

Two Electivity Indices for Feeding with Special Reference to Zooplankton Grazing¹

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The electivity indices E_i and E_i' of predator-prey interaction are currently used to quantify particle-size selection by grazers. Under conditions of passive, mechanical particle-size selection predicted by the leaky-sieve model, these indices yield electivity vs. particle-size curves that vary with the shape of the particle-size spectrum of food offered to the zooplankton. In addition to this bias, poor estimates of electivity will be obtained unless only a small fraction of the food is eaten in such experiments. The selectivity coefficient (W_i) used by modelers in feeding constructs and the electivity index E_i^* , derived here, are recommended instead because they do not suffer from the shortcomings described for E_i and E_i' . Moreover, use of W_i 's and E_i^* 's is recommended for quantifying selection for many other cases of predator-prey interaction.

Key words: electivity indices, selectivity, selective grazing, predator-prey intraction

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On utilise communément les indices d'électivité E_i et E_i' de l'interaction prédateurs-proies quand il s'agit de quantifier le choix de la grosseur des particules par les brouteurs. Dans les conditions de la sélection mécanique passive de la grosseur des particules prédite par le modèle du tamis, ces indices donnent des courbes électivité vs grosseur des particules qui varient en fonction de la forme du spectre de grosseurs des particules offertes au zooplancton. En plus de ce biais, on obtiendra de pauvres estimations de l'électivité à moins qu'une petite fraction seulement de la nourriture soit mangée au cours de telles expériences. Au lieu de cela, on recommande le coefficient de sélectivité (W_i) utilisé dans la construction de modèles d'alimentation et l'indice d'électivité E_i^* , tel que déduit ici, parce qu'ils n'ont pas les défauts qui ont été décrits pour E_i et E_i' . On recommande en outre d'utiliser W_i et E_i^* pour quantifier la sélection dans plusieurs cas d'interaction prédateurs-proies.

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THE electivity indices E_i and E_i' (Ivlev 1961) have been used to quantify size-selective grazing by zooplankton (Poulet 1973, 1974; Frost 1977). These indices are used to answer the following two questions. First, are particles of certain sizes "selected" in preference to others? Second, does this selection depend on the shape of the particle-size spectrum of food offered? The second question is currently of special interest to zooplankton ecologists. Some work suggests that size selection by copepods is passive and mechanical, a function only of the pore-size distribution of the grazer's filtering sieve and morphology of other mouth parts (Nival and Nival 1973, 1976; Boyd 1976; Frost 1977). Although we recognize the possible importance of mouth parts other than the one or ones with a sieve, this model of size selection will be called the leaky-sieve model, after Boyd (1976). Other work suggests

that copepods somehow select peaks of abundance in the particle-size spectrum of food (Poulet 1973; Richman et al. 1977).

In this paper we will show that E_i and E_i' cannot be used to answer the above questions. Boyd (1976) has demonstrated graphically that E_i can vary with the shape of the offered particle-size spectrum. We will support his results analytically and show that the passive size selection predicted by the leaky-sieve model gives values of E_i' that can vary with the shape of the offered particle-size spectrum. Further, we propose the use of two electivity indices that do not suffer from this theoretical shortcoming. A further difficulty with E_i and E_i' is that the experimenter must allow the zooplankton to remove only a small portion of the food offered; otherwise, biased estimates of E_i and E_i' will result. This technical difficulty does not apply to the proposed indices. One proposed index is O'Neill's (1969, 1971) selectivity coefficient (W_i) calculated

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from filtering rates or mortality rates (Vanderploeg and Scavia 1979). The other index is derived here. Although we advocate using the proposed indices for zooplankton, these indices should be useful for other predators as well.

To show that E_i and E_i' vary with the shape of the offered particle-size spectrum under the conditions of the leaky-sieve model, we need the definitions of E_i and E_i' as well as the definition of the filtering rates (F_i) given by the leaky-sieve model:

$$(1) \quad E_i = \left[P_i - \left(X_i / \sum_i^n X_i \right) \right] / \left[\left(P_i + \left(X_i / \sum_i^n X_i \right) \right) \right],$$

$$(2) \quad E_i' = P_i / \left(X_i / \sum_i^n X_i \right),$$

and

$$(3) \quad F_i = \phi_i \psi \quad (\text{Nival and Nival 1973, 1976; Boyd 1976}),$$

where P_i = probability that when feeding occurs the i^{th} kind or size of prey will be selected from all n kinds of prey, X_i = concentration of prey i , ϕ_i = probability that a particle in size category i will be retained by the filtering apparatus and ingested, and ψ = volume of water filtered per unit time by the predator.

Poulet (1973, 1974) and Frost (1977) have approximated P_i by

$$(4) \quad P_i \simeq R_i / \sum_i^n R_i,$$

where R_i = ration of the i^{th} prey over the time interval of the experiment. Because feeding rate (dR_i/dt) is $F_i X_i$, it follows from equation 3 that $dR_i/dt = \phi_i \psi X_i$. Thus, the relation of R_i to ϕ_i is

$$(5) \quad R_i = \phi_i \int_0^t \psi X_i du,$$

where t = time and u is the dummy variable of integration. Substituting equation 5 for R_i in equation 4 and placing this result for P_i in equation 2, we obtain

$$(6) \quad E_i' = \frac{\phi_i \left(\int_0^t \psi X_i du \right) \left(\sum_i^n X_i / X_i \right)}{\sum_i^n \phi_i \left(\int_0^t \psi X_i du \right)}.$$

For the special case where all R_i 's are small relative to X_i (i.e. for short experiments), X_i in equation 6 may be treated as a constant. In this case,

$$(7) \quad E_i' = \frac{\phi_i \sum_i^n X_i}{\sum_i^n \phi_i X_i}.$$

It is easily seen from equation 7 that E_i' is proportional to ϕ_i but that the value of E_i' can vary with the shape of the offered particle-size spectrum since the quantity $\sum X_i / \sum \phi_i X_i$ can vary with the shape of the offered par-

ticle-size spectrum. The same is true for the general case (equation 6). Equations 6 and 7 predict that although the value of E_i' can vary with the particle-size spectrum offered, the shape of an E_i' vs. particle-size curve will not.

By combining equations 1 and 2, we obtain

$$(8) \quad E_i = (E_i' - 1) / (E_i' + 1).$$

Equations 6 and 8 imply that both the values of E_i and the shape of an E_i vs. particle-size curve can vary with the shape of the offered particle-size spectrum, which has been discussed earlier by Boyd (1976).

We also checked the behavior of the Q and D indices of Jacobs (1974), which were derived from the special case of two kinds of prey. When extended to the case of more than two kinds of prey, Q and D —like E_i' and E_i —vary with the shape of the offered food spectrum.

The selectivity coefficient, W_i , is the weighting factor appearing in the following expression for the probability, P_i , of selection of a given kind of prey (O'Neill 1969, 1971):

$$(9) \quad P_i = W_i X_i / \sum_i^n W_i X_i.$$

Vanderploeg and Scavia (1979) constrain the definition of W_i by requiring that $\sum W_i = 1$. If the W_i 's are constants for any set of X_i 's, W_i corresponds to the probability that the i^{th} kind of prey will be selected when all kinds of prey are equally abundant (Vanderploeg and Scavia 1979). Chesson (1978) has recently derived a measure of selective predation identical to W_i from a simple stochastic model of prey encounter and capture.

Vanderploeg and Scavia (1979) have shown that W_i is related to filtering rates or mortality rates (m_i) for the n kinds of different prey as follows:

$$(10) \quad W_i = F_i / \sum_i^n F_i = m_i / \sum_i^n m_i.$$

Combining equations 3 and 10 yields

$$(11) \quad W_i = \phi_i / \sum_i^n \phi_i.$$

Since ϕ_i is a fixed property of the filtering animal, equation 11 implies that W_i is independent of the shape of the particle-size spectrum of food available and is only a function of the hole sizes in the filtering apparatus and the animal's ability to handle different sizes of food. If size-selective grazing deviates from that predicted by the leaky-sieve model, W_i for a size category will vary with the shape particle-size spectrum offered. The leaky-sieve model is a specific case of a more general model that may apply to many predator-prey interactions. ϕ_i is the conditional probability (W_i') that if encountered, prey i will be eaten (Vanderploeg and Scavia 1979). ψ corresponds to the volume of space searched per unit time by the predator. W_i 's in other

applications may depend on such factors as palatability, prey escape abilities, or defense mechanisms (O'Neill 1969). Thus, W_i is a useful index for pointing out deviations from the leaky-sieve model or deviations in the assumption of constant W_i 's for the more general case.

Vanderploeg and Scavia (1979) showed how to estimate W_i from E_i , E_i' , feeding rates, mortality and filtering rates, but recommended using the latter two variables (equation 10) since in that way the experimenter can allow large portions of the available prey to be eaten. The filtering rates are calculated in the usual way:

$$(12) \quad F_i = (V/t)[\ln X_i(0) - \ln X_i(t)] \quad (\text{Gauld 1951}),$$

where V = volume of water available per animal in the experiment and t = length of the experiment. It is possible that if the animals eat a large portion of the available food, F_i will vary with time over the period of the experiment. One might wonder whether time variability in F_i will affect the calculation of W_i . It can be seen that variations in F_i (calculated by equation 12) are due only to changes in ψ (equation 3) for the leaky-sieve model and that W_i is independent of ψ (equation 11). Thus, W_i 's can be calculated from F_i 's given by equation 12 regardless of whether F_i 's are time varying.

In calculating E_i or E_i' from P_i as given by equation 4, zooplankton ecologists must be concerned about the length of the experiment because, as the amount of prey eaten becomes large, equation 4 becomes a poor approximation for P_i . As more food is eaten, concentrations of "desired" (or easily sieved) prey will diminish relative to the less-desired prey. As the less-desired prey increase relative to other prey, the probability of encounter and capture of less-desired prey will be increased, with the end result that estimated values E_i and E_i' for less-desired prey will be biased upwards. Thus, in addition to its theoretical advantage (i.e. constant for the leaky-sieve model), W_i can be more accurately computed since the experimenter can allow the zooplankton to graze down a substantial fraction of the particle-size spectrum.

W_i is defined between 0 and 1. E_i , the electivity coefficient most often used, is defined between -1 and +1, with neutral electivity indicated by zero. Since ecologists are used to working with E_i , we derive an index that has the desirable properties of W_i and ranges between -1 and +1, with neutral electivity indicated by zero. If equation 1 is examined for the case of equal concentrations of food items, then P_i and $X_i/\sum X_i$ are equal to W_i and $1/n$, respectively. Thus, by analogy our new electivity index, E_i^* , is

$$(13) \quad E_i^* = [W_i - (1/n)]/[W_i + (1/n)].$$

E_i^* is not a function of the food spectrum if the leaky-sieve or constant W_i model holds, since by combining equations 11 and 13

$$(14) \quad E_i^* = \left[\phi_i / \sum_i^n \phi_i - (1/n) \right] / \left[\phi_i / \sum_i^n \phi_i + (1/n) \right].$$

As was recommended above, W_i (appearing in equation 13) should be estimated from equation 10. Further, E_i^* , like W_i , is not affected by the length of time the experiment is run.

The practical significance of the advantages of E_i^* over E_i can be demonstrated by calculating values of E_i and E_i^* from results of hypothetical experiments done with a zooplankter having an assumed ϕ_i distribution. The final food spectra $[X_i(t)]$ were generated from assumed initial spectra $[X_i(0)]$ using the relation

$$X_i(t) = X_i(0)e^{-(\phi_i \psi / V)t}$$

(from equations 3 and 12), the assumed values of ϕ_i , and various values for $(\psi/V)t$. From the initial and final spectra, values of E_i were calculated with equation 4. Values of E_i^* , which are independent of the shape of the offered food spectrum or duration of the experiment, were calculated directly from the values of ϕ_i (equation 14). The assumed ϕ_i distribution was estimated from filtering rates (F_i) determined in a typical grazing experiment with *Diatomus sicilis*, a freshwater calanoid copepod. Equation 3 was used to calculate ϕ_i , where ψ was assumed to be equal to the largest F_i measured in the experiment. Four different initial food spectra, including a spectrum having the same shape as the ϕ_i distribution, were considered in our analyses (Fig. 1). The effect of the duration of an experiment on E_i , determined for a uniform initial distribution of food is shown in Fig. 2. From the basic definitions of W_i , E_i , and E_i^* , one would expect E_i to approach E_i^* for the case of a uniform distribution of food when the fraction of the available food that is eaten is small. As greater proportions of food are eaten, the departure of the E_i curve from the E_i^* curve gets larger and, as predicted above, values of E_i

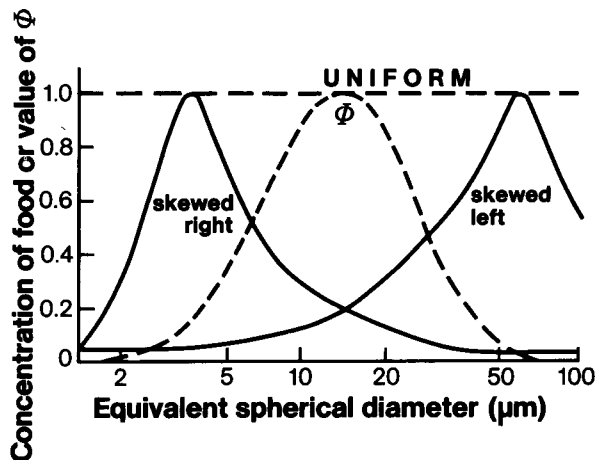


FIG. 1. ϕ distribution and particle size spectra for initial food concentrations.

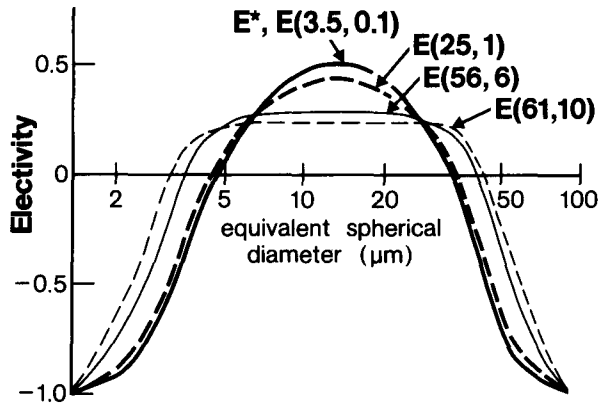


FIG. 2. Curves of electivities vs. particle size as a function of duration of feeding experiment for a uniform offered food spectrum. E^* is the new index and $E(a,b)$ is Ivlev's index with a = percent of food eaten and $b = \psi t/V$ (see text).

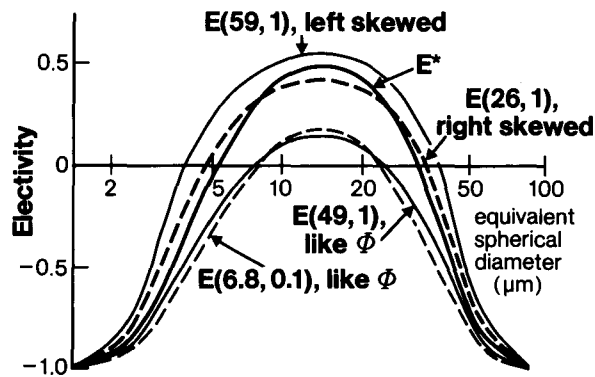


FIG. 3. Curves of electivities vs. particle size as a function of the shape of the offered particle size spectrum. E^* is the new index and $E(a,b)$ are as in Fig. 2.

for small values of ϕ_i (less-desired prey) are biased upwards (Fig. 2).

The shape of the initial food spectrum has a significant effect on the E_i curve (Fig. 3). The E_i curves for the skewed initial distributions of food are considerably different from each other as well as from the E_i^* curve. The E_i curve for the initial distribution shaped like the ϕ_i distribution (Fig. 1) is grossly different from the E_i^* curve and from the E_i curves for the skewed initial distributions. In fact the values of E_i for some size categories even change sign as a function of the initial food spectrum (Fig. 3).

In summary, we recommend the use of the electivity indices W_i and E_i^* to quantify feeding preferences of zooplankton and other animals where W_i 's are expected to be constant. Further, the validity of the assumption of constant ϕ_i 's or W_i 's can be tested with these indices. Not only size selection can be investigated with these indices but also preferences based on taste or other factors. Even if the assumption of constant W_i 's is only an approximation, one would still expect to get better estimates of selectivity under various conditions of relative prey abundance from W_i and E_i^* than from their analogues, E_i' and E_i .

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