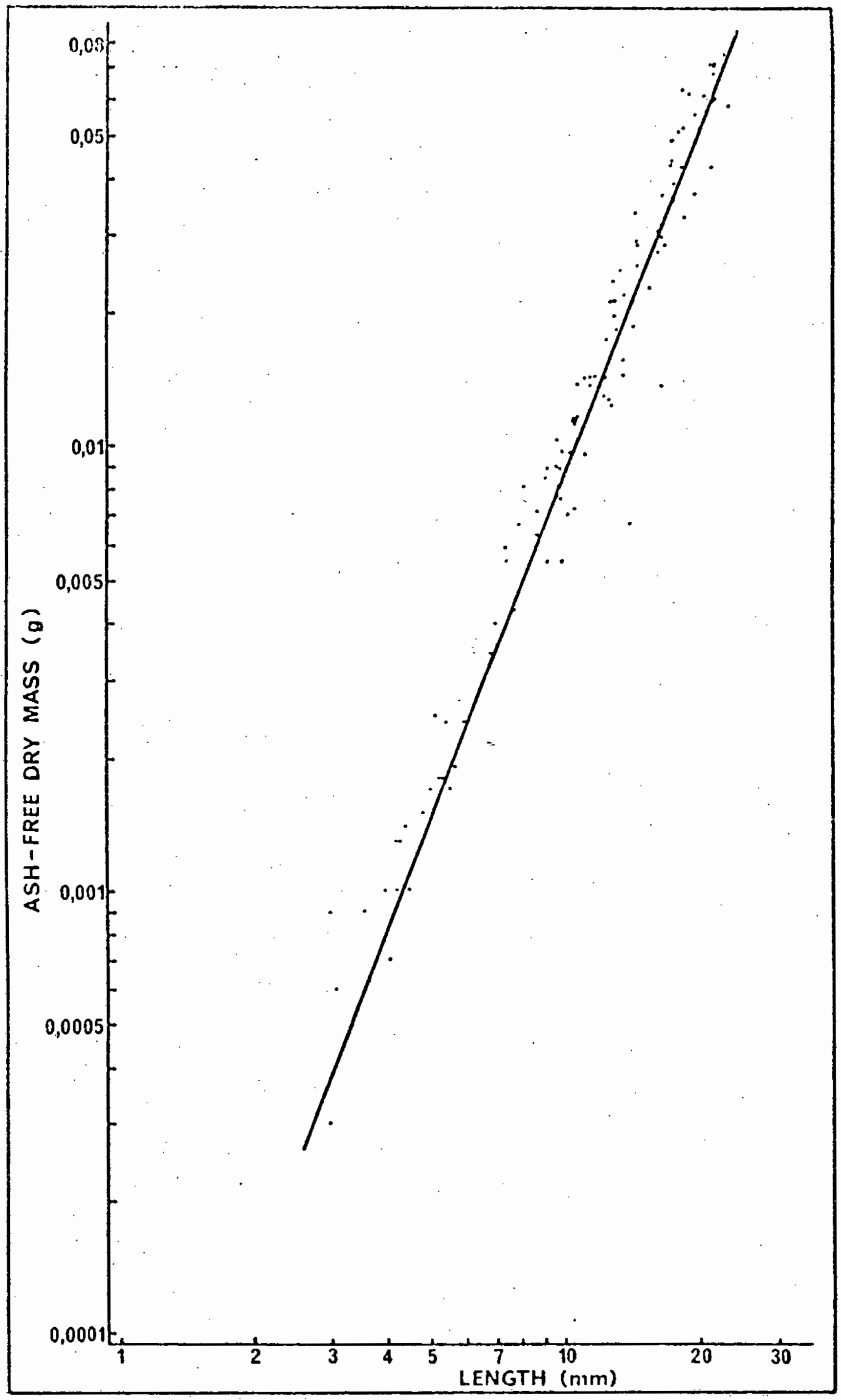

Fig. 3.9

Log - log length - ash-free dry mass regression for Ligia dilatata for spring, summer and autumn of the study period.

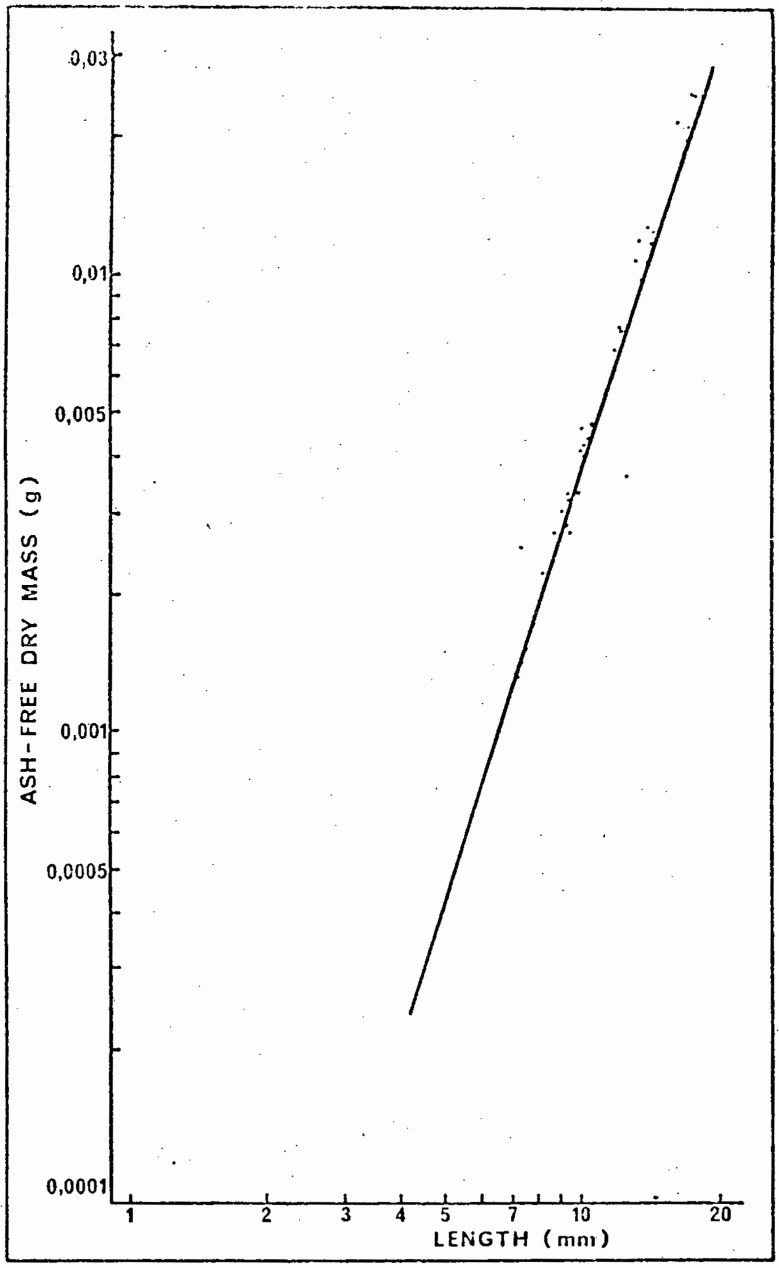

Fig. 3.10

Log - log length - ash-free dry mass regression for Ligia dilatata for winter of the study period.

## Production

The production of each cohort was calculated over the entire study period by two methods. Mean length of animals in the different cohorts were derived using the NORMSEP computer program (Section 3.2). These were converted to mean ash-free dry mass using the appropriate length-mass regressions (this section).

(1) Monthly production was estimated by multiplying the average number of animals during that month ($\bar{N}_t$) by the mass gained by an animal of mean cohort length in that period ($\Delta W_t$) :

$$P_t = \bar{N}_t \cdot \Delta W_t$$

$$\text{or } P_t = \frac{(N_{t1} + N_{t2})}{2} \cdot (W_{t2} - W_{t1})$$

where $P_t$ = monthly production

$N_{t1}$ = number of animals at the beginning of the month

$N_{t2}$ = number of animals at the end of the month

$W_{t1}$ = mass of mean sized animal at the beginning of the month

$W_{t2}$ = mass of mean sized animal at the end of the month

The assumption in this calculation is that during the time interval $t_2 - t_1$ on the average $\bar{N}_t = (N_{t1}+N_{t2}).2^{-1}$ animals exist and produce an average $\Delta W = W_{t2}-W_{t1}$ in mass (i.e. production estimate based on survivorship) (Petrusewicz and Macfadyen, 1970).

(2) The second method of estimating production involves assuming that during the time interval $t_2-t_1$ a number of animals $\Delta N_t = N_{t1}-N_{t2}$ having an average mass of $\bar{W}_t = (W_{t1}+W_{t2})/2$ are eliminated from the population. This is calculated as production by the formula (estimate based on elimination) (Petrusewicz and Macfadyen, 1970)

$$P_t = \Delta N_t \cdot \bar{W}_t$$

$$\text{or } P_t = (N_{t1} - N_{t2}) \cdot \frac{(W_{t1} + W_{t2})}{2}$$

Production for each cohort for the whole study period was then estimated by adding the monthly production figures (Table 3.7) (overleaf).

From the data in Table 3.7 production of a cohort of L. dilatata for its whole lifespan can be estimated. Although no cohort was followed throughout its lifespan the production estimate may be obtained by combining results from cohort B, which was sampled for most of its lifespan, with the first few months of cohort C. There is every reason to be confident that the resulting production estimate is a good one because (as discussed

| Cohort | Total Production over 20 Months<br>g AFDM . $m^{-1}$<br>Survivorship | <br>g AFDM . $m^{-1}$<br>Elimination | <br>kJ . $m^{-1}$<br>Survivorship | <br>kJ . $m^{-1}$<br>Elimination |
|---|---|---|---|---|
| A | 19,25 | 32,67 | 429,08 | 728,21 |
| B | 27,88 | 28,37 | 621,45 | 632,37 |
| C | 34,10 | 20,41 | 760,09 | 454,94 |
| D | 1,12 | 0,96 | 24,96 | 21,40 |
| Total Pop. | 82,35 | 82,41 | 1835,58 | 1836,92 |
| Annual Prod. | 70,99 | 46,58 | 1582,37 | 1038,27 |

Table 3.7

Production estimates for *Ligia dilatata* for May 1976 to November 1977, i.e. the 20 month study period and annual production for the year July 1976 - June 1977.

in Section 3.2) the reproductive patterns as well as the population structure and dynamics were remarkably constant from year to year. Production of a hypothetical cohort of *L. dilatata* over its lifespan estimated by this method is 35,07 g AFDM . $m^{-1}$ or 781,71 kJ . $m^{-1}$ of shoreline.

Since *L. dilatata* brood their young in brood pouches production estimates include both somatic growth ($P_g$) and reproductive effort ($P_r$). Energy channelled into reproduction was estimated by multiplying the number of females with embryos about to hatch per m of beach in monthly samples by average fecundity calculated in Section 3.1. The total amount of reproductive material produced by the population during the study period is estimated to be 9,43 g AFDM . $m^{-1}$ or 269,60 kJ . $m^{-1}$ of shoreline. This represents 14,68% of the total energy of production. By difference production of somatic tissue amounts to 72,98 g AFDM . $m^{-1}$ or 1567,32 kJ . $m^{-1}$ of shoreline. Annual reproductive output for the period July 1976 to June 1977 is estimated at 152,4 kJ . $m^{-1}$ of shoreline.

## Standing Crop

Standing crop estimates for the L. dilatata population were obtained by multiplying density (i.e. $\hat{N}$ . $m^{-1}$ of shoreline) by mean ash-free dry mass ($\bar{w}$) each month. Fluctuations in standing crop in energy units over the full sampling period are shown in Fig. 3.11, indicating two peaks in the standing crop of the isopod population. They occurred in December 1976 and October 1977 and are explained by the rapid growth in the preceding months together with the emergence of new cohorts from October of both years (Section 3.2). The drop in standing crop between January 1976 and July 1977 is a result of the slow growth that all cohorts exhibited during summer until March 1977, coupled with the high mortality of the largest

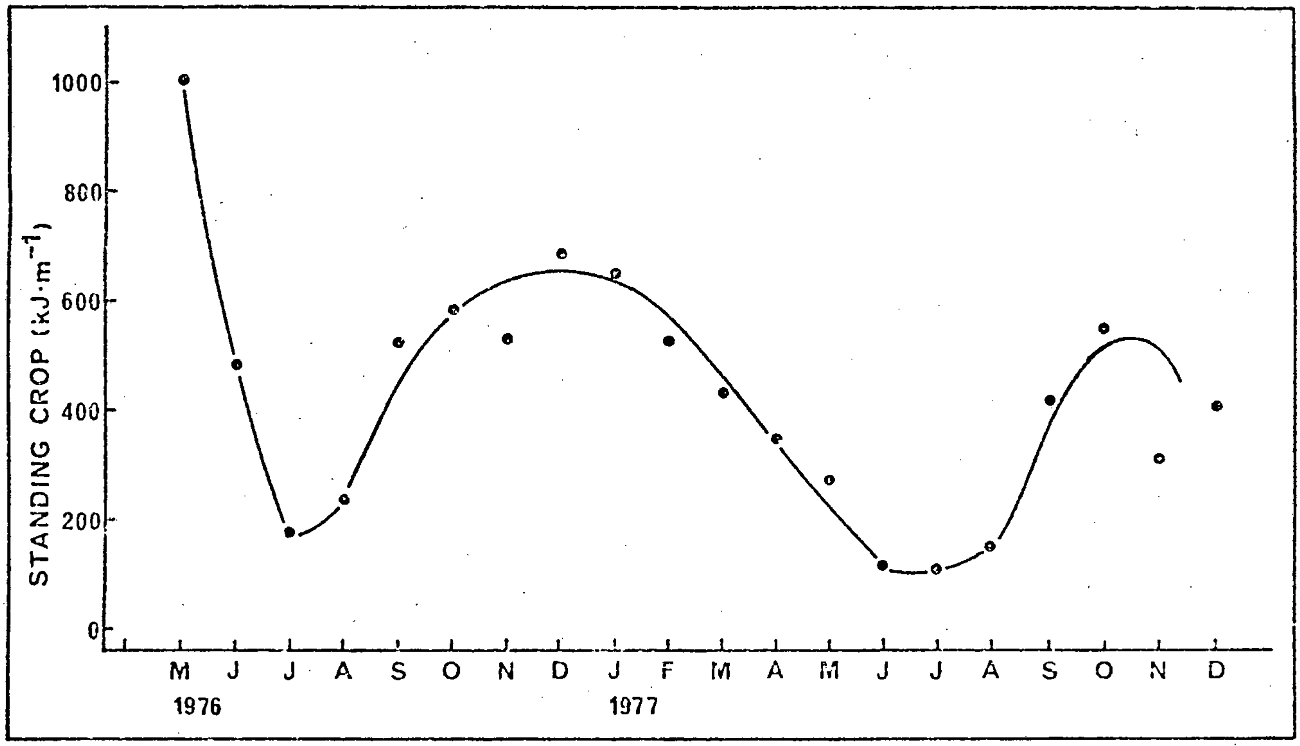

Fig. 3.11

Fluctuations in standing crop of the Ligia dilatata population at Kommetjie for the entire sampling period of 20 months.

cohort in the population over this period.

Although the general pattern of fluctuations in standing crop repeated itself during the study period, the magnitude of these fluctuations was not identical in different years. Peak standing crop in late 1976 was higher than that recorded in late 1977. The indications are also that the 1975 standing crop was much higher than at any time during the study period. It cannot be assessed whether this difference in the magnitude of the standing crop of the population during different years has a significant effect on the stability of the population. The mean standing crop for the period July 1976 to June 1977 was 422,1 kj . $m^{-1}$ of shoreline and for the entire study period 425,5 kJ . $m^{-1}$ of shoreline. The annual $P/\bar{B}$ ratio (Petrusewicz and Macfadyen, 1970) for the year July 1976 to June 1977 was 2,54.

Consumption

Feeding rates for *L. dilatata* of different size classes are shown in Table 3.8 (overleaf). Daily consumption rates as a function of body mass were quantified using a power curve regression of the form

$$C = aW^b$$

where $C$ = wet mass of food consumed (g) per 24h

and $W$ = ash-free dry mass of animal (g).

| Body length (mm) | Mean food uptake (g wet mass) per animal per 24 h<br>June | S.D. | n | December | S.D. | n |
|---|---|---|---|---|---|---|
| 4- 6 | - | - | - | 0,0281 | 0,0053 | 5 |
| 6- 8 | 0,0493 | 0,0140 | 5 | 0,0534 | 0,0060 | 5 |
| 8-10 | 0,0554 | 0,0108 | 4 | - | - | - |
| 10-12 | 0,1091 | 0,0093 | 5 | 0,1153 | 0,0103 | 5 |
| 12-14 | 0,1019 | 0,0079 | 4 | 0,1250 | 0,0090 | 5 |
| 14-16 | - | - | - | 0,1684 | 0,0074 | 5 |
| 16-18 | 0,1601 | 0,0380 | 5 | 0,1632 | 0,0119 | 5 |
| +16-18 | - | - | - | 0,1316 | 0,0175 | 5 |
| 18-20 | - | - | - | 0,2399 | 0,0326 | 5 |
| 20-22 | 0,2094 | 0,0059 | 5 | - | - | - |

+Ovigerous females

Table 3.8

Feeding rates of *Ligia dilatata* for different size classes of the population measured at different times of the year.

The equations for the two periods of the year are shown in Table 3.9 below.

| Time of Year | Regression Equation | n | $r^2$ |
|---|---|---|---|
| June | $C = 0,72 \, . \, W^{0,40}$ | 6 | 0,95 |
| December | $C = 1,15 \, . \, W^{0,56}$ | 8 | 0,95 |

Table 3.9

Seasonal regression equations for daily consumption of *Ligia dilatata*. Consumption is expressed in g wet mass and body mass in g ash-free dry mass.

## Egestion

The mean rate of faeces production of individual isopods for the whole size range of the population is shown in Table 3.10 (overleaf). The daily rate of faeces production (g AFDM) by individuals as a function of their body mass (g AFDM) is expressed by the power curve regression

$$F = aW^b$$

The two regression equations calculated from the data in Table 3.10 are :

| Body length (mm) | Faces Production (g AFDM . 24h$^{-1}$ . individual$^{-1}$) June | S.D. | n | December | S.D. | n |
|---|---|---|---|---|---|---|
| 4- 6 | - | - | - | 0,0036 | 0,0010 | 5 |
| 6- 8 | 0,0066 | 0,0019 | 5 | 0,0071 | 0,0008 | 5 |
| 8-10 | 0,0071 | 0,0012 | 4 | - | - | - |
| 10-12 | 0,0144 | 0,0023 | 5 | 0,0150 | 0,0017 | 5 |
| 12-14 | 0,0136 | 0,0017 | 4 | 0,0171 | 0,0013 | 5 |
| 14-16 | - | - | - | 0,0214 | 0,0022 | 5 |
| 16-18 | 0,0198 | 0,0057 | 4 | 0,0209 | 0,0018 | 5 |
| 18-20 | - | - | - | 0,0316 | 0,0054 | 5 |
| 20-22 | 0,0269 | 0,0019 | 5 | - | - | - |
| 16-18 ovigerous females | - | - | - | 0,0177 | 0,0028 | 5 |

Table 3.10

Rate of faeces production of individual *Ligia dilatata* covering the whole size range of the population.

Winter : $F = 0{,}09 \cdot W^{0{,}38}$ ($r^2 = 0{,}94$; $n = 6$)

Summer : $F = 0{,}15 \cdot W^{0{,}56}$ ($r^2 = 0{,}95$; $n = 8$)

Assimilation

The assimilation/consumption ratio (often referred to as assimilation efficiency) was calculated from the formula

$$\frac{A}{C} = \frac{C - (F + U)}{C} \qquad \text{(Holme and McIntyre, 1971)}$$

Energy lost through dissolved organic matter was considered to be negligible because the isopods live in air; therefore the factor U in the equation was ignored and the formula reduced to

$$\frac{A}{C} = \frac{C - F}{C}$$

Using the data from Section 3.2 and calorific values from Section 3.3, the assimilation efficiency for various size classes of L. dilatata in the laboratory yields a mean of 25,90% ± 2,07 (S.D.) for June and 25,04% ± 1,90 (S.D.) for December.

Ligia dilatata falls into the category of "more or less continuous feeders . . . which live in their food medium, which also defaecate regularly and whose time of retention of the food in the gut varies only slightly so that any mixing of food does not seriously affect the measurement of ingested and egested energy" (Duncan and Klekowski, 1975). Under such conditions and given an abundant food supply assimilation efficiency is expected to be low (Hubbell *et al.*, 1965). The recorded efficiencies of various size classes of the *L. dilatata* population of between 21,94 and 29,34% agree well with the literature value of 22 - 27% for detritus feeders (Duncan and Klekowski, 1975).

Comparison of the assimilation efficiency of different size classes of the *L. dilatata* population showed that this was not related to body size. The general trend reported in the literature is one of decreasing efficiency with increasing size of individuals (Tshikon-Lukanina and Lukasheva, 1970; Johnson 1974) although Shafir (1978) reports the opposite trend for the marine isopod *Cirolana imposita*. Relationships between assimilation efficiency and sex or reproductive state have been reported by Prus (1971) who found, among other things, that ovigerous females of the isopod *Asellus aquaticus* showed the highest efficiency in the population. This was not the case in *L. dilatata* and assimilation efficiency of 23,23% for ovigerous females lies near the bottom of the range recorded in this study.

Table 3.5 shows that inorganic material makes up 47,0% of the food of *L. dilatata*. Faeces have only 11,4% ash content. Thus a large proportion (75,7%) of the inorganic material is assimilated, something that had previously been reported by Tsikhon-Lukanina and Lukasheva (1970), Prus (1971) and Lasenby and Langford (1973).

## Respiration

Fig. 3.12 shows a typical graph of hourly oxygen consumption of one isopod measured over 25 h. It is apparent from the graph that L. dilatata exhibited no clear endogenous rhythms of metabolic activity. The recorded rates are routine rates fluctuating between values approaching standard rates (the lowest values) and active rates of oxygen consumption (i.e., the highest values).

Fig. 3.13 shows graphs of hourly oxygen consumption per individual plotted against ash-free dry mass for the four seasons of the year. The regression equations of the form

$$R = a \cdot W^b \qquad \text{(Newell, 1979)}$$

where $R$ = respiration rate ($O_2 \cdot \text{individual}^{-1} \cdot h^{-1}$)
and $W$ = ash-free dry mass of the individual (g)

are listed in Table 3.11. Weight specific respiration rates are shown in Fig. 3.14. These were obtained by plotting oxygen consumption per g ash-free dry mass of

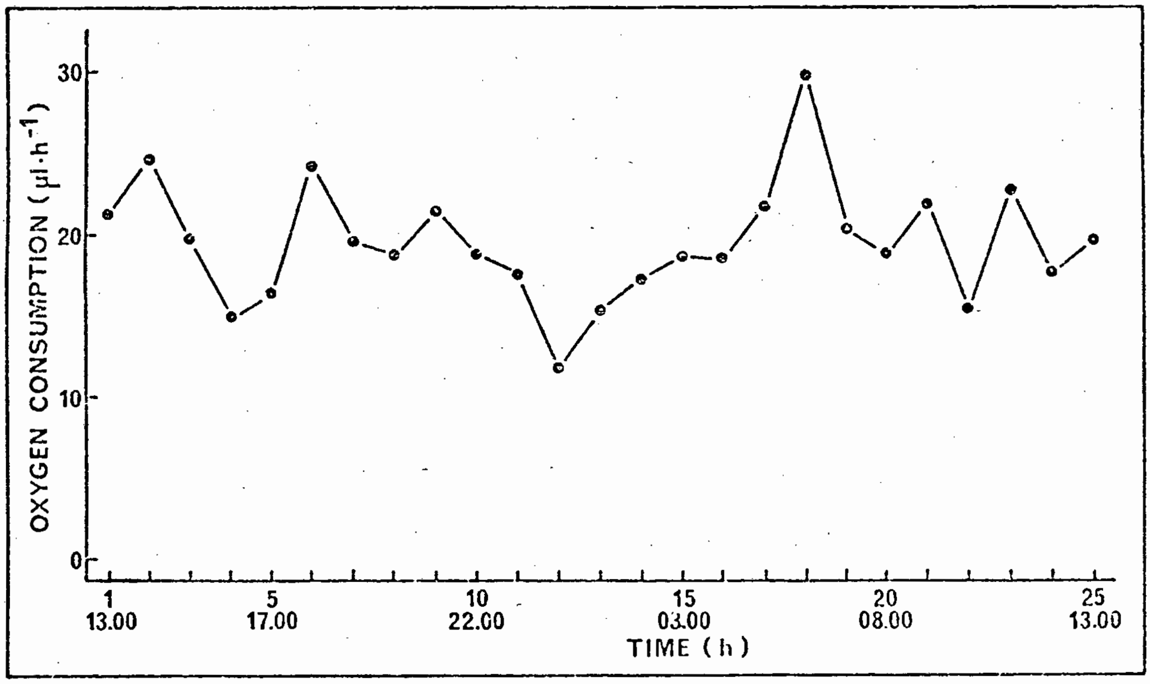

Fig. 3.12

Typical graph of oxygen consumption of an individual isopod measured every hour for 25 hours; recorded in August 1976 for an animal of 12,1 mm body length (0,0067 g AFDM).

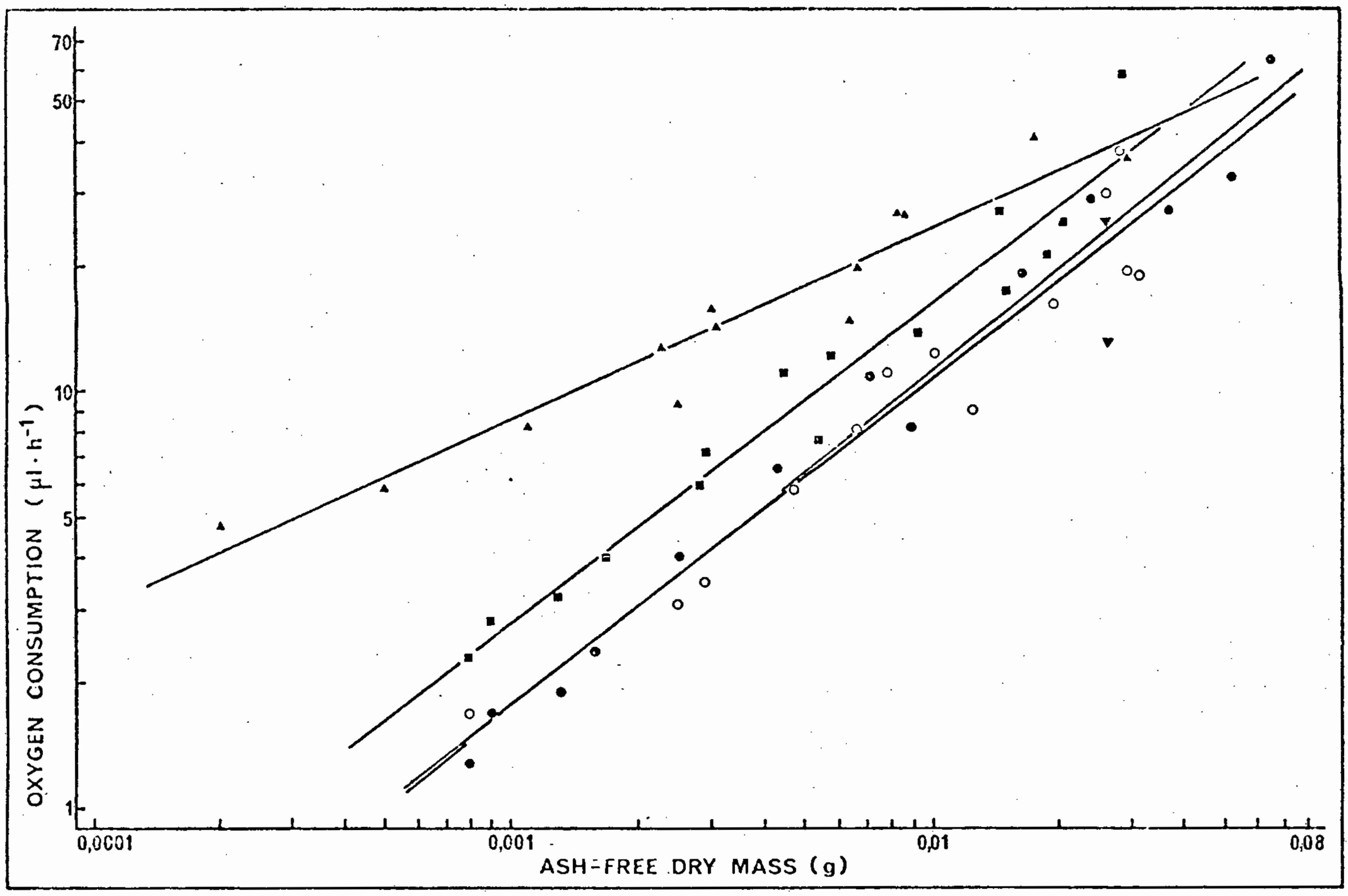

Fig. 3.13

Oxygen consumption (ul.h$^{-1}$) per isopod plotted against body mass (g AFDM) on log - log scale.

▲ -August 1976, ● -October 1976, ■ -January 1977, ○ -April 1977.

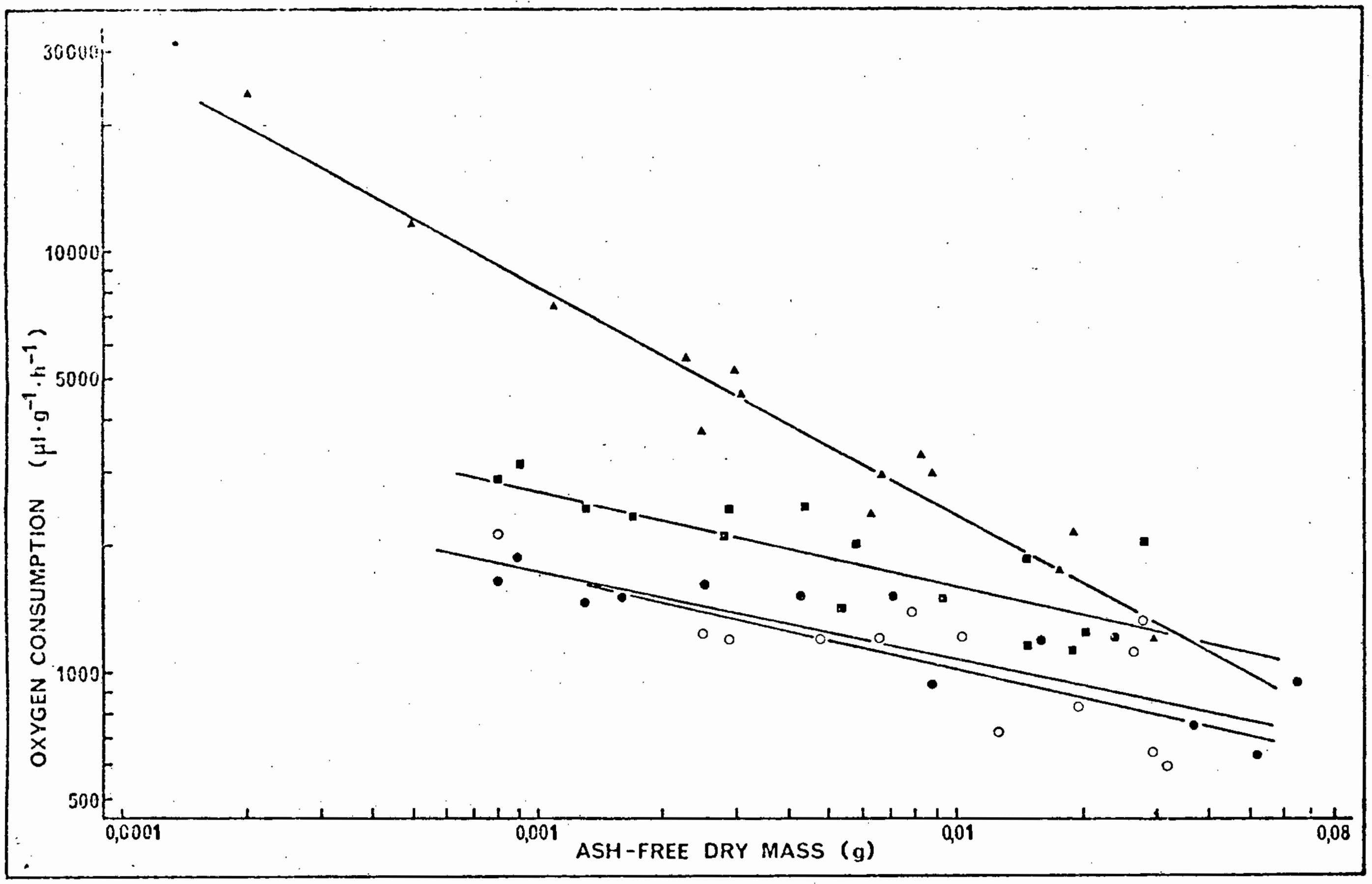

Fig. 3.14

Weight specific oxygen consumption of isopods spanning the whole size range plotted against body mass (g AFDM) on log-log scale.

▲ -August 1976, ● -October 1976, ■ -January 1977, ○ -April 1977.

individuals per hour against body mass (AFDM). The regression equation has the form

$$\frac{R}{W} = a \cdot W^{b-1} \qquad \text{(Newell, 1979)}$$

These equations are listed in Table 3.11 (overleaf).

A t-test for the difference between slopes and intercepts of two regression lines (Zar, 1974) was applied to all combinations of the equations in Fig. 3.13. This was repeated for the weight-specific equations of Fig. 3.14. The slope of the August regression line differed significantly at the 5% level from those of the other three lines in both cases, indicating that metabolic activity of _L. dilatata_ increased more slowly with body mass in winter than at other times of the year.

Values for the exponent b in the respiration regression equations agree well with those given in the literature. Zeuthen (1953) and others (in Grodzinski _et al._, 1975) give a value for b of 0,751 ± 0,015 whereas Winberg (1971) states that the value for freshwater and marine crustaceans is 0,81. Only the slope of the August regression line deviates from these values indicating a slower increase in metabolic rate with body size in winter.

| Month | T($^{\circ}$C) | Respr. Equation $R = aW^{b}$ | n | $r^2$ | Weight Specific Respr. Equation $\frac{R}{W} = aW^{b-1}$ | n | $r^2$ |
|---|---|---|---|---|---|---|---|
| August | 12,9 | $R = 200,32.W^{0,46}$ | 14 | 0,94 | $\frac{R}{W} = 200,31.W^{-0,54}$ | 14 | 0,96 |
| October | 14,2 | $R = 491,60.W^{0,82}$ | 13 | 0,98 | $\frac{R}{W} = 491,61.W^{-0,18}$ | 13 | 0,73 |
| January | 15,4 | $R = 588,69.W^{0,78}$ | 15 | 0,95 | $\frac{R}{W} = 588,70.W^{-0,22}$ | 15 | 0,63 |
| April | 15,9 | $R = 375,67.W^{0,78}$ | 13 | 0,93 | $\frac{R}{W} = 375,67.W^{-0,22}$ | 13 | 0,52 |

Table 3.11

Respiration and weight-specific respiration equations for *Ligia dilatata* at different times of the year.

## 3.4 The Energy Budget

### Population Consumption, Egestion and Assimilation

Estimates of energy ingested as food and energy lost through faeces of the *L. dilatata* population were obtained from the consumption and egestion rate regressions presented in Section 3.3 and from data in Sections 3.2 and 3.3 according to a method described by Sameoto (in Shafir, 1978). For each size class the total mass of food consumed and faeces produced per 24h were estimated every month and summed to give total daily consumption and egestion for N animals in the sample for that month. These figures were then multiplied by the formula

$$\frac{D \cdot n}{N}$$

where $D$ = density of animals at the time

$n$ = number of days in month

$N$ = number of animals in monthly sample

The sum of the values calculated thus is the total consumption and egestion for the population for the study period. These values were then converted to energy units.

Consumption from July 1976 to June 1977 was 123 258,2 $\mathrm{kJ.m^{-1}}$. Egestion for the same period was 88 395,9 $\mathrm{kJ.m^{-1}}$.

## Population Respiration

Population respiration was estimated from results of laboratory respiration experiments (Section 3.3), again following Shafir (1978). The oxygen consumed per hour by all the animals in each size class in the monthly sample was estimated using the respiration regression equations (Section 3.3) and summed to give total hourly oxygen consumption for N animals in the sample. The monthly values were then multiplied by

$$\frac{D \, . \, n \, . \, 24}{N \, . \, 10^3}$$

where D = density of animals at the time
n = number of days in month
N = number of animals in monthly sample

to obtain monthly population respiration in ml $O_2$. All the monthly values were then added to obtain an estimate of the total amount of oxygen consumed annually by the population per metre of beach. To convert this figure to energy units an energy value of 20,18 joules . $ml^{-1}$ was used (Brody, 1945; Hughes, 1970b; Johnson, 1976; Shafir, 1978). The energy lost by the population through respiration for the period July 1976 to June 1977 is estimated to be 5194,1 kJ . $m^{-1}$.

## Terms of the Energy Budget

The various terms of the energy budget which have been estimated in this work are shown in Table 3.12. This represents a summary of energy flow through the Ligia dilatata population for the year July 1976 to June 1977.

| C | = | P | + | R | + | F | + | U |
|---|---|---|---|---|---|---|---|---|
| 123258,2 | | 1038,3 | | 5194,1 | | 88395,9 | | - |
| 100% | | 0,8% | | 4,2% | | 71,7% | | - |

$P = P_g + P_r = 885{,}9\ \mathrm{kJ.m}^{-1} + 152{,}4\ \mathrm{kJ.m}^{-1}$

$A = P + R = 6232{,}4\ \mathrm{kJ.m}^{-1}$

The deficit on the loss side of the equation is 28 629,9 $\mathrm{kJ.m}^{-1}$ or 23,2%.

Table 3.12

Annual Population Energy Budget in $\mathrm{kJ.m}^{-1}$ for the population of Ligia dilatata at Kommetjie, Cape Peninsula.

To facilitate comparisons with other published energy budgets the estimates presented in Table 3.12 were converted to $\mathrm{kJ.m}^{-2}$. Since the isopods inhabit a narrow strip of 15 m width at the top of the beach (between 10 m above and 5 m below HWS) each estimate was divided by 15 to yield an energy budget in kJ.m$^{-2}$ of habitat. This gave the following estimates :

C = 8217,2 kJ.m$^{-2}$ of habitat
P = 69,2 "
R = 346,3 "
F = 5893,1 "

In order to relate energy turnover of the *L. dilatata* population to the total area of the beach at Kommetjie, the energy budget estimates in Table 3.12 were divided by the length from the top of the distribution of the isopods to LWS, a total of 83 m. This gives energy budget estimates in kJ.m$^{-2}$ of beach :

C = 1485,0 kJ.m$^{-2}$ of beach
P = 12,5 "
R = 62,6 "
F = 1065,0

The basic terms of energy budgets are often related to one another in the form of coefficients of efficiency. These ratios characterise the physiological state of populations in relation to changes in life cycle and environmental conditions as well as providing indices of energy flow within populations and between trophic levels (Kozlovsky, 1968; Petrusewicz and Macfadyen, 1970; Crisp, 1971;

Grodzinski _et_ _al_., 1975). The various coefficients of efficiency calculated for the _L_. _dilatata_ population are listed in Table 3.13.

| Ratio | | Estimate |
|---|---|---|
| Assimilation efficiency | A/C | 25 5,1% |
| Gross growth efficiency | P/C | 0,8% |
| Net growth efficiency | P/A | 16,7% |
| | logP/logR | 0,81 |
| | P/R | 0,20 |
| Turnover | $P/\overline{B}$ | 2,5 |

_Table 3.13_

Ecological efficiencies of the _Ligia_ _dilatata_ population calculated from energy budget data. Assimilation calculated as $A = P + R$.

The annual log P/log R ratio of 0,81 and the P/R ratio of 0,20 were compared to values for a large number of ectotherms given by McNeill and Lawton (1970). Log P/log R ratios for _Asellus_ _aquaticus_, _A_. _militaris_ and _Ligidium_ _japonica_ (the three isopods listed) were 0,71, 0,76 and 0,45 respectively while the P/R ratios were 0,32, 0,22 and 0,22 respectively. This shows agreement between these values and the ratios calculated for _L_. _dilatata_. Thus the imbalance in the energy budget is unlikely to be due to errors in the estimates for Production and Respiration, the two parameters entering into the ratio unless there are compensatory errors. Production is defined as the total amount of body tissue generated by a population, comprising production of body tissues, reproduction and exuvia. Although the first two parameters were estimated in this study it was impossible to estimate moulting rates since animals could not be kept to moult in the laboratory. The production figure in the energy budget omits exuvia and is therefore likely to be an underestimate of the true value. However, the amount of energy lost through exuvia is generally considered to be very small (Tsikhon-Lukanina *et al.*, 1970; Johnson, 1974) and this is supported by the arguments above.

The value calculated for gross growth efficiency of the *L. dilatata* population is low when compared to the ratios given in the literature for other invertebrates. However, values as low as 3 - 7% for *Nerita spp.* or 4 - 10% for *Pontogammarus maeoticus* are on record (in Shafir, 1978). As pointed out by Klekowski and Duncan (1975) estimation of consumption is the least developed part of energy budget studies. This is linked directly to practical difficulties involved firstly in determining what the food source is and secondly in quantifying the amount of food consumed per unit time especially when extrapolating laboratory data to field conditions. These practical problems have led many workers to calculate theoretical consumption rates as the amount of energy required to produce an assimilation rate calculated from the sum of production and respiration (Sameoto, 1972; Johnson, 1974). In energy budgets of this kind, however, it is impossible to compare the estimates of the various parameters. In the present study consumption was measured in the laboratory. Although some degree of error is introduced by extrapolating laboratory rates to the field this approach was adopted because direct field measurements were impossible. The very low gross growth efficiency seems to indicate that the consumption estimate may be too high. However, if it were assumed, for argument's sake, that the total (23%) imbalance in the energy budget were due to too high a consumption estimate and the consumption rate were corrected accordingly, gross growth efficiency would still be only 1,1% which remains low when compared to values in the literature. It seems likely, therefore, that the consumption estimate may be too high accounting for the bulk of the imbalance in the energy budget. However, the gross growth efficiency is genuinely low, of the order of 1%.

A comparison between population assimilation calculated as the sum of respiration and production and as the difference between consumption and egestion stresses the importance of including estimates of urinary excretion (U) in energy budget studies. Assimilation estimates are 6232,4 kJ.m$^{-1}$ and 34 862,3 kJ.m$^{-1}$ respectively. Even if a large proportion of this difference is due to an overestimate of the consumption figure, the very much higher value obtained by calculating A as C - F suggests that energy loss due to dissolved organic matter could account for some of the imbalance in the energy budget for L. dilatata.

In most energetic studies U has been assumed to be insignificant (Hughes, 1970b, 1971; Paine, 1971; Johnson, 1974; Shafir, 1978). This approach has been criticised by Hargrave (1971) who stated that the fraction accounts for 5% of the energy ingested by the amphipod Hyalella azteca and quotes data by Johannes and Satomi who reported that it accounts for 33% of the carbon ingested by the freshwater shrimp Palaemonetes pugio. Field (1972) found that energy lost through dissolved organic matter can be substantial and more recently Shafir (1978) presented evidence that at least some of the discrepancy in his estimated energy budget of the benthic isopod Cirolana imposita could be attributed to the loss of dissolved organic matter.

However, the above organisms are all aquatic and it is unlikely that D.O.M. could account for as high an energy loss in a semi-terrestrial air-breathing isopod such as L. dilatata. Nevertheless, it is believed that this factor may contribute to the imbalance in the energy budget estimate.

As stated in Section 3.3, estimates of population metabolism were calculated from laboratory respiration experiments. There are potentially large errors in extrapolating respirometer rates measured in the laboratory to the field where conditions are quite different. The experimental apparatus imposes significant restrictions on the activity of the animals and activity level has been found to have a distinct effect on the respiration rates of animals (Kamler, 1970; Newell, 1970; Johnson, 1976). This poses a problem since metabolic rates recorded in studies of population energetics are usually of some average level of activity (Petrusewicz and Macfadyen, 1970). Hughes (1970) states, however, that fairly representative estimates of monthly respiration rates can be obtained from laboratory experiments if they are carried out at temperatures equal to field temperatures at the time. It seems likely that errors involved in estimating population metabolism were relatively small and this is confirmed by the above discussion of P/R ratios.

In summer, temperatures are generally high, causing raised levels of metabolism. At the same time the isopods are in the middle of their breeding season (Section 3.2) and the energy demand of the population is high. However, food supply at this time is at its lowest for the year (Fig. 3.2). As can be seen from the temperature profiles (Fig. 3.1) the highest temperature experienced by L. dilatata in their habitat in summer is 6,6°C lower than the air temperature. Thus choice of habitat appears to be an important energy conserving mechanism since less energy is used for metabolic processes because of the moderate ambient temperature. This energy saving may be channelled into reproduction at a time when energy input in terms of food is low.

A large number of energy budgets have now been reported in the literature (see Shafir, 1978). This study of Ligia dilatata presents data for a semi-terrestrial detritivore and can be used for comparative purposes. The most common efficiency used in comparing the utilisation and flow of energy in populations from different habitats and different trophic levels is assimilation efficiency. It should be noted in this context that there is some confusion in the literature concerning the calculation of this ratio. As has been pointed out, the assumption has often been made that the term U of the balanced energy equation is negligible. Consequently, assimilation efficiency has been calculated as $\frac{A}{C} = \frac{C - F}{C}$ (Carefoot, 1973b; Shafir, 1978). This could lead to a serious overestimate of the efficiency if the assumption proved to be erroneous as has been shown for a number of species (Hargrave, 1971; Shafir, 1978). The present study shows that assimilation efficiency calculated by this method is 5,5 times higher than if it were calculated as $\frac{A}{C} = \frac{P + R}{C}$ (28,3% as opposed to 5,1%). It is believed that in the present study the greatest part of this discrepancy is due to an overestimate of the consumption rate of L. dilatata. However, in studies where there is evidence that energy is lost through nitrogenous excretion is likely to be substantial, assimilation efficiency should preferably be calculated by the latter formula. Unfortunately, it is not always clear from the literature how assimilation efficiency was calculated and so comparisons are not necessarily valid.

Several factors have been shown to influence assimilation efficiency. Food preference was found to be the most important (Conover, 1966; Tsikhon-Lukanina et al., 1968; Carefoot, 1970, 1973a) since the proportion of the food assimilated depends on the chemical composition of the food and the digestive potential of the animal. The preferred food species of L. dilatata determined in laboratory experiments was also the main food source in the field. Other important factors affecting assimilation efficiency are food supply (Hubbell *et al.*, 1965) and population density (Prus, 1971; Carefoot, 1973a).

Carefoot (1973a) has shown that assimilation efficiency for *Ligia pallasii* dropped from 74% in isolated animals to 55% recorded for groups of isopods while Prus (1971) recorded the opposite phenomenon for *Asellus aquaticus*. Hubbell *et al.* (1965) working on *Armadillidium vulgare* found that laboratory specimens supplied with abundant food consumed 2,5 times more than animals in the field. Simultaneously the assimilation efficiency dropped from 59 - 84% to 19 - 27%. In view of these different absorption values Hubbell *et al.* (1965) stress the need for caution in extrapolating laboratory feeding data to the field, especially when food availability is low in the natural habitat. They postulate a phase of "excess feeding" in animals with an abundant food supply leading to lowered values of assimilation efficiency.

In the light of the above arguments the assimilation efficiency recorded for *L. dilatata* does not appear excessively low.

# CHAPTER 4

# CONCLUSIONS

The energy budget shows a deficit of 23,2%. It seems likely that the bulk of this imbalance is accounted for by an overestimate of Consumption; energetic losses due to loss of D.O.C. may further contribute to the discrepancy underlining the criticism of Hargrave (1971) that estimates of this term should be included in energy budget studies.

Although this study has quantified many aspects of the biology and energetics of _L. dilatata_, a number of points require further study.

It has been found in this work that the isopods have a low assimilation efficiency of 25,5% (Section 3.3). This has been linked to the fact that the animals at the study site had an abundant food supply through most of the study period. Populations of _L. dilatata_ from beaches with less abundant food supply should be investigated to test the hypothesis that assimilation efficiency is inversely proportional to the amount of food available to the isopods.

_L. dilatata_ assimilate 75,7% of the inorganic material contained in the food. This is a very high value when compared to the low overall assimilation of 25,5%. Further study is required to determine which fraction of the ash is assimilated and how this is utilized by the animals. The study has shown that the isopod population consumed kelp that had been aged on the beach for three days. The reasons for this are not known but it is hypothesised that microheterotrophs growing on the kelp debris might constitute an additional food source. Stranded kelp should be sampled regularly to determine what chemical changes take place after stranding, at what rate the population of microheterotrophic organisms increases, which properties of aged kelp make it more palatable to the isopods and whether the food supply is supplemented by bacteria.

Since this study was undertaken within the framework of the kelp bed research effort, the following aspect of the work is particularly significant.

The study population of L. dilatata consumed some 76 kg wet mass of cast up kelp per metre of beach annually during the study period, equivalent to 123 258,2 kJ (Section 3.3). Of this total consumed energy only 0,8% was channelled into production.

The major portion of energy input into the population was extruded as faeces. This fraction accounted for 71,7% of the total energy consumed annually.

During the study period of 20 months no predation on L. dilatata was observed and it is not known what predators might exist. Thus ecological efficiency defined as yield to predators/ingestion (Slobodkin, 1960) cannot be estimated. However, the energetic contribution of the isopod population to the community, both intertidal and littoral is substantial. The primary role appears to be one of breaking down into smaller units, the large plants thrown ashore. This produces two kinds of products : particles of intermediate size created by the mechanical action of chewing and biting and faecal pellets of relatively high calorific value (see Section 3.3). A possible third product is dissolved organic matter released from algal cells by the action of the mouthparts. These products are washed into the sea by wave action at high tide.

Whereas initially this work was designed to determine how energy produced in the kelp bed and exported in the form of plants torn loose from the sediment is utilised by animals in the adjacent rocky shore ecosystem, the study has indicated that L. dilatata must be considered an important contributor to the energetics of the kelp bed.

The results of this work have shown that they are active agents in the transformation of energy, making available large amounts of detritus (over 88000 kJ . $m^{-1}$ of shoreline per annum in faeces alone at Kommetjie) to filter feeders and detritivores in the neighbouring systems.

# CHAPTER 5

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