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Letter

# THE USE OF MEASURABLE COEFFICIENTS IN PROCESS FORMULATIONS — ZOOPLANKTON GRAZING

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ABSTRACT

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This paper redefines a construct previously used to model phytoplankton—zooplankton interactions in such a way as to permit the use of measurable quantities as construct coefficients. The new construct can use unaltered values of the half-saturation constant for zooplankton grazing on total available food ($k_s$) and the minimum food concentration necessary to stimulate effective feeding ($B$MIN) reported in the literature. Typical values for these coefficients are 0.1—15 and 0.016—0.19, respectively.

Modellers of aquatic ecosystems strive to obtain realistic process formulations in their models. In developing expressions to mimic functional processes in these models, one should obtain an equation whose coefficients can be estimated from either existing literature or tractable laboratory and/or field experiments. In this way, the calibration step in model development can be performed more readily and the assumptions surrounding the conversion of existing process coefficient values can be kept to a minimum.

The purpose of this note is to redefine a construct used for modelling zooplankton grazing so that its coefficients are readily estimable.

The original construct was developed by O'Neill et al. (1972) and modified by Bloomfield et al. (1973). It has been used in various ecosystem models (Park et al., 1974, 1975) and is described in detail by Scavia and Park (1976). The basic equation

$$C_{ij} = C\mathrm{MAX}_j \left[ \frac{W_{ij}(B_i - B\mathrm{MIN}_{ij})}{K_j + \sum_i W_{ij}(B_i - B\mathrm{MIN}_{ij})} \right] B_j, \tag{1}$$

where

$CMAX_j$ = maximum consumption rate of $j$
$B_i$ = concentration of biomass of prey $i$
$B_j$ = concentration of biomass of predator $j$
$W_{ij}$ = preference factor of $j$ for $i$
$BMIN_{ij}$ = minimum concentration of $i$ for $j$ to begin feeding
$K_j$ = constant

describes the loss term of one prey group "$i$" due to the predator group "$j$". When this term is summed over all prey, the relationship between total food and zooplankton grazing ($C_j$) becomes

$$C_j = CMAX_j \left[ \frac{\sum_i W_{ij}(B_i - BMIN_{ij})}{K_j + \sum_i W_{ij}(B_i - BMIN_{ij})} \right] B_j \qquad (2)$$

The coefficient values necessary for this construct are $CMAX_j$, $W_{ij}$, $BMIN_{ij}$, and $K_j$. $CMAX$ is available from the literature (e.g., Richman, 1966; Hutchinson, 1967) and can be determined in the laboratory. The preference factor $W_{ij}$ for herbivorous zooplankton has received attention recently and experimental results are starting to become available for its estimation (Wilson, 1973; Bogdan and McNaught, 1976). The two remaining coefficients are more difficult to obtain. $BMIN_{ij}$ represents the minimum concentration of prey $i$ necessary for consumer $j$ to begin feeding. This concentration is not available in the literature since it would be most difficult to ascertain for a mixed prey population. Additionally, subtracting this minimum term from each food supply confounds the meaning of $K_j$; it no longer corresponds to the half-saturation constant available from the literature ($k_s$). However, this note will show how it is possible to calculate $BMIN_{ij}$ and $K_j$ from measurable quantities.

Experimentalists have determined a minimum value of *total* food necessary to stimulate feeding (Parsons et al., 1969; McAllister, 1970), which will be denoted here as $BMINj$. Also, the relationship between total available food and consumption has been reported quite often (although not always in weight-specific terms) and can be obtained in the laboratory. Eq. 2 in terms of total food supply and $BMIN_i$ is

$$C_i = CMAX_j \left[ \frac{(\sum_i W_{ij}B_i) - BMIN_j}{K_j + (\sum_i W_{ij}B_k) - BMIN_j} \right] B_j, \qquad (3)$$

where $BMIN_j = \Sigma_i BMIN_{ij}$.

Estimates for $BMIN_{ij}$, the minimum concentrations for the individual prey groups, can be determined by assuming $BMIN_{ij}$ is related to $BMIN_j$ as $W_{ij}$ is related to $\Sigma_i W_{ij}$ or

$$BMIN_{ij} = \left[\frac{W_{ij}B_i}{\sum_i W_{ij}B_i}\right] BMIN_j. \tag{4}$$

One can also find a relationship between the measurable quantity $k_s$ and the modified half-saturation constant $K_j$. Since

$$\frac{(\sum_i W_{ij}B_i)}{k_s + (\sum_i W_{ij}B_i)} = \frac{(\sum_i W_{ij}B_i) - BMIN_j}{K_j + (\sum_i W_{ij}B_i) - BMIN_j},$$

one may solve this equation for $K_j$ to obtain

$$K_j = \left[\frac{(\sum_i W_{ij}B_i) - BMIN_j}{(\sum_i W_{ij}B_i)}\right] k_s \tag{5}$$

Thus, the modified half-saturation constant $K_j$ can be calculated directly from measurable quantities (e.g., see Table I).

The overall construct for zooplankton grazing on a mixed assemblage is then

$$C_j = CMAX_j \left[\frac{(\sum_i W_{ij}B_i) - BMIN_j}{K_j + (\sum_i W_{ij}B_i) - BMIN_j}\right] B_j \tag{6}$$

TABLE I

Coefficient values

| Species | mg C/l | Reference |
|---|---|---|
| $B$MIN | | |
| *Calanus pacificus* | 0.016 | McAllister (1970) |
| 14 marine species | 0.04—0.19 | Parsons and LeBrasseur (1970) |
| $k_s$ | | |
| *Diaptomus oregonensis* | 1.6 * | Richman (1966) |
| *Bosmina coregoni* | 0.1—4.0 | Semenova (1974) |
| *Daphnia magna* | 9.6 ** | McMahon and Rigler (1963) |
| | 15.0 ** | Ryther (1954) |
| *Daphnia rosea* | 0.16 *** | Burns and Rigler (1967) |

* Food was *Chlamydomonas reinhardti* and *Chlorella vulgaris*: $0.124 \times 10^{-6}$ mg C/cell.
** Food was *Chlorella vulgaris*: $0.124 \times 10^{-6}$ mg C/cell.
*** Food was *Rhodotorula glutinis*: ovoid cells, 4.2 $\mu$ long, $0.776 \times 10^{-8}$ mg C/cell.

and the loss term for one particular prey group $i$ is

$$C_{ij} = CMAX_j \left[ \frac{W_{ij}B_i - XMIN_{ij}}{K_j + (\sum_i W_{ij}B_i) - BMIN_j} \right] B_j, \quad (7)$$

where $XMIN_{ij}$ is defined in eq. 4 and $K_j$ in eq. 5.

This revised construct is used in an ecosystem model developed for Lake Ontario (Scavia et al., 1976a) and for investigating the dynamics of all of the Laurentian Great Lakes (Scavia et al., 1976b).

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