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Modeling and simulation of physiology and population dynamics of copepods. Effects of physical and biological parameters

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A detailed model of the physiology and vertical migration behaviour of marine copepods of the *Calanus* is developed. A two-dimensional population model calculates the size and developmental structure of the population in relation to its own dynamics and the environment. Examination of the effect on the population dynamics and production of copepods by changing the physical and biological parameters is performed.

1. Introduction

A long range research and development programme was started in Norway around 1974 under the title HAVBIOMODELLER (English translation OCEAN BIO-MODELS). The goal of this programme is to establish the capability of producing mathematical/numerical models of a total marine ecosystem of the Barents Sea, north of Norway (Balchen 1980). The total ecological system of the Barents Sea is modelled by a set of submodels describing the physical oceanography, chemical oceanography, and production and distribution of phytoplankton, zooplankton and fish. The main objective of this paper is to establish a submodel of zooplankton, but a submodel describing distribution and production of nutrients and phytoplankton will also be included.

Most models used in the management of fish stocks assume some density and age-dependent growth and death rates. Density dependent rates are based on the assumption that the amount of food available for a certain population is constant. A weakness with this assumption is that several species of fish may exploit the same or a similar food resource. Since not all species are caught equally by humans, some species may increase their relative abundance and thereby decrease the food available for the most commercially important fish stocks. The physical properties of the sea may also change as a result of meteorological phenomena. These changes will contribute to imposing variations of food supply for the fish stocks and thereby affect their mortality and, especially, their growth rates.

Since a major part of the energy transfer, from primary production to fish, passes through the herbivore zooplankton, it seems to be important to understand the biological processes at this tropic level. Our intention here, therefore, will be to

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make a model of the most dominant herbivore zooplankton species in our area—*Calanus finmarchicus*. However, even for this intensively studied species, data are missing to build a comprehensive model. Data from related species, such as *C. helgolandicus* and *C. pacificus*, will be used when necessary and the model may, therefore, be taken to apply to a more general class of animals—the herbivore copepods. The main problem when using data found in literature is the experimental temperature. Most experiments are performed at temperatures of 10–15°, whereas the temperature in our area of interest lies between −2 and 10°.

Models of zooplankton have usually been relatively primitive biomass models with no size or age structure, though size structure information may often be more important than the biomass. This is certainly the case with the fish larvae, which must have food of proper size in order to survive their first weeks of life. In addition to biomass and size structure, spatial distribution of zooplankton is important when assessing the amount of available food that the fish sees. Spatial distribution is probably a result of several interacting processes, such as behaviour of the individuals of the population, intertrophic relations and physical processes (Ebenhöh 1980).

Studying dynamics of zooplankton in the open ocean is usually a difficult task. You never know if you are sampling the same population during a given time period because of the water movements. Neither do you know the prehistory of the water masses in which you are sampling.

Any population of animals consists of single individuals. The dynamics of the population is the integrated dynamics of its single individuals. Our approach here is to establish a population model of copepods. Based on the available literature, most of what we believe to be the relevant physiological processes of the single individual will be represented in the model. Since the copepod production is strongly related to primary production, it has been necessary to build a dynamic model of phytoplankton. This model calculates growth of phytoplankton from light, nutrients and grazing from copepods. By perturbating the parameters in the model, the importance of the different physiological processes can be tested. Using this method, we can put more effort into obtaining more and better data for those processes which seem to be most important, and we can simplify the representations for those which appear unimportant for the model results.

We also hope to obtain some insight into the dynamics of the plant–herbivore system by studying the integrated behaviour of the sub-processes represented in the model.

2. Formulation of a copepod population model

2.1. *Introduction*

Whatever the complexities of ecological systems, we can be certain of one thing: populations surely obey a conservation law in the form

$$\frac{dx_1}{dt} = \text{births} - \text{deaths} \pm \text{migrations} \tag{1}$$

where x_1 is the number of individuals in the population. In order to say anything about the number of individuals in the population, we must know something about the three terms on the right hand side of eqn. (1). This is not as easy as it seems because these terms depend on a large number of factors both within the population and its environment. A great deal of mathematical ecology has been elaborations

of various birth and death laws from assumptions about resource consumption, including time lag to account for maturation delays, adding stochastic terms to model fluctuating environment and combining logistic-like equations to model competitions between species (Oster 1977).

A major deficiency in these types of models becomes apparent if we ask what is an adequate state description of a population. The number of individuals, $x_1(t)$, is insufficient to predict the future course of the population growth. What if all members of the population were males? Or too starved to bear viable offspring? The effect that the population exerts on its food resources depends on the age structure of the population because younger animals usually have a higher metabolic rate than older ones. This gives rise to the problem of how to define an average animal in the population. More information about the population is required than just its numbers, and we must expand our description to include the age structure and other phenotypic characteristics which might influence population growth, such as mass, size, behaviour, etc. That is, we must write our population law (eqn. (1)) for a density function, $\eta(t, x)$, where x is a vector of the relevant phenotypic characteristics.

What are the relevant phenotypic characteristics for a population of copepods? To answer this question, we may list which features we want our copepods' population model to contain:

(1) An internal structure which gives information regarding the size (biomass) of the population and its ability to grow and reproduce as a function of the environmental variables, such as food, temperature, light, etc.

(2) Give the effect on the algal populations on which the copepods are grazing.

(3) Give the availability to predators (fish, fish larvae, etc.).

In general, the development of a population depends on the age structure and its ability to find proper food. Growth and development of poikiloterms depends much on the environmental temperature. Therefore, in a changing environment, age will not necessarily tell anything about the reproductive potential of the populations. Copepods, which develop by moulting, are usually characterized by developmental stage. After a fixed number of moultings, they reach adult stage and start a reproductive period before dying. The time spent in each developmental stage is, for a given food concentration, a direct function of temperature.

The availability of food for a filter-feeding animal depends, largely, on the filtering apparatus. There is probably a size range of food organisms outside which the animal cannot catch and handle satisfactorily. This size range must, again, be some function of the size of the animal. Thus, it is not enough to calculate the biomass of phytoplankton in order to assess the available amount of food for the copepods, but its size distribution has to fit the size distribution of the copepods' population, too.

The spatial distribution of phytoplankton is not even. It is rather patchy, both in the vertical and horizontal directions. The behaviour of the copepods (vertical migration and feeding behaviour), will, therefore, influence the amount of phytoplankton that the copepods see. This behaviour (especially vertical migration), is probably a function of developmental stage. From a predator point of view, several properties of the prey (copepod) may be important. These properties may be size, visibility, mobility and behaviour which affect the local concentration (small scale patchiness) of copepods. Visibility and mobility are likely to be functions of size.

From this discussion, we may conclude that the most important characteristics for describing growth and reproduction of a copepod population in relation to its environment are *size* (*or mass*) and *developmental stage*.

One may argue that size and developmental stage are not independent of each other, and that a relationship may be found between these two variables. However, copepods which are reared at different temperatures will differ widely in size at a particular stage (Wiborg 1954). Food supply during rearing will also affect the size at a particular stage (Paffenhöfer 1970, 1976). This means that both the temperature and the food supply affect the growth and the developmental rate in different ways, which results in adult animals of different sizes. In order to have this feature built into the model, therefore, we have to employ size and developmental stage distribution for describing the population. The observability of the model will probably be improved, compared to biomass models, because the output of the model can be compared not only with biomass and size distribution but also with size distribution within different developmental stages.

Before formulating the population model, it is, for mathematical reasons, necessary to make some definitions and approximations regarding size and developmental stage. As mentioned earlier, the growth of copepods is stepwise through successive moults if the growth is measured by size. On the other hand, if growth is measured in energy or carbon units, we may expect more continuous growth. Therefore, we use the increase in mass or weight (μg C) as a measure of growth.

The development of copepods may be more continuous than the size, but measurements of development are usually performed along a discrete scale—stage of development. Here, we define a continuous developmental scale which we shall call *level of development*. This scale ranges from 0·0 to 2·0, where 0·0–0·3 corresponds to the eggs and naupliar stages, 0·31–1·0 to the copepodite stage and 1·0–2·0 to the adult stage. For more details, see § 3.1.

2.2. *The population model—formulation*

We now introduce a density function $\eta(t, x_3, x_4)$, where t is time. x_3 is weight (μg C) and x_4 is level of development of a single individual. The subscripts 3 and 4 on the variables are used because 1 and 2 are used for the state variables x_1 (total number of individuals in the population), and x_2 (level of satiation). For details, see § 3.1. The density function, $\eta(t, x_3, x_4)$, has the following properties: the total number of individuals between weights x'_3 and x''_3, and developmental levels between x'_4 and x''_4 at time t are given by

$$x'_1 = \int_{x'_3}^{x''_3} \int_{x'_4}^{x''_4} \eta(t, x_3, x_4)\, dx_3\, dx_4 \tag{2}$$

For $x'_3 = 0$, $x''_3 = \infty$, x'_1 is the total number of individuals whose developmental levels are between x'_4 and x''_4 at t. If x'_4 and x''_4 coincide with the limits for a particular developmental stage (see § 3.1), x'_1 is the total number of individuals at this stage. With $x'_3 = 0$, $x''_3 = \infty$ and $x'_4 = 0$, $x''_4 = \infty$, we find the total number of individuals in the population

$$x_1 = \int_0^{\infty} \int_0^{\infty} \eta(t, x_3, x_4)\, dx_3\, dx_4 \tag{3}$$

Since there are no heavy animals at low developmental level and nor are there any individuals at high developmental level with very low weight, η approaches zero as

either $x_3 \Rightarrow$maximum, $x_4 \simeq 0$ or $x_4 \Rightarrow$maximum, $x_3 \simeq 0$. If we imagine a plane with axis x_3 and x_4, then $\eta(t, x_3, x_4)$, at a specific time t, can be visualized as a surface above the plane. Figure 1 shows such a surface with the volume delineated by the surface, and the planes x'_3, x''_3, x'_4, x''_4, equal the population between those weights and developmental levels as given by eqn. (2). The total volume under the surface equals the total population (eqn. (3)).

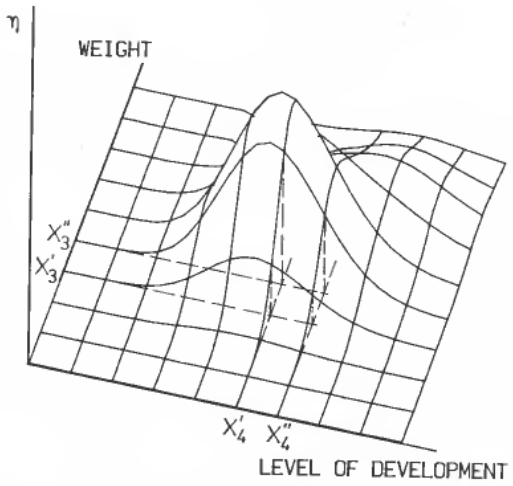

Figure 1. A sample weight–developmental level distribution at a particular time t. The volume delineated by the surfaces, x'_3, x''_3, x'_4, x''_4 equals the population between x'_3, x''_3 and x'_4, x''_4. The total volume under the surface equals the total population.

The density function η contains a great deal of information about the population. For example:

The total biomass at t

$$B_t = \int_0^\infty \int_0^\infty x_3 \eta(t, x_3, x_4)\, dx_3\, dx_4 \tag{4}$$

The weight distribution at t

$$\eta_w(t, x_3) = \int_0^\infty \eta(t, x_3, x_4)\, dx_4 \tag{5}$$

It can be shown (Himmelblau and Bischoff 1968, Sinko 1969) that the density function $\eta(t, x_3, x_4)$, with properties as mentioned above, satisfies the partial differential equation

$$\frac{\partial \eta}{\partial t} + \frac{\partial}{\partial x_3}(v_3 \eta) + \frac{\partial}{\partial x_4}(v_4 \eta) = -D\eta \tag{6}$$

where $v_3(t, x_3, x_4)$ is the growth rate of animals of weight x_3 and developmental level x_4 at time t and $v_4(t, x_3, x_4)$ is the developmental rate of animals of weight x_3 and developmental level x_4 at time t. $D(t, x_3, x_4)$ is the death rate for animals of weight x_3 and developmental level x_4 at time t. v_3 and v_4 are calculated by means of a physiological model of a single individual which is described in § 3. The death rate is partly calculated from the physiological model (death caused by starvation)

and partly from a predator model which is assumed to be a function dependent on time, only.

To make eqn. (6) well posed, we must specify boundary conditions, i.e. the weight–developmental level distribution of animals at time zero, $\eta_0(x_3, x_4)$, and the weight density distribution of newborn $\eta_B(x_3, x_4, t)$

$$\eta_0(x_3, x_4)=\eta(0, x_3, x_4) \tag{7}$$

$$\eta_B(t, x_3)=\eta(t, x_3, 0) \tag{8}$$

The newborn are expected to have developmental level zero but might have weights which depend on the weight of their parents (McLaren 1963). Assuming that the function $f_B(t, x_3, x'_3, x'_4)\,dx_3$ gives the rate at which animals of weight x'_3 and developmental level x'_4 give birth to neonates with weight between x_3 and x_3+dx_3, we find the density function of newborn

$$\eta_B(t, x_3)=\int_0^\infty \int_0^\infty f_B(t, x_3, x'_3, x'_4)\eta(t, x'_3, x'_4)\,dx'_3\,dx'_4 \tag{9}$$

We observe that the mathematical problem is complicated by the fact that the boundary condition (9) is dependent upon the density function itself. In certain special cases, it is possible to find an analytic solution of eqn. (6) (Courant and Hilbert 1962). However, in the general case, numerical solutions are probably necessary.

2.3. *Mortality*

The ability of a copepod to survive periods of starvation depends largely on its stage of development. The death rate of nauplii is probably very sensitive to starvation, whereas stage V may survive for months, apparently without any food supply. The weight of an animal, at a particular stage, will probably also be a factor affecting the survival success during periods of starvation. Since the satiation level, x_2, reflects an animal's ability to obtain proper food (see § 3.1), we assume the death rate caused by starvation, D_{st}, to be a function of x_2 and the developmental level x_4

$$D_{st}=d_{st}f_{st}(x_2, x_4) \tag{10}$$

where d_{st} is a parameter which represents the maximum mortality of starving nauplii and f_{st} is a function that describes how this death rate is modified by the level of satiation and development. Few quantitative data exist to construct this function. Therefore, we construct a relationship as shown in Fig. 2. The relationship mimics the qualitative description given above of the mortality, starvation and level of development. For simulation runs we will use the following relationship:

$$D_{st}=\begin{cases} 0, & x_2 \geqslant 0{\cdot}5 \\ 1-2x_2, & x_2<0{\cdot}5,\ x_4 \leqslant 0{\cdot}45 \\ \dfrac{1-2x_2}{1+10(x_4-0{\cdot}45)}, & x_2<0{\cdot}5,\ x_4>0{\cdot}45 \end{cases} \tag{11}$$

The reason why we choose these limits is that, for a satiation level above 0·5, we have more than 80% of maximum growth, and death caused by starvation is probably near zero. x_4 equals 0·45 means a stage of development corresponding to

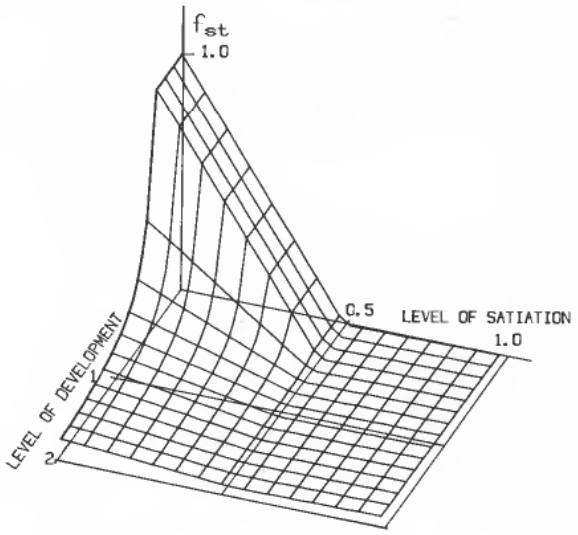

Figure 2. Mortality as function of satiation and developmental levels.

copepodite IV. We assume that animals above this stage of development are gradually less affected by starvation.

Predators on the copepods consist of numerous species, each of which will interact with the numbers and size distribution of their prey. The functional representation of this prey–predator relationship should be, in principle, similar to that used in the phytoplankton–copepod system and numerical representation of the predators should be comprised in a dynamic model. The latter seems to be especially important when dealing with predators of ctenophores type (Reeve and Walter 1978). Since the aim here is to set forward a model for the population dynamics of copepods, we will not go into details about the predator dynamics. This implies that we make the predator system largely independent of the prey, and give it predefined characteristics.

For simplicity we assume a time function which gives an increasing predator pressure during the spring

$$D_{pr}(x_3, x_4) = P_0 \frac{t^2}{t^2 + t_0^2} \tag{12}$$

where P_0 is a parameter giving maximum death rate caused by starvation and t_0 is the time at which the predation pressure has reached 50% of its maximum. Total death rate is the sum of death caused by starvation and predation.

2.4. *Sex differences*

We will assume here that there are no differences between the sexes before they reach adult stage (developmental level 1). Adult males are usually of much smaller size than the females and feeding is considerably lower (Paffenhöfer 1970). In the ocean, males seem to disappear very soon upon becoming adults. There are some discussions about the sex ratio in the literature (McLaren 1963), but we will assume here that this ratio is 1, and that the sexes have identical behaviour and development until they reach adult stage. To take into account the relatively short life span and

low feeding rate of the adult males, we assume that they all die upon reaching a certain level of development.

Thus, we may add an additional term to the mortality and predator functions (eqns. (11) and (12)), to allow the male fraction of the population to disappear,

$$D_{sex}(x_4)=0{\cdot}5\delta(x_4-x_{4s}) \tag{13}$$

where x_{4s} is the level of development at which the male fraction of the population is assumed to disappear. $\delta(\cdot)$ is a dirac pulse.

3. Formulation of a physiological model of a copepod

3.1. *The structure of the physiological model*

The mathematical model of the physiological state of an individual copepod will be based on the principal of energy balance (Slagstad 1980, Balchen 1976). This means that ingested food is converted to produce growth, reproduction, activity and losses. In addition to the energetic state variables, we have three state variables which describe the developmental stage (or level), number of animals in the population and the depth at which an animal is found. The state variables are defined as follows:

x_1—number of animals in population,

x_2—satiation level. May be associated with the energy stored in blood, liver, muscles and fat droplet,

x_3—energy contained in the animal, exclusive x_2,

x_4—level of development,

z—the depth from surface in the water column at which the animal is found.

Energy stored in gut will not be a dynamic storage but a function of ingestion, faeces and assimilation. This can be done since the time constant for filling up the gut is very much smaller than time constant of x_3 and x_4. Comments on this will be given later. A block diagram which shows the structure of the physiological model is exhibited in Fig. 3.

Satiation level

The level of satiation is a state variable which is meant to give a picture of the hunger state of the animal. It is represented by an energy storage that is filled up when the animal is feeding and used for metabolic demands when food supply diminishes. The energy storage associated with the satiation level may be carbohydrate stored in the blood, midgut gland and muscles. Part of this energy storage may also be stored as fat, which has been shown to be utilized as fuel in zooplankton (Lee *et al.* 1970). Several authors (Mullin 1963, McAllister 1970, 1971, Frost 1972, Hargrave and Geen 1970) have shown that when animals were starved before feeding, the ingestion rate increased several fold during the initial exposure to algal food compared with animals in steady state food conditions.

In this model, the satiation level will, besides having an effect on the ingestion rate, influence the growth, behaviour, development and reproduction of a single individual. The differential equation that describes changes in the satiation level is

$$\frac{dx_2}{dt}=(v_{as}-v_r-v_g x_3-v_e)/V_{sat} \tag{14}$$

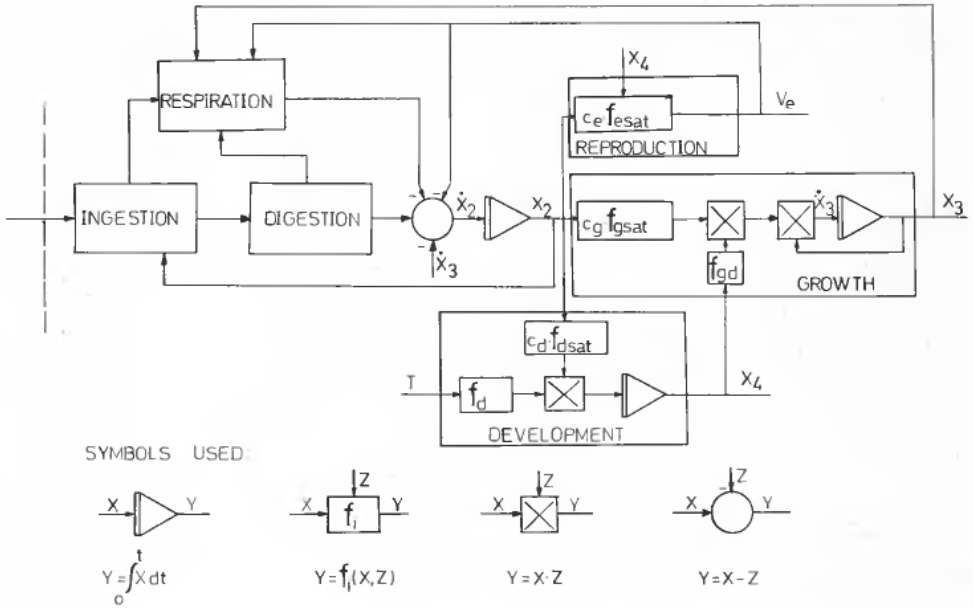

Figure 3. Block diagram structure of the physiological model.

where v_{as} is the rate of assimilation (μg C hr^{-1}), v_r is the rate of respiration, v_g is the rate growth per unit weight (hr^{-1}), v_e rate of reproduction (energy put into eggs, μg C hr^{-1}) and V_{sat} is the maximum size of the energy storage associated with the level of satiation. V_{sat} must be some function of the size and, perhaps, the stage of development of the animal. There are no data available to indicate this relationship but we will suppose that V_{sat} is proportional to the weight of the animal, only. Comparison of data from McAllister (1970) and Frost (1972), with simulation runs of the model, indicates that this V_{sat} is about 5–10% of the total weight of the animal. Sensitivity analysis described later shows that the model is not very sensitive to this parameter.

Growth

Growth is a function of the internal state of the animal and external factors of which we shall take into account temperature, only. The effect of food supply acts through the satiation level, which is function of quantity and quality of food. It is usually believed that growth rate is proportional to the weight of the animal

$$\frac{dx_3}{dt} = x_3 f_g(x_2, x_4, T) \tag{15}$$

where $f_g(x_2, x_4, T)$ is a function that describes growth rate as a function level of satiation, level of development and temperature. If we now regard the effect of one variable on the growth rate, independent of the other variables, we can split $f_g(\cdot)$ into product functions

$$f_g(x_2, x_4, T) = c_g f_{gsat}(x_2) f_{gd}(x_4) f_{gT}(T) \tag{16}$$

where c_g is a parameter that represents the maximum growth rate at a given temperature, when level of development is zero, f_{gsat} is a function that describes the effect

of the level of satiation on the growth rate, f_{gd} is a function that describes the effect of the level of development on the growth rate and f_{gT} is the function that describes the effect of the temperature on the growth rate. T is the temperature. The functions f_{gsat} and f_{gd} are normalized such that their maximum value is one.

Nothing, of course, is known about $f_{gsat}(\cdot)$ and we have to choose this function. The choice will not be a critical factor determining growth rate because feedback from x_2 to the filtering rate will adjust the ingestion rate to a level which gives maximum growth rate. If x_2 decreases, the filtering rate will be increased until its maximum value is reached. If food concentration is low and energy used for growth cannot be supplied even with maximum filtering rate, the growth rate will decrease until a steady state level is reached. During a starvation period, the animal metabolizes body tissue and the growth rate will be negative. We, therefore, choose the following function

$$f_{gsat}(x_2)=1-2\exp(-5x_2) \tag{17}$$

The weight specific growth tends to decrease as the animal approaches the adult stage (Paffenhöfer 1976, Vidal 1980). When reproduction starts, the growth ceases and the energy is directed towards the reproductive products. Paffenhöfer (1976) used the relationship

$$x_3(t)=x_3(0)\exp(kt) \tag{18}$$

to calculate what he called "coefficients of daily exponential growth, k". $x_3(0)$ is the weight of one animal at the beginning of a time period, and $x_3(t)$ is its weight at the time t. He found that k was a function of the developmental stage, food species and amount of food offered. The largest growth rate and the largest final size were attained when the unarmoured dinoflagelate *Gymnodinium splendens* was offered as food. If we assume that this is the maximum growth rate of *Calanus helgolandicus* at 15°C, we may construct a function from his data which describes the maximum growth rate at a specific level of development at a given temperature (Fig. 4).

A commonly applied relationship between temperature, T, and the rate of a biological process, v_b, is

$$v_b=Q_{10}{}^{0.1(T-T_r)} \tag{19}$$

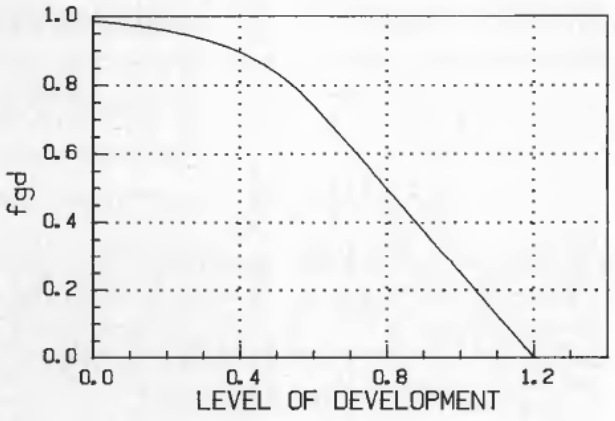

Figure 4. Growth rate of *C. helgolandicus* as a function of developmental level (data from Paffenhöfer (1976), Table 7).

where T_r is the reference temperature at which the rate of the biological process is measured and Q_{10} is the ratio of the biological process for a difference of 10°C from any temperature reference T_r. This relationship will be used to describe the temperature effect on different physiological processes. For the growth process, we choose Q_{10g} and T_{rg} equal 3·35 and 15·0, respectively, according to an experiment of Mullin and Brooks (1970 a).

Development

Eggs of *Calanus* take between 5 and 1 days to hatch into nauplii, when the temperature ranges from 0–20°C (McLaren 1963). The growth is, as in other crustacea, through successive moults. There are six naupliar stages and six copepodite stages, where the last one is the adult stage, consisting of male and female animals. Several factors may influence the moulting frequency, but temperature and food supply seem to be the most important factors. Although development is measured in distinct stages, we shall here define a continuous developmental scale ranging from 0–2. Each value of the continuous scale corresponds to a specific developmental stage. Horwood (1973) calculated from his own and others' data that the proportion of the developmental time spent in each stage is independent of temperature. His results are given in Table 1. Using data from this table, we may construct a continuous developmental scale (Fig. 5). The rate of development is assumed to be a function of the level of satiation and temperature

$$\frac{dx_4}{dt}=f_{dev}(x_2, T) \tag{20}$$

Assuming that $f_{dev}(\cdot)$ can be split into product functions, we obtain

$$f_{dev}(x_2, T)=c_d f_{dsat}(x_2) f_{dT}(T) \tag{21}$$

where f_{dsat} is a function that describes the effect of the satiation level on the rate of development, f_{dT} is a function that describes the effect of temperature on the rate of development and c_d is a parameter which represents the maximum rate of development at a given temperature. The inverse of c_d is the minimum time of development from hatching until the adult stage is reached.

E	N1	N2	N3	N4	N5	N6	C1	C2	C3	C4	C5
2·21	1·53	1·96	7·89	4·42	6·77	6·80	5·82	8·90	9·83	11·35	32·52

Table 1. Percentages of egg to adult time spent in each stage (from Horwood (1973)).

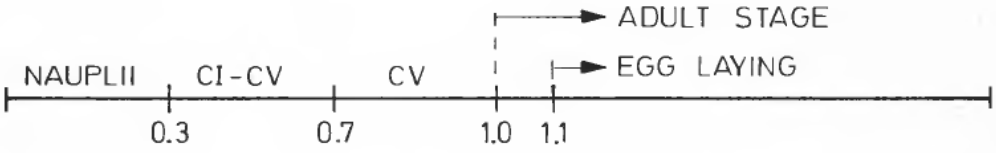

Figure 5. Relationship between discrete developmental stage scale and the continuous developmental level scale.

Paffenhöfer (1970) found that developmental time from egg to adult was inversely proportional to the amount of food offered. He also found that food species had a certain effect on the developmental rate. As the satiation level is a function of the amount and quality of food, we will assume the developmental rate to be a function of the satiation level rather than the amount of food. This function must be slightly different from f_{gsat} in order to obtain animals which differ in weights when food supply changes. Since we have no data, we chose the function

$$f_{dsat}(x_2)=\begin{cases}0, & \text{if } x_2<0{\cdot}13\\ 1-\exp\left[-5(x_2-0{\cdot}13)\right], & \text{if } x_2\geqslant 0{\cdot}13\end{cases} \tag{22}$$

If the influence of temperature on growth and development were identical, the weight of an animal at a particular stage would be independent of temperature. However, it is commonly believed that crustacea reared in a cold environment will reach a larger size than animals reared at higher temperature. This has also been found in laboratory experiments with *C. pacificus* (Vidal 1980). He concluded that with increasing body size the growth rate tends to become temperature-independent, but that the developmental rate remains proportional to temperature. This means that Q_{10g} of growth is less than Q_{10d} of development. Using $Q_{10g}=3{\cdot}35$, we find that Q_{10d} equal to 3·65 will give adult animals weighing three times as much when reared at 5°C than those reared at 15°C. Minimum time from hatching to adulthood is about 20 days for *C. helgolandicus* when reared at 15°C (Paffenhöfer 1970, Mullin and Brooks 1970 a), which gives the maximum rate of development c_d equal to $2{\cdot}08\times10^{-3}$ hr^{-1}. Assuming the weight of nauplii, when feeding starts, to be equal to 0·1 μg C and adult weight to be equal to 60 μg C, we find from eqns. (15) and (20) that c_g equals $1{\cdot}75\times10^{-2}$ hr^{-1}.

3.2. *The ingestion submodel*

The most common way to describe the feeding rate of planktonic herbivores in simulation models is by some non-linear function of phytoplankton concentration (Wroblewski and O'Brien 1976, Steele 1974, Mullin, Stewart and Fuglister 1975). An Ivlev or Michaelis–Menten function is often used to describe this relationship. However, we know from several experiments in recent years that, in addition to food concentration, the size of the algal cells and the satiation level (or hunger state) affect the ingestion rate as well (Frost 1972, 1977, McAllister 1970). The ingestion model of a copepod presented here will be based on the following assumptions:

—the animal is a 'true filter feeder' and does not capture food by predation,

—the filtering rate (ml hr^{-1}) is determined by the internal state (weight and satiation level) of the animal and temperature,

—the efficiency of the filter is related to the size of the animal and the size of the algal cells.

In a suspension of particles of size distribution $P(V_0)$, the rate of ingestion q_I is calculated by equation

$$q_I=FR(x, x_g, T)\int_0^\infty h_e(V_0, x_3)P(V_0)V_0\,dV_0 \tag{23}$$

where q_I is the rate of ingestion, FR is the filtering rate of an animal of physiological

state x, gut content x_g at temperature T. h_e is the filtering efficiency of an animal of weight x_3 which feeds on particles of volume V_0 ($0 \leqslant h_e \leqslant 1$).

For simplicity we assume that the algal cells are of uniform size and consist of a single species. Equation (23) reduces to

$$q_I = FR(x_2, x_3, x_g, T)h_e(V_0, x_3)PV_0 \tag{24}$$

where P is the number of algal cells per millilitre.

Filtering rate

A typical relationship between the filtering rate, ingestion rate and food concentration is shown in Fig. 6. The area of constant ingestion arises probably when the energy supply equals the energy demands of the animal. The critical concentration, P_c, defined as that cell concentration at which the maximal ingestion rate is first achieved will, therefore, be a function of the size of the algal cells and their nutritional value. At food concentrations between the lower threshold P_1 and the critical, the animal filters at its maximum rate to obtain as much energy as possible. At low food concentrations the energy spent in filtering may exceed the energy gain from the feeding process. It is, therefore, often assumed that the filtering rate is reduced at this lower end of food concentrations. How this reduction comes about is still unclear, but we assume here that there is a threshold below which the copepods cease to filter. At food concentrations above this lower threshold, the filtering rate is assumed to be a function of the internal state of the animal and temperature.

$$FR(x_2, x_3, x_g, T) = f_{FRw}(x_3)f_{FRs}(x_2)f_{FRg}(x_g)f_{FRT}(T) \tag{25}$$

where $f_{FRw}(x_3)$ is a function describing the effect of weight on the maximum filtering rate, $f_{FRs}(x_2)$ is a function describing the effect of satiation level on the filtering rate, $f_{FRg}(x_g)$ is a function describing the effect of gut filling on the filtering rate and $f_{FRT}(T)$ is a function describing the effect of temperature on the maximum filtering rate.

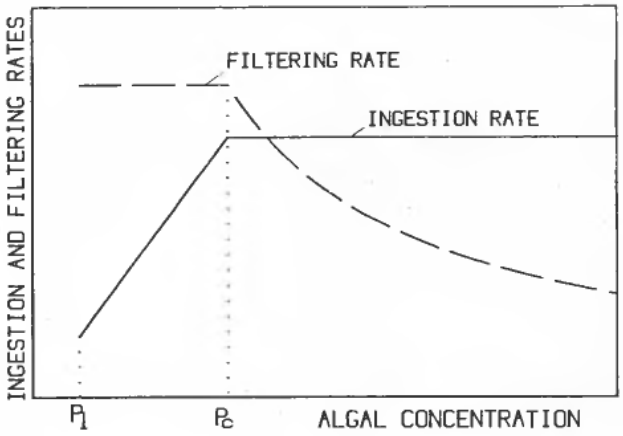

Figure 6. Typical ingestion and filtering rates as function of algal concentration. P_c is the critical concentration and P_1 is called the lower critical concentration below which the copepods cease to filter.

The geometry and size of the filtering apparatus is determined by the size of the animal. Therefore, the maximum filtering rate will be a function of the size of the animal. Using data from Paffenhöfer (1970), we find that the filtering rate is close to an exponential function of weight

$$f_{FRw}(x_3)=FR_0x_3^{\beta} \tag{26}$$

where FR_0 is the maximum rate of filtering of an animal of unit weight and β is an exponential constant. Parameter values may also be found from Paffenhöfer's data. We found $FR_0=1{\cdot}25$ ml $hr^{-}{}_1$ and $\beta=0{\cdot}77$.

The ingestion rate in the plateau area seems to be determined by the energy demands of the animal, only. It is not limited by factors such as maximum gut passage rate or physiological constraints of the feeding mechanisms because starved animals may have an ingestion rate which is two or three times higher than the plateau area for several hours when excess of food is offered (Frost 1972, McAllister 1970). We therefore assume a relationship between the filtering rate and the satiation level which is such that filtering rate is maximum when the satiation level is low and decreases as the level of satiation reaches maximum. The following relationship will be used

$$f_{FRs}(x_2)=\begin{cases}1{\cdot}0-\exp\left[-5(1{\cdot}4-x_2)\right], & x_2\leqslant 1{\cdot}4\\ 0, & x_2\geqslant 1{\cdot}4\end{cases} \tag{27}$$

The maximum ingestion rate is defined as that rate at which a starved animal ingests when food is given in excess. What limits that rate? Data obtained from *Calanus* with which to answer this question are rather scarce, but Geller (1975) found that by comparing ingestion rates of *D. pulex* for seven species of phytoplankton, the maximum ingestion rates are most similar between species when the values are expressed on a volumetric basis (μm^3 animal^{-1} hr^{-1}) rather than on the basis of cell carbon contents. This may imply that maximum volume of the gut imposes an upper limit on ingestion.

We assume

$$f_{FRg}(x_g)=\begin{cases}1, & x_g\leqslant 1\\ 0, & x_g>1\end{cases} \tag{28}$$

Maximum filtering rate generally increases with temperature (Geller 1975, Kibby 1971). Data on this temperature dependence are scarce but we will use the kind of temperature function as employed for growth and developmental rate (eqn. (19)). Using data from Geller (1975) on *D. pulex*, we assume $Q_{1\,0f}$ of filtering rate equal to 2·10.

Filtering efficiency

The size of phytoplankton may markedly influence the ability of planktonic herbivores to obtain enough food to sustain growth and reproduction (Parsons and LeBrasseur 1970). For a copepod, there must be some lower limit of particle size where the ability to obtain particles from a suspension ceases. At the other end of the size spectra, some maximum particle size must exist which cannot be ingested. These upper and lower boundaries are probably a function of the weight of the animal. But few data are available to make any assumption about these limits,

especially the uppermost one. In the size range between the two extreme limits, there are some theories and data to suggest a relationship between filtering rate and particle size. Thus, Frost (1977) proposed a hypothesis that size-selective feeding tendency, observed in several species of *Calanus*, was due solely to the mechanical operation of feeding appendages and reflects the relative efficiency at which copepods collect, handle, and ingest cells of different sizes. We adopt this hypothesis here because it gives a simple and realistic explanation for size-selective feeding to be used in our model. We define a filtering efficiency function ($h_e(V_0)$) of a copepod's ability to collect, handle and ingest cells at a specific volume.

The filtering efficiency function is defined as

$$h_e(V_0)=\frac{FR_m(V_0)}{FR_{opt}} \tag{29}$$

where $FR_m(V_0)$ is the actual measured maximum filtering rate when cells of volume V_0 are offered as food and FR_{opt} is the maximum filtering rate when cells of optimal size are offered as food. Optimal size of algal cells is that size which gives maximum filtering rate for a starved animal. Using Frost's (1977) log-lin relationship between cell size and maximum filtering rate, we find

$$h_e(V_0)=\theta_1 \log (V_0)+\Theta \tag{30}$$

where V_0 is cell volume in μm^3. This relationship is based on adult animals of weight 68 μg C, which gives values of θ_1 and Θ equal to 0·22 and 0·36, respectively. The filtering efficiency must also be a function of the size of the animal. If we assume that the form of this relationship is independent of the size of the animals and is only shifted to the right as the animal becomes larger, the size change will affect the parameter Θ only.

Assuming the coarseness of the filtering mesh is proportional to a given length scale of the animal, we find, when using $x_3 \sim L^3$,

$$h_e(V_0)=\theta_1 \log (V_0)-\theta_2(x_3)^{1/3}+\theta_3 \tag{31}$$

where θ_1, θ_2 and θ_3 are parameters. Using Frost's (1977) data, we find $\theta_2=0{\cdot}19$ and $\theta_3=0{\cdot}41$. For a more comprehensive discussion, see Slagstad (1980).

3.3. *The digestion submodel*

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 constituents. Porter (1975) has found that some gelatinous green algae even seem to survive a passage through the gut and thus, probably, have been of no nutritional 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 constituents 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

$$\frac{dV(t)}{dt} = -aV(t), \quad t > t_{g0} \tag{32}$$

where $V(t)$ is the volume of a cell after t time units inside the gut, a is the rate of digestion per unit cell volume (hr^{-1}) and t_{g0} is time delay between ingestion and the onset of digestion. Solution of eqn. (32) gives

$$V(t) = \begin{cases} V_0, & \text{if } t < t_{g0} \\ (V_0 - V_f) \exp[-a(t - t_{g0})] + V_f, & \text{if } t \geq t_{g0} \end{cases} \tag{33}$$

where V_0 is the initial volume of a cell when ingested and V_f is the minimum indigestible volume of the cell. The volume of an individual algal cell versus time is plotted in Fig. 7.

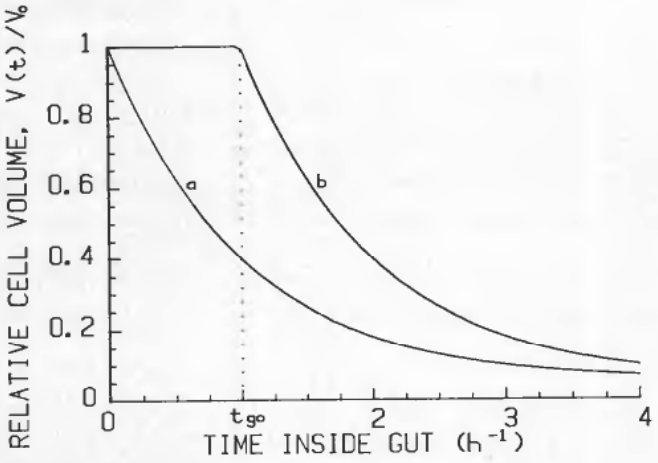

Figure 7. Relative volume of an algal cell versus time inside the gut. (*a*) Cell wall broken when ingested and digestion starts immediately upon ingestion. (*b*) Cell wall is resistant against digestive enzymes for some time (t_{g0} time units) before digestion of cellular constituents starts.

From this figure we note 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. Thus gut passage time seems to be an important factor for the assimilation process. Assuming now that the velocity of algal cells through the gut is proportional to the gut filling (Holling 1966), we can find the following expression for the gut passage times (Slagstad and Tande 1981)

$$t_g = \frac{t_{min}}{x_g} \tag{34}$$

where t_{min} is the minimum gut passage time which occurs when the gut is completely filled. In steady state (i.e. $dx_g/dt=0$), the gut filling is given by

$$x_g=\frac{N_I t_g V_{av}}{V_g} \tag{35}$$

where $N_I=FR\cdot h_e\cdot P\cdot V_0$=number of algal cells ingested per unit time. V_{av} is the average cell volume inside the gut. V_g is the maximum volume of the gut.

3.4. *Respiration and excretion*

All heterotropic organisms ultimately obtain their energy from oxidation reduction reaction. Aerobic organisms obtain most of their energy through respiration. The processes which demand energy are mainly growth, reproduction, digestion and filtering work. Since these processes are more or less independent of each other, it is convenient to split them into sub-processes.

Standard metabolism

Standard metabolism is defined as the energy cost to keep life going when no physical or digestive work is being done. We assume that this is a function of weight of the animal and temperature

$$R_s=R_{s0}(x_3)^b Q_{10r}{}^{0\cdot 1(T-T_{rr})} \tag{36}$$

where R_{s0} is standard metabolic rate of an animal of unit weight (μg C hr^{-1}), Q_{10r} is the Q_{10} of respiration, T_{rr} is the temperature at which R_{s0} is measured and b is an exponential constant.

Energy of filtering

Based on theoretical considerations, we may assume that the energy expended in filtering is given as the product of the force which the copepod exerts in setting up a circulation pattern and the speed of the moving water (Lam and Frost 1976). The drag forces on the moving appendages of a copepod have not been studied very much so that it is not possible to decide, from data, whether the drag is viscous or turbulent. Lehman (1976) indicated that the flow may be viscous and, for lack of better information, we will use the same suggestion here. Thus, the energy expended in filtering can be expressed as

$$R_f=c_1 Dv \tag{37}$$

where D is the drag force given by $D=c_2 A_f v$, v is velocity at which the water moves through the filtering apparatus, A_f is the effective area of the filtering mechanism and c_1 and c_2 are constants. Assuming now that the area of the filtering mechanism is proportional to the square of a given length scale of the animal ($A_f\sim L^2$) and weight is proportional to the volume of the animal ($x_3\sim L^3$). The filtering rate is $FR=A_f V$. Using these assumptions and eqn. (37), we obtain

$$R_f=c_f(x_3)^{-2/3}FR^2 \tag{38}$$

where c_f is a constant.

Energy cost of digestion

It has been known for a long time that respiration is lower in copepods living in water, with an inadequate supply of food, than in the same species living in a nutrient

rich environment (Marshall 1973). Increased respiration by feeding is caused by two sources; one is from the energy used in filtering and handling the prey and the other is from specific dynamic action defined as energy used to digest and biochemically transform the food.

According to Kleiber (1975), we will here assume that the specific dynamic effect is proportional to the amount of food ingested. The energy spent in digestion may then be calculated from the following relationship

$$R_d = d_0 c_{as} \tag{39}$$

where c_{as} is the assimilation rate (μg C hr^{-1}) and d_0 is a parameter determining the fraction of the assimilated food that is put into digestive work. Total respiration may now be found by summing up the sub-processes

$$R = R_{s0}(x_3)^b Q_{10r}^{0\cdot1(T-T_{rr})} + c_f(x_3)^{-2/3} F R^2 + d_0 c_{as} \tag{40}$$

3.5. *Reproduction*

Reproduction is assumed to take place after the animals have reached the adult stage. In our notation, that means above the level of development equal to 1. The rate of egg production is taken proportional to the level of satiation, which means that reproduction will be closely related to quantity of food. Evidence for this assumption can be found in Marshall and Orr (1972). The reproduction equation can be formulated like this:

$$E = \begin{cases} e_n(1-\exp[-5(x_2-0\cdot2)]), & x_2 > 0\cdot2 \quad \text{and} \quad x_4 > x_{4e} \\ 0, & \text{else} \end{cases} \tag{41}$$

where E is the number of eggs laid per unit time, e_n is the parameter giving the maximum rate of egg production of an animal when food is in excess and x_{4e} is the level of development above which an animal is able to reproduce. No temperature dependence is assumed for the rate of egg laying. The parameters of the reproductive model e_n and x_{4e} are taken equal to 2·0 hr^{-1} and 1·1, respectively. When food is abundant, this gives approximately a total production of 900 eggs per animal during their adult life period. Each egg is assumed to contain 0·1 μg C (Mullin and Brooks 1970 b).

3.6. *Vertical migration*

Copepods usually undertake diurnal vertical migration journeys, ranging from a few metres to several hundred metres. The main stimulus for this migration behaviour is probably change in light intensity. However, the biological state of the animal and phytoplankton concentration seem to interact and modify the dependence of light intensity. The migration model will be based on the following assumptions:

(1) The direction of migration is such that the animals tend to stay in the depth where light intensity is equal to their internal reference level. If there is complete darkness, the animals are assumed to move randomly in the water column.

(2) The light reference level is a function of the stage of development and has a diurnal variation during midnight sun conditions.

(3) The speed of migration depends on the difference between the reference level and ambient light intensity, the weight of the animals, and food concentration.

Assuming that the effect of each factor on the migration speed can be split up into a product function, we find

$$\frac{dz}{dt}=\begin{cases} f_{bw}(x_3)f_{bI}(I_z, I_{ref})f_{bp}(P), & I_z>0 \\ \text{white noise}, & I_z=0 \end{cases} \tag{42}$$

where f_{bw} is a function describing how maximum migration speed depends on the weight of the animal. We assume this speed to be proportional to the weight.

$$f_{bw}=v_{z0}+v_{z1}x_3 \tag{43}$$

v_{z0} and v_{z1} are parameters. f_{bI} is a function that describes how the migration speed and direction depend on the light intensity

$$f_{bI}=\begin{cases} 10(I_z-I_{ref}), & \text{if } |I_z-I_{ref}|\leqslant 0{\cdot}1 \\ 1, & \text{if } I_z-I_{ref}>0{\cdot}1 \\ -1, & \text{if } I_z-I_{ref}<-0{\cdot}1 \end{cases} \tag{44}$$

I_z is the light intensity at depth z and I_{ref} the reference level of the animals. We assume that this reference level takes one value for the naupliar stages and one for the copepodites.

f_{bp} is a function that describes how the migration speed depends on the food concentration. The reason why we choose this dependence is because several authors have found that there is a positive correlation between chlorophyll maximum layer and maximum concentration of copepods (Anderson, Frost and Peterson 1972, Mullin and Brooks 1972). This may indicate that phytoplankton concentration (or its gradient) may affect the direction of migration. The following relationship is assumed to describe this behaviour.

$$f_{bp}=\begin{cases} 1, & \text{if } P\leqslant P_s \\ \exp\left(-\dfrac{(P-P_s)}{a_p}\right), & \text{if } P>P_s \end{cases} \tag{45}$$

where

P_s is algal concentration below which the migration speed is not affected.

a_p is a parameter.

4. Phytoplankton model

4.1. *Introduction*

The production of herbivore copepods in the marine environment is usually limited by the phytoplankton. Simulation experiments with the population and the physiological model of copepods have, therefore, little value if a proper phytoplankton model is not included. What is a proper phytoplankton model? In principle, it should have a structure which gives information about the growth of the population in relation to its environment, effect of its chemical environment (removal of nutrients) and information about the availability, digestibility and nutritional value

Parameter name	Units	Value	Meaning
a	hour^{-1}	3·3	Rate of digestion per unit cell volume
t_{min}	hour	0·17	Minimum gut passage time
V_{g0}	mm^3	$2{\cdot}5\times10^{-4}$	Gut volume of an animal of unit weight
FR_0	ml/hour^{-1}	1·25	Filtering rate of an animal of unit weight
β		0·75	Exponential constant of the filtering rate–weight relationship
θ_1		0·22	Parameters concerning size-selective feeding
θ_2		0·19	
θ_3		0·41	
Q_{10f}		2·10	Q_{10} of filtering
Q_{10d}		3·67	Q_{10} of development
g_t	hour	480	Generation time at 15°C when excess of food is given
V_{s0}		0·075	Fraction of the animal associated with the satiation level
c_g	hour^{-1}	0·017	Growth constant
Q_{10g}		3·35	Q_{10} of growth
e_n	hour^{-1}	2·0	Rate of egg production when excess of food is given
X_{4e}		1·1	Level of development above which egg production starts
R_{s0}	hour^{-1}	$1{\cdot}14\times10^{-3}$	Standard respiration of an animal of unit weight
b		0·81	Exponential constant of respiration–weight relationship
Q_{10r}		2·0	Q_{10} of respiration
d_0		0·3	Fraction of assimilated energy spent in digestion
c_f	gC(ml/hr)$^{-2}$	$7{\cdot}8\times10^{-4}$	Constant related to energy spent in filtering
V_{z0}	m/hour	10·0	Maximum migration speed of an animal of unit weight
V_{z1}	(gC)$^{-1}$	0·03	Parameter giving the increase in migration velocity with weight
a_p	mM N/m^3	1·14	Parameters which determined decrease in migration Velocity with increasing algal concentration
p_s	nM N/m^3	1·0	
I_{rn}	W/m^2	1·0	Light reference level of the nauplii
I_{rc}	W/m^2	0·3	Light reference level of copepodites

Table 2. Parameters of the physiological model used in the simulation runs.

for the copepods. Here, we will make a simplification and take the properties of the phytoplankton to be constant, whereas the concentration depends on growth and grazing pressure. The limiting nutrient is assumed to be nitrogen which is supplied from two sources, nitrate and ammonia. Ammonia is mainly produced by the copepods and bacterial decomposition of detritus, whereas the detritus is assumed to consist of dead phytoplankton.

4.2. *The dynamic equations*

The dynamic equations describing the growth and vertical distribution of phytoplankton, nutrients and detritus are:

Phytoplankton

$$\frac{\partial P}{\partial t} = -(w+w_p)\frac{\partial P}{\partial z} + \frac{\partial}{\partial z} D_z \frac{\partial P}{\partial z} + V_m f_1(I_z)\{G_N(P, A) + G_A(P)\} - \phi_r P - q_I(P) \quad (46)$$

Nitrate

$$\frac{\partial N}{\partial t} = -w\frac{\partial N}{\partial z} + \frac{\partial}{\partial z} D_z \frac{\partial N}{\partial z} + \phi_a A - V_m f_1(I_z) G_N(P, A) \quad (47)$$

Ammonia

$$\frac{\partial A}{\partial t} = -w\frac{\partial A}{\partial z} + \frac{\partial}{\partial z} D_z \frac{\partial A}{\partial z} - \phi_a A + \phi_d D + E^z - V_m f_1 G_A(P) \quad (48)$$

Detritus

$$\frac{\partial D}{\partial t} = -(w+w_d)\frac{\partial D}{\partial z} + \frac{\partial}{\partial z} D_z \frac{\partial D}{\partial z} + \phi_r P - \phi_d D \quad (49)$$

The first two terms of the r.h.s. of the equations represent the vertical transport and vertical turbulent mixing, respectively. The third term of eqn. (46) represents the phytoplankton growing term. Growth of phytoplankton is accompanied by a decrease in the concentration of nutrients. This is accounted for by the last terms in eqns. (47) and (48). The fourth term of eqn. (46) represents the respiration and mortality of the phytoplankton. These losses are assumed to give a supply to the detritus pool (third term in eqn. (49)).

V_m is the maximum uptake rate of nitrogen. For the relationship between photosynthesis and light, we choose Steele's (1962) function

$$f_1(I_z) = \frac{I_z}{I_{max}} \exp(1 - I_z/I_{max}) \quad (50)$$

where I_z is the light intensity at depth z. I_{max} is the light intensity giving the maximum photosynthetic rate. I_{max} depends on the chlorophyll content of the algae, and this on its light history. We, therefore, take I_{max} as a function of depth and season (see Jamart *et al.* 1977). The uptake rate of nitrate is depressed with increasing ammonia concentration (Walsh and Dugdale 1972, Packard and Blasco 1974). To account for this depression we multiply the Michaelis–Menten expression by an exponential

$$G_N(P, A) = \frac{NP}{k_N + N} \exp(-\psi A) \quad (51)$$

where k_N is the Michaelis constant and ψ is a parameter determining the decrease in nitrate uptake by the ammonia. For $G_A(P)$, uptake of ammonia, we also assume a Michaelis–Menten form.

The last term in eqn. (46) represents the grazing pressure from the copepods. The third term in eqns. (47) and (48) represents the oxidation of ammonia into nitrate, whereas the fourth term in eqns. (48) and (49) represents bacterial decomposition of detritus into ammonia.

The sinking rate of phytoplankton, w_p, is taken to be a function of nutrients of the surrounding water masses

$$w_p = \frac{w_0}{1+\left(\frac{N+A}{n_s}\right)^2} + w_\infty \tag{52}$$

where w_0 is the sinking rate when the nutrients are completely depleted, w_∞ is the sinking rate at high nutrient level and n_s is a constant. The sinking rate of detritus, w_d, is assumed to be constant.

The amount of solar radiation is calculated from the sun's angle to the horizon, which again depends on latitude, sun's declination and hour angle.

4.3. *Parameter values*

In Table 3, the parameters of the phytoplankton and chemical models are collected. The choice of values was guided by comparison with Wroblewski (1977) and Jamart *et al.* (1977). Because this model is related to a comprehensive ecological model of the Barents Sea, we always start our simulation runs according to a winter situation, with nitrate (10 mM N/m^3) homogeneously distributed throughout the water column.

5. The dynamics of the zooplankton–phytoplankton model

5.1. *Introduction*

The model, describing the growth of phytoplankton and zooplankton and their interactions, contains a vast number of parameters. Their numerical value is usually uncertain. It is, therefore, of great interest to analyse the behaviour of the model as a function of its parameter values. This is done by a technique called *sensitivity analysis.*

There are two methods of sensitivity analysis. Analytical analysis involves the derivation of partial differential equations describing the rate of change of the dependent variables with respect to change in the parameter values (Wroblewski and O'Brien 1979). If the model equations are too complex, analytical analysis becomes impractical. One changes, therefore, the parameter values, runs the model once more, and looks at the displacement of one or several output variables (e.g. biomass, population, spatial or temporal structure, etc.). This method is less elegant than the analytical technique but is often necessary in models with spatial dependence. The latter method will be used here.

As a measure of how change in different parameters affects our plant herbivore system, we have chosen the produced biomass of copepods, B^z, during a time period, t_s, defined by

$$B^z = \int_0^{t_s} \int_0^{\infty} \int_0^{\infty} \eta(t, x_3, x_4)(V_{as}(t, x_3, x_4) - R(t, x_3, x_4))\, dx_3\, dx_4\, dt \tag{53}$$

Parameter name	Units	Value	Meaning
V_m	hour^{-1}	0·086	Maximum uptake rate of nitrogen
ψ	mM N/m^3	1·46	Parameter denoting the concentration of ammonia which reduces the uptake of nitrate by 37%
k_N	mM N/m^3	1·0	Half-saturation constant for nitrate
k_A	mM N/m^3	1·0	Half-saturation constant for ammonia
ϕ_r	hour^{-1}	$4{\cdot}17\times10^{-3}$	Respiration rate of phytoplankton
ϕ_a	hour^{-1}	$1{\cdot}57\times10^{-3}$	Rate of oxidation of ammonia into nitrate
ϕ_d	hour^{-1}	0·043	Rate of bacterial decomposition of detritus into ammonia
w_d	m/hour	0·36	Sinking rate of detritus
w_0	m/hour	0·083	Sinking rate of phytoplankton when nutrients are depleted
w_∞	m/hour	0·02	Sinking rate at high nutrient level
n_s	mM N/m^3	2·5	Parameter concerning sinking rate
V_0	mm^3	$3{\cdot}6\times10^{-6}$	Volume of a single algal cell
V_f	mm^3	$1{\cdot}8\times10^{-7}$	Indigestible volume of an algal cell
ρ_{alg}	mg/mm^3	85·0	Specific carbon content
C_N^c		7·0	Carbon/nitrogen ratio (atomic)
t_{g0}	hour	0·075	Delay of digestion

Table 3. Parameters of the nutrient and phytoplankton models used in the simulation runs.

where $\eta(x_3, x_4)$ is the weight–developmental distribution, $V_{as}(t, x_3, x_4)$ is the assimilated amount of carbon and R is the total respiration of an animal of weight x_3 and level of development x_4.

The time course of depth integrated biomass, vertical structure of phytoplankton and nutrients and population structure of copepods will also, in some cases, be discussed.

5.2. *The basic run*

For the basic run (Figs. 9–13), we have chosen the depth variation of vertical mixing coefficients as in Fig. 8. No horizontal water exchange is assumed. Maximum depth is 100 m, below which a pool of nitrate is assumed to be constant (10 mM N/m^3) throughout the simulation period. The distance between the grid points is taken to be equal to 5 m. Each layer is assumed to be homogeneous and the vertical mixing coefficient describes the turbulent mixing between the layers. A pycnocline is assumed at 20 m.

Maximum death rate for starved nauplii D_0 and maximum predation rate P_0 are put equal to 0·002 animals hr^{-1} and 0·004 animals hr^{-1}, respectively (see § 2.3). Time from simulation start to 50% of maximum predation rate occurs: $t_0=25$ days (see eqn. (12)).

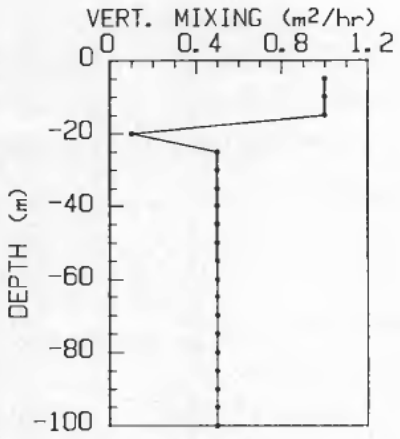

Figure 8. The basic run. Depth variation of the vertical mixing coefficient. The dots show the border between the layers.

Our ecosystem is assumed to be placed at a latitude of 72°, which means that half of the usual simulation period (100 days) is performed during midnight sun conditions. The start of simulation (day 0) is always on March 22nd. The transmission coefficient, τ_0, is taken equal to 1, which means that no damping through clouds is assumed. The biological parameters of the copepods and phytoplankton are as given in Tables 2 and 3, respectively.

Temperature is taken equal to 15°C throughout the whole water column.

Time series of depth integrated biomass copepod and phytoplankton are shown in Fig. 9. From day 1 to about day 12, phytoplankton population growth depends mainly on its own dynamics—controlled by light and nutrients.

From about day 12, the copepod population becomes a significant factor, interacting with phytoplankton both in terms of biomass and size composition. Total produced biomass of copepods and phytoplankton during the simulation period (100 days) is 8·2 gC/m² and 52·8 gC/m², respectively.

The vertical structure of phytoplankton, nitrate and ammonia throughout the simulation period is shown in Fig. 10. From day 1 to day 40, the plant production takes place above the pycnocline. When the nutrients are exhausted here, the algal cells partly sink or disappear through grazing from this upper mixed layer. Removal of phytoplankton near the surface makes more light penetrate below the pycnocline and sustains growth in this area. A depth profile of phytoplankton with maximum concentration below the pycnocline will develop. The production will now depend on the supply of nutrients from below and the light that penetrates through the mixed layer.

The copepod population is assumed to consist of adult animals, only, at day 0. These animals (1000 individuals/m²) give rise to the first generation, which develops relatively fast during the spring boom of phytoplankton (Fig. 11). After day 20, the phytoplankton is at a very low level and the copepod population is reduced by predation and starvation. The youngest individuals especially will be reduced in numbers during this period. Plotting the satiation level as a function of weight and developmental level gives information about how different parts of the population are able to obtain food for growth or reproduction (Fig. 12). From day 4 to day 16,

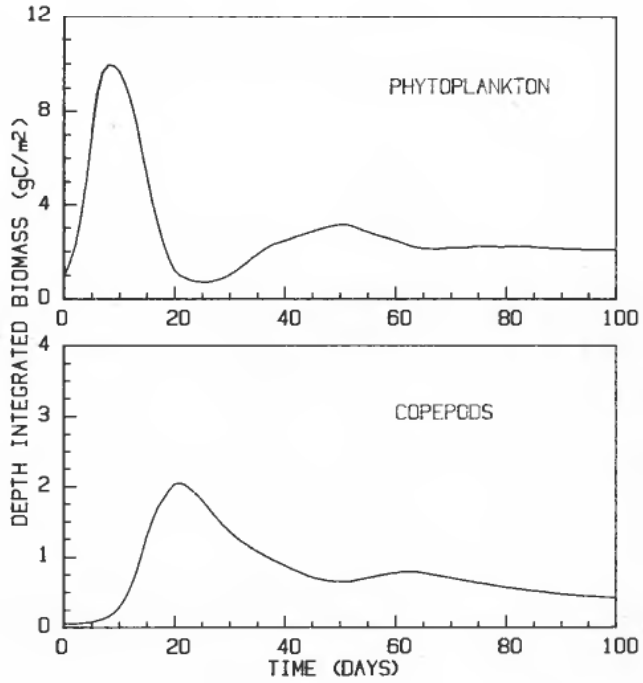

Figure 9. The basic run. Depth integrated biomass (gC/m^2) of phytoplankton and copepods. ($t=0$ equals March 22nd.)

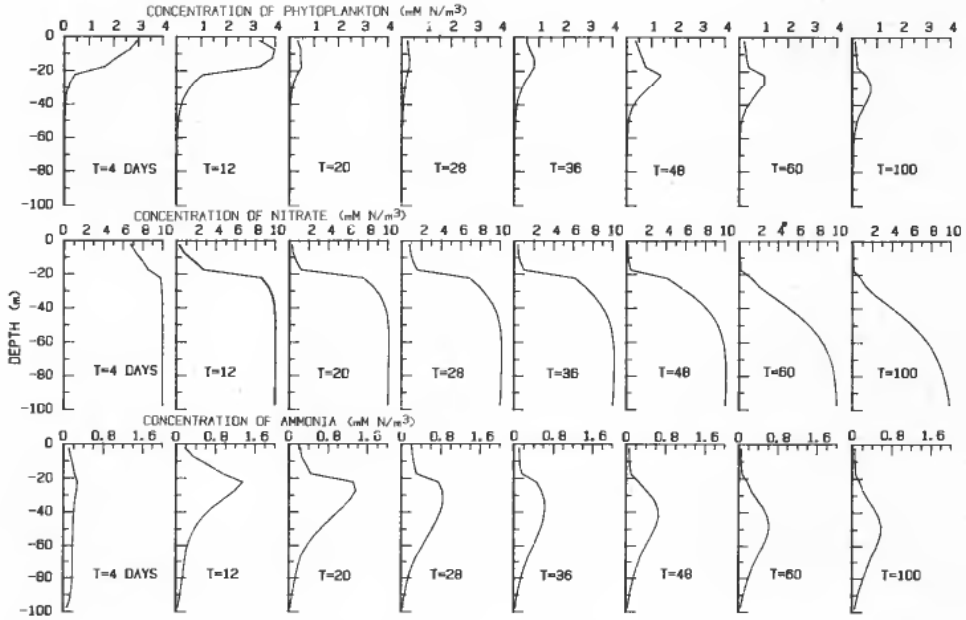

Figure 10. The basic run. Vertical profiles of phytoplankton, nitrate and ammonia throughout the simulation period.

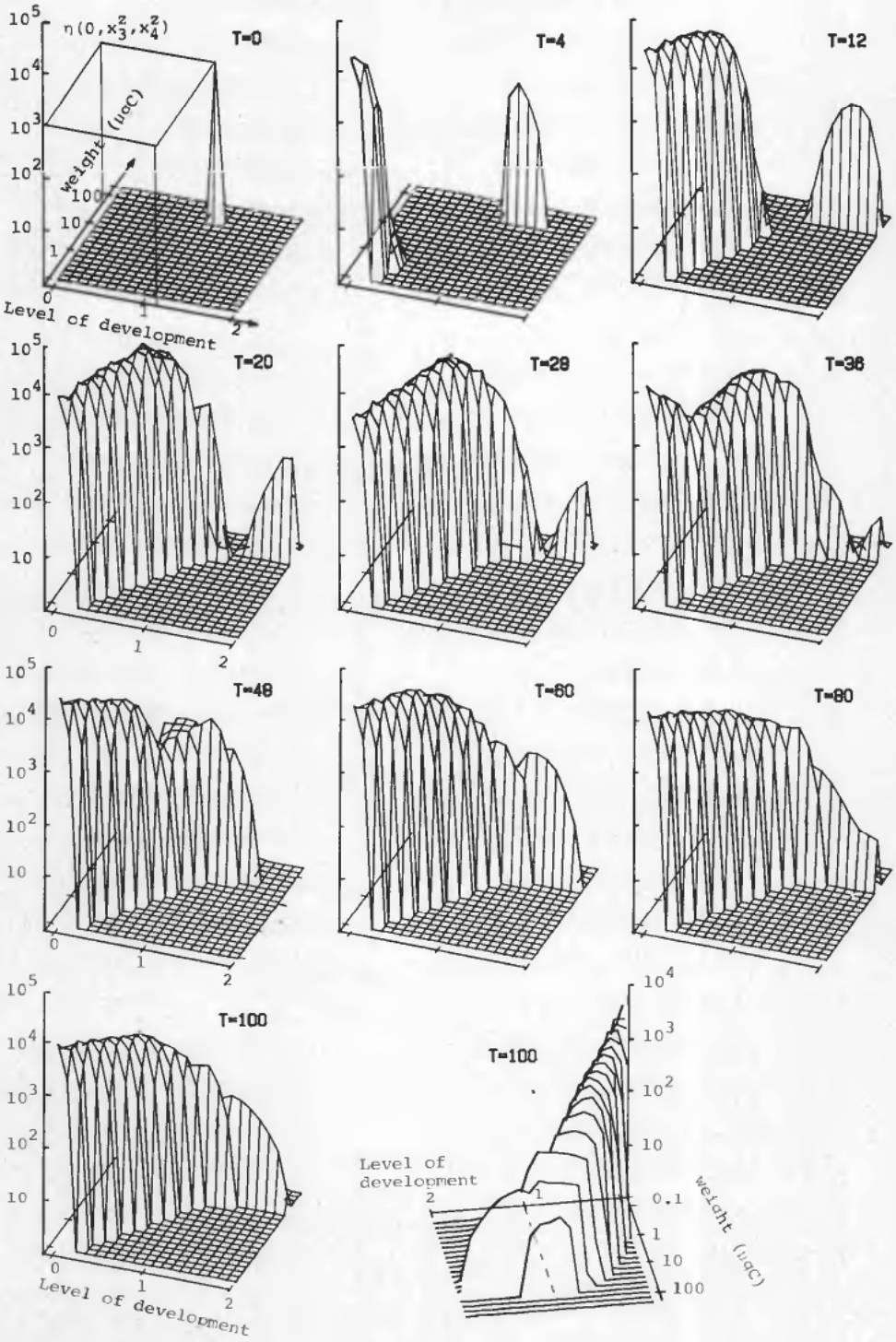

Figure 11. The basic run. Population dynamics of copepods.

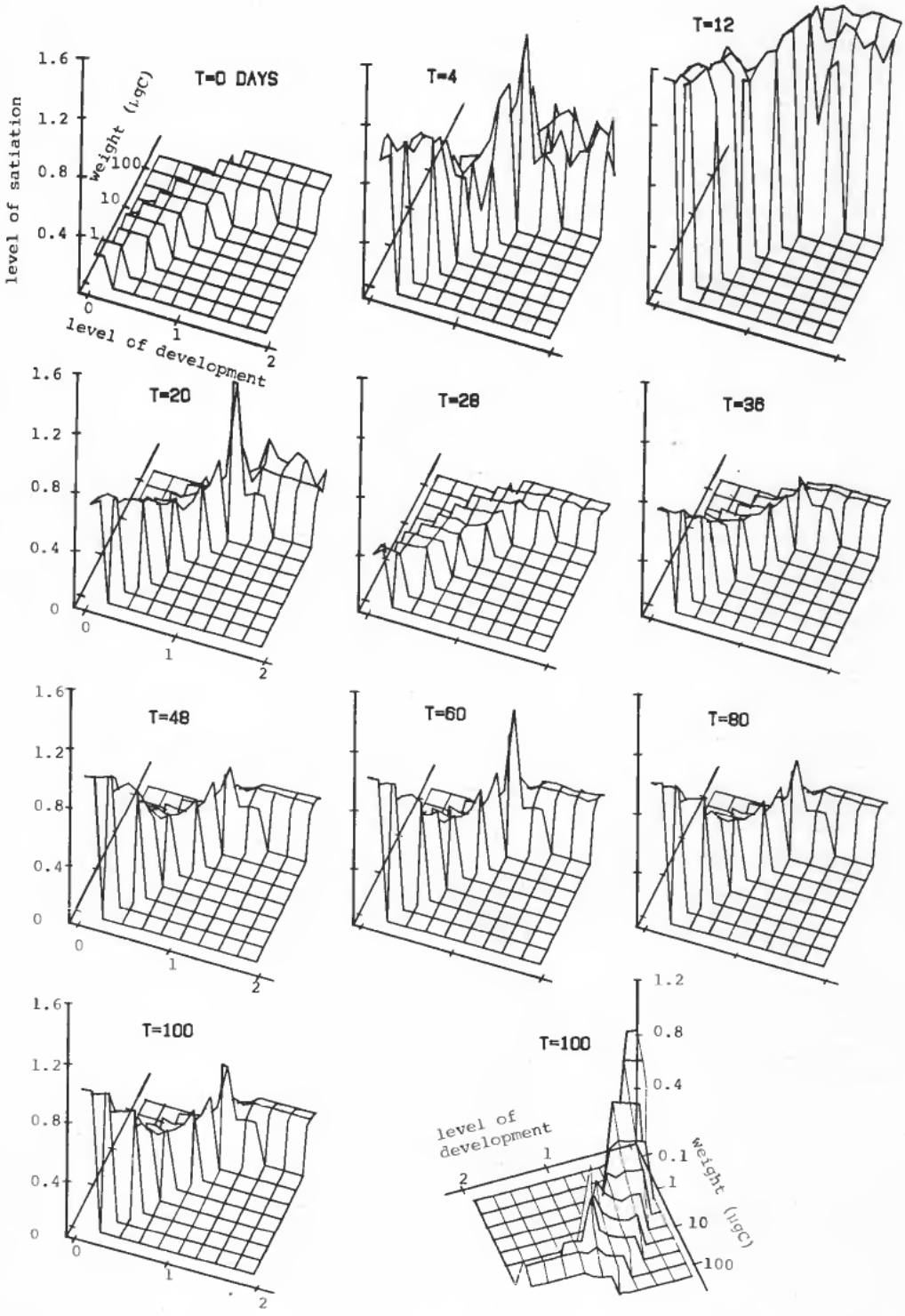

Figure 12. The basic run. Daily average level of satiation as a function of weight and levels of development.

all animals have a relatively high daily average level of satiation. When the phytoplankton is at its minimum, from day 20 to 32, the whole copepod population is starving. The youngest animals will decrease in numbers (Fig. 11). When the phytoplankton population starts growing again, the youngest animals will be able to obtain more food, relative to their energy demands, than the older ones. The main reason is the relatively small size of the algae chosen, which makes the filtering efficiency for the largest animals relatively low.

Another contributory factor is the light reference level, which is higher for animals with a low developmental level than for the others. The youngest animals will thereby stay more together with the phytoplankton than the older ones, with a lower reference level.

The adult animals are able to reproduce from day 32. From about day 40, we reach more stable conditions where the average satiation level is low but still enough to sustain some growth and reproduction. Animals in the model do not start reproducing before they reach a level of development equal to 1·1. After becoming adult (developmental level 1), and until they start reproducing, they do not use much energy for growth. Therefore, these animals will have a relatively high level of satiation, as shown in Fig. 12, from day 48 onwards.

In some cases, the weight distribution can give as much information as the simultaneous weight–developmental distribution. This distribution (Fig. 13) is obtained by integrating the weight–developmental level distribution over all developmental levels and then dividing by the total number of individuals in the population

$$\eta_w(t, x_3) = \frac{1}{x_1} \int_0^{\infty} \eta(t, x_3, x_4)\, dx_4 \tag{54}$$

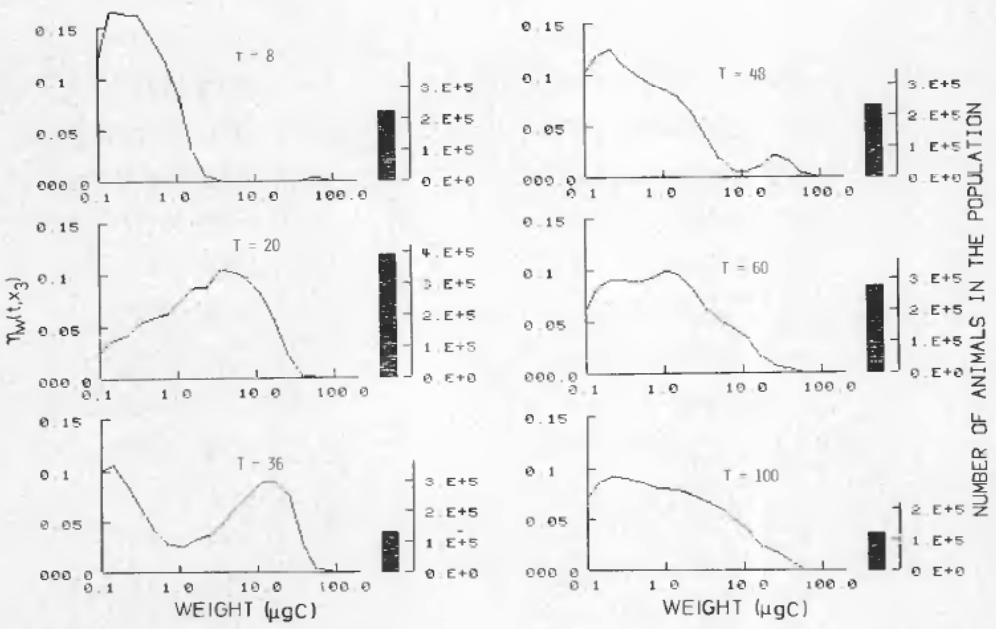

Figure 13. The basic run. Weight distribution as function of time. The columns on the right-hand side of the figures show the total number of animals in the population.

The total number of individuals in the population is shown by the column on the right-hand side of the figure. We can easily distinguish between the first two generations. The second generation starts its growth at about day 32 and can be identified until day 50. Thereafter, the reproduction will be almost continuous and will depend more on the food supply available for the whole adult population than on numbers of adults. The size distribution will then reach an equilibrium.

5.3. *The effect of change in predation*

The function giving predation pressure on the copepods was described in § 2. In this section, we will discuss how its parameters affect production and population structure of the copepods. Decreasing the predation pressure gives an increase in the standing stock of copepods. Since this large population needs a relatively large amount of the available phytoplankton for respiration purposes, we may expect that the production of biomass will be reduced. On the other hand, a high predation pressure will give a low standing stock of copepods. Concentration of phytoplankton will increase, digestion efficiency will decrease and less of the algae produced will turn into copepod biomass. In addition, a low copepod biomass may not be able to utilize all the algal cells and parts of them may sink out of the region accessible to them. As both low and high predation pressure lead to a decrease in the produced biomass, a predation pressure in between these two extremes must give a maximum production (Fig. 14).

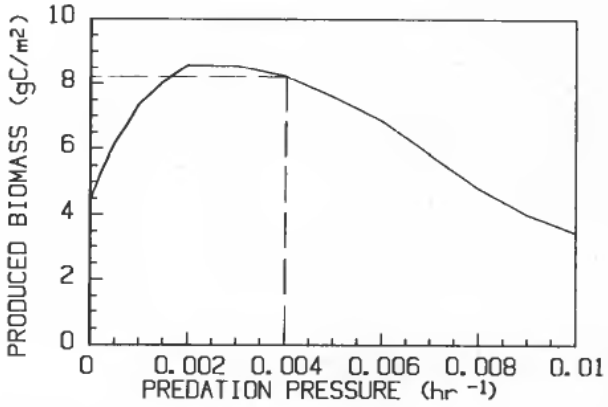

Figure 14. Total biomass of copepods produced during the simulation period (100 days) as a function of the predation pressure.

Changing the predation pressure will not only affect the standing stock of copepods (Fig. 15), but its structure will also be affected (Fig. 16). The weight distribution is not much affected during the first 20 days of simulation. From day 20 onwards, the animals of the high predation case are able to start reproduction and a second generation can start to develop. Since there is always food enough to sustain growth and reproduction, eggs and nauplii are produced continuously and the different generations will soon lose their identity. In the low predation case, the second generation cannot be seen until 20 days later because food shortage does not allow reproduction during this period. Since there are a larger number of adults still alive when

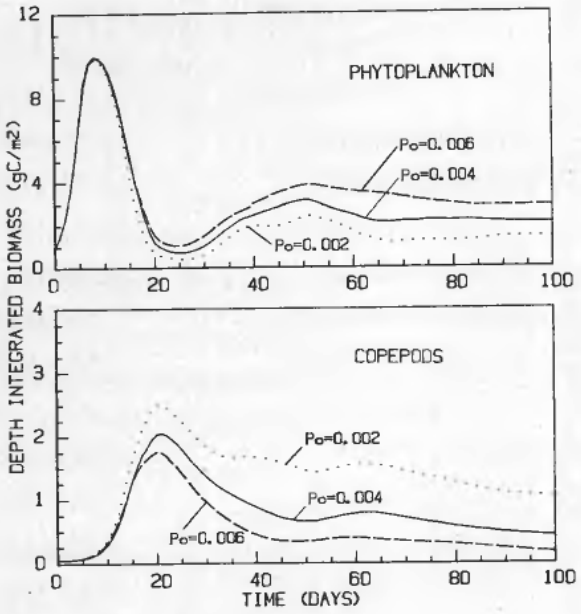

Figure 15. Depth integrated biomass (gC/m^2) of phytoplankton and copepods versus time for various predation pressures.

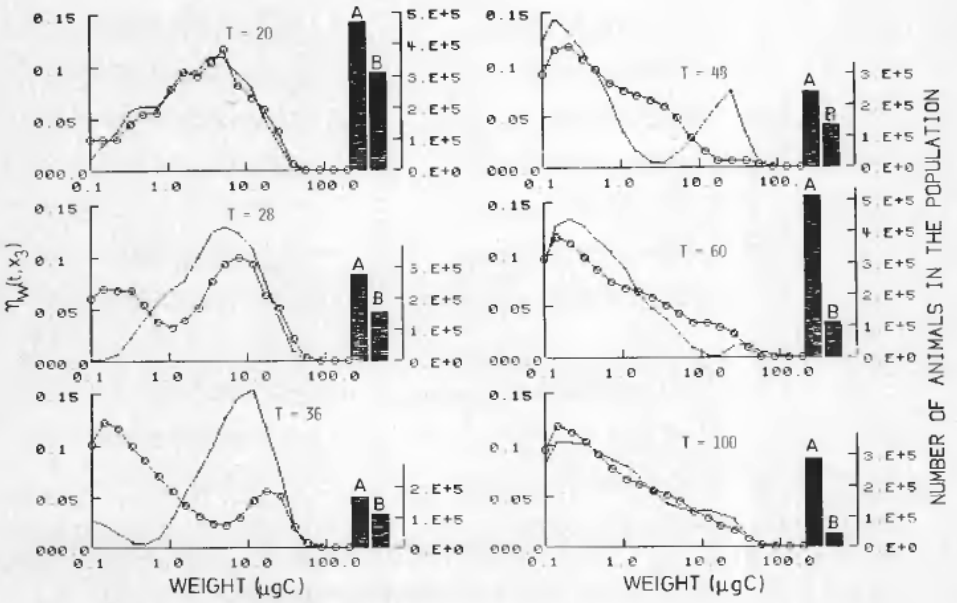

Figure 16. Weight distribution of the copepod population. Effect of different predation pressures. The columns on the right-hand side show the total number of animals in the population. Low pressure, $P_a = 0{\cdot}002\ hr^{-1}$ (———) corresponding to column A and high predation pressure, $P_0 = 0{\cdot}006\ hr^{-1}$ (–o–o–o–) corresponding to column B.

reproduction starts at day 40, a large number of young ones will be produced. But the growth rate of single individuals in the population is very low, which is seen from the static weight structure.

5.4. *The effect of change in vertical turbulence*

It is assumed that vertical turbulent mixing can be modelled by means of an eddy diffusion coefficient K_V. This coefficient can take any value between zero, for highly stratified water, and almost infinity for very turbulent water which turns the water column down to several hundred metres during a few hours. In the absence of necessary physical measurements or calculations from other physical parameters, we choose a depth dependence of K_V. The effect of different choices of this depth dependence on the production of phytoplankton and copepods will be discussed in this section.

(1) *No pycnocline*

Assuming the vertical turbulence to be independent of depth, we may plot the total produced biomass during the simulation period as a function of the turbulent mixing parameter, K_V (Fig. 17). The simulation period chosen is 100 days and the simulation starts (time=0) on March 22nd. We also assume that the mixing is constant throughout the simultion period. The other parameter values (biological and physical), are the same as used in the standard run.

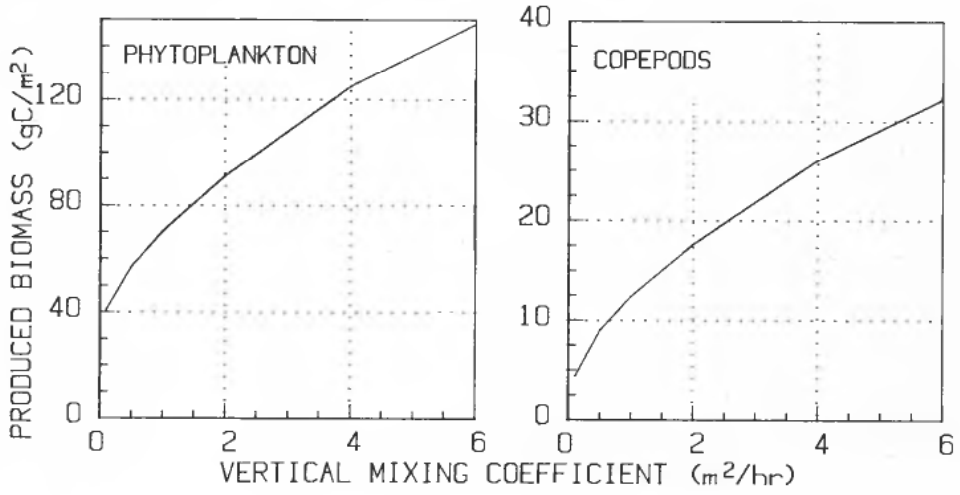

Figure 17. Total produced biomass (gC/m²) of phytoplankton and copepods during the simulation period (100 days) as a function of the vertical mixing parameter.

We observe that the produced biomass is almost proportional to the vertical mixing. This is what we might have expected because the rate of nutrient supply, to the productive upper layer from the nutrient-rich deep water, is proportional to the vertical mixing.

Studies of the vertical distribution of the phytoplankton show that the depth of the chlorophyll maximum layer decreases as the vertical turbulence increases (Fig. 18). This is because high turbulence will disperse the phytoplankton from the surface

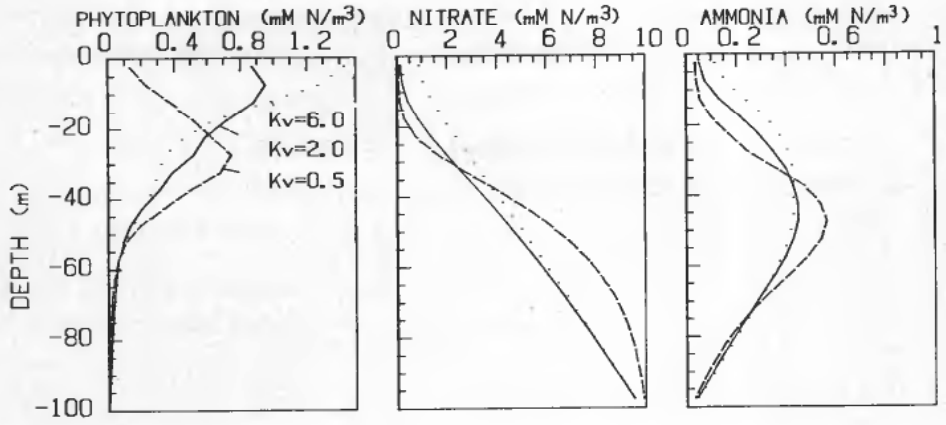

Figure 18. Vertical structure of phytoplankton and nutrients at time 80 days for various values of the vertical mixing parameter.

and downwards. Self-shading of the phytoplankton will lead to an area of maximum production which approaches the surface as the turbulence increases.

(2) *Vertical transport inhibited by a density gradient (pycnocline)*

Very often a density gradient is situated within or below the euphotic zone which inhibits the transport of nutrients from deeper water. We will discuss here the effect of such a gradient on our ecosystem. The magnitude of the gradient will be mimicked by the vertical mixing parameter, K_V. A small value of this parameter means that the gradient is strong. We will always assume that the gradient is fixed throughout the simulation period.

If we place a density gradient at 20 m ($z_T=20$), the produced biomass of phytoplankton and copepods during the simulation period can be plotted as a function of the strength of this gradient (Fig. 19). We observe that the produced biomass increases as the mixing through the pycnocline increases.

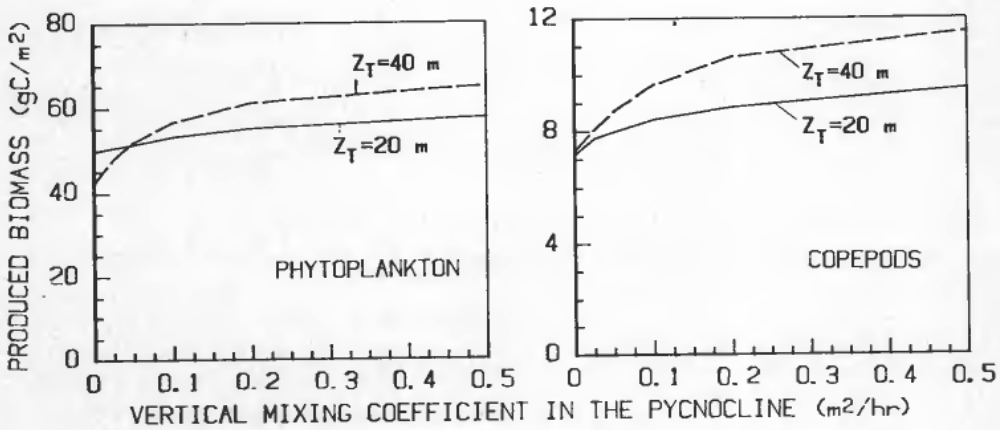

Figure 19. Total produced biomass (gC/m^2) of phytoplankton and copepods as a function of mixing through the pycnocline. Two cases are shown, the pycnocline placed at 20 m ($z_T=20$) and the pycnocline placed at 40 m ($z_T=40$).

The depth integrated biomass of phytoplankton and copepods versus time is plotted in Fig. 20. Three cases of pycnocline mixing are shown: low mixing, $K_{VT}=0{\cdot}025$; intermediate, $K_{VT}=0{\cdot}1$; and no pycnocline, $K_{VT}=0{\cdot}5$. From the figure, we find that a strong pycnocline includes a second bloom of phytoplankton at about day 50, whereas a weak pycnocline tends to give a more stable phytoplankton population after the first bloom. The first bloom occurs above the pycnocline, whereas the second takes place below. A strong pycnocline limits the supply of nutrients to this area and the algae almost disappear due to grazing and sinking. Since the phytoplankton concentration is now very low above the pycnocline, light can penetrate down to the nutrient-rich water beneath and production can start in this area. By increasing the mixing through the pycnocline, nutrients will be transported through the pycnocline after the first bloom and keep some production going. The light conditions below will not be as suitable as for the low mixing case. In addition, parts of the algae produced below the pycnocline will be transported upwards and give self-shading effects on the population below (Fig. 21). Therefore, a weak gradient will tend to damp the second bloom below the pycnocline.

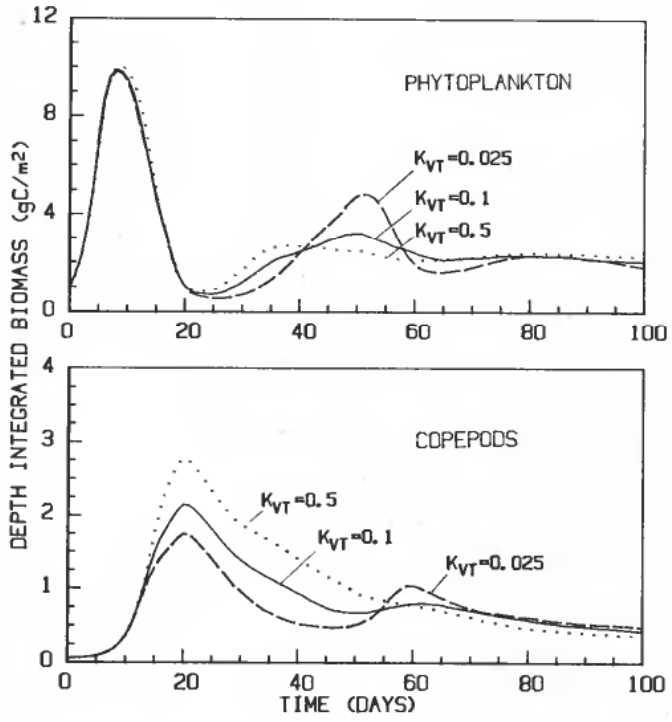

Figure 20. Depth integrated biomass (gC/m^2) of phytoplankton and copepods versus time for three different values of the pycnocline mixing, K_{VT}. The pycnocline is placed at 20 m.

If we place the pycnocline at a depth of 40 m, the total produced biomass of copepods increases about 20% (Fig. 19), during the simulation period, compared with a pycnocline at 20 m. During the first 40 days of simulation, there is no difference in copepod production between high and low pycnocline. After 40 days, however,

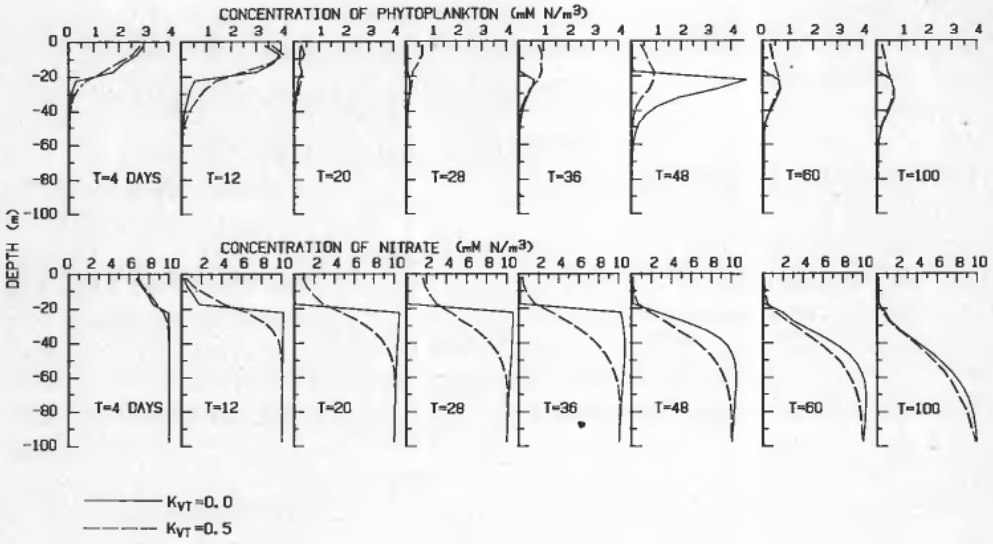

Figure 21. Vertical profiles of phytoplankton and nitrate for two different values of pycnocline mixing. (———) no mixing through the pycnocline ($K_{VT}=0{\cdot}0\ m^2\ hr^{-1}$), (- - - - -) high mixing through the pycnocline ($K_{VT}=0{\cdot}5\ m^2\ hr^{-1}$).

the production is entirely dependent on the transport of nutrients through the pycnocline. Since the pycnocline is placed at a depth to which only a small part of the light can penetrate, significant production cannot take place below this depth.

To sum up this vertical mixing discussion, we may produce some conclusions.

The production of phytoplankton and, thereby, of copepods during the spring phase (first 30–40 days), is controlled by the total available nutrients. In addition to regeneration, there are two sources:

(1) Initial concentration which increases with the depth of the pycnocline.

(2) Transport through the pycnocline.

After this spring phase, a new period, which we may call summer conditions, starts. If the pycnocline is situated near the surface, the production is controlled by the supply of nutrients from deep water. On the other hand, if the pycnocline is placed far from the surface the phytoplankton production has to take place above the pycnocline. Nutrient transport across this gradient will now be the controlling factor.

5.5. *The effect of change in biological parameters*

The effect on produced biomass of copepods by changing parameters in their physiological model is shown in Fig. 22. The parameters were changed by a certain percentage from their nominal value, given in Table 2. All other parameters were as in the basic run.

(A) *Ingestion submodel*

A surprising effect of increasing the maximum filtering capacity of a single individual (FR_0 and β) is a decrease in produced biomass during the simulation

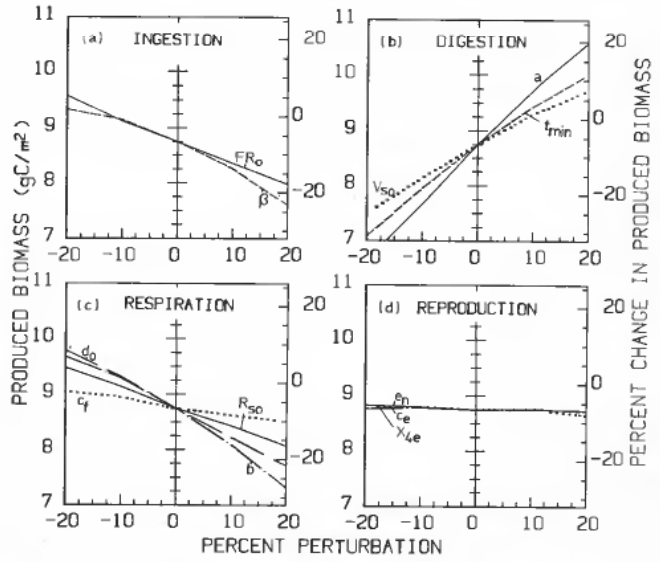

Figure 22. Effect on produced biomass of copepods by change in the parameters of the physiological model. The parameters were perturbated by a certain percentage from their nominal value, one at a time, and kept constant throughout the simulation period.

period (Fig. 22 (*a*)). Since the produced biomass must be equal to zero when FR_0 equals zero, there must exist a FR_0 which gives maximum value of the produced biomass. Plotting the produced biomass of copepods as a function of FR_0 (Fig. 23), we find that the 'optimal' value of FR_0 is about 65% of that used in the basic run. This takes place due to the high filtering capacity of a vertical migrating animal which, since it is more or less starved upon reaching water rich in phytoplankton, will quickly fill up the gut and the percentage of assimilation will decrease. A larger part of ingested phytoplankton will be excreted as faecal pellets and this will be lost from the euphotic zone.

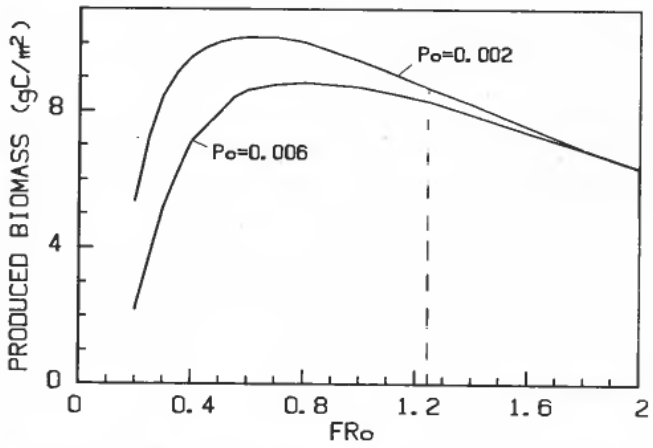

Figure 23. Produced biomass of copepods during the simulation period (100 days) as function of the maximum filtering capacity, FR_0. Two cases are shown. One with low predation pressure, $P_0 = 0{\cdot}002$, and the other one with high predation pressure, $P_0 = 0{\cdot}006$.

Increasing the exponential constant, β, will also increase the filtering capacity of the animals and we observe a similar effect on the produced biomass. The parameters concerning the filtering efficiency (θ_1, θ_2 and θ_3) have only a minor effect on the produced biomass when their numerical values are changed.

(B) *Digestion submodel*

It is the parameters of this submodel which exert the largest changes in produced biomass of copepods when they are perturbed. This submodel is concerned with the utilization of the available phytoplankton—percentage of assimilation. An increase in the utilization will cause increased growth and reproduction by the same amount of phytoplankton. On the other hand, a decrease in utilization will lead to larger production of faecal pellets and, thereby, remove parts of the produced phytoplankton from the system. Increasing the digestion rate, a, gives a rapid increase in produced biomass. The numerical value of this parameter seems to be of great importance (Fig. 22) and has to be specified carefully. There are some indications that the digestion rate is not a constant but rather a function of the ambient food concentration during the last 1–10 days (Mayzaud and Poulet 1978, Tande, pers. comm.).

Increasing $t_{\min}$ (minimum gut passage time) allows a better assimilation of phytoplankton from gut. The utilization of the available phytoplankton increases and the production of copepods increases (Fig. 22 (*b*)).

The velocity of food through the gut was assumed, in § 3.3, to be proportional to the gut filling, x_g. It is, therefore, likely that B^z is sensitive to variations of the parameter giving the volume of gut, α_g. This is also confirmed in this simulation.

Another parameter, which directly affects the assimilation efficiency, is the digestion delay constant, t_{g0}, which depends on the algal species. Increasing this parameter means that the content of the algal cell will be exposed to the digestive enzymes for a shorter time period before leaving the gut, which results in less absorption.

The main reason that B^z is most sensitive to change in the parameters affecting the assimilation efficiency, is the assumption that faeces are removed from the pelagic ecosystem. Lowering of the assimilation percentage will increase the production of faeces for a certain amount of ingested phytoplankton.

(C) *Respiration submodel*

Perturbating the parameters of this submodel causes only a minor change in B^z, except d_0. The reason is that we have assumed protein to be the fuel for the respiration needs. Ammonia will, therefore, be excreted and give an increase in the production of phytoplankton which, again, can be utilized by the copepods.

The energy spent in digestion and biochemically transforming the food was assumed to be 30% of the assimilated energy, § 3.4. This is probably a rather high value and it should be observed (Fig. 22 (*c*)) that perturbating this parameter (d_0) by 20% gives 17% change in B^z.

(D) *Growth and developmental submodels*

The parameters giving the maximum growth and developmental rate for a given temperature (c_g and c_d) cannot be varied independently because this may produce animals of abnormal sizes, which tend to grow outside the grid used for solving the

population equation. However, varying c_g and c_d, such that the ratio between them is constant, gives variation of generation time but no change in the adult size. Increasing the generation time means a slower growth and the production decreases. If the predation rate is high, relatively few animals will reach a reproductive stage and too few nauplii will be reproduced to account for the losses by predation during the longer generation time (Fig. 24).

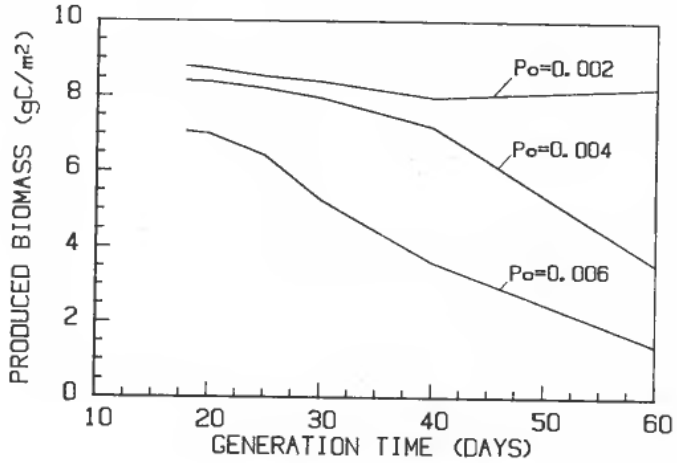

Figure 24. Produced biomass of copepods during the simulation period as a function of the generation time for various predator pressures.

Increasing the potential reproductive rate (parameter e_n) will not be sufficient to compensate for the longer generation time.

Change in the parameter, V_{s0} (giving the size of energy storage associated with the satiation level), does not affect B^z.

(E) *Reproduction submodel*

Perturbating e_n (the maximum rate of egg production) does not affect B^z (Fig. 22 (*d*)) because the number of young ones produced and reared to copepodite stages is mostly a function of food supply. However, during bloom conditions, when food is in excess, the number of eggs and nauplii produced will depend on this parameter (Fig. 25). This may be important for fish larvae, which feed on this size group of copepods.

(F) *Vertical migration model*

The most pronounced effect on B^z is the change in the light reference level, especially for the copepodite stages. The reason is that increasing the light reference level will bring the copepods and the phytoplankton closer together during the day-time. Several factors will now contribute to increase the production. More of the excreted ammonia from the copepods can directly be utilized by the phytoplankton, since it is released near the surface. The supply of food to the copepods will be more even and thereby increase the percentage of assimilation. Another effect of bringing the copepods more together with the phytoplankton is the oscillative behaviour of the plant–herbivore system.

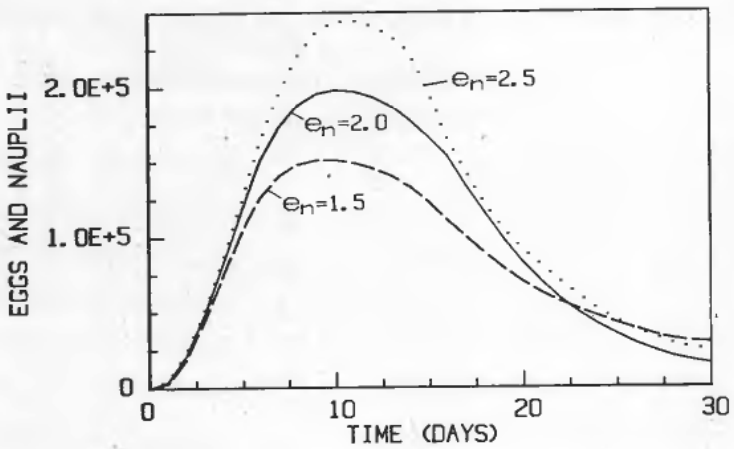

Figure 25. Depth integrated amount (number/m^2) of eggs and nauplii ($0 < x_4 < 0{\cdot}3$) as a function of time for various values of the parameter giving the maximum rate of eggs produced for a well-fed female.

During the vernal bloom, the copepod population increases its biomass much faster and reaches a higher maximum at a high reference level compared with a lower one. The 'high reference' animals are able to do this because their parents were able to produce more nauplii during the first few days of the simulation (Fig. 26). When these animals are given excess of food by the phytoplankton bloom they will increase its biomass faster simply because there are more animals. The large copepod population will keep control of the phytoplankton for a relatively long period. Nutrients can now be supplied into the euphotic zone without being utilized by the phytoplankton. When the copepod populations are reduced by starvation and predation, the phytoplankton can start a new bloom which will last until the nutrients are exhausted again.

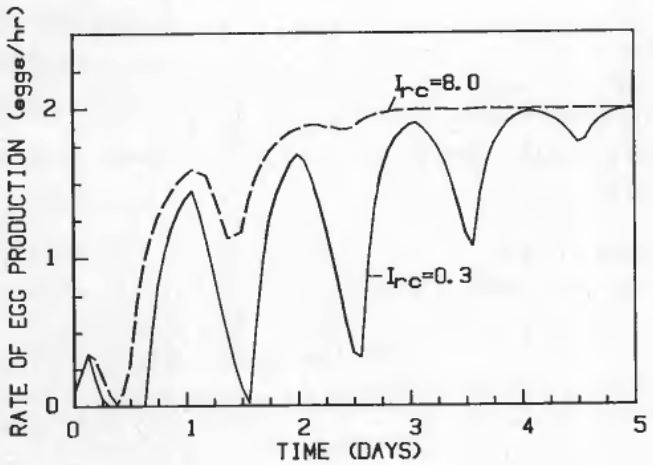

Figure 26. Rate of egg production by a single copepod during the first 5 days of simulation for two different values of the light reference level parameter of the copepodites, I_{rc}.

The results shown here may lead to the conclusion that it is an advantage for the copepods not to migrate but to stay close together with the phytoplankton. However, two important factors are omitted which would certainly have changed the results.

The predation pressure is probably a function of light intensity, especially predation due to fish. If we had included such a relationship in our model, we would probably have obtained less increase or even a decrease in produced biomass, as the reference level is increased.

Another advantage of the copepod's having a low reference level is that migrating animals are transported in a horizontal direction relative to the phytoplankton (Isaacs, Tont and Wick 1974). This transport is possible because the shear currents of the ocean, relative to the surface, increase generally with depth, and organisms which descend deeper will experience more horizontal displacement relative to the surface. In areas with a low standing crop of phytoplankton, daylight penetrates far into the ocean, causing animals to descend deeper. In areas with high standing crop, the migrating animals remain closer to the surface (Fig. 27). Their interactions with the current shear will then, in general, result in their transport out of areas of low standing crop and in their maintenance within areas of high standing crop.

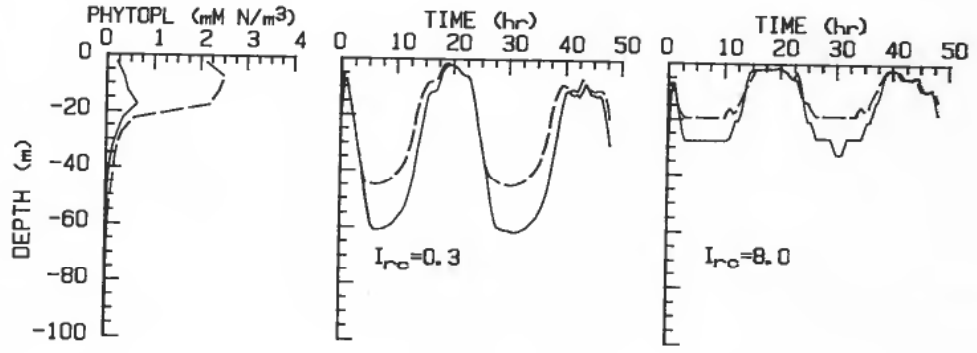

Figure 27. Vertical migration of adult animals in different phytoplankton concentrations. (- - - -) high phytoplankton concentration. (———) low phytoplankton concentration. The simulations are performed at surface light conditions corresponding to days 16 and 17.

Change of other parameters in the migration submodel gives only minor effect on the copepod production. Decreasing the threshold of phytoplankton at which the copepods begin to retard their migration, P_s, had, surprisingly, a negative effect on the copepod production. The reason why this happens is that the copepods can remove the yield of the phytoplankton production by passing through the chlorophyll maximum layer twice a day. If they are not retarded, they move into the upper layer and remove phytoplankton in this area. Removal of phytoplankton near the surface causes more light to penetrate down to the layers, rich in nutrients, where phytoplankton grows. Phytoplankton will grow faster and slightly more food will be available for the copepods.

(G) *Phytoplankton and nutrient models*

The parameters of the phytoplankton and nutrient models are listed in Table 3. Perturbating the parameters gives only a small effect on the produced biomass of copepods. The results are presented in Fig. 28, for those parameters giving more than 5% change in B^z when perturbated by 20%.

After the vernal bloom, most of the primary production takes place at a relatively low light intensity below the pycnocline. If there are sufficient amounts of nutrients, the production depends on the steepness of the photosynthesis–light curve, V_m/I_{max}. It is, therefore, not unexpected that V_m and I_{max} seem to be the most important parameters when calculating primary production.

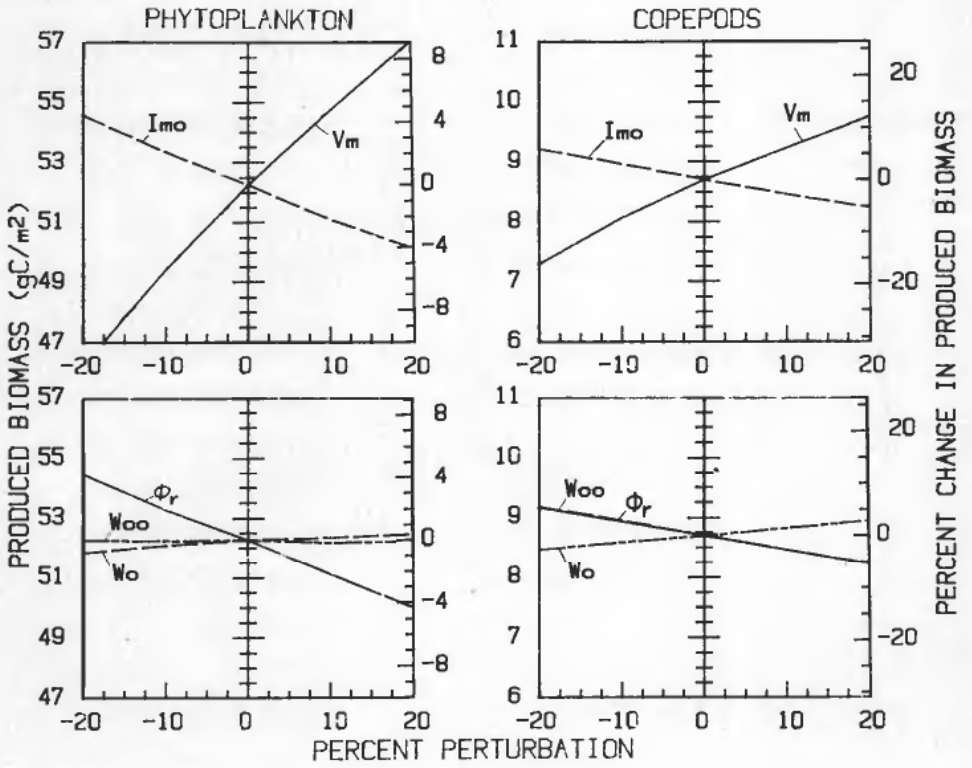

Figure 28. The effect on the produced biomass of phytoplankton and copepods by change in some of the parameters of the chemical and phytoplankton models. The predation pressure was equal 0·002 hr^{-1} (see legend of Fig. 22).

We also observe that sinking velocity affects B^z, whereas production of phytoplankton is practically unchanged. The respiration rate and death of phytoplankton, ϕ_r, has a negative effect on primary production because the detritus formed by this process is assumed to sink relatively fast (0·36 m/hr). Regeneration of nutrients from this detritus will take place, therefore, below the productive zone.

6. Conclusions and critique

Production of copepods is mainly a function of available phytoplankton which again depends on the availability of light and nutrients. After the first vernal bloom the production is solely dependent on nutrient supply from below. The coastal area of Norway and the Barents Sea is not especially known to be one of upwelling areas. However, it has been shown that wind from certain directions may cause upwelling, temporary and spatial, along the Norwegian coast (Ellertsen *et al.* 1981, Saetre 1978). On the basis of the sensitivity analysis performed in § 5, we may conclude that knowing the physical processes, which supply nutrients into the euphotic zone, will probably be more important than details of the biology when assessing herbivore production. Upwelling and vertical mixing are strongly related to the bottom topography and the meteorological processes. It is, therefore, of great importance to know the response to the hydrodynamics from the atmosphere. This calls for a hydrodynamic model which can quantify those physical processes in which we are interested.

The copepod production was found to be relatively sensitive to change in the vertical migration behaviour. It is often argued that vertical migration is a mechanism to avoid visual predation. In the northern areas of Norway, however, there is continuous light during most of the productive season. How the herbivore copepods manage two counteracting stimuli (food and predators) seems to be important for their utilization of the phytoplankton. Should the vertical migration be coupled to the level of satiation?

In the rather complicated physiological model of a single individual, the parameters concerning the utilization of the phytoplankton are very important. The main reason for this is the assumption that the part of the algal cells which is not assimilated is lost from the pelagic system as faeces. The losses of nutrients through respiration is not as serious as losses through faeces because the metabolites of the respiration processes are put back into the system again.

When assessing the significance of these findings, we must be aware that the model cannot draw any conclusions about those mechanisms which are not included in the model. Thus, the effect of size selective feeding has not been really tested because it implies modeling of the size structure of the phytoplankton.

The predation on the copepods is not well represented in the model. The time dependent function used ignores the dynamics of the predators. This is especially important for predators of ctenophore type, which can increase their abundance extremely fast when given proper conditions (large amounts of copepods of proper size). In a very short time these can remove a large population of copepods (Kamshilov 1960). On the other hand, regeneration of nutrients from these animals can contribute to an increased primary production. Thus, a necessary condition for herbivore production is high primary productivity, but the amount of food available for fish depends also on the dynamics of the non-fish predators.

There has been no comparison of the model with real data. The main reason for this is that our parameters are too uncertain and allow too large freedom when fitting the model to the data. It would probably be possible to fit the model to almost any data. Therefore, we have tried to reproduce a text-book like production pattern and discuss the importance of the different parameters and submodels.

Within a population there is always some variance of the physiological parameters from one animal to another. If variation of the parameters gives a non-linear effect on the output of the model, omitting the variance will introduce bias in our

results. However, in § 5.3 we have shown that the produced biomass of copepods depends almost linearly on the biological parameters, at least within $\pm 20\%$ range from the mean. It is, therefore, likely that our results will not be affected if the variance is included during simulation. The environmental parameters such as temperature, predation pressure, nutrient supply and light have certainly a much greater range of variation than the physiological parameters of the population. As the environment is continuously changing, non-linear effects such as influence on the mean and skew distribution around the mean must be expected in our results. In a future model system, this effect should be included by modeling first, second and third-order moments and their interactions. These moments can be found by repeated simulation runs with stochastic perturbation of the parameters.

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