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Seasonal variation in the carbon and energy contents and assimilation of a Mysis relicta population in Pääjärvi, southern Finland

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Assimilation of a *Mysis relicta* population was studied in the light of the previous population and respiration studies on this species in the oligotrophic lake Pääjärvi. Background information was obtained from a study of the variation in the organic carbon content of the mysids during 1 year. The amount of organic carbon in the animals was measured by a new technique based on the infrared gas analyser and converted to the energy equivalent.

The organic carbon content varied seasonally from about 50 to 63 %. The values were highest in the young embroys and lowest in young mysids about 2 months after liberation, in males after copulation and in females liberating their embryos in the spring after the winter starvation period.

In mature animals carbon contents were high just before the breeding season, in the second cohort in August—September, when about 13—15 months old, and in the first cohort in November—December, when about 7 months old. The former cohort attained 62—63 % and the latter 57—59 % organic carbon. The males accumulated carbon faster and earlier, but lost it almost totally in copulation. The females lost about 8 % of their stored carbon in egg-laying, but still had a reserve for the winter.

Active feeding was necessary during the winter because the stored carbon was sufficient for only 2 weeks' respiration.

A male maturing in the first year assimilated 426.4 Joules and a female 628.0 A male maturing in the second year assimilated 858.4 Joules and a female 1287.6 Joules. The corresponding production efficiencies were 34.3, 23.6 and 15.7.

The mysid population produced 1.016×10^7 kJ, respired 2.670×10^7 kJ and assimilated 3.684×10^7 kJ in Pääjärvi. The production efficiency of the population was 27.58.

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1. Introduction

Assimilation, the sum of the energy needed for production and maintenance (e.g. Petrusewicz & Macfadyen 1970), is the aspect of the energy budget usually studied. Of the many papers published on the subject, however, few consider the energy relations at population level. This applies especially to studies of organisms in the water ecosystem, although this system is of great importance in modern ecology.

The energetics of *Mysis relicta* has been studied by Lasenby & Langford (1972, 1973), but their studies do not concern the population level. The present study is based on previous work on population dynamics and production (Hakala 1978) and on respiration studies by Ranta & Hakala (1978).

In determining energy content I did not use the normal microbomb calorimetry (Phillipson 1964). Instead, I measured the organic carbon content. This new technique was developed by Salonen (unpublished and is based on the infra-red carbon analyser. The values for organic carbon were the converted to their energy equivalents in the light of a study of the carbon-energy relations of some freshwater invertebrates in Pääjärvi, including M. *relicta* (Salonen et al. 1976).

2. Material and methods

Determination of carbon and energy contents

The material for this study was collected in 1976 in connection with studies on the population dynamics and production of *M. relicta*. A representative sample (20—150 individuals depending on size and including females and males of both cohorts, immatures, ovigerous females and embryos) was taken from the population samples. The mysids were dried at 60°C for 12 h and then carefully homogenized. The homogenized samples were frozen at -20 °C for further studies. The samples were taken at seven periods scattered through the year 1976.

The ash-free dry weight (AFDW) of each homogenized sample was determined by igniting four small (1.0—3.0 mg) subsamples at 505 °C for 6—8 h. Weighing was done with a Cahn automatic electrobalance (accuracy 0.001 mg).

Organic carbon was measured in four subsamples (0.5—3.0 mg) taken from each homogenized sample. These were placed in thin platinum foil cups, and fired at 900 °C in a quartz tube. The carbon dioxide formed was driven to the infra-red gas analyser (Hartmann & Braun, Uras II) with pure, dustfree oxygen. The amount of organic carbon in the samples was determined by comparing the observed peak of carbon dioxide on the recorder graph with the peak from a known amount of some organic standard. The procedure described was developed and fully described by Salonen (unpublished).

The values for organic carbon in the samples were converted to their energy equivalents according to the regression of carbon against energy (Salonen et al. 1976).

3. Results

A. Seasonal variation in carbon and energy contents

The carbon and ash contents are given in Table 1, and their seasonal variation in Fig. 1.

During early embryonic development (January—February) mysids have a high carbon content (observed maximum 62.72 %). This was the maximum value observed for any stage. The carbon lost during embryonic development represents energy expended in maintenance and moulting. The small loss indicates a very low rate of metabolism compared with that of active mysids. Actually the carbon content should have fallen immediately after egg-laying, but it was kept at a high level by the high carbon pulse from the late-laid eggs of the first-cohort females (Hakala 1978), which were included in the same samples. By the time liberation starts (April) the carbon content has dropped to about 58 % and continues to fall steeply after liberation, reaching a minimum almost 50 %, in August. At the time of liberation the young mysids still had a visible carbon reserve. This was probably consumed during the 2-or 3-week period of inactivity after liberation (Hakala 1978). In the beginning of the rapid growth period in July and August the young mysids probably use the energy they assimilate for growth of tissue with a low carbon content (proteins) and start to accumulate high-carbon lipids only after the necessary growth is completed. By this time the mysids have attained a mean weight of 1.0—1.5 mg (AFDW).

In autumn carbon accumulates rapidly in connection with maturation and propagation. Part of the population then lays down a winter store of carbon. At this time the maturing mysids can be distinquished from those that remain immature. The maturing group rapidly acquires a high carbon content for propagation, wheareas the immature group is slower and only reaches a maximum at the end of the year. The males lose all their stored carbon in copulation in late autumn (Fig. 1) and die shortly after (Hakala 1978). The females use about 8 % of the stored carbon for egg production. The males apparently store energy only for propagation. The two sexes seem to invest equal proportions of their carbon contents in reproduction, because the females have 55 % carbon after egg-laying, the males 50—51 %, but as the males are smaller the relative carbon losses are equal. The females consumed the remaining 4—5% of stored carbon during the winter.

The immature mysids do not lose as much carbon as the ovigerous females. Their carbon content is lowest in early May (52.74 %). After this they (now separable as cohort II) grow rapidly and begin to store carbon immediately. The highest value was observed in August (62.04 %), but the actual maximum is probably still higher, being reached during the long interval between samples in late August or in September.

The mixed samples in late autumn prevent separate estimates of the carbon content differences between the cohorts. The second (older-generation) cohort probably attains a higher carbon content before breeding and reaches a peak 1.5—2 months earlier than the maturing subcohort of the first (younger generation) cohort. The actual maximum of the first cohort

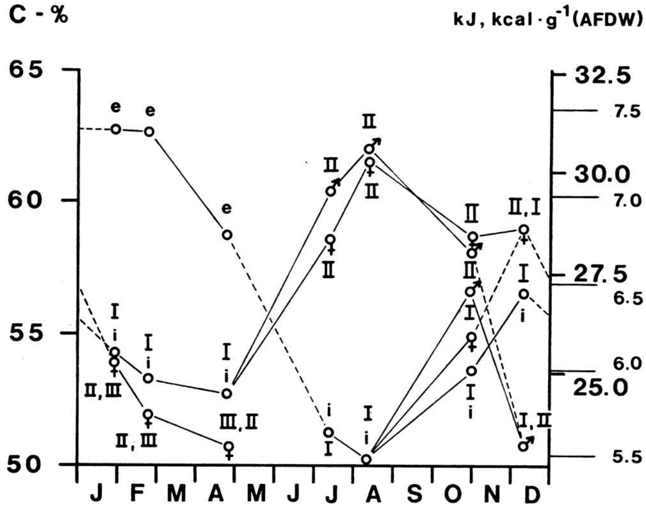

Fig. 1: The seasonal variation in the organic carbon content of *Mysis relicta* (right) and in the energy content (left; larger numbers Joules, smaller kcal). Sex and cohort symbols are shown, (e) embryos, (i) immatures. The dashed lines are extrapolations. The dashed lines in November indicate the mixed cohort samples.

Table 1. Ash and carbon content of *Mysis relicta* expressed as percent of dry weight (DW, mean and SD) and of AFDW.

	Ash (DW)		C (DW)		C (AFDW)
28.I.1976					
juveniles	7.65	0.24	50.20	1.24	54.33
embryos	7.81	0.41	57.86	3.71	62.72
ovigerous ♀♀	7.95	0.24	49.61	2.86	53.89
cohort I ♂♂	8.59	0.97	47.24	0.98	51.68
24.II.1976					
juveniles	7.62	0.72	49.21	1.38	53.27
embryos	7.55	0.32	57.91	8.81	62.64
ovigerous ♀♀	9.53	0.32	48.91	0.90	51.99
cohort I ♂♂	11.62	0.32	44.78	2.85	50.67
24.IV.1976					
juveniles	8.70	–	48.15	0.98	52.74
embryos	9.96	0.59	52.23	0.79	58.74
ovigerous ♀♀	9.41	0.81	45.97	1.44	50.75
12.VII.1976					
juveniles	10.14	0.31	46.08	1.07	51.28
cohort II ♂♂	7.23	0.20	56.04	1.58	60.41
cohort II ♀♀	7.36	0.19	54.29	2.28	58.60
11.VIII.1976					
juveniles	9.72	0.30	45.36	1.88	50.24
cohort II ♂♂	6.00	0.40	58.32	2.67	62.04
cohort II ♀♀	6.61	0.14	57.48	3.87	61.55
30.X.1976					
juveniles	8.78	0.53	48.89	0.82	53.60
cohort I ♂♂	8.24	0.80	51.95	2.32	56.62
cohort II ♂♂	7.65	0.22	53.57	2.05	58.01
cohort I ♀♀	7.17	0.10	50.72	2.58	54.92
cohort II ♀♀	8.09	2.19	53.63	1.83	58.65
10.XII.1976					
juveniles	7.52	0.19	52.33	1.39	56.59
embryos	7.60	0.38	54.70	1.96	59.20
cohort I ♂♂	9.97	0.40	46.62	3.03	51.78
ovigerous ♀♀	7.47	0.76	54.58	0.71	58.99

is also higher than the values observed, but probably less so than that of the second cohort.

Mysid females have been reported to breed twice (Lasenby 1971, Fürst 1972a), but this was not observed in Pääjärvi (Hakala 1978). The explanation may be that stored carbon is almost totally lost during the winter. Most ovigerous females reach this low pergentage long before primary production starts in the spring and are not able to recover.

The amount of carbon the females lose during the winter starvation period would not be enough to support life. In Pääjärvi the winter starvation period is assumed to be about 150 days. During this time the older second-cohort females lost 0.657 mg carbon and the first-cohort females 0.338 mg. Growth stops during this time, so they do not moult and all the carbon consumed is used for maintenance. These calculations are based on the mean weights of the females and the percentages of carbon lost. According to respiration studies (Ranta & Hakala 1978), a second-cohort mysid weighing about 8 mg (AFDW) consumes 0.0576 mg C daily in respiration and a total of 8.64 mg during the starvation period. The carbon lost corresponds to only about 7.6 % of the carbon respired, and would support life for only 2 weeks. A first-cohort female weighing about 4 mg (AFDW) consumes 0.0371 mg C daily and 5.57 during the starvation period. The carbon lost is 6.1 % of the total carbon respired. An immature loses 0.0886 mg

C and consumes 3.9 mg in respiration. The carbon lost is only 2.6 % of the carbon respired. The stored carbon seems to be even less important for the immatures than for the ovigerous females. The heavy load of embryos in the brood pouches may interfere with the feeding of the females, preventing them from capturing active and valuable food items.

The time the mysids can live on their stored carbon (lipids) is surprisingly short, but this observation is supported by the study of Pechen-Finenko et al. (1975). These authors found that the energy stored in *Eudiaptums graciloides* corresponded to the maintenance costs of about 20 days in winter. This indicates that the importance of the stored energy has been overestimated. Owerwintering mysids must acquire most of their maintenance energy by active feeding. However, the ability to store energy has obvious adaptive value. It enables the population to survive short spells of unpredictably adverse conditions without serious fluctuations in population size.

Comparison of the values obtained for the carbon needed for egg production and that lost by the females during egg-laying showed a discrepancy — the amount lost was not sufficient to produce the observed number of embryos. The mean number of embryos in second-cohort females was 22.9 and in first-cohort females 16.4. The just-laid eggs had an AFDW of 0.101 mg. A second-cohort female thus needed 1.443 mg C to produce the observed number of embryos and a first-cohort female 1.033 mg. The carbon loss observed was 0.640 mg in the second-cohort females, which is only about 44 % of the carbon necessary for embryo production. The discrepancy is great and is only partly explained by the higher carbon content presumably accumulated before the breeding season. The main explanation is the error in the estimated weights of the females before and after egg-laying.

The AFDW of the females had been estimated from the lengthweight relation (Hakala 1978). This was fitted to the population as a whole. To chek the validity of this relation I collected all values for females that were measured and weighed either before or after egg-laying and fitted separate power functions to the two groups (Fig. 2). As Fig. 2 shows, the original relation underestimated the weights before egg-laying and overestimated the weights of the ovigerous females. The comparison, though based on small numbers (15 and 12), explains the missing amount of carbon for the weight range that includes most of the ovigerous females (5—10 mg). For example, a female with a carapace length (the dimension used to estimate weight) of 5 mm weighed 6.5 mg according to the original calculation, but after correction it weighed 8.0 mg before and 6.0 mg after egg-laying. The difference in carbon is 1.750 mg, which amply covers the amount of carbon consumed in egg production (1.443 mg).

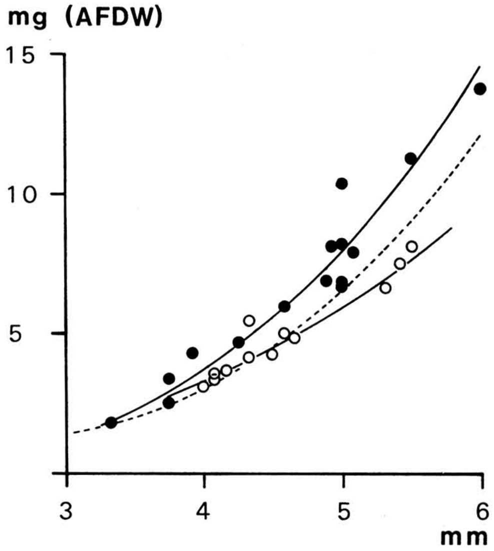

Fig. 2: Length-weight relations in females. Dashed line=average values, solid lines=corrected relations: black circles before egg-laying, open circles after egg-laying.

The annual variation in the energy content of *M. relicta* individuals is shown in Fig. 1. The organic carbon content was converted to the equivalent energy value according to the regression y = (—8.415 + 0.620) × (Salonen et al. 1976), where y is energy (kJ × g^{-1} AFDW) and × is carbon content as a percentage. The values may therefore be read as carbon content (on the left) or energy content (one the right).

The energy content of the mysids fell from 30.47 kJ g^{-1} (7290 cal) in young embryos to 22.73 kJ (5440 cal) in the young mysids in August. Low values were also observed in old ovigerous females and in copulated males (23.5 kj 5510 cal and 23.69 kj 5670 cal).

The highest energy values observed indicate a large accumulation of lipids, while the lowest imply an almost total absence of lipids, the energy value approaching that of body proteins. According to the regression of lipid content against AFDW by Griffiths (1977), the highest energy values represent about 59 % lipids in the mysids and the lowest values about 26 %. The latter percentage is evidently an overestimate, due to the small and scattered data on which he based his regression. According to Winberg (1971), »any values below 5 kcal g^{-1} organic matter should be treated as suspect». Thus the latter lipid percentage is totally unrealistic. I suggest that at the 50 % carbon level mysids contain only structural lipids. This means, according to Giese (1966) (quoted in Griffiths 1977), a lipid content of 2.3—5.2 %. If the highest of these values is subtracted from the lowest energy values in mysids (5.4 kcal g^{-1}), then about 5 kcal g^{-1} is obtained.

If the values below 5 kcal are omitted the observed annual variation in the energy content of *M. relicta* falls within the range of energy contents observed in other freshwater invertebrates (e.g. Gummins & Wuyscheck 1971, Wissing & Hasler 1971, Snow 1972 and Gorecki 1975). However, few reports present energy data covering the whole year (e.g. Snow 1972). Thus comparison of the annual energy cycles is impossible. Moreover, many authors still use dry weight and even wet weight instead of ash-free dry weight, which excludes a considerable amount of otherwise useful data.

B. Assimilation in Mysis relicta

The instantaneous daily growth, respiration, assimilation and production efficiencies of the mean inviduals are shown in Fig. 3. Growth rates were calculated from the new logistic models, which were recalculated from the original AFDW values after these had been converted to carbon. The carbon data were then converted to energy according to the regression of carbon content on energy (p. 132).

The respiration rates were calculated from original (AFDW) growth models (Hakala 1978) according to the regression of the respiration rate against the AFDW of the mysids (Ranta & Hakala 1978). Respiration rates were then converted to the corresponding energy values, i.e. multiplied by the oxycalorific coefficient (O_{ox}) 14.75 (Elliot & Davison 1975), which is rather high and assumes that the animals feed on carbohydrates. This may not be so, but is probably justified by the RQ (close to 1) in our respiration studies (Ranta & Hakala 1978).

Assimilation rates were calculated by adding the instantaneous production and respiration rates, and the production efficiences from the equation $K_2 = 100\, P/A$, according to Duncan & Klekowski (1975).

The energetics of the immature mysids is based on subjective growth data, because the first cohort actually includes two subcohorts. No objective method was found for separating them, because their weight ranges overlapped too much. The subcohort that is liberated later remains immature during the first winter, but its mean weight could not be determined accurately even in subsequent sampling periods. An estimate was made by calculating the mean weight of individuals without the distinctive sings of maturation at a time when a considerable number of first-cohort individuals showed them. This estimate is inaccurate and perhaps explains the unrealistic growth rates in winter, when actually there should not be any growth. An alternative explanation is the disappearance (due to predation or death) of the mysids weighing less than 1 mg.

The cumulative production, respiration, assimilation and production efficiencies of the individual mysids reaching different ages are as follows (I):

	Production	Respiration	Assimilation	K_2
Males breeding in the first year	146.4	280.0	426.4	34.3
Females breeding in the first year	150.0	478.0	628.0	23.9
Males breeding in the second year	193.6	664.8	858.4	22,9
Females breeding in the second year	201.6	1086.0	1287.6	15.7

All these values, especially those for females, might have been slightly different if the length-weight correction had been applied to all the measurements.

The animals actually show negative growth in winter, although this was not visible from the AFDW data (Hakala 1978). The corresponding production efficiencies were also negative. The maximum growth periods are more clearly separated in these energy curves (Fig. 1) than in the AFDW data (Fig. 2). The growth period of the second cohort is skewed towards the early summer owing to the rapid accumulation of carbon when growth is resumed. The separation of the female and male growth periods is likewise obvious, especially in the first chort, but also in the second if account is taken of the larger size of the females of this cohort (Fig. 3). The more rapid accumalation of energy in the males is probably simply an example of protandry, as observed in many insect species (e.g. Wiklund & Fagerström 1977); it ensures that the females are fertilized immediately after maturation, so minimizing the pre-reproductive death of females.

The first-cohort individuals show higher instantaneous production efficiencies (50—60) and are relatively efficient throughout the growth period (Fig. 3A). The highest efficiencies of the second cohort are lower and persist for a shorter period, owing to their greater age (senility) and size. Males seem to reach higher efficiencies than females, but only briefly.

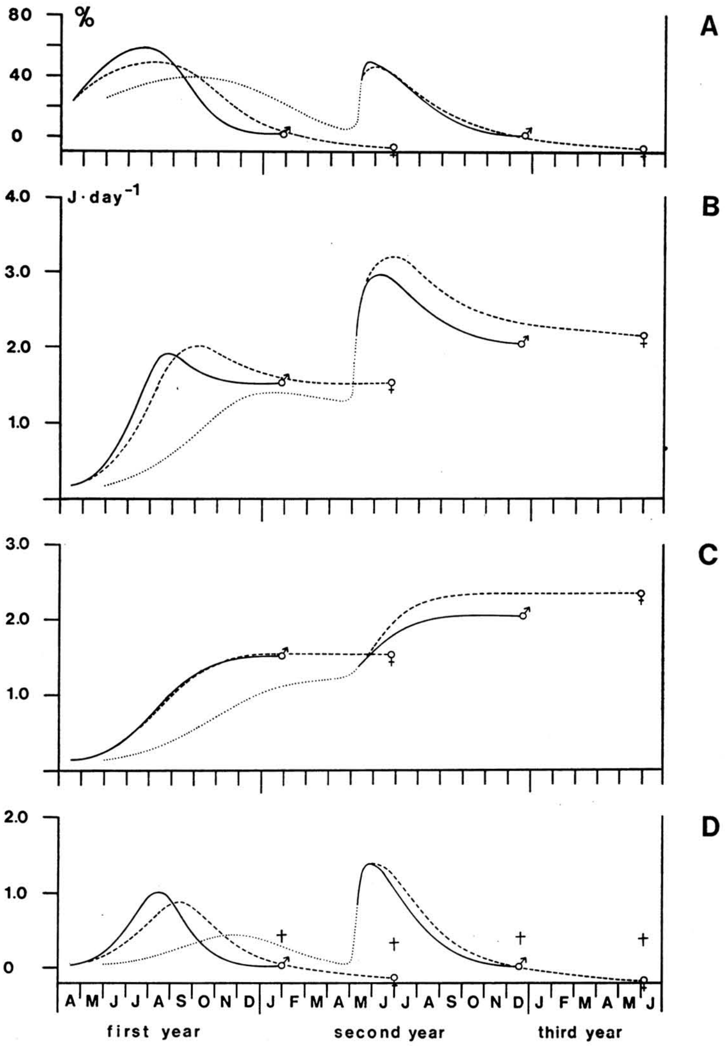

Fig. 3: The production efficiency (A), assimilation rate (B), respiration rate (C) and instantaneous daily production rate (D) of *Mysis relicta*. Solid line males, dashed line females, dotted line hypothetical values for immatures.

The increasing senility with age and size is clearly seen in the production efficiencies of *M. relicta*, the efficiency of the long-lived second-cohort female being only about half that of the short-lived first-cohort male.

The production efficiencies of *M. relicta* seem to lie within the range of efficiencies observed in other short-lived poikilotherms with high-respiratory-cost non-productive stages (Duncan & Klekowski 1975). For example, *Asellus aquaticus* has a K_2 of 24.1, *Pisidium virginium* of 47.3 and *Gammarus pseudolimneus* of 15.0. Crustaceans, especially amphipods, seem to have lower efficiencies than, for example, the *Pisidium* species. Some *Pisidia* of Pääjärvi showed efficiencies even higher than those mentioned above (Holopainen, unpublished).

C. Population assimilation

Values for assimilation, respiration, production and production efficiency of the population are shown in Fig. 4. The mean weights of the cohorts were used to transform the AFDW to energy and to calculate the respiration rate. These were then converted to values for the population by multiplying by the respective numbers of individuals on the cohorts.

The production rate of the population was highest (90000 kJ/day) in June. This peak coincided with the maximum assimilation rate (about 200000 kJ/day). Thus the maximum instantaneous production efficiency remained below 50. The assimilation rate was lowest at the end of April, i.e. at the time when the females started to liberate the embryos (25000 kJ/day).

There is a great unexplained variation in these variables in winter, which is due to the sample variation caused by the low population density (Hakala 1978). The downward trend in the assimilation rate during the winter is due to the mortality of males after copulation and of females after releasing their embryos.

The *M. relicta* population of Pääjärvi assimilated 3.684×10^7 kJ and produced 1.016×10^7 kJ in 1976. The production efficiency was 27.58, which is comparable with the few values calculated for other freshwater poikilotherms (Duncan & Klekovski 1975).

This estimate of the production efficiency of the population is relatively high compared with the cumulative efficiencies of individuals. According to Ivanova & Alimov (1973), the efficiency of the population should be lower than that of the individuals that compose it. In *Eudiaptomus graciloides* they found efficiency values of 20 for the individual and of 13 for the population. The explanation may be that my values for individual growth rates were calculated from the population mean, which is evidently always lower than that of individual growth.

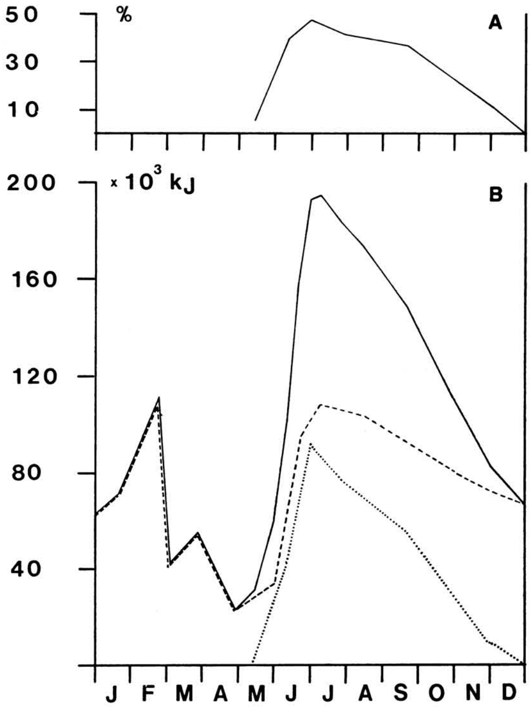

Fig. 4: (A) Production efficiency of the *Mysis relicta* population in Pääjärvi. (B) Population assimilation. Instantaneous daily production rate (dotted line), respiration rate (dashed line) and assimilation rate (solid line).

4. Discussion

Concerning the energy content and especially its annual variation, data are still surprisingly scanty. This is partly because of the laborious methods used for measuring energy. Bomb calorimetry requires a relatively large amount of material and it is almost impossible to obtain sufficient data about the smallest freshwater invertebrates. The determination of organic carbon is more accurate and quicker. With this method samples can be studied at submicrogramme level, and even with individuals of the smallest freshwater invertebrates the energy content can be studied with satifactory accuracy, and a great number of samples can be treated.

According to Slobodkin & Richman (1961) (quoted in Griffiths 1977), animals that are liable to encounter unpredictable food shortages have larger food reserves, this being an adaptation to the unpredictable environment. Griffiths (1977), after examining data from various sources, favours this hypothesis. However, my data show both the lovest possible and almost highest observed energy values in one and the same species. I suggest that both S & R and G based their conclusions on scattered data and without sufficient knowledge of the seasonal variations in energy content. It would perhaps be better to say that the seasonal variation in the energy content increases with increasing unpredictability of the environment and that animals living in such environments are able to store more energy than those living in more stable environments.

It seems to me too early to draw theoretical conclusions about the variation in the energy content of different taxa, especially in view of the lack of standardization of methods and the unrealistic values obtained.

Most of the energy accumalated by *M. relicta* is invested in propagation. The proportion the males invest in propagation is surprisingly high, being almost the same as in females. This and the low fecundity (Hakala 1978) indicates that this mysid is an equilibrium species (K-selected). The stored energy is of small importance for the maintenance of life, as in *Eudiaptomus graciloides* (Pechen-Finenko *et al.* 1975). This leads me to suggest that a deep boreal lake is not actually an unpredictable environment. The pelagial of a lake is supposed to be less stable than the benthos (e. g. Griffiths 1977). The mysids have become adapted to feed and accumalate energy in the pelagial during the season of high production and remain in the more stable benthic environment during the starvation period, where the amount of food, though small, fluctuates less. The death of the males before the winter leaves more food for the ovigerous females, ensuring their survival over the critical period.

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