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A mathematical model of the assimilation process in the copepod Calanus finmarchicus (Gunnerus): computer simulations discussed in relation to experimental results

D. Slagstad[1] and K. S. Tande[2]

[1] The Foundation of Scientific and Industrial Research (SINTEF), Division of Automatic Control, The Norwegian Institute of Technology, Trondheim, Norway

[2] Aquatic Biology Group, Institute of Biology and Geology, University of Tromsø, Tromsø, Norway

Abstract

Feeding, digestion and assimilation are usually treated as separate aspects in studying the physioecology of copepods. A general model predicting the assimilation rate from ingestion rate, phytoplankton species compositon and digestive or physiological state of the animal is presented. The assumption is made that digestion is accompanied by a subsequent decrease in cell volume, which is equal to the assimilated part of the cell. In addition, a time delay between ingestion and the onset of digestion is assumed to describe the digestion properties of the algal cells. The model predicts a decrease in assimilation efficiency with increasing ration. The minimum gut passage time and the digestion rate seem to be the most important parameters for the production of copepods. These and other characteristics of the model are discussed in relation to available information.

Introduction

A long-range research and development program was started around 1974 under the title HAVBIOMODELLER (English translation: Ocean bio-models) (BALCHEN 1980). The goal of this program is to establish the capability of producing mathematical/numerical models of a total marine ecological system of the Barents Sea, north of Norway. The model system consists of submodels describing physical and chemical oceanography, growth and distribution of phytoplankton and zooplankton, and the biological state and migratory pattern of the main fishing stocks.

In marine food webs, calanoid copepods constitute prominent pathways for energy flow between primary producers and predatory species of zooplankton and fish. In the Barents Sea *Calanus finmarchicus* and *C. glacialis* are by far the most dominant herbivorous copepods. Accordingly, a mathematical model describing their physiology, behaviour and population structure has been developed essentially based on data available in the scientific literature.

Simulation models of marine planktonic communities usually describe the feeding rates of herbivorous copepods by some nonlinear function of the concentration of phytoplankton (e.g. STEELE 1974, WROBLEWSKI and O'BRIEN 1976). Assimilation rate is usually taken as a constant fraction or some fixed function of the ingestion rate (see

CONOVER 1978 for a review). Furthermore, little conclusive data exist about interdependent processes such as feeding, digestion and assimilation in calanoid copepods.

Data on filtration and ingestion are available for several copepods feeding on a variety of food particles and on a broad range of food concentrations. Feeding in copepods has been found to be affected by food concentrations, particle size and type (PAFFENHÖFER 1971, FROST 1972, 1975) season and level of satiation (McALLISTER 1970, RUNGE 1980). Digestive enzyme activity is supposed to vary with the nutritional state of the animal (BOUCHER and SAMAIN 1974, MAYZAUD and POULET 1978), and presumably affects the digestion rate.

The lack of agreement between various models describing the interrelationship between ingestion and assimilation rates seems to stem from the strictly empirical basis they are built on. Little theory exists to account for the dynamic rather than static processes that are likely to be involved in the assimilation process.

Model hypotheses

The hypothesis advanced here will constitute the framework of a physiological model of the digestion process. This model will be used to predict the assimilation rate from ingestion rates, phytoplankton species composition and digestive or physiological state of the animal.

Gut dynamics

In general, the dynamics of gut filling are described by the equation

$$\frac{dx_g}{dt} = (q_l - q_e - q_{as})/V_g \qquad (1)$$

where x_g is the gut filling ($0 \leq x_g \leq 1$), V_g volume of gut (mm^3), q_l is the ingestion rate or flow (mm^3h^{-1}), q_e is the egestion rate (mm^3h^{-1}), and q_{as} is the volume of organic matter assimilated per unit time (mm^3h^{-1}). Filling of the gut is a rather fast process compared with other physiological processes that may affect ingestion and digestion. Therefore, we may ignore the dynamics of gut filling, which implies $\frac{dx_g}{dt} = 0$ and

$$q_l = q_{as} + q_e \qquad (2)$$

If a feeding interval is of sufficient duration to reach steady state the number of cells inside the gut, N_g, can be described by the following equation

$$N_g = N_l \cdot t_g \qquad (3)$$

where N_l is the ingestion rate (number of cells h^{-1}), t_g is the gut passage time, (i.e. time elapsed between a cell entering the gut to its being egested). If these cells were ingested uniformly over time, their average volumes, V_{av}, would be

$$V_{av} = \frac{1}{t_g} \int_0^t V(t) \, dt \qquad (4)$$

where V(t) is the undigested volume of an algal cell after t units of time inside the gut. The gut filling is the ratio of the volume actually occupied by the cells and the maximum volume which the gut may attain. That is

$$x_g = \frac{N_g \cdot V_{av}}{V_g} \tag{5}$$

or

$$x_g = \frac{N_l \cdot t_g \cdot V_{av}}{V_g} \tag{6}$$

The maximum ingestion rate is limited by these constraints, since gut filling cannot become larger than one.

$$(N_l)_{max} = \frac{V_g}{t_g \cdot V_{av}} \tag{7}$$

There are two ways that an animal can adjust its maximum ingestion rate, providing that ingestion is not limited by lack of food or high level of satiation. One way is to adjust the gut passage time whereas the other is to change the average cell volume inside the gut, which is the same as changing the rate of digestion. Evidence for the first alternative has been found by GELLER (1975) for *Daphnia pulex* and indications of a variable digestion rate is suggested by MAYZAUD and POULET (1978).

Gut passage time

It is reasonable to believe that the defaecation rate is proportional to the amount of food in the gut ((see HOLLING 1966). Here we will make a similar suggestion and take the velocity of algal cells through the gut to be proportional to the gut filling

$$v_g = \alpha x_g + v_{gm} \tag{8}$$

where α is a constant of proportionality and v_{gm} is some minimum velocity of cells through the gut. Assuming that the cells have to go some equivalent distance, l_g, at this velocity, we find the gut passage time

$$t_g = \frac{l_g}{\alpha x_g + v_{gm}} \tag{9}$$

Manipulating this equation, we can find parameters that have other physiological implications and may be easier to measure:

$$t_g = \frac{t_{min} \cdot t_{max}}{x_g (t_{max} - t_{min}) + t_{min}} \tag{10}$$

where t_{min} is the minimum gut passage time, and t_{max} is the maximum gut passage time occuring when gut filling approaches zero. If $t_{max} >> t_{min}$ equation (10) can be approximated by

$$t_g \simeq \frac{t_{min}}{x_g} \tag{11}$$

Digestion

The digestion of a single algal cell may depend on several factors such as algal species, physical state when ingested (ruptured or not), concentration of digestive enzymes and environmental temperature. Cells which are ingested unruptured have a cell wall which may be of different quality from one algal species to another. Some cells have a thin wall enclosing the cell constituents which digestive enzymes may soon rupture, whereas others are covered with a thick gelatinous layer which temporarily prevents digestion of cellular constitutents. PORTER (1975) has found that some gelatinous green algae even seem to survive passage through the gut and thus probably have been of no nutrient value to the animal.

Our digestion model is based on the following assumptions:

1. a time delay between ingestion and the onset of digestion depending on algal species

2. digestion of individual algal cells is accompanied by a subsequent decrease in cell volume. When the cell constitutents are exposed to the digestive enzymes the rate of digestion is proportional to the undigested volume of the cell.

In mathematical terms this can be expressed as

$$\frac{dV(t)}{dt} = -aV(t) \qquad t > t_{go} \tag{12}$$

where a is the rate of digestion per unit cell volume (h^{-1}), and t_{go} is the time delay between ingestion and the onset of digestion. Solution of equation (12) gives

$$V(t) = \begin{cases} V_o & \text{if } t < t_{go} \\ (V_o - V_f)e^{-a(t-t_{go})} + V_f & \text{if } t \geq t_{go} \end{cases} \tag{13}$$

where $V(t)$ is the volume of a cell after t time units inside the gut, V_o is the initial volume of a cell when ingested, and V_f is the minimum undigestible volume of the cell. The volume of an individual algal cell versus time is plotted in Fig. 1. This figure shows that time spent inside the gut before egestion takes place is important for the amount of the cell which can be utilized by the animal. When the gut passage time is less than or equal to t_{go}, the cell will pass through the gut without being digested at all.

Rate of assimilation

The goal of the digestion process is to transform the ingested food into a form which can be assimilated through the gut wall. Here, digestion is defined as loss of cell volume. Since this decrease in cell volume is equal to the assimilated part of the cell, the rate of assimilation and digestion will be equal. The rate of assimilation will then depend on the same variables as the digestion rate of a single algal cell (equation
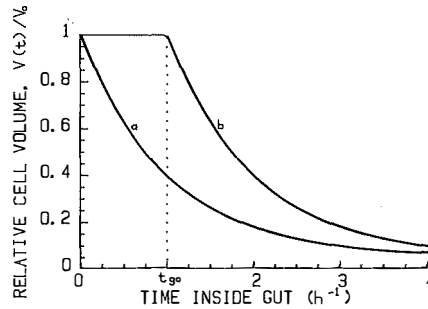
Figure 1

Relative volume of an algal cell versus time inside the gut. (a) cell wall broken when ingested and digestion starts immediately upon ingestion. (b) cell wall is resistant against digestive enzymes for some time (t_{go} time units) before digestion of cellular constituents starts.

(12)). A function can then be found which allows us to calculate the rate of assimilation from the amount of ingested food, digestion properties of the algae, and gut passage time.

The assimilation rate through the gut wall is proportional to the undigested fraction of cells in the gut which have been in gut more than t_{go} time units

$$q_{as} = aN_l (t_g - t_{go}) \bar{V} \qquad\qquad t_g \geq t_{go} \tag{14}$$

where $\bar{V}$ is the average volume of the digestible part of the cells which are under digestion (i.e. have been inside the gut more than t_{go} time units, see Table 1).

Table 1

Specific relations used to evaluate the equations of the assimilation process

$$V_{av} = \begin{cases} V_o & t_g \leq t_{go} \tag{15} \\[2em] (V_o - V_f)\left(\dfrac{t_{go}}{t_g} + \dfrac{a}{t_g}(1 - e^{-a(t_g - t_{go})})\right) + V_f & t_g > t_{go} \end{cases}$$

$$\bar{V} = \frac{V_o - V_f}{t_g - t_{go}} a (1 - e^{-a(t_g - t_{go})}) \qquad\qquad t_g > t_{go} \tag{16}$$

It is not certain that all the cell constitutents are absorbed at the same rate. However, data is not available to allow us to construct such a function. We, therefore, assume that cell constitutents are absorbed in proportion to cell volume. Substituting equation (16) into equation (14) we obtain

$$V_{as} = N_l (V_o - V_f) \varrho_{alg} (1 - e)^{-a(t_g - t_{go})} \tag{17}$$

where V_{as} is the assimilation rate of carbon, and ϱ_{alg} is the specific carbon content of the digestible part of the algal cell. The percent of assimilation (the ratio between absorbed and ingested carbon) is found from

$$A = \frac{\varrho_{alg} \ (V_o - V_f - V(t_g))}{\varrho_{alg} \ (V_o - V_f)}$$

$$= \begin{cases} 0 & t_g \leq t_{go} \\ 1 - e^{-a(t_g - t_{go})} & t_g > t_{go} \end{cases} \tag{18}$$

Choice of parameters

Preliminary results from experiments on gut passage time in copepodite stage V of C. finmarchicus indicate that minimum gut passage time is ca. 45 min. at 6 °C (TANDE and SLAGSTAD in prep). Assuming that an animal feeds on phytoplankton cells which have digestion delay parameter, t_{go}, of 18 minutes, one has to use digestion rate equal 1,0 h^{-1} to simulate GAUDY's (1974) results on the percent of assimilation versus daily food intake.

Table 2

Parameters used in the model

PARAMETERS	VALUES
a	1,0 h^{-1}
t_{min}	0,17 h
t_{max}	1,0 h
t_{go}	0,3 h

General characteristics of the model

Use of the above mentioned parameters and equations in the digestion model shows that the percent of assimilation decreases as the ingestion rate per unit gut volume increases (Fig. 2). We also note that the gut filling increases when the ingestion rate per unit gut volume increases.
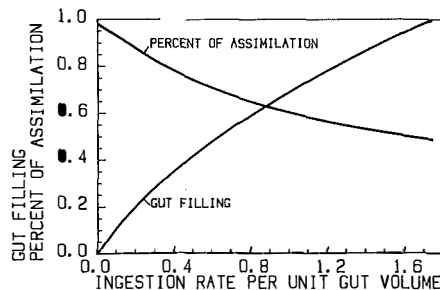
Figure 2

Gut filling and percent of assimilation as function of ingestion rate per unit of gut volume

Sensitivity analysis

This model is used in a larger system of models describing the growth and interactions of phytoplankton and copepods (SLAGSTAD 1980). The assimilation model is tested as a function of its parameter values. It was evident from sensitivity analysis that in determining production of *Calanus*, the digestion rate, a, and the minimum gut passage time, t_{min}, were the most important biological parameters. One possible explanation for this is that these two parameters control the assimilation efficiency by the copepods. Low percent of assimilation means that the production of fecal pellets is relatively high compared with the ingestion rate. As the fecal pellets usually sink out of the euphotic zone (SMALL et al. 1979), a large amount of phytoplankton biomass will in this way be lost from the phytoplankton/copepod system. Therefore, the digestion rate and minimum gut passage time have a great influence on the utilization of the phytoplankton and thereby the production of copepods. Other parameters dealing with metabolism (i.e. respiration) do not have the same effect on the copepod production because respiration products are mainly regenerated and reused by the primary producers again.

Digestion rate

Recent evidence indicates that the digestive enzyme activity is related to the trophic position of the animal and varies with the season and the quantity of food ingested (BOUCHER and SAMAIN 1974; PANDIAN 1975; MAYZAUD and POULET 1978).

Calanus finmarchicus from Balsfjorden, northern Norway, produces only one generation a year (TANDE 1979). In Fig. 3, the specific trypsin activity in copepodite stage V and VI shows a pronounced seasonal variation in which differences between copepodite stage V and adult females are apparent. Evidence for a short-term variation in enzyme activity regulated by the food offered is shown in Fig. 4. Trypsin activity in copepodite stage V seems to undergo variations as a consequence of differences in feeding and starvation time.
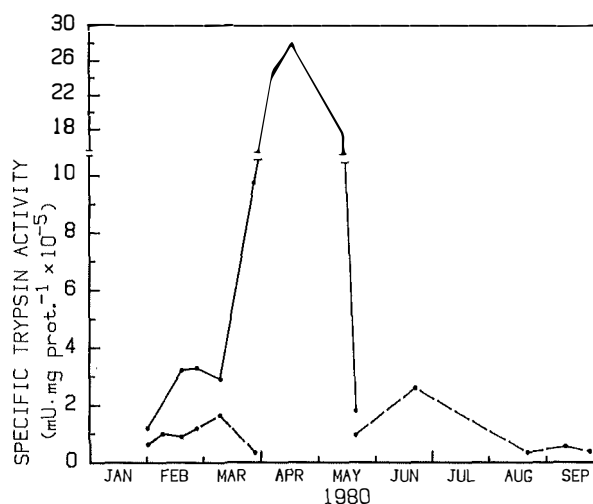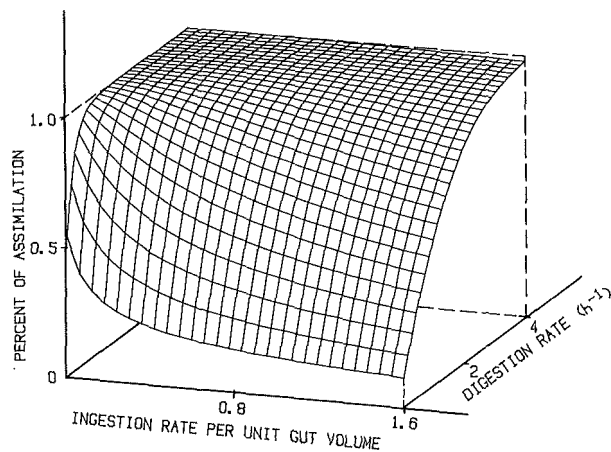

Figure 3

Calanus finmarchicus. Seasonal variation in trypsin activity of copepodite stage V (·---·) and adult females (·——·) from Balsfjorden, northern Norway
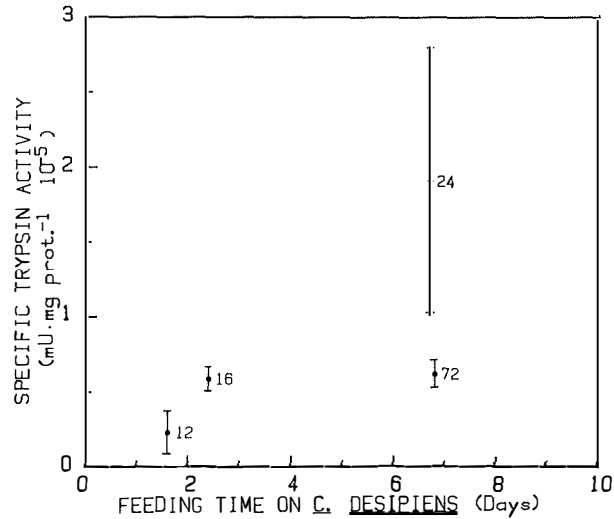
Figure 4

Calanus finmarchicus. Trypsin activity in relation to feeding and starvation time. Number besides the mean values is starvation time in hours.

Figure 5

The percent of assimilation as function of the ingestion rate per unit gut volume and digestion rate

It is reasonable to believe that the digestion rate depends strongly on the level of enzyme activity. This means that a is not a parameter but a function of the nutritional history of the animal.

Fig. 5 shows how the model predicts the percent of assimilation as a function of the ingestion rate per unit gut volume and the digestion rate. We observe that the percent of assimilation becomes independent of ingestion rate when digestion rate is sufficient high.

Discussion

Production of phytoplankton in boreal and Arctic areas is mainly controlled by the environmental physical conditions such as light and supply of nutrients. Herbivore production is usually constrained by food limitations (STEELE 1972). Given a certain primary production, the utilization of phytoplankton by herbivores must be of great importance both with respect to the overall zooplankton production and to competition between species. Our findings that the digestion rate was a key parameter both in the present model and in a larger model system indicate the necessity of examining the different factors controlling the digestion rate.

PANDIAN's (1975) review of the mechanism of heterotrophy in marine organisms shows that the amount of digestive enzyme is related to the quantity of food ingested. MAYZAUD and POULET (1978) suggested that the stimulus for enzyme secretion may be the degree and frequency of filling the gut. The assumption in our model that the amount of enzymes will highly influence the rate of digestion raised the question of the regulatory mechanism controlling the level of enzyme activity in copepods. Acclimation to a significant change in the food supply seems likely to be governed by both time and quantitative thresholds (MAYZAUD and POULET 1978).

In a study of the nutritive adaptations in *Artemia* SAMAIN et al. (1981) indicate that in spite of different ingestion rates, assimilation is optimized by regulating the digestive enzyme system. The requirements of the animals, changing with developmental stage and environmental conditions, would seem to regulate the nutritional behaviour and assimilation in *Artemia*.

Little conclusive data exist about the assimilation efficiency of copepods (CORNER 1961; CONOVER 1964, 1966; CORNER et al. 1967; BUTLER et al. 1969; TAGUCHI and ISHII 1972; GAUDY 1974). CONOVER (1966), provided evidence for the fact that copepods do not reduce assimilation efficiently at higher food levels. However, values were higher for naked flagellates and dinoflagellates than for diatoms, indicating that the digestability of the food organisms can influence the assimilation rate.

Although the model predicts an inverse relationship between assimilation efficiency and ingestion, much research must be done before further conclusions can be made about the digestion and assimilation in copepods. The aspects of assimilation and digestion discussed in this paper indicate that the previous history and acclimation of individuals will play an important part in the experiments to test the various hypotheses in our *Calanus* model.

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