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C.M.1974/L:23
Plankton Committee

Search Rate and Food Size Preference in Two Copepods

by

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Introduction

The paper is based on data published by Frost (1972) and Poulet (1973).

In an attempt to expand the Beverton and Holt (1957) model of fish population dynamics into a multispecies model (Andersen, Lassen and Ursin, C.M. 1973/H:2o, and an unpublished paper available on request to the authors) it became necessary to develop handy expressions for the rules governing the search for food by marine animals. At the time the hypotheses advanced were largely unsupported but have since turned out fairly realistic. For details of the reasoning the reader is referred to the above mentioned contributions.

There were two problems to attack namely, the rules governing a predator's accept of an encountered food item as being of suitable size, and the frequency of encounters. The idea was that the predator may estimate its food relative to its own size in such a way that an item twice the preferred size is as suitable as another half the preferred size. This suggests a size preference curve the shape of the log-normal probability function. The exponential term suffices when prey of the preferred size is allotted a value of one:-

$$G_{ij} = \exp\left(- \frac{\left(\log \frac{w_i}{w_j} - \eta_i\right)^2}{2\ \delta_i^{\,2}}\right); \quad 0 < G_{ij} \leq 1 \qquad (1)$$

The index i represents the predator, j the prey. w is body weight and η_i the logarithm of the preferred ratio w_i/w_j (more specifically, the median in the size ratio distribution). $\delta_i^{\,2}$ is the variance indicating how particular the predator in question is in its selection of prey. Curves for cod and dab (Ursin 1973) are shown in Fig. 1. The abscissa is the predator-size/prey-size ratio.

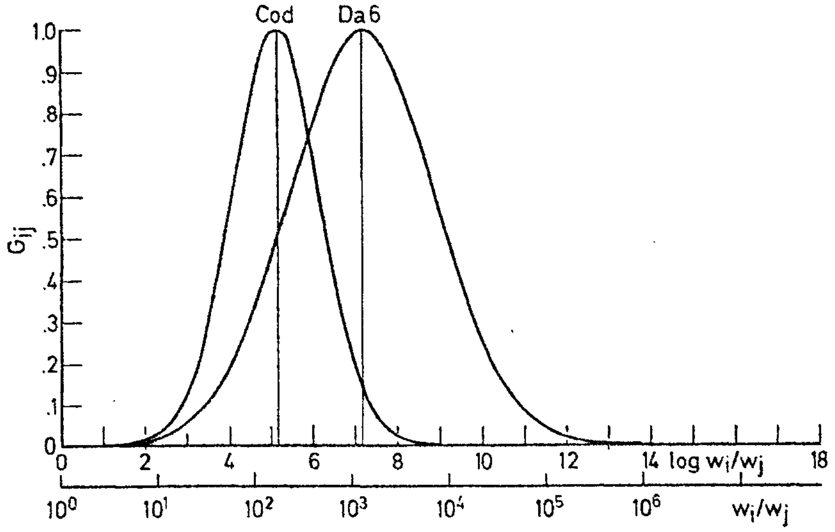

Fig. 1. Prey size selection curves for cod and dab. The ordinate is the size preference index, G.
From Ursin (1973), redrawn.

The impression is that the dab gets more food than the cod because the curve is broader: food items of a wide size spectrum are readily accepted. Other mechanisms, however, may counteract this difference; one is described in a later paragraph based on observations by Frost (1972).

Consider the effective amount of food available to predator i:-

$$\varphi_i = \sum_j \varphi_{ij} = \sum_j G_{ij} w_j N_j \qquad (2)$$

namely, the biomass of all kinds of food each weighted by its "size value" as expressed by G_{ij}.

Now assume the rate of search for food proportional to the maximum rate of food consumption by the predator in question:-

$$\frac{d\hat{V}_i}{dt} = q_i \left(\frac{dR}{dt}\right)_{max} \qquad (3)$$

where $\hat{V}_i$ is the volume searched for food and R_i the food ingested. Further, introduce the feeding level, f_i, of the predator as the fraction achieved of the maximum feeding rate. Reasoning (Andersen, Lassen and Ursin, l.c.) leads to the formulation

$$f_i = \frac{\varphi_i/V}{\varphi_i/V + \frac{1}{q_i}} \qquad (4)$$

where V is the water volume (φ_i/V the effective food concentration, e.g., g/m^3). $^1/q_i$ is known in the literature on primary production as the half saturation constant.

The amount consumed by a predator is determined by the volume searched and the selection of food items in that volume: two predators may get the same amount of food if one moves little but eats almost everything in its way and another is very active, but particular about the size of food items. In order to determine the consumption of each species in a multispecies interactive model it is therefore paramount to know for each predator i the preferred relative food size as expressed by η_i, the spread δ_i of the food size selection curve, and the search rate coefficient q_i.
It is shown below how these parameters can be estimated for two planktonic copepods, Calanus pacificus and Pseudocalanus minutus.

1. Calanus pacificus

Frost (1972) fed adult females of Calanus pacificus five kinds of diatoms of different size one kind at a time in varying concentrations, and measured their rate of ingestion. So little was consumed of the smallest diatom that it could not be measured although a few fecal pellets were produced, but for the other four species a large number of observations is published.

A disturbing influence is an interspecific difference in carbon contents. The body weights given below are recalculated assuming wet weight = 12.5 x carbon contents. Thus,

w_i = 8.5 E-4g
$w_j = \{$1E-1o, 1.18E-9, 1.o5E-8, 2.o6E-8, 4.17E-8$\}$
$w_i/w_j = \{$8.5E6, 7.2E5, 8.1E4, 4.1E4, 2.oE4$\}$

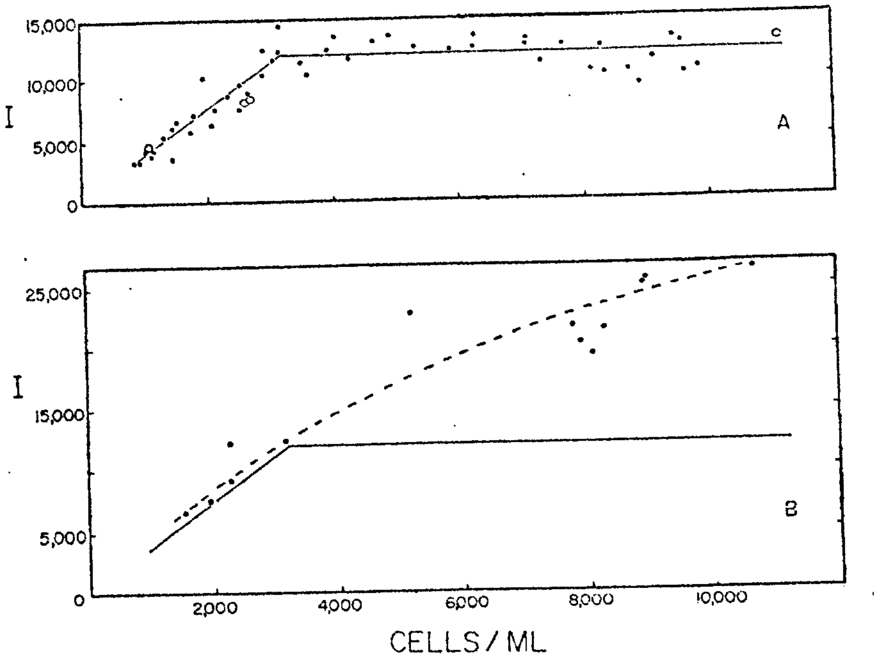

Fig. 2. Food consumption as a function of food concentration: Calanus pacificus eating Thalassiosira fluviatilis.
A. Well nourished animals. B. Hungry animals, with the curve for well nourished animals inserted. From Frost (1972).

As an illustration of Frost's work see Fig. 2 (his Fig. 2A and 2B) showing the consumption of Thalassiosira fluviatilis (w_j= 1.18E-9g) by Calanus as cells ingested per hour related to cells per ml in the vessel. The curvilinear relation in Fig. 2B is in accordance with the model (Ursin 1967):

$$\frac{dR_i}{dt} = f_i h_i w_i^{2/3} \qquad (5)$$

where h is an instantaneous ingestion coefficient of the predator and f the feeding level as expanded above, eq (4). Points on that curve were produced when the copepods were hungry at the beginning of the experiment and the ingestion measured after less than 12 hours. Points in Fig. 2A were produced when the copepods were in good feeding condition at the beginning of an experiment. Up to a point the two curves coincide, but at a certain food concentration (the "critical concentration") the ingestion for well fed animals becomes independent of concentration: Calanus has the appetite predicted above (eqs.(4)and(5)), but is let down by its metabolism which cannot keep pace.

No model is available for describing the interaction of the two mechanisms, but the maximum feeding level achieved by well-fed Calanus is estimable as are also the other parameters. The procedure is easily followed in Table 1.

First is stated the concentration in cells/ml as read from Fig.2. Next the calculated concentration in g/ml. The ingestion is read as cells/hour and calculated as g/hour. The product $f_i w_i$ for Calanus is calculated from eq. (5) where w_i and dR_i/dt are known. To separate f_i and h_i insert eq. (2) into eq. (4) and rearrange:-

$$\frac{1}{G_{ij}\, q_i} = \frac{1-f_i}{f_i}\, w_j\, \frac{N_j}{V} \qquad (6)$$

where the diatom weight w_j and the cell concentration N_j/V are known. As we are dealing with one size of predator i and one size of prey j, $G_{ij}q_i$ = constant. Therefore, find by iteration a value of f_i for one concentration (e.g., the largest) which makes $G_{ij}q_i$ constant. One value of f_i chosen (in Table 1 f=.46 for N/V= lo.ooo cells/ml) provides the other f_i values because for any two values of f_i (f_{ia} and f_{ib}) we have $f_{ia}/f_{ib} = dR_{ia}/dR_{ib}$.

Values of f_i widely different from .46 for N/V = lo.ooo produced a marked trend of the calculated values of $G_{ij}q_i$. For the concentration mentioned we find $f_i h_i$ = .00333 from which by division by f_i = .46, h_i = .oo72o $g^{1/3}$ $hours^{-1}$ = 63.1 $g^{1/3}$ $years^{-1}$.

The feeding level corresponding to the critical food concentration at which the bottom curve of Fig. 2 turns horizontal (12ooo cells/hour, 32oo cells/ml) is f_{ci} = .219

There remains to separate q_i and G_{ij}. The clue lies in the observation by Frost that the quantity ingested at the critical food concentration (by weight) is independent of cell size. That means that we can put in eq. (6) $f_i = .219$ for the critical concentration of all four kinds of diatoms. A plot of the resulting values of $G_{ij}q_i$ (Table 2) against log (w_i/w_j) according to eq. (1) has the shape, but not the height, of the food preference curve for Calanus, analogous to those for cod and dab in Fig. 1. The four points are plotted in Fig. 3 with the addition of a dubious fifth point for the very small diatom about which is known only that G_{ij} is almost negligible.

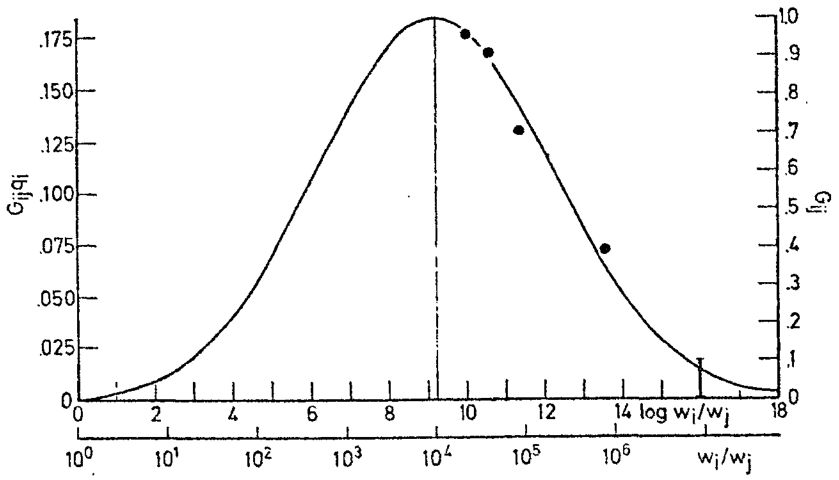

Fig. 3. Prey size selection curve for Calanus eating diatoms. Dots calculated from Frost's observations. The vertical line indicates an observation about which is known only that it is small.

The log-normal curve drawn in Fig. 3 is a mere guess. A sound parameter estimation might have been possible had Frost included a food item 5o times the size of the biggest diatom. The maximum of the curve has the ordinate $G_{ij}q_i = q_i =$ 1.85E5 ml/g =.185 m^3/g because $G_{max} = 1$ by definition (eq.(1)). Values of G_{ij} for each diatom j can be calculated by means of the estimate of q_i(right-hand column of Table 2) and hence the critical effective food concentration $\varphi_{i,crit} = G_{ij} w_j N_j / V$.

The estimated size preference parameters for Calanus are, for what they are worth,

$$\eta_i = 9.2 \ , \quad \delta_i = 3 \ , \quad e^{\eta_i} = 99oo.$$

The last figure is the predator/prey size ratio preferred by Calanus.

As a check the ingestion curve for starved Calanus eating Th. fluviatilis (Fig. 2) can now be calculated because from the equations given above we have

$$\frac{dN}{dt} = \frac{dR_i}{dt} \Big/ w_j = f_i h_i \frac{w_i^{2/3}}{w_j}$$

where

$$f_i = \frac{G_{ij} w_j \frac{N_j}{V}}{G_{ij} w_j \frac{N_j}{V} + \frac{1}{q_i}}$$

the parameters of which are estimated. The last two columns of Table 1 are feeding levels and cells ingested per hour thus calculated. Both are underestimated by 5-8 pct which is not alarming considering the crude methods of parameter estimation and the absence of variance estimates.

The standard deviation of the food size preference curve for Calanus ($\delta_i = 3$) is high as compared to similar values for cod ($\delta_i = 1.0$) and dab ($\delta_i = 1.7$) referred to above. As demonstrated by Frost the effect apparently is counteracted by the inability of Calanus to eat all it can accept except at low food concentrations. Similar phenomena may be widespread in marine life but it is suggestive that it was observed in a planktonic copepod, a group of animals subject to excessive variation in food supply. The mechanism may be an adaptation to life in diluted environments because it ensures a maximal growth rate even at fairly low food concentrations.

2. Pseudocalanus minutus

Poulet (1973) used a different experimental set-up permitting, however, estimation of the same parameters as Frost's work.

Details are deferred to a later publication. Here are given only the parameter values as crudely estimated as for Calanus above, and a few illustrations of the observations.

The estimates are:-

$\eta_i = 8.4$; $\delta_i = 4.47$; $e^{\eta_i} = 4400$;

$q_i = .066\ m^3/g$; $h_i = .0561\ g^{1/3} days^{-1} = 20.5\ g^{1/3} years^{-1}$.

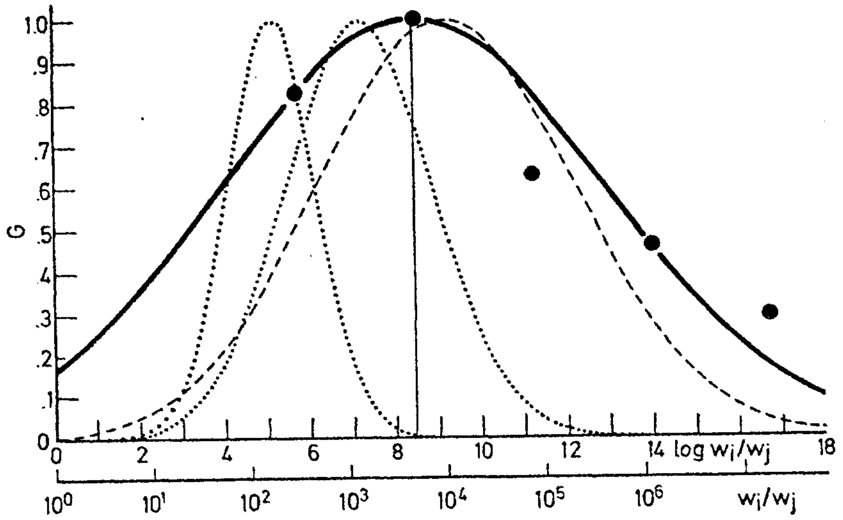

Fig. 4. Full line: prey size selection curve for Pseudocalanus minutus with dots indicating Poulet's observations from which the parameters were crudely estimated. Broken line: similar curve for Calanus pacificus (from Fig. 3). Dotted lines: similar curves for cod and dab (from Fig. 1).

The food size preference curve is drawn in Fig. 4, with the previous curves (cod dab, Calanus) inserted for comparison. It seems that on designing his experiments Poulet, like Frost, underestimated the copepods' interest in large prey which again made parameter estimation rather hazardous. It would be interesting to know if the curve holds for very large prey or has a skewness due to inability of the copepod to attack effectively prey of its own size or over.

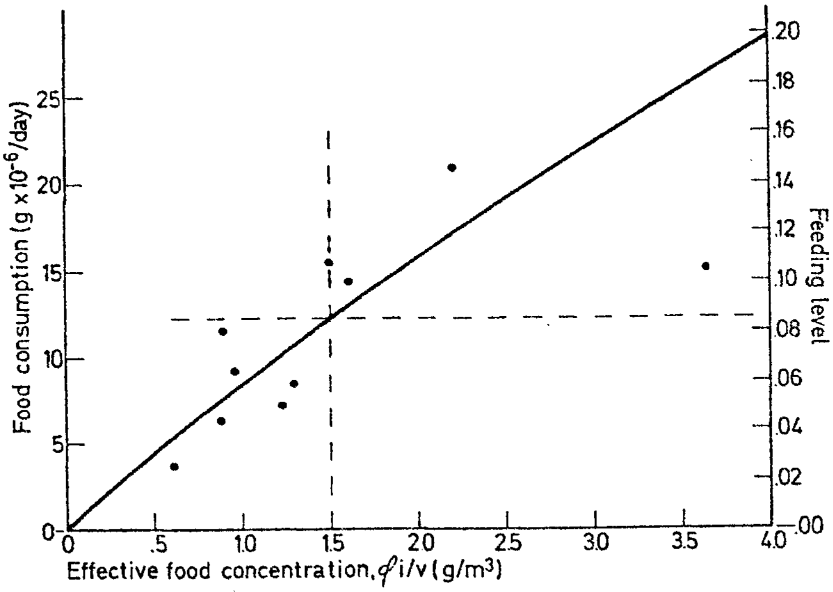

Fig. 5. Food consumption by Pseudocalanus minutus as a function of effective food concentration, i.e., each size category of food weighted by its "size value", G_{ij}. The vertical line indicates the "critical concentration" for Calanus (from Frost) above which consumption is independent of concentration except for starved animals. The horizontal line (normal to the vertical line at the latter's intercept with the curve) corresponds to Frost's observations on well-fed animals. The single observation at a high food concentration agrees fairly well with it (cf. Fig. 2).

Fig. 5 should be compared with Frost's illustration of food consumption as a function of food concentration for Calanus (Fig. 2). The curve is based on the estimated parameter values. The vertical line indicates the critical food concentration for Calanus as estimated in the preceding paragraph. It is not known if Poulet's Pseudocalanus became hungry before the beginning of the experiment, but the low value of the single observation at a high food concentration is suggestive. It recalls the horizontal part of Frost's curves. If the low value is not an accidental deviation from the curve it determines the maximum feeding level for well-fed Pseudocalanus as $f_{ci} \sim .1$, which is half the value estimated for Calanus.

Summary

Published data on copepod food consumption is shown to supply information for estimating parameters of a model of food search and selection although the design of experiments was not entirely adequate for the purpose. The hypotheses of the model could not be rejected, but were found incomplete inasmuch as an extra parameter (easily introduced) seems necessary because only hungry copepods and copepods exposed to low food concentrations acted as predicted by the model; well fed ones exposed to high food concentrations did not consume as much as their rate of search would allow.

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Table 1. Thalassiosira fluviatilis fed to Calanus pacificus at various concentrations. Estimation of feeding levels and of the coefficient h_i of ingestion for Calanus.

Food concentration		Ingestion rate			By iteration		Calc. with estimated parameter values	
		$\frac{dN}{dt}$	$\frac{dR_i}{dt}$	$f_i h_i$	f_i	$q_i G_{ij}$	f_i	dN/dt
cells/ml	g/ml	cells/hour	g/hour	$g^{1/3}$ $hour^{-1}$		ml/g		cells/hour
2000	2.35E-6	8000	9.40E-6	1.05E-3	.1455	7.25E4	.135	7400
4000	4.70E-6	14500	1.70E-5	1.90E-3	.2636	7.62E4	.238	13100
6000	7.05E-6	19000	2.23E-5	2.49E-3	.3455	7.49E4	.320	17600
8000	9.40E-6	22700	2.67E-5	2.97E-3	.4127	7.48E4	.385	21200
10000	11.75E-6	25300	2.97E-4	3.33E-3	.46	7.25E4	.439	24100

$$h_i = 3.33E\text{-}3/.46 = 7.20E\text{-}3 \text{ g } 1/3 \text{ hours}^{-1}$$

$$h_i = 63.1 \text{ g}^{1/3} \text{ years}^{-1}$$

Table 2. Estimation of the parameter product q_iG_{ij} for each species of diatom (j) when consumed by Calanus (i). Using Fig. 3 estimates of individual values of G_{ij} are provided.

Species of diatom	Critical concentration (f_{ki}=.219) cells/ml	Rate of ingestion at critical concentration cells/hour	Body weight w_j g	q_iG_{ij}	$\log\frac{w_i}{w_j}$	$\eta_i=9.2$ G_{ij}(obs)	$\delta_i=3$ G_{ij}(calc)	Critical concent. $G_{ij}W_jN_j/V$ g/m^3
Thalassiosira pseudonana		(small)	1.00E-10	(small)	15.96	-	.08	-
Thalassiosira fluviatilis	3200	12000	1.18E-9	7.4403E4	13.49	.40	.36	1.36
Coscinodiscus angstii	204	1250	1.05E-8	1.3060E5	11.30	.71	.78	1.67
Coscinodiscus eccentricus	81.2	597	2.06E-8	1.6765E5	10.63	.91	.89	1.49
Centric sp.	37.6	343	4.17E-8	1.781E5	9.92	.96	.97	1.52