PART III: CONSUMPTION BY ZOOPLANKTON AND BENTHOS

33. In studies of the flow of any substance through an ecosystem, be it energy, biomass, or nutrients, it is critical to know the transfer pathways from one ecosystem component to another. This transfer occurs in animal communities through a series of predator-prey interactions which we call consumption. For example, a simple food chain in which phytoplankton is consumed by zooplankton which in turn is eaten by fish is one pathway. Modeling such a simple flow of material would be relatively easy, but, unfortunately, it would probably have little relation to the real world. The aquatic communities of temperate lakes and reservoirs are highly complex, and trophic relations can best be described as interacting food webs. Modeling of all these feeding relationships is beyond the present state of the art. As a result, most modelers attempt to portray only the major energy flow pathways of which we have some knowledge. Other feeding relations are recognized but presently cannot be adequately quantified. In this section of the report we review what is currently known about the feeding relations of zooplankton and benthos and attempt to place this information in a modeling perspective.

34. In conducting this review, we stressed the quantitative aspects of feeding. Food habits, although often interesting, have generally been ignored because they tell nothing of the rate and control of consumption. We have also stressed those areas most amenable to modeling and have related our analyses to previous modeling efforts. In addition, we have reviewed several subjects of current topical interest to modelers, including the role of organic detritus as a food supply, zooplankton grazing on blue-green algae, and the comparability of field and laboratory data.

35. More information is available on the dynamics of zooplankton feeding than is available for benthos. The rather functionally homogeneous nature of zooplankton, the relative ease in culturing and experimenting with zooplankton as compared to benthos, and its importance in phytoplankton dynamics have led to a better documented literature.

Benthic communities of reservoirs are not as homogeneous a unit as zooplankton, taxonomically or functionally, and they are often difficult to culture in the lab or study in the field.

Section A: Zooplankton Grazing

36. The zooplankton community of freshwater lakes and reservoirs consists of widely divergent taxonomic groups of organisms. Crustaceans of the subclass Copepoda and order Cladocera make up the bulk of the community biomass in most lakes. Rotifers are also an important part of the zooplankton community in many lakes.

37. The mathematical formulation of zooplankton feeding is a critical element in the equation describing zooplankton population dynamics. Most of the products of primary production pass through zooplankton in the aquatic ecosystem model as a direct result of grazing; zooplankton feeding, therefore, serves as a resource pathway to other model compartments, i.e., benthos and fish.

38. The primary zooplankton groups, Cladocera, Copepoda, and Rotatoria, generally can be classified as either herbivorous filter feeders or as carnivores, based on their feeding mechanisms and food habits. In reality, many zooplankters are omnivores and do not fit into neatly defined trophic groups. Nevertheless, some groupings and distinctions must be made in deference to our limited knowledge of individual taxa and the logistics of describing all possible interactions. Filter-feeding zooplankton make up a greater proportion of the zooplankton community, both numerically and as biomass, than do the carnivores. They are also more important to our understanding of the dynamics of phytoplankton populations, and phytoplankton dynamics are especially important to water quality modeling. Consequently, the feeding relations of filter feeders have been more heavily emphasized in this report.

39. The quantitative feeding relations of zooplankters have been studied in some detail for only a few major taxonomic groups. Feeding relations of copepods and cladocerans were documented for the more

common forms, but little quantitative information was available on feeding by rotifers and protozoans. Of the 127 species of Cladocera listed by Brooks (1959) as occurring in North America, filtering or grazing rates have been examined to some degree for only 18 species, or 14 percent of the total. Within the Cladocera, the genus Daphnia has been most intensively studied. Brooks (1957) listed 30 species in this genus occurring worldwide. Our review indicates that feeding of only 12 Daphnia species, or 40 percent of the total, has been studied. Of the 15 North American species of Daphnia, 9 (60 percent of the total) have been studied. Because Daphnia represents the most intensively studied genus within the Cladocera, and because data are available for many United States species, our analysis is biased toward this genus.

40. Calanoid copepods constitute a major group of filter-feeding zooplankton. Wilson (1959) listed 92 species for North America and our review revealed that the feeding for only 7 species (8 percent of the total) has been studied. Six of the seven species are in the genus Diaptomus (= Eudiaptomus), which includes 78 North American species.

41. Rotifers constitute the third major group of filter-feeding zooplankters. The literature on the number of North American species is contradictory, but easily exceeds 200. Feeding rate values are available for only six species.

42. This brief statistical summary illustrates that the feeding relations of most filter-feeding zooplankters are unknown and indicates that caution must be used in extrapolating grazing results to all species.

Consumption by Filter-Feeding Zooplankton

43. Factors that influence food consumption by filter-feeding zooplankton include animal density, size, sex, reproductive state, nutritional or physiological state, as well as the type, quality, concentration, and particle size of food. Other factors include water quality and temperature. Some of these variables are more important

than others in controlling feeding. The effects of many are poorly understood and synergistic effects among variables do occur.

44. The purpose of this section of the report is to examine in detail those variables of primary importance in regulating zooplankton feeding and which are considered suitable for mathematical description. Table 2 summarizes factors influencing feeding and lists information sources. Concerning the difficulties of comparing feeding data, Geller (1975) stated:

> It is difficult or impossible to compare the results obtained by these authors, because they used different methods of investigation. The size of the animals is not specified precisely or is omitted; the habitation and acclimation periods cited in many publications are obviously insufficient, and the food particles used range from clay particles, yeasts, algae, and bacteria to synthetic particles and 'artificial detritus.' The measuring units employed for determining food biomass also differ, and may be either the number of cells, wet weight, dry weight, carbon content, or energy content, and conversion from one unit to another is possible only in exceptional cases.

45. We found Geller's comments to be wholly justified. Appendix B presents a comparison of zooplankton filtering rates found in the literature.

46. The objectives of this section are as follows: (a) to describe the effect of food concentration, type of food, and temperature on feeding rates, including a review of field versus laboratory results, as well as synergistic effects; (b) to examine the role of diel and annual variations in feeding rates; and (c) to discuss possible model formulations for grazing by filter-feeding zooplankton. Further information on the biology of filter feeding was presented by Jorgensen (1966), and a critique of experimental methods employed to measure filtering and feeding rates was given by Rigler (1971).

Effect of food concentration

47. Literature synopsis. The question of how zooplankton grazing rates are influenced by changes in food concentration is central to the development of a model describing zooplankton biomass dynamics. The first workers to examine the effects of food concentration on feeding

Table 2

Factors Reported to Influence the Feeding of Filter-Feeding Zooplankton and a List of References

Factor	References
Food concentration	Ryther (1954), Richman (1958), Monakov and Sorokin (1960), Rigler (1961a), Galkovskaya (1963), McMahon and Rigler (1963), Richman (1964), McMahon (1965), McMahon and Rigler (1965), Richman (1966), Burns and Rigler (1967), Kryutchkova and Sladecek (1969), Ivanova (1970), Tezuka (1971), Ivanova and Klekowski (1972), Crowley (1973), O'Brien and DeNoyelles (1974), Chisholm et al. (1975), Green (1975), Geller (1975), Kersting and Leeuw-Leegwater (1976), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977).
Size of food	Ryther (1954), McMahon and Rigler (1965), Gliwicz (1969), McQueen (1970), Berman and Richman (1974), Kryutchkova (1974), Bogdan & McNaught (1975), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977).
Age of food	Ryther (1954), McMahon and Rigler (1965), Stross et al. (1965).
Type of food	Ryther (1954), Comita (1964), Burns (1968b), Schindler (1968), Burns (1969a), Gliwicz (1970), McQueen (1970), Kersting and Holterman (1973), Haney (1973), O'Brien and DeNoyelles (1974), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Pourriot (1977), Webster and Peters (1978).
Temperature	McMahon (1965), Burns and Rigler (1967), McMahon (1968), Schindler (1968), Burns (1969b), Kibby (1971a), Chisholm et al. (1975), Green (1975), Geller (1975), Gophen (1976), Hayward and Gallup (1976).
Light intensity	McMahon (1965), Schindler (1968), Buikema (1973), Hayward and Gallup (1976).

(Continued)

Table 2 (Concluded)

Factor	References
Water quality	McMahon (1968), Schindler (1968), Tezuka (1971), Ivanova and Klekowski (1972), Kring and O'Brien (1976).
Size of animal	Ryther (1954), Richman (1958), McMahon (1965), Burns and Rigler (1967), Schindler (1968), Kryutchkova and Sladecek (1969), Burns (1969b), Ivanova and Klekowski (1972), Buikema (1973), Kibby and Rigler (1973), Bogdan and McNaught (1975), Chisholm et al. (1975), Haney and Hall (1975), Green (1975), Geller (1975), Hayward and Gallup (1976), Pilarska (1977a), Webster and Peters (1978).
Sex of animal	Haney and Hall (1975), Green (1975), Hayward and Gallup (1976).
Nutritional state of animal	Ryther (1954), McMahon and Rigler (1965), Geller (1975).
Reproductive state of animal	Schindler (1968), Hayward and Gallup (1976).
Circadian rhythms and behavior	Nauwerck (1959), Burns and Rigler (1967), McMahon (1968), Burns (1968a), Haney (1973), Starkweather (1975), Chisholm et al. (1975), Haney and Hall (1975), Hayward and Gallup (1976), Duval and Green (1976), Gulati (1978), Andronikova (1978).
Animal density	Schindler (1968), Buikema (1973), Hayward and Gallup (1976).
Acclimation period	McMahon (1965), Schindler (1968), Buikema (1973), Geller (1975), Hayward and Gallup (1976).

investigated the marine copepod Calanus finmarchicus (Fuller and Clarke 1936, Fuller 1937, Harvey 1937). They and their contemporaries concluded that the filtering rates (volume of water filtered per unit of time) of marine filter-feeding zooplankton were independent of food concentration. The corollary to this hypothesis was that grazing rates (weight of food eaten per unit body weight per unit of time) were directly proportional to food concentration (Figure 9). These results suggested that a species-specific filtering rate could be established.

48. It was not until Ryther's 1954 paper on the filtering response of Daphnia magna that attention was directed to freshwater zooplankters. The most significant result of Ryther's work was that he demonstrated that filtering rate per animal decreased as food concentration increased. This relation was found to hold for all three algal species tested and was the first evidence to suggest that zooplankton did not filter at a constant rate at all food concentrations. Ryther's results suggested that filtering rate may be reasonably constant and high at very low food densities (less than ca 700 mg C/m^3 for Chlorella), decline sharply at

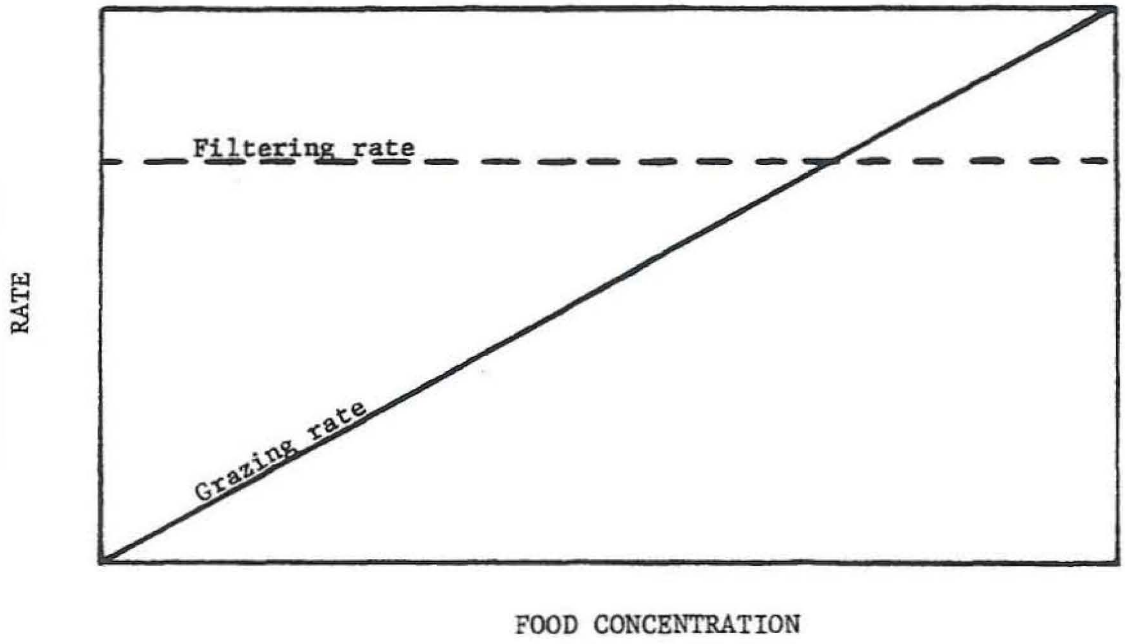

Figure 9. Relation among food concentration, filtering rate, and grazing rate, based upon early studies of filter-feeding marine zooplankton

intermediate densities, and possibly reach a minimum filtering level at high food densities (greater than ca 2000 mg C/m^3).

49. With all three species of algae introduced as food by Ryther, grazing rate increased with increased food density (the one exception was Daphnia fed senescent Chlorella). In examining Ryther's data where Daphnia were fed growing algal cultures (Figure 10), it is clear that grazing increased with food density in a linear or near linear fashion.

50. The results of Ryther's work stimulated other workers to examine zooplankton feeding relationships over a wide range of food concentrations. Rigler (1961a) demonstrated that the grazing rate of the zooplankter Daphnia magna may approach a maximum as food concentration is increased. The grazing response changed markedly at a food concentration of approximately 600 mg C/m^3. The grazing rate was nearly constant above this concentration, but too few data points prevent firm conclusions. Similar results were obtained by McMahon and Rigler (1965) (Figure 11).

51. Rigler (1961a) offered this hypothesis:

> ...when a filter-feeding Crustacean encounters low concentrations of food, the feeding rate is limited by the ability of the animal to filter water and hence feeding rate is proportional to concentrations of food. But above a critical concentration of food, which will vary with the species of Crustacean and food organisms, feeding rate is constant and limited by the ability of the animals to ingest or digest the food....

52. Subsequent studies by Rigler and his associates (McMahon and Rigler 1963, 1965; McMahon 1965, 1968; Burns and Rigler 1967; Burns 1968a, 1969a, b) have validated the above hypothesis and clearly support the earlier conclusion that "above a critical concentration of food, the feeding rate is independent of concentration of food" (Rigler 1961a). The concentration of food at which feeding becomes constant, called the "critical concentration" by Rigler, is now usually termed the "incipient limiting level" after Fry (1947). This relationship is illustrated in Figure 12.

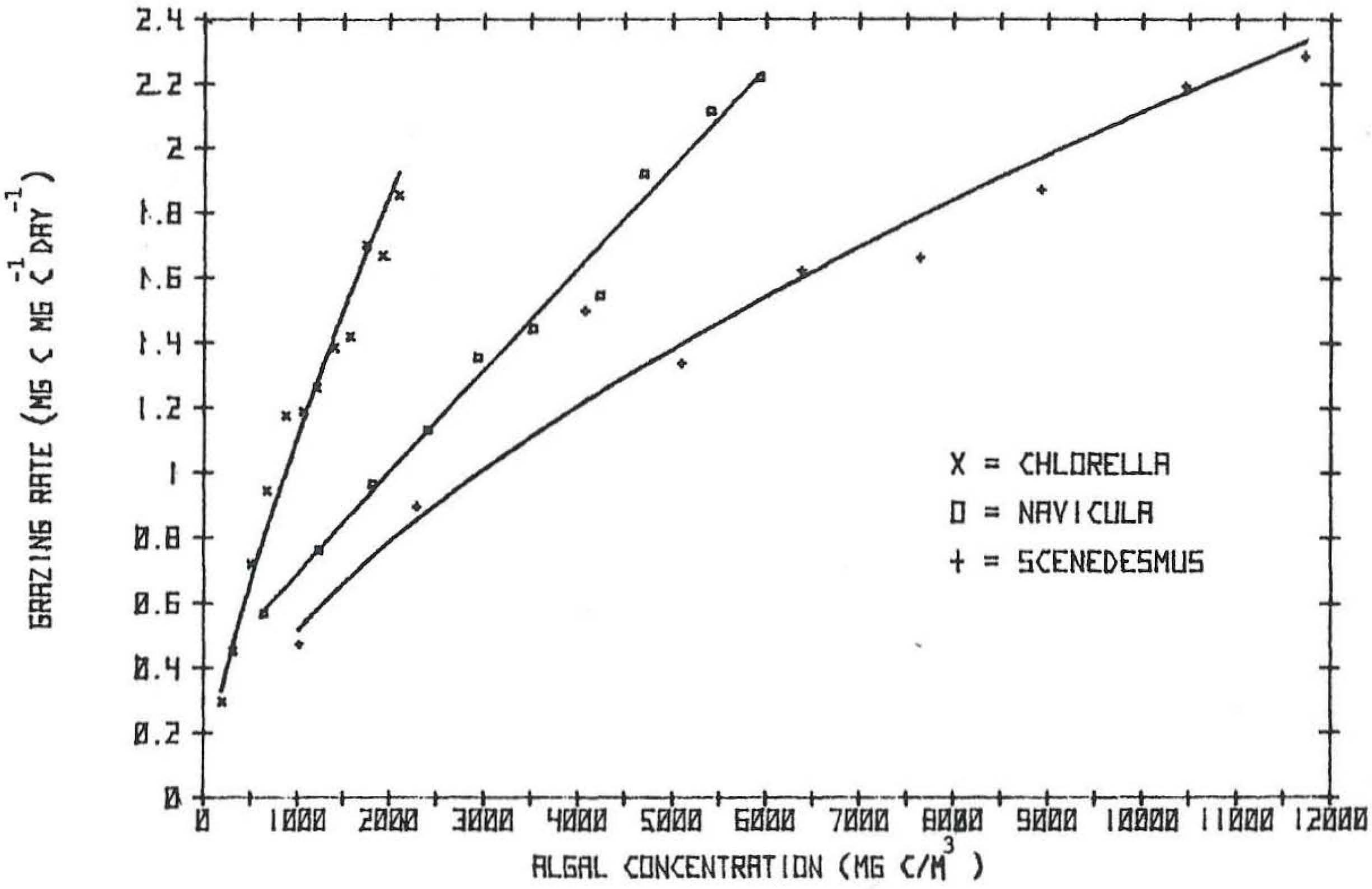

Figure 10. Grazing rate of Daphnia magna at various concentrations of three algal species bease on the data of Ryther (1954)

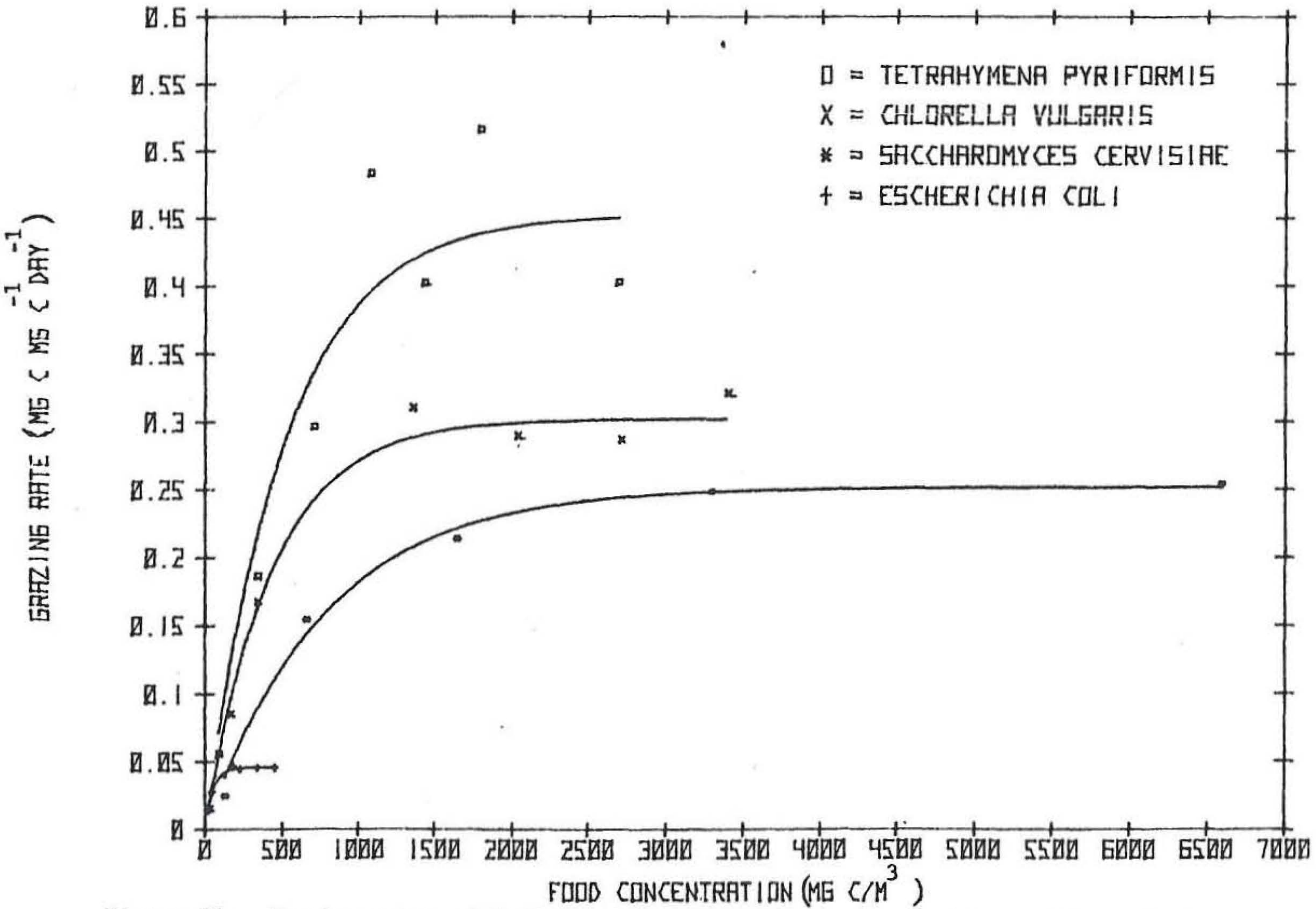

Figure 11. Grazing rates of Daphnia magna at various concentrations of four food sources based on the data of McMahon and Rigler (1965). An Ivlev function was fitted to the values (see Saturation Response Models)

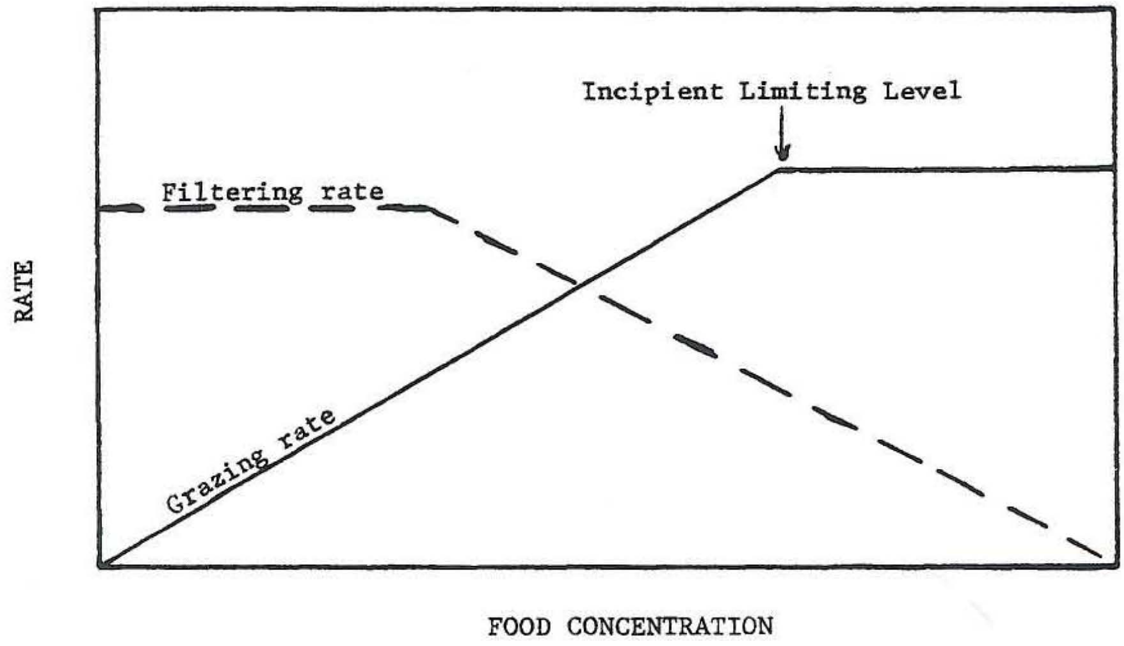

Figure 12. Relation among food concentration, filtering rate, and grazing rate first proposed by Rigler (1961a)

53. Work by Mayzaud and Poulet (1978) on marine zooplankters suggested that the earlier conclusions (that filtering rate was independent of high food concentrations) were not incompatible with results showing a declining filtering rate with increasing food concentration. In a 1-year field study they found a linear relationship between feeding rates and food supply for five copepod species. However, they also found that if the marine zooplankter *Pseudocalanus minutus* was fed a range of food concentrations over an 18- to 20-hr period, a saturation-type curve, showing a maximum feeding rate, was obtained. Their experimental work indicated that the levels of digestive enzymes of the copepod population also varied linearly with food concentration on a seasonal basis. These results suggest that both ingestion and digestion by copepods were seasonally acclimated to the concentration of food particles. The authors noted:

> From our results and those published earlier it becomes evident that saturation curves have been obtained in experiments where time and season are eliminated as influential parameters. The feeding saturation level found by so many workers is very likely partially a function of the time needed by the copepods to acclimate their ingestion and digestion to the qualitative and quantitative variations of their food.

54. Thus, it may be that zooplankton grazing rates are proportional to food concentration, if the animals have had time to acclimate, and that a maximum grazing rate of the saturation type only is approached in the field under very high food concentrations, as might occur during a phytoplankton bloom.

55. Model constructs. Scavia (1979) reviewed various mathematical constructs for describing consumption by filter-feeding zooplankton. Our purpose is to synthesize existing information and to present a mathematical expression describing the relation between feeding rate and food concentration. The terms feeding rate and grazing rate are used interchangeably.

56. Based on the work of Mayzaud and Poulet (1978) in the preceding section, we noted that the two divergent viewpoints on the relation between food concentration and feeding rate may not necessarily be incompatible. The first viewpoint held that a linear relationship exists between feeding rate and food concentration (Figure 9). Evidence by Mayzaud and Poulet (1978) indicated that if the time is sufficiently long (probably more than 24 hr but less than 6 days), zooplankters can adjust their ingestion rates, through changes in digestive enzyme activity, to acclimate to varying food concentrations. Over the range of naturally occurring food densities, the relation is essentially linear. The second viewpoint held that as food concentration increases, feeding rate also increases but reaches a maximum rate at the incipient limiting food concentration. At higher food densities, feeding is constant and maximal (Figure 12). Many workers have demonstrated the second viewpoint to be generally true in short-term feeding experiments. Mayzaud and Poulet (1978) also found the same result for Pseudocalanus minutus when it was exposed to varying food concentrations after short-term incubation periods of 18 to 20 hr.

57. Research results suggest two conclusions. First, for short-term incubation periods, zooplankters respond to increasing food concentrations in a curvilinear manner, often described as a "saturation curve," where feeding rate attains a constant maximum value. Second, if zooplankton are allowed to incubate at the test concentrations for longer periods (>24 hr but <6 days), then digestive enzyme acclimation may occur and the feeding rate response is linear. These conclusions emphasize the importance of specifying duration when comparing laboratory and field studies. Of the papers that examined the effects of food concentration on feeding rate, we found none that involved food incubation periods exceeding 24 hr. Thus, the results of laboratory experiments conducted to date must be interpreted as short-term feeding responses of incompletely acclimated zooplankters.

58. The above hypothesis concerning the functional response of field populations of zooplankton to varying food concentrations was first outlined by Mayzaud and Poulet (1978). Because little experimental work has been conducted to support or refute this proposal, it must be tentatively accepted. It is our opinion that this hypothesis will be verified, and we have accepted the conclusions and proposals of the above authors in presenting a model construct for zooplankton consumption.

59. Saturation response models. The currently accepted saturation response models are easily verified by existing laboratory data, and because of the limited verification of the Mayzaud-Poulet model to follow, the reader may wish to use one of these constructs instead. Because the Mayzaud-Poulet model is an elaboration of saturation response models, a basic understanding of these functions is needed.

60. Scavia (1979) described three expressions normally used to describe the saturation type of response of zooplankton feeding on varying food concentrations. The first is a rectilinear form presented by Rigler (1961a), which consists of two straight lines with different slopes above and below the incipient limiting food concentration (Figure 12). The remaining two forms are curvilinear and have been represented by Michaelis and Menten (1913) and Ivlev (1966) formulations:

Michaelis-Menten

$$G = G_{max} \left(\frac{B}{k + B}\right) \qquad (2)$$

where, G = observed grazing rate

G_{max} = maximum grazing rate

B = food concentration

k = half-saturation constant

Ivlev

$$G = G_{max} \left(1 - e^{-kB}\right) \qquad (3)$$

where the parameters G, G_{max}, and B are the same as described for the Michaelis-Menten equation and k is a proportionality constant. According to Mullin et al. (1975), using the results of Frost (1972), none of these three model formulations differ significantly in representing the filtering rate response of Calanus pacificus. At food concentrations below the half-saturation constant, the Ivlev equation produces relative feeding rates that are slightly less than those determined by the Michaelis-Menten relationship. The opposite is true of feeding rates at food concentrations above the half-saturation constant (Swartzman and Bentley 1977) (Figure 13).

61. We have selected the Ivlev formulation for use in our model constructs for two reasons. First, the determination of the proportionality constant, k, is straightforward. Second, the Ivlev formulation is used in the model of Mayzaud and Poulet (1978) thus eliminating conversions to the Michaelis-Menten expression.

62. Both the Michaelis-Menten and Ivlev equations have been modified in some models to include a lower threshold food concentration below which zooplankton do not feed. The Ivlev equation then becomes,

$$G = G_{max} \; (1-e^{-k(B-B_o)}) \qquad (4)$$

where B_o is a threshold food concentration at which grazing commences. Experimental evidence for such a threshold came from work on marine species (Parsons et al. 1967, McAllister 1970). However, Frost (1975), also studying a marine zooplankter, found no clear threshold at low food concentrations but rather greatly reduced feeding. We have found no evidence to support the concept of a threshold food concentration for feeding in freshwater zooplankton. McMahon and Rigler (1963) reported that, in the absence of food, both the collecting and ingesting mechanisms function in Daphnia magna, and Crowley (1973) noted that, in Daphnia pulex, the movement of the thoracic appendages serves respiration as well as feeding. He concluded that it was essential for

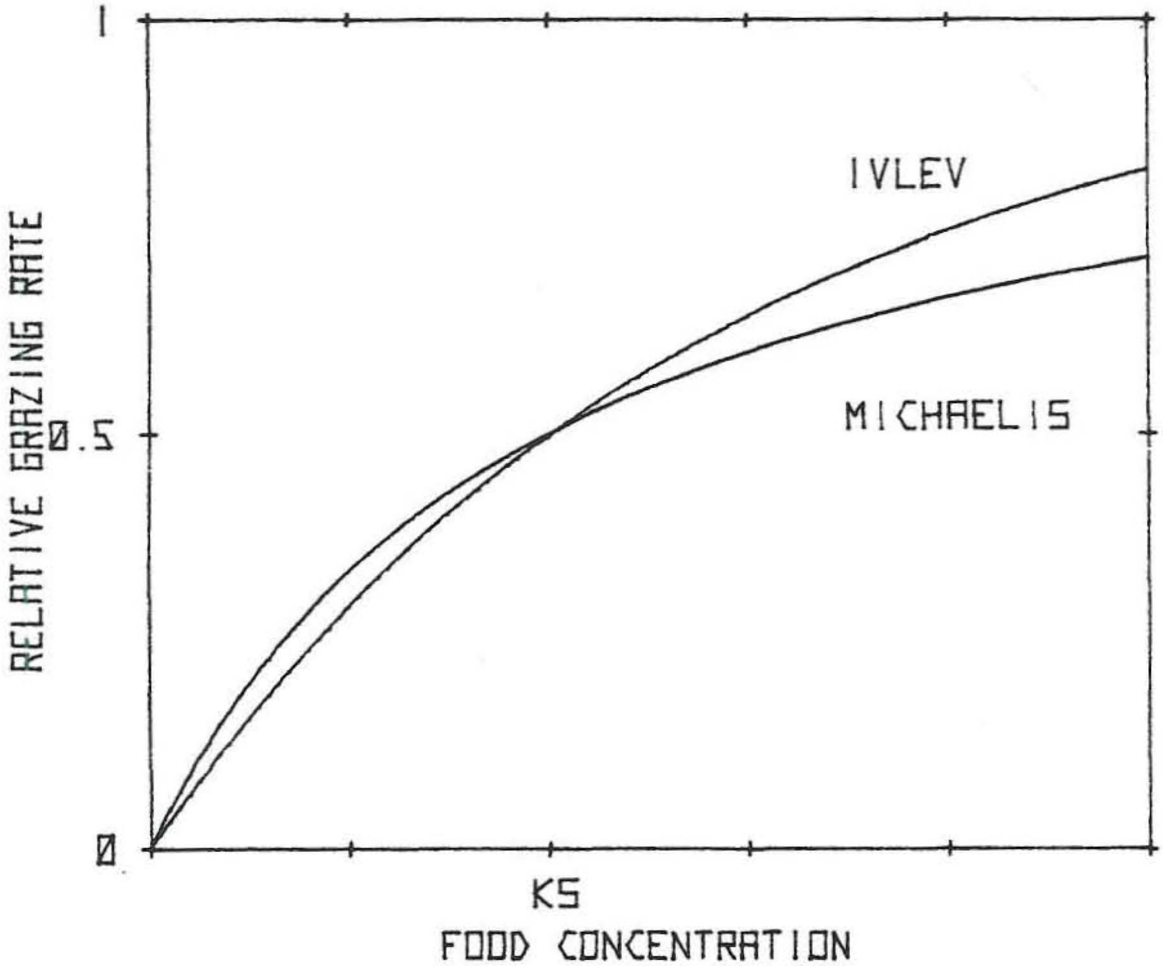

Figure 13. Comparison of the Ivlev and Michaelis-Menten functions with the same half-saturation value, k_s (based on Swartzman and Bentley 1977)

filtering to continue, even when food was absent. It has been suggested that threshold levels are needed to prevent the zooplankton from grazing algal foods to extinction. This simulation phenomenon appears to be the primary reason for including threshold levels in most models. It is likely that extinction is an artifact of the simulation process and results from inappropriate assumptions or our ignorance of zooplankton grazing dynamics. Wroblewski and O'Brien (1976) showed that the addition of zooplankton vertical migration to their model made threshold levels unnecessary. Grazing pressure was not sufficient to drive food supplies to extinction. In light of these results and because threshold food concentrations have not been demonstrated for freshwater zooplankters, threshold levels are not included in our model construct.

63. Parameters of the Ivlev equation. Filtering and feeding rates are seldom presented in biomass units, particularly as carbon. The results of a few papers were deemed to be suitable for conversion to carbon units. Our analysis method was to convert the raw data to carbon units and then to find the best fit to the data using the Ivlev function (Table 3). Variability of values for the grazing rate parameters can be attributed to variations in animal size, species, and physiological state, as well as to differences in food source, temperature, and assumptions made in our conversion of the literature data. The results presented in Table 3 are only for studies that made it reasonably clear that a maximum grazing rate existed.

64. Values for the maximum grazing rates ranged from 0.045 to 3.44 $\mathrm{mg\ C \cdot mg\ C^{-1} \cdot day^{-1}}$. Several investigators found a linear or nearly linear increase in the grazing rate with increasing food concentration but did not state the maximum grazing rate. Because these studies only allowed for short-term acclimation, we assumed that the ranges of food concentrations tested were below the incipient limiting level. The variability among values (Table 4) was high.

65. Many studies reported grazing as a percentage of the organism's body weight consumed daily (Table 5). These results are not directly comparable to carbon grazing rates but probably are reasonably close approximations.

Table 3

Grazing Rate Parameters of the Ivlev Equation Calculated From Experimental Studies That Demonstrated the Existence of a Maximum Grazing Rate

Taxon	Food	Approximate Range of Food Concentrations, B (mg C/m^3)	Food Concentration When Observed Grazing Rate Reaches 95% of the Maximum Grazing Rate, 0.95 B_{lim} (mg C/m^3)	Maximum Grazing Rate, G_{max} (mg C mg C^{-1} Day^{-1})	Value of Empirical Constant, k	Reference
Class: Crustacea						
Order: Cladocera						
Family: Daphnidae						
Daphnia magna	*Saccharomyces cervisiae*	132-6,600	2,346	0.251	0.001277	McMahon and Rigler (1965)
Daphnia magna	*Tetrahymena pyriformis*	90-2,700	1,559	0.452	0.001922	McMahon and Rigler (1965)
Daphnia magna	*Chlorella vulgaris*	34-3,400	1,302	0.301	0.002300	McMahon and Rigler (1965)
Daphnia magna	*Escherichia coli*	22-450	155	0.045	0.01936	McMahon and Rigler (1965)
Daphnia magna	*Chlorella vulgaris*	64-2,157	2,140	0.760	0.0014	Kersting and Leeuw-Leegwater (1976)
Daphnia magna	*Saccharomyces cerivisiae*	33-6,336	1,275	0.350	0.00235	Rigler (1961a)
Daphnia pulex	*Chlorococcum* sp.	150-7,150	1,362	1.200	0.0022	Monokov and Sorokin (1961) as reported by Ivanova (1970)
Daphnia rosea	*Rhodotorula glutinis*	250-5,000	1,664	0.900	0.0018	Burns and Rigler (1967) as reported by Ivanova (1970)
PHYLUM: ROTATORIA						
Family: Brachionidea						
Brachionus rubens	*Chlorella vulgaris*	160-134,000	10,699	3.438	0.00028	Pilarska (1977a)

Table 4

Range of Grazing Rates Calculated From Experimental Studies in Which A Maximum Grazing Rate Could Not be Demonstrated

Taxon	Food	Approximate Range of Food Concentrations, B (mg C/m^3)	Range of Calculated Grazing Rates, G (mg C mg C^{-1} day^{-1})	Reference
Class: Crustacea				
Order: Cladocera				
Family: Daphnidae				
Daphnia longispina	*Chlorococcum* sp.	347-5,805	0.935-2.697	Monakov and Sorokin (1960) and Monakov (1972)
Daphnia longispina	Bacteria	961-31,636	0.837-1.736	Monakov and Sorokin (1960 and Monakov (1972)
Daphnia magna	*Chlorella vulgaris**	174-2,100	0.106-1.857	Ryther (1954)
Daphnia magna	*Navicula pelliculosa**	588-5,935	0.460-2.219	Ryther (1954)
Daphnia magna	*Scenedesmus quadricauda**	1,020-11,730	0.474-2.286	Ryther (1954)
*Daphnia pulex***	*Chlamydomonas reinhardti*	4,975-19,900	1.332-13.764	Richman (1958)

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* Results combined for scenescent and growing cell cultures. Also includes prefeeding study for *Chlorella vulgaris*.

** The results are combined for the three sizes of *Daphnia* tested.

Table 5

Literature Values for the Daily Ration of Filter-Feeding Zooplankters

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Cladocera			
Family: Holopedium			
Holopedium gibberum	Phytoplankton Bacteria	12.1 7.5	Gutel'mackher (1973)
Family: Chydoridae			
Acroperus harpae	Detritus	253	Smirnov (1969)
Family: Bosmidae			
Bosmina coregoni	*Chlorella* sp. Bacteria	32.9-177.8 13.5-125.0	Semenova (1974)
Bosmina longirostris	*Chlorella* sp.	96	Sorokin (1966b)
Bosmina longirostris	Phytoplankton Bacteria	42.2 16.4	Gutel'mackher (1973)
Family: Daphnidae			
Daphnia longispina	*Chlorella* sp.	93	Sorokin (1966b)
Daphnia magna		56	Duncan et al. (1974)
Simocephalus espinosus	*Chlorella* sp.	59	Sorokin (1966b)
Simocephalus vetulus	*Chlorella* sp.	108	Sorokin (1966b)

(Continued)

Table 5 (Concluded)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Eucopepoda			
Family: Diaptomidae			
Diaptomus graciloides	Phytoplankton Bacteria	40.0 17.3	Gutel'mackher (1973)
Diaptomus graciloides	*Chlamydomonas eugamentos* *Chlorella vulgaris*	23-700 20-366	Kryutchkova and Rybak (1974)
PHYLUM: ROTATORIA			
Family: Brachionidae			
Brachionus plicatilis	*Dunaliella salina*	1000	Doohan (1973)
Brachionus rubens	*Chlorella vulgaris*	58-250	Pilarska (1977a)

66. Because only nine maximum grazing rates could be estimated from literature data, and because of the variability of those values, a frequency distribution of maximum grazing rates could not be established. Therefore, we attempted to develop several empirical formulations to estimate the maximum grazing rate, G_{max}, the constant, k, and the incipient limiting food concentration, B_{lim}.

67. When the Ivlev equation is solved for k at any given incipient limiting food concentration, B_{lim}, the value of k decreases as B_{lim} increases for <u>any</u> maximum grazing rate (Figure 14). If G_{max} is plotted against k, based on literature data (Table 3), a similar relationship is apparent (Figure 15). As G_{max} increases, k decreases. G_{max} appears to be linearly related to B_{lim}, as shown in Figure 16. Even though only a limited number of data points are available to plot Figures 15 and 16, we believe that the data are of good quality and the apparent relations among G_{max}, k, and B_{lim} are valid. These relationships are true <u>only</u> if zooplankton foods are edible and of a size range suitable for filtering. In general, these two requirements would be met under field conditions. The three equations based on literature data relating G_{max}, k, and B_{lim} can be written as follows (Note: For calculation, we have arbitrarily let B_{lim} equal the food concentration at which the observed grazing rate, G, is within 5 percent of the maximum grazing rate, G_{max}. Equations 6 and 7 are based on a temperature of 20°C):

$$k = 10^{(0.4773 - 1.0002 * \log (B_{lim}))} \quad ; R^2 = 1.00 \tag{5}$$

$$k = 10^{(-2.9664-0.9787 * \log (G_{max}))} \quad ; R^2 = 0.77 \tag{6}$$

$$G_{max} = 0.0788 + 0.0003105 * B_{lim} \quad ; R^2 \;\; 0.89 \tag{7}$$

68. If any one parameter is known, the above equations, although tentative, allow the calculation of any other grazing parameter. The following hypothetical argument supports Equation 7 as potentially the most useful relationship.

69. As we previously stated, Mayzaud and Poulet (1978) found a

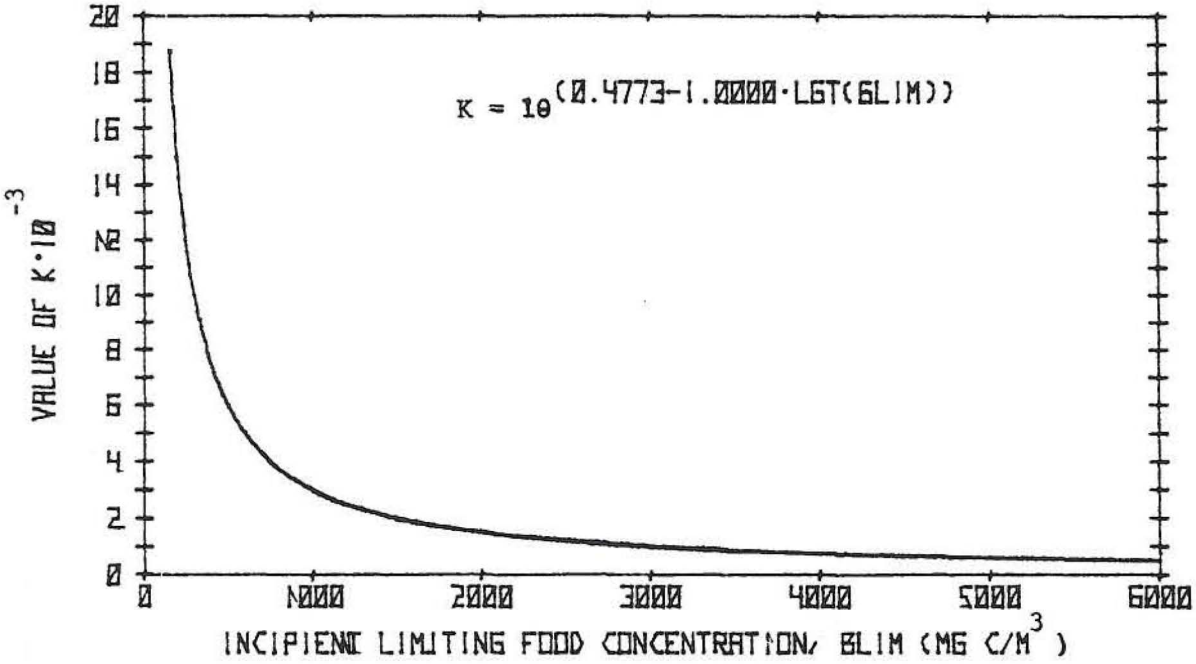

Figure 14. The relation of the constant, k, to the incipient limiting food concentration, B_{lim}. This relation is true for any value of G_{max}

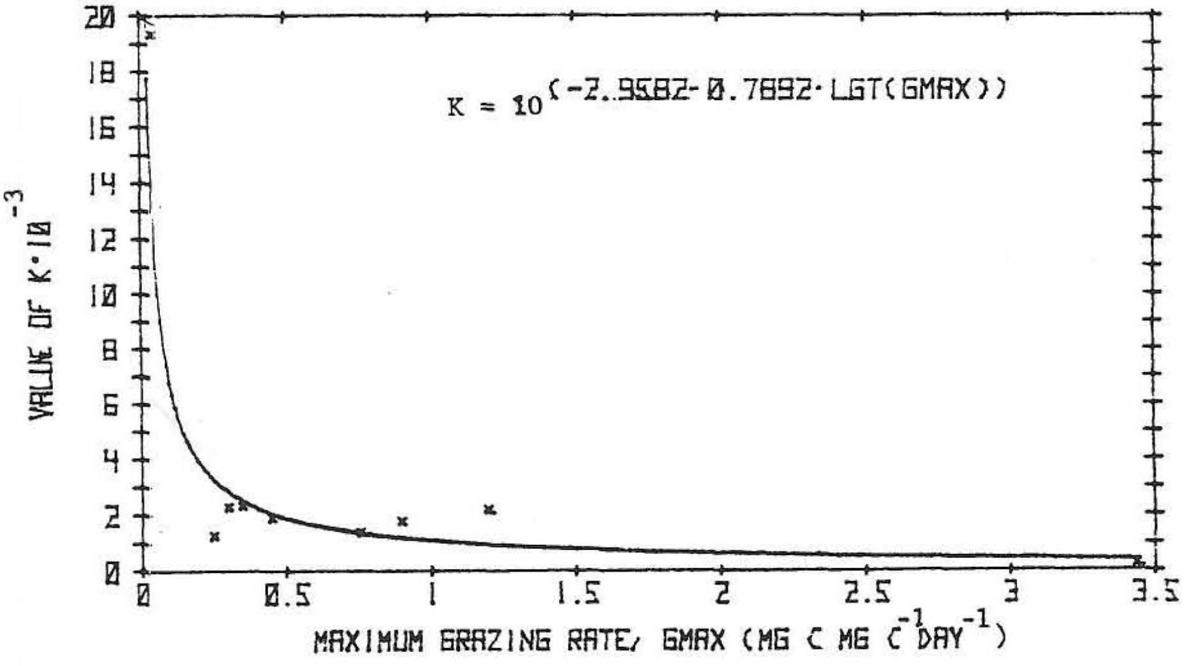

Figure 15. The relation of the constant, k, to the maximum grazing rate, G_{max}. The curve was fitted to values of k and G_{max} from Table 3

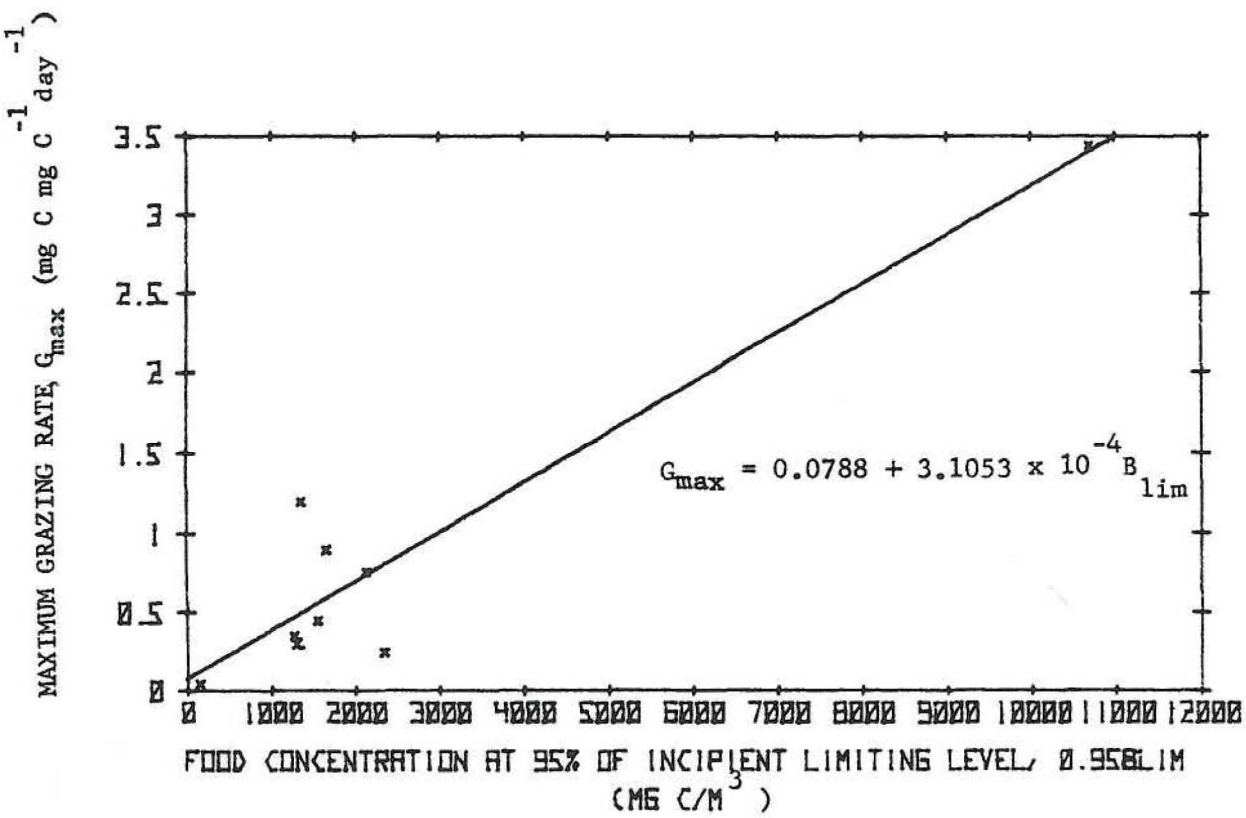

Figure 16. The relation of the maximum grazing rate, G_{max}, to the incipient limiting food concentration, Blim (values for 0.95 B_{lim} have actually been plotted because the Ivlev equation can not be directly solved for B_{lim}). The line was fitted from values in Table 3

linear relationship between food concentration and ingestion for five marine copepods. They also found that ingestion was linear up to the ambient concentrations, when copepods were feeding in a range of food concentrations that were below and above the ambient level. This result suggests that under most field conditions, when the zooplankters are acclimated to the ambient food concentration, they feed maximally at the ambient level. For all practical purposes, then, the ambient food concentration is equivalent to the incipient limiting concentration of laboratory studies. At higher food concentrations, grazing rate approaches an asymptote at G_{max}. If this argument is valid, it becomes clear that the observed grazing rate at the ambient food concentration is equivalent to, or closely approximates, the maximum grazing rate. If true, Equation 7 can be used to estimate the grazing rate for any ambient food concentration. The benefit of such a relationship is obvious. Zooplankton grazing could be described by a linear relationship for any food concentration. Only the biomass of zooplankton and the biomass of available food would need to be measured in the field.

70. The above argument, although supported by the results of Mayzaud and Poulet (1978), is not sufficiently documented in the literature to be generally accepted. Our analysis of the available data provides additional support. Perhaps Equation 7 could be incorporated into some preliminary simulations and these compared to simulations based on the more generally accepted zooplankton feeding constructs. Further experimental work should clarify these relationships.

71. In concluding this analysis, we describe the feeding construct of Mayzaud and Poulet (1978). Although problems are presented in applying the grazing relationship, we believe that it is more realistic than alternative formulations and should be used in the simulation of zooplankton feeding.

72. Mayzaud and Poulet proposed the following feeding construct, which we have changed to our terminology. The acclimation time for a significant increase in food supply, B, occurring over a period t is defined as Γ. Acclimation time corresponds to the maximum ingestion and digestion rates reached at a given food concentration. For $t \leq \Gamma$ the physiological response will follow a saturation-type curve. For $t > \Gamma$ the maximum grazing rate is shifted upward according to a linear relationship. For $t \leq \Gamma$ the grazing rate can be defined by Equation 3. If $0 < t < \Gamma$, the maximum grazing rate remains constant and independent of time. If $\Gamma < t < \infty$, and B is within natural limits, G_{max} can be defined as

$$G_{max} = ZB_t \tag{8}$$

where Z is a constant and B_t is the food concentration at time t. By substitution Equation 3 becomes

$$G = ZB_t \; (1-e^{-kB_t}) \tag{9}$$

This equation becomes linear when B_t is increasing. Values for Z for different G_{max} and B_t are presented in Table 6.

Table 6

Relationship Among G_{max}, B_t, and Z as Defined by Equation 8 and Based on the Data in Table 3

G_{max} (mg C mg C^{-1} Day^{-1})	B_t (mg C/m^3)	Z
0.5	1,356.5	3.68×10^{4}
1.0	2,966.8	3.37×10^{-4}
1.5	4,577.1	3.28×10^{-4}
2.0	6,187.4	3.23×10^{-4}
2.5	7,797.7	3.21×10^{-4}
3.0	9,408.0	3.19×10^{-4}
3.5	11,018.4	3.18×10^{-4}

The constant, k, can be determined by using either Equation 5 or Equation 6. The relationship between B_t and Z can be described mathematically by

$$Z = 10^{(-3.2295 - 0.06787 * \log (B_t))} \tag{10}$$

$$R^2 = 0.93$$

Mayzaud and Poulet (1978) report:

> Equation [9] can account for three ecological situations found in various data: a sudden large increase in phytoplankton results in saturation of the feeding system until acclimation has had sufficient time to take place; over a long time such as a yearly cycle, ingestion is directly proportional to food supply, and because the...environment has a highly variable energy supply the feeding system of herbivorous zooplankters is in a more or less continuous state of being acclimated. Hence we could sample a copepod population in a state of equilibrium with a saturation level at or close to the environmental particle concentration. If the sampling takes place during acclimation to an increase in particle

> concentration, the saturation will be obtained for values significantly smaller than the environmental concentration. If sampling occurs during an acclimation to a decrease in particulate concentration, a linear relationship with no apparent saturation will be observed.

Mayzaud and Poulet concluded by stating,

> At the moment we do not have experimental values for Γ but from the results of Mayzaud and Conover (1976) it should be <6 days and probably >24 h. Whether all copepods have such an acclimation ability remains to be seen. In the neritic environment off Nova Scotia it appears that both adult copepods and copepodites have it (Poulet 1977).

73. Brandl and Fernando (1975) found that, for three species of cyclopoid copepods, the predation rate was different among groups differing in their previous diet up to the fourth day after the transfer to the same diet. This suggests that Γ may be equal to or greater than 4 days. The acclimation time Γ can be empirically determined by varying its value within the above noted limits during simulation runs.

Food Selectivity by Zooplankton

74. All zooplankters are selective feeders resulting from a combination of (a) an organism's mechanical limitations in capturing and processing food items of varying size and configuration, (b) the chemical nature of the food, and (c) feeding behavior. Herbivorous filter feeders predominate in freshwater zooplankton communities. For purposes of describing a general zooplankton model, species in this group can all be regarded as passive, indiscriminate filter feeders subject to the mechanical and chemical restraints mentioned above. Scavia (1979) discussed selective feeding in a modeling context and commented on aspects needing further research.

75. Zooplankters have a wide variety of potential food sources available to them. Two questions are of central concern to any modeling effort: "What is the size range of food items eaten by zooplankton?" and "Is preference shown to one type of food over another?".

76. Size range of food particles consumed. The size of food

particles that are suitable for consumption vary by species. Generally, the larger the animal, the larger the size of food that can be eaten (Burns 1968b). For discussion we treat all zooplankton as a single community and hence are interested in the range of usable food sizes. Edmondson (1957), Jorgensen (1962), and Kryutchkova (1974) have reviewed literature on this subject and our conclusions draw heavily on these summaries.

77. No absolute size range can be established for a zooplankton community. We have defined size to mean the length in microns of the long axis of a food particle. Clearly, width and volume are also important factors. Reported literature values for the size of ingested particles range from approximately 0.2 to 100 μm in diameter, but most values are less than 20 μm. The preferred or most efficiently consumed particles are generally between 1 and 10 μm. Rotifers clearly feed on smaller particles, with the exception of Asplanchna, a predaceous genus. Ascertaining the maximum size of food consumed by predators is difficult because many species are raptorial feeders capable of tearing prey items into smaller particles before consumption. The range of sizes consumed (0.2 to 100 μm) potentially covers organisms from bacteria to large algae or algal colonies. We suggest that the grazing construct only allow the zooplankton community to feed on particles of 100 μm or less. Further division of the zooplankton community into smaller groups, i.e., rotifers, copepods, predators, etc., would necessitate establishing a maximum and minimum food size for each group. Although division of the zooplankton community may be highly desirable for some model applications, data needed to establish particle-size preference for subcategories of zooplankton are too few and variable within the major taxa.

78. Preference among food sources. Food preference is demonstrated if an organism consumes a food item in a proportion greater than the food item's relative contribution to the total of all available foods in the environment. Preferences among variable food sources have been incorporated into recent models (e.g., Scavia 1979). Most of these models use a food preference term or electivity index for each food source. Seldom are more than two types of food available to the grazing

community in simulation models, i.e., phytoplankton or detritus. Often values for the food preference terms are the modeler's best guess because little sound documentation exists.

a. Detritus and microflora as food

79. Detritus, or unidentifiable, particulate organic and inorganic material, is a significant food source for zooplankton in some models. Although ample evidence exists to show that detritus is consumed by zooplankton, no evidence exists to show that detritus is consumed preferentially. Several studies have shown that detritus is ingested in proportion to its composition in the environment. When detritus is included as a food source in a grazing formulation, it should be given equal ranking with other suitable foods.

80. Since Odum and de la Cruz (1963) first described organic detritus, a fairly extensive body of literature has developed that is concerned with the functional role of detritus in trophic webs of aquatic ecosystems. Detritus consists of organic carbon that is lost from any trophic level by nonpredatory means (e.g., nonpredatory mortality, egestion, excretion) or that is derived from allocthonous sources. The detritus food chain is any route by which chemical energy from detritus is made available to biota (Wetzel 1975). These definitions recognize bacterial action on detrital substrates as trophic transfer (Wetzel 1975). Goldman and Kimmel (1978) reviewed much of the previous work conducted on energy flow and matter cycling through detrital pathways and emphasized the importance of detritus in reservoirs.

81. The upper reaches of reservoirs typically act as sediment traps for tremendous loads of clay, silt, and detritus. As a result, river impoundments may receive a significant portion of their driving energy from inflowing allocthonous detritus. In Tuttle Creek Reservoir, Kansas, Marzolf (1978) found that 1200 mg $C \cdot m^{-2} \cdot day^{-1}$ came from allocthonous sources and only 70 mg $C \cdot m^{-2} \cdot day^{-1}$ from autochthonous origins. Sorokin (1972) suggested that 25 percent of the driving energy in Rybinsk Reservoir, USSR, was derived from allocthonous organic substances. Twenty-three percent of the organic matter in a Texas reservoir came from upstream areas (Lind 1971). In addition to the detritus flowing

into reservoirs, a substantial quantity may enter impoundments when new areas are inundated by high water levels (Romanenko 1966, Winberg 1972).

82. Diets of nonpredatory zooplankton often include significant quantities of detritus or bacteria (Smirnov 1962, Conover 1964, Petipa 1967, Andronikova et al. 1972, Poulet 1976). Edmondson (1957) discussed the potential importance of detritus in zooplankton diets and cited previous observations of zooplankton consuming detritus and bacteria. Bacteria made up 58 percent of the nonpredatory zooplankton diet during the freezing period in Red Lake, USSR (Andronikova et al. 1972). Marzolf (1978) observed zooplankton gorged with clay particles and detritus. Gutel'mackher (1973) determined that dispersed bacteria composed 28 to 38 percent of the diets of Bosmina longirostris, Holopedium gibberum, and Diaptomus graciloides.

83. Bacteria probably make indigestible detritus available to nonpredatory zooplankton (Edmondson 1957, Sorokin 1972). In some cases, microflora on the detritus may represent the primary source of energy (Overbeck 1972). That bacteria colonize detrital particles is well established (Rodina 1963; Paerl 1973, 1974). According to Rodina (1963), the mass of bacteria on detritus is often enormous, and an aggregate often consists of a small organic core with an overgrowth of bacteria and bacterial filaments.

84. Bacteria also may appear as free-living plankton (Azam and Hodson 1977, Kimmel 1978, Sieburth and Smetacek 1978). In fact, Sieburth and Smetacek (1978) found that the bacteria attached to the seston which passed through a 20-μm screen consisted of only about 0.1 percent of the total cells they concentrated on 0.2-μm nucleopore membranes. Although most dispersed bacteria probably are not filterable by zooplankton (Monakov and Sorokin 1972), colonization of detritus may increase the availability of dispersed bacteria for zooplankton consumption (Goldman and Kimmel 1978). Haney (1973), however, considered particles within the size range of 0.45 to 30 μm to be available for zooplankton consumption. Some dispersed bacteria probably are at the lower end of this size range.

85. Few data exist on the assimilation of detritus and bacteria

by zooplankton (Appendix C). Assimilation efficiencies of Cladocera feeding on phytoplankton (8 to 99 percent; $\bar{X} = 47.4$) tend to be higher than that of Cladocera fed detritus and bacteria (8 to 55 percent; $\bar{X} = 23.3$; Appendix C). Similarly, Copepoda assimilate algae (10 to 99 percent; $\bar{X} = 59.5$) somewhat more efficiently than they do yeast and bacteria (21 to 67 percent; $\bar{X} = 44.2$; Appendix C) (Gutel'mackher 1973; Green 1975).

86. Nonpredatory zooplankton fed detritus and bacteria apparently can survive, even though assimilation of these foods is relatively low. Baylor and Sutcliffe (1963) observed that *Artemia* sp. fed particulate, organic detritus grew as well as those shrimp fed yeast, through the fourth day of their experiment. Thereafter, *Artemia* continued to grow but at a slower rate than yeast-fed specimens. Cladocera fed sterile, crushed plant and animal detritus survived 38 days but did not reproduce effectively (Rodina 1963). When fed detritus that was colonized by bacteria, the Cladocera survived and reproduced through several generations. Apparently the bacteria provided certain vitamins needed by the Cladocera for reproduction and development. Other zooplankters also have been observed to survive, mature, and reproduce on diets of detritus and/or bacteria (Gellis and Clarke 1935, Rodina 1963, Yesipova 1969, Monakov 1972, Winberg et al. 1973).

87. Zooplankters apparently must feed on detritus and bacteria to balance their energy budgets when phytoplankton production is insufficient to support the biomass of zooplankton present. In the tropical Atlantic, food needs for zooplankton were 1.5 to 4 times greater than chlorophyll *a* primary production (Finenko and Zaika 1970). Nauwerck (1963) calculated that the July growth rates of *Diaptomus* sp. could not have been maintained with the available phytoplankton production. Like inefficient benthic herbivores that feed on detritus and bacteria (e.g., Hargrave 1971), zooplankters may have high tissue growth efficiencies and simply process large quantities of poorly assimilated food. Welch (1968) demonstrated an inverse relation between assimilability and growth efficiency.

88. In field studies, large temporal discrepancies have been observed between peaks in phytoplankton and the abundance of herbivorous

zooplankton. In fact, zooplankton dynamics occasionally correlate better with the production of bacteria than with that of phytoplankton (Moskalenko and Votinsev 1972, Jassby 1975). Colonization and partial decomposition of senescent algae by bacteria and fungi may make them secondarily available for zooplankton consumption (Edmondson 1957). Jassby and Goldman (1974) concluded that a majority of the phytoplankton losses in Castle Lake, California, were the result of natural senescence and not grazing.

89. A tremendous quantity of chemical energy in the form of bacteria has been largely ignored by limnologists. While bacterial biomass typically is low in most waters throughout the year (1 g wet weight per m^3 was a common estimate by Rodina (1963) and Sieburth and Semtacek (1978)), turnover time is rapid (e.g., 3 to 48 hr). As a result, bacterial production can exceed primary production under certain conditions (Winberg 1972, Jassby 1975). On a yearly basis, bacterial production is usually less than primary production, but of the same magnitude (Kuznetsov et al. 1966, Overbeck 1972, Pechlander et al. 1972, Tilzer 1972). Such a potential source of energy in reservoirs is of too great a magnitude to be ignored, even if inefficiently utilized.

90. If detritus is considered a second food source for zooplankton, then a term indicating preference for detritus or phytoplankton should be incorporated into a model's grazing construct. Four zooplankton models include detritus as a source of food for zooplankton (i.e., Menshutkin and Umnov 1970, Umnov 1972, MacCormick et al. 1974, Patten et al. 1975). The Wingra Model (MacCormick et al. 1974) includes a preference term for detrital and algal foods that usually was set at unity (i.e., indicating no preference), or that was empirically derived. Patten et al. (1975) assumed that small zooplankton feed 20 percent on phytoplankton and 80 percent on particulate organic matter. These values are similar to the percent composition (by weight) of these components in net seston. Menshutkin and Umnov (1970) and Umnov (1972) assigned zooplankton preferences for detritus or phytoplankton on the basis of the percent composition (by weight) of these components in the ecosystem. Data of Ryther (1954) and Lampert (1974) suggested that the

use of a preference term, based on the concentration of food particles of a filterable size, may be reasonable. Particle selection by Cladocera in these studies depended on the concentration of filterable-sized particles and not on the type of particles present. Particles are not rejected simply because they have limited food value. Copepods ingest and form fecal pellets of particles of India ink (Marshall and Orr 1952) or polystyrene pellets (Paffenhofer and Strickland 1970).

91. The seasonal abundance of phytoplankton, bacteria, and detritus may be the main factor determining the percent composition of these components in the diets of many zooplankton. For example, Poulet (1976) determined that the balance between living and nonliving particle consumption in Pseudocalanus minutus was related to the relative concentrations of these components within each particle peak (i.e., the size range of particles which are filtered at a maximum rate). Riley (1970) stated that such nonselective feeding, based on available particle size, should not distinguish between living and nonliving particles. Detrital carbon constituted 71 percent of the food ration of Pseudocalanus minutus (Poulet 1976). This figure is about the same as the percent composition of detritus in the seston of the sea (78 to 95 percent, Finenko and Zaika 1970; 76 percent, Beers and Steward 1969; 70 to 93 percent, Poulet 1976).

92. In some models, animals are limited to one food source. DiToro et al. (1971) and Steele (1974) developed models in which zooplankton fed exclusively on phytoplankton. Food of benthic organisms was limited to detritus in a model by Zahorcak (1974). Other models primarily have been concerned with particle size selection (e.g., Scavia et al. 1976, Taghon et al. 1978). Elaborate constructs dealing with food selection based on prey availability, catchability, and desirability (e.g., Park et al. 1974, Zahorcak 1974, Scavia et al. 1976) may not represent substantial improvements over single-food models if they cannot be effectively evaluated. While such interactions and behavior probably exist, they have not yet been adequately quantified.

93. Clesceri et al. (1977) presented a model simulating free and attached microflora, particulate and dissolved organic matter, and nitrogen and phosphate in limnetic areas. Feeding terms for bacteria were

the same as those used for zooplankton and benthos feeding in the Lake George model (Park et al. 1974). Insofar as we know, the effort of Clesceri et al. (1977) represented the first attempt to model bacteria dynamics.

94. In reviewing the literature on assimilation and feeding, we became aware of several gaps in the knowledge needed to effectively model zooplankton. We urgently need accurate methods for determining the percent composition and turnover of detritus, bacteria, and phytoplankton in seston. With these methods, we could better elucidate the seasonal dynamics of these components and determine their relationship to zooplankton feeding. In addition, more studies are needed of assimilation and survival when zooplankton are fed protozoa, detritus and/or bacteria, or various combinations for several generations. Until these data are available and incorporated into models of reservoir zooplankton, simulations of the real environment may be inaccurate.

95. Dissolved organic matter (DOM) is another potential source of food for benthos and zooplankton of which we know little. We do know that DOM is about 10 times more abundant than particulate organic matter (POM) in marine and freshwater ecosystems (Jorgensen 1962, Wetzel 1975). Data on the use of DOM by aquatic invertebrates are rare. Peloscolex multisetosus, an oligochaete, actively took up glycine from solution (Brinkhurst and Chua 1969). Epidermal tissues of soft-bodied marine invertebrates have been shown to actively transport dissolved, free amino acids. Larval forms with large surface-area-to-volume ratios, especially, may benefit from such uptake (West et al. 1977). Southward and Southward (1971) believed that some marine polychaetes can meet all of their nutritional requirements by absorbing DOM. Gellis and Clarke (1935) found that Daphnia magna could not survive in a glucose solution but could effectively use unfilterable, colloidal organic matter as food. The osmotic assimilation efficiency of DOM by Daphnia pulex in sterile water is about 2 percent (Monakov and Sorokin 1972). More research is necessary to determine what types of animals in reservoirs, if any, can directly (by uptake) or indirectly (via a bacterial trophic link) utilize the energy in DOM.

b. Selectivity among algae

96. Conflicting evidence on the nutritional value and grazability of blue-green algae has appeared for many years. Our review of assimilation, in a later section, clearly shows that blue-green algae are generally not as assimilable as are other algal species. This does not mean, however, that blue-green algae are ignored as a food source by zooplankton. Birge (1898) may have been the first worker to speculate on the ability of zooplankton to graze filamentous blue-green algae. He suggested, on the basis of qualitative observations, that Chydorus could utilize Anabaena but not Lyngbya.

97. Lefevre (1942) compared the suitability of many algal species as food for Daphnia magna and Daphnia pulex. Blue-green algae were not included in the analysis, but his results showed that species differences within the same genus could produce widely divergent suitability ratings. Because Lefevre did not measure actual consumption of the algal species he examined, his results are not directly comparable to more recent work. However, they do illustrate the contention that it is not necessarily the taxonomic position of the algae that makes it suitable or unsuitable as food but rather the attributes of each algal species such as size, shape, and toxicity.

98. Lefevre (1950) found that the filamentous blue-green Aphanizomenon gracile was unsuitable as food for Daphnia magna and D. pulex. Both species of Daphnia could filter the algae but rejected it because they could not ingest the filaments.

99. Ryther (1954) considered the possibility that Daphnia magna filtered large algal cells less efficiently than small cells. In a group of experiments in which Daphnia was fed mixed cultures containing equal numbers of the large Scenedesmus and the smaller Chlorella, each prey species was eaten in equal numbers suggesting no difference in filtering efficiency.

100. Ryther also suggested, then experimentally demonstrated, that the age of the algal culture was important in determining filtering rate. For all species investigated, Daphnia magna filtered senescent cells at a much lower rate than it filtered growing cells. Ryther

hypothesized that antibiotics produced by the senescent cultures inhibited Daphnia feeding. His results were supported by McMahon and Rigler (1965) and Stross et al. (1965).

101. Blazke (1966) found that Daphnia pulicaria was able to grow and reproduce when feeding on a bloom of blue-green algae. However, Arnold (1971) noted that bacteria may have been consumed along with the blue-green algae in Blazka's study.

102. In her study of Daphnia feeding in Heart Lake, Canada, Burns (1968a) found that the filamentous blue-green algae Anabaena, Oscillatoria, and Lyngbya were numerically dominant during the summer. Also present were colonies of Gomphosphaeria and Microptis. Daphnia filtering rate declined as the concentration of Anabaena colonies in the water increased. Burns noted,

> When Daphnia were feeding in lakewater, many of the colonies were drawn into the thoracic chamber. Most of the colonies were cast out by movements of the postabdomen alone, but many of the filaments came to lie in the food groove parallel to the long axis of the body. In D. rosea, an immediate and vigorous labral rejection occurred whenever an Anabaena filament, or cell from a filament, reached the region of the maxillules. Several rejections were sometimes necessary to dislodge a filament.

Burns suggested that the decline in Daphnia filtering rate could be due to the presence of the filamentous blue-green algae which interrupted the filtering process. Her results supported the conclusion that Daphnia rosea was not utilizing the predominant phytoplankton of Heart Lake for 5 months of the year.

103. Burns found, in contrast, that Daphnia galeata ingested single cells or small fragments of Anabaena at times when the food level in Heart Lake was low. Her hypothesis was that perhaps Daphnia galeata could use less desirable food sources in times of inadequate food supply.

104. Although Daphnia rosea and D. galeata showed similar filtering rates and feeding behavior in Heart Lake water, Burns noted,

> ...that during June, D. galeata adults ingested small colonies of a chrysophycean alga whereas D. rosea adults did not. This implies not only that an active selection of food particles in lakewater might occur in nature, as

has been suggested by other authors (Smith, 1936; Gajevskaya, 1961), but also that two species of *Daphnia* might differ in an ability to select food.

105. Schindler (1968) fed *Daphnia magna* three algal species separately (*Chlorella* sp., *Chlamydomonas* sp., and *Anabaena* sp.) and found no significant difference in the feeding rate. The assimilation rates of *Daphnia* fed *Chlorella* sp. and *Chlamydomonas* sp. were not significantly different, but the assimilation rate for *Anabaena* sp. was significantly lower. Food energy content (2 to 5 calories/mg) had a significant effect on feeding and assimilation.

106. Schindler noted that planktonic Copepoda and Cladocera from a turbid Minnesota lake, when observed in the laboratory, ate particles of different origin nonselectively, although there was some selection for size and shape of particles.

107. Experiments conducted by Gliwicz (1969) on eight zooplankton species fed various sizes of mineral grains and diatom frustules support the hypothesis that filtering may be primarily passive and mechanical. Gliwicz found that as the proportion of mineral particles in the food suspension increased, the amount consumed also increased. He concluded that when large amounts of valueless food which cladocerans cannot avoid or reject are present, filtering rates did not decrease. He also examined the contents of alimentary canals of various zooplankton species from Lakes Mikolajskie and Taltoursko, Poland. This quantitative study revealed that the following species consumed blue-green algae along with other foods: *Daphnia cucullata*, *D. longispina*, *Bosmina coregoni*, *B. longirostris*, *Brachionus angularis*, and *Asplanchna priodonta*.

108. McQueen (1970) found that *Diaptomus oregonensis* did not feed on the platelike colonies of the blue-green *Merismopedia* in Marion Lake, British Columbia (although this species was of a filterable size), nor on two species of the diatom *Cyclotella* that were within the size range normally eaten by *Diaptomus*. McQueen concluded that cell type, rather than size and concentration alone, is important in determining filtering rates.

109. Schindler (1971) fed *Daphnia longispina*, *Diaptomus gracilis*,

and Cyclops strenuus 11 algal species, three of which were blue-green algae. The zooplankters ate each of the 11 species, although the assimilation efficiencies were highly variable.

110. Arnold (1971), who examined the effects of seven species of blue-green algae on Daphnia pulex, found that ingestion, assimilation, survival, and reproduction were lower in specimens fed blue-green algae than in those fed green algae. The degree to which the different blue-green algae affected the Daphnia was variable. Arnold concluded that the blue-green algae tested did not supply sufficient nutrition to support the Daphnia pulex population unless additional food sources were available.

111. Porter (1973), who examined in situ the selective grazing of algae by a zooplankton community in Fuller Pond, Connecticut, reported that artificial increases in grazing pressure resulted in a decline of the phytoplankton community as a whole. The most heavily grazed groups were ciliates, small algal species, large diatoms, flagellates, and nanoplankton. Unaffected groups were large algal species, small blue-green algae, small diatoms, large desmids, large dinoflagellates, and large chrysophytes. Large blue-green algae showed a variable response and large green algae increased.

112. Anabaena affinis and A. flos-aquae were rarely consumed by the zooplankton and were unaffected by increased grazing pressure. The green algae that were enhanced by grazing were encased in gelatinous sheaths and passed through the gut intact. Sphaerocystis schroeteri and Elakatothrix gelatinosa reproduced after gut passage.

113. Porter suggested that gelatinous green algae must be included with blue-green algae and other very large species as being poorly utilized as food by zooplankton. She concluded,

> By their responses to grazing, algae can be divided into three major groupings that cut across taxonomic lines. One contains species that are large, rare, or filamentous and seldom found in the guts of the zooplankton, either because they are not eaten or are actively rejected. They are unaffected by manipulations of grazing pressure. The second contains small, edible species that are eaten, digested and suppressed by grazers. The third contains species encased in thick gelatinous sheaths that pass through the grazers, frequently intact and in viable condition. These are

> increased by an increase in grazers. Grazing pressure, like physical and chemical factors, may determine the relative proportions of algal species and drive seasonal succession from a spring association dominated by edible flagellates and diatoms to gelatinous greens and filamentous blue-greens in autumn. The impact of grazing on the phytoplankton community is determined by the proportions of suppressed, increased and unaffected algae present.

114. In a continuation of her study, Porter (1975) found blue-green algae to be consumed in limited quantities by three zooplankters in Fuller Pond, Connecticut. _Cyclops scutifer_ fed to a very small extent on _Aphanothece_ sp. (4.3 percent of gut volume) and _Chroococcus limneticus_ (3.5 percent). Only _Daphnia galeata_ consumed _Anabaena flos-Aquae_ (0.2 percent), along with seven other species of blue-green algae. She presented evidence to show that some species of blue-green and green algae with gelatinous sheaths can be consumed and pass through the digestive tract of zooplankters intact and viable.

115. Haney (1973) contrasted his work with that of Burns (1968a). Contrary to Burn's conclusions, he found that it was unlikely that _Anabaena_ filaments were the direct cause of the rapid decline in zooplankton filtering rates in the spring in Heart Lake, Canada.

116. O'Brien and DeNoyelles (1974), who fed _Ceriodaphnia reticulata_ on a natural assemblage of phytoplankton, with and without the colonial blue-green algae _Microcystis aeruginosa_ added to the culture, found that the presence or absence of _M. aeruginosa_ had no significant effect on the filtering rate. The authors did not state whether or not _Ceriodaphnia_ consumed any of the blue-green algae.

117. Geller (1975), after examining the filtering rate of _Daphnia pulex_ on eight algal species in pure culture, showed that _Scenedesmus_, _Nitzchia_, and _Asterionella_ were all filtered at about the same rate. _Staurastrum_ and the blue-green _Microcystis_ were filtered at a much lower rate, which Geller attributed to cell size and shape and the cells gelatinous sheath. _Anabaena_ was filtered very little if at all. The green alga _Stichococcus_ was filtered at a reduced rate that was explained by the small cell size and reduced filtering efficiency of _Daphnia_. Geller stated,

> The ingestion rates measured during feeding with blue-green algae permit the assumption that they are accepted if they are individual cells in suspension, though the ingestion rates do not reach those for green algae and diatoms, which are taken up quite readily. Filamentous forms, e.g., colonies of Anabaena, which in the present investigation were short filaments of 50-200 cells, are taken up to a very small extent.

118. Hayward and Gallup (1976) examined the filtering and feeding rates of Daphnia schodleri fed seven species of algae. Feeding occurred for all species except the filamentous Anabaena and Aphanizomenon, both blue-green species. Both species were rejected by Daphnia, and high mortality rates occurred. Daphnia schodleri did not eat single cells of Anabaena when the filamentous chains were broken up. The authors suggested that Daphnia may be able to recognize Anabaena by chemical and physical detection.

119. Pourriot (1977), who reviewed the food habits of rotifers, stated, "The polyphagous Keratella species (quadrata group) feed on many kinds of food including detritus and small living cells (Flagellates, green algae) but none ingested the cyanophycean Synechocystis which is of suitable size."

120. Pourriot also listed 28 species of filter-feeding rotifers and their foods. Of the 18 species of freshwater rotifers listed, 17 did not ingest Cyanophyceae. One species, Brachionus diversicornis, ingested blue-green algae (species unspecified) and exhibited moderate reproduction. None of the seven raptorial feeding species of rotifers listed fed on blue-green algae, but rather on large Cryptomonadales, Chyrsomonadales, and some diatoms and Centrales. Two of the three brackish or alkaline water species listed fed on blue-green algae and reproduced successfully. Both of these species were in the genus Brachionus. It appears that Brachionus is the only rotifer genus utilizing blue-green algae. Many of the 28 species did not feed on other algal groups or on detritus and bacteria. Most species except the raptorial feeders maintained themselves reasonably well on detritus.

121. Webster and Peters (1978), who performed experiments to see if large zooplankters were differentially affected by blue-green algal

filaments over small zooplankters, indicated that in large zooplankters (Daphnia pulex, D. ambigua, Simocephalus vetulus) the filtering rate declined and the rejection rate increased as the filament concentration increased. The filtering rates for Bosmina longirostris, the smallest animal, showed little change with variations in filament concentrations. Results for Ceriodaphnia quadrangula were variable. These results show that filtering of large zooplankters is impeded by the presence of filamentous blue-green algae.

122. Published data generally indicate that the zooplankton community, as a whole, is capable of filtering and consuming all major algal groups, including the blue-green Myxophyceae. The size, shape, and chemical nature of the algae available as food appear to be of primary importance in controlling the rate of consumption. Senescent cells have been shown to inhibit feeding, and this chemical inhibition is not limited to blue-green algae. Large species with gelatinous sheaths are consumed by zooplankton but may pass through the digestive tract undamaged and perhaps enhanced in terms of increased growth rates. Rejection and reduced feeding may occur in the presence of large quantities of filamentous algae.

123. With respect to water quality problems resulting from eutrophication, the blue-green algae pose the most serious problem. The blue-green "bloom" species, such as Anabaena and Aphanizomenon, are filamentous forms that are unlikely to be consumed by the zooplankters. Even under unperturbed conditions, such as might be found in natural lakes, filamentous blue-green algae may predominate in the lake phytoplankton during the summer and early fall. In any situation where filamentous algal forms become a significant proportion of the phytoplankton community, grazing rates are affected. Grazing on these species should not be modeled at the same rate as that on other nonfilamentous forms.

124. Model construct. In view of the water quality orientation of the model which this report is intended to supplement, we propose the following construct based on our literature evaluation. First, food preference is equal among all potential food sources except filamentous algae.

Filamentous noncyanophyte species are normally not water quality problems, nor do they predominate phytoplankton of reservoirs. We do not believe sufficient justification exists to separate these species from the bulk of the phytoplankton community. Filamentous blue-green algae should be distinguished from other algal groups and should be grazed at a lower rate. To reduce the grazing rate on filamentous blue-green algae, the modeler should introduce a preference term into the grazing equation. The magnitude of the term is not supportable quantitatively by literature data but probably should be allowed to range from 0 (no grazing) to 0.3. The greater the concentration of filamentous blue-green algae in the total algal concentration, the lower the total grazing rate. This construct can be written as:

$$G_i = ZB_t \left[1 - e^{-kB_i \left(\frac{W_i B_i}{\Sigma W_i B_i} \right)} \right] \tag{11}$$

where

G_i = observed grazing rate on food type i
Z = proportionality constant defined by Equation 10
B_t = concentration of food at time t
B_i = concentration of food type i
W_i = preference coefficient for food type i
k = proportionality constant

Effect of Temperature on Consumption

125. Temperature is known to influence many types of biological functions, including the filtering rates and hence the grazing rates of filter-feeding aquatic organisms. We next review information on the effects of temperature on zooplankton grazing rates, analyze these results critically, and, finally, propose a model construct incorporating temperature into the grazing function. Although alluded to here, lethal temperature limits are discussed in the section "Nonpredatory Mortality," page 166.

126. Literature synopsis. The earliest reference to temperature effects on the grazing rates of freshwater zooplankters is that of Cohn (1958). His study of *Daphnia pulex* and *D. schodleri* showed no change in the grazing rates over the limited temperature range of 17° to 21°C. Nauwerck (1959), who conducted in situ experiments at Lake Erken, Sweden, with *Daphnia longispina* and *Diaptomus* sp., found that over a temperature range of 8° to 18°C, they both filtered most rapidly between 16° and 18°C.

127. The first comprehensive examination of the influence of water temperature on feeding behavior was conducted by McMahon (1965) on *Daphnia magna*. The feeding response was recorded at temperatures ranging from 5° to 35°C. At food concentrations above the incipient limiting level, the grazing rate reached a maximum at 24°C. McMahon found that at food concentrations below the incipient limiting level, the maximum grazing rate was reached at 28°C, but it was not clear whether this rate was significantly different from the rate at 24°C. Kryutchkova and Kondratyuk (1966) found that *Daphnia pulex* achieved a maximum filtering rate at 24°C, over the temperature range of 18° to 26°C.

128. Burns and Rigler (1967) found the optimum temperature for *Daphnia rosea* to be 20°C. McMahon (1968) studied the rate of movement of the thoracic appendages in *Daphnia magna*, as a reflection of filtering rate, and found that *Daphnia* cultured in the laboratory at 24°C had a slightly higher rate of thoracic appendage movement than those cultured in open field tanks of natural lake water at 16° ± 4°C. Schindler (1968) found no significant difference in the grazing rate of *Daphnia magna* at 10° and 20°C.

129. Burns (1969b) examined the filtering rates of immature and adult instars of four species of *Daphnia* at three temperatures: 15°, 20°, and 25°C. Adult and immature *D. magna* showed increasing filtering rates with increasing temperature. Adult *D. schodleri* showed a peak at 20°C, while the immatures reached a maximum filtering rate at 15°C with declining rates as temperatures increased. Adult *D. pulex* and *D. galeata* reached a maximum filtering rate at 20°C, while the immatures of these species showed increasing filtering rates at temperatures up to 25°C. These results indicate that there are species differences as well as age

differences in the filtering response to temperature.

130. Daphnia rosea raised at 12°C were used in a study of the effects of temperature on feeding behavior by Kibby (1971a). The maximum filtering rate was at 14°C but was not significantly different from the rate at 12°C. These results differ from those reported earlier by Burns and Rigler (1967) and illustrate the importance of acclimation temperature in determining optimum temperatures for grazing.

131. Chisholm et al. (1975) studied the effects of temperature on the filtering rate of Daphnia middendorffiana, a species of primarily Arctic and alpine distribution. The maximum filtering rate was at temperatures near 12°C for ages of Daphnia tested and decreased at higher and lower temperatures.

132. Perhaps the most comprehensive examination of the influence of temperature on the grazing rate of a zooplankter was conducted by Geller (1975) on Daphnia pulex. He showed that the previous temperature exposure of the animals is very important in determining grazing rate. Geller made a distinction between short-term acclimation of hours to days and long-term acclimation from weeks to months. Animals acclimated to 15°C and then tested at 10°, 15°, 20°, and 25°C had higher grazing rates at temperatures other than their acclimation temperature. At an acclimation temperature of 15°C the grazing rate reached a maximum at 20°C. Temperature responses were similar for animals acclimated to the other test temperatures. In another set of experiments, in which Geller examined the grazing rate of Daphnia that had been acclimated to the test temperatures for periods up to 3 years, grazing rate increased in a linear manner with temperature. Such a linear relation might be expected under field conditions, provided ambient temperature did not change too rapidly (i.e., on the order of 1° to 2°C per week over a seasonal period).

133. In support of Geller's results, Zankai and Ponyi (1976) found the filtering rate of Eudiaptomus gracilis (= Diaptomus gracilis) to be linearly related to temperature over the temperature range of 0° to 27°C. Gophen (1976) found that the grazing rate of Ceriodaphnia reticulata increased linearly over the range of 15° to 27°C. Hayward and

Gallup (1976), who studied the grazing rate of Daphnia schodleri at temperatures of from 5° to 30°C, found an increase in grazing rate with temperature up to a maximum at 20°C. At higher temperatures grazing declined.

134. Calamoecia lucasi, a freshwater copepod of a primarily tropical marine genus, was studied by Green (1975). He examined the filtering rate of adults and immature instars of this species from 10° to 25°C. Results indicate that filtering rates increased with temperature up to 20°C. At higher temperatures filtering declined for adult females and copepodite stages III, IV, and V. Filtering remained relatively constant between 20° and 25°C for nauplii, and filtering increased slightly for copepodites I and II and for adult males.

135. No information is available on the effects of temperature on the grazing rates of rotifers. Table 7 summarizes the results of the papers cited in this review.

136. Analysis. With the exception of Nauwerck (1959), all information on the effects of temperature on grazing rates was derived in controlled laboratory studies. Consequently, it is imperative that the previous thermal history of the test animals be known. In attempting to model temperature effects, a data base that closely reflects the natural environmental conditions is needed. With respect to temperature, zooplankton in a natural environment are acclimated at any period of time to a specific thermal regime, usually diel in character. Changes in the thermal regime over days to months normally occur gradually and allow zooplankton to acclimate physiologically and behaviorly to meet these changes. Seldom are zooplankters faced with sudden temperature changes such as might be experienced upon entrainment in a thermal plume from a power plant. Laboratory studies in which test animals are allowed to fully acclimate to the test temperatures can be expected to best reflect field conditions.

137. Work by Geller (1975) on Daphnia pulex represents the most comprehensive examination of the role of temperature acclimation yet undertaken. Geller concluded that the maximum time required for temperature acclimation for newly established cultures was proportional to the

Table 7

Summary of Literature Data on the Effects of Temperature on the Grazing Rates of Filter-Feeding Zooplankton

Taxa	Temperature (°C) to Which the Animals Were Assumed to be Acclimated	Period Allowed for Animals to Adjust to the Test Temperature	Grazing Rates of Adult Zooplankters Expressed as a Percentage of the Maximum Observed Rate (100% = Maximum Observed Rate)																				Reference
			Temperature (°C)																				
			5	7	8	10	12	14	15	16	17	18	20	22	24	25	26	27	28	30	33	35	
ORDER: Cladocera																							
Family: Daphnidae																							
Ceriodaphnia reticulata	Variable	24 hr							39					94				100					Gophen (1976)
Daphnia galeata	15,20, or 25	Several weeks							26				100			91							Burns (1969b)
Daphnia longispina	Variable	Na								100	100	100											Nauwerck (1959)
Daphnia magna	20	1 hr	8			16			25				41		100				49		45	5	McMahon (1965)
Daphnia magna	15,20, or 25	Several weeks							54				88			100							Burns (1969b)
Daphnia middendorffiana	Variable	1 hr	21				100				66												Chisholm et al. (1975)
Daphnia pulex	Variable	24 hr**										52	58		100		61						Kryutchkova and Kondratyuk (1966) as reported by Geller (1975)
Daphnia pulex	15,20, or 25	Several weeks							81				100			59							Burns (1969b)
Daphnia pulex	15	None				60			45				100			91							Geller (1975)
Daphnia pulex	7,10,15,20, or 25	Up to 3 years		24		35			54				74			100							Geller (1975)
Daphnia rosea	20	48 hr	48			63			87				100			90							Burns and Rigler (1967)
Daphnia rosea	12	48 hr	67		82	90	98	100		94		89	85			81							Kibby (1971a)
Daphnia schedleri	15,20, or 25	Several weeks							53				100			68							Burns (1969b)
Daphnia schedleri	20	12 hr?	26			60			87				100			91					71		Hayward and Gallup (1976)
ORDER: Eucopenpoda																							
Family: Centropagidae																							
Calamoecia lucasi	Variable	48 hr				29			51				100			86							Green (1975)
Family: Diaptomidae																							
Diaptomus sp.	Variable	Na*								100	100	100											Nauwerck (1959)
ORDER: Eucopepoda																							
Family: Centropagidae																							
Calamoegia lucasi	Variable	48 hr				29			51				100			86							Green (1975)
Family: Diaptomidae																							
Diaptomus sp.	Variable	Na*								100	100	100											Nauwerck (1959)

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* Not applicable; experiment was conducted in situ in a natural lake.

** Test temperatures ranged from 18° to 30°C.

growth rate. He estimated this time period to be about 6 weeks at temperatures near 7° to 10°C, and about 4 weeks at temperatures of 15°C or higher. Geller noted, "The physiological adaptability of Daphnia to environmental temperature can be fully realized only if they are reared from eggs at a constant temperature."

138. A comparison of literature values of the time periods allowed for animals to acclimate to test temperatures (Table 7) clearly indicates that most experimental results are based on insufficient acclimation periods to reflect the gradual adjustments made to thermal change by field populations. Only the work by Geller (1975), and possibly Burns (1969b), allowed sufficient time for acclimation. The fact that the results of different authors do not agree led Geller (1975) to the conclusion that it was impossible to calculate the temperature effect for even a single species of Daphnia (Figure 17).

139. Early workers recognized the importance of thermal history on the feeding behavior of zooplankton (Cohn 1958, Nauwerck 1959), but for many years information was unavailable on the period of time necessary to fully acclimate animals to test temperatures. Kibby (1971a) was first to examine acclimation temperature as a factor influencing filtering rates. His results for Daphnia rosea acclimated to 12°C, when compared with results for this species acclimated to 20°C (Burns and Rigler 1967), indicated that filtering rates may be higher at lower temperatures than previously demonstrated (Figure 18). Since the acclimation period of Burns and Rigler was 48 hr, it is evident that this time period is insufficient to allow for complete acclimation.

140. Burns (1969b) allowed four species of Daphnia to acclimate for "several weeks" before conducting her tests. By the standards for acclimation time presented by Geller (1975), a period of about 4 weeks would be needed for Daphnia pulex at temperatures above 15°C. Therefore, it is not clear whether Burns allowed sufficient acclimation time. Her results show that the filtering rate of Daphnia magna increased over the range of temperatures tested, while rates for D. pulex, D. schodleri, and D. galeata reached a maximum at 20°C and declined at higher temperatures. Geller (1975) found that acclimated Daphnia pulex showed

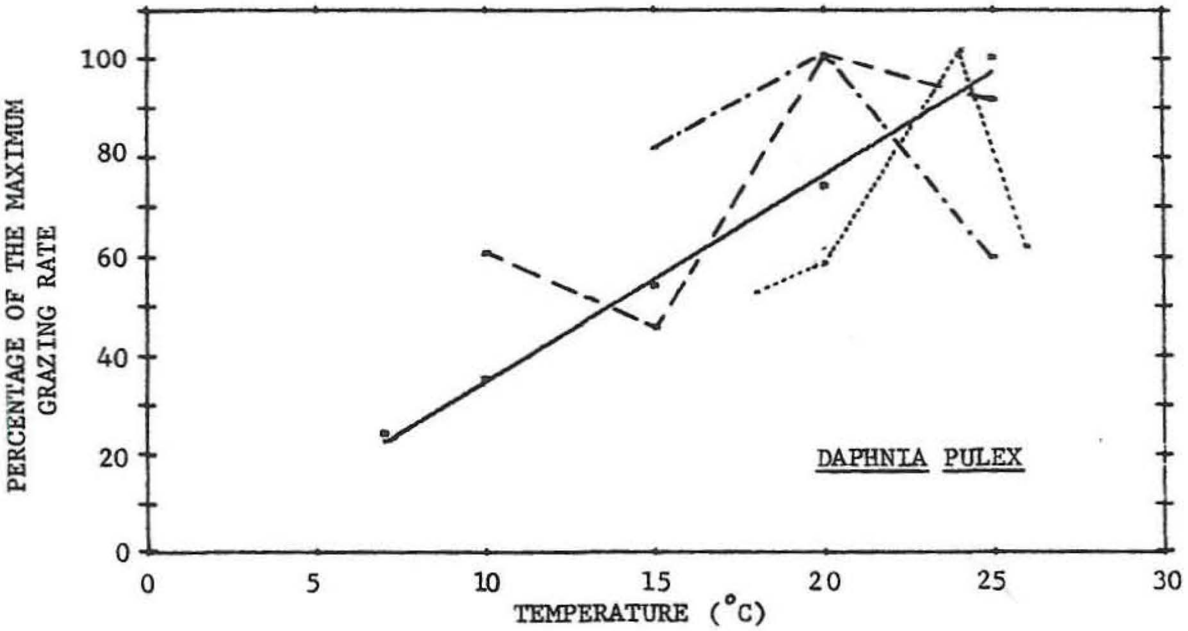

Figure 17. Grazing rate as a function of temperature for Daphnia pulex. Based on the data of Kryutchkova and Knodratyuk (1966) (······), Burns (1969b) (-·-·-·), Geller (1975) (——— for long-term acclimation), and Geller (1975) (— — — for short-term acclimation)

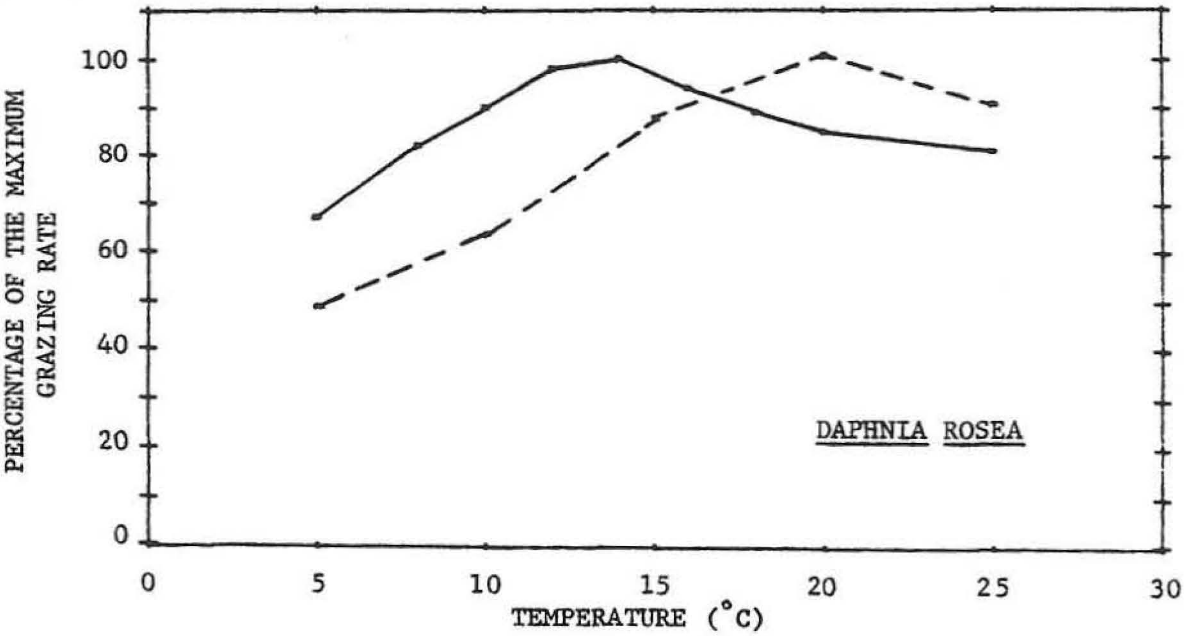

Figure 18. Grazing rate as a function of temperature for Daphnia rosea. Based on the data of Kibby (1971a) (———) and Burns and Rigler (1967) (— — —)

linearly increasing filtering rates with increasing temperature over the range of temperatures tested. Most reported temperature "optima" for grazing must, therefore, be considered to be responses of incompletely acclimated animals to temperature stress. Such results do not reflect the normal physiological response of acclimated animals. These results are, however, valuable when one is considering short-term responses of zooplankters to abrupt changes in temperature, such as might occur upon entrainment in the thermal plumes of power plants.

141. Temperatures of 20° or 25°C are the optimum temperatures for grazing (Table 7). It is clear that these optima are to a great extent artifacts of experimental design. Most authors measure grazing rates at fairly wide intervals, for example 5°, 10°, 20°, 25°, and 30°C. Because these experimental designs did not allow for a continuum of temperatures, it could not be ascertained whether the optimum grazing rate occurred at the cited temperature. Referring to Table 7, one can determine that 20° and 25°C are almost the most frequently measured temperatures.

142. Model construct. The form of the relationship between temperature and grazing rate is unclear for reasons previously discussed. Based on a theoretical argument, a maximum (or optimum) grazing rate must exist at some temperature, for a given food concentration, near the upper lethal limit of the organism. Beyond this temperature one would expect grazing to decline or cease completely as physiological processes become impaired. For field populations not under stress from thermal pollution, it is unlikely that lethal or near-lethal temperatures would occur for long periods (1 day or more in the model).

143. Based on this argument and on the assumption that field populations gradually acclimate to temperature changes, we propose a linear model to describe the relationship between grazing rate and temperature (Figure 19). The equation for Figure 19 can be written,

$$y = 0.67T - 0.33 \qquad (12)$$

where y = scalar of the grazing rate and T = temperature (°C). Such a relationship, although lacking some biological reality, is in

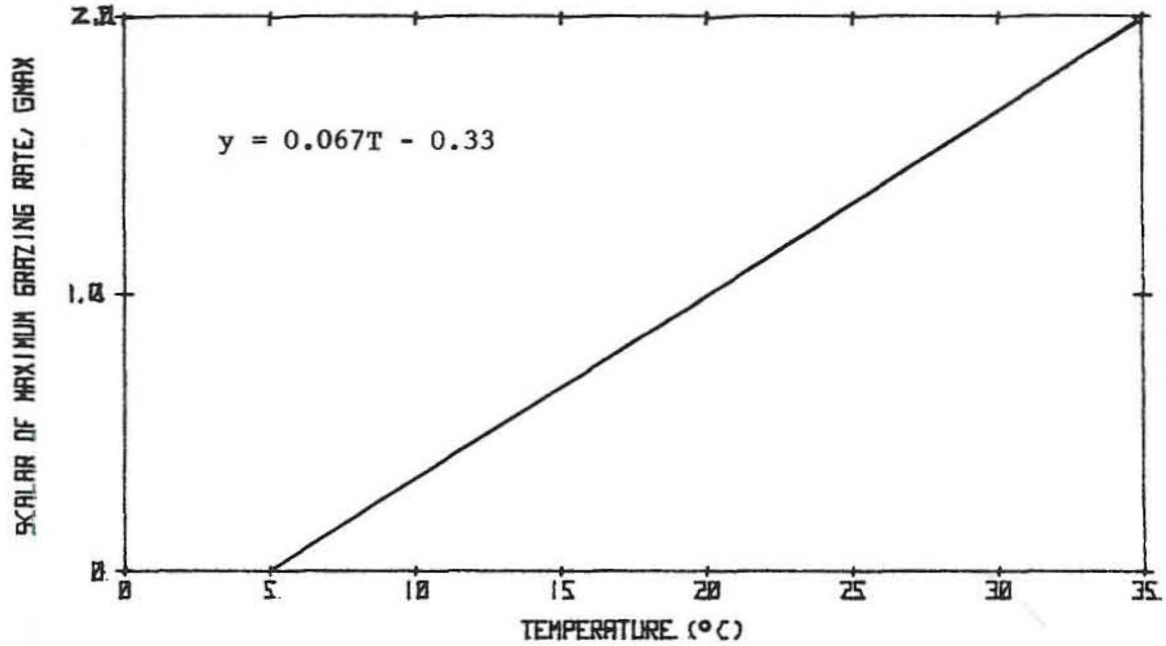

Figure 19. The relation of temperature to the relative increase in grazing rates for animals fully acclimated to test temperatures. The maximum grazing rate is equal to one on the ordinate

accordance with the results of Geller (1975). The bounds of the model are the lower and upper lethal temperatures for the species, approximately 0° to 34°C. This model is predicated on zooplankton populations from temperate lakes and does not consider the synergistic effects of temperature with metabolic processes and food concentration, although these factors are recognized as influencing variables (Chisholm et al. 1975, Hayward and Gallup 1976).

144. Clearly, a second construct is needed if abrupt thermal changes need to be incorporated into the modeling framework. Again, thermal pollution effects serve as an example. The grazing response increases with temperature to a maximum value and then declines at higher temperatures, with a cessation of grazing at the upper lethal limit (Figure 20).

145. Most laboratory studies support a function of this form. The optimum grazing rate usually occurs at or only slightly above the acclimation temperature of the animal. Therefore, the temperature at which the maximum grazing rate occurs differs for an animal acclimated

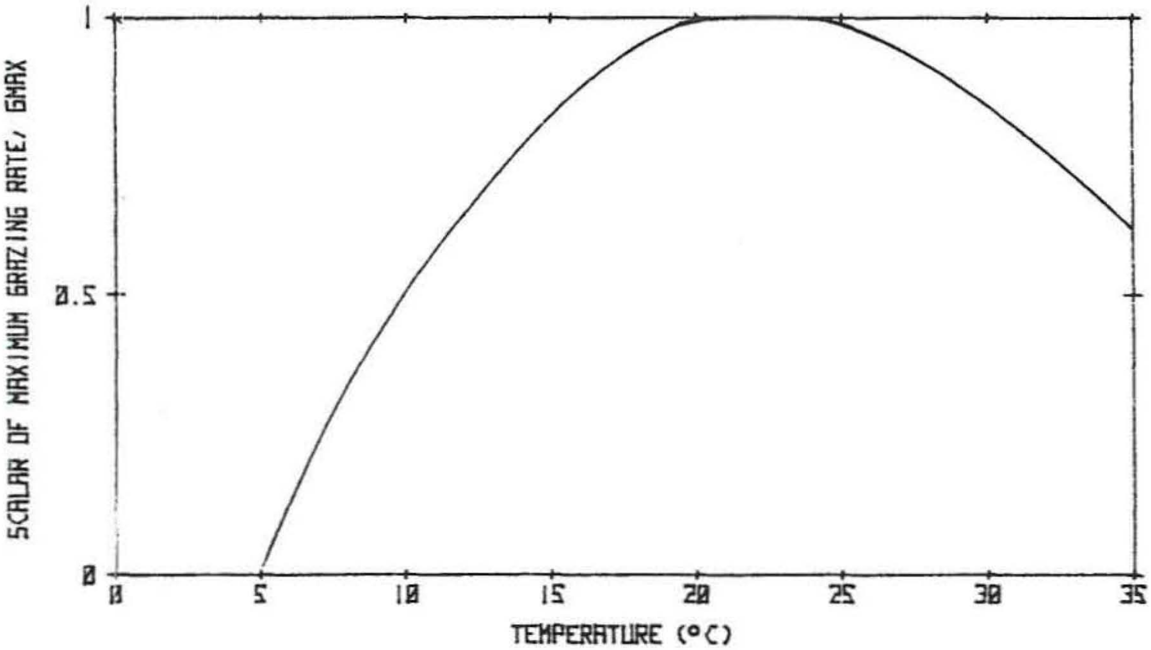

Figure 20. The relation of temperature to the relative increase in grazing rate for animals incompletely acclimated to test temperatures. In this example, the animal is fully acclimated to 20°C. The maximum grazing rate is equal to one on the ordinate

to 10°C, and subjected to a sudden heat stress, than it will be for an animal acclimated to 20°C and subjected to the same relative stress. Furthermore, upper and lower lethal temperature limits will vary.

146. Because no data are available on the maximum grazing rates of animals fully acclimated to various temperatures, the following construct is proposed. For animals acclimated to temperatures between 0° and 30°C, the maximum grazing rate is assumed to occur at the acclimation temperature and to remain constant with increasing temperature until the acclimation temperature plus 20 percent is reached. If the acclimation temperature is 30° to 34°C, the maximum grazing rate is assumed to be constant up to 34°C. Temperatures above 34°C are considered lethal. Temperatures at 30°C and above are not likely to normally occur in the field for periods long enough for acclimation to occur. Indeed, Geller (1975) stated that Daphnia pulex could not be successfully raised for any length of time at temperatures above 27°C. Burns (1969b) noted that temperatures above 25°C rarely occur in temperate lakes inhabited by Daphnia pulex or D. galeata, two widely distributed zooplankters.

147. To complete this construct we must define the form of the function above and below the temperatures at which maximum grazing occurs. Experimental results indicate that grazing tapers off less rapidly as temperatures decline from the maximum grazing temperature than occurs as temperatures increase above the maximum grazing temperature. Furthermore, filter-feeding zooplankters tend to graze at a greater rate at temperatures closer to their upper lethal limit than to their lower lethal limit (Figure 20). A generalized biological reaction rate curve similar to that described by Thornton and Lessem (1978) would adequately define this function. The reader is referred to this paper for details. The upper and lower lethal temperature limits must be known for each acclimation temperature. These data are unavailable for all temperatures for even one zooplankton species. In light of this, we have proposed such limits based on qualitative judgment (Table 8).

Diel Variations in Filtering and Feeding Rates

148. Most modelers of zooplankton grazing assume that the grazing rate remains constant on a diel basis, the rate being determined only by food concentration and temperature. In recent years it has become increasingly clear that grazing is a complex interaction among food supply and its distribution, zooplankton food habits, feeding behavior, and environmental variables. The role of zooplankton migratory behavior and endogenous rhythms is now recognized as a major influence on phytoplankton dynamics. A number of models now include diel vertical migrations of zooplankton. Bowers (1979) reviewed the role of vertical migration of zooplankton and its incorporation into simulation models of zooplankton grazing. The objective of the present section is to review the experimental evidence for diel variations in the grazing of freshwater zooplankton and to propose a simplified construct for including these changes in the grazing function.

149. Literature synopsis. Nauwerck (1959) in his study of the plankton of Lake Erken was the first worker to comment on diel changes in zooplankton grazing. He found that Eudiaptomus graciloides fed more

Table 8

Acclimation Temperature, Upper and Lower Lethal Temperatures, and the Temperature Range for a Constant Maximum Grazing Rate for Zooplankters Exposed to Rapid Temperature Stress

Acclimation Temperature, °C	Lower Lethal Temperature Limit, °C	Upper Lethal Temperature Limit, °C	Temperature (°C) Range Over Which the Maximum Grazing Rate Remains Constant (Ta to 1.2 Ta)
0	--	--	Lethal
5	0	25	5-6
10	0	30	10-12
15	2	33	15-18
20	5	34	20-24
25	7	34	25-30
29	10	34	29-34
30	10	34	30-34
31	12	34	31-34
34	15	34	34
35			Lethal - No Grazing

actively during the day than at night. However, he found the opposite to be true for Daphnia longispina. Haney (1973) reported on unpublished data of Gliwicz, who found that zooplankton feeding declined at night by 7 to 20 percent in two Polish lakes. Haney (1973) found contradictory evidence in Heart Lake, Canada. He found that zooplankton migrated toward the surface at night, but found no difference between the grazing rate at noon and midnight. Repeating the experiment later in the year, he again found vertical migration by some species and a nearly twofold increase in grazing from noon to midnight. Haney noted that the results may reflect differences in environmental conditions and changes in the species composition of zooplankton between the two sampling dates. Starkweather (1975), who subjected laboratory populations of Daphnia pulex to a light:dark cycle of 16:8 hr (16L:8D), found that the maximum filtering rate occurred during the dark phase and that the filtering rate increased significantly with the onset of darkness (Figure 21). The maximum filtering rate, which occurred during the dark phase, was two to three times greater than the minimum rate. Based on additional experiments, Starkweather concluded that his results provided circumstantial evidence that diel changes in filtering rate may be endogenous in nature.

150. Chisholm et al. (1975) observed diel changes in the grazing rate of Daphnia middendorffiana and that feeding peaks occurred consistently at 2400 hr and 1400 hr, times when the water temperature passed through 11°C, the optimum temperature for this species. The authors suggested that Daphnia may maximize their activity when the temperature is optimum. The maximum grazing rate was approximately double the minimum rate.

151. In a series of detailed studies at Lawrence Lake and Little Mill Lake, Michigan, Haney and Hall (1975) found that the filtering rates of Daphnia pulex and D. galeata were significantly higher at midnight than at noon. The filtering rate of medium-sized Daphnia was five to ten times higher at night than during the day. Furthermore, the magnitude of change in filtering rate between noon and midnight was not influenced by water temperature in species of Daphnia, but only by body

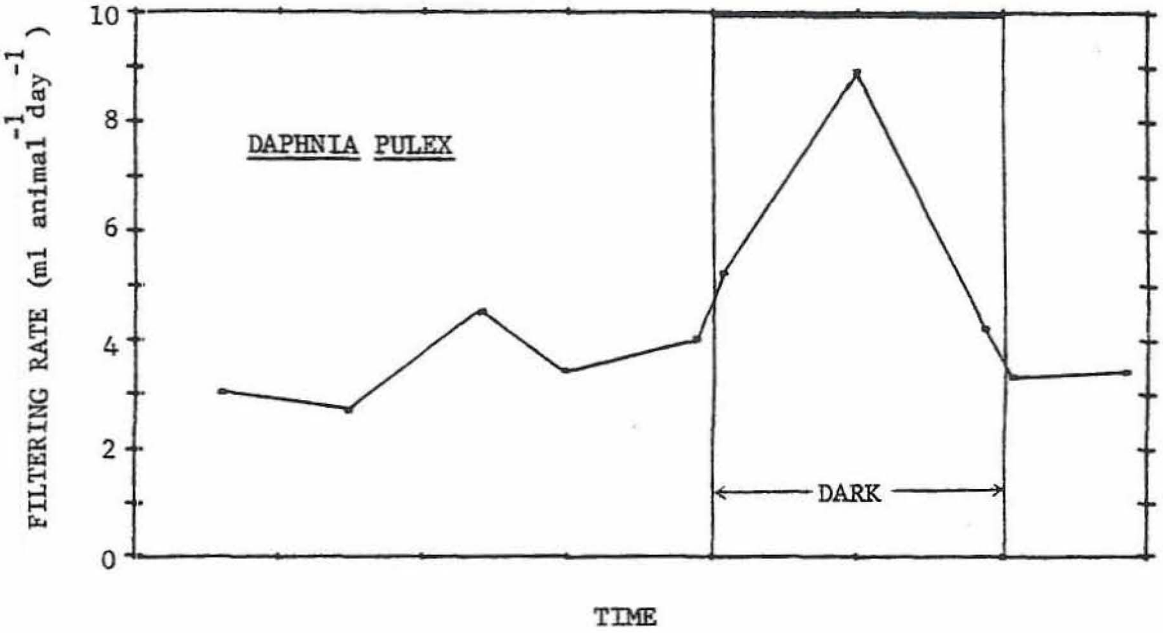

Figure 21. The diel pattern of filtering rate change at 18°C in a light:dark 16:8 photocycle. Based on data from Starkweather (1975)

size. Large animals had a greater increase in filtering rate. Both migrating and nonmigrating populations of Daphnia showed the change in filtering rate between day and night, and the authors concluded that vertical migration was not a necessary prelude to high night filtering. In contrast to these results, Diaptomus pallidus showed no significant difference between the noon and midnight filtering rates, even though some vertical migration toward the surface at night was detected.

152. Haney and Hall (1975) examined the role of light intensity and vertical migration on filtering in Daphnia. Daphnia galeata in Wintergreen Lake, Michigan, and D. pulex in Three Lakes, Michigan, increased filtering rates during the night. The filtering rates of both species were clearly related to photoperiod and showed a bimodal peak (Figure 22). The maximum filtering rate was approximately six times the minimum rate for Daphnia galeata and from 5 to 27 times the minimum, depending on animal size, for D. pulex. Differences in temperature and quantity of filterable particles showed no clear relationship to the daily filtering rate changes. Two species of Diaptomus were also studied

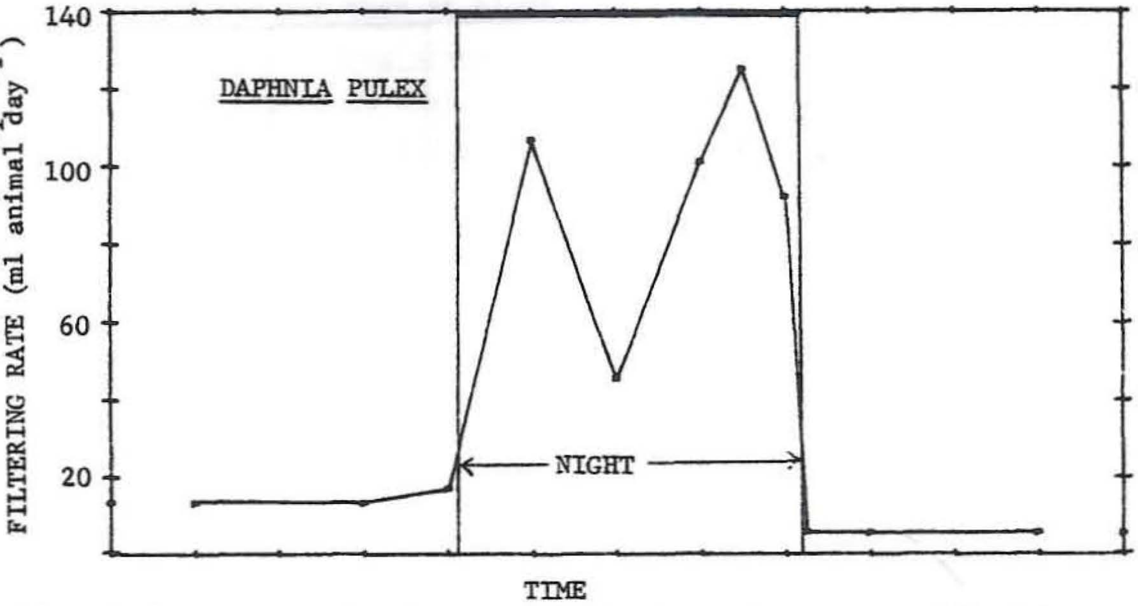

Figure 22. The diel pattern of filtering rate change of Daphnia pulex in Three Lakes, Michigan. Based on data from Haney and Hall (1975)

in Three Lakes. No clear increase in the filtering rate could be demonstrated during the night, although the evidence suggested that it may have increased slightly between 2100 and 0200 hr.

153. Haney and Hall noted that Daphnia in Wintergreen Lake and Three Lakes should be considered nocturnal grazers because 85 percent of the filter feeding in both lakes occurred during the night period. The authors calculated the error that would result if only the daytime value for grazing rate were used in the estimate of grazing pressure. For Three Lakes, the daytime calculations underestimated Daphnia grazing by a factor of 4.2.

154. Haney and Hall concluded that the diel activity patterns of vertical migration and change in filtering rate in Daphnia are strongly correlated with light intensity. They suggested that these are endogenous cycles synchronized to a 24-hr time period by relative light changes.

155. Duval and Geen (1976), who examined diel feeding of the zooplankton community of Eunice Lake, British Columbia, also found bimodal grazing during the night period, with maxima occurring at 0200

and 1800 hr or times just prior to sunrise and sunset. Similar results were obtained for populations of Daphnia pulex and Cyclops scutifer from Deer Lake, British Columbia. The maximum feeding rate varied by a factor of 8 over the minimum rate for the Eunice Lake population, and by 5 and 14 for the winter and summer populations, respectively, from Deer Lake. Extrapolation of the diurnal values of feeding to a diel basis resulted in an underestimate of grazing pressure ranging from 37 to 72 percent.

156. Similar diel grazing rhythms have been described by Mackas and Bohrer (1976) for marine filter feeders.

157. Model construct. Although the preceding results are by no means definitive, they do suggest the potential importance of diel grazing cycles for some species of zooplankton. Many models currently employing data based on diurnal grazing values may considerably underestimate the impact of zooplankton populations on their food supply. Diel cycles have been demonstrated for several species of Daphnia. These cladocerans often compose a significant, if not overwhelming, part of the zooplankton biomass of temperate lakes. Therefore, it may be reasonable to treat zooplankters of the entire community as if they behaved like Daphnia.

158. For discussion, we adopted this treatment. The data base developed in this report is designed to function in a model that simulates zooplankton and benthos dynamics, normally on a daily basis. Such a design presents problems in incorporating diel grazing rhythms which ideally must be simulated at a time interval less than 1 day. Additionally, diel cycles in vertical migration could potentially improve model performance by more realistically portraying zooplankton grazing behavior. Bowers (1979) discussed the simulation of vertical migration.

159. Four approaches to including diel changes in grazing rate are presented. Whether one method is better than another cannot be determined until test simulations are conducted against field data. Numerical simulation results may indicate that a diel grazing cycle is unnecessary for certain applications. Because the magnitude of increases in grazing from daytime to nighttime is highly variable and

dependent on species, size, temperature, and possible other factors, we have elected to increase daytime grazing by a factor of five to represent the night value in our examples. The factor five was selected based on the mean of literature values.

a. Method No. 1

160. The most straightforward approach to adjusting the grazing rate to reflect average diel grazing is to correct the maximum grazing rate by either increasing its value, if you assume that the maximum rate is representative of daytime conditions, or by decreasing its value, if you assume that it better reflects nocturnal grazing. There is no evidence to support one of these alternatives as superior to the other. In our opinion the maximum grazing rate better reflects nocturnal conditions, but only simulation with a range of values will clarify this hypothesis. Nighttime grazing rates have been shown to range from 2 to 27 times the daytime rate, depending on such factors as species, food, and water temperature.

b. Method No. 2

161. A second approach to including diel grazing involves these points: (a) set the maximum nighttime grazing rate equal to the maximum grazing rate; (b) calculate the diurnal grazing rate, i.e., $G_{night}/5 = G_{day}$; and (c) assume that zooplankton grazes at the nocturnal rate for the entire period between sunset and sunrise, or some other threshold light concentration (Table 9). For a 16-hr day and 8-hr night (16L:8D), this grazing construct could be written as follows:

$$G_{diel} = \left(G_{day}/24\right) 16 + \left(G_{night}/24\right) 8 \qquad (13)$$

Substituting $G_{night} = 5\ G_{day}$ (14)

$$G_{diel} = \left(G_{day}/24\right) 16 + 5 \left(G_{day}/24\right) 8 \qquad (15)$$

$$= 2.33\ G_{day}$$

The appropriate Ivlev function or linear relationship can be substituted for G_{day}.

Table 9

Values for Relative Change in Light Intensity, as Cited by Haney and Hall (1975), that Represent Threshold Light Intensity for Positive Phototaxis

Species	Rate of Light Change When Vertical Migration Began, $\sec^{-1}$	Reference
Daphnia magna	-0.0013 to 0.0024	Ringelberg (1964)
Daphnia galeata	-0.0007	Haney and Hall (1975)
Daphnia pulex	-0.0021	Haney and Hall (1975)
Daphnia longispina	-0.011	Siebeck (1960)
Bosmina longispina	-0.011	
Cyclops tatricus	-0.011	

c. Method No. 3

162. With the same assumptions presented in Method No. 2, we assumed that a unimodel peak occurs during the night. This peak is the maximum grazing rate. The temporal bounds are set as above, and Figure 23 illustrates this construct for a 16L:8D period. The curve in Figure 23 is one of many possible functions that could be used to describe a unimodal peak. Integrating this curve and simplifying the result indicates that the average diel grazing rate can be written,

$$G_{diel} = 1.48\ G_{day} \tag{16}$$

d. Method No. 4

163. This method is identical to Method No. 3 except that a bimodal peak occurs during the night (Figure 24). Bimodal peaks have been observed in several studies. We have simplified the experimental results by making the two maxima equal in value (they may not be according to some studies) and have set the minimum grazing value between the maxima at 70 percent of the maximum (literature values range from 35 to 89 percent of the maximum). The bimodal curve can be integrated and simplified to show that:

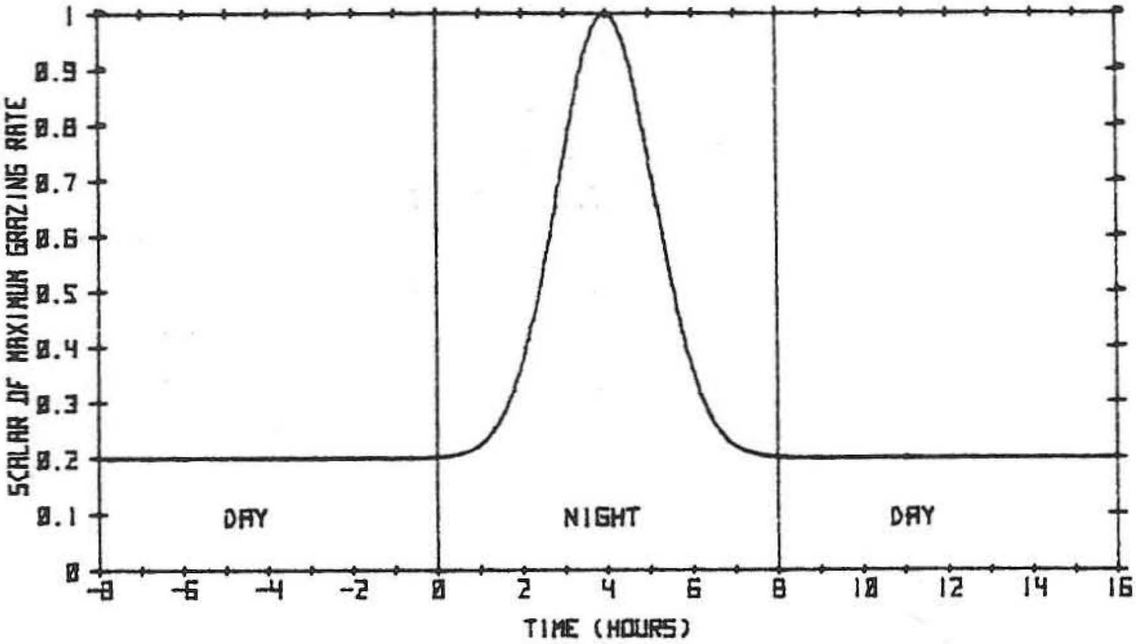

Figure 23. The diel grazing function of filter-feeding zooplankton exhibiting a unimodal peak in grazing during the night. Hour 0 represents the time at which increased grazing begins and hour 8 the time when increased grazing ceases

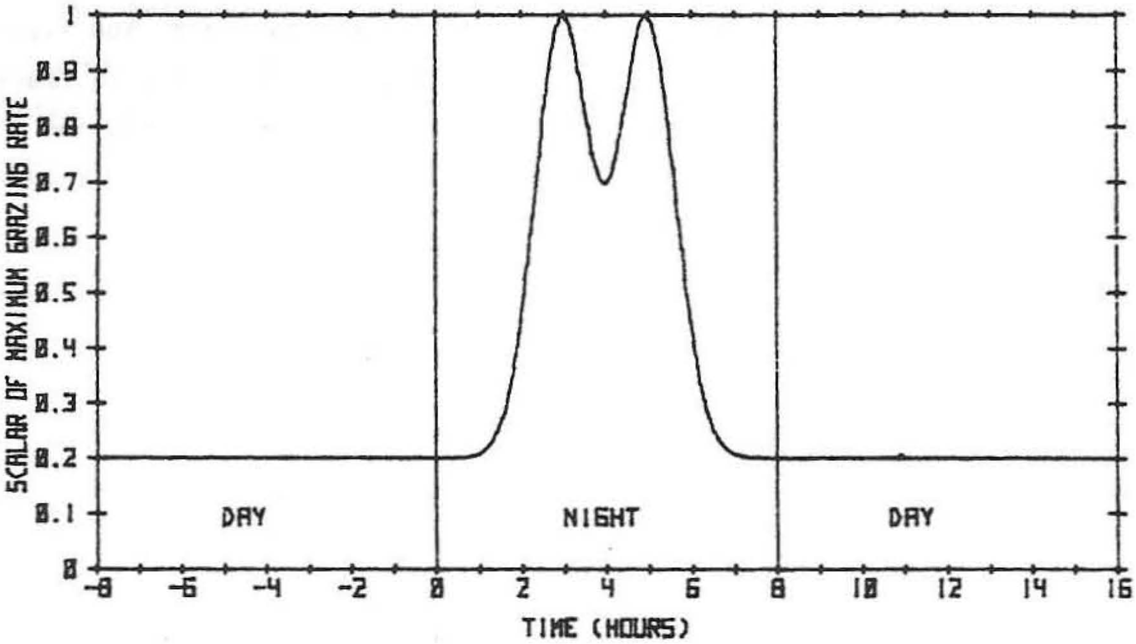

Figure 24. The diel grazing function of filter-feeding zooplankton exhibiting a biomodal peak in grazing during the night. Hour 0 represents the time at which increased grazing begins and hour 8 the time when increased grazing ceases

$$G_{diel} = 1.54\ G_{day} \qquad (17)$$

Other solutions are possible.

164. We suggest using Method No. 3 for initial simulation runs.

Consumption by Predatory Zooplankton

165. A predatory zooplankter is difficult to define. In temperate fresh waters, cyclopoid copepods, the cladocerans *Leptodora kindtii* and *Polyphemus pediculus*, and several rotifers, particularly *Asplanchna*, are usually considered predators. However, as Fryer (1957) has pointed out, many of the so-called predatory zooplankters should more appropriately be classed as omnivores. The problem in definition partly arises from the mode of feeding employed by most of the "predatory" species. Almost without exception these species are raptorial feeders; that is, they grasp or seize their prey, whether it be animal or plant material. In the past, most raptorial feeders have been automatically considered predators, the assumption being that raptorial feeding is characteristic of carnivority. The few carefully executed food studies that are available have revealed that this assumption is not always warranted.

166. The central question relevant to this review is whether or not the form of the feeding response by predatory zooplankton species differs from that of herbivorous filter feeders. Quantitative information on the feeding of predatory zooplankters is scarce. The scarcity is partly due to problems in designing experiments to measure food consumption by raptorial feeders. For example, when a carnivorous copepod such as *Cyclops* captures a prey item, possibly *Ceriodaphnia*, not all of the prey is consumed. The process of raptorial feeding often leaves prey dismembered, with a resultant loss in biomass. Brandl and Fernando (1975) estimated that the three species of cyclopoid copepods they studied ingested only about one third of the prey biomass that they attacked. Similar results have been found for the carnivorous marine amphipod *Calliopius laeviusculus* (Dagg 1974).

167. Because data are poorly detailed for predatory feeding, we

have included a summary of reported values for daily ration for both omnivores and predators (Table 10). Daily ration, when expressed as a percentage of body weight, is a good approximation of grazing rate. A synopsis of the literature for freshwater predatory zooplankters follows.

Literature synopsis

168. Shushkina and Klekowski (1968) examined how the daily ration of Macrocyclops albidus varied with food concentration. Although their results are not directly convertible to carbon units, they do show that under conditions of short-term food acclimation, consumption increased with increasing food concentration until a maximum rate was reached; thereafter, consumption remained constant with further increases in food concentration (Figure 25). This relation appeared to be true for all developmental stages when fed Paramecium aurelia at concentrations from

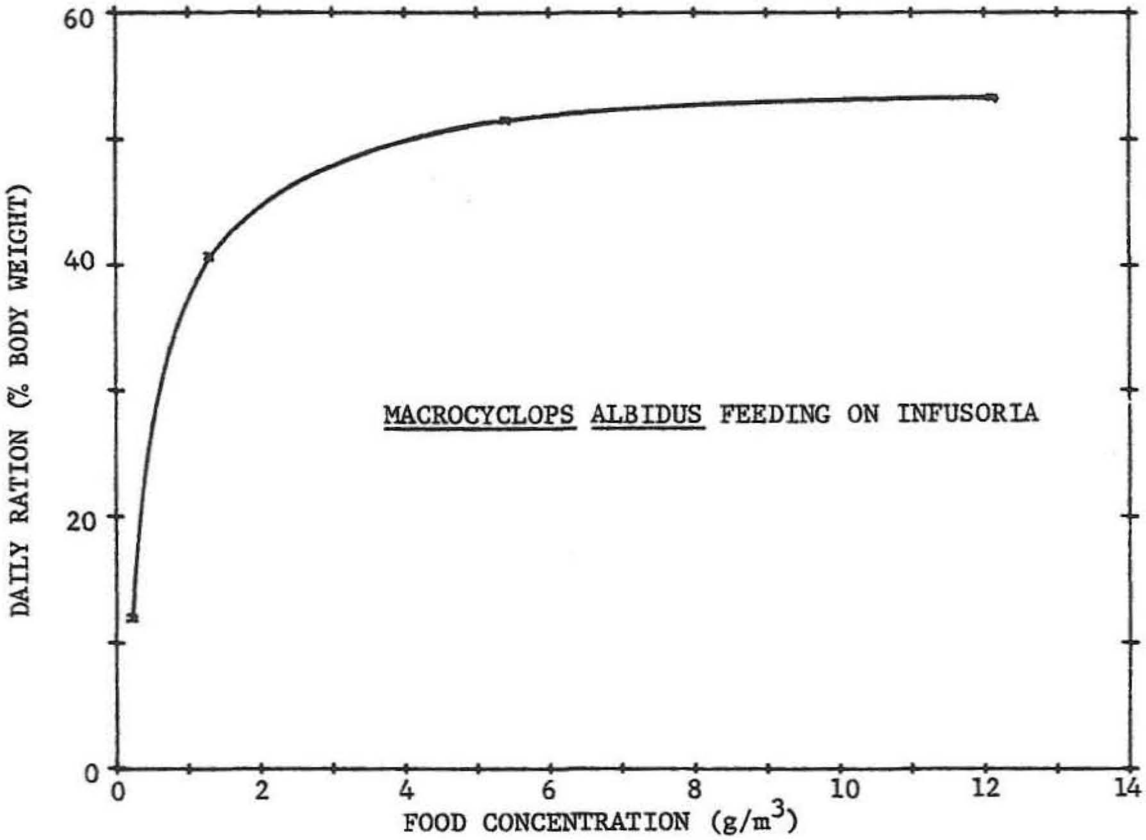

Figure 25. The daily ration of Macrocyclops albidus females as a function of food concentration. Based on the data of Shushkina and Klekowski (1968)

Table 10

Published Values for the Daily Ration of the Planktonic Omnivores and Predators

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Cladocera Family: Leptodoridae			
Leptodora kindtii	Natural assemblage of zooplankton	30-48	Hillbricht-Ilkowska and Karabin (1970)
Leptodora kindtii	Zooplankton	5-20	Stepanova (1972)
Order: Eucopepoda Family: Cyclopidae			
Cyclops vicinus	*Chilodonella* sp. *Stylonychia pustulata* *Paramecium caudatum* *Askenasia* sp.	9.6-79.2($\bar{X}$=29.3)	Korniyenko (1976)
Macrocyclops albidus	*Paramecium aurelia*	12-240	Klekowski and Shushkina (1966a)
Mesocyclops leuckarti	Zooplankton	10-34	Stepanova (1972)
Mesocyclops leuckarti	*Ceriodaphnia reticulata* *Artemia salina*	63-113 30-200	Gophen (1977)
Acanthocyclops vernalis	*Stylonychia pustulata* *Paramecium caudatum* *Askenasia* sp.	27.4-64.8($\bar{X}$=41.2)	Korniyenko (1976)
Family: Tortanidae			
Tortanus discaudatus	*Calanus pacificus*	ca 4-98*	Ambler and Frost (1974)

* Marine species. These values are probably overestimates because the authors assumed that any *Calanus* attacked was ingested.

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start
here

0.1 to 10 g/m^3 wet weight. Their results clearly showed that the grazing rate of this predatory zooplankter can be defined by an Ivlev function identical to the construct used to describe herbivorous zooplankton grazing. Data presented showed that daily grazing rates for Macrocyclops albidus may be as high as 240 percent of body weight, depending on zooplankter age and food concentration (Klekowski and Shushkina 1966a, 1966b).

169. McQueen (1969) found that the predator Cyclops bicuspidatus thomasi fed most extensively on copepod nauplii, both its own and those of Diaptomus, and on rotifers. Few cladocerans and diaptomid copepodids were eaten. Laboratory results showed that as prey density increased, predation rate also increased, usually linearly or with a maximum feeding rate being reached at high prey densities. Field measurements of predation rates on nauplii of Diaptomus oregonensis, D. hesperus, and Cyclops bicuspidatus thomasi, in Marion Lake, British Columbia, agreed well with laboratory results. The predation rate increased linearly with increasing prey density. The rotifer Keratella cochlearis was readily eaten in laboratory studies but was seldom preyed upon in the field, suggesting selective grazing by Cyclops.

170. Confer (1971) examined predation rates of Mesocyclops edax on natural densities of the prey Diaptomus floridanus. When fed Diaptomus copepodite stages V and VI, Mesocyclops showed an increasing predation rate with increasing prey density. This relationship was linear.

171. Stepanova (1972), who discussed the daily rations of Mesocyclops leukarti and Leptodora kindtii, showed (although poorly) that Mesocyclops approached a maximum grazing rate of about 34 percent of body weight per day as food concentration increased. Leptodora, on the other hand, reached a peak grazing rate of 20 percent of wet weight per day as food concentration increased; the rate then declined at higher food densities. No explantion was offered for this occurrence.

172. Fedorenko (1975) found that predation rates of the larval phantom midges Chaoborus americanus and C. trivittatus on the copepod Diaptomus tyrelli increased as prey density increased. The relation of

predation to prey density followed a saturation curve. When Chaoborus was fed Diaptomus kenai and Diaphanosoma, the results were similar. In one experiment, Chaoborus showed a linear feeding response to increasing density of Diaphanosoma.

173. Korniyenko (1976) found in laboratory studies that Acanthocyclops vernalis, when fed various concentrations of four species of infusorians, consumed between 27.4 and 64.8 percent (mean = 41.2 percent) of its body weight per day. Cyclops vicinus ate between 9.6 and 79.2 percent (mean 29.3 percent) of its wet weight per day. The authors noted that their results were in agreement with daily ration values given by Bogatova (1951) for Cyclops strenuus and C. viridis.

174. When adult female Mesocyclops leuckarti were fed Ceriodaphnia reticulata, the daily ration ranged from 63 to 113 percent of the wet body weight per day, depending on temperature (Gophen 1977). As temperature increased from 15° to 27°C, so did the daily ration. Similarly, the rations of adult male and female Mesocyclops also increased when they were fed Artemia salina nauplii at various temperatures. Male daily rations (30 to 200 percent of their body weight) were greater than those of females (30 to 130 percent). These results are generally higher than values reported by Stepanova (1972) under similar temperature regimes.

175. Similar feeding responses to those outlined above have been found for predaceous marine zooplankton (Ambler and Frost 1974, Landry 1978).

Model construct

176. Little quantitative work on feeding by predatory zooplankton has been undertaken. No data are available for freshwater predators to allow the calculation of grazing in carbon units. We have therefore based our proposed model construct for predatory zooplankton grazing on three assumptions:

a. For short-term feeding experiments, the available evidence indicates that grazing follows a linear or saturation curve response to increases in prey density. We assume the saturation curve response to be characteristic and that this response can be described by an Ivlev function (Equation 3). This type of response has been previously demonstrated for herbivorous filter feeders.

b. Under field conditions, wherein zooplankton populations are acclimated to ambient conditions, we assume that grazing by predatory species is linearly related to food concentration (Equation 9). There is currently no literature documentation to support this assumption.

c. Daily rations (Table 10) of predatory zooplankters are an approximation of grazing rates and are within the range of daily grazing rates reported previously for filter-feeding zooplankton. We assume that the entire range of grazing rates is similar for herbivorous and carnivorous zooplankters. Metabolic similarities among herbivores, omnivores, and carvivores support this assumption.

177. We believe the assumptions outlined above are reasonable and will be documented as additional information becomes available. The acceptance of these assumptions will allow the modeler to design a predatory zooplankton grazing function, if desired. Predators could be assigned about 20 percent of zooplankton biomass in the event that herbivorous and predatory zooplankton are divided. This figure was based on ecological growth efficiencies tabulated by Welch (1968).

Seasonal Changes in Grazing

178. Seasonal changes in grazing are highly variable and dependent on the species composition of the zooplankton community, available food supply, temperature, and many other environmental variables. Generally, in temperate lakes minimum grazing rates occur during the winter, followed by increased grazing in the spring and peak rates in early summer. A gradual decline may follow through late summer to fall. Often another minor fall peak in grazing is observed. Major pulses in grazing activity are usually well correlated with peaks in the population density of the predominate zooplankters. A summary of several field studies is presented in Table 11.

Synergistic Effects of Environmental Variables

179. With many model processes, such as grazing, the understanding

Table 11

Seasonal Changes in the Grazing Rate of Zooplankton Communities

Lake	Season	Year	Mean Grazing Rate (% of Wet Weight Per Day)	Percent of Total Annual Grazing	Reference
Heart Lake, Canada	Jan-May	1969	19.2	17.4	Haney (1973)
	Jun-Sep		80.1	61.7	
	Oct-Jan		35.2	20.9	
Lake Vechten, The Netherlands	Mar-Apr	1976-77	9.8	22.0	Gulati (1978)
	May-Sep		24.0	69.0	
	Oct-Nov		5.5	4.5	
	Dec-Feb		2.1	4.5	
Lake Krasnoye, USSR Littoral zone	May	1973	4	1	Andronikova (1978)
	Jun		32	11	
	Jul		120	43	
	Aug		80	28	
	Sep		32	11	
	Oct		16	6	
Pelagic zone	May	1973	0.6	0.6	
	Jun		12	12	
	Jul		37	36	
	Aug		35	34	
	Sep		14	14	
	Oct		4	4	
Lake Balaton, Hungary	Spring	1974-75		30	Zankai and Ponyi (1976)
	Summer			46	
	Fall			20	
	Winter			4	

of system dynamics results from the interpretation of studies that are often designed to examine single variable effects (e.g., the effects of food concentration or temperature on grazing). As a result, we end up mathematically describing model processes by a series of variables that we assume are independent. In many situations this is not a valid assumption. Most modelers realize the inherent problems in attempting to combine experimental results for variables that may not be independent. Unfortunately, few data are available on synergistic effects to clarify these relationships.

180. Hayward and Gallup (1976) are the only workers who have examined potential synergistic effects on zooplankton feeding. Their objective was to identify how feeding would be affected when two or three parameters were altered simultaneously in one experiment. A partial abstract of their work follows.

> Feeding and filtering rates of Daphnia schoedleri were measured at different temperatures, light intensities, food concentrations, crowding conditions, and with different diet species. The rates were compared as well for different sizes, sexes, and reproductive states of the experimental animals. All of the above factors were found to affect feeding rates in a significant fashion in single variate experiments. However, when two or more environmental parameters were varied simultaneously, the previously defined relationships did not hold, and indeed were obscured as extremes of temperatures or cell concentrations were approached. The effects of these parameters which most dramatically altered feeding rates were then determined for assimilation rates and digestive efficiency estimates ... .
>
> Results showed that a change in one environmental parameter can significantly alter Daphnia schoedleri's response to a change in a second parameter. The incipient limiting food concentration was found to be significantly different at different temperatures. Similarly, different shaped temperature curves were obtained as food concentrations were changed, the most dramatic alterations being evident in the extremes. When comparable experiments were performed with ^{14}C-labeled algae, no incipient limiting level was observed for assimilation rates, but rather, peaked curves became evident. Three environmental parameters: temperature, food concentration, and diet species, were found to alter responses to other parameters in a measurable manner. This would seem to indicate that feeding behavior of the zooplankton must be thoroughly understood before results from

> laboratory or field studies can be applied to even approximate estimates of secondary production in natural conditions.

Model constructs to handle synergistic effects are generally unavailable. Clearly, further research on this subject is needed.

Section B: Benthic Grazing

181. The benthos of freshwater lakes and reservoirs is highly diverse, both taxonomically and functionally, complicating the modeling process. Current understanding of the role of the benthic community in the energy and nutrient dynamics of lentic ecosystems is poor. Indeed, little information is available on the basic life history of most species.

182. Little quantitative information exists on food consumption by benthos. We were unable to find a single reference that documented, in units convertible to carbon, the change in benthic grazing as food concentration increased.

183. The functional diversity of benthic organisms contributed to the problem of defining feeding relationships. Filter feeders, predators, deposit feeders, and surface grazers are all represented in most benthic communities.

184. Because of the lack of quantitative feeding data, it is our opinion that benthic communities are better treated as a whole in any modeling effort. Daily rations (an approximation of the daily grazing rate) of some benthic species are listed in Table 12. Unfortunately, the values listed in this table include most of what is quantitatively known of consumption by benthic organisms.

Effect of Food Concentration

185. Sorokin (1966b), who reviewed data on the filtering rate of Dreissena polymorpha on bacteria, showed that the relative feeding intensity increased nearly linearly with increasing bacterial concentration.

Table 12

Daily Ration of Benthic Organisms

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
PHYLUM: NEMATODA			
Plectus palustris	*Acinetobacter* sp.	650	Duncan et al. (1974)
Aphelenchus avenae	fungal mycelia	26	Soyza (1973)
PHYLUM: MOLLUSCA			
Dreissena polymorpha	bacteria	1-12*	Sorokin (1966b)
Goniobasis clavaeformis	aufwuchs	1-24**	Malone and Nelson (1969)
PHYLUM: ARTHROPODA Class: Crustacea Order: Amphipoda			
Hyalella azteca	surface sediments	17-103	Hargrave (1970)
Pontogammarus robustoides	*Cladophora* sp. *Tubifex* sp.	7.4-98.0 18.7-163.0	Kititsyna (1975)
Order: Isopoda			
Asellus aquaticus	*Alnus glutinosa*	25†	Prus (1972)

(Continued)

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* It is unclear whether these values are for live weight, shell-free weight, or dry weight.

** Shell-free, ash-free dry weight based on a shell-free weight of 68.5 mg/snail.

† Based on energy units of food and organism.

(Sheet 1 of 3)

Table 12 (Continued)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Podocopa			
Herpetocypris reptans	*Spirogyra* sp.	128	Yakovleva (1969)
	Zygnema sp.	93	
	Mougeotia sp.	93	
	Chironomus plumosus	66	
	Asellus aquaticus	66	
	fish fry	109	
Heterocyris incongruens	*Spirogyra* sp.	240	Liperovskaya (1948) as cited by Yakovleva (1969)
Class: Insecta††			
Order: Diptera			
Chaoborus flavicans	Natural plankton assemblage	3.6-11.4	Kajak and Dusoge (1970)
Procladius choreus	Chironomidae and Crustacea	7-11	Kajak and Dusoge (1970)
Chironomidae	Variable	100-300	Results of several Russian studies reported by Olah (1976)
Order: Ephemeroptera			
Stenonema pulchellum	*Navicula minima*	23.4-21.4‡	Trama (1972)

(Continued)

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†† Larval forms only

‡ Based on dry weights of food and organism.

(Sheet 2 of 3)

Table 12 (Concluded)

Taxon	Food	Daily Ration (% of Wet Body Weight)	Reference
Order: Plecoptera			
Acroneuria californica	*Hydropsyche* sp. *Simulium* sp.	0.2-8.7‡ 1.1-9.0‡	Heiman and Knight (1975)

---

‡ Based on dry weights of food and organism.

Morton (1971) studied the filtering rate of D. polymorpha on various concentrations of several algal and infusorian species. We converted his results to feeding rates and compared the number of cells per animal per day to cell concentration. For all of the six food species offered, the number of cells consumed increased linearly or almost linearly as cell concentration increased. These results (Table 13) suggest that filter-feeding benthic mollusks may have the same functional relationship to changes in food concentration as do filter-feeding zooplankton. At extremely low food concentration levels, filtering continued with no threshold food concentration apparent. Morton's experiments allowed for short-term acclimation to the varying food concentrations. Because the results indicated nearly linear responses to increasing food concentration, it may be reasonable to assume that the food densities tested were below the incipient limiting food concentrations.

Effect of Temperature

186. Although data are limited, it may be reasonable to assume that benthic organisms show the same grazing response to temperature as that shown by zooplankton. Kititsyna (1975) found that the amphipod Pontogammarus robastoides increased its daily ration linearly as temperature was increased from 9° to 29°C. Elwood and Goldstein (1975) acclimated the snail Goniobasis clavaeformis for 1 week to 13.8°C before testing the snail's grazing response over the temperature range of 10° to 19.3°C. The temperature at which the maximum grazing rate occurred was 14°C. These results indicate a short-term grazing response to temperature similar to that demonstrated for zooplankton (see "Effects of Temperature on Consumption," page 66).

Effect of Diel Variations

187. Although quantitative documentation of diel changes in grazing rate is virtually nonexistent, other evidence (primarily for

Table 13

Filtering Rates of Molluscs Reported in the Literature

Mollusca Taxon	Length (mm)	Temperature (°C)	Type of Food	Range of Food Concentrations Tested (cell/ml)	Range of Measured Filtering Rates (ml/animal/day)	Reference
Sphaerium rivisola	19	?	?	?	up to 2400	Alimov (1965) as reported by Mitropol'skii (1966)
Sphaerium corneum	7	13–15	*Chlorella* sp.	$7.35 \times 10^3 - 3 \times 10^6$	0.23–4976	Mitropol'skii (1966)
Dreissena polymorpha	2–30	20–22	*Chlorella* sp.	?	24–1536	Mikheev (1966)
			bacteria	?	72–1080	
			detritus-*Chlorella* sp.	$5 \times 10^4 - 1.5 \times 10^6$ particles	72–1584	
			reservoir seston	?	3–1200	
Dreissena polymorpha	1.6–3.5	?	colloidal graphite	?	ca 115–1800	Morton (1971)
			colloidal graphite and *Chlamydomonas globosa*	ca 1×10^4 to 80×10^4	ca 460 3530	
			colloidal graphite and *Pedinomonas minar*	ca 1.6×10^3 to 1.4×10^5	ca 450–1060	
			colloidal graphite and *Pediastrum boryanum*	ca 4 to 160	ca 265–720	
			colloidal graphite and *Euglena spirogvra*	ca 3 to 430	ca 185–1120	
			Colloidal graphite and *Cosmarium botrytis*	ca 56 to 2820	ca 670–1700	
			Colloidal graphite and *Pleodorina illinoiensis*	ca 6 to 640	ca 300–1300	

stream macrobenthos) indicates that some benthic invertebrates feed more at night. Kroger (1974) suggested that nocturnal activity may have evolved, in some aquatic insects, as a protective mechanism against trout predation. Elliott (1968) documented a significant diel foraging pattern for the mayfly Baetis rhodani. Nymphs moved to the upper surfaces of stones to feed at night, and foraging apparently peaked right after sunset. Baetis flavistriga, collected 2 hr after sunset, contained significantly more food biomass than those nymphs collected 4 hr earlier (Ploskey 1978). Although we realize that some species are day active (e.g., some caddisflies), for modeling purposes we recommend that diel grazing constructs for zooplankton be tested in benthos simulations to determine whether such a construct improves results. Only future work on diel grazing of reservoir benthos will unequivocally justify such a formulation.

Section C: Model Constructs

188. A sound data base does not exist on which to establish firm model constructs for benthic grazing, and much more research is needed. Consequently, we propose to model benthic grazing in the same manner as described for zooplankton. The only major change is that food concentration should be expressed on a square meter basis, and a diel grazing correction should not be employed unless its use improves simulations. We again recommend the use of Equation 9, which corrects for the effects of food concentration in acclimated animals, and Equation 12, which corrects for the effects of temperature in acclimated animals. We base this grazing proposal on the same assumptions outlined under the model construct of consumption by predatory zooplankton. Most modelers have used this approach when simulating the benthic community.

Summary of Constructs

189. The constructs described below are equally applicable to zooplankton and benthos except as noted. Consult the text for analyses and details.

Definitions

b = zooplankton or benthos biomass

$B = B_t$ = concentration of food at time t (mg $C \cdot m^{-3}$ - zooplankton; mg $C \cdot m^{-2}$ - benthos)

B_i = concentration of food of type i (mg $C \cdot m^{-3}$ - zooplankton; mg $C \cdot m^{-2}$ - benthos)

G = observed grazing rate (mg $C \cdot$mg $C^{-1} \cdot day^{-1}$)

G_{max} = maximum grazing rate (mg $C \cdot$mg $C^{-1} \cdot day^{-1}$)

G_{diel} = diel grazing rate (mg $C \cdot$mg $C^{-1} \cdot day^{-1}$)

G_{day} = diurnal grazing rate (mg $C \cdot$mg $C^{-1} \cdot day^{-1}$)

G_{night} = nocturnal grazing rate (mg $C \cdot$mg $C^{-1} \cdot day^{-1}$)

W_i = preference factor for food of type i (unitless; ranging from 0 to 1)

k and Z = proportionality constants

y = scalar of the maximum grazing rate, G_{max} (unitless; ranging from 0 to 2)

T = temperature (°C)

Step 1 - Food Concentration

190. To obtain a baseline grazing rate that is corrected for the effects of food concentration, solve for G in the equation:

$$G = ZB_t \left[1 - e^{-kB_t}\right] \tag{9}$$

where B_t is measured in the field, Z is defined by:

$$Z = 10^{(-3.2295 - 0.0678 \log B_t)} \tag{10}$$

k is defined by:

$$k = 10^{(-2.9664 - 0.9787 \log G_{max})} \tag{6}$$

G_{max} is defined by:

$$G_{max} = ZB_t \tag{8}$$

We assume that most natural populations are fully acclimated to food concentrations and therefore recommend the use of the above construct (Equation 9). However, occasionally populations may be incompletely acclimated and, in such cases, solve for G in the equation:

$$G = G_{max}\left(1 - e^{-kB}\right) \qquad (3)$$

where B is measured in the field, k is defined by:

$$k = 10^{(-2.9664 - 0.9787 \log G_{max})} \qquad (6)$$

and G_{max} is defined by:

$$G_{max} = 0.0788 + 0.0003105B \qquad (7)$$

The rate of consumption obtained above (G) may also be obtained for zooplankton and benthos communities that have more than one food source. This procedure is given in Step 2. If only one food type is available, proceed to Step 3.

Step 2 - Food Selectivity

191. The grazing rate of zooplankton or benthos on a particular food item (i) is given by the equation:

$$G_i = ZB_t\left[1 - e^{-kB_i \cdot \left(\frac{W_iB_i}{\Sigma W_iB_i}\right)}\right] \qquad (11)$$

where Bi measured in the field, k is defined by Equation 6 (Step 1), Bt = concentration of food at time t (measured in the field), Z is defined by Equation 10 (Step 1), and W_i is the same for all potential food sources, except for filamentous blue-green algae (where $W_i = 0 - 0.3$). When data are available on the fractional composition of foods in the environment, W_i should be set equal to the fraction that a particular food contributes to the total. The baseline grazing rate G, corrected for food concentration, is given by the sum of the grazing rates on all individual food items obtained from Equation 11. Proceed to Step 3.

Step 3 - Temperature

192. After obtaining a grazing rate G that has been corrected for the effects of food concentration (from Equation 9, Step 1) or for the effects of food concentration and selection (Equation 11, Step 2), the rate must also be corrected for the effects of temperature. This correction may be accomplished by multiplying G by a scalar (y) that is defined by:

$$y = 0.67T - 0.33 \tag{12}$$

where y is a scalar and T = temperature (°C). Equation 12 is based on the assumption that most natural populations are fully acclimated to temperature. For incompletely acclimated animals, refer to Figure 20 in the text and to Thornton and Lessem (1978). Proceed to Step 4.

Step 4 - Diel Variations

193. To correct zooplankton grazing rates for the effects of diel variations in consumption, we recommend Method 3. This method assumed that the grazing rates obtained from Equation 9 (Step 1) and Equation 11 (Step 2) represent mean daytime rates and as such should be multiplied by a correction factor to account for increased nighttime grazing (G_{diel} = Factor × G_{day} = Factor × G). G_{diel} is the average diel rate, and the correction factor is obtained from Method 3 (paragraph 162).

Step 5

194. Grazing rates obtained from Steps 1-4 above must be multiplied by the biomass of the model compartment to yield the weight of

carbon consumed daily [i.e., b (mg carbon) times G (mg carbon$\cdot$mg carbon^{-1} $\cdot$day^{-1}) = biomass of food consumed daily (mg carbon$\cdot$day^{-1})]. For use in Equation 1, consumption should be left as a weight-specific rate G.

Section D: Conclusions

195. The mathematical formulation for feeding is one of the most critical elements in the equation describing zooplankton and benthos population dynamics. Filter-feeding zooplankton make up a greater proportion of the zooplankton community, both numerically and as biomass, than do the carnivores. Consequently, the feeding relations of filter feeders have been more heavily emphasized. More information is available on the dynamics of zooplankton feeding than is available for benthos. Even so, the feeding relations of most filter-feeding zooplankters are unknown and caution must be used in extrapolating grazing results to all species.

196. Factors which influence food consumption by filter-feeding zooplankton include animal density, size, sex, reproductive state, nutritional or physiological state, as well as the type, quality, concentration, and particle size of food. Other factors include water quality and temperature.

197. Papers that examined the effects of food concentration on feeding rate must be interpreted as short-term feeding responses of incompletely acclimated zooplankters. We believe the following hypothesis to be true. For short-term incubation periods, zooplankters respond to increasing food concentrations by increasing their grazing rate in a curvilinear manner, where feeding rate attains a constant maximum value. If zooplankton are allowed to acclimate at the test concentrations for longer periods (possible 1 to 6 days), then digestive enzyme acclimation may occur and the feeding rate response is linear.

198. Threshold food concentrations for feeding have not been demonstrated for freshwater zooplankters. Further, most zooplankton feed on particles of 100 μm or less. Little quantitative data exist on the feeding of predatory zooplankton and virtually nothing suitable for

modeling purposes could be found for the benthic community.

199. When detritus is included as a food source in a grazing formulation, it should be given equal preference, according to availability, with other suitable foods. Published data generally indicate that the zooplankton community, as a whole, is capable of filtering and consuming all major algal groups, including the blue-green Cyanophyta. Filamentous algal forms are difficult for most zooplankters to consume. Rejection and reduced feeding may occur in the presence of large quantities of filamentous algae.

200. There are species differences as well as age differences in the filtering response of zooplankton to temperature. In addition, the previous thermal history of the animal is extremely important in determining the grazing rate. Most reported temperature "optima" for grazing must be considered to be responses of incompletely acclimated animals to temperature stress. These results are valuable when one is considering short-term responses of zooplankters to abrupt changes in temperature. Fully acclimated animals, such as might be found in a field population, show a linear increase in grazing with temperature over the temperature range normally experienced in temperate lakes and reservoirs.

201. Not all zooplankters or benthos show diel variations in grazing rate. For those that do, diel patterns of foraging often are correlated with light intensity and can result in significant changes in the grazing rate. Grazing rates often are highest during the dark period.

202. Synergistic effects of environmental variables on grazing are poorly understood and model constructs to handle synergistic effects are currently unavailable.