CALCULATION AND USE OF SELECTIVITY COEFFICIENTS OF FEEDING: ZOOPLANKTON GRAZING *

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ABSTRACT

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A straightforward method of calculating selectivity coefficients (W_{ij}) of predation from raw data, mortality rates of prey, filtering rates, feeding rates and electivity indices is derived. Results from a comparison of selectivity coefficients for the copepod *Diaptomus oregonensis* grazing under a number of experimental conditions suggest that W_{ij}'s for size-selective feeding are invariant, a conclusion also supported by the leaky-sieve model. Recommendations are made on how to use W_{ij}'s in linear and nonlinear feeding constructs for zooplankton and other animals.

INTRODUCTION

Many recent aquatic ecosystem models have been designed to simulate seasonal succession of phytoplankton and zooplankton. In order to accomplish this, the models have included several phytoplankton and zooplankton groups (Bloomfield et al., 1973; Park et al., 1974; Canale et al., 1976; Scavia et al., 1976a and b; Bierman, 1976). A main factor controlling successional change in both phytoplankton and zooplankton is zooplankton selective feeding (cf. Porter, 1977). Many field and laboratory studies have been carried out to quantify the selection process; however, the forms in which the data are reported are not immediately applicable to models. This paper describes how the selectivity coefficients (W_{ij}'s) used in most models can be easily derived from data collected in these feeding experiments.

The use of W_{ij}'s and other similar selectivity constants has become common in feeding constructs (O'Neill, 1971a and b; Bloomfield et al., 1973; Kitchell et al., 1974; MacCormick et al., 1974; Shugart et al., 1974; Park et al., 1974; DeAngelis et al., 1975; Smith et al., 1975; O'Neill, 1975, 1976; Canale et al., 1976; McNaught and Scavia, 1976; Bierman, 1976; DePinto et al., 1976; Scavia and Park, 1976; Scavia et al., 1976a and b). The W_{ij}'s appearing

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in most formulations are based on O'Neill's (1969) original concept of the selectivity coefficient. O'Neill (1969) stated that W_{ij} could be measured in the laboratory by presenting a predator with equal quantities of each prey and determining the amount of each prey eaten. In a later paper, O'Neill (1971a) also calculated W_{ij}'s for a web spider feeding on various prey having different availabilities. In this paper, we extend his method to calculate W_{ij}'s from the different parameters given by selective grazing experiments of zooplankton: filtering rates, prey mortality rates, feeding rates, and Ivlev's (1961) electivity indices, E'_i and E_i. Also, recommendations are made on how to use W_{ij}'s in time-dependent linear and nonlinear feeding constructs.

An important assumption in the use of W_{ij}'s is that W_{ij}'s are time invariant. Evidence is presented below that suggests that the W_{ij}'s of size-selective feeding in zooplankton do not vary with the particle-size spectrum of food available. Further, we point out bias in estimates of W_{ij}'s arising from use of particle-size analyzers to measure grazing. Although selective grazing is emphasized here because of our interest in herbivorous zooplankton, the methods apply as well to other predators.

DERIVATIONS

O'Neill (1969) defined W_{ij} as the relative frequency, or the ratio, in which various prey would be eaten by predator j if present in equal standing crops. He also defined the probability that organism j would select the ith kind of prey from all n kinds of prey as

$$P_{ij} = \frac{X_i W_{ij}}{\sum_{i=1}^{n} X_i W_{ij}} \tag{1}$$

where X_i is standing crop of organism i. P_{ij} is equivalent to the fraction of total food eaten that was taken from group i by predator j. He noted that $\sum_{i=1}^{n} P_{ij} = 1$; we normalize W_{ij} so that $\sum_{i=1}^{n} W_{ij} = 1$. Thus our normalized W_{ij} corresponds to the probability that the ith kind of prey will be selected from all n kinds of prey when all kinds of prey are equally abundant. For simplicity of notation, we drop the subscript j and note that all further summations are over i. Implicit in both O'Neill's and our definitions of W_{ij} is that W_{ij} is a constant. If it is not a constant it is a weighting factor that varies with X_i. The assumption that W_{ij} is a constant will be critically examined below.

Consider a feeding experiment where various concentrations of prey are offered to a predator and the experimenter determines the concentration of prey left after a period of time. Under the conditions of the experiment, P_i, the fraction of total ingested food taken from group i is

$$P_i = \frac{X_i - R_i}{\Sigma(X_i - R_i)} \tag{2}$$

From Eq. (21), feeding rate on the ith kind of prey is

$$G_i = G_{max} \frac{\Sigma W_i' X_i}{K + \Sigma W_i' X_i} P_i$$

$$= G_{max} \frac{\Sigma W_i' X_i}{K + \Sigma W_i' X_i} * \frac{W_i' X_i}{\Sigma W_i' X_i}$$

$$= G_{max} \frac{W_i' X_i}{K + \Sigma W_i' X_i} . \tag{22}$$

To calculate W_i''s required in Eq. (22) or other similar nonlinear constructs from W_i's, one must know one W_i'. As done by Scavia et al. (1976a), one could assume that the highest W_i for size-selective grazing by zooplankton corresponds to a W_i' of 1. The remaining W_i's can then be scaled proportionately. One can see by the definition of ϕ_i that $W_i' = \phi_i$ for zooplankton grazing. Thus, W_i' is the conditional probability that, if encountered (i.e. entered the filter chamber), prey i will be retained by the sieve and eaten.

The stratagem of assigning a W_i' of 1 to the highest W_i observed may be a useful approximation for other predators as well. For example, in some cases, W_i's may be determined from E_i's or E_i''s reported for stomach content analyses and concentrations of different prey in the environment. In fact, it is possible to derive values for W_i' for any predator that demonstrates time-invariant preferences (or nonpreferences) for food sizes or types, regardless of the mode of feeding.

ESTIMATION OF SELECTIVITY COEFFICIENTS OF A FRESHWATER COPEPOD

In this section we will estimate W_i's and W_i''s of size-selective feeding of *Diaptomus oregonensis*, a freshwater copepod, from feeding experiments performed under a number of conditions of food concentration and relative abundance of different sized food. This application will serve two purposes. First, in arguing for constant W_i''s we assumed that the leaky-sieve model is correct. Strong support for the leaky-sieve model in marine copepods comes from the qualitative arguments of Boyd (1976), synthesized from the results of Nival and Nival (1973, 1976) and others, and Frost's (1977) experiments in the laboratory. On the other hand, Poulet (1974) and Richman et al. (1977) in their studies of a marine copepod conclude that copepod grazing is not entirely mechanical and passive but that copepods can preferentially select, or "track", peaks of abundance in natural particle size spectra. By calculating W_i's and W_i''s for *Diaptomus oregonensis* we will test the leaky-sieve model. Second, in examining the data on *Diaptomus* we will discuss limitations of data from this and other studies because these limitations can lead to potentially serious errors in analysis of data from grazing experiments. In fact, Frost (1977) invokes these limitations to explain some of the results of Poulet (1974) and Poulet and Chanut (1975).

Data used here come from the study of McQueen (1970) and three experiments performed by one of the authors (HAV). The latter experiments were done to compare the selective feeding of *D. oregonensis* on natural lake seston with that of *D. sicilis* and *D. ashlandi* in a much larger study nearing completion.

Our experimental method, in broad outline, follows that of other workers (Parsons et al., 1967; McQueen, 1970; Poulet 1973, 1974; Richman et al., 1977) and, thus, it serves as a model of the technique generally employed. Lake water that had been poured through a 153-μm screen to remove large zooplankton was poured among four 300-ml bottles in the order: control 1, experimental 1, experimental 2, control 2. The two experimental bottles received an equal number — between 24 and 41 — of barren adult *D. oregonensis* females obtained from Crooked Lake (Washtenaw County, Michigan). To keep seston in suspension and limit algal growth, the bottles were placed on a rotating wheel at 0.25 rpm in the dark at lake temperature (McQueen, 1970). After 20—23 h of incubation, the bottles were removed from the wheel and poured through a 200-μm screen. The screening served to remove zooplankton from the experimental containers before counting with the Coulter Counter. The controls were also screened to make sure they received the same handling. Because the concentration of seston in lake water during summer was very high and the desired zooplankton were difficult to capture, seston in lake water was diluted to a half or a third of its original concentration by dilution with 0.22-μm filtered lake water. This then allowed the relatively small number of animals to graze down a significant fraction of the seston in the experimental bottles.

Particle-size spectra (both number and volume concentration of particulate matter in different size categories) were obtained with a TA II Coulter Counter using the basic method of Sheldon and Parsons (1967). In the experiments of 1977, 50- and 200-μm aperture tubes were used. In the 1978 experiment 50-, 140- and 400-μm aperture tubes were used. Lake water was made conductive by the addition of enough 25% NaCl to make a final solution of 0.5% NaCl. After adding salt, samples were stirred for 4 min before analysis to allow bubbles, which would be counted by the Coulter Counter, to escape from suspension. Aliquots from each bottle were run in quadruplicate on each aperture tube in the same order they were originally filled. An hour of analysis per aperture tube was required to do all four bottles. Any differences in particle concentration owing to instrument drift or time changes of the particle spectra in bottles would thus show up as differences between controls. Coincidence (simultaneous passage of particles through the aperture that results in two or more particles being counted as a larger particle) was monitored by the concentration index meter of the TA II. In all experiments reported here, coincidence was less than 1.5%, a value shown by experiment to cause little distortion in measurement of the true particle-size spectra.

Filtering rates were calculated for each experimental bottle using Eq. (13). The concentration of prey (seston) offered was taken to be the mean counts

per milliliter of the two control bottles at the end of the feeding period. Mean filtering rates were calculated from the filtering rates of the two experimental bottles. In certain size categories, counts per milliliter in experimental bottles were higher than in control bottles owing to particle modification, an artifact of these experiments which will be explained below. A higher concentration in the experimental bottle yields a negative filtering rate, a physical impossibility. As is the usual practice (e.g. Richman et al., 1977), negative mean filtering rates were assigned values of zero. Three experiments in this series were rejected because of gross differences between controls, lack of feeding, or excessive coincidence biasing the particle-size spectra measured.

Figure 1 shows concentration of particulate material in the controls and
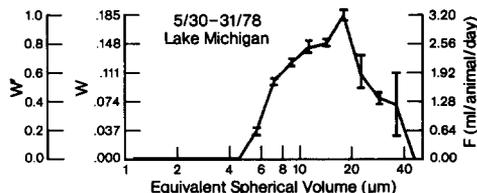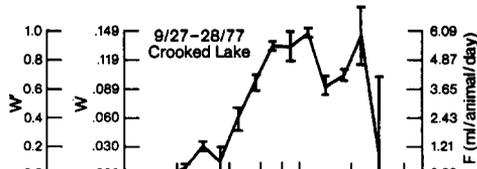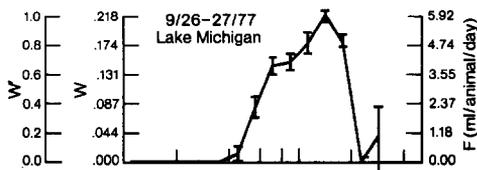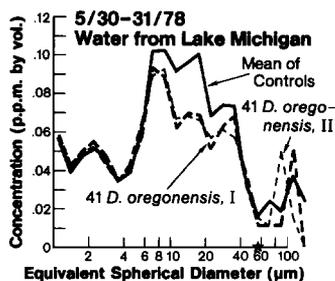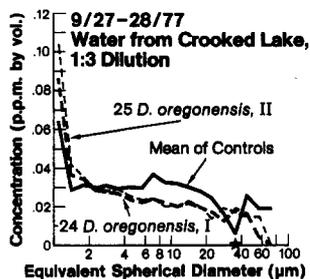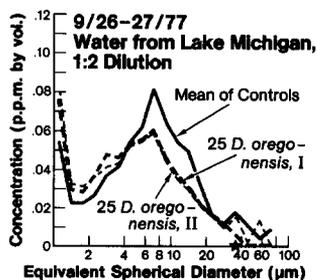
Fig. 1. Concentration of seston in control and experimental containers at the end of feeding period. I and II are container identifier numbers. Arabic numerals refer to number of animals in each experimental container. Data to right of star are statistically uncertain.

Fig. 2. W_i''s, W_i's, and F_i's calculated from concentrations of seston in experimental and control containers.

the experimental bottles at the end of the feeding period. The three experiments represent three very different feeding conditions. The shapes of the particle size spectra for the controls of the experiments are quite different. The types of food available to the zooplankton in each of the experiments differed as well. Lake Michigan water of 26—27 September 1977 contained a great deal of organic detritus, with the flagellate *Ceratium* and various colonial green and blue-green algae being the dominant forms of large algae. The 27—28 September 1977 sample from Crooked Lake contained a moderate amount of organic detritus, with diatoms as well as colonial greens and blue-greens being the dominant large algae. Lake Michigan water of 30—31 May 1978 had very little detritus, and diatoms were the dominant form of large algae. Temperatures also varied between the summer (18°C) and spring (7°C) experiments.

Filtering rates, W_i's and W_i''s are shown in Fig. 2. Concentrations of individual particles in natural waters are roughly inversely proportional to particle size (Sheldon and Parsons, 1967; Poulet, 1973, 1974). As a result, fewer particles are counted by the Coulter Counter in the larger size categories. Since counting follows Poisson statistics, precision of number and volume concentration decrease with increasing particle size. The asterisks on the abscissa of Fig. 1 indicate the first size category where the (predicted) concentration recorded by the Coulter Counter in a control container has a percent standard error equal to or greater than ±25%. Such errors or larger errors may be acceptable for looking at trends in the shape of the particle-size spectrum in control and experimental bottles but can lead to enormous errors in calculation of the filtering rate. For this reason, filtering rates were calculated only for size categories to the left of the asterisks.

For easy comparisons, results in Fig. 2 were plotted as W_i''s. W_i''s were calculated by dividing the filtering rate of a size category by the highest filtering rate observed. This assumes that the highest filtering rate observed corresponds to a W_i' of 1. The number of size categories for which filtering rates were calculated varied among experiments because of varied precision of the data. Since $W_i = F_i/\Sigma F_i$ (Eq. (15)), W_i is dependent on the number of size categories analyzed and, thus, is not as useful as a parameter for comparison of these experiments.

Even though the particle-size spectra of food available to the zooplankton varied among experiments and maximum filtering rates varied considerably between summer and spring experiments, the W_i' plots are quite similar. In Fig. 3, we have plotted mean W_i''s averaged from the three experiments along with the standard errors. Along with our data we have reported W_i''s and their standard errors calculated from mean filtering rates and standard errors given for two large sets of experiments performed by McQueen (1970) with *D. oregonensis*. One set of experiments was done using a mixture of different sized species of *Navicula* diatoms from pure cultures. The other was done with natural algae in lake water. The particle-size spectra available as food and the maximum filtering rates on them varied greatly between the two sets.
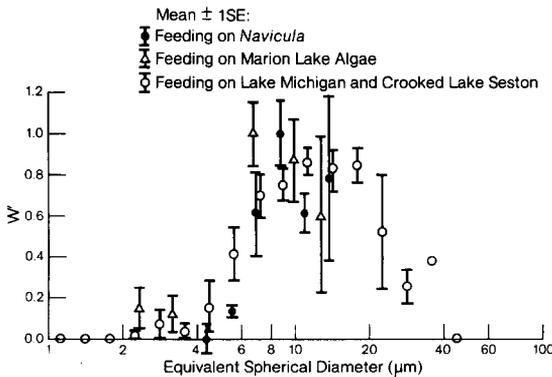
Fig. 3. Mean W'_i's calculated from present study and study of McQueen (1970).

The general pattern of W'_i's for McQueen's (1970) experiments is not greatly different from ours, although his *D. oregonensis* possibly selected smaller particles than our *D. oregonensis*, as evidenced by the position of the maximum W'_i. One possible explanation for his animals selecting smaller particles is the animals' size. He used a mixture of stage V and adult female animals. Stage V animals are considerably smaller than adult females (Comita and Anderson, 1959). Also size of adult females may vary considerably with season and year (Comita and Anderson, 1959; Maly, 1973). Since the filtering mesh size is proportional to animal length (Nival and Nival, 1976) the apparent difference in size selection may be caused by his using smaller animals.

We assert that these results support the leaky-sieve model. We intend to show that part of the roughness in the W'_i pattern reported here and the "tracking" behavior observed by others could follow from limitations in the data. We will also indicate how part of the discrepancies may follow from misinterpretation or presentation of results. Finally, we will also discuss situations where it might be expected that the leaky-sieve model does not hold.

In addition to removing phytoplankton or seston from the water while feeding, zooplankton add particles of different sizes to the water. While chewing and handling individual phytoplankton cells or seston, small fragments may be lost and added to the water (Conover, 1966; Frost, 1977). Furthermore a zooplankter may reject particles after chewing them if they do not have the proper taste (Poulet, 1978). Certain delicate chain-forming phytoplankton may be broken and lost to the water as smaller chains (O'Connors et al., 1976). Calanoid copepods produce fecal pellets that are large relative to other seston in the water. These pellets may remain intact (Reeve, 1963; Rigler, 1971) or become fragmented (Poulet, 1974) during feeding experiments. Cladocerans produce fecal material of small size (Christensen, 1973; Berman and Richman, 1974).

Particle addition is evident in Fig. 1 in the smaller size categories, where

the concentrations of particulate material in experimental bottles are higher than in the control bottles. This addition is especially evident for the 26—27 September 1977 experiment with Lake Michigan water. Particle addition has been observed in both small and large size categories in other experiments with calanoid copepods (Parsons et al., 1967; Parsons and Seki, 1970; Poulet, 1973, 1974; O'Connors et al., 1976; Nival and Nival, 1976; Frost, 1977; Richman et al., 1977).

The effects of particle addition are obvious. If an animal is filtering particles from one size group and modifying particles from other groups in such a way as to add to the former group, then the net change in particle concentration for that size group would not represent the animal's actual selectivity. In addition to potential errors introduced by particle addition, statistical errors may contribute to results that apparently deviate from the leaky-sieve model. In all recent studies of zooplankton grazing on natural particle-size spectra, one control bottle and one experimental bottle were used. Filtering rates or electivity indices are often calculated from small differences between particle-size spectra in control and experimental bottles. The accuracy claimed by the manufacturer for the Coulter Counter is about 2% on counts per milliliter in each channel. Thus, in size categories where differences between controls and experimental containers is small, very large errors in filtering rates, W_i's, or electivity can propagate owing only to instrumental and counting uncertainties.

From the two examples discussed above, particle addition and statistical uncertainty, it can be seen that great care must be taken to minimize these limitations in the data. As demonstrated in the data presented in Fig. 1, statistical artifacts can be reduced by replication; however, the problem of particle additions requires further study.

Use of the electivity index E_i (notably Poulet, 1973, 1974) has complicated the evaluation of selectivity because E_i varies with shape of the particle-size spectra of food offered (Boyd, 1976; Vanderploeg and Scavia, 1979) even when food selection conforms to the leaky-sieve model. Further, E_i is sensitive to the amount of food eaten in an experiment (Vanderploeg and Scavia, 1979). Thus, use of E_i in studies of selectivity may bias results away from the leaky-sieve model. W_i and E_i^*, an electivity index derived by Vanderploeg and Scavia (1979), do not suffer from these defects. Thus, it is clear that W_i (or E^*) should be used to evaluate the soundness of the leaky-sieve model.

There are certain conditions under which the leaky-sieve model might not be expected to hold exactly. First, capture efficiency of the filtering apparatus may change somewhat with pumping velocity of the water through the filter (Bernstein and Koehl, 1977) and distensibility of the food and filtering mesh (Boyd, 1976). Second, the zooplankton may reject cells that do not taste good or ones that have no taste (Poulet, 1978). If taste of the food is important, it can be introduced into the conditional probability model as follows. Change the definition of ϕ_i slightly so that it becomes ϕ_i', the proba-

bility that the prey will be captured by the filtering apparatus and brought to the "mouth". In the mouth, the food will be tasted and have a certain probability of being swallowed, T_i. Thus, W_i' is the product $\phi_i' T_i$. Further research is needed to determine the significance of food taste. If it is a significant phenomenon in nature, research will be needed to determine whether T_i varies with the relative abundance of different tasting foods.

SUMMARY AND CONCLUSION

In this paper, several methods of calculating selectivity coefficients (W_{ij}) of predation were derived. The resulting equations allow calculation of W_{ij} from raw data, mortality rates of prey, filtering rates, feeding rates and electivity indices. The use of W_{ij} in linear and nonlinear feeding constructs was discussed and the definition of W_{ij} in probabilistic terms was given.

Data from feeding experiments with *D. oregonensis* were used to illustrate the estimation of W_{ij} and give support for the leaky-sieve model of zooplankton filter-feeding. The limitations, statistical artifacts and poor presentation of typical feeding data were discussed relative to their effects on tests of the leaky-sieve model.

It appears that the leaky-sieve model conforms, at least approximately, to experimental observations — considering the limitations of those observations — under many conditions. In any event, W_{ij} is useful for evaluating the leaky-sieve model and for use in linear and non-linear feeding contructs to approximate partitioning of grazing among different classes of prey.

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where R_i is the concentration of prey i left after the feeding period. Equating Eqs. (1) and (2) and rearranging

$$W_i = \frac{X_i - R_i}{\Sigma(X_i - R_i)} * \frac{\Sigma W_i X_i}{X_i}$$

or

$$W_i = \frac{f_i \Sigma W_i X_i}{\Sigma(X_i - R_i)} \tag{3}$$

where $f_i = (X_i - R_i)/X_i$ is the fraction of available prey i that has been eaten. Using the constraint $\Sigma W_i \equiv 1$ and summing Eq. (3), we obtain

$$\frac{\Sigma W_i X_i}{\Sigma(X_i - R_i)} = \frac{1}{\Sigma f_i} . \tag{4}$$

Placing Eq. (4) in Eq. (3) and solving for W_i results in

$$W_i = \frac{f_i}{\Sigma f_i} . \tag{5}$$

Thus, W_i, the normalized selectivity coefficient, is easily obtained from experiments where various proportions of prey are available as long as both the initial and final food concentrations are reported. Since prey removed by the predator are not replaced, the experiment should not be run too long as a significant fraction of the "desired" prey will be removed and the predator will be forced to move on to less desired prey, causing the estimates of W_i's for the less desired prey to be biased upwards. The method presented here differs somewhat from that given by O'Neill (1971a). To calculate his (unnormalized) W_i, he set $\Sigma W_i X_i$ equal to some arbitrary number and solved for W_i in Eq. (1). The relation between the unnormalized W_i, which we will designate as W_i^*, and W_i is $W_i = W_i^*/\Sigma W_i^*$.

Results from selective grazing experiments are often not left in the form of particle spectra or f_i's, but are instead converted to electivity coefficients, filtering rates or feeding rates. Below we derive the relation between W_i and these other parameters.

The relationship between W_i and E_i' may be derived as follows:

$$E_i' \equiv \frac{P_i \Sigma X_i}{X_i} . \qquad \text{(Ivlev, 1961)} \tag{6}$$

Substituting Eq. (1) in (6) and rearranging results in

$$W_i = \frac{E_i' \Sigma X_i W_i}{\Sigma X_i} . \tag{7}$$

Using the constraint $\Sigma W_i \equiv 1$, summing, and rearranging Eq. (7) results in

$$\Sigma E_i' = \frac{\Sigma X_i}{\Sigma W_i X_i} . \tag{8}$$

Combining (7) and (8) and solving for W_i,

$$W_i = \frac{E'_i}{\Sigma E'_i}. \tag{9}$$

We now derive the relation between W_i and E_i by relating E_i to E'_i. E_i is given by the definition (Ivlev, 1961)

$$E_i = \frac{P_i - (X_i/\Sigma X_i)}{P_i + (X_i/\Sigma X_i)}. \tag{10}$$

Dividing numerator and denominator of Eq. (10) by $X_i/\Sigma X_i$ (noting $P_i \Sigma X_i / X_i$ is E'_i) and solving for E'_i gives

$$E'_i = \frac{1 + E_i}{1 - E_i}. \tag{11}$$

Placing Eq. (11) in Eq. (9) results in

$$W_i = \left(\frac{1 + E_i}{1 - E_i}\right) \Big/ \sum\left(\frac{1 + E_i}{1 - E_i}\right). \tag{12}$$

Filtering rates (F_i) are calculated from the equation

$$F_i/V = (\ln X_i - \ln R_i)/t \qquad \text{(Gauld, 1951)} \tag{13}$$

which is derived from the differential equation describing the exponential loss of prey during a feeding experiment

$$\frac{dX_i}{dt} = \frac{-F_i}{V} X_i \tag{14}$$

where X_i = concentration of prey i or size category i,

F_i = filtering rate of zooplankton on prey i (volume/time),
V = volume of water per animal in the experiment, and
t = time.

F_i/V is m_i, the mortality rate of i, that is, the instantaneous fraction of i removed. Thus, from Eq. (5),

$$W_i = \frac{m_i}{\Sigma m_i} = \frac{F_i}{\Sigma F_i}. \tag{15}$$

When food supply is below a specific critical concentration, F_i does not vary with food concentration (Rigler, 1971). In this case, W_i's can be accurately estimated from F_i's even though great fractions of the prey have been removed. In contrast, f_i, which by definition equals $(1/X_i)(\Delta X_i/\Delta t)$, can be a poor estimator of m_i and can lead to overestimates of W_i's for less desired prey as discussed above. Even above the critical concentration, F_i or m_i, although varying, is still a better parameter for estimating W_i's than f_i. In fact, if one imposes the "leaky-sieve" model (see below) for zooplankton filtering, W_i's calculated from F_i's determined from Eq. (13) will be correct regardless

of whether filtering rate varies over the interval of the experiment.

The (instantaneous) feeding rate (G) of a zooplankter is defined as

$$G_i = F_i X_i$$

where G = amount of food eaten per unit time. One can see, then, that

$$W_i = \frac{G_i/X_i}{\Sigma G_i/X_i} \tag{16}$$

and, unless the initial food concentrations (X_i) of all groups are equal, G_i must be converted back to F_i by dividing by the original food concentrations. The equations derived above for calculating W_i from various forms of data are summarized in Table I.

For the W_i construct to be useful, W_i should not vary appreciably with the shape of the particle-size spectrum of food or the amount of food available. Support for constant W_i's in copepods comes from papers by Nival and Nival (1973, 1976), Boyd (1976) and Frost (1977), which suggest that the filtering apparatus of copepods functions like a leaky sieve, a sieve that has a certain frequency distribution of different-sized holes. This frequency distribution determines the probability that a particle of a given size will be retained by the filtering apparatus. Filtering rate on size category i (F_i) is then

$$F_i = \phi_i \psi \tag{17}$$

where ϕ_i = probability that a particle in size category i will be retained by the filtering apparatus, and

ψ = volume of water passing through the filtering apparatus of the zooplankter per unit time.

TABLE I

Summary of equations used to calculate W_i from different forms of data

Form of data	Equation	Number in text
From proportions of each category eaten (f_i)	$W_i = \dfrac{f_i}{\Sigma f_i}$	(5)
From electivity coefficient (E_i')	$W_i = \dfrac{E_i'}{\Sigma E_i'}$	(9)
From electivity coefficient (E_i)	$W_i = \left(\dfrac{1+E_i}{1-E_i}\right)\Big/\Sigma\left(\dfrac{1+E_i}{1-E_i}\right)$	(12)
From filtering (F_i) or mortality (m_i) rates	$W_i = \dfrac{F_i}{\Sigma F_i} = \dfrac{m_i}{\Sigma m_i}$	(15)
From feeding rates (G_i)	$W_i = \dfrac{G_i/X_i}{\Sigma(G_i/X_i)}$	(16)

Since $W_i = F_i / \Sigma F_i$, Eq. (17) leads to

$$W_i = \frac{\phi_i}{\Sigma \phi_i}. \tag{18}$$

Because ϕ_i is a fixed property of the sieve, the leaky-sieve model implies that W_i's are independent of the particle-size spectra of food available. Particles small relative to the frequency distribution of holes have a low probability of being retained, while particles large relative to this distribution have a high probability of being retained. Particles larger than the largest holes are expected to be retained with a 100% efficiency; however, there is an upper limit to the size of particles zooplankton can handle so that F_i and W_i should eventually decrease with increasing size of food.

USE OF SELECTIVITY COEFFICIENTS IN FEEDING CONSTRUCTS

The relation of feeding rate (G_i) on the ith kind of prey to feeding rate (G) on the entire assemblage of prey is

$$G_i = G P_i . \tag{19}$$

O'Neill (1969) discusses how to calculate G for linear ecosystem models. P_i in Eq. (19) is estimated from W_i's as discussed in this paper.

The use of W_i in feeding constructs of nonlinear ecosystem models requires explanation here as its use has not been clearly explained, and in some cases it has been misapplied. The basic idea behind most feeding constructs in nonlinear ecosystem models is that feeding rate on a single kind of prey follows Michaelis—Menten kinetics:

$$G = G_{\max} \frac{X}{K + X} \tag{20}$$

where $G_{\max}$ = the maximum feeding rate,
$\quad K$ = the half saturation coefficient, which may be a function of predator concentration, and
$\quad X$ = the biomass concentration of the prey.
In time-dependent models, both $G_{\max}$ and X vary in time due to variations in temperature and other ecosystem components.

To handle the case of more than one kind of prey, most modellers take the basic approach that the total effective food supply available to the predator is $\Sigma W_i' X_i$, where W_i' is the conditional probability that feeding will occur when the ith kind of prey is encountered (O'Neill, 1971b, 1975; Bloomfield et al., 1973; Park et al., 1974; Shugart et al., 1974; DeAngelis et al., 1975; Smith et al., 1975; McNaught and Scavia, 1976; Scavia and Park, 1976; Scavia et al., 1976a and b). This conditional probability W_i' is proportional to W_i. Placing $\Sigma W_i' X_i$ for X in Eq. (20) gives

$$G = G_{\max} \frac{\Sigma W_i' X_i}{K + \Sigma W_i' X_i}. \tag{21}$$

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