

AN ENERGY BUDGET FOR *MENIPPE MERCENARIA* LARVAE  
FED *ARTEMIA* NAUPLII

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Only a few of the published reports on the energetics of marine crustaceans include data for larval stages or juveniles (Marshall and Orr, 1955; Corner, Cowey, and Marshall, 1967; Lasker, 1966; Reeve, 1969b; Regnault, 1969; Tsikhon-Lukanina and Lukasheva, 1970; Clutter and Theilacker, 1971), and only one (Tsikhon-Lukanina and Lukasheva, 1970) is complete from time of hatching. In addition, there have been no total energy budgets (meaning all energy sources and sinks accounted for) for commercially important shellfish in the available literature. In the present work we have studied the entire larval life (five zoeal stages and one megalopal stage) of the stone crab, *Menippe mercenaria*. We have accounted for the major flows of energy into and out of the organism through the period of larval development.

The energy balance in an organism may be described using the terms proposed by Petruszewicz and Macfadyen (1970). Matter consumed (C) is either digested (D) or egested (F). Digested material may be assimilated (A) or lost to excretion (U). Energy which has been assimilated is either channeled into energy for maintenance of vital life processes or into production (P), which may be subdivided into growth of new body tissue ( $P_g$ ), exuvia (E), reproductive products ( $P_r$ ), and secretions. The former is measured by oxygen consumption and/or carbon dioxide production and is termed respiration (R). In the present study, consumption (C), growth of new body tissue ( $P_g$ ), exuvia (E), and respiration (R) have been measured. Egestion (F) and excretion (U) are considered together as rejecta (FU) and obtained by subtraction. For larvae, growth of reproductive products is not applicable.

MATERIALS AND METHODS

Ovigerous females were obtained from Florida and held in small recirculating seawater systems. Larvae were collected soon after hatching and placed in finger bowls of filtered seawater at  $30.0 \pm 1.0\%$  salinity. Animals used in the feeding experiments were reared individually in plastic compartmented boxes. Three inch finger bowls with ten zoeae per bowl were used to determine survivorship and molting frequency, and eight inch bowls with up to five hundred larvae per bowl were maintained for growth, respiration, and caloric determinations. All cultures were kept at  $25.0 \pm 0.5^\circ$  C on a 12:12 light-dark cycle. Rearing techniques were modified from Costlow and Bookhout (1959). Larvae were changed daily to freshly filtered seawater and fed newly-hatched *Artemia salina* nauplii at a density of approximately 5/ml. Food was always in excess. Number of exuvia present and mortality were recorded daily for all except the mass culture bowls.

Energy consumed was measured daily as the difference between the number of *Artemia* nauplii initially offered to each individual and those remaining after twenty-four hours. Since the concentration of *Artemia* has been shown to affect the rate of development in decapod larvae (Reeve, 1969a, 1969b; Mootz, 1973), each larva was provided with 100 *Artemia* nauplii in 20 ml of seawater. This was consistent with the food density present in cultures used to determine growth, molting frequency, caloric content, and respiration.

Replicate samples of larvae were taken every second day from hatching to day 24, counted, dried at room temperature in a desiccator, and weighed on an analytical balance to the nearest 0.01 mg. The values were plotted on semi-logarithmic paper and a least squares linear regression line fitted to the data. Dry weight data were also obtained for animals that had just molted to the first juvenile crab stage and the exuvia for each stage. Standard deviations and confidence limits were calculated for these data.

Caloric content was determined by wet oxidation in the presence of an acid-dichromate mixture (Maciolek, 1962; American Public Health Association *et al.*, 1965) for larvae at two-day intervals, exuvia of each stage, first juvenile crabs, and newly-hatched *Artemia* nauplii. Standard deviations and confidence limits were calculated for the data. Feeding rates and growth expressed as dry weight were converted to energy units using the values obtained.

Metabolic energy expenditure was measured on a daily basis through megalopa in an all-glass differential microrespirometer. The procedures were modified from Grunbaum, Siegel, Schulz, and Kirk (1955). Readings were taken in the middle of the day to avoid any diurnal effects which were not considered in this study. The experimental animal was placed in the respiration chamber with 0.5 ml filtered seawater, and a piece of filter paper containing 10  $\mu$ l of 10 per cent potassium hydroxide was attached. The two flasks were connected to a 0.3 mm bore capillary tube. The unit was allowed to equilibrate for 15 minutes after which it was sealed

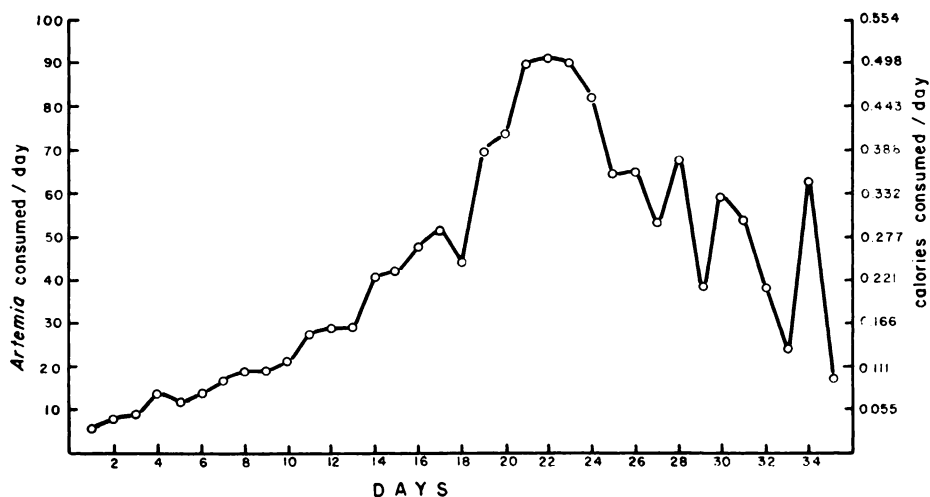


FIGURE 1. Feeding rate for larvae of *Menippe mercenaria* at a density of 5 *Artemia* nauplii/ml.

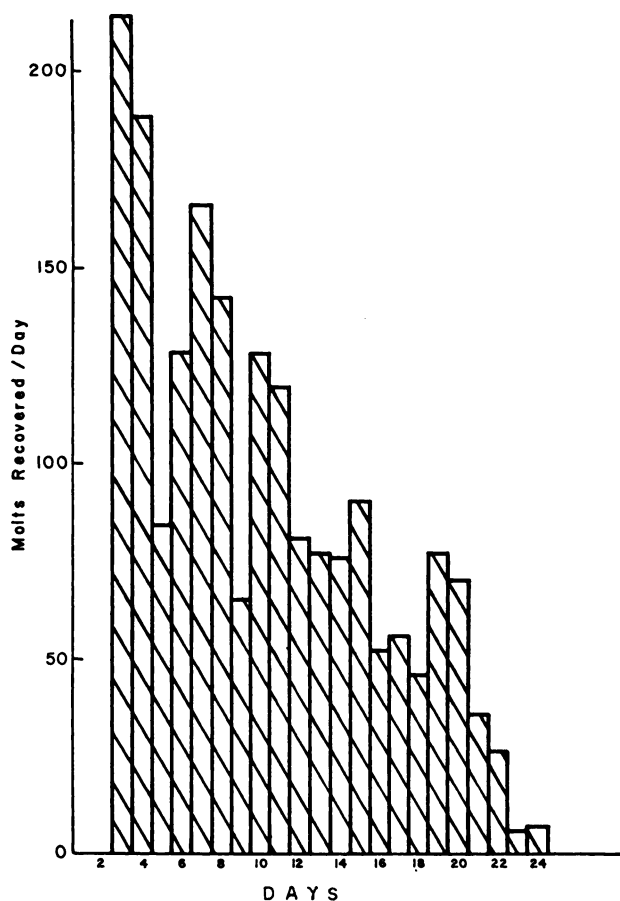


FIGURE 2. Molting frequency of larvae of *Menippe mercenaria* showing duration of each stage.

and placed in a water bath at 25° C. Each daily run consisted of an initial reading and four consecutive hourly readings. The number of larvae used per determination varied as follows: 10 larvae on day 0; 5 larvae on days 2, 3, and 4; 4 larvae on day 5; 2 larvae on day 6; and 1 larva each day thereafter. After four hours, the larvae were removed from the chamber, dried to constant weight in a room temperature desiccator, and weighed on an analytical balance. Animals were not fed during the experiments or for several hours prior to each determination. The results were plotted on double logarithmic paper and a least squares linear regression line fitted to the data for the zoeal stages. Oxygen consumption by the megalopa was averaged and a standard deviation calculated for the data. A caloric equivalent for oxygen consumption of  $4.825 \times 10^{-8}$  calories/ $\mu$ l O<sub>2</sub> consumed was used to convert the data to energy units (Brody, 1945).

#### RESULTS

The average daily feeding rate is shown in Figure 1. Consumption reaches its peak during megalopa and declines several days prior to the onset of meta-

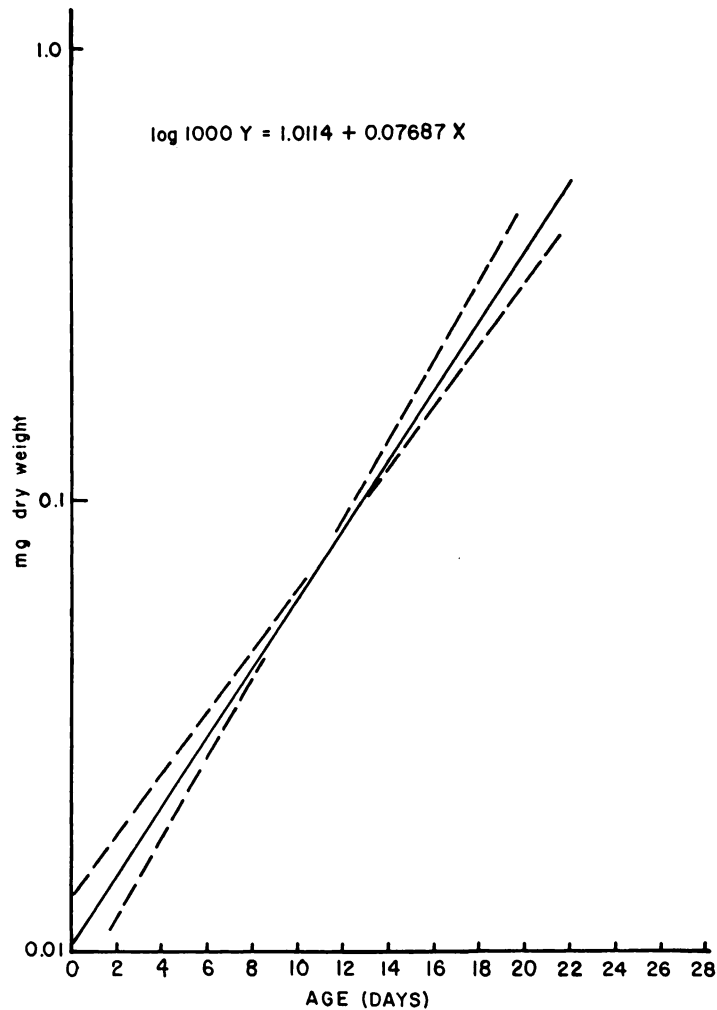


FIGURE 3. Growth expressed as dry weight of the zoea of *Menippe mercenaria* showing 95% confidence limits for the regression coefficient.

morphosis. A decrease in food consumption at molting in crustacean larvae has also been noted by others (Reeve, 1969b; Regnault, 1969). *M. mercenaria* larvae consume up to an average of 91 *Artemia* nauplii per larva per day, which is equivalent to 22 per cent of the dry weight of one animal on day 22. When converted to energy units using a value of  $4.538 \pm 0.179$  calories/mg determined by wet oxidation, individual larvae are seen to consume up to 0.502 calories/day and a total of 7.329 calories from hatching to first juvenile crab.

The rate at which larvae grow and develop was measured in three ways: duration of each larval stage, increase in dry weight, and caloric content. The number of molts recovered per day in survivorship experiments is plotted as a histogram (Fig. 2) with peaks representing the end of each stage. The peaks diminish in

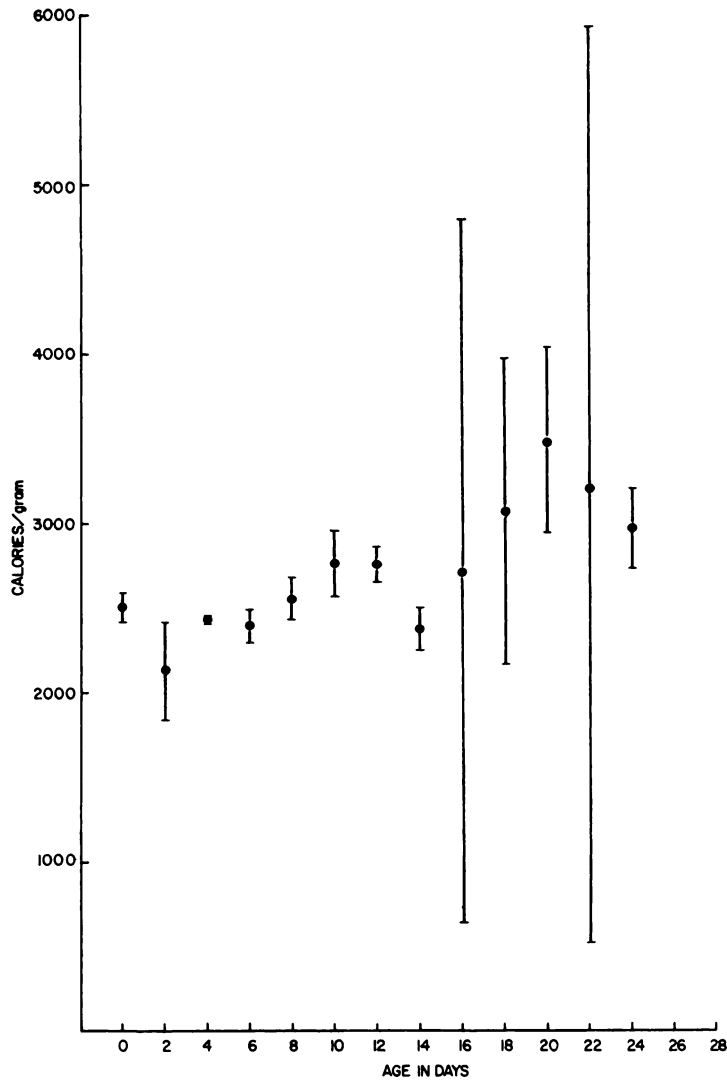


FIGURE 4. Caloric content of *Menippe mercenaria* at two-day intervals from hatching to first juvenile crab, showing the 95% confidence interval.

height as a result of variations in individual developmental time and mortality. For purposes of constructing an energy budget, each stage has been defined as follows: stage 1 from day 0 to 4; stage 2 from day 5 to 8; stage 3 from day 9 to 11; stage 4 from day 12 to 15; stage 5 from day 16 to 20; and megalopa from day 21 to 28.5. The value 28.5 is the mean number of days to first crab determined from the survivorship and molting frequency experiments. It is lower than the value 32.4 given by Ong and Costlow (1970) for *M. mercenaria* under similar conditions of temperature and salinity.

The results of least squares linear regression of log transformed dry weight data with time are shown in Figure 3. Statistical analysis on the fit of the data to the function  $\log 1000Y = 1.0114 + 0.0768X$  indicates that the slope is significantly different than 0 ( $t = 18.129$ ;  $t_{0.01, 11} = 3.106$ ) at the 0.01 probability level. Ninety-five per cent confidence limits for the regression coefficient are plotted (Fig. 3).

Growth is exponential throughout the zoeal stages, representing the exponential phase of the sigmoid growth curve, and levels off at megalopa to an average first crab dry weight of 0.69 mg. Dry weight at hatching is calculated to be 0.0102 mg; by day 20, the beginning of megalopa, the average weight is 0.354 mg, an increase of 35 times over the initial value.

The results of wet oxidation analysis are shown as calories per gram dry weight in Figure 4, with limits for the 0.05 confidence interval. Due to a lack of sufficient replicate samples, the intervals for days 16 to 22 are wide. Values range from a low of 2.129 calories/mg at day 2 to a high of 3.746 calories/mg for newly molted first crabs. Samples of exuvia from each stage were averaged and contain 1.296 calories/mg. In general, the energy content of the larvae increases with age, although it is apparent that a cyclic pattern may exist which could be related to the molting cycle. After hatching, the caloric content drops from an average of 2.503 calories/mg to 2.129 calories/mg. It is assumed that this is due to absorption of yolk material after hatching, which is primarily fat in many marine crustaceans (Pandian and Schumann, 1967) and may contain up to 9.35 calories/mg (Petrusewicz and Macfadyen, 1970). The values obtained are in accordance with other workers using a similar method of analysis (Tsikhon-Lukanina, Soldatova, and Nikolayera, 1968; Tsikhon-Lukanina and Lukasheva, 1970; Soldatova, 1970). They are, however, lower than values obtained for comparable material by the methods of bomb calorimetry.

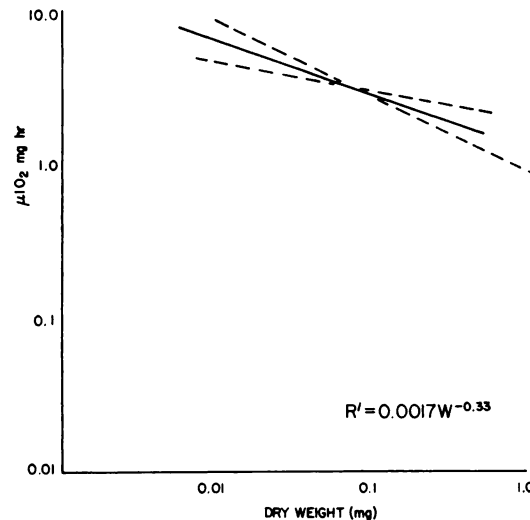


FIGURE 5. Weight specific respiration rate for the zoea of *Menippe mercenaria* with the 95% confidence interval plotted.

TABLE I  
*Energy budget for each zoeal stage and the megalopa of Menippe mercenaria*

Stage	Energy consumed (C) (cal.)	Growth (Pg) (cal.)	Energy of exuvium (E) (cal.)	Respiratory energy expenditure (R) (cal.)	Rejecta (FU) (cal. by diff.)
1	0.211	0.025	0.003	0.060	0.123
2	0.347	0.054	0.005	0.082	0.208
3	0.376	0.085	0.006	0.093	0.192
4	0.838	0.192	0.030	0.188	0.428
5	1.590	0.671	0.057	0.404	0.458
Megalopa	3.980	1.181	0.402	1.105	1.292

Weight specific oxygen consumption, as a measure of energy expended for maintenance, is shown in Figure 5. The data obtained approximate active metabolism rather than basal or resting metabolism since the animals were free to swim within the confines of the respiration chamber. Energy expended on locomotion is therefore taken into account. The energetic cost of feeding and digestion was not included since it was not measured directly and could not be obtained by subtraction. Regression analysis on logarithmically transformed data gives the relationship  $R' = 0.0017W^{-0.33}$  where  $R'$  is the weight-specific oxygen consumption and  $W$  is the dry weight of the animal. The alternate equation,  $R = 0.0017W^{0.67}$ , where  $R$  is the oxygen consumption per unit time for one organism, fits the theoretical assumption that respiration rate is proportional to the two thirds power of body weight. Statistical analysis on the data indicates that the regression coefficient is significantly different than 0 ( $t = 4.714$ ;  $t_{0.01, 16} = 2.921$ ). Ninety-five per cent confidence limits for the regression coefficient are plotted. Richman's (1958) values for *Daphnia pulex* are 0.0014 and 0.881 for  $a$  and  $b$ , respectively, corresponding to 0.0017 and  $-0.67$ , above. Clutter and Theilacker (1971) give  $a$  as 2.0 and  $b$  as 0.62 to 0.68 in *Metamysidopsis elongata*. Generally,  $b$  is between 0.67 and 1.00 for Crustacea (Wolvekamp and Waterman, 1960). The results of this study compare well with similar studies on oxygen consumption in Crustacea.

#### DISCUSSION

The data presented above are used in the calculation of an energy budget and various energetic efficiencies for the larvae of *Menippe mercenaria*. Table I shows the partitioning of consumed energy among the various life processes for each zoeal stage and the megalopa. In the second column, the energy consumed represents the total calories ingested per larva for each stage. Consumption increases over ten times from stage one to megalopa while the average dry weight increases thirty-five times, indicating an increase in the efficiency with which energy is utilized for growth. Energy expended on growth is equal to the sum of the calculated weight gain per day multiplied by the caloric content per unit weight for the corresponding day. The amount of energy channeled into growth is greater for each succeeding stage. When considered on a daily basis, however, energy of growth increases through stage 5 and levels off at megalopa, similar to growth as dry weight. Production of exuvia represents a loss to the organism at each suc-

cessive molt. While this loss is small compared to growth for zoea, it represents approximately 26 per cent of total production at megalopa (Table I).

Respiratory energy expenditure is the caloric equivalent of oxygen consumption for an average RQ of 0.82 (Brody, 1945), which corresponds to  $4.825 \times 10^{-3}$  calories/ $\mu$ l O<sub>2</sub> consumed (Table I). The maximum error obtained by estimating RQ rather than experimentally determining it is only about 3.5 per cent when oxygen consumption rather than carbon dioxide production is used (Brody, 1945). This is well within the limits of experimental error in metabolic measurements. More energy is channeled into respiration with succeeding stages and increasing size. When respiratory energy expenditure is compared with that utilized for production (growth and exuvia), the reverse is seen. A larger proportion of the assimilated calories are used for respiration at stage 1; respiration and production equalize at stage 3, while energy going into production exceeds that for respiration by stage 5, when growth is at its peak. Due to the increased mass of the megalopal exuvium, respiratory energy expenditure exceeds production during megalopa.

Rejecta as used here (Table I) is the difference between energy consumed and assimilated (sum of growth, energy of exuvia, and respiration). It represents energy not utilized by the organism, a possible example being the exoskeleton of the *Artemia* nauplii. It includes fecal and urine production. Due to the size of the animals used in this study, it was not feasible to obtain the values directly.

From the energy budget presented above, efficiencies are calculated which give the proportions of energy utilized for each process. Assimilation efficiency, gross growth efficiency, and net growth efficiency are the most relevant to larval stages where development of reproductive tissue is negligible. Per cent assimilation (Table II) is the ratio between assimilated calories and calories consumed and represents the proportion of the energy consumed by the organism which is actually available for growth and respiration. For *Menippe mercenaria* larvae it increases from 41.70 per cent during stage 1 to 85.43 per cent at megalopa. The values obtained may be biased since only whole *Artemia* nauplii were counted in determining feeding rate; however, no recognizable fragments of *Artemia* were ever seen.

Assimilation efficiency is highly variable depending on the species, the age of the organism, the type of food and its concentration, internal physiological factors, the environmental conditions, and the way in which it is measured (Petrušewicz and Macfadyen, 1970). For example, excretion is generally considered negligible

TABLE II  
*Energetic efficiencies of zoeal stage and the megalopa of Menippe mercenaria*

Stage	Percent assimilation (A/C)	Gross growth efficiency (P <sub>g</sub> /C)	Net growth efficiency (P <sub>g</sub> /A)
1	41.70	11.84	28.41
2	40.40	15.56	38.30
3	48.91	22.61	46.19
4	48.93	22.91	46.83
5	71.19	42.20	59.93
Megalopa	85.43	29.67	43.94



in energy studies, but it has been shown to be as much as 36 per cent of the assimilated calories (Hargrave, 1971). When assimilation is measured as consumption minus egestion, excretion is ignored. The indirect methods of this study consider excretion and egestion together. While assimilation efficiency is important to the individual organism, particularly in nutritional studies where optimization of feeding and growth are desired (*i.e.*, agriculture or mariculture), comparison of data for different species may be of little value. For example, values reported range from 6.6 per cent for pre-adult *Daphnia pulex* (Richman, 1958) to 100 per cent for the wolf spider (Edgar, 1971) and from 15 to 99 per cent for *Calanus finmarchicus* (Marshall and Orr, 1955).

Gross growth efficiency is defined as the proportion of consumed energy utilized for growth ( $P_g$ ), while net growth efficiency is the ratio between growth ( $P_g$ ) and assimilated energy. The net growth efficiency is always higher than the gross growth efficiency, with one exception—the case where assimilation is 100 per cent.

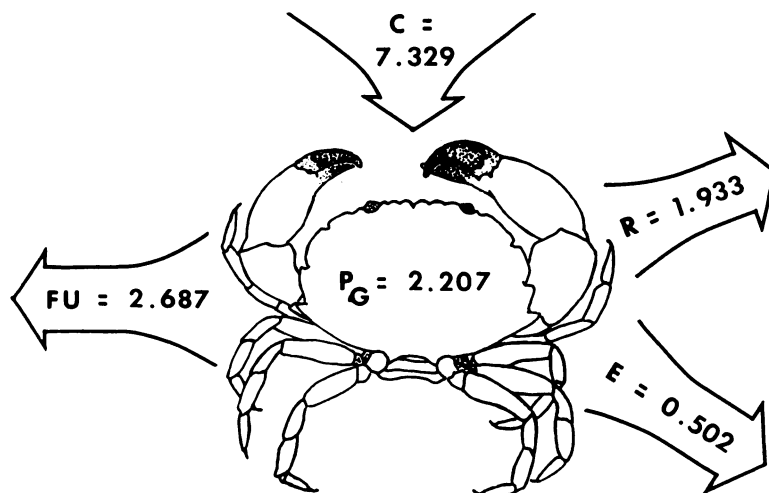


FIGURE 6. Cumulative energy budget from time of hatching to first juvenile crab showing all energy sources and sinks.

In this study, exuvia (E) were not included in the growth efficiency calculations since they represent a loss of energy to the organism. The larvae of *M. mercenaria* utilize energy most efficiently for growth during the third, fourth, and fifth zoeal stages. With decreased growth rate during megalopa, the efficiency with which energy is utilized for growth also decreases. Reeve (1969b) found growth efficiency to decrease from 70 to 35 per cent over larval development in *Palaemon serratus*. However, his work was based on dry weight values alone, so changes in caloric content of the larvae with time were not taken into account. The growth efficiencies obtained compare with literature values for developing stages of *Daphnia pulex* (Richman, 1958) and *Calanus hyperboreus* (Conover, 1964) but are considerably higher than those of young isopods (Tsikhon-Lukanina and Lukasheva, 1970).

A cumulative energy budget from hatching to first crab is presented in Figure 6. It represents the total amount of energy utilized during larval development in

calories. Of the 7.329 calories consumed (C), 2.207 calories are used for growth ( $P_g$ ), 1.933 calories for respiratory energy expenditure (R), 0.502 calories for production of exuvia (E), and 2.687 calories are eliminated through egestion and excretion (FU). The cumulative assimilation efficiency is 63.33 per cent, gross growth efficiency is 30.11 per cent, and net growth efficiency is 47.54 per cent. Conover (1964, 1966) suggests an assimilation efficiency for crustaceans of at least 60 per cent and perhaps greater. Reeve (1969b) found a cumulative gross growth efficiency of 35 per cent for *Palaemon serratus* fed *Artemia* nauplii. Both compare with the results obtained in this experiment.

In general, maintenance of vital life processes constitutes the major energy expenditure for invertebrate populations. Production (growth and reproduction) accounts for only 10 to 20 per cent of the total (Phillipson, 1966). However, when only a portion of the life cycle is considered, energy utilized for growth may equal or exceed that used for maintenance. Richman (1958) found that pre-adult *Daphnia pulex* expend 55.36 to 58.64 per cent of assimilated energy on growth; and adults, at the time of reproduction, utilize 52.08 to 70.46 per cent of the energy assimilated on production of young. The copepod *Calanus hyperboreus* exhibits a net growth efficiency of up to 89 per cent by storing fat during the short-lived phytoplankton blooms of the Arctic summer (Conover, 1964). In the fifth zoal stage, *Menippe mercenaria*, as shown in this study, can convert up to 59.93 per cent of the energy it assimilates into new body tissue. When production of exuvia is taken into account, this increases to 64.31 per cent. The ability to channel large amounts of energy into production presents an obvious advantage to the organisms. Arctic copepods can store enough energy to sustain them through much of the winter. Larvae of benthic invertebrates, as *Menippe mercenaria*, can take advantage of the food supply available in the plankton to maximize growth and possibly shorten developmental time before settling to the bottom.

The construction of an energy budget is important both from a nutritional and ecological point of view. Unfortunately, the data must be obtained under laboratory conditions which, at best, can only approximate the natural state, making application to the field difficult (Petrusewicz and Macfadyen, 1970). Some energy budget parameters are difficult to measure, particularly on very small organisms. Feeding rate and growth are the easiest parameters to measure with minimal disturbance to the organisms. Consequently, energy consumed and energy of growth are the most reliable data in this study. Maintenance energy data are the least accurate of the parameters measured since the animals were confined to small chambers and unfed during the respiration experiments. Had the animals been fed, it would have been impossible to account for the oxygen demand of fecal matter produced during the experiments. The methods used were intended to give the most uniform results possible.

This study is the most complete one to date on energetics of marine crustacean larvae. Analysis of the data by larval stage, as well as cumulatively from hatching to first crab, shows significant changes during development in growth, efficiency of food utilization for growth, and assimilation efficiency. The limited scope of the study (single temperature regime, single food source at one density, and single salinity investigated) prevents construction of an ecological energy budget. An extension of this study to investigate the effects of environmental parameters on the energetics of the species would allow a more complete and natural picture.

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#### SUMMARY

1. An energy budget was constructed for *Menippe mercenaria* from hatching to first juvenile crab when fed newly-hatched *Artemia* nauplii.
2. Larvae of *M. mercenaria* grow exponentially through the zoeal stages. Growth rate decreases during megalopa.
3. Consumption reaches its peak during megalopa where one individual may consume 91 *Artemia* nauplii/day. Feeding rate decreases prior to molting to first crab stage.
4. The caloric content per unit dry weight increases from 2.503 cal/mg at hatching to 3.746 cal/mg at first juvenile crab. Molts contain 1.296 cal/mg.
5. Respiration by zoea is proportional to the two thirds power of body weight and is described by the function  $R = 0.0017W^{0.67}$ .
6. Over the period of larval development, 7.329 calories are consumed, 2.207 calories are used for growth, 0.502 calories are lost to production of exuvia, 1.933 calories are expended for maintenance, and 2.687 calories are lost as rejecta.

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