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Feeding rate of *Diaptomus sicilis* and its relation to selectivity a effective food concentration in algal mixtures and in La Michigan[1]

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Abstract. The concept of effective food concentration (EFC), a means of predicting food cc sumption from selectivity and food concentration data, is explained, tested, and applied to und standing food consumption by the freshwater copepod *Diaptomus sicilis* on mixtures of algae different sizes and on Lake Michigan seston. Experiments on mixtures of different sized *Chlamyc monas* spp. showed that selection (W′) was an invariant function of particle size when the algae w counted microscopically. When the Coulter counter was used, a more variable pattern of selectivity similar to the peak tracking response reported by some investigators – was obtained. This was due bias of zooplankton-produced particles. Size-selective selectivity coefficients (W′) were used to weig the food concentration in each size category and the weighted values summed to give EFC. Food cc sumption in experiments with seston and with cultured algae was better described by EFC than total food concentration (TFC), the unweighted sum. Moreover, use of EFC diminished t magnitude of the apparent threshold concentration required for feeding to commence. Althou selectivity in algal mixtures and lake seston was approximately the same, the food consumption vers EFC curve saturated more quickly for the algal mixtures than for the lake seston. Since expression food concentration as EFC allowed direct comparison of experiments having different particle-si spectra of food, we concluded the difference resulted from the lower food quality of lake seston, th is, its lower digestibility and sensory quality for zooplankton capture.

Introduction

Recently, Vanderploeg (1981a) showed *Diaptomus sicilis* exhibited a relativel invariant bell-shaped selectivity versus particle-size curve for Lake Michiga seston for varying particle-size spectra. This result was significant because it wa the first demonstration of an invariant pattern of selection for a copepod feedin on natural seston. Invariant selectivity is necessary for use of the effective foo concentration model (Vanderploeg and Scavia, 1979a; Bartram, 1980). Thi model provides a simple means of predicting feeding rates in mixtures of differer kinds of food from knowledge of the food-type concentrations (X_i) and thei invariant selectivity coefficients (W_i'). The results for *D. sicilis* represent th special case in which the different kinds of food are size categories. Effectiv food concentration (EFC) is the weighted sum of food concentrations, where th weighting factors are the selectivity coefficients:

$$EFC = \sum_{i=1}^{n} W_i' X_i \qquad (1$$

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Traditionally, ecologists have reported environmental food concentration as total food concentration (TFC), the unweighted sum of the X_i (i.e., TFC = ΣX_i). The selectivity coefficient W_i' is, in the most straightforward manner, determined from clearance rates (F_i) of the different kinds of food in mixtures from the relation $W_i' = F_i/F_{pref}$, where F_{pref} is the clearance rate of the most preferred food (Vanderploeg and Scavia, 1979a). [Previously F_{pref} was called F_{max} (Vanderploeg and Scavia, 1979a; Vanderploeg, 1981a) to indicate it was the highest clearance rate in a mixture. The notation was changed to avoid confusion with the overall maximum clearance rate (e.g., Frost, 1972) that would be expected at a low concentration of that alga.]

The EFC model states that ingestion rate (G) on any mixture of foods is given by a simple functional relation G = f(EFC). The function f(EFC) may be any of the relations used to predict ingestion of a single kind of food such as the linear, Michaelis-Menten or Ivlev (Mullin *et al.*, 1975). By substitution of EFC for food concentration in the Michaelis-Menten expression for food consumption, one obtains the following expression for total ingestion rate on all kinds of food (Vanderploeg and Scavia, 1979a):

$$G = \frac{G_{max}\,(EFC)}{K + EFC} = \frac{G_{max} \Sigma W_i' X_i}{K + \Sigma W_i' X_i} \quad (2)$$

Bartram (1981), using a slightly different approach, arrived at a similiar result. The probability (P_i) that the ith food would be eaten is given by the expression

$$P_i = \frac{W_i' X_i}{\Sigma W_i' X_i} \quad (3)$$

Multiplying equation (2) by the expression for P_i gives the following expression for ingestion (G_i) of the ith food (Vanderploeg and Scavia, 1979a):

$$G_i = \frac{G_{max} W_i' X_i}{K + \Sigma W_i' X_i} = \frac{G_{max} W_i' X_i}{K + EFC} \quad (4)$$

Equation (1) may be thought of as converting the quantity of each kind of food to the equivalent amount of the 'most preferred' ($W_i' = 1$) food by means of the selectivity coefficient, W_i'. A consequence of this is that the functional response G = f(EFC) should be the same as the functional response for the most preferred food alone. Thus, $G = F_{pref} \Sigma W_i' X_i$ (since for a single kind of food, G = FX where F is clearance rate and X is concentration of food), and by substituting this expression in Equation (2),

$$F_{pref} = F_i/W_i' = \frac{G_{max}}{K + \Sigma W_i' X_i} \quad (5)$$

The same substitution procedure leads to results appropriate for the linear and Ivlev models. Results for the linear model are given in Appendix I.

The essence of the EFC model is that each unit of effective food concentration results in the same ingestion response as another regardless of its composition whether for example the unit consists of large cells or of small cells, or of both. In practical terms, the model implies that W_i' values and f(EFC) from simpl

feeding experiments can be used to predict ingestion on any mixture of foo [provided all information necessary to predict W′ (e.g., taste and size) is inclu ed]. Evaluation of the model involves two steps: (i) it must be demonstrated th W_i' values are invariant; (ii) the same functional response [e.g., the Michael Menten relation of equation (2) or (5)] with invariant coefficients must work f all kinds of food or mixtures thereof.

In this paper we examine data from Coulter counter experiments with la seston (Vanderploeg, 1981a) and parallel experiments with three different-siz species of *Chlamydomonas* using both microscopic and Coulter counting evaluate the EFC feeding construct and to explore the feeding biology of *D sicilis*. The *Chlamydomonas* spp. chosen were ovoid or round, and all we readily eaten and highly digestible. Thus, problems in Coulter experiments asso ated with particle taste, particle shape, and production of grazer-produced pa ticles should be minimized (Vanderploeg, 1981a). In addition, *Chlamydomon* are ideal subjects for Coulter counting and sizing, in contrast to lake sesto which required special precautions for accurate sizing (Vanderploeg, 1981b Moreover, by using *Chlamydomonas* mixtures, it was possible to determine si selectivity of *Diaptomus* on particle-size spectrum shapes very different fro those found in nature. One series of *Chlamydomonas* experiments that was an lyzed by Coulter counting allowed us to compare directly selectivity and feedir on natural seston with that on a continuous size spectrum of *Chlamydomona* Another series utilizing both microscopic and Coulter counting allowed us t determine W′s and feeding rates that were not biased by particle production an to evaluate the magnitude of this bias.

Methods

Experiments with lake seston

The methods for experiments with lake seston are detailed in Vanderploe (1981a, 1981b). Offshore Lake Michigan water taken from the upper hypc limnion, the depth at which the adult female *D. sicilis* feeds, was screene through a 153 μm mesh to remove most zooplankton; 20–50 *D. sicilis* female were added to duplicate 275 ml bottles, and two 275 ml bottles served as controls Bottles were placed on a rotating wheel (0.25 r.p.m.) in the dark at ambient lak temperature. After 19–24 h, the bottles were removed from the wheel and par ticle concentrations as a function of equivalent spherical diameter in control an experimental bottles were determined with a Coulter counter. From these data the clearance rate and the selectivity coefficient W_i' (Vanderploeg and Scavia 1979a; Vanderploeg, 1981a) were calculated for each size category; W_i' wa determined by dividing the clearance rate in each size category by F_{pref}, th highest clearance rate of all size categories. F_{pref} may be thought of as the effect ive volume searched per unit time by the copepod (Vanderploeg and Scavia 1979b).

Two feeding rate quantities were calculated for each experimental containe (Vanderploeg, 1981a). The first, net feeding rate (NFR), identical to Poulet's (1973, 1974) food consumption, was calculated for each experimental containe

by summing, over all size categories, the difference between mean particle concentration in the controls and concentration in the experimental container after feeding. Gross feeding rate (GFR) was calculated in the same way, except that only positive differences were summed. Because food concentrations in control containers changed very little over the duration of the experiments, food concentration available to the animals over the experimental period was approximated by the arithmetic mean of concentration in control and experimental containers. These concentrations and feeding rate values were used to obtain the feeding rate-concentration response of the animals. This approximation yields results under these conditions that have a negligible difference from those predicted by the 'average-concentration' method of Frost (1972).

Coulter experiments with Chlamydomonas spp.

Experiments with mixtures of species of *Chlamydomonas* were similar to those with lake seston, except that cultured *C. oblonga* (UTEX 219), *C. proteus* (UTEX 216), and *Chlamydomonas* sp. (UTEX 796) were used as food. Again the Coulter counter was used to measure feeding. Algae were cultured in filter-sterilized unbuffered WC medium (Guillard and Lorenzen, 1972) at a light intensity of about 70 μEinst $m^{-2} s^{-1}$ at 15°C on 16:8 L:D cycle. Cells used for feeding experiments were in exponential phase growth. Feeding suspensions were made by pipetting algae into 0.22 μm filtered, 5°C hypolimnetic water to the desired concentration.

In experiments comparing feeding on eaeh species of *Chlamydomonas* separately, the suspension was poured among four 275 ml bottles and 20–30 animals were added to two of the bottles; two bottles without animals served as controls. Bottles were placed on a rotating wheel (0.25 r.p.m.) in a dark incubator at 5°C for 19–25 h. Algal growth rate during this period was very low. In experiments with mixtures of *Chlamydomonas*, algal suspensions were dark acclimated for 16–27 h before they were added to the bottles. At the same time, the zooplankton were preconditioned to the suspension in a 250 ml beaker. Algal concentrations in the controls did not change during the feeding experiments.

W_i' values for experiments with mixtures of *Chlamydomonas* spp. were calculated by the same method described for lake seston. For experiments with individual species of algae, W_i' values were approximated by determining the clearance rate for the peak in the biomass spectrum of each alga and dividing this value by the highest value obtained. (See Appendix I for justification.)

Microscope/Coulter experiments with Chlamydomonas spp.

Experiments were done with *Chlamydomonas* spp. using both microscopic and Coulter counting. The microscopic counts allowed estimation of W' that was unbiased by zooplankton-produced particles (Bartram, 1980). These results could then be contrasted with results from Coulter analyses. Because it was difficult to distinguish clearly between all three species of *Chlamydomonas* in a mixture during microscopic counting or by size for Coulter counting, only the largest and smallest species (*C. oblonga* and *C.* sp.) were used. *C. oblonga* and *Chlamydomonas* sp. were operationally defined by Coulter counting as particles within the size ranges of 3.17–8.00 μm and 8.00–20.2 μm, respectively. Most *C. oblonga*

and *Chlamydomonas* sp. were restricted to respective Coulter size ranges 3.17–6.35 μm and 10.08–16.0 μm. Algae were grown as described above, b algae and zooplankton were preconditioned at 10°C in dim light on a 14:10 L cycle. Excess nutrients, trace metals, and vitamins were added. After Coul analyses, subsamples of water were preserved in 1% acid Lugol solution for la counting on the inverted microscope. Usually on a given date (between June a October), experiments were run at approximate initial total concentrations of 0. 0.9, and 2.7 mm l^{-1} using a fixed biomass ratio of *C. oblonga* to *C.* sp. Ea experiment consisted of duplicate initial bottles (for estimate of initial algal co centration), duplicate control bottles, and duplicate experimental bottles. Fros (1972) equations were used to calculate ingestion as a function of 'average' co centration of food. In the case of microscopic counts, the equations were appli to each alga separately. In the case of the Coulter counts, the equations we applied to each Coulter channel.

Carbon concentrations

Carbon contents of seston, algae and zooplankton were determined on a Oceanography International Carbon Analyzer (nondispersive infrared, CO_2 se sitive) following wet oxidation by potassium persulfate and phosphoric ac (Menzel and Vaccaro, 1964) at 95°C or 150°C for 4 h in sealed precombuse (400°C, 4 h) ampoules (Oceanography International Corp., 1978). Seston ar algae were concentrated on precombusted (400°C, 4 h) 25 mm Gelman A/E gla fiber filters. For seston carbon contents, three 100 ml samples were filtered fro water remaining in control bottles after Coulter analyses. Carbon contents fc *Chlamydomonas* were determined similarly for cultures grown under conditior identical to those used for the feeding experiments. Specific carbon concer trations were calculated by dividing carbon content by total volume of particulat material measured by the Coulter counter.

Body volumes of zooplankton

Body volumes of all zooplankton were determined by assuming an ellipsoi metasome and a urosome having the cross section of an ellipse. From measure ments of metasome length (a), width (b) and depth (c) and urosome width (d depth (f) and length (l), the volumes (V) of the zooplankton were calculated b $V = \pi[(abc)/6 + (dfl)/4]$.

Comparison of W′ curves

A W′ curve may be thought of as a vector $(W_1', W_2', \ldots, W_n')$, where W_i refers to the W′ value of the ith size category. W′ vectors from one set of exper imental conditions were compared to those from another by use of multivari ate analysis of variance (MANOVA). Error degrees of freedom (df) are $df = N - n - 1$, where N = total number of experimental replicates, and n = numbe of size categories. The computer programs SPSS-MANOVA (Northwestern Uni versity), which employs Wilk's lambda, Hotelling's trace criterion, Roy's larges root criterion, and Pillai's trace criterion to test for differences (Anderson, 1958) was used. Univariate F-tests were used to identify particular size categorie

having significant differences in W′ between experimental conditions. Since we could not be sure that the assumptions of normality and homogeneity of variance implicit in these tests would be strictly adhered to for a limited number of observations, the data in each size category were transformed to ranks, and the MANOVA was performed on the rank-transformed data (Conover, 1980, p. 337) as well. Since nearly identical results were obtained for the MANOVA on unranked and ranked data, we are confident that the statistical analyses reported here on the unranked data are valid (Conover, 1980, p. 337).

Results

Selectivity patterns in Coulter counter experiments with Chlamydomonas spp. and lake seston

Table I shows W′ values obtained for *D. sicilis* feeding on the species of *Chlamydomonas* offered individually at low concentrations. All experiments were run on the same date (15 June 1979) to avoid potential effects of time-varying feeding rates owing to the physiological condition of the zooplankton (Mayzaud and Poulet, 1978). Lowest W′ values were associated with small cells.

Experiments with mixtures of *Chlamydomonas* were intended to represent four experimental cases: (i) low concentration (TFC = 1.18, EFC = 0.50 $mm^3 l^{-1}$), small-cell-rich mixture (Figure 1a); (ii) high concentration (TFC = 1.82, EFC = 0.67 $mm^3 l^{-1}$), small-cell-rich mixture (Figure 1b); (iii) low concentration (TFC = 0.55, EFC = 0.35 $mm^3 l^{-1}$), large-cell-rich mixture (Figure 1c); and (iv) high concentration (TFC = 1.70; EFC = 0.94 $mm^3 l^{-1}$), large-cell-rich mixture (Figure 1d). Note that the curves for the two concentrations of large-cell-rich mixture are virtually identical; the same holds true for the two concentrations of small-cell mixtures. The curves for the small-cell-rich mixtures are similar to those for the large-cell-rich mixtures, although the W′ values for the latter are somewhat lower in the smaller size categories. Mean W′ curves from the 23 experiments with lake seston and the four experiments with *Chlamydomonas* spp are shown in Figure 2, along with the W′ values obtained with individual species of *Chlamydomonas*. The same general W′ pattern is seen for both natural seston and *Chlamydomonas* spp. Despite this similarity, MANOVA of the W′ vectors having nine size categories between 3.17 and 25.4 μm, from the experiments with seston and with *Chlamydomonas* showed their curves were highly significantly (p = 0.002) different. Univariate F-tests comparing W′ size category by size cat

Table I. Clearance rates (±s.e., N = 2) and W′ calculated for peaks in biomass spectra of *Chlamydomonas* spp. offered individually at low concentrations (TFC = 0.34–0.37 $mm^3 l^{-1}$). All experiments were run on the same day.

Species	Size category of biomass peak (μm)	Clearance rate (ml d^{-1})	W′
Chlamydomonas oblonga	4.00 – 5.04	1.64 ± 0.77	0.21
C. proteus	6.35 – 8.00	4.26 ± 0.29	0.53
C. sp.	12.7 – 16.0	8.00 ± 1.31	1.00

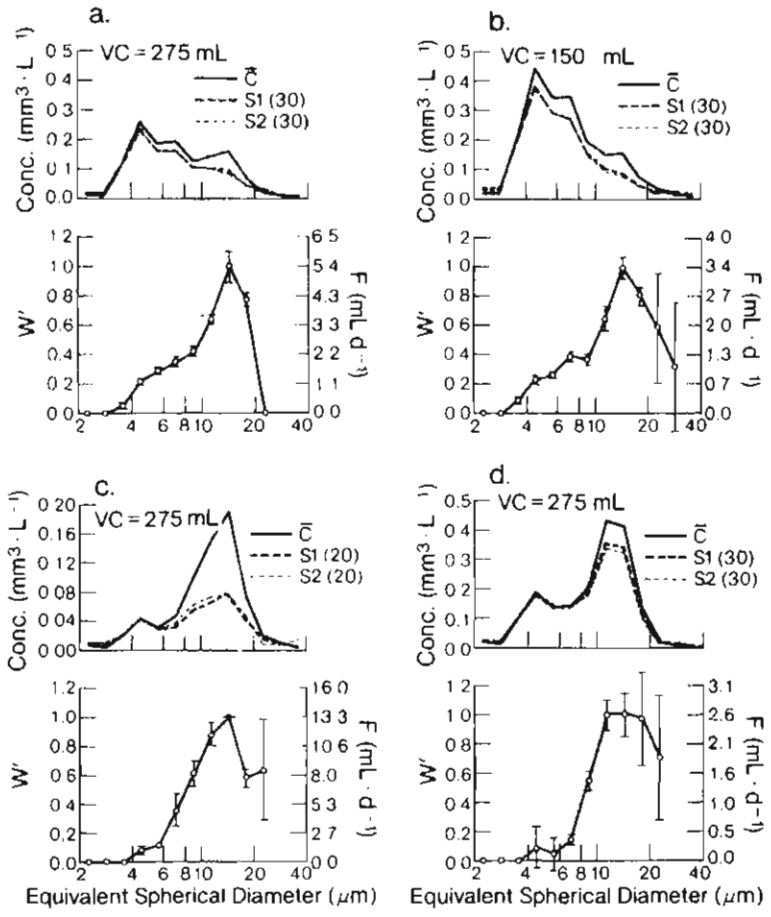

Fig. 1. Effect of particle-size spectrum of *Chlamydomonas* spp. on W′. $\bar{C}$ is mean concentration control containers. S1 and S2 refer to respective experimental containers, each containing the numb of zooplankton indicated in parentheses. VC = volume of bottles.

egory showed no significant ($p < 0.05$) differences; thus, no particular categor or categories could be singled out as significantly different.

MANOVA was also done to determine if the W′ results from the large-cell-ric *Chlamydomonas* mixtures were different from the small-cell-rich *Chlamyc omonas* mixtures. To provide enough error degrees of freedom for the test, th nine size categories were reduced to three by combining data from three adjacer size categories to produce each of the three new size categories (3.17 − 6.35 μm 6.35 − 12.7 μm, and 12.7 − 25.4 μm). The MANOVA indicated the W′ curve were significantly ($p = 0.014$) different. The univariate tests indicated that onl W′ values from the 3.17 − 6.35 μm size category were significantly different.

Feeding rate patterns in Coulter experiments with Chlamydomonas

As a preliminary test of the EFC concept, Michaelis-Menten expressions wer

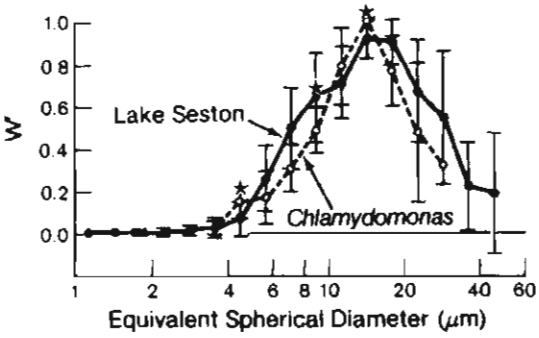

Fig. 2. Mean W' versus particle size for experiments with Lake Michigan seston, with mixtures of *Chlamydomonas* spp., and with individual species of *Chlamydomonas* (stars). Error bars are ± 1 s.d

Table II. Coefficents and r^2 values from fit of Michaelis-Menten expression to feeding rate versus TFC or EFC data for Coulter experiments with *Chlamydomonas* spp. Approximate 95% leve confidence intervals are given in parentheses following the coefficients.

Case	G_{max} (10^7 μm³ d⁻¹)	K (mm³ l⁻¹)	G_{max} (% body C d⁻¹)	r^2
NFR versus TFC	0.401 (0.114 – 0.689)	0.350 (– 0.447 – 1.15)	12.0	0.26
NFR versus EFC	0.480 (0.186 – 0.773)	0.318 (– 0.208 – 0.844)	14.4	0.54
GRF versus TFC	0.607 (0.295 – 1.18)	0.698 (– 0.912 – 2.31)	18.1	0.33
GFR versus EFC	1.01 (0.110 – 1.92)	1.11 (0.658 – 2.89)	30.2	0.63

fitted to NRF versus EFC, NFR versus TFC, GFR versus EFC, and GFR versus TFC data from Coulter-analyzed experiments performed with individual species of *Chlamydomonas* and mixtures (Table II). These experiments (Figure 3) include those reported above (Table I and Figure 1) and four more experiments with *Chlamydonas* sp. alone. To calculate the EFC for both the experiments with seston and with *Chlamydomonas*, we used the W_i' values calculated for each size category from the 23 experiments with lake seston (Vanderploeg, 1981a). These regressions show: (i) an improvement in explained variance (r^2) when food concentration is expressed in terms of EFC (Table II and Figure 3); (ii) slightly better correlation for regressions with GFR than with NFR; and (iii) the apparent threshold concentration below which feeding ceases that is suggested by the individual data points in Figure 3a diminishes when food concentration is expressed as EFC (Figure 3b).

Feeding rate patterns for lake seston

Figure 4 shows the time histories of temperature, TFC, EFC and NFR expressed as a percentage of body volume (NFR/V) and as a percentage of body carbon (NFR/ C). The relationship between feeding rate and seston concentration was explored by linear regression because visual inspection of the data points (Figures 5 and 6) suggested there was no evidence of saturation of feeding rate. All regressions were significant at the 1% level. The results for lake seston parallel those for

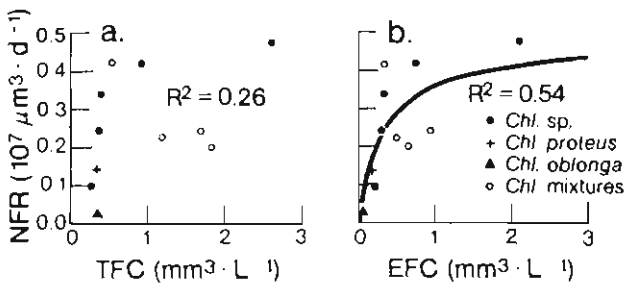

Fig. 3. Net feeding rate (NFR) as function of (a) total food concentration (TFC) and (b) effective fo concentration (EFC).

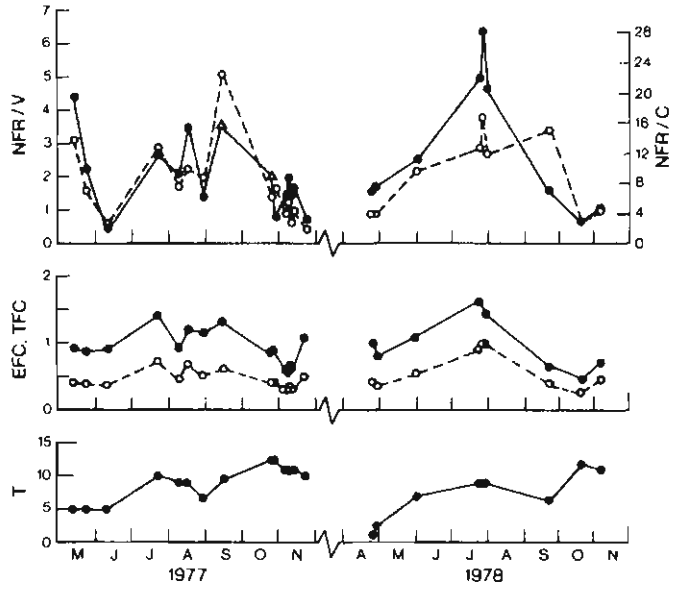

Fig. 4. Time histories of water temperature (T, °C), effective food concentration (EFC, mm³ l⁻¹), total food concentration (TFC, mm³ l⁻¹) and net feeding rate (NFR) expressed as percentage of body volume per day (NFR/V ●), and as a percentage of body carbon per day (NFR/C, ○). The triangles on the NFR/V curves for September and October 1977 indicate calculated results determined from feeding experiments on lake water diluted by factors 1/4 and 1/3, respectively; actual feeding rates were divided by these dilution factors to give results shown.

Chlamydomonas in that, although a reasonably good fit was obtained for NFR versus TFC (Figure 5a), a slightly higher r^2 was obtained when seston concentration was expressed as EFC (Figure 5b). The same pattern was seen for the GFR regression in Figure 6. The NFR versus TFC (Figure 5a) and GFR versus TFC (Figure 6a) regression lines intersect the abscissa at values appreciably larger than zero, suggesting an apparent threshold below which feeding ceases. This threshold was not as appreciable when seston concentration was expressed as EFC (Figures 5b and 6b). However, none of the y interepts is statistically differ-

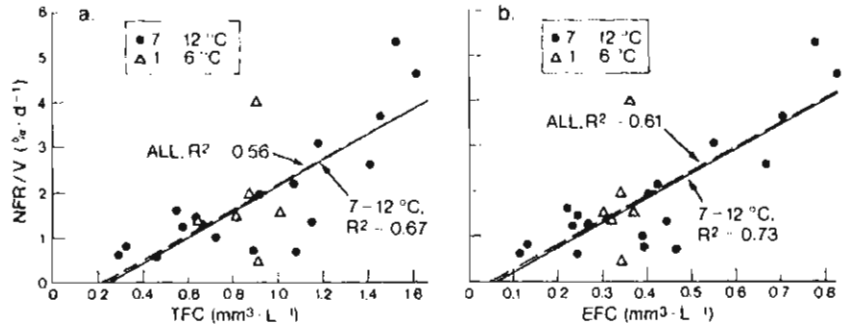

Fig. 5. (a) Linear regressions of NFR/V (NFR expressed as percent body volume d^{-1}) versus TFC for all data and the 7 – 12°C data. (b) Regressions of NFR/V versus EFC.

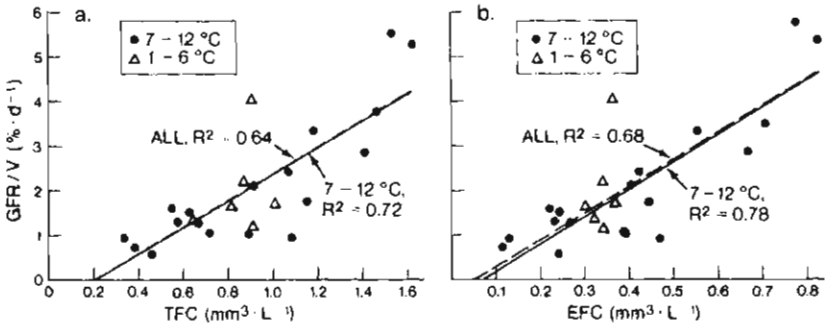

Fig. 6. (a) Linear regressions of GFR/V (GFR expressed as percent body volume d^{-1}) versus TFC for all data and for 7 – 12°C data. (b) Regressions of GFR/V versus EFC.

ent ($p < 0.05$) from zero. Although the results for experiments with seston are similar to those with *Chlamydomonas* spp., a much greater improvement in correlation when converting TFC to EFC was seen for the latter. This follows from the great diversity of EFC/TFC ratios seen in the *Chlamydomonas* data (Table III).

The high r^2 and significance of the linear regressions of feeding rate on EFC (and on TFC) suggest that EFC is below the incipient limiting concentration. This conclusion is also supported by the lack of correlation between F_{pref}/V (F_{pref} per 10^8 μm^3 of zooplankton body volume) and TFC (Figure 7a) and between F_{pref}/V and EFC (Figure 7b). Body size of the zooplankton was not a major contributor to the residual variation since the coefficient of variation for body volume among experiments was 7.7%. Since average body volume was 1.04×10^8 μm^3, F_{pref}/V values are nearly identical to F_{pref} values of individual zooplankton.

Microscope/Coulter experiments with Chlamydomonas spp.

The W′ curves obtained from the Coulter experiments with *Chlamydomonas* spp. (Figure 1) were very similar to those obtained with lake seston, thus supporting the conclusion of invariance drawn from the previous study (Vanderploeg 1981a). Individual W′ curves for different *Chlamydomonas* mixtures were quit

Table III. EFC/TFC ratios (±s.d.) for Coulter-analyzed experiments with seston and mixtures c algae. EFC was calculated from overall mean W′ values determined from experiments with sest

Experiment	N	EFC/TFC
Chlamydomonas oblonga	1	0.131
C. proteus	1	0.490
C. sp.	5	0.818 ± 0.01
Small-cell-rich *Chlamydomonas* mixtures	2	0.415 ± 0.03
Large-cell-rich *Chlamydomonas* mixtures	2	0.640 ± 0.05
Lake Michigan seston	23	0.459 ± 0.05

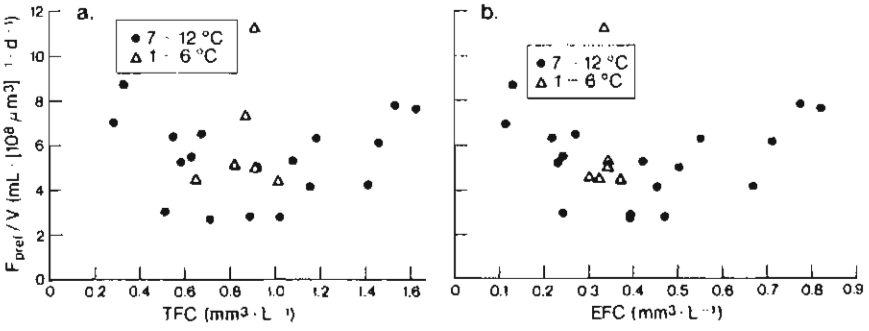

Fig. 7. (a) F_{pref}/V (F_{pref} per body volume) versus TFC. **(b)** F_{pref}/V versus EFC.

similar despite great differences in particle-size spectrum shape for the concer tration range studied. Apparently W′ for small cells increased as their concer tration relative to larger cells increased (Figure 1); however, this increase could b an artifact of particle production (Frost, 1977; Vanderploeg and Scavia, 1979a Deason, 1980; Bartram, 1981; Vanderploeg, 1981a).

Both the selectivity results and observed improvement in r^2 when food concen tration is expressed as EFC are consistent with the EFC model, but are not proo of the model. With the publication of Bartram's (1981) study, which used micro scopic counting of algae to obtain the relatively invariant patterns in selectio reported, we decided a careful test of the EFC model could only be made i microscopic instead of Coulter counts were made.

Selectivity patterns. To test directly whether *Diaptomus* was peak tracking that is preferentially selecting peaks in the biomass spectrum (Poulet, 1973, 1974 1978; Poulet and Chanut, 1975; Richman *et al.* 1977, 1980; Cowles, 1979), w tested the following regression model:

$$F_1/F_2 = a_0 + a_1(X_1/X_2) + a_2(X_1 + X_2) + a_3(X_1/X_2)(X_1 + X_2)$$

where F_1 and F_2 are clearance rates on *C. oblonga* and *Chlamydomonas* sp. (ml d^{-1}) respectively, and X_1 and X_2 are 'average' concentrations ($mm^3\ l^{-1}$) zooplankton see over the duration of the experiment (Frost, 1972). If peak tracking is significant, a_1 should have a significant non-zero value. The coef- ficients a_2 and a_3 allow for interactions with total concentration and with the total

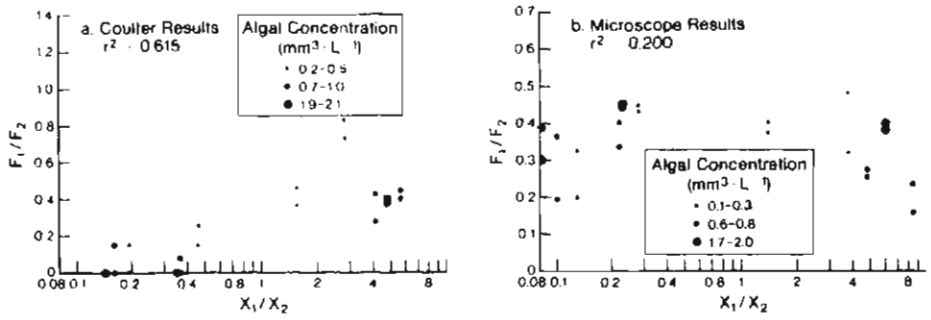

Fig. 8. Results of multiple linear regressions for F_1/F_2 as a function of X_1/X_2, $X_1 + X_2$ and cross product for **(a)** Coulter results and for **(b)** microscope count results. A log-scale abscissa is used to spread out the X_1/X_2 ratios at low values and to emphasize the geometric spread of these ratios. Regressions were done on untransformed data. Note that the diameter of the data points corresponds to the total biomass of the mixture that each point represents. Regression obtained for Coulter results was $W_1' = F_1/F_2 = 0.244 + 0.0842(X_1/X_2) - 0.135(X_1 + X_2)$. The regression obtained for microscope results was not significant; $W_1' = F_1/F_2 = 0.343 \pm 0.020(22)$.

concentration and relative concentration cross product. Note that if clearance rate of *Chlamydomonas* sp. is always greater than clearance on *C. oblonga*, $F_1/F_2 = W_1'$ by definition. The use of F_1/F_2 instead of W' (range: $0-1$) allows the dependent variable to have the same range ($0-\infty$) as the independent variable X_1/X_2. Regression analyses, using the all regressions approach (Draper and Smith, 1966), showed that for the results based on microscopic analyses $F_1/F_2 = W_1' = a_0$, and $F_1/F_2 = W_1' = a_0 + a_1(X_1/X_2) + a_2(X_1 + X_2)$ for the Coulter results. The data are plotted in Figure 8 with the values of the coefficients and r^2 values. From the Coulter results (Figure 8a), which are affected by the bias of particle production, we might conclude that selection for the small cell increases as its relative biomass increases and decreases as total biomass increases. In contrast, the unbiased microscope results showed no dependence on relative or total concentration.

Feeding rate patterns. As one test of the EFC model, we fitted equation (5) to the clearance rate of *Chlamydomonas* sp. versus food concentration data for both microscopic and Coulter results (Figure 9). The excellent correlation ($r^2 = 0.933$) obtained from the EFC microscope data (Figure 9d) and lower correlation ($r^2 = 0.748$) obtained for the TFC microscope data (Figure 9c) strongly support the EFC hypothesis. Interestingly, relatively low correlations of approximately the same value ($r^2 = 0.6$) were obtained for both TFC Coulter and EFC Coulter results (Figure 9a and b). The considerably lower clearance rates for the Coulter results (Figure 9a and b) derive from zooplankton-produced particles obscuring feeding on the large alga. The low correlation for both TFC Coulter and EFC Coulter regressions probably reflects the dominating influence of particle production. Like the F_1/F_2 regression for Coulter data, the influence of particle production on the clearance rate versus concentration relation will vary with relative proportions and total concentration of food.

We also evaluated the EFC model by fitting equation (2) to the food consump

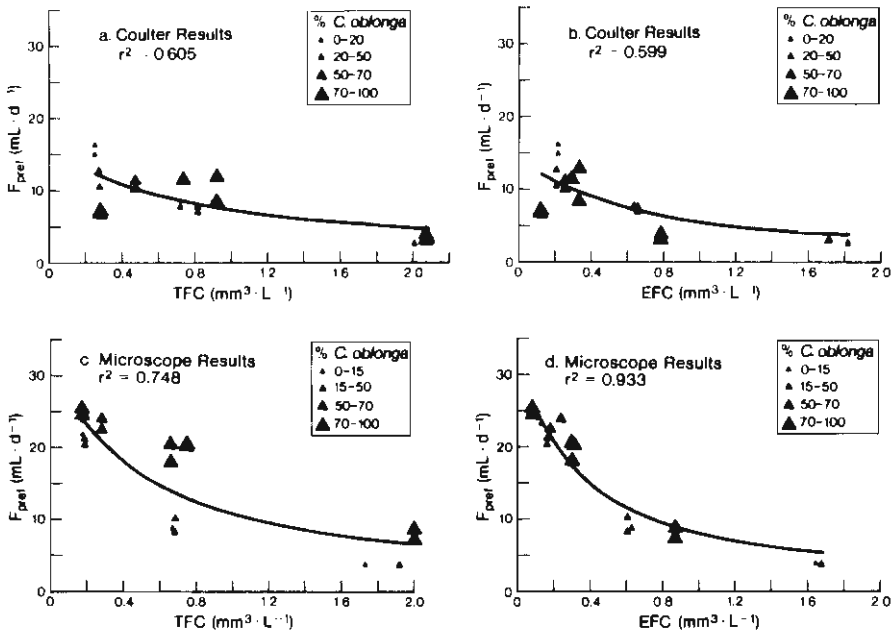

Fig. 9. Fit of equation (5) to clearance rate of *Chlamydomonas* sp. (F_{pref}) versus food concentrati data: **(a)** TFC of Coulter results, **(b)** EFC of Coulter results, **(c)** TFC of microscope count results, a **(d)** EFC of microscope count results. Note that size of triangles indicates percent of the total bioma in the mixture that is *C. oblonga*.

tion (NFR or GFR) versus food concentration data (Table IV, Figure 10). Lik the clearance rate regressions, the food consumption regressions support the EF model because of the high r^2 (0.916) for the microscope EFC results as compare with the lower r^2 (0.796) for the microscope TFC results (Figure 10, Table IV Also similar to the clearance rate regressions is the improvement in r^2 observe for the microscopic as compared with Coulter results (Table IV). As was observe for Coulter experiments with lake seston (Figures 5 and 6) and with *Chlamyd omonas* mixtures (Figure 3, Table II), r^2 improves in going from the NFR to GFI regressions and in going from TFC to EFC regressions (Table IV). For all re gressions (Table IV) the value of G_{max} is about the same. However, expression o food concentration as EFC instead of TFC lowered K, the half saturation co efficient.

The feeding rate response for the algal mixtures is different from that for lak seston (Figure 10). GFR for the microscopically counted algae saturated mor quickly than GFR for Coulter-counted seston whether food concentration wa expressed as TFC or EFC. Comparison of seston GFR or NFR curves with all th corresponding Coulter regressions in Table IV also yielded similar results.

Table IV. Coefficients, 95% confidence intervals (CI), and r^2 values for fit of Michaelis-Menten expression [Equation (2)] for G (expressed as NFR or GFR) versus TFC or EFC data from the microscope/Coulter experiments. To calculate EFC, the following W' values were used: (i) W' for *Chlamydomonas* sp. or size categories corresponding to it was 1; (ii) W' of *C. oblonga* for the microscopically counted results was the mean overall W' (0.343) calculated for microscopic results (Figure 8b); and (iii) W' of *C. oblonga* size categories was the mean overall W' (0.250) calculated from Coulter results (Figure 8a).

Regression	Kind of analysis	G_{max} (10^7 μm^3 d^{-1})		K(mm^3 l^{-1})		r^2	G_{max} (% body C d^{-1})
		$\bar{X}$ ± s.d.	95% CI	$\bar{X}$ ± s.d.	95% CI		
NFR versus TFC	Coulter counter	0.683 ± 0.062	0.553–0.813	0.358 ± 0.106	0.137–0.581	0.664	20.4
NFR versus EFC	Coulter counter	0.690 ± 0.052	0.582–0.798	0.221 ± 0.053	0.110–0.333	0.733	20.6
GFR versus TFC	Coulter counter	0.771 ± 0.061	0.644–0.896	0.403 ± 0.097	0.200–0.605	0.756	23.1
GFR versus EFC	Coulter counter	0.773 ± 0.048	0.673–0.873	0.244 ± 0.046	0.147–0.341	0.817	23.1
GFR versus TFC	Microscope	0.684 ± 0.034	0.613–0.755	0.209 ± 0.040	0.127–0.292	0.796	20.5
GFR versus EFC	Microscope	0.697 ± 0.022	0.652–0.743	0.149 ± 0.017	0.113–0.184	0.916	20.8

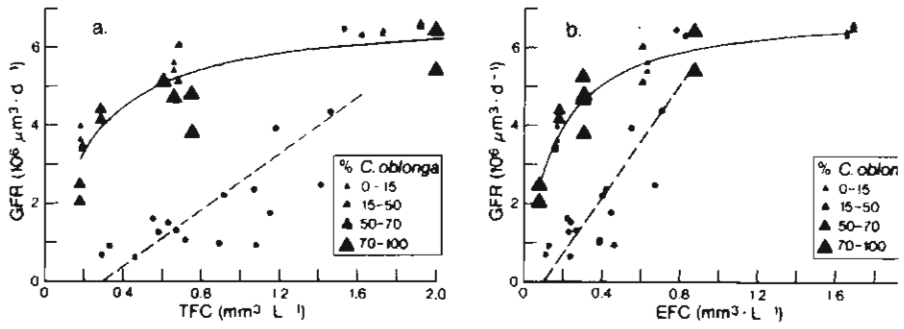

Fig. 10. Fit of equation (2) to GFR (solid line) versus TFC (**a**) and EFC (**b**) data (△) of microsco results (Table IV). Note that the size of the triangle indicates percent of the total biomass in the m ture that is *Chlamydomonas oblonga*. The dashed line is the best linear regression of GFR versus fo concentration for the 7 – 12°C field results (●).

Discussion

Selectivity

The keystone of the EFC model is that the food-selection pattern is invarian or at least approximately so. The question of invariance for copepod feeding h been a controversial issue. The counter hypothesis to invariance is peak trackir (Poulet, 1973, 1974, 1978 Poulet and Chanut, 1975; Richman *et al.*, 1977, 198 Cowles, 1979) whereby copepods preferentially select peaks in the particle-si spectrum. Peak tracking is what would be expected from optimal foraging theo (e.g., Lacher *et al.*, 1982). Vanderploeg (1981a) has reviewed in detail previo experimental work on this question. On the side of invariance were the Coult results of Frost (1977) for *Calanus* feeding on mixtures of diatoms, Bartram (1980) microscope results for *Paracalanus parvus* feeding on mixtures of alga and Vanderploeg's (1981a, 1981b) Coulter results for lake seston. It is not worthy that invariance was quite strictly adhered to in Bartram's microscop study but only approximately in the studies of Frost (1977) and Vanderploe (1981a, 1981b). On the side of peak tracking, or variable selection, were all oth studies with natural seston (Poulet, 1973, 1974, 1978; Poulet and Chanut, 197 Richman *et al.*, 1977, 1980; Cowles, 1979). Frost (1972) and Vanderploeg (1981 1981b) argued that variable selection observed in these studies may have resulte from: (i) improper methods of quantifying selection (e.g., in the studies o Poulet, 1973, 1974; Poulet and Chanut, 1975; Cowles, 1979); (ii) bias fro grazer-produced particles (e.g., Richman *et al.*, 1977, 1980; Poulet, 1978); an (iii) taste of seston (Richman *et al.*, 1977, 1980). Another possibility (Vande ploeg, 1981a) is that some copepod species, the '*Calanus*-like' species, ma exhibit invariant selection, while others with different feeding methods (e.g. *Acartia*: Donaghay and Small, 1979) may exhibit more variable selection.

Our microscope/Coulter experiments clearly show that *Diaptomus* exhibits a invariant pattern of particle section in algal mixtures over nearly two orders o magnitude of X_1/X_2 ratios (Figure 8) and food concentrations (0.17 – 2.1 mm³

l^{-1}, equivalent to 39–490 μg C l^{-1}) when algae are counted microscopically. The range studied here is considerably broader than the range found during the annual cycles in Lake Michigan (Figure 4). It is also broader than the range (0–34 μg C l^{-1}) studied by Bartram (1981). Moreover, our experiments show how particle production can bias the results of Coulter experiments. The Coulter biased results (Figure 8a) were exactly what would be expected from optimal foraging theory (e.g., Lacher *et al.*, 1982): selection for the small, 'less-preferred' cell increased as its concentration increased relative to the large alga, and its selection decreased as total biomass of both algae increased. These experiments underscore the criticisms voiced by Vanderploeg (1981a) on the effects of particle-production on Coulter experiments with natural seston: (i) subtle changes in particle-size selection with changes in particle-size spectrum shape (like those in Figure 1) should not be regarded as evidence for peak tracking or variable selectivity; and (ii) extreme peaks in the particle-size spectrum are going to lead to gross underestimates of selection at low points in the spectrum as, for example, the zero W′ values in Figure 8a for low X_1/X_2 ratios.

We will contrast the Coulter experiments of Richman *et al.* (1980) on Green Bay seston with the combined results of our study and Vanderploeg's (1981a). This discussion is relevant because Richman *et al.* (1980) claimed varying selection for another herbivorous diaptomid (*Diaptomus siciloides*) and because certain aspects of these experiments not discussed by Vanderploeg (1981a) are worth examining. Richman *et al.* (1980) reported results for three experiments (their Figures 1, 2 and 3) in which in each experiment an experimental and control bottle were analyzed at three different times (e.g., 8, 12 and 16 h) subsequent to beginning each experiment. Particle-size spectra in control and experimental containers were reported along with clearance rates as a function of particle size. We can use the clearance rate versus particle-size curves to approximate selectivity because W′ is a normalized clearance rate ($W_i' = F_i/F_{pref}$). In addition, Richman *et al.* (1980) put brackets on their particle-size spectra to enclose those size categories in which there were significant differences between control and experimental bottles, as evaluated by a 5% level t-test. This bracketed range was called the size range of feeding. From these time interval experiments, they concluded that *D. siciloides* starts feeding on the peaks in the particle-size spectra and extends its range of feeding to both larger and smaller particles as particles within the initial feeding ranges are removed.

In an approximate way, the clearance rate curve shapes resemble each other and Vanderploeg's (1981a) W′ curves in that large particles were preferred to small particles even when, as in their Figure 3, a large peak in the small size categories dominated the spectrum. Moreover, there was little change in selectivity with time in their Figure 3. In all experiments, the statistically defined feeding range expanded with time; however, this apparent behavior could be a statistical artifact and could be expected with only invariant selection operating (Appendix II). Likewise, the width of the size range of non-zero valued clearance rates would also increase with time, especially in the very early phases of the experiment before much seston was grazed. This artifact is a stochastic one, a result of the fact that clearance rates cannot be accurately measured on size

categories in which nothing or little has been eaten. This bias is not as strong that for the t-test criterion, which forces its bias by its implicit functional relat with time [Appendix II, Equation (B4)].

Inspection of the particle-size spectra and clearance rate curves of Richmar *al.* (1980) (their Figures 1, 2, 3) shows that particle production occurs in all exp iments. Particle production is clearly a factor in causing variability in the W′-s relation since, as the peaks are grazed down, they will gradually contribute fev particles to low points in the spectrum, allowing feeding to increase relative particle production in the low points. [See Equation 3 of Vanderploeg (1981a) f formal result.]. This time-dependent process is analogous to the response obse ed in W′ in Figure 8a in moving to the right from an X_1/X_2 ratio of zero.

Particle scent or taste could have been a dominant factor in Figure 2 of Ric man *et al.* (1980). In addition to the broadening of the clearance rate curve w time, clearance rate on larger particles (10 – 20 μm) dropped. Particle producti was probably a factor, but some of the drop could have been real because t region of the drop coincided with the peak in the spectrum, where the partic production artifact could have been expected to be relatively small. Much of t available seston was grazed in this time-series experiment. Preference for lar particles is thought to be a result of active capture of these particles where cop pods smell 'large' algae at significant distances from their bodies and use c ordinated movements of the mouth-parts to bring these particles to the mou and then ingest them if they have the proper taste (e.g., Alcaraz *et al.*, 198 Koehl and Strickler, 1981; Paffenhöfer *et al.*, 1982). This probably explains wl large dead cells (Bartram, 1980) and large inert particles (Frost, 1977; Huntley *al.*, 1983) are captured at a lower rate than large live cells. Since live cells const tute only a fraction of natural seston [e.g., 30 – 50% of the particulate organ carbon for Lake Michigan (Robertston *et al.*, 1971)], the decreasing clearan rates with time may have resulted from removal of a significant fraction of tl algae from this large-particle region of the spectrum.

In the case of Lake Michigan seston, the relatively invariant selection observe there was explained by the large particles generally having a high food quality an at least some of the small particles being of good food quality (Vanderploe 1981a). The relatively invariant selection would result from passive and activ capture modes operating simultaneously, with particles of low food quality (e.g detritus and mineral particles) captured along with small particles of high foo quality in the passive ('filtering') mode (Vanderploeg, 1981a; Vanderploeg an Ondricek-Fallscheer, 1982). Food quality and particle production probabl explain the difference between seston and *Chlamydomonas* curves in Figure 2.

Part of the popularity of the 'peak-tracking' paradigm may result from th attractiveness of the idea of optimal foraging, as witnessed by the great numbe of theoretical papers on this general principle. Another part results from th linkage between the 'leaky-sieve' model (Boyd, 1976; Frost, 1977) and invariance This model predicted that particle-size selection should be invariant, a functio only of the pore-size distribution in the second maxilla of the copepod. With th filmed observations on copepod feeding that showed an active mode of capture both the leaky-sieve model and invariance, by its linkage to the model, were dis

credited. The idea of invariance suffered another blow from filmed observations of Price *et al.* (1983), who showed that the marine calonoid copepod *Eucalanus pileatus* used the passive, small particle-capturing mode only when small algae were abundant. This mode switching mechanism could, in theory, lead to variable selection. On the other hand, filmed observations on *Diaptomus* (Vanderploeg and Paffenhöfer, in preparation) show that both active and passive modes of feeding operate simultaneously. Thus, certain '*Diaptomus*-like' copepods would be expected to exhibit invariant selection in mixtures of algae and relatively invariant selection under the conditions described for Lake Michigan, and others, like *Eucalanus*, more variable selection.

The feeding rate-EFC response: a useful unifying principle?

The second criterion of the EFC model, namely, that the same functional response works for all mixtures of food, appears reasonable for algal mixtures in view of the excellent fits of both microscopically-determined clearance rate (Figure 9) and food consumption rate (Figure 10) with EFC data, and the poorer fits with TFC data. The clearance rate versus EFC regression (Figure 9d) resembles Bartram's (1981, Figure 9) regression of these variables for *Paracalanus*. Again as with selectivity results, Coulter feeding rates were biased by particle production. This led to the lower correlation coefficients for Coulter results (Figure 9a and 9b, Table IV).

In addition to improving the fit of feeding rate versus food concentration response for the Coulter-analyzed experiments with *Chlamydomonas* spp. and lake seston by representation of food concentration as EFC, the size (absolute and relative) of the threshold concentration for feeding to begin (Figures 3, 5, and 6) was reduced. Recent work with unialgal cultures (Muck and Lampert, 1980; Porter *et al.*, 1981) suggests that feeding thresholds do not exist for freshwater copepods or cladocerans. By converting food concentration to EFC, the threshold was removed in Figure 3 because we essentially converted TFC to food concentration of a single kind of food, namely, the preferred alga. The same force is at work in Figures 5 and 6; however, the story is more complicated for lake seston since the food consumption versus EFC responses for lake seston and algal mixtures are different.

The EFC model provides the framework for comparing different studies on feeding on natural seston and for comparing laboratory and field experiments. The EFC for *D. sicilis* in Lake Michigan was relatively stable (Figure 4) because of the relatively stable total concentration of seston and a very stable EFC/TFC ratio (0.459 ± 0.050; Table III). Because of the stability of this ratio, food consumption on Lake Michigan seston was reasonably well correlated with TFC. In contrast, Dagg and Grill (1980) obtained very poor correlation (r^2 = 0.39) between food consumption and TFC of natural marine seston. This may have resulted from greatly varying EFC/TFC ratios since they mentioned that location of peaks in particle-size spectra varied considerably. The EFC/TFC ratio also tells us what proportion of the environment's food concentration is useful to the animal. It would be interesting to know what EFC/TFC ratios are for other environments. Our comparison of the feeding response for lake seston and for

laboratory algae is more appropriate for the GFR versus EFC data (Figure 1
than for the GFR versus TFC data (Figure 10a) because the difference in parti
size spectra between experimental conditions has been theoretically remo
from the EFC data by weighting the food concentration by size-selective sel
tivity coefficients [equation (1)]. Low food quality of the seston and particle p
duction are the probable causes of the difference between lake seston and al
mixture results (Figure 10b). As noted above, only 30–50% of Lake Michig
particulate organic material is living algae, and the nonliving particulate orga
material would be expected to be ingested at a lower rate. Moreover, if t
material is poorly digested, both Coulter-measured NFR and GFR will be mu
lower than true ingestion because of the particle-production artifact. In additic
some of the seston will be mineral particles [e.g., calcite (Vanderploeg, 1981
and these particles, like plastic beads (Frost, 1971; Donaghay and Small, 197
Huntley *et al.*, 1983), will be captured at a lower rate and not digested at a
Thus, although the general features of the selectivity-size cure were not su
stantially altered by food quality and particle production, the ingestion ra
response was greatly affected. Interestingly, Dagg and Grill (1980) also observ
lower feeding rates on natural seston than would be predicted from laborato
feeding studies; however, they compared only food-consumption versus TF
responses. The challenge of the future will be to predict feeding rate on natur
seston. To do this, it will be necessary to know what the different particles are
the different size categories and develop selectivity coefficients that include se
sory qualities of the food.

The EFC model is a potentially useful unifying principle not only for copepo
feeding but for other predators as well. Predation by *Mysis relicta*, which use
mechanoreceptors to sense disturbances its zooplankton prey make in the wate
was well correlated ($r^2 = 0.72$) with EFC but poorly correlated with TFC ($r^2 =$
0.14) for *in situ* feeding on Lake Michigan zooplankton (Bowers and Vande
ploeg, 1982). The EFC model would *a priori* be expected to be a useful approx
mation for filter feeders, e.g., salps (Harbison and McAlister, 1979) and clad
ocerans (Porter *et al.*, 1983). However, some deviations from invariant selectivit
can occur for filter feeders because of the piggyback phenomenon, which allow
small particles to be more efficiently captured because of the presence of larg
particles that clog the filter or make it sticky (Porter *et al.*, 1983). One situatio
where the model will definitely not work is where the predator strongly switche
feeding modes in response to different relative concentrations of prey, as fo
example the switching between biting and filtering modes by the northern an
chovy (O'Connell, 1972).

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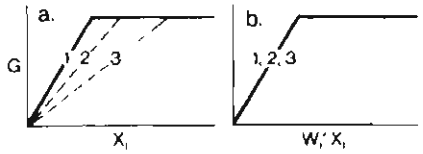

Appendix Fig. 1. The three curves (**a**) obtained from three different-sized algae (1, 2, 3) in Frost's (1972) experiments can be represented by a single curve (**b**) if concentration of algae is expressed as EFC.

Appendix I: Relations for linear model

Because the linear model is useful for some points we wish to make here, we give the corresponding results for the linear model. For EFC below the incipient limiting concentration (ILC),

$$G = K'(EFC), \text{ and} \tag{A1}$$

$$G_i = K' W_i' X_i \tag{A2}$$

For EFC $\geq$ ILC,

$$G = G_{max} \text{ and} \tag{A3}$$

$$G_i = \frac{G_{max} W_i' X_i}{\Sigma W_i' X_i} \quad \frac{G_{max} W_i' X_i}{EFC} \tag{A4}$$

Frost's (1972) results for *Calanus pacificus* feeding on individual species of diatoms of different sizes are consistent with equations (A1)–(A4). His results are schematized in Appendix Figure 1. We see in Appendix Figure 1a that all algae have the same G_{max} and that the slopes of the lines below the ILC diminish in going from largest (1) to smallest algae (3). From equation (A1) the slope (or clearance rate), K_i', for any alga is $K' W_i'$, implying:

$$W_i' = K_i'/K' \tag{A5}$$

K' may be taken as K_1, the K_i' of the largest alga, the 'preferred' alga. Appendix Figure 1b shows that, if results for each alga are plotted as G versus EFC (where $EFC = W_i' X_i$ for the case of a single alga), the same curve applies to all algae.

We have suggested elsewhere (Vanderploeg and Scavia, 1979a; Vanderploeg, 1981a) that W_i' values should be determined from experiments with mixtures of different kinds of food; specifically, $W_i' = F_i/F_{pref}$, where F_i is clearance rate on the ith kind of food and F_{pref} is the highest clearance rate observed for a food in that mixture. If equations (A1)–(A4) are correct, W_i' determined from experiments with single species [equation (A5)] should be the same as those determined from mixtures. This is also approximately true for the Michaelis-Menten functional response at low concentrations since it is approximated by equation (A1) as $EFC \to 0$.

Appendix II: Effect of time on the statistically defined size range of feeding

Richman *et al.* (1980) used a t-test criterion to indicate size categories in which there were significant differences between concentration in control and exper-

imental containers. The size range over which there were significant differer was defined as the size range of feeding. They noted that the size range of feed started near peaks and gradually broadened with time suggesting that copep became less selective as the peaks were grazed down. We will show here t under conditions of invariant selection the size range broadening with time car concomitant of the use of the t-test to define this range.

The t statistic for two means $\bar{X}_1$ and $\bar{X}_2$ having variances σ_1^2/n_1 and σ_1^2/n_i

$$t = (\bar{X}_1 - \bar{X}_2)/(\sigma_1^2/n_1 + \sigma_2^2/n_2)^{1/2} \quad (\text{e.g., Snedecor and Cochran, 19}$$

Assume equal volumes of water were counted in control and experimental b tles. Number of particles $[N(T)_i]$ counted in size category i at time T in the exp imental container, assuming invariant selection, is:

$$N(T)_i = N(0)_i \exp[-F_{pref} W_i')(n/V)T] \quad (\text{e.g., Vanderploeg and Scavia, 19}$$

where $N(0)_i$ = count initially in size category i in both control and experimer containers, F_{pref} = clearance rate on the preferred size category (size categ exhibiting highest clearance rate), n = number of animals in the experimen bottle, V = volume of bottles, and T = elapsed time. Since Poisson statist apply, the variance on a total count will equal that count, and equation (B1) m be rewritten as:

$$t = (N(0)_i - N(T)_i)/(N(0)_i + N(T)_i)^{1/2}$$

Substituting equation (B2) for $N(T)_i$ in equation (B3) results in:

$$t = N(0)^{1/2}\{1 - \exp[(-F_{pref} W_i')(n/V)T]\}/\{1 + \exp[(-F_{pref} W_i')(n/V)T]\}^1$$

Thus, from equation (B4), t increases with time. Moreover, whether a particu size category first exceeds a critical t value depends on $N(0)_i$ and W'. Thus a s category with a high particle concentration and W' will be the first to exceec critical t value.

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