PART IV: ASSIMILATION EFFICIENCY, EGESTION, AND EXCRETION OF ZOOPLANKTON AND BENTHOS

Introduction

203. Assimilation (A) is the food absorbed from an individual's digestive system. Assimilation efficiency (A/G) is the proportion of consumption (G) actually absorbed (Sushchenya 1969, Odum 1971, Wetzel 1975). Although the term A/G is usually used in reference to individual organisms, it also can be applied to populations. Egestion is food that is not assimilated by the gut and which is eliminated as feces (Pennak 1964). By contrast, excretion is a waste product formed from assimilated food and generally is eliminated in a dissolved form.

204. Energy flow refers to the assimilation of a population and is designated as the sum of production (P) and respiration (R), i.e., $A = P + R$ (Sushchenya 1969; Odum 1971). The efficiency of energy flow in a population, $\frac{P + R}{G}$, may be approximately equal to the assimilation efficiency of an individual in that population (Sushchenya 1969). However, since A/G often depends on age (Schindler 1968, Waldbauer 1968, Winberg et al. 1973, McDiffett 1970, Lawton 1970, Fischer 1972, Pilarska 1977b), the A/G of an individual may differ significantly from that of the population. Population A/G is essentially the mean A/G of the individuals composing the population and therefore depends on the age-class structure of the population. At the community level, the efficiency of energy flow through trophic webs ultimately influences the rates of fish production and eutrophication, both of which are important to man.

205. The importance of assimilation efficiencies in the modeling of zooplankton and benthos is paramount, particularly when models approach trophic dynamics by way of feeding equations. Assimilation efficiencies may be used in feeding equations to modify consumption and to yield the quantity of energy entering an individual or population. In most models, a constant A/G value is used to modify consumption (e.g. 0.70, Menshutkin and Umnov 1970; 0.70, Umnov 1972;

0.57, MacCormick et al. 1972; 0.80, Male 1973; 0.70, Steele 1974; 0.20, Thomann et al. 1975; 0.20 and 0.50, Scavia et al. 1976), but in other models A/G ratios were varied (e.g., 0.50 to 0.76, DiToro et al. 1971; 0.50 to 0.70, Baca et al. 1974; 0.64 to 0.90, Ross and Nival 1976). Assimilation was determined by the difference in consumption and the quantity: excretion (E) plus egestion (F), in models by Zahorcak (1974) and MacCormick et al. (1974). A potential drawback to this method is that literature data on E and F are relatively scarce. However, if assimilation efficiency and consumption data are used to estimate E and F, a fairly large data base is available in the literature. Assimilation efficiencies have been used to determine the quantity of matter or energy entering a detrital pool from egestion or excretion (Menshutkin and Umnov 1970, Patten et al. 1975, Swartzman and Bentley 1978). The difference in consumption (i.e., when G = 1) and A/G represents the fraction of consumption that is egested and excreted. We have used this method to estimate E and F losses from zooplankton and benthos.

206. Our approach to assimilation, egestion, and excretion was to tabulate A/G (Appendix C) and to set up frequency distributions of A/G and $\frac{F + E}{G}$ for potential model compartments (Figures 26-35). In doing so, we hoped to attain the largest possible data base and determine the degree of variation among values within potential model compartments. The following discussion primarily concerns assimilation efficiencies and factors influencing A/G. Because A/G and $\frac{F + E}{G}$ are additive inverse functions (i.e., $\frac{A}{G} + \frac{(F + E)}{G} = 1$), the discussion also indirectly applies to egestion and excretion (i.e., as A/G changes in response to environmental conditions, $\frac{F + E}{G}$ also must exhibit changes that are of equal magnitude but opposite in direction). Thus, Figures 26 and 27 are mirror images of Figures 34 and 35, respectively. Both A/G and $\frac{F + E}{G}$, from frequency distributions, are to be used as multiplicative modifiers of consumption to yield the quantities of carbon assimilated and lost, respectively.

207. Energy equations of individuals or populations are essential to a thorough understanding of assimilation efficiency. A complete energy equation may be expressed as:

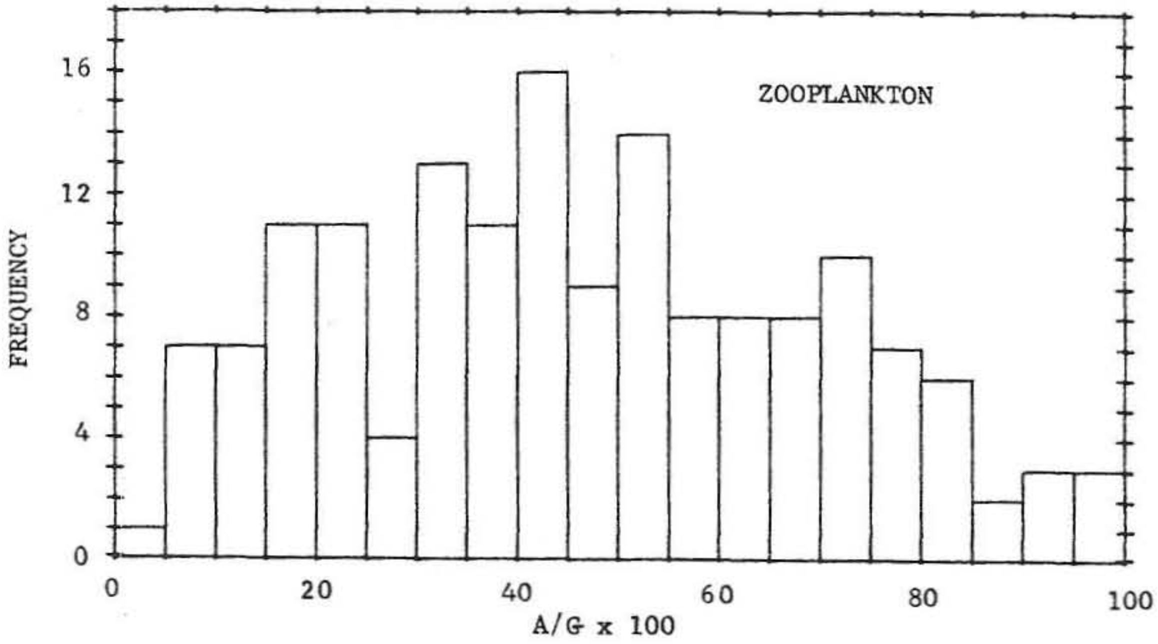

Figure 26. Frequency histogram of zooplankton assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

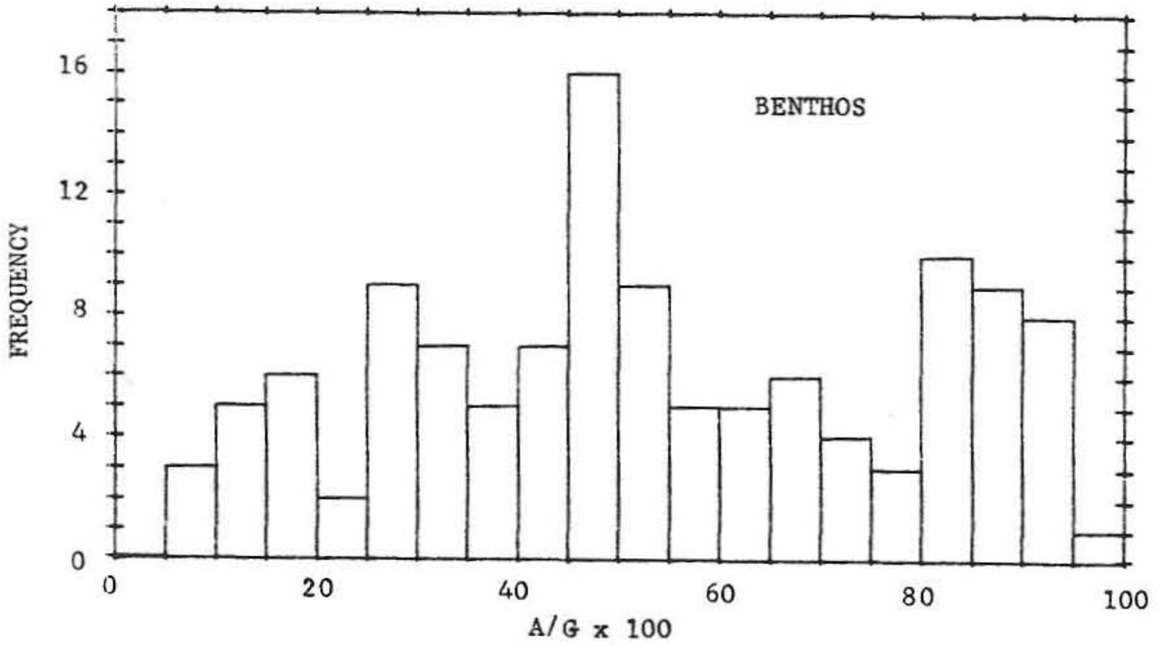

Figure 27. Frequency histogram of benthos assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

$$G = P_{(g + r + ev + s)} + R + F + E \qquad (18)$$

where G = consumption; P = production, elements of which are growth (g) reproduction (r), exuvia (ev), and secretion (s); R = respiration; F = egestion; E = excretion. Assimilation efficiencies can be estimated in two ways from the basic energy equation, i.e., $\frac{A}{G} = \frac{P + R}{G}$, and $\frac{A}{G} = \frac{G - F - E}{G}$.

208. In the last two decades, radioactive-isotope methods that directly measure uptake have been applied (see Appendix C for a tabulation of methods). These methods use radioisotope movements to evaluate energy parameters in Equation 18. Conover (1966a) developed an ash-ratio method that did not require quantitative measurements of G and F. All methods have technical problems, and results produced by the various methods are often far from similar (Conover 1966a, Streit 1976, Pechen'-Finenko 1977). To better understand why the assimilation efficiencies cited in the literature are so variable (ca 2 to 99 percent, Figures 26 and 27), we have examined the methods and environmental factors which influence them.

Methodology

209. One of the earliest methods was to evaluate:

$$\frac{A}{G} = \frac{P + R}{G} \qquad (19)$$

Production (P) in Equation 19, often is measured in terms of growth (Pg) (Czeczuga and Bobiatynska-Ksok 1972, Fischer 1972, Trama 1972) or perhaps as growth and exuvial production (Pg + Pev) (Lasker 1966) or as growth and reproduction (Pg + Pr) (Richman 1958, Kryutchkova and Rybak 1974, Duncan et al. 1974). However, rarely are all components of production, including estimates of secretion (Ps), determined.

210. Secretions lost to the environment during feeding and upon egestion may constitute a significant portion of production (McDiffett 1970). Otto (1975) estimated Pg, Pev, and Ps in larval Potamophylax

cingulatus (Trichoptera) and found that Pev and Ps constituted 16.3 percent (4.1 and 12.2 percent, respectively) of total production. Had he neglected these parameters, A/G would have been significantly underestimated.

211. Potential errors in the estimation of respiration or consumption are discussed under their respective headings. It is sufficient to conclude that potential errors are numerous, and they all decrease the accuracy of A/G estimates.

212. When A/G is calculated with three independently determined parameters (i.e., P, R, and G), researchers may encounter fairly high variation among results. This variability often results because independent determinations of P, R, and G are conducted under different experimental conditions. For example, Comita (1964) estimated the consumption of Diaptomus siciloides by measuring changes in the concentration of one food item (Pandorina or Chlamydomonas) before and after feeding, in 50 ml of pond water. Respiration was determined in small, 2-ml vials which contained no algae. Production was estimated by evaluating reproduction (Pr) exclusively. This estimation was made by computing the daily egg production of females that were collected from the field 8 years earlier.

213. The equation used to calculate assimilation efficiency (Zimmerman et al. 1975) is:

$$\frac{A}{G} = \frac{G - F - E}{G} \qquad (20)$$

However, most authors omit the excretion term (E) because it is difficult to quantify and is sometimes considered negligible (Lawton 1970, McDiffett 1970, Daborn 1975, Sweeney and Schnack 1977). Technically, the following equation measures absorption efficiency (Ricker 1968) or incorporation (Lasker 1960, Bell and Ward 1970) and not assimilation efficiency:

$$\frac{A}{G} = \left(\frac{G - F}{G} \right) \qquad (21)$$

214. The excretion component (E) sometimes appears to be insignificant and probably could be eliminated from assimilation estimates. When Daphnia pulex swallowed algae whole, it lost only 4 percent of its ingested carbon as dissolved organic carbon (DOC) (Lampert 1978). Excretion by Hexagenia limbata was generally less than 1 percent of consumption (Zimmerman et al. 1975).

215. In contrast, Johannes and Satomi (1967) found that Palaemonetes pugio (an estuarine decapod) lost DOC one third as fast as it consumed particulate organic carbon (POC). This estimate is probably high, because some of the DOC measured undoubtedly was derived from food items ruptured during ingestion (Conover 1966a). Up to 17 percent of the algal carbon filtered by Daphnia pulex was lost as DOC from ruptured cells (Lampert 1978). Perhaps the best quantitative approach is to combine F and E and simply measure all losses (Johannes and Satomi 1967). Until more research is conducted, researchers cannot be certain of the magnitude of error involved when E is not evaluated. Apparently it varies among taxa. For the purpose of this model, this potential overestimation of A/G is considered as part of the random error affecting all values.

216. Quantitative collection of feces, especially from small zooplankton, is perhaps the most serious problem with the $\frac{G - F - E}{G}$ method. In macrobenthos, however, the quantitative collection of feces is not always a problem (Lawton 1970, McDiffett 1970). Torn fecal pellets and the subsequent loss of feces, as DOC or POC, usually results in an overestimation of A/G (Conover 1964, 1966a). The situation is complicated by the suspension and reconsumption of zooplankton feces. Coprophagy results in underestimates of F and G and overestimates of A/G (Conover 1966a, Schindler 1968). Unless precautions are taken (e.g., short feeding periods), these errors can be very significant. Though the loss of feces is the most common source of error, the collection of foreign matter such as algae, exuvia, bacteria, fungi, or detritus with the feces, especially in prolonged experiments, may result in an underestimation of A/G (Conover 1962, 1966b). Lawton (1970) discussed

in some detail the potential sources of error in determinations of A/G by Equation 21. He concluded as did Conover (1964) that most of the potential errors tend to overestimate A/G.

217. Since previous methods failed to yield comparable results, Conover (1966a) developed an ash-ratio method. His method does not require quantitative collection of feces nor measurements of consumption. The method is based on the assumption that the inorganic fraction (ash) of ingested foods is unaffected during gut passage. Assimilation efficiency is defined as

$$\frac{A}{G} = \frac{F' - E'}{(1-E')\ (F')} \times 100 \qquad (22)$$

where F' and E' are the fractions of organic matter (i.e., ash-free dry wt:dry wt ratio) in the ingested food and feces, respectively.

218. Prus (1971), who calculated the A/G of Asellus aquaticus (Isopoda) by the ash-ratio and $\frac{G - F}{G}$ methods, found that Asellus aquaticus excreted minerals in excess during the winter and absorbed them during the summer. The differential use of minerals by this species thus rendered the ash-ratio method unreliable (Prus 1971).

219. At one time, the most promising methods appeared to be those in which foods were labeled with radioisotopes of phosphorus (Marshall and Orr 1955a, 1956; Cohn 1958) or carbon (Monakov and Sorokin 1960, Schindler 1968, Vannote 1969). Using these methods, investigators can directly measure the accumulation of isotopes in the body, excreta, and feces of an animal, as well as provide an estimate of consumption. Though many variations exist, the basic steps of the method are as follows: (a) label food items and correlate the radioactivity, in counts per minute (cpm), to the caloric value of the food; (b) feed animals labeled food (preferably for a short period of time so that defecation and excretion of isotopes are minimal); and (c) feed animals unlabeled food until all radioisotopes in the gut have been eliminated. By measuring the difference in radioactivity accumulated in the body of the animal before and after the elimination of radioisotopes, a researcher can estimate consumption and assimilation, respectively. Radioactivity of

the respired CO_2 and feces provides estimates of E and F, respectively. Thus, A/G can be calculated by using the terms A = (cpm in the body and CO_2) or (cpm consumed minus cpm in F and CO_2) in the numerator, and G = (cpm consumed) or (cpm in the body, F, and CO_2) in the denominator.

220. Radioisotope methods often are considered to be significantly more accurate than the other methods of determining A/G (Marshall and Orr 1955b, Sorokin 1966a, Pechen'-Finenko 1977). The basis for this belief is that radioisotope movements into an animal constitute the only direct measurements of consumption and assimilation. By contrast, a number of researchers seriously question the value of most tracer studies conducted to date.

221. Johannes and Satomi (1967) stated that most A/G values determined by radiocarbon methods are overestimates. Overestimates result from losses of unlabeled materials from the gut wall to the gut lumen. Unless the worker is absolutely sure that no ^{14}C is excreted, respired, or lost to the environment, the experiment is uninterpretable without detailed information on reaction kinetics (Conover and Francis 1973). Lampert (1975) demonstrated that ^{14}C losses (i.e., as $^{14}CO_2$) can be accurately measured only during feeding experiments. Carbon losses as $^{14}CO_2$ usually are negligible when measured at the end of feeding periods (Schindler 1968, Kibby 1971b); however, in Daphnia pulex monitored during feeding, ^{14}C losses were about 10, 20, and 30 percent of assimilated carbon in 10-, 60-, and 300-min experiments, respectively (Lampert 1975). Unmonitored losses of this magnitude result in significant overestimates of A/G. Lampert (1975) developed a model of ^{14}C loss for Daphnia pulex.

222. Some of the assumptions on which the isotope methods are based apparently are invalid. For example, the specimen is assumed to be a single compartment system in which there is instantaneous and complete mixing of labeled and unlabeled compounds. In addition, labeled compounds are supposedly evenly distributed and do not recycle. Unfortunately, several pools of carbon and phosphorus with different turnover rates have been demonstrated and tracer recycling does occur (Conover 1964, Conover and Francis 1973, Lampert 1975). Conover (1961)

recognized two phosphorus pools in Calanus finmarchicus, and Lampert (1975) stated that Daphnia pulex was not a single compartment system. Conover and Francis (1973), who developed a multicompartment model to account for tracer recycling among compartments, stated,

> Unless it is known that no recycling of isotope has occurred, the assumption of linear uptake, when in fact the system is not linear, even for short periods, can lead to significant errors in the estimation of ingestion or feeding.

223. In summary, none of the methods of assessing assimilation, egestion, and excretion are invariably foolproof, but one method may be significantly more accurate than another for a particular species or under specific experimental conditions. Although assimilation efficiencies have been calculated for many animals (Appendix C), many of the estimates are probably of limited value. Variation in experimental results is a function of a multitude of factors, but major discrepancies probably result from variable experimental conditions (Marshall 1973). Apart from variation among species, age groups, and sex, factors such as temperature, light, container size, animal density, animal size, and quality of food all exert a marked influence on experimental results (Marshall 1973). Thus, methodology is not the only cause of variability in A/G estimates.

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Factors Affecting Assimilation Efficiency

Food type

224. Undoubtedly the most significant factor affecting assimilation efficiency is food type. The effect is not very apparent in carnivores, like the odonate Pyrrhosoma nymphula (Lawton 1970), the plecopteran Acroneuria californica (Heiman and Knight 1975), and the amphipod Calliopius laeviusculus (Dagg 1976; Appendix C), because the food type, energy content, and digestibility of animal foods do not vary greatly. For example, most benthic carnivores have A/G ratios between 0.80 and 0.95 (Figure 28). By contrast, ranges in A/G are wide in herbivore-detritivores (Figure 29) because these animals often consume foods of varying energy content and digestibility--e.g., the

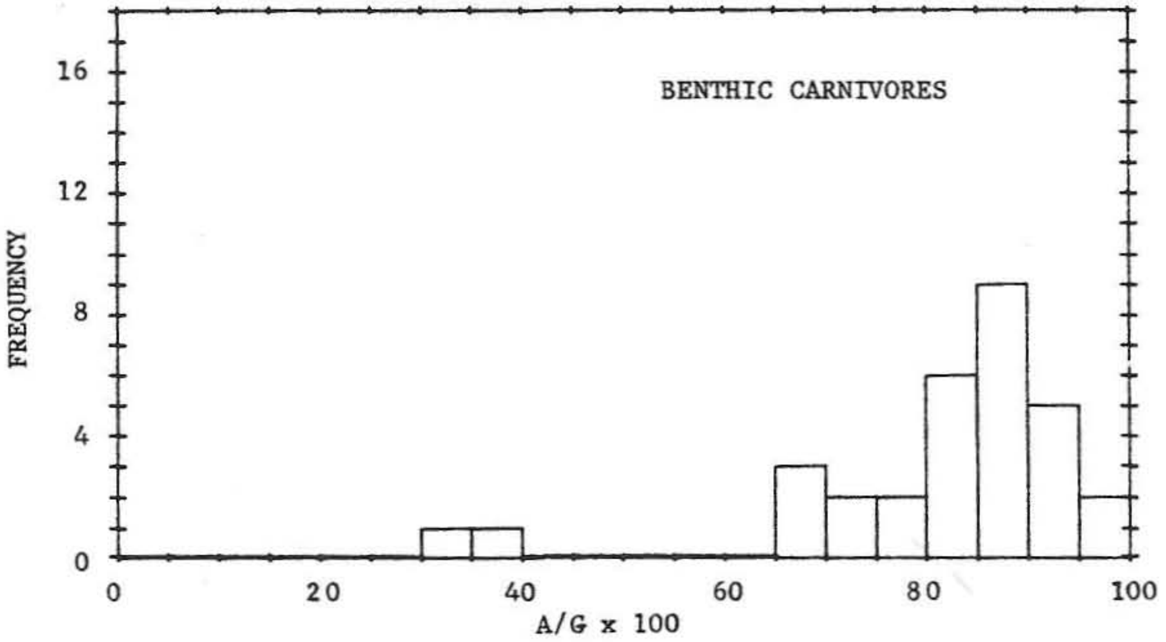

Figure 28. Frequency histogram of benthic carnivore assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

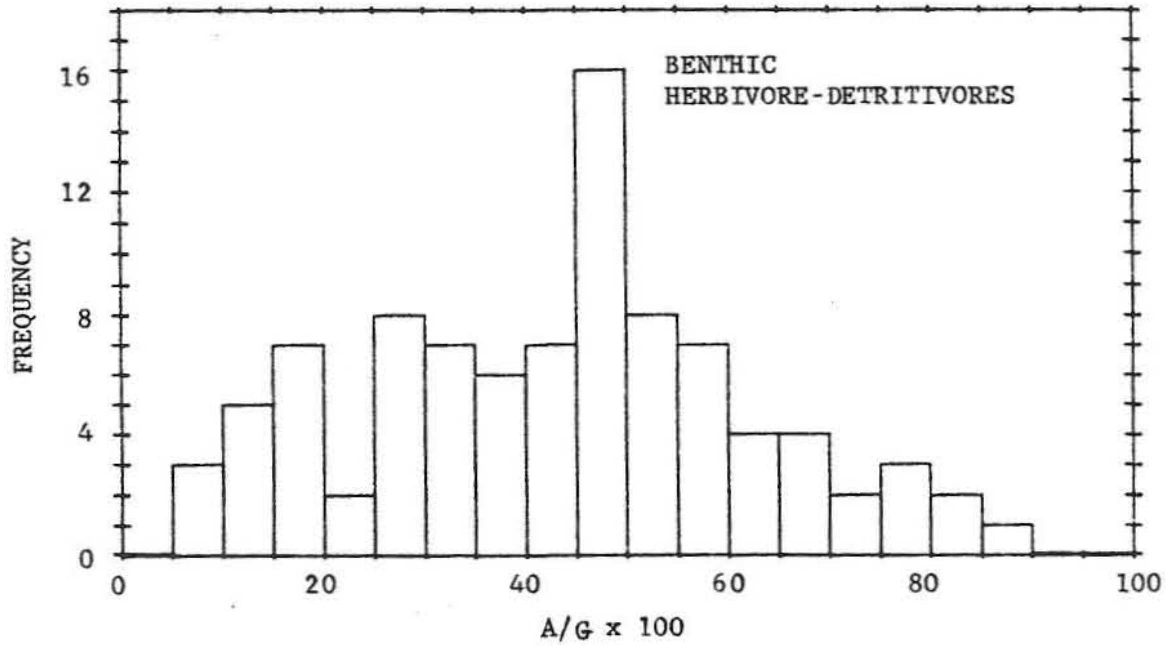

Figure 29. Frequency histogram of benthic herbivore-detritivore assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

cladocerans Daphnia longispina (Schindler 1971) and Sida crystallina (Monakov and Sorokin 1972) and the amphipod Gammarus pseudolimnaeus (Barlocher and Kendrick 1975).

225. Many workers have correlated A/G with the caloric value of foods (Odum 1971, Wetzel 1975). Schindler (1968) found that the assimilation efficiency of Daphnia magna increased from about 10 to 99 percent as the caloric content of its diet increased from 1.3 to 5.3 calories/mg dry weight. Thereafter, further increases in caloric value resulted in decreasing A/G--perhaps due to decreased digestibility of these foods. Similar correlations have been cited for planktonic crustaceans (Pechen'-Finenko 1971) and suggested for Asellus sp. and Gammarus sp. (Swiss and Johnston 1976).

226. Assimilation efficiencies also depend directly upon the quality and digestibility of foods (McDiffett 1970, Fischer 1970, Odum 1971, Wetzel 1975) and apparently are inversely related to the ash content (Conover 1966a, Schindler 1968). By contrast, Lawton (1970) found that the A/G of Pyrrhosoma nymphula was not correlated to ash content nor to caloric content.

227. In general, the A/G of animals fed living or senescent plant matter is less than that of animals fed living or dead animal tissue (Sushchenya 1969, Monakov 1972, Monakov and Sorokin 1972). This observation was substantiated by most of the literature values for benthic carnivores and herbivore-detritivores (cf Figures 28 and 29). Certain phytoplankters, however, may be assimilated very efficiently by zooplankton (e.g., see Schindler 1971, Monakov and Sorokin 1972, Hayward and Gallup 1976). Digestibility is probably more related to the high caloric and low cellulose contents of some phytoplankters than to increased efficiency of digestion by zooplankton. We separated zooplankton assimilation efficiencies on the basis of diet. Blue-green algae and detritus are apparently assimilated less efficiently than are green algae (Figures 36 and 37, respectively). The data for the assimilation of green algae are highly variable, perhaps reflecting the tremendous diversity of structure within the Chlorophyta.

228. Though the use of detritus and/or microflora as food by

benthos is widely accepted (Cummins et al. 1966, Hynes 1970, Fisher and Likens 1972, Marzolf 1964, Barlocher and Kendrick 1975, Rodina 1966), the use of these items by zooplankton is not generally acknowledged. In most models, zooplankton and benthos depend primarily upon phytoplankton as a food source. This basic premise probably is inaccurate for reservoir benthos and zooplankton. A detailed discussion of this topic was given in the section "Detritus and Microflora as Food" in Part III of this report, page 53.

Food concentration and feeding rate

229. Assimilation efficiencies have been observed to decrease significantly with increasing food concentration or ration in filter-feeding zooplankton, e.g., *Daphnia magna* (Ryther 1954, Schindler 1968), *Daphnia pulex* (Richman 1958), *Brachionus pilcatilis* (Doohan 1973), *Diaptomus graciloides* (Kryutchkova and Rybak 1974), and seven species of Entomostraca (Winberg et al. 1973). The same trend also has been observed in other animals such as the nematode *Plectus palustris* (Duncan et al. 1974), the gastropod *Goniobasis clavaeformis* (Elwood and Goldstein 1975), and various Crustacea (Sushchenya 1969). The above findings seem to support the theory of superfluous feeding (Harvey et al. 1935, Beklemishev 1962), which holds that animals assimilate food most efficiently when it is present in small quantities. When food is abundant and consumption exceeds the animal's food requirement, the efficiency of digestion decreases because of the animal's inability to efficiently process the large quantities of food. In filter-feeding Cladocera, Copepoda, and perhaps Rotatoria, filtration rates cannot be reduced enough to limit the intake of food, when the food is present at very high concentrations. Under these conditions extra or superfluous feeding can occur (Monakov and Sorokin 1961, as cited by Monakov 1972). Field observations also seem to substantiate superfluous feeding. King (1967) noted that undigested algae appeared in the feces of the rotifer *Euchlanus dilitata* only when the algae were present at very high concentrations. A similar observation also was made for *Daphnia magna* (Ryther 1954).

230. Some authors have observed constant A/G with increasing food concentration and therefore disagree with the theory of superfluous feeding. Pechen'-Finenko (1973) noted that in raptorial zooplankters (mostly predators), A/G remains constant over a wide range in food concentration. Presumably, these types of animals can regulate consumption and therefore optimize A/G. *Pyrrhosoma nymphula*, a carnivorous odonate (Lawton 1970), and *Neanthes virens*, a carnivorous polychaete (Kay and Brafield 1972), also exhibit fairly uniform A/G regardless of the quantity of food consumed. Even the filter-feeding copepods *Diaptomus gracilis* (Kibby 1971b) and *Calanus hyperboreus* (Conover 1964, 1966a) exhibit fairly uniform assimilation efficiencies (64.2 to 68.4 percent and 39.6 to 71.1 percent, respectively) when food concentrations are varied significantly.

231. Pechen'-Finenko (1973) argued that the concentration at which superfluous feeding occurs exceeds the concentrations of food found in nature. In addition, he suggested that automatic filter feeders can regulate assimilation by altering their filtration rate and A/G. Pechen'-Finenko (1977) expressed the belief that the apparent discrepancies in previous results of experiments on food concentration were entirely due to variations in methodology. For example, he viewed the downward trend in the A/G of *Daphnia pulex* (Richman 1958) as an artifact generated by Richman's use of the $\frac{P + R}{G}$ method. However, Schindler (1968) and Hayward and Gallup (1976), using radiocarbon techniques, also observed decreasing A/G as food concentrations were increased. Schindler (1971) believed that superfluous feeding may become evident only when zooplankton are feeding on certain types of food. He concluded that assimilation efficiency varies inversely with the ingestion rate, when different foods are consumed.

232. Firm conclusions cannot be made regarding the relation of assimilation efficiency to food concentration. Lawton (1970) noted that the A/G of *Pyrrhosoma nymphula* may increase, decrease, or remain constant as feeding rates increase. He suggested that all three responses are possible in nature. Hayward and Gallup (1976) pointed out that the situation is even more complicated than most people believe. According

to their work, A/G is a function of food concentration, but this function varies with temperature. They stressed the need for multivariate information on assimilation and suggested that great care be exercised in the interpretation of results.

233. Practically all models we reviewed used grazing constructs that were dependent on food density. In other words, these authors believed that assimilation efficiency remains constant at all food concentrations, whereas consumption changes at low to moderate food concentrations. This premise may or may not be correct, but it is practical in that the effects of concentration on grazing are easier to examine and simulate than are those same effects on assimilation efficiency. DiToro et al. (1971) used a density independent (i.e., linear) grazing relationship based on the idea of superfluous feeding and made assimilation efficiencies vary with food concentration. The relation of feeding rate to food concentration is essentially linear over most food concentrations and though a linear function may be appropriate in most cases, difficulties in determining the exact effect of food concentration on assimilation efficiencies render this approach less appealing.

Temperature

234. Changes in A/G have been positively correlated with water temperature for Cladocera (Webb and Johannes 1967, Schindler 1968, Hayward and Gallup 1976), Copepods (Conover 1962), various Crustacea (Sushchenya 1969, Pechen'-Finenko 1971), Insecta (Heiman and Knight 1975, Otto 1975), and Gastropoda (Elwood and Goldstein 1975). Effects of temperature on metabolism have been described by the Q_{10} law (Prosser and Brown 1961), which states that ectotherm metabolism increases two to three times with a 10° increase in temperature. Under ideal conditions, A/G should be low at low temperatures, increase to a maximum as temperature increases to a species-specific optimum, and gradually decline as temperature approaches the upper tolerance limit for the species.

235. Unfortunately, the ideal relationship of A/G to temperature is not always observed. The A/G of Calanus hyperboreus (Conover 1962), between 2° and 11°C, did not vary significantly (64.5 to 68.0 percent). In the gastropod Goniobasis clavaeformis A/G remained constant between

10° and 20°C (Elwood and Goldstein 1975). Assimilation efficiency also was unaffected by temperature in a number of other animals (Lawton 1971, Kibby 1971b, Dagg 1976).

236. A possible explanation for these discrepancies in published data is that temperature not only affects P and R but also consumption (G) through the effects of food concentration and temperature on filtration rates (Hayward and Gallup 1976). There is a good possibility that increased temperature, within a certain range, may not increase the A/G of an organism. This response could occur if the increase in assimilation (P + R) was matched by a concomitant increase in consumption (G also increases with temperature; see "Effects of Temperature on Consumption" in Part III of this report, page 66). In short, several variables are interrelated and the final result may have emergent properties (i.e., properties that cannot be predicted by separately examining the effects of the individual variables).

Animal development

237. Assimilation efficiencies have been observed to change significantly as animals develop. Whether this result is a function of age or weight is not certain, but, in some organisms at least, the change is clearly related to life history events such as metamorphosis (Fischer 1966). Many organisms change their diet during development (e.g., nauplii of predaceous copepods often are herbivorous until they reach a certain size). Because food type probably is the most significant factor influencing assimilation efficiency, changes in diet during the course of development may significantly alter A/G ratios (Schindler 1968, Waldbauer 1968).

238. Assimilation efficiencies have been observed to decrease, remain constant, or even increase during the development of various aquatic invertebrates. Decreasing A/G ratios during development were noted in the zooplankters *Daphnia magna* (Schindler 1968) and *Macrocyclops albidus* (Shushkina et al. 1968), and in the insects *Pyrrhosoma nymphula* (Lawton 1970), *Pteronarcys scotti* (McDiffett 1970), *Hedriodiscus truquii* (Stockner 1971), and *Lestes sponsa* (Fischer 1972). However, assimilation efficiencies remained constant during the development of the copepod

Macrocyclops albidus (Klekowski and Shushkina 1966b), the mollusc *Dreissena polymorpha* (Monakov 1972), the amphipods *Gammarus pulex* (Nilsson 1974), and *Calliopius laeviusculus* (Dagg 1976). *Brachionus rubens* (Rotatoria) exhibited increased A/G during development (Pilarska 1977b), and Lawton (1970) believed that the A/G of *Pyrrhosoma nymphula* (Odonata) could increase, decrease, or remain constant under a given set of environmental conditions.

Reproductive state

239. Few data are available that describe the effects of an animal's reproductive state on assimilation efficiency. *Daphnia magna* and *D. schodleri* bearing eggs or embryos assimilate at a higher rate than nonovigerous females (Schindler 1968, Hayward and Gallup 1976). The assimilation efficiency of *Assellus aquaticus* varied from 26 to 44 percent depending on reproductive condition, sex, and population density (Prus 1976).

Summary of Constructs

240. First, users should select the frequency histogram (Figures 26-33, 36, and 37) that best describes the model compartment they are considering. Second, the frequency histogram should be transformed into a probability distribution of A/G ratios (restricted by the confidence limits placed on the probability distribution by the user), and a range of A/G ratios should be selected. Third, consumption (mg carbon·mg carbon^{-1}·day^{-1})--generated by grazing constructs in Part III--should be multiplied by the selected A/G ratios, according to Equation 1. The resulting products describe the range of weight-specific assimilation (mg carbon·mg carbon^{-1}·day^{-1}) by the compartment. To determine the range of weight-specific loss (egestion + excretion--mg carbon·mg carbon^{-1}·day^{-1}), users should subtract A/G ratios from one and multiply weight-specific consumption by the resulting difference. The product of the weight-specific rates of assimilation or egestion + excretion (as determined above) and the biomass of the model compartment (mg carbon) yields the weight of carbon assimilated or lost, respectively.

241. Because the distribution of A/G values for cladocerans (Figure 32) was essentially uniform, we recommend that zooplankton be considered as a single compartment (Figure 26). However, when greater resolution is required, the frequency histograms of rotifer and copepod A/G (Figures 30 and 31, respectively) may be used, but cladoceran A/G ratios should be randomly selected from a range of 0.05 to 0.55. Biomass of zooplankton should be arbitrarily assigned as follows: Cladocera = 60 percent, Copepoda = 35 percent, Rotatoria = 5 percent, unless more accurate data are available. Rotatoria assimilation, for example, may be calculated as $0.05b\ [G(A/G)]$, where b = total zooplankton biomass (mg carbon), G = zooplankton consumption ($\text{mg carbon}\cdot\text{mg carbon}^{-1}\cdot\text{day}^{-1}$), and A/G = Rotatoria assimilation efficiency (from Figure 30).

242. Benthos should be compartmentalized into carnivores and herbivores-detritivores on the basis of their respective assimilation efficiencies (Figures 28 and 29). Based on the ecological growth efficiencies of a nematode (Duncan et al. 1974), a chironomid (Kajak and Dusoge 1970), and an oligochaete (Ivlev 1939), we believe that carnivores should constitute 20 ± 10 percent of total benthic biomass, when the benthos compartment is divided. Assimilation by benthic herbivores-detritivores may be calculated as $0.80b\ [G(A/G)_1]$ and that of benthic carnivores as $0.20b\ [G(A/G)_2]$, where b = total benthic biomass (mg carbon), G = benthos consumption ($\text{mg carbon}\cdot\text{mg carbon}^{-1}\cdot\text{day}^{-1}$), $(A/G)_1$ = A/G ratio for herbivore-detritivores (Figure 29), and $(A/G)_2$ = A/G ratio for carnivores (Figure 28).

Conclusions

243. Assimilation efficiencies are important in biological models because they can be used to modify consumption and thereby yield the rate of energy flow into model compartments. Egestion (F) and excretion (E), which technically differ, are defined as a single loss in the model--the additive inverse of assimilation efficiency $\left(A/G + \frac{(F + E)}{G} = 1\right)$.

244. Because methods employed to estimate A/G are inaccurate, we

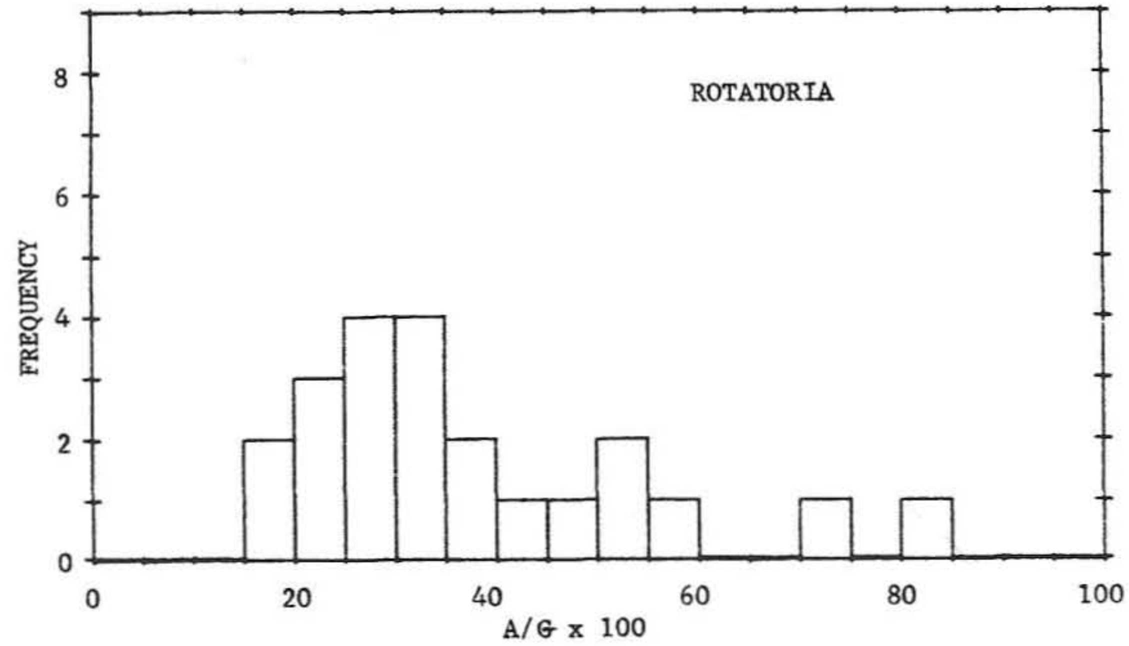

Figure 30. Frequency histogram of Rotatoria assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

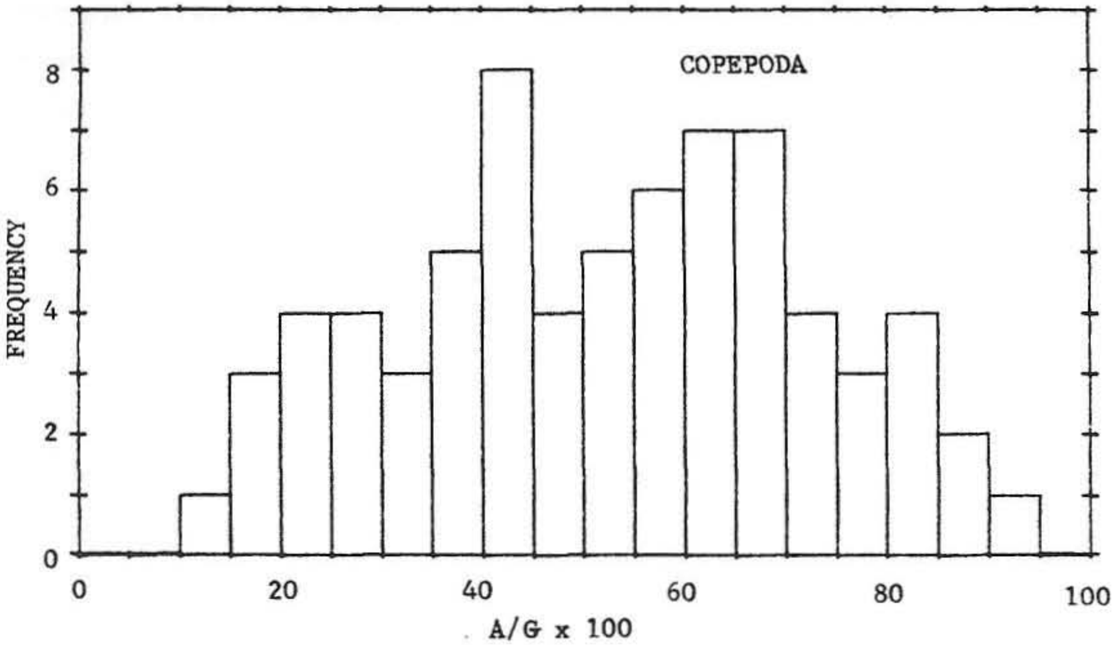

Figure 31. Frequency histogram of Copepoda assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

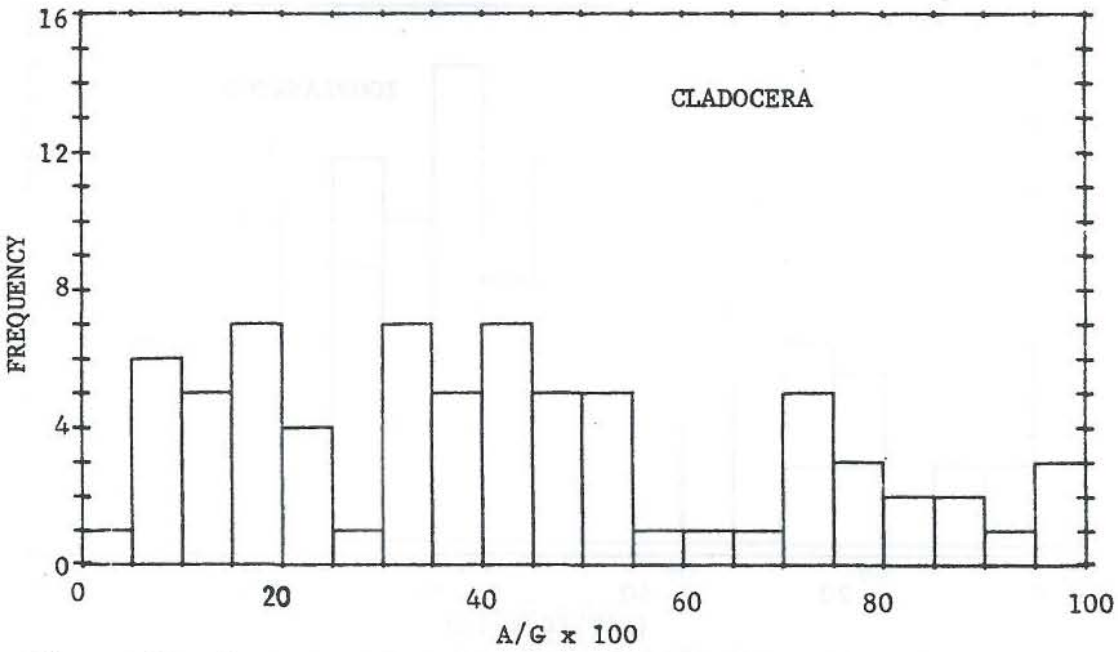

Figure 32. Frequency histogram of Cladocera assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

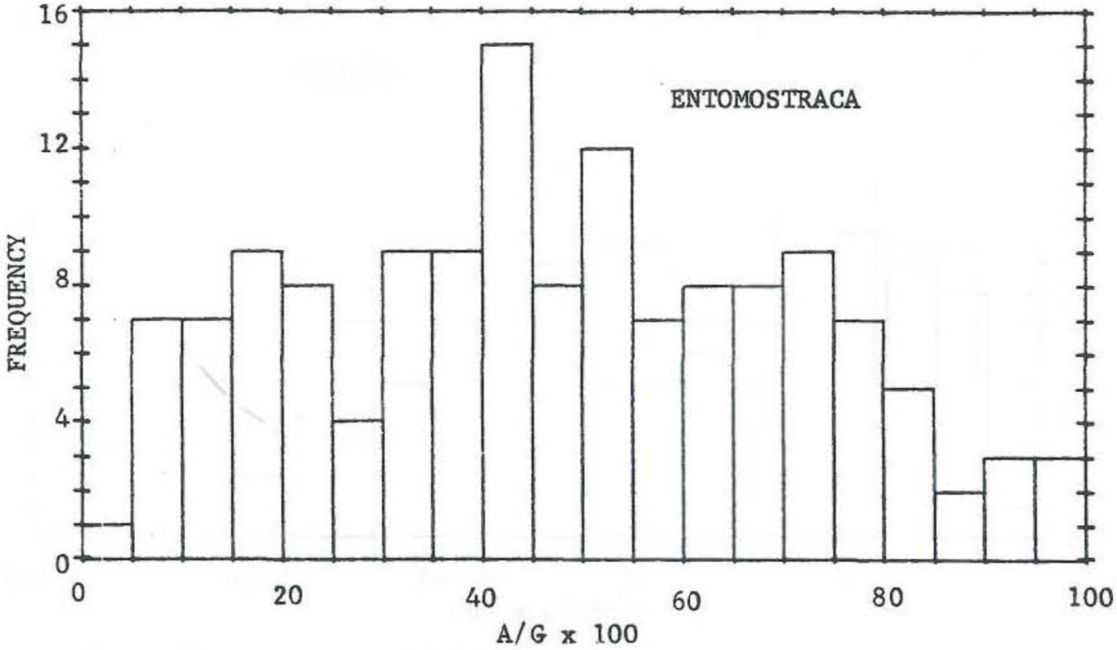

Figure 33. Frequency histogram of Entomostraca assimilation values (A) as a percentage of consumption (G). Based on data in Appendix C

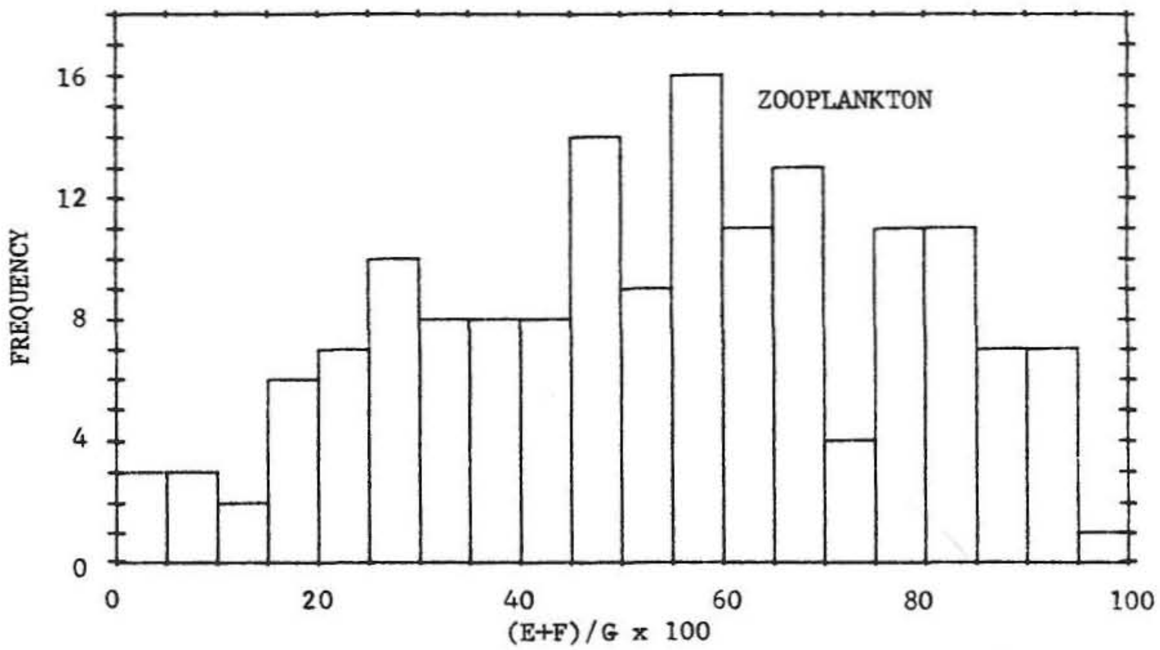

Figure 34. Frequency histogram of zooplankton egestion (F) and excretion (E) values as a percentage of consumption (G). Based on data in Appendix C

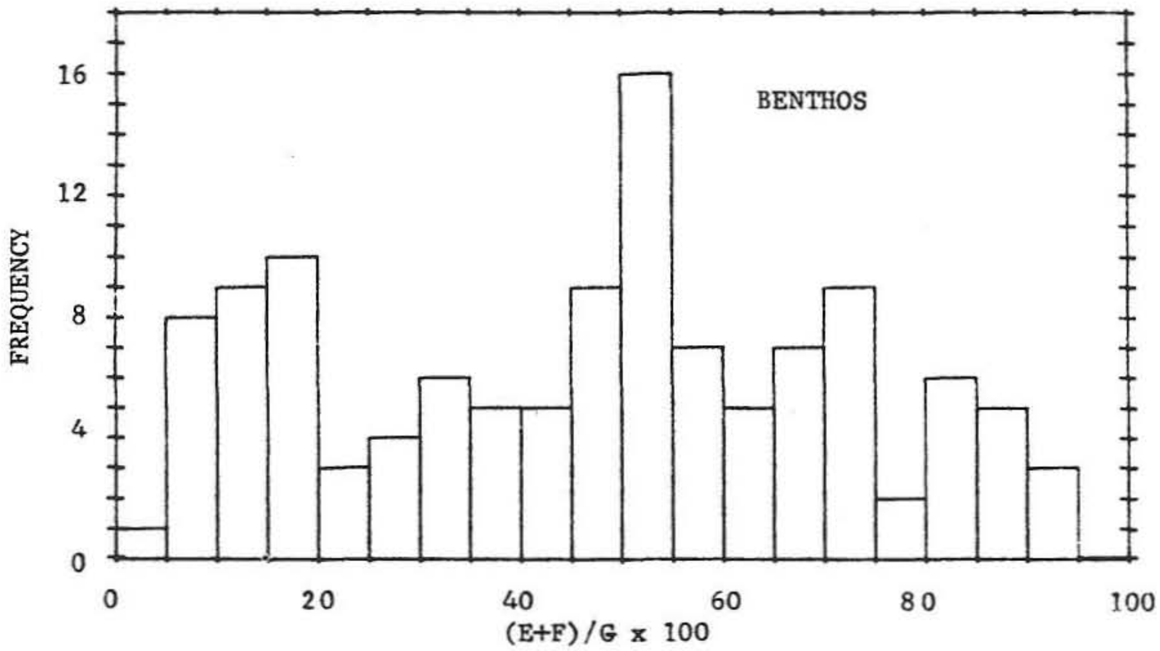

Figure 35. Frequency histogram of benthos egestion (F) and excretion (E) values as a percentage of consumption (G). Based on data in Appendix C

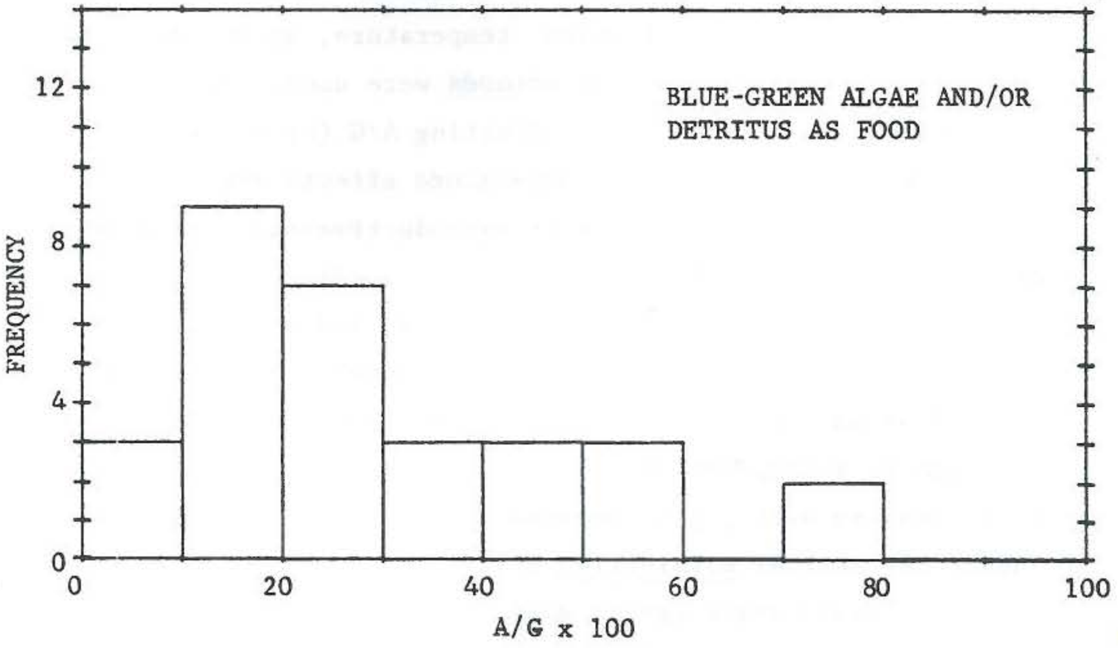

Figure 36. Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed blue-green algae and/or detritus

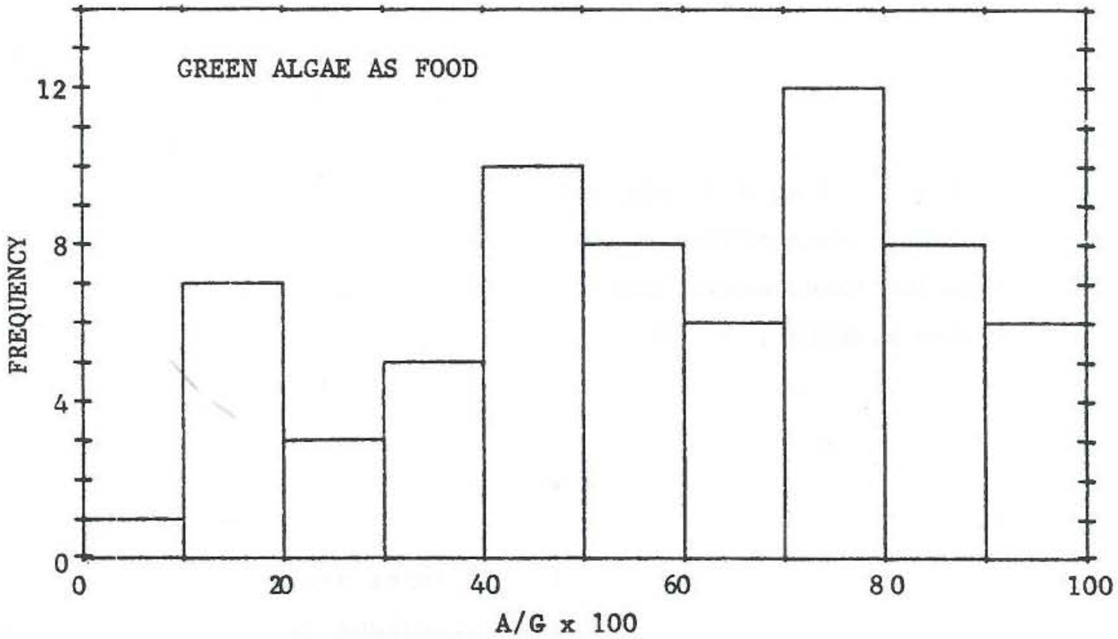

Figure 37. Frequency histogram of assimilation values (A) as a percentage of consumption (G) when zooplankton were fed green algae

did not develop constructs to predict cause-effect relations between A/G and factors such as food concentration, temperature, animal development, or reproductive state. When similar methods were used, food type generally was the most important factor affecting A/G (cf Figures 28-29 and 36-37), but food concentration and temperature effects were inconsistent. Few data that illustrate the effects of reproductive state or animal development have been published.