

ENERGY BUDGETS¹

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ABSTRACT

Introduction

Assuming that the functioning of ecosystems can best be described in terms of energy flow and nutrient cycling, it is prediction and manipulation relative to these two functional aspects which holds the greatest promise in the area of ecosystem management. Energy budgets for ecosystems--that is, how much energy is required per unit time to operate a system and how is the energy apportioned between the various components--can be prepared by summation of data at the level of populations. Such assessments seem more useful than monitoring total energy flow, e. g. light income = heat output. Even though our apparent goal is the management of ecosystems, there will probably be no instances in which this will be of interest independent of manipulations of specific populations within the system.

The energy flow diagram shown in Fig. 1 illustrates some of the summations and rate functions to be determined in estimating a budget at the ecosystem level. The model shown is for a semi-controlled stream, but the essentials of the macroconsumer portions would be the same for all natural lotic systems. The herbivore, detritivore and carnivore categories shown in Fig. 1 would be calculated by summation of all populations (or portions of populations - see below) fitting each of the three designations. Fig. 2 represents a budget for a natural population of a benthic stream macroconsumer. Both the summation of energy expenditures in various "compartments" and the transfer rates between components are depicted.

Investigators which have produced energy budgets for invertebrate macroconsumers (e.g. Richman, 1958; Kuenzler, 1961; Phillipson, 1963; Comita, 1964; Woodland *et al.*, 1968; Cummins *et al.*, 1969) have not dealt with lotic organisms except for the work of Trama (1957).

Methods for Determining Energy Budgets for Lotic Macroconsumers

Since population energy budget determinations require the processing of extensive amounts of diverse data and a great many populations must be analyzed before a useful budget estimate at the system level can be obtained, automation

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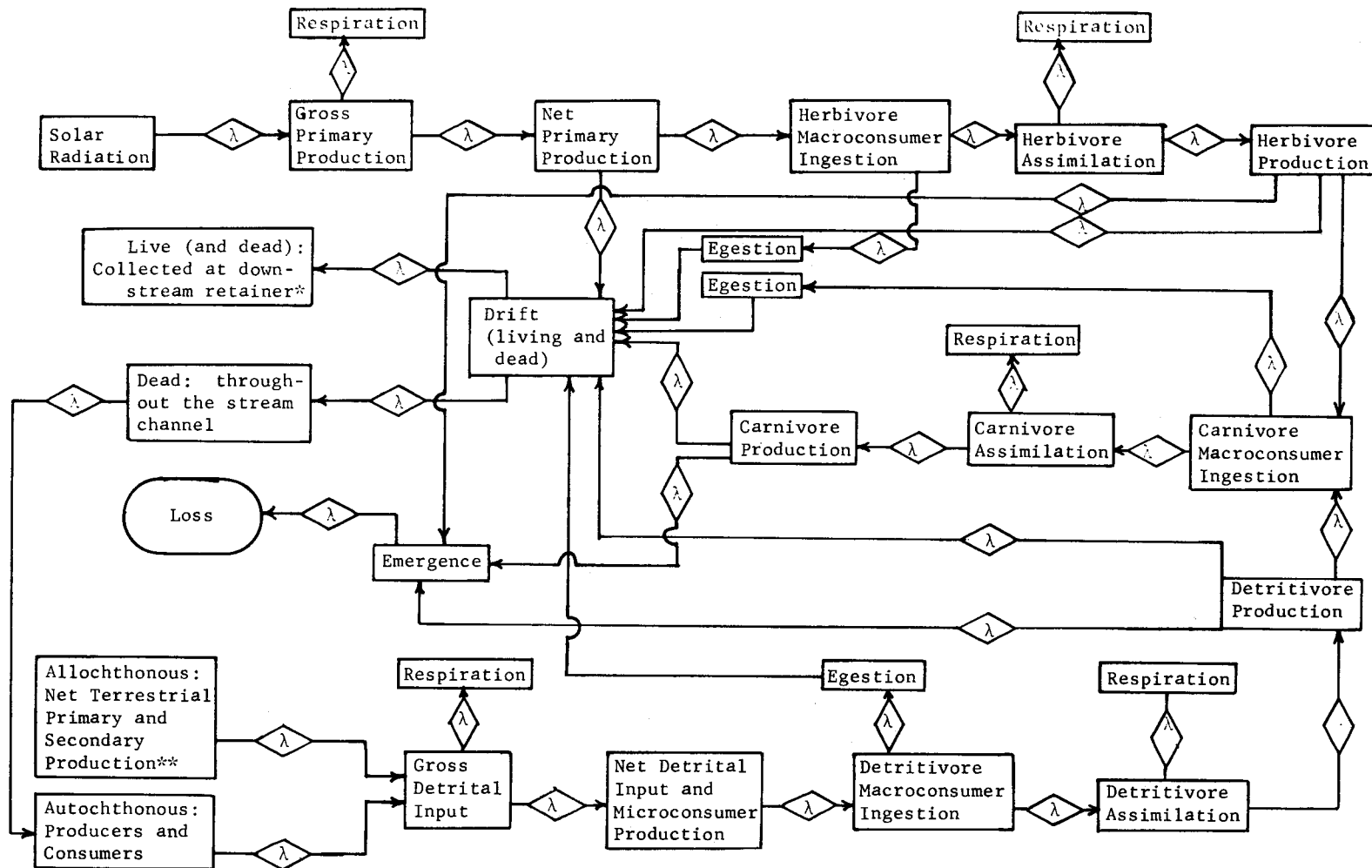


Fig. 1. Components of an annual energy budget for a semi-controlled stream ecosystem. The symbol λ stands for transfer rates. *Retainer contents reintroduced at upstream position on a regular schedule. **Added to system in known amounts.

of data gathering and analysis is critical. We are attempting to establish a standard processing package for determining such energy budgets, as summarized in Fig. 3. The aim is to obtain data output in the form of punch tape which can be processed by computer terminal utilizing standard routines kept on file. Reduced handling of the data and computer manipulation not only increases the volume of data that can be processed, but significantly reduces errors. Particularly useful are subroutines that sort out aberrant pieces of data which violate previously set limits.

Ingestion and Egestion

In order to determine instantaneous ingestion, representatives of each size class of a given species are dissected and the gut contents concentrated on Millipore filters for counting. Enumeration is in three categories, algae, detritus (including the microbial biota) and animals. The final result is an estimate, on a per individual basis, of the calorie content of the algal, detrital and animal components of the food in the gut.

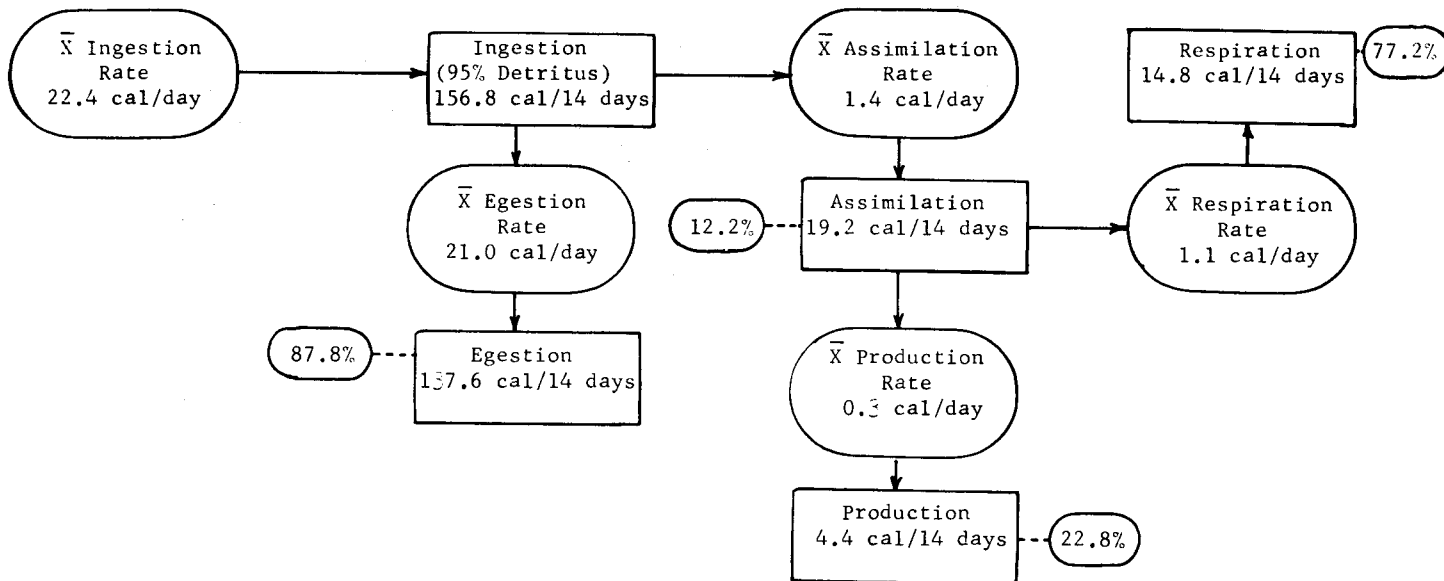
Based on these relative caloric ingestion of the three food categories, portions of the standing crop of each age class of a given species are assigned to herbivore, detritivore and carnivore trophic categories. Thus, organisms are placed in trophic categories on the basis of tissue support.

In addition to the tracer methods discussed below, ingestion and egestion rates are determined in the laboratory under controlled temperature conditions and with known diets. Leaf detritus from the stream (including the microflora) cut into discs with a cork borer, dried and preweighed, attached algae grown on preweighed cover slips and preweighed pellets made from prey species can be used as food material. Weight loss of food, weight gain of feeding animals and weight of feces produced, all per unit time, are measured directly. Collection of fecal pellets is particularly easy for species which produce a peritrophic membrane.

Assimilation (Tissue Incorporation)

The measurement of tissue incorporation using carbon-14 as a tag must take into account the nutritional history of the feeding organism and the biochemical composition of the food. In the normally functioning stream macroinvertebrate, assimilated products of carbohydrate digestion are probably utilized rapidly for respiration (maintenance cost), whereas fatty acids and glycerol from lipids, and amino acids from proteins are probably incorporated more permanently. That is, fat bodies and structural protein would result from anabolic processes, the energy expenditure of which is part of the maintenance cost. Animals which have been starved before the initiation of the experiment would be expected to behave differently with respect to incorporation and respiration of carbohydrate, fats and proteins.

Regardless of the method the intent is to measure the rate at which material entering the anterior end of the "plumbing" becomes incorporated into the tissues, or the assimilation rate as calories per time, and the efficiency of this incorporation per unit of ingested material. The latter allows for the conversion of ingestion data to an assimilation base. This is particularly important since



Stable Age Distribution

Sample	Age Class (%)							Total Number of animals measured
	1	2	3	4	5	Prepupae	Pupae	
7/23/69	0	0.56	5.08	14.40	27.68	24.29	27.96	354
8/6/69	0	1.17	8.23	14.11	27.12	23.50	27.05	85

Fig. 2. Components of an energy budget for a benthic stream macroinvertebrate, *Glossosoma nigrior* (Trichoptera)

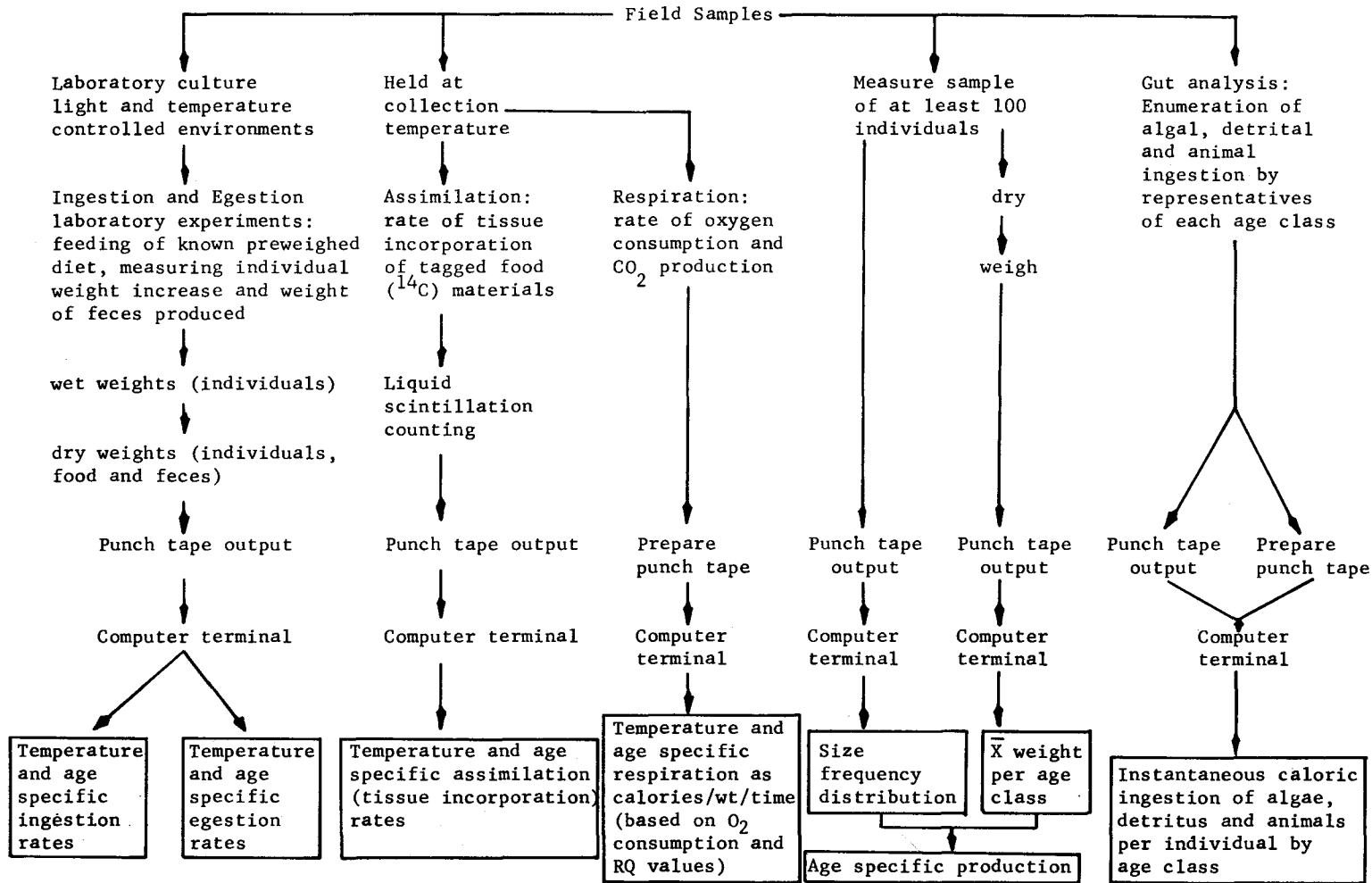


Fig. 3. General methods for the estimation of energy budgets for lotic benthic macroinvertebrates.

various food substances are undoubtedly assimilated with different per unit weight efficiencies.

Respiration (Maintenance Cost)

Maintenance cost for the population is estimated by gathering age and temperature specific data on individuals in the laboratory (e.g. with a Gilson differential respirometer) and projecting it to the entire population under a given set of conditions. Unfortunately, the literature is saturated with oxygen consumption values that are essentially useless to ecologists; they represent animals under stress conditions. It is probably accurate to assume that at any given temperature, unless the animals are dying, the lowest oxygen consumption value measured is the best representation of the natural condition. The age and nutritional state of the animals, the substrate available, water movement and light conditions are among the more important factors to be considered, all of which bear on the locomotory behavior of the organism.

Also, it is of little use for energy budget determinations to measure respiration rates at temperatures to which the organisms are never naturally exposed. Evidence is accumulating that many freshwater invertebrates exhibit maintenance cost plateaus. That is, over the range of temperatures normally encountered, the energetic cost to the organism is essentially constant.

Production (Growth and Reproduction)

The problem of production has already been discussed as part of this symposium. Suffice it to say that there are several ways of estimating biomass increments through time. Certainly of critical importance is the adjustment of the population census schedule so that it is equal to or less than the biomass turnover time. Our approach has been to determine numerical shifts in population age structure and utilize age-specific mean weights per individual in estimating production.

There are two components of production to determine: 1) the weight gain per individual between time 1 and time 2 multiplied by the number of individuals surviving to time 2 and, 2) the weight gain made by individuals not surviving the entire time 1 to time 2 interval. With regard to the second component, if all individuals are lost the instant following the initial census at time 1 the production to be added to the estimate, obtained as the first component, is zero. If all individuals are lost the instant before the census at time 2, the additional production would be the weight gain per individual over the period multiplied by the number of individuals lost (i.e. the number per unit area at time 1 minus the number per unit area at time 2). Actually, the loss is undoubtedly spread over the time interval, so that some median point may serve as a reasonable estimate. Thus production might be calculated as follows:

N_1 = number/unit area at time 1*

N_2 = number/unit area at time 2*

wt = weight gain/individual from time 1 to time 2

$$\text{Production} = (N_2)(wt) + \frac{1}{2}[(N_1 - N_2)(wt)].$$

(*Assuming no new recruitment over the period)

If "natural" or physiological death is negligible and the loss to predators has been assessed independently, then a more accurate estimate is possible. This sort of analysis can only be attempted when all major macroconsumer components of a stream system are receiving close scrutiny--a rare occurrence.

A Representative Short-Term Energy Budget
(Glossosoma nigrior:Trichoptera)

The intra-instar weight gains can be determined directly if a stable age distribution is approached, as shown for the 14 day Glossosoma nigrior budget in Fig. 2. Each census was based on three 900 cm² bottom samples in a small cold water Michigan stream (Augusta Creek, Barry County).

The rapid and accurate determinations of energy budgets for stream macroconsumers should form a critical facet of lotic ecosystem investigations. Such data, together with energy budgets for primary producers and microconsumers will allow for the assessment of ecosystem functioning necessary for predictive manipulation of stream communities.

A great deal remains to be done in the development and refinement of techniques (e.g. see Fig. 3), but particular attention should be directed toward standard methods for determining ingestion and assimilation rates. In order to obtain realistic rates and efficiencies of tissue incorporation, a great deal of information is needed on nutritional biochemistry of benthic stream macroconsumers and feeding habits under natural conditions.

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