ECOLOGICAL EFFICIENCY OF A PELAGIC MYSID SHRIMP; ESTIMATES FROM GROWTH, ENERGY BUDGET, AND MORTALITY STUDIES[1]

ROBERT I. CLUTTER[2] AND GAIL H. THEILACKER[3]

ABSTRACT

The net ecological efficiency (yield/assimilated) of a population of *Metamysidopsis elongata* (Crustacea, Mysidacea) is estimated to be 32 %. The gross ecological efficiency (yield/ingested) is probably between 19 % and 29 %.

Energy use by the field population was calculated from estimates of age specific natural mortality rates and data on growth, molting, reproduction, and respiration. Average growth and molting rates were determined by rearing the mysids in the laboratory. Size specific fecundity was determined from field and laboratory observations. The calorie contents of the mysids, their molts, eggs and larvae were estimated by bomb calorimetry and in part from biochemical composition. The energy used in metabolism was calculated from size specific respiration and data on body composition.

Biological systems are organized by the flow of energy. Trophic structure, numbers of steps in food chains, and numbers of conjunctions in food webs depend on the amount of energy passed through populations to other populations. Energy units provide a means of expressing productivity in terms common to all organisms.

The energy produced in the breakdown of biomass by organisms is stored as chemical energy in the pyrophosphate bonds of adenosine triphosphate (Morowitz, 1968). The overall thermodynamic efficiency of this process is similar in all animals, about 60 to 70 % according to Krebs and Kornberg (1957). It has been suggested (e.g. Slobodkin, 1961, 1962) that the efficiency of energy transfer between populations of animals is also fairly constant. This efficiency is necessarily of lower order because, for example, there are losses involved in synthesizing macromolecules, in continually resynthesizing proteins that undergo thermal denaturation, in transforming foodstuff energy into work energy (about 65 % efficiency), and in the degradation of energy during the performance of work. All energy that passes through a population is either lost as heat or passes on to another trophic level. If one assumes that all mortality is caused by predation, the gross ecological efficiency (Phillipson, 1966) of energy transfer through that population is the ratio of the energy yield in mortality to the energy ingested.

Through laboratory studies of growth, molting, reproduction, respiration, body composition, and energy content, we have constructed an energy budget for the pelagic mysid shrimp *Metamysidopsis elongata* (Holmes). Various aspects of the distribution, behavior, and population biology of this species have been described by Clutter (1967, 1969) and Fager and Clutter (1968). The energy budget data, together with estimates of natural population mortality rates, are used to estimate net and gross ecological efficiencies for the field population.

GROWTH AND DEVELOPMENT

Metamysidopsis elongata is a member of the Mysidae, a family that is ubiquitous and often very abundant in most of the neritic zones of the world ocean. This species is free-swimming and occurs in shoals and swarms just above the sand bottom in areas where surf is common

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[2] Formerly of National Marine Fisheries Service Fishery-Oceanography Center, La Jolla, Calif. 92037.

[3] National Marine Fisheries Service Fishery-Oceanography Center, La Jolla, Calif. 92037.

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(Clutter 1967, 1969).

As is characteristic of mysids, the eggs and larvae are held by the oostegites (brood pouch) of the adult females until they develop into juveniles that are similar in form to the adults. The juveniles grow by shedding their exoskeletons (ecdysis) at intervals that become progressively longer until they reach maturity. Males and females develop distinguishable morphological features during the period of rapid growth prior to maturity. Growth becomes progressively slower after maturity. Although there is no evidence that death occurs because of physiological aging, the maximum age observed was about 9 months. Most animals survive less than 3 months in the natural environment . We assume that most of the natural mortality is caused by predation, especially by fishes.

Some growth experiments have been reported for other species of Mysidae. Blegvad (1922) determined the growth rates of a few individuals of *Mysis inermis* from first stage juveniles through early maturity. Nouvel and Nouvel (1939) made disjunct determinations of time between molt stages for some size groups of *Praunus flexuosis.* Nair (1939) observed the time sequence in the egg and larva development of *Mesopodopsis orientalis,* determined the size and age at liberation, and noted the size at sexual maturity of males and females. In his review of growth in some marine Crustacea, Kurata (1960) presented the results of growth studies made by Ishikawa and Oshima on *Neomysis japonica* and by Matsudaira et al. on *Gastrosaccus vulgaris.* Mauchline (1967) maintained adult *Schistomysis spiritus* in the laboratory, estimated the time they take to attain sexual maturity, and estimated the minimum incubation time. Considering differences between species, sizes, and environmental temperatures, these reported patterns of development and size increase per molt are compatible with the results of our study.

CULTURE METHODS

Experimental animals were collected during the day from the middle of their habitat with nets (Clutter, 1965; Fager, Flechsig, Ford, Clutter, and Ghelardi, 1966). They were placed in large (20-50 liter), opaque plastic containers with covers and transported to the laboratory within 1 to 2 hr after the time of capture.

The culture methods were about the same as those described by Lasker and Theilacker (1965) for euphausid shrimps. Individual animals were placed in rectangular clear plastic containers in about 500 ml of sea water. The small containers were partly immersed in trays of running sea water. Since the running sea water was pumped continuously into the aquarium from midwater offshore, within the *Metamysidopsis* habitation zone, the laboratory temperatures (14°-20° C) were about the same as those that the animals would have experienced in their natural environment.

Animals of both sexes and of several sizes were selected for the experiments. Young juveniles were procured by placing pregnant females in containers and recovering the young on the day following their release from the brood pouch, which occurred at night. These young were then placed in separate containers. To determine the incubation time, i.e. the time from fertilization of the eggs to release from the brood pouch as juveniles, pregnant females with known times of fertilization were placed in individual containers so that larval development could be observed.

Mysids of all ages were fed freshly hatched nauplius larvae of brine shrimp, (*Artemia salina*). Twice each week the mysids were removed while their containers were emptied of excess food and cleaned with hot fresh water followed by a sea water rinse. They were then provided with excess quantities of fresh nauplii in clean sea water.

The containers were examined every day for the presence of molts or, occasionally, carcasses. The molts and carcasses were removed and placed individually in small vials of 5 % Formalin for subsequent microscopical examination and measurement.

OOGENESIS AND INCUBATION

Since *Metamysidopsis* has a transparent cara-

pace and body wall, it is possible to observe the late stages of oogenesis in live animals without dissecting them. The ovary (cf. Nair, 1939, for description) is situated in the interspace between the alimentary canal and the pericardial floor. Its most obvious feature is the pair of larger tubes that lay side by side. It is in these tubes that the eggs to be extruded into the brood pouch are invested with yolk. The process of yolk formation takes about a week in *Metamysidopsis* and is completed just before the female molts and copulates. By observing the ova in these tubes it is possible to estimate the size or age at first reproduction in maturing females, and to count the number of eggs that will be spawned by reproducing females of all ages.

Copulation occurs at night within 2 to 3 min after the mature female molts, during which time sperm are passed into the empty brood pouch by the attending adult male. The eggs are subsequently extruded into the brood pouch where they are fertilized. The eggs hatch from the vitelline membrane after 2 to 3 days. According to Manton (1928) and Nair (1939) a larval ecdysis occurs in the brood pouch shortly before the larvae are liberated. These late stage larvae have movable appendages and pigmented eyes that show through the transparent oostegites of the brooding female. The small quantity of yolk that is present after the larval ecdysis is absorbed, or nearly so, prior to liberation from the brood pouch.

After liberation the larvae tend to sink, then, according to Nair (1939), they undergo a second larval ecdysis after which the statocysts appear and they are capable of swimming. The mysids assume this highly mobile juvenile form within a few minutes after liberation. Although we did not attempt to distinguish sexes of larvae and juveniles, the observations of Nair (1939) indicate that dimorphism is exhibited by the antennules and abdominal appendages even though neither the brood pouch nor the penis is developed.

Incubation time was determined in the laboratory. Adult females and adult males were observed in an aquarium during molting and copulation. Ten females were caught after being observed *in copulo* and were placed in separate containers of sea water at the temperature of their natural environment at that time (17°-19° C). Five of them were removed, at various times, to determine the stages of development of the young. The remaining five all released their young as juveniles on the tenth day after fertilization.

In addition, a large number of nonpregnant adult females were kept in separate containers for various periods up to 157 days. The range of intermolt periods in 218 observations was 5 to 13 days; the median and modal values were both 10 days. There was no obvious temperature effect. The adult females molt just before fertilization and just after liberation of the young; therefore, the average incubation time was taken to be 10 days. This is intermediate between incubation times given for Mysidae that live and reproduce at higher and lower temperatures. Nair (1939) determined the incubation time of *Mesopodopsis orientalis* to be 4 days at 25° to 29° C. Mauchline (1967) reports a minimum incubation time of 3 weeks for *Schistomysis spiritus* at 12.5° C.

MOLTING

To avoid handling and possible injury of the experimental animals, the growth rates were determined by measuring molts. The molts suffered no appreciable decomposition because they were collected on the day following ecdysis. The morphological development of the animals was usually discernable from their molts. But the molts are fragile, split just back of the carapace where the animals emerge, and easily stretched out of shape. Therefore, to measure growth it was necessary to measure a part of the molt that always retained its form and bore a consistent relationship to the body length.

Uropod-Body Length Relationship

The exopod of the uropod (tail fan) was used to estimate the body length of each animal for its previous intermolt period. The uropods were measured from the base (end of last abdominal segment) to the tip, not including spines, which were sometimes broken, with an ocular micro-

meter, at 27.5 × magnification.

The relationship between uropod length and body length was established from a selected series of 94 animals that had been collected in the field and preserved. The series included animals that ranged in body length from 0.8 mm to 7.2 mm, and included late stage larvae, juveniles, immatures, and adults. Both sexes were included; there was no difference between sexes in this relationship.

The body length was measured from the end of the last abdominal segment (base of uropod) to the anterior edge of the carapace, behind the insertion of the eyestalk. Mysids tend to curl when preserved, and they can be distorted to appear longer if they are stretched when measured. To avoid this we chose specimens that were at most only slightly curved, and measured the length of the arc through the midline of those that had significant curvature, rather than the straight line distance between head and tail.

As shown in Figure 1, the relationship between uropod length and body length is linear. The body length is 4.5 times the uropod length.

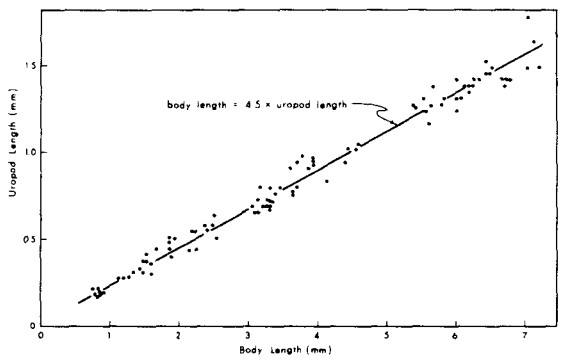

FIGURE 1.—Relationship between uropod length and body length of *Metamysidopsis*.

Molting Frequency

Average intermolt periods were estimated from 414 observations, 146 on males and 268 on females. In many cases several observations were made on the same animal. The maximum period of laboratory survival for a single animal was 157 days, and the maximum number of molts observed for a single animal (not the same animal) was 21. The molting frequency data for animals reared in the laboratory are summarized in Table 1. The sex of the juveniles was established after they had grown large enough to develop obvious morphological differences.

TABLE 1.—Frequency of molting periods observed for *Metamysidopsis* in the laboratory.

Sex and length	Intermolt Period (days)													
	3	4	5	6	7	8	9	10	11	12	13	Mode	Median	Mean
Females														
Body length (mm) 2		8										4	4	4.0
3		6	2									4	4	4.3
4		5	3	1								4	4-5	4.6
5		3	7	7	1	5	2					5-6	6	6.2
6			10	7	9	13	13	28	17	5	8	10	9-10	9.2
7			11	8	6	9	16	12	28	9	9	11	10	9.4
Males														
Body length (mm) 2	11											3	3	3.0
3	2	11	1									4	4	3.9
4	2	15	8	1	1							4	4	4.4
5		6	29	20	4							5	5-6	5.4
6		6	11	8	7	3						5	5-6	5.7

Supplementary data on molting frequency in the field population were obtained indirectly. Over a period of 3 days, 1,211 juveniles + immatures and 2,979 adults were brought into the laboratory late in the day and placed in large aquaria. The following morning all the animals and their molts were collected and counted. Of the juveniles + immatures 218 or 18 % had molted, and of the adults 356 or 12 % had molted. The reciprocal of the relative number molting is an estimate of molting period. The observed reciprocals were 5.6 for juveniles + immatures and 8.3 for adults. Since these values are midway in the ranges shown by laboratory animals (3-8 days for juveniles + immatures and 4-13 days for adults) we assume that the laboratory observations are valid estimates of molting frequency in the population as a whole.

Although our observations were made from February to October, and the water temperatures in the rearing troughs varied from 14° to 20° C, we were unable to detect any obvious effects of temperature or time of year on molting

frequency or growth rates. Nouvel and Nouvel (1939) stated that the intermolt period for *Praunus flexuosis* is least during the warmest months, and the incubatory period is 15 days in August and 3 to 4 weeks in September. Lasker (1966) showed that *Euphausia pacifica* intermolt periods varied as the water temperature fluctuated, and that the intermolt period was shortened by an artificially produced warm period, but that temperatures above 12° C did not accelerate molting further.

Since we do not have evidence to the contrary, we must assume that our laboratory observations on molting frequency provide adequate average values. From the median values given in Table 1 and estimated average growth rates (see below) we have estimated the molting schedules of females and males from juveniles to mature adults as follows:

Females: first six molts — 4 days
seventh molt — 5 days
eighth molt — 6 days
ninth molt — 8 days
tenth molt and thereafter — 10 days

Males: first four molts — 3 days
fifth to eighth molts — 4 days
ninth and tenth molts — 5 days
eleventh molt and thereafter — 6 days

GROWTH AND MATURATION

Evidence of the temporal sequence of growth and maturation can be obtained from following peaks of abundance of size groups in natural populations. We sequentially sampled the mysids in the field and observed some shifting peaks. But we consider that the results are not very reliable because of temporal changes in age-specific mortality rates (Fager and Clutter, 1968). Therefore, all the age-specific growth estimates presented here were obtained from laboratory studies.

Observed Growth

A few mysids were reared in the laboratory from fertilized egg to adult. Several were reared from egg through the juvenile stage. In addition, larger numbers of various sizes were collected in the field and kept in the laboratory for several molts.

The growth data from these animals were combined as shown in Figure 2 (females) and Figure 3 (males). The sexes were separated because the growth and molting rates of males and females are different. As they are shown in Figures 2 and 3, these individual growth curves are simplified and slightly incorrect representations of true growth, for two reasons. First, the growth of the body integument is represented to be continuous, whereas it actually occurs in discrete increments. Second, the age

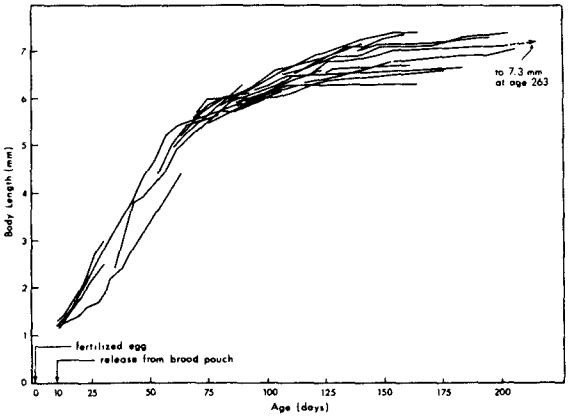

FIGURE 2.—Observed growth in length (from molts) of *Metamysidopsis* females in the laboratory.

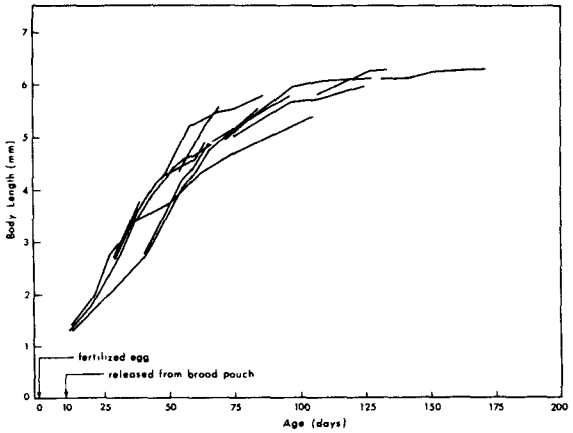

FIGURE 3.—Observed growth in length (from molts) of *Metamysidopsis* males in the laboratory.

shown is the age of the animal at the time it molted, rather than the age at the time that the molted integument was first formed. The procedure for combining the various growth curves of individual animals was to first plot the growth of the animals of known age, and then plot the other growth curves (actual ages unknown) in a manner that showed the least variation from the apparent trend.

Some of the apparent variability in growth rates may be attributable to differences in the temperature at which the growth occurred, but we did not detect any obvious temperature effect. Considerable individual variability occurred among animals of the same size or age that were reared simultaneously.

Maturation

Changes in morphology in relation to size, and known or estimated age, were observed in the molts of animals reared in the laboratory. Observations were made on live females collected from the field population to determine the size at which yolk invested ova first appear in the ovaries. Supplementary observations on the relationship between size and body form were made on preserved animals that had been collected in the field. There is some evidence from previous samples taken for other purposes (Clutter, 1967, 1969) that the relationship between size and stage of development may vary seasonally. But during the period of observations reported here, this did not appear to be significant.

In particular, we wished to determine (1) the size (and subsequently the age) at which males and females were easily distinguishable by their secondary sexual characteristics, (2) the size at the onset of maturity, and (3) the size at which spawning and brooding of eggs and larvae occurs. The external characteristics that most obviously separate males from females of this species are the enlarged oostegites (brood pouches) of the females and the enlarged pleopods (abdominal legs) and antennae of the males.

There is some variability in the size at which the stages of development occur. Therefore, our estimates are average values. The larvae are released and juvenile form is attained at age 10 days; at this time both sexes are about 1.2 mm long (body length; excluding antennae, eyes, and tail fan). Males exhibit sub-adult morphology when about 3.7 mm long, and become mature at 4.3 mm. Females exhibit sub-adult form at 4.0 mm, the ova become infused with yolk at 4.5 mm, and the eggs are extruded into the brood pouch, fertilized, and incubated at slightly less than 5.2 mm.

Average Growth in Length

Average continuous growth curves were fitted by eye to the combined growth data plotted in Figures 2 and 3. These curves are represented by the lower curves (fine, continuous unbroken lines) in Figure 4 (females) and Figure 5 (males). These continuous curves represent the size of the molt at the time—days from fertilization—that the molt was shed. Actually the integument of the animal had attained that size by the beginning of the intermolt period in question. The true growth of the integument of the average animal is represented by the stair-step pattern, which is based on the molting frequency analysis. The broken curved line of continuous growth (Fig. 4 and 5) represents the probable pattern of temporal change in average organic weight of the animal. This curve connects the points halfway between the beginnings and endings of the intermolt periods.

Since the average sizes at various stages of development were determined, it was possible to estimate the average time schedules of maturation and reproduction for females and males on the basis of the growth curves. The average female begins to develop a brood pouch at the seventh molt, 39 days after becoming a fertilized egg. Yolk invested ova begin to be formed at 45 days, during the ninth intermolt period; the ova are extruded into the developed brood pouch and fertilized at the beginning of the tenth intermolt period, at 53 days; and reproduction can occur at 10 day intervals thereafter.

Males and females grow at rates that are indistinguishable up to the age of about 30 days, even though the juvenile males molt more frequently than juvenile females. After that the

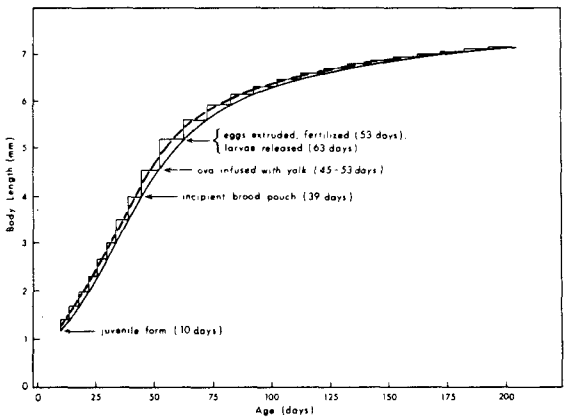

FIGURE 4.—Average growth in length of female *Metamysidopsis* in the laboratory. The lower curve (fine continuous line) was fitted to molt size data (Fig. 2). The steps represent changes in integument size. The upper curve (heavy broken line) represents the average size of the animals, assuming that the addition of body tissue is continuous.

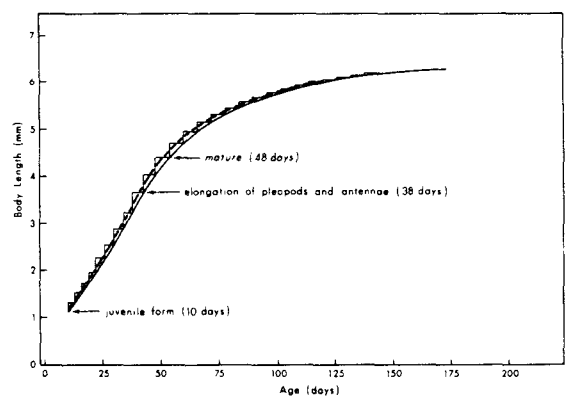

FIGURE 5.—Average growth in length of male *Metamysidopsis* in the laboratory. The lower curve (fine continuous line) was fitted to molt size data (Fig. 3). The steps represent changes in integument size. The upper curve (heavy broken line) represents the average size of the animals, assuming that the addition of body tissue is continuous.

males grow more slowly. The males develop easily recognized secondary sexual characteristics at an average age of 38 days and become sexually mature after about 48 days. Average age at maturity was estimated from observations of testes and copulatory behavior in the laboratory as well as from external morphology.

Average Growth in Weight

To estimate growth in terms of energy it is necessary to translate growth in length into growth in dry weight. This growth in dry weight is then translated into growth in organic (ash-free) weight and thereafter into calories.

The dry weights of *Metamysidopsis* of body lengths ranging from 1.9 mm to 6.5 mm were determined. The animals were captured alive, measured, washed very briefly with distilled water, and dried at 60° C in an oven for 24 hr. They were then weighed individually on a Cahn electrobalance immediately after they were removed from the oven.

The observed relationship between body length and dry weight is shown in Figure 6.

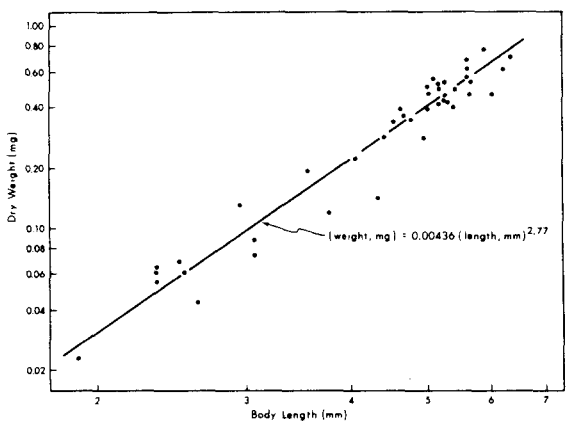

FIGURE 6.—Relationship between body length and dry weight of *Metamysidopsis*.

The equation for the relationship was determined empirically by fitting a straight line to the logarithms of body length and dry weight by the method of Bartlett (1949). The relationship is:

$$\log_e (\text{weight}) = -5.436 + 2.77 \log_e (\text{length})$$

or

$$\text{weight} = 0.00436\,(\text{length})^{2.77}$$

where weight is expressed in mg and length in mm.

It is common to assume that body weight and body volume have a linear relationship, and that body volume is proportional to the third power of length. Therefore dry weight is expected to

be proportional to the third power of body length (Bertalanffy, 1951). The observed relationship does not quite conform to the expected. The relationship between body length and body diameter appears to be linear (Fig. 7); therefore the body volume must be proportional to the third power of the body length. The observed relationship between weight and length could be the result of orthogonal growth of the appendages, which become progressively larger as the animals mature.

From the average length-weight relationship and the average continuous growth in length curves (Fig. 4 and 5) we have calculated the average growth in weight curves shown in Figure 8. The average continuous growth in length curves represented by the heavy broken lines in Figures 4 and 5 were used to calculate growth in weight, because we assume that growth in organic weight is continuous during intermolt periods even though growth of the integument occurs in discrete steps. The estimated growth in weight of males was extrapolated by eye from age 175 days to age 204 days. We do not have laboratory growth estimates for these larger males, but they occurred in the field population.

The average dry weight per egg (140 eggs in sample) was 5.5 μg. Larvae weigh slightly less than this because they lose weight through metabolism while in the brood pouch, even though their ash content is slightly higher than that of the eggs.

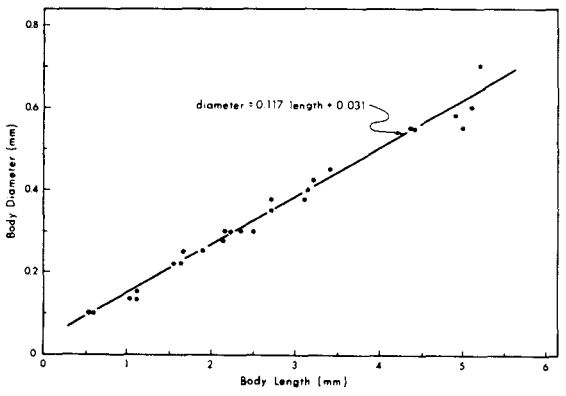

FIGURE 7.—Relationship between body length and body diameter of *Metamysidopsis*.

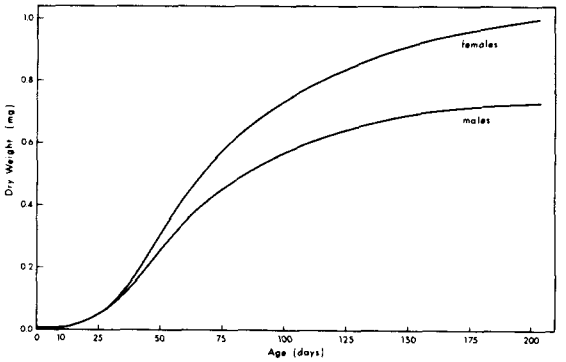

FIGURE 8.—Average growth in dry weight of *Metamydisopsis* females and males in the laboratory.

REPRODUCTION

Data on reproduction and associated energy use are easier to obtain for Mysidae than for most pelagic invertebrates. The eggs and larvae are carried in the brood pouch of the female, and the incipient eggs can be counted prior to their full development and extrusion because the body walls of the mysids are transparent. In addition, copulation and fertilization can be observed in the laboratory, and frequency of pregnancy among mature females can be observed in the natural population through sequential sampling because all stages live in the same area while gestating as they do when not reproducing. Nevertheless, average reproduction rate in these animals is not easy to assess with absolute certainty.

FECUNDITY

Minimum Estimate

The most straightforward way to estimate fecundity is to collect animals in the field, preserve them, and count the number of eggs or larvae carried by females of different sizes. Figure 9 shows the relationship between body lengths and number of young for 310 females collected in the field at various times during the year. The data include 125 females bearing eggs and 185 bearing larvae; we excluded animals that had obviously lost young during capture and preservation. For both eggs and lar-

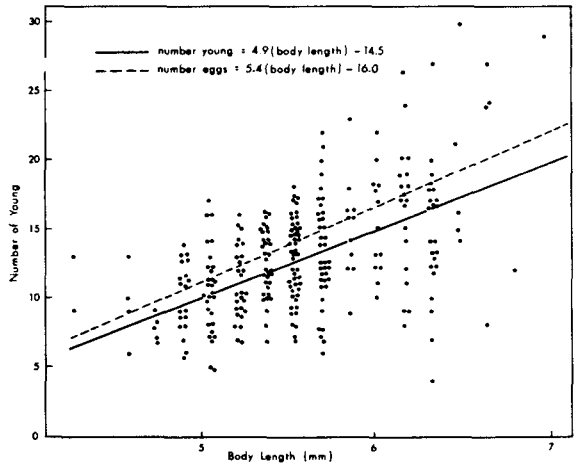

FIGURE 9.—Relationship between body length and number of brood pouch young (eggs and larvae) of preserved animals that were collected in the field. The lower line (continuous) was fitted to the points by the method of Bartlett (1949). The upper line (dashed) represents the equivalent relationship for newly laid eggs, assuming a brood pouch mortality of 0.013/day (see text).

vae, the number of young per female is highly variable. The average relationship between the size of the female and the number of young, calculated by the method of Bartlett (1949), is represented by the straight line: number of young = 4.9 (body length, mm) – 14.5.

This estimate of fecundity is not quite correct because it was made from counts of eggs and larvae that were a few days old. Some eggs and larvae apparently are lost from the brood pouch during the incubation period. Therefore, we adjusted the relationship to account for the mortality which occurs during the incubation period. To estimate the mortality during incubation, counts were made of the maturing ova in the ovaries of 40 adult females and counts were made of late stage larvae in the brood pouches of 27 females of the same size, collected at the same time. The ratio of mean number of larvae/mean number of ova was 0.90. The larvae were estimated to be 8 days old, giving an instantaneous mortality rate of 0.013/day.

The average age of the eggs and larvae from the 310 preserved females (Fig. 9) was estimated to be 7 days. Therefore, the relative survival of the young in the brood pouch between the time of extrusion of the eggs and the estimated average age at which they were counted (7 days) was estimated to be about 0.91. The number of brood pouch young per female was adjusted to the equivalent number of eggs extruded per female by multiplying the number of young by 1/0.91 = 1.10. The relationship (Fig. 9) then becomes: number of eggs = 5.4 (body length, mm) – 16.0, which is shown in Figure 9 as the upper, dashed line.

We consider this to be a minimum estimate of fecundity, because some females that had lost eggs and larvae from the brood pouches during collection and preservation were probably included, despite our attempt to exclude them.

Maximum Estimate

We observed that the females that had released young during the laboratory experiments had a higher apparent fecundity than those that were collected and preserved in the field. It is possible that there was some bias in selecting animals for the laboratory experiments, but we were not aware of any. The number of young released per female is plotted against the body length of the female for those 17 specimens in Figure 10. The average relationship between

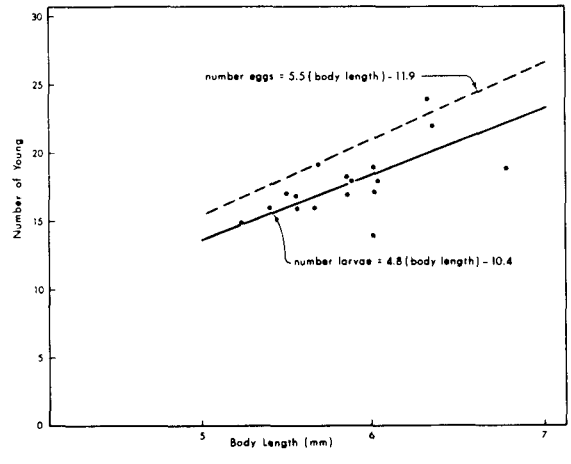

FIGURE 10.—Relationship between body length and number of young released by experimental animals in the laboratory. The lower line (continuous) was fitted to the points by the method of Bartlett (1949). The upper line (dashed) represents the equivalent relationship for newly laid eggs, assuming a brood pouch mortality of 0.013/day (see text).

body length and number of young, calculated by the method of Bartlett (1949), was: number of young = 4.8 (body length, mm) − 10.4. This is represented by the lower, unbroken straight line in Figure 10.

This relationship gives estimates of fecundity that are about 1.5 to 2 young per female higher than the relationship calculated from preserved animals. But this is not quite a maximum estimate of fecundity because it does not include the reduction from mortality that occurs during incubation.

As already demonstrated, we can assume a brood pouch mortality rate of 0.013 per day. The relative survival of young in the brood pouch during the 10 days between the extrusion of eggs and the release of larvae was therefore estimated to be 0.87. The number of young released per female was adjusted to the equivalent number of eggs extruded per female by multiplying the number of young by 1/0.87 = 1.15. The relationship (Fig. 10) then becomes: number of eggs = 5.5 (body length, mm) −11.9, which is shown in Figure 10, as the upper, dashed line.

This relationship gives estimates of fecundity that are about four eggs per female higher than the minimum estimates calculated from preserved animals. We consider this to be the maximum estimate of fecundity. It is the same as that used by Fager and Clutter (1968).

COPULATION AND FERTILITY

The fecundity estimates given above apply only to the females that engage in copulation and are fertilized. Mature females that are not fertilized apparently extrude some eggs, but only about one-half the usual number.

Many observations of copulation were made in the laboratory (Clutter, 1969). It occurs in artificial light as well as in the dark, but only at night, between about 2000 and 2400 hr. It occurs within only 2 to 3 min after the mature females molt, and apparently only when the female exudes a pheromone to attract adult males of the same species.

Ten females were captured immediately after they were observed *in copulo* and kept in separate chambers for 10 days. Impregnation had been successful and the usual number of eggs were extruded in every instance. Some adult females that molt do not stimulate males to attend them. Ten adult females were captured after they had been observed to be unattended by males during molting and recovery. They later extruded only about one-half of the normal number of eggs, which eventually disappeared from the brood pouch, presumably because they were infertile. Therefore, the unfertilized females expended only about half the amount of energy in eggs that the fertilized females expended.

Since the mature females are subject to fertilization for only a few minutes following molting, and they apparently do not always attract males during the time, copulation does not always occur. Therefore, not all produce young every 10 days. In a large number of field collections during all seasons, the observed fraction of mature females carrying eggs or larvae in their brood pouches varied from 18 % to 78 %; the mean was 51 %. We are not certain of the source of this variability; there is some evidence that it could be related to population density (Clutter, 1969). We have assumed an average value of 50 % for the purpose of calculating the amount of energy used in reproduction.

On the average, mature females extrude the usual number of eggs about one-half of the time, and they otherwise extrude only one-half of the usual number of eggs. Therefore, the effective average fecundity, in terms of energy used in reproduction (but not in terms of the number of viable young produced), is 0.5 + (0.5) (0.5) = 75 % of the fecundity estimated from counts of young produced/female. For the purpose of calculating the amount of energy used in reproduction the fecundity equations are:

minimum — number of eggs = 4.1 (body length, mm) − 12.0

maximum — number of eggs = 4.1 (body length, mm) − 8.9

The second of these relationships is used in the ensuing energy budget calculations.

RESPIRATION

A polarographic oxygen electrode (Kanwisher, 1959) was used in a closed system to measure the respiration rates of *Metamysidopsis*. Both temperature and oxygen were recorded continuously on a strip chart.

The experimental animals were taken from large constant-flow holding tanks (temperature 14°-17° C) and acclimated overnight at the temperature used in the experiments (13.8°-18.1° C), to avoid the overshoot in oxygen consumption described by Grainger (1956). They were then washed in millipore-filtered seawater, counted, and transferred to previously filtered seawater in the oxygen electrode system. In each experiment an attempt was made to use animals of a limited size range. During the run they were held within a 10-ml chamber, baffled at each end with silk screen cloth of 282 μ mesh aperture size. The water in the closed system circulated through this chamber and then past the electrode at a constant rate. The whole system was immersed in a temperature-controlled water bath.

Oxygen use by bacteria was measured by making blank runs with the same water both before and after each test run. Bacterial use amounted to less than 2 %. Oxygen consumption by the mysids was corrected for bacterial uptake. The decrease in relative oxygen tension with time was nearly linear in both the blank runs and the test runs.

The results of the respiration experiments are shown in Table 2. Observed weight-specific respiration rates (μl O_2/mg dry weight hr) were corrected for the initial percent oxygen saturation and for temperature. In correcting for temperature, a Q_{10} of 1.9 was used (Grainger, 1956). All values were corrected to 16° C, which is about the median of the year-round temperatures that occur in the natural environment of the mysids.

TABLE 2.—Summary of respiration experiments on *Metamysidopsis*.

Specimens	Number	Mean dry weight	Water temperature	Weight-specific respiration rate	
				Uncorrected	Corrected[1]
		Mg.	° *C*	*(µl O₂/mg dry wt hr)*	
Juveniles	99	0.03	13.8	7.71	7.54
Juvenile and immature males and females	176	0.07	18.0	5.40	4.76
"	297	0.08	18.1	5.08	4.48
"	297	0.08	18.1	6.78	5.93
"	132	0.14	13.8	3.92	3.82
Immature females	85	0.28	15.2	1.95	2.46
Males	51	0.31	13.8	3.60	3.53
Brooding females	27	0.47	13.8	3.22	3.16
"	27	0.66	13.8	2.65	2.59

[1] Corrected for oxygen saturation level and corrected to temperature of 16.0° C by using Q_{10} = 1.9 (Grainger, 1956).

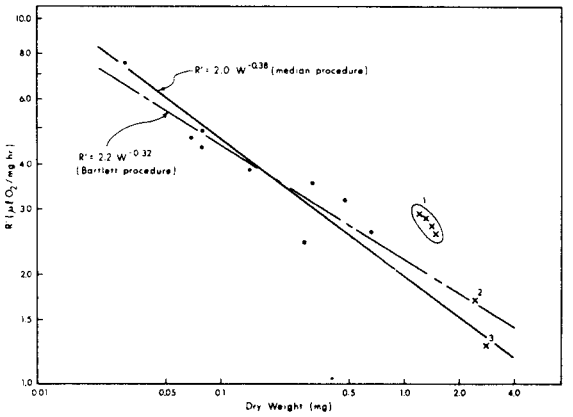

FIGURE 11.—Relation between respiration rate of *Metamysidopsis* and size at 16° C. The symbol R' represents respiration rate per dry unit weight (R/W). The lines were fitted to the circle points by two statistical pocedures. The x points are values calculated from published data on other species of Mysidae: 1-*Neomysis americana* (Raymont and Conover 1961); 2-*Neomysis integer* (Raymont, Austin and Linford 1966); 3-*Hemimysis labornae* (Grainger 1956).

The corrected weight-specific respiration data are plotted in Figure 11 on log-log scales. The symbol R' (Conover, 1960) represents the respiration rate per unit dry weight (R/W). The average relationship between mean dry weight and R' was estimated by two statistical procedures. First, a straight line was fitted to the logarithmically transformed data by the median procedure (Tate and Clelland, 1957). This gave the relationship:

$$R' = 2.0\ W^{-0.38}$$

or

$$R = 2.0\ W^{0.62}$$

where R = respiration rate in μl O_2/hr
and W = mean dry weight in mg.

Second, a straight line was fitted to the logarithmically transformed data by the method of

Bartlett (1949). This gave the relationship:

$$R' = 2.2\ W^{-0.32}$$

or

$$R = 2.2\ W^{0.68}$$

Theoretically, the respiration rate is expected to be proportional to the $^2/_3$ power of weight. Since our estimates are slightly above (0.68) and slightly below (0.62) the expected value of 0.67, we consider that the $^2/_3$ power relationship is the best estimate for *Metamysidopsis* and that the best estimate of respiration rate (μl O_2/hr) is given by the equation:

$$R = 2.1\ W^{0.67}$$

Estimates of weight-specific respiration for three other, somewhat larger, species of Mysidae are compared with *Metamysidopsis* in Figure 11. The upper four points ("1" on Fig. 11) represents results for *Neomysis americana* from Raymont and Conover (1961) that were adjusted from 4° C or 10° C to 16° C by using a Q_{10} value of 1.6 that was estimated from their data. The intermediate point is an estimate of the median value oxygen consumption rate calculated from 12 determinations on *Neomysis integer* (Raymont, Austin, and Linford, 1966) that had been adjusted to 16° C by using a Q_{10} of 1.9 (Grainger, 1956). The lower point was estimated from the results of Grainger (1956) for *Hemimysis lamornae*. The ranges of values for these three larger species are about the same as the range (1-3 μl/hr) calculated from the seasonal change data of Raymont et al. (1966) that had been adjusted to 16° C. The estimates for *Metamysidopsis* and the other three Mysidae all lie well above the relationships calculated for marine planktonic Crustacea by Conover (1960).

BODY COMPOSITION AND ENERGY CONTENT

To estimate the amounts of energy used in respiration, molting, and reproduction it was necessary to determine the body composition of the mysids, their molts, and their young. For these analyses the animals were captured alive and, within 2 hr, placed in a constant-flow holding tank at 15° to 17° C where they were kept for a short time prior to analysis.

BODY COMPOSITION

The estimates of body composition of dried animals and molts are summarized in Table 3. The estimates for ash, protein, lipid, carbohydrate, and chitin are not considered to be accurate past the first decimal point. The fractional percentage values are entered so that the sums will equal 100 %. The methods by which these values were determined will be explained item by item.

To determine dry weights, the animals were washed very briefly with distilled water while still alive, then were oven-dried to constant weight at 60° C. Materials that were available only in small quantities were weighed on a Cahn electrobalance.

Ash

Ash content was estimated by incinerating

TABLE 3.—Average composition and energy content of dry *Metamysidopsis* bodies, molts, eggs, and larvae. Tabulated values for composition are %, and for energy content are cal/mg. The sums of % ash, "protein", lipid, carbohydrate and chitin = 100 %.

	Nitrogen	Carbon	Ash	"Protein"[1]	Lipid	Carbohydrate	Chitin	Energy
	%	%	%	%	%	%	%	*Cal/mg*
Body, whole	11.5	36.8	12.5	69.0	10.0	1.5	7.0	4.60
Body, organic	13.2	42.0	0	79.0	11.4	1.6	8.0	5.24
Molt, whole	--	23.5	44.8	30.9	0	0	24.3	2.48
Molt, organic	--	42.5	0	56.0	0	0	44.0	4.49
Egg, whole	--	58.0	6.0	35.2	58.8	0	0	7.16
Egg, organic	--	61.8	0	37.5	62.5	0	0	7.62
Larva, whole	--	45.7	6.6	60.8	28.9	0	3.7	5.78
Larva, organic	--	48.8	0	65.0	31.0	0	4.0	6.20

[1] "Protein" may include free amino acids.

whole animals or molts in a muffle furnace at 500° C and weighing the residue. Ash determinations were made on six samples composed of mixed animals, juveniles, immatures, adult males, and adult females. The samples contained from 2.7 to 7.3 mg of dried animals; the mean ash content was 12.5 % of the dry weight, and the range was 9.4 to 13.3 %. There was no obvious difference between age groups or sexes. This ash content is within the range, but slightly higher than the mean, of values reported for other Mysidae: *Mysis flexuosa* — 16 % (Hensen, 1887) and 11.9 % (Delff, 1912, quoted by Vinogradov, 1953); *Neomysis integer* — 7.9 % (Raymont, Austin, and Linford, 1964); *Siriella aequiremis* — 10.2 % (Omori, 1969).

Molts used for ash determinations were collected in the laboratory immediately after they were shed. Two samples, weighing 1.1 and 0.6 mg, composed of molts from a wide size range of mysids of both sexes had ash contents of 44.4 % and 45.7 %; the mean was 44.8 %. Lasker (1966) reported a similar value (46 %) for *Euphausia pacifica*. This high ash content in the molts suggests that a large fraction of the total body ash resides in the integuments of the whole animals. From 10 observations, we have found that the dry weight of the molt is on the average 13 % of the dry weight of the animal that sheds the molt. Assuming that the ash content of the molt is the same as the ash content of the integument of the whole animal, we estimate that 47 % of the body ash resides in the integument.

Ash content of brood pouch young was estimated from a large number of specimens taken from live females. A dry sample of 0.6 mg of newly hatched larvae had an ash content of 6.1 %. A sample of 1.2 mg of late stage larvae had an ash content of 6.6 %. Ash content of eggs was not determined; we assume that the ash content is slightly less than that of the newly hatched larvae, and we have used a value of 6.0 %.

Nitrogen and Carbon

Nitrogen content was determined by the micro-Kjeldahl method from three samples of mixed juvenile-adult animals. The dry weights of the samples were 12, 24, and 63 mg, and contained 13.1 %, 11.7%, and 11.2 % nitrogen respectively; the mean was 11.5 % of total dry weight. From a large number of determinations, Raymont et al. (1964) found a value of 11.4 % for *Neomysis integer*. Omori (1969) reported 11.0 % for *Siriella aequiremis,* and Jawed (1969) found 11.9 % for *Neomysis rayii.*

Carbon content was determined with an F and M carbon analyser model 180, described by Lasker (1966). We assume that all organic carbon, including that in chitin, is liberated by this method.

Three samples of females, without young, that weighed 0.2 to 0.4 mg, had carbon fractions between 35.6 % and 38.1 % of dry weight; the mean was 36.8 %. This estimate is intermediate among other values reported for mysids: *Lophogaster* sp. (family Lophogastridae) — 46.8 % (Curl, 1962a); *Neomysis integer* — 30.2 % and 29.5 % (Raymont et al., 1964, 1966); mixed mysids and euphausids — 40.7 % (Beers, 1966); *Siriella aequiremis* — 42.4 (Omori, 1969). From his analysis of several kinds of arthropods, Curl (1962a) found an average of about 38 % of the dry weight as carbon. He points out that this is about ¾ of the commonly assumed value of 50 % (Krogh, 1934).

In our carbon analysis of molts and young, we found that a 0.2-mg sample of fresh dried molts had 23.5 % carbon, a 0.4-mg sample of eggs had 58.0 % carbon, a 0.4-gm sample of midstage larvae had 47.1 % carbon. The carbon contents of the ash-free organic fractions of the material were calculated from these values. Lasker (1966) found 17 % carbon in the molts of *Euphausia pacifica* and 50 % carbon in the eggs.

Macromolecular Components

We assume that the body nitrogen of our species, *Metamysidopsis,* is present as protein, free amino acids, and chitin (Raymont, Austin, and Linford, 1968). We made no evaluation of chitin content, but used the value of 7 % determined for *Neomysis integer* by Raymont et al. (1964). The percent "protein" (may include free amino acids) was estimated by the following relationship, given that 16 % of "protein"

is nitrogen, 6.5% of chitin is nitrogen, and 7 % of the dry body is chitin: 0.16 ("protein") + (0.065) (0.07) = 0.115. From this relationship, the "protein" content of the whole dry body was estimated to be 69 %, which is similar to the value to 71 % protein estimated directly by Raymont et al. (1964) for *Neomysis integer*. According to the estimates of Raymont et al. (1968), the percent nitrogen in proteins of Mysidae may be lower than the value of 16 % commonly assumed for animal tissues. They found 13.3% N in the body protein of *Neomysis integer*, and estimated that about 17 % of what we would have designated as "protein" nitrogen was actually free amino acid nitrogen. They suggest that the amino acids may function in osmoregulation for *Neomysis integer*, which is a euryhaline-brackish water species. We know nothing directly about this for *Metamysidopsis*. Our species lives in a constant oceanic salinity, and we estimated the ash content to be higher than that of *N. integer*. Therefore, a high concentration of free amino acids may not be necessary for osmoregulation in our species. Whatever the ratio of protein/free amino acids may be in *Metamysidopsis*, our energy calculations should not be affected materially.

The lipid content of the mysid bodies was estimated by placing samples of dried, crushed bodies successively for 1 hr in each of two 10-ml portions of ethyl alcohol and two 10-ml washes of petroleum ether. The lipid content was estimated as the difference in dry weight before and after extraction. Two dry samples of mixed animals, weighing 62.9 mg and 13.4 mg, gave values of 9 % and 11 % lipid respectively. A third sample, containing 24.1 mg of brooding females that had full complements of young in their brood pouches, gave a value of 19 % lipid. Linford (1965) found that large females of *Neomysis integer* carrying young had higher lipid contents than males. From our knowledge of the number of young per female and the estimated percent lipid in the young, we calculate that ¼ to ½ of the 19 % lipid value could be contributed by the brood pouch young. Therefore, we have excluded the 19 % value from our estimate, and we have used 10 % as the estimate of average lipid content of the dry bodies. This is slightly less than the value of 13 % estimated for *Neomysis integer* by Raymont et al. (1964), but within the range of means for three species estimated from a large number of determinations by Linford (1965): *Mesopodopsis slavveri* — 9.0 %; *Neomysis integer* — 10.1 %; *Praunus neglectus* — 9.3 %.

The carbohydrate content of the mysids was estimated as the amount of macromolecular material remaining after the average estimates for ash, protein, chitin, and fat are subtracted from the dry weight. This remainder is 1.5 %. Apparently the carbohydrate fraction is low in all pelagic Crustacea. Raymont and Conover (1961) found that 1 % of the dry weight of *Neomysis americana* was glucose; Raymont and Krishnaswamy (1960) found 1.3 % carbohydrate in dry *Neomysis integer;* and Raymont et al. (1964) found 2.4 % carbohydrate in dry *Neomysis integer*.

We did no detailed analyses of the composition of molts, but we assume that the molt is composed of structural materials rather than energy storage materials. Since we consider that carbohydrates and lipids are virtually absent, we entered zero values for them in Table 3. The "protein"/chitin relationship was determined indirectly. First, we estimated the amount of carbon in the average protein of the mysids from the relationship:

$$\begin{aligned}(\%\ \text{C as protein}) = {} & (\%\ \text{C in body}) \\ & - (\%\ \text{C as chitin}) \\ & - (\%\ \text{C as lipid}) \\ & - (\%\ \text{C as carbohydrate}).\end{aligned}$$

The percent carbon in the organic fraction of the body is 42 %, the chitin fraction is taken as 8 %, the chitin is assumed to be 50 % carbon (Curl, 1962a), the lipid content of the organic fraction is 11 %, the lipid is assumed to be 77 % carbon (Lasker and Theilacker, 1962), the carbohydrate fraction is about 2 %, and the carbohydrate is assumed to be 40 % carbon (Curl, 1062a). Therefore, the percent carbon in the

mysid protein is calculated as:

$$\% \text{ C} = \frac{1}{0.79}[0.42 - (0.08)(0.50) - (0.11)(0.77) - (0.02)(0.40)]$$
$$= 0.364$$
$$= 36.4\ \%$$

This is considerably less than the average value of 52 % carbon in protein given by Hawk, Oser, and Summerson (1954), but similar to an estimate of 37 % made from the data of Lasker (1966), and higher than an estimate of 23 % made from the data of Raymont et al. (1964).

The second step in finding the relationship between chitin and protein in the molts was to estimate the chitin fraction from the following relationship:

(chitin fraction) (% C in chitin) + (protein fraction) (% C in protein) = (% C in molt)

where

chitin fraction + protein fraction = 1.0.

The chitin fraction calculated from this relationship is 44 % for the organic molt. The protein fraction is therefore estimated to be 56 %. This result suggests that a large fraction of the chitin may be reabsorbed by the animals before molting. This seems reasonable because in Crustacea the new endocuticle is formed during the intermolt period (between 2 % and 46 % of the time between molts, according to Passano, 1960).

To estimate the protein content of eggs and larvae, we have made some arbitrary assumptions that seem reasonable, and that do not measurably affect our energy calculations in any event. We have assumed that the eggs do not contain a measurable amount of carbohydrate, and that they contain little or no chitin because the integument is not yet formed. Therefore, we have assumed that the organic fraction of the eggs is either protein or lipid. For late stage larvae we have also assumed that carbohydrate is absent, but that some chitin is present because they form integument and molt once before they are released. We have assumed that the organic fraction of the larvae contains half the amount of chitin as the adults, or 4 %.

The protein-lipid composition of the eggs was calculated from the carbon content of the ash-free fraction. We have estimated (above) that 36.4 % of the mysid protein is composed of carbon, that 77 % of the lipid is carbon, and that 61.8 % of the ash-free egg is carbon. By using these values we calculate that the organic fraction of the eggs is 62.5 % lipid and 37.5 % protein. The carbon content of intermediate age brood pouch young (about 5 days old) was less than that of eggs and more than that of late stage larvae. For these intermediate age young we calculate a lipid content of 43 %.

ENERGY CONTENT

Juveniles - Adults

The ash-free calorie content of *Metamysidopsis* was determined in a Parr non-adiabatic calorimeter. The data, converted to ash-free values, are given in Table 4. Three of the samples contained so little material that Nujol supplement had to be added to raise the heat of combustion to a measurable level. All three of these measurements fell outside the 95 % confidence limits of the six determinations made without the Nujol supplement. The variability among the three supplemented determinations can be attributed to the ± 2 % variation of the caloric content of the Nujol supplement (10,791 ± 200 cal/g), because the weight of the supplement greatly exceeded the weight of the sample material in each case.

TABLE 4.—Ash-free[1] caloric content of *Metamysidopsis*.

Specimens	Dry weight	Calorie content
	Mg	*Cal/g*
Young juveniles	1.05	[2]3028.9
Juveniles	2.65	[2]6462.6
Young females	4.80	[2]4242.3
Advanced juveniles	12.55	5021.7
Immature males	17.30	5049.0
Immature males	17.30	5358.0
Mature males	15.75	5123.8
Mature females	12.40	5185.7
Mature females	17.25	5699.1

[1] Ash content 12.5 % used in all calculations.
[2] Nujol supplement used in determinations.

The mean for the six nonsupplemented samples is 5,240 cal/g (shown as 5.24 cal/mg in Table 3). No significant differences in energy content among developmental stages nor between sexes were found.

This mean calorie content estimate is somewhat lower than those reported for other crustacea. Slobodkin and Richman (1961) gave values of 5.4 to 5.6 cal/ash-free mg; Lasker (1965) reported a range of 4.9 to 5.4 cal/mg (including ash) for two species of copepods. Our mean value is also lower than the value that can be calculated from the information on body composition, together with reported average values of the calorie content of animal protein, fat, and carbohydrate. Conversion factors given by Morowitz (1968) are: protein, 5.5 cal/mg; fat, 9.3 cal/mg; and carbohydrate, 4.1 cal/mg. Since chitin is glucosamine, we have assumed that it, like carbohydrate, has a calorie content of 4.1 cal/mg. From these conversion factors and the composition data given in Table 3, we calculated an expected value of about 5.77 cal/ash-free mg.

We use the empirical value, 5.24 cal/ash-free mg, in our subsequent energy budget calculations. We consider this to be a conservative estimate, because it assumes that the mysid protein has an energy content of only 4.8 cal/mg. This lower than expected estimate may be related to the empirical observation that the mysid protein contains only 36 % carbon, rather than about 50 % as is commonly assumed for animal protein.

The juvenile and adult *Metamysidopsis* contained 12.5 % ash; therefore, the energy in the whole dry body of an adult or juvenile is estimated to be: (4.6 cal/mg) × (dry weight, mg).

Molts

We estimated the energy content of molts indirectly, because it was difficult to obtain enough material for calorie measurements. The ash-free fraction (55 %) of the molts was estimated to be composed of 44 % chitin and 56 % protein. By assuming that chitin has an energy content of 4.1 cal/mg, and that the mysid protein has an energy content of 4.8 cal/mg, we calculate that the ash-free fraction of the molts has an energy content of 4.5 cal/mg.

From a sample of 10 animals and their molts we found that the dry weight of molts is on the average 13 % (range 9-19%) of the dry weight of the animals that shed them. Lasker (1964, 1966) and Jerde and Lasker (1966) found that the dry molts of a euphausiid were about 10 % of the dry weight of the animals that produced them (range 4-14 %).

The energy lost by molting *Metamysidopsis* is therefore proportional to the size of the animal:

$$(0.13)(0.55)(4.5 \text{ cal/mg}) \times (\text{dry weight of animal, mg})$$

or

$$(0.32 \text{ cal/mg}) \times (\text{dry weight of animal, mg}).$$

Eggs and Larvae

We estimated that eggs were 6 % ash, 35 % protein, and 59 % lipid. The energy content of an egg is estimated to be: (0.35) (4.8 cal/mg) + (0.59) (9.3 cal/mg) = 7.16 cal/mg. A sample of 140 eggs was dried and weighed; the mean dry weight per egg was 0.0055 mg. The energy content per egg is therefore 0.039 calorie.

We estimated that, just before being released from the brood pouch, the larvae are about 6 % ash, 61 % protein, 29 % lipid, and 4 % chitin. The energy content of a late stage larva is estimated to be: (0.61) (4.8 cal/mg) + (0.29) (9.3 cal/mg) + (0.04) (4.1 cal/mg) = 5.78 cal/mg. The mean dry weight per larva, estimated from 110 individuals, was 0.0051 mg. The energy content per larva is therefore 0.029 calorie.

ENERGY BUDGET AND EFFICIENCY OF ENERGY TRANSFER

From the data on average growth, age-specific fecundity, respiration rate, and energy content we have calculated cumulative curves of energy use by individual mysids in attaining various stages of development. Data on age-specific natural mortality rates (Fager and Clutter 1968) were used to estimate l_x (probability

of animal being alive at age x) schedules and average generation time of the field population. The field and laboratory data were combined in an analysis of the efficiency of energy transfer through the *Metamysidopsis* population to the organisms that feed on them.

CUMULATIVE ENERGY CURVES

At age zero the egg contains about 0.04 cal. Ten days later, at the time it is released from the brood pouch, the larva contains about 0.03 cal. Thereafter the average calorie content increases in proportion to the dry weight (4.6 cal/mg). The average schedules of energy incorporation differ between males and females after about 30 days; the rate of incorporation becomes lower and levels off sooner in males. The accumulation of body energy is shown as the lowest curves in Figure 12 (females) and Figure 13 (males).

The amount of energy lost in molts varies with age because the size of the molt increases and the molting frequency decreases. Females and males have different cumulative losses of energy from molting because their growth rates are different after age 30 days, and their molting frequencies are different (Table 1.) Although the actual loss of energy in molting occurs at discrete intervals, we have plotted the cumulative energy loss as smooth curves, because the accumulation of energy for integument formation probably is continuous. Cumulative energy loss in molting is shown as the second curve in Figure 12 (females) and Figure 13 (males). The cumulative energy curves are additive, i.e. the area between the first curve (body energy) and second curve (molting energy) represents the cumulative energy loss in molts.

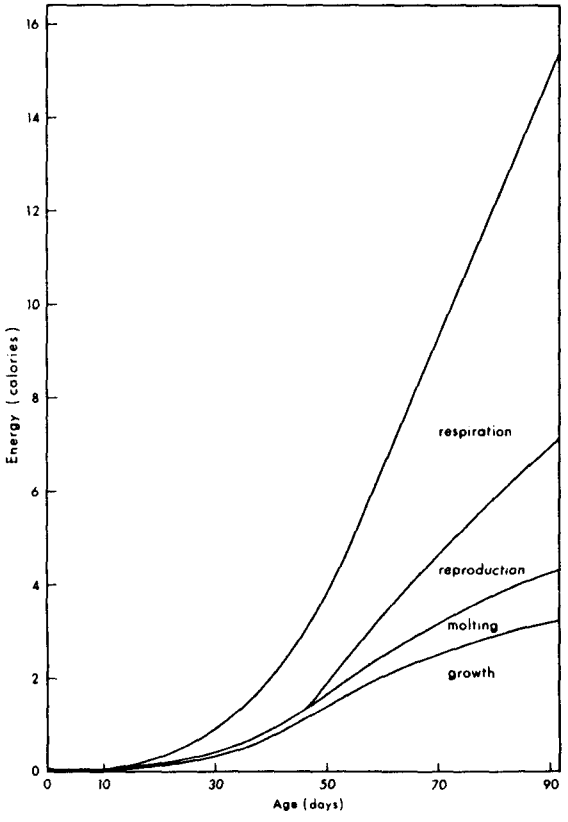

FIGURE 12.—Cumulative energy used by individual *Metamysidopsis* females. The curves are additive, i.e. the space between the lower two curves represents the cumulative energy lost in molts, the next higher space represents energy used to produce eggs (both fertilized and unfertilized), etc.—so that the upper curve represents cumulative energy used for all processes.

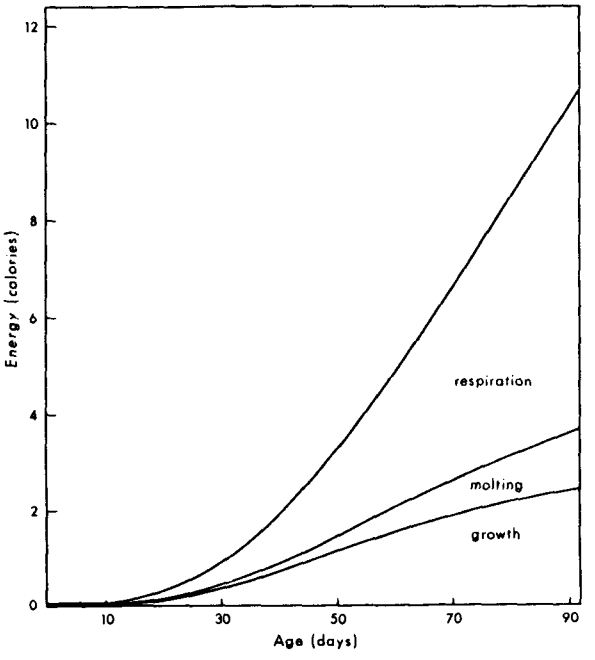

FIGURE 13.—Cumulative energy used by individual *Metamysidopsis* males. The curves are additive (see Fig. 12).

Males use a small amount of energy in producing sperm, but we assume that this is negligible. In females, the ova begin to be infused with yolk about age 45 days. The actual discharge of eggs occurs at discrete intervals of about 10 days, beginning at age 53 days. We assume that the accumulation of energy for reproduction is more continuous than this, therefore we have shown reproductive energy use as a smooth curve. The reproduction energy curve shown in Figure 12 is based on the maximum fecundity estimate given previously [number of eggs = 4.1 (body length, mm) — 8.9]. A reproduction energy curve based on our minimum estimate of fecundity [number of eggs = 4.1 (body length, mm) — 12.0] would be 0.12 cal (3.1 eggs) lower per spawning. This would make the minimum estimate 72 % of the maximum estimate at the age of first spawning (53 days) and progressively higher in percentage thereafter, e.g. 85 % at the age of fifth spawning (93 days). All our reproduction energy calculations take into account the observation that, on the average, mature females extrude the usual number of eggs only one-half of the time and otherwise extrude only one-half the usual number of eggs.

The amount of energy used in respiration was calculated from the weight-specific respiration equation: $R' = 2.1$ (dry weight, mg) $^{-0.33}$, and from energy conversion factors based on our estimates of body composition.

We do not know what substrate *Metamysidopsis* catabolizes. The organic fraction of the body is largely protein; the storage product (carbohydrate and lipid) content is low. Raymont and Krishnaswamy (1960) observed that the carbohydrate content of *Neomysis integer* decreased slightly, from about 1.30 % (of dry weight) to 1.06 %, when a marked reduction in feeding occurred. For the same species, Linford (1965) found no significant change in lipid level whether the animals were starved, fed a lipid-free diet, or fed a high lipid diet. Raymont et al. (1968) asserted that *N. integer* uses protein as an energy source.

We agree with Linford (1965) that it seems likely that the mysids must live largely on their daily ingestion. We think that the food they ingest has composition similar to their bodies. Therefore, our energy calculations assume that they use catabolic substrates in proportion to their presence in the body. This is supported by the results of Jawed (1969). To convert the amount of oxygen used in respiration into the equivalent energy lost as heat we have used the following values for calories lost/μl O_2 consumed (Hawk et al., 1954; Prosser, 1950): protein, 4.5×10^{-3}; lipid, 4.7×10^{-3}; carbohydrate, 5.0×10^{-3}. Therefore, our estimate of the average amount of energy used in respiration is about 4.5×10^{-3}cal μl O_2.

The cumulative energy used in respiration is shown as the uppermost curve in Figure 12 (females) and Figure 13 (males). The area between that curve and the next lower curve represents the catabolic heat loss. These respiration data were calculated for a temperature of 16° C, which was the median temperature of the natural environment of *Metamysidopsis*. Our respiration measurements were made in flowing water during the daylight hours. Therefore, they represent basal metabolism + energy expended in active swimming. There is some evidence (Clutter, 1969) that the mysids may be less active at night, even though they continue to swim at all times. For this reason we think that the field population may use somewhat less than this amount of energy in respiration.

Our estimated rate of energy loss in catabolism is higher than that estimated by Jawed (1969) in his study of nitrogen excretion in *Neomysis rayii*. He suggested that protein is catabolized in relatively large quantities, therefore nitrogenous excretion may provide a good estimate of catabolism. He found an average catabolism of about 2.5 % of body nitrogen per day in adult animals that were probably 8 to 10 mg dry weight, that were held at 10° C. The rate for adult *Metamysidopsis* of average size (0.6-0.8 mg) was 5 to 6 % of the body energy per day. This disparity in catabolism may result from differences between the size and between the environmental temperatures of the two species.

Jawed (1969) showed that about 15 % of the nitrogen was excreted as amino acids. We did

not investigate this in *Metamysidopsis*, therefore, our estimate of total catabolism could be slightly low because it includes only losses of heat energy.

NET ECOLOGICAL EFFICIENCY

Mortality and Generation Time

Estimates of natural mortality in the field population were made during the same period that the laboratory growth experiments were done (Fager and Clutter, 1968).

Brood pouch mortality rate was estimated to be 0.013/day (maximum of 0.017/day). Mortality rates for juveniles, immatures, and adults were estimated from consecutive series of field collections. The field mortality rates varied during the year. Survival curves (l_x = probability of being alive at age x) for periods of at least mortality, median mortality, and greatest mortality are shown in Figure 14. The mortality rates that we used to calculate these l_x curves are shown in Table 5. The greatest mortality rate results in a declining population; at the median mortality rate the population size remains about constant; and at the least mortality rate the population increases.

An average female first reproduces at about age 53 days. The generation length for the population is somewhat longer because the females reproduce more than once. The generation length for the field population varied between 67 days and 71 days; the median was 68 days (Fager and Clutter, 1968).

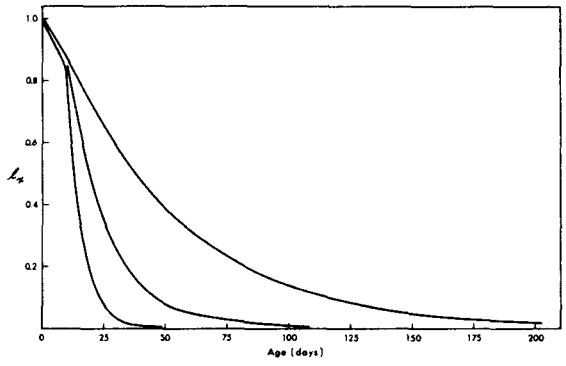

FIGURE 14.—Age specific survival (l_x = probability of being alive at age x) of *Metamysidopsis* calculated from estimates of greatest, median, and least mortality in the field population (Table 5).

TABLE 5.—Mortality rates (per day) used to calculate l_x schedules for the *Metamysidopsis* field population.

Specimens	Least mortality	Median mortality	Greatest mortality
Brood pouch young	0.013	0.013	0.017
Juveniles	0.02	0.06	0.15
Immatures	0.02	0.05	0.14
Adults	0.02	0.04	0.13

Relative Energy Use by Individuals

We determined the calories of energy used by average individual female and male mysids, and the fractions used for growth, molting, reproduction, and respiration from the estimates of cumulative energy use (shown in part in Figures 12 and 13). The amounts and the percentage distributions required to reach selected stages of development are shown in Table 6.

TABLE 6.—Energy used by individual *Metamysidopsis* to reach selected stages of development.

	Age	Energy	Relative use			
			Respiration	Reproduction	Molting	Growth
	Days	*Cal*	*%*	*%*	*%*	*%*
Females:						
Egg yolk production	45	2.7	52	0	8	40
First reproduction	53	4.6	49	9	7	35
Generation	68	8.7	50	15	7	28
l_x = 0.01	[1]103	18.4	55	19	7	19
Males:						
Maturity	48	3.0	54	0	10	36
l_x = 0.01	[1]103	12.8	67	0	12	21

[1] *Approximate age at which l_x = 0.01 in a nearly stable population ($r \sim 0$).*

The indicated age at which the probability of being alive reaches 0.01 applies to the stable population (median death rates).

The males require less energy to reach maturity than females, but relatively more of this energy goes into molting and respiration and less is incorporated. Two-thirds of the energy used in reproduction remains in the population; one-third is lost as unfertilized eggs.

The estimates of relative use of assimilated food by *Metamysidopsis* females during a life span are compared with estimates for a copepod and a euphausid (Corner, Cowey, and Marshall, 1967) in Table 7. The mysids apparently use a fraction of assimiliated energy for growth that is intermediate between the other two species, a lower fraction for metabolism, and a higher fraction for producing eggs.

TABLE 7.—Use of assimilated food by *Metamysidopsis* females (life span 103 days) compared with the copepod *Calanus finmarchicus*[1] (life span 10 weeks) and the euphausid *Euphausia pacifica*[2] (life span 20 months).

	Assimilated energy used by *Metamysidopsis*	Assimilated N used by *Calanus*	Assimilated C used by *Euphausia*
	%	%	%
Growth	19	25.3	10.1
Metabolism	55	61.4	72.3
Molts	7	0.9	16.6
Eggs	19	12.4	1.0

[1] From Corner, Cowey, and Marshall (1967).
[2] From Lasker (1966), revised in Corner et al.

Relative Energy Use by the Population

The values of relative energy use given in Tables 6 and 7 apply to individuals, or to populations wherein all members live a full life span. They do not apply to the natural population, because some die during all stages of growth.

We have estimated the relative amounts of energy that would be lost by populations in respiration, production of infertile eggs, molting, and mortality at the observed minimum, median and maximum mortality rates shown in Table 5. This was done by calculating the fraction of the population that died during each intermolt period (Δl_x), and multiplying this times: (1) the mean body energy content for the midpoint of that period, (2) the quantity of cumulative energy lost in infertile eggs up to the midpoint of that period, and (4) the quantity of cumulative energy used in respiration up to the midpoint of that period. The product values for each of these loss categories (mortality, molting, etc.) were then summed over all ages (to $l_x \sim 0.001$). The relative energy use values were calculated as fractions of the overall sum for all categories combined. We excluded fertilized eggs because this reproduction energy is retained in the population.

The age specific distribution of energy use (representing energy loss, because fertilized eggs are excluded) by a population (females and males) of *Metamysidopsis* at the median mortality rate is illustrated in Figure 15. All the curves are plotted with reference to the base line, zero. The rate of energy loss is low among eggs and larvae, and much higher among the juveniles that have just emerged from the brood pouch and begun to swim. In the larger animals, the respiration per unit weight is lower, but the respiration per animal is higher, so that the respiration rate per day is highest among the animals that are about 25 days old. The loss of energy per day from all causes is highest among the animals that are about 30 days old. After this the curve declines because the effect of larger size becomes less than the effect of smaller numbers.

The estimated relative amounts of energy lost by the population of females, males, and both sexes combined, for each loss category and

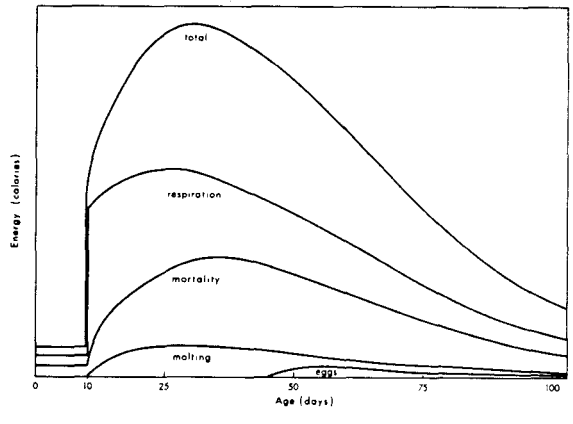

FIGURE 15.—Age specific distribution of energy loss by a *Metamysidopsis* population at the median mortality rate. Production of fertilized eggs is excluded.

for each of three mortality rates, are shown in Table 8. The percentages for females and males combined are not quite the same as the means of the separate percentages for females and for males. At the minimum death rate 55 % of the energy loss would pass through the female half of the population (58 % if fertile eggs are included). At the median death rate 52 % would pass through the females, and at the maximum death rate, 50 %.

TABLE 8.—Relative amount (%) of energy lost by *Metamysidopsis* populations in respiration, production of infertile eggs, molting, and mortality; at minimum, median and maximum mortality rates.

Sex	Death rate	Respiration	Infertile eggs	Molting	Mortality
		%	%	%	%
Females	minimum	63.7	6.7	8.6	20.9
	median	55.6	3.7	7.7	33.0
	maximum	45.4	0.1	6.1	48.4
Males	minimum	67.4	0.0	12.6	20.0
	median	58.3	0.0	9.9	31.8
	maximum	47.9	0.0	6.5	45.6
Females and Males	minimum	64.5	3.7	10.4	20.5
	median	56.9	1.9	8.8	32.4
	maximum	46.7	0.1	6.3	47.0

If we assume that all the mortality is yield to predators (Odum and Smalley, 1959; Engelmann, 1961), our mortality fractions are an estimate of net ecological efficiency (energy yield/energy assimilated). Apparently some Crustacea regularly die from natural causes other than mortality (e.g. *Daphnia*, Slobodkin, 1959). Many mysids of all ages died in our laboratory cultures, but we do not attribute this to senescence. In the field and in the laboratory we observed *Metamysidopsis* much older than the oldest animals that are involved significantly in our energy calculations. Our best estimate of the net ecological efficiency of the mysid population, for transfer of energy to a higher trophic level, such as fishes, is about 32 %. The net efficiency of transfer to all trophic levels is 1 — respiration fraction = 43 %.

ASSIMILATION AND GROSS ECOLOGICAL EFFICIENCY

Assimilation Efficiency

Gross ecological efficiency (energy yield/energy ingested) is the product of net ecological efficiency (energy yield/energy assimilated) × assimilation efficiency (energy assimilated/energy ingested). Therefore, an estimate of assimilation efficiency is required to estimate gross ecological efficiency for the mysid population.

We attempted to estimate the assimilation efficiency of *Metamysidopsis* directly by a carbon-14 method described by Lasker (1960). This failed because the mysids did not filter sufficient amounts of radioactive phytoplankton. An experiment with another member of the family Mysidae, taken from the same area, was successful. This gave an estimate of 90 % assimilation efficiency.

Lasker (1966) obtained a similar high value (84 %) for the morphologically similar *Euphausia pacifica;* and Marshall and Orr (1955) found values greater than 90 % for the copepod *Calanus finmarchicus.* In his detailed reviews of assimilation in zooplankton, Conover (1964, 1966) suggests that these values probably are too high. The very large number of observations, many of them his own, that are cited by Conover seem to be evidence that, although variable, the mean assimilation efficiency for crustacean zooplankton is at least 60 % and perhaps greater.

Gross Ecological Efficiency

From the information presently available we consider that the assimilation efficiency of the mysids is between 60 % and 90 %. Our best estimate of net ecological efficiency (yield/assimilated) is 32 %. Therefore, the minimum estimate of gross ecological efficiency (yield/ingested) is 19 % and the maximum estimate is 29 %.

These estimates are well within the broad range of available estimates of gross ecological efficiency (see reviews by Patten, 1959; Slobodkin, 1961; Phillipson, 1966; Reeve, 1966), and within the range of 8 % to 30 % that Engelmann (1961) considers to be acceptable. They are about 2 to 3 times as high as the median value of 10 % that is suggested by Slobodkin (1961, 1962), but lower than the values of 30 % to 50 % suggested for marine zooplankton by

Ketchum (1962), Steemann Nielsen (1962), and Curl (1962b).

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