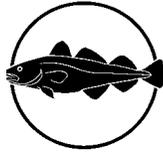


# **The Faroese Fisheries Laboratory**

**Fiskirannsóknarstovan**



## **Zero-Dimensional Model of the Lowest Trophical Levels of the Marine Ecosystem on the Faroe Shelf.**

by

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**Technical Report No.: 04-02**

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the Faroe Shelf**

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# 1 Introduction

The Faroese society is critically dependent upon the living resources of the surrounding ocean areas and knowledge about their variations is a necessary tool for sustainable management. The Faroese Fisheries Laboratory (FFL) has since its foundation collected a large set of data on various components of the ecosystem, from fish to plankton and on the physical and chemical environment. These investigations have given a solid background on the biology of the various species and have shown links between them and between the abiotic and the biotic parts of the ecosystem. The complete ecosystem is, however, so complicated that the various links have to be integrated in a mathematically consistent manner in order to be able to describe the system as a whole. FFL has therefore initiated a program to develop a mathematical model of the Faroese Marine ecosystem.

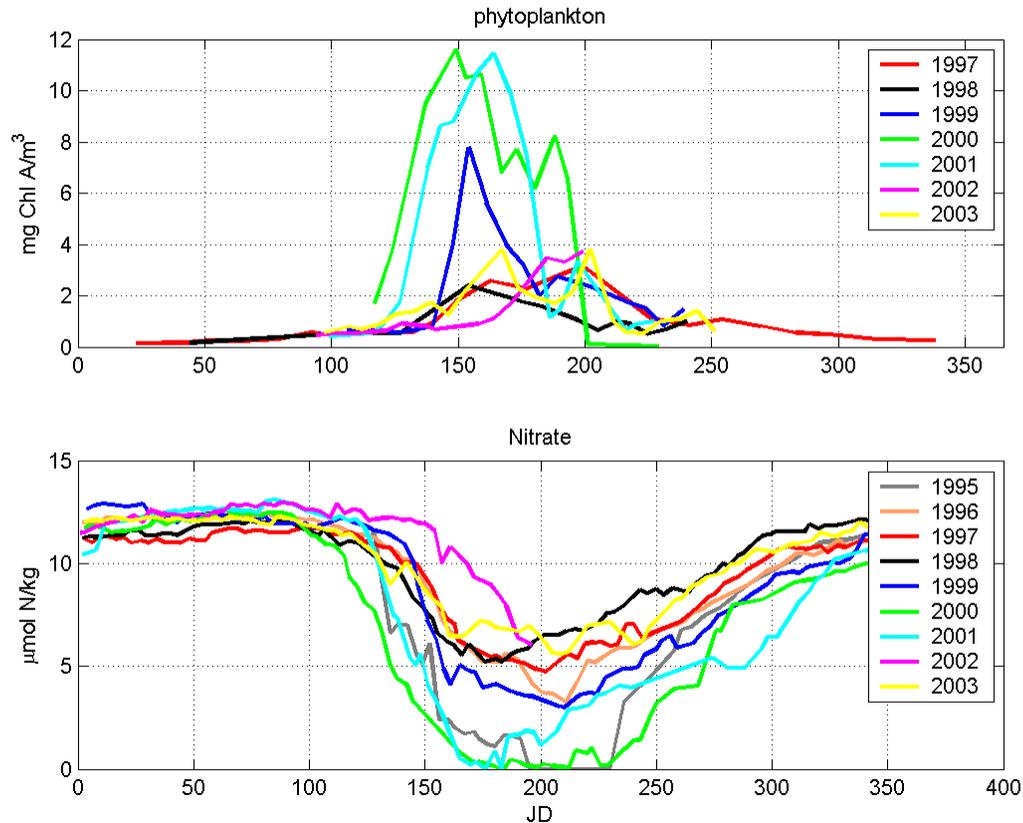
The development of a comprehensive Marine Ecosystem Model for the Faroe Islands (MEMFIS) is a task that will require many years to complete and must be done in parts. It was therefore decided to start by focusing on the lowest trophical levels on the shallow parts of the Faroe Shelf and their dependence on the physical environment. A main reason for that is the indication that the primary production on the shelf varies considerably between years (Figure 2-1) and that these variations are transmitted throughout the ecosystem (Gaard *et al.*, 2002). It furthermore appears that oceanic zooplankton, especially *Calanus finmarchicus*, which are advected onto the shelf in spring, may control the primary production (Gaard *et al.*, 1998).

The possibility to initiate the modeling activity was given by a grant to the FFL from The Faroes Partnership.

Here the Ecosystem Model is reviewed with special focus on phytoplankton growth versus zooplankton grazing.

## 2 Phytoplankton

First we will take a look at the observed growth on the Faroe Shelf. In Figure 2-1 we see the phytoplankton concentration (upper panel) and we see that it is negatively correlated with the nitrate concentration (lower panel).



**Figure 2-1. Observations of phytoplankton (upper panel) and nitrate (lower panel) on the Faroe Shelf.**

In Figure 2-2 we see the observed net increase of phytoplankton. If we ignore influence from horizontal and vertical movements, the observed growth is given as:

$$\frac{1}{P} \frac{dP}{dt} = g_P - r_P - m_P - g_Z$$

**Equation 2-1**

where  $P$  is phytoplankton biomass,  $g_p$  is the nutrient absorption or growth,  $r_p$  is the respiration,  $m_p$  is the mortality and  $g_z$  the grazing by zooplankton given in daily rates.

Rearranging this equation to biomasses we have:

$$\frac{dP}{dt} = G_P - R_P - M_P - G_Z$$

**Equation 2-2**

where  $G_p$  are nutrients absorbed,  $R_p$  is the amount respired,  $M_p$  is the amount which has died and  $G_z$  the amount grazed during one time-step.

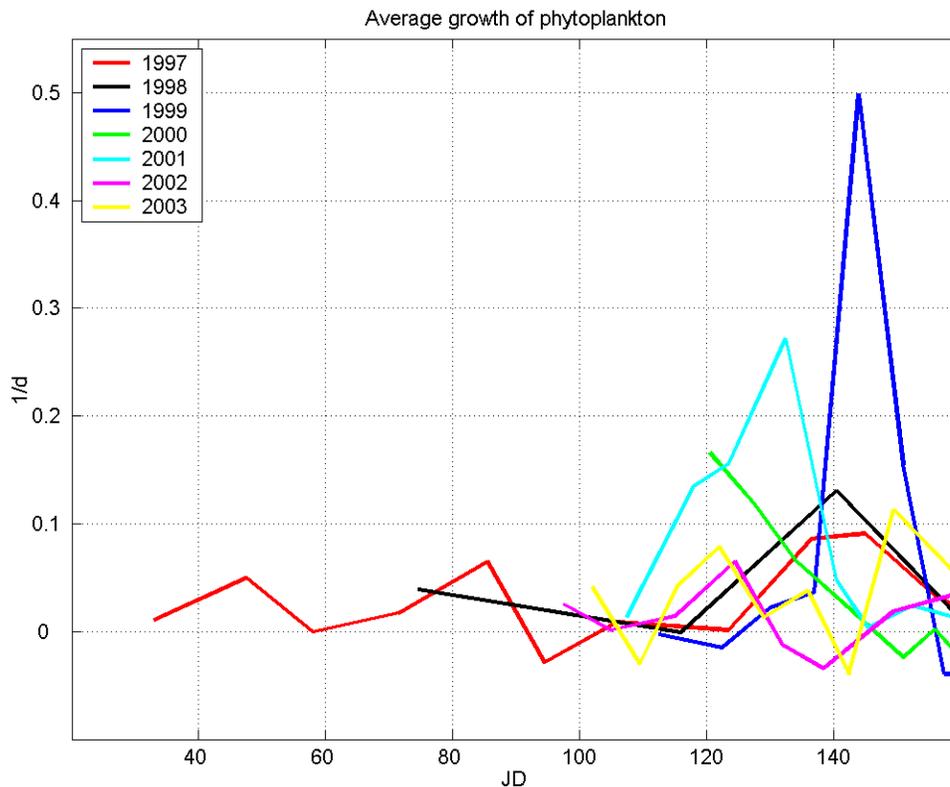


Figure 2-2. Observed average net growth ( $\frac{1}{P} \frac{dP}{dt}$ ) of phytoplankton the first 160 days of the year.

It can be seen that the net growth of the phytoplankton concentration in average is positive during the spring. In the pre-bloom phase it is up to 0.05 while the increase in the bloom period can be as high as 0.3-0.5 pr day. This growth is seen in reality, with grazers present. This means that the growth rate probably is higher than this, and can be still higher in June-July when the irradiance is maximum.

In reality the phytoplankton community is differing during the year. During the winter the phytoplankton biomass is dominated by small flagellates while larger diatoms become more dominant in the spring and usually are dominant in the spring bloom.

## 2.1 Photosynthesis

The model is a 0-dimensional model where all horizontal and vertical variation is ignored. The phytoplankton growth in the model is dependant on nutrient absorption, respiration and mortality. First we will look at the growth  $g_p$ . The factors influencing  $g_p$  are:

1. The irradiance  $I$
2. The attenuation coefficient of the light  $k$
3. The half saturation constant for light absorption  $\kappa_I$
4. The half saturation constant for nutrient uptake  $\kappa_N$
5. The maximum growth rate  $P_{max}$
6. The depth  $d$

The light in the water is used by the phytoplankton for photosynthesis. The photosynthesis depends on the irradiance and nutrients available. In Faroese waters, nitrate usually is the limiting nutrient. The growth rate of phytoplankton can be given as two combined Michaelis-Menten functions (Lalli & Parsons, 1997):

$$g_P = P_{\max} \cdot \min\left(\frac{I}{\kappa_I + I}; \frac{N}{\kappa_N + N}\right)$$

**Equation 2-3**

where  $P_{\max}$  is the maximum photosynthesis,  $I$  is irradiance,  $N$  is nitrate concentration, and  $\kappa_I$  and  $\kappa_N$  are half saturation constants for irradiance and nitrate, respectively. Depending on whether the light or the nutrient concentration is the limiting factor for photosynthesis, the smallest is multiplied with  $P_{\max}$ .

The Faroese Shelf is vertically mixed, and therefore no vertical variation is assumed for the nitrate and phytoplankton concentration, but the irradiance decreases downwards, and therefore it is necessary to compute an average growth rate for the whole water column.

To compute photosynthesis in the water column it is assumed that the irradiance is exponentially dependent on the depth:

$$I(z) = I_0 e^{-kz}, \quad z \leq 0$$

**Equation 2-4**

where  $I_0$  is the surface light and  $k$  the attenuation coefficient.

The average photosynthesis is computed by integrating the photosynthesis in the whole water column, and thereafter dividing by the depth. It is also assumed that it is only the irradiance that depends on  $z$  (perfectly mixed water column). Here the computations are carried out assuming  $z \leq 0$  and  $D < 0$ :

$$\left\langle \frac{I}{\kappa_I + I} \right\rangle = \frac{1}{-D} \int_D^0 \frac{I(z)}{\kappa_I + I(z)} dz = \frac{1}{-D} \int_D^0 \frac{1}{\frac{\kappa_I}{I(z)} + 1} dz = \frac{1}{-D} \int_D^0 \frac{1}{\frac{\kappa_I e^{-kz}}{I_0} + 1} dz$$

Integrating this gives:

$$\begin{aligned} \left\langle \frac{I}{\kappa_I + I} \right\rangle &= \frac{1}{-D} \left[ z - \frac{1}{k} \ln\left(1 + \frac{\kappa_I}{I_0} e^{-kz}\right) \right]_D^0 = \frac{1}{-D} \left[ -\frac{1}{k} \ln\left(1 + \frac{\kappa_I}{I_0}\right) - D + \frac{1}{-k} \ln\left(1 + \frac{\kappa_I}{I_0} e^{-kD}\right) \right] \\ &= 1 + \frac{1}{kD} \ln\left(\frac{I_0 + \kappa_I e^{-kD}}{I_0 + \kappa_I}\right) \end{aligned}$$

**Equation 2-5**

So when the photosynthesis is computed it actually looks like:

$$g_P = P_{\max} \cdot \min\left(1 + \frac{1}{kD} \ln\left(\frac{I_0 + \kappa_I e^{-kD}}{I_0 + \kappa_I}\right); \frac{N}{\kappa_N + N}\right)$$

**Equation 2-6**

and it is an average value for the whole water column.

Before continuing we will discuss what this average photosynthesis implies. If we assume a mixed water column, it means that the phytoplankton is equally distributed in the water column at the beginning of the day. In reality, the photosynthesis is highest in the uppermost part of the water column, while in the lowest part, the respiration and mortality will be higher than the photosynthesis, i.e. a negative growth, because of the irradiance distribution. If the photosynthesis is faster than the mixing, this will cause the phytoplankton to be unequally distributed in the water column, and this means that in the topmost part of the water column, where there is a large number of phytoplankton, there will be growth and in the lowest part of the water column, where the number of phytoplankton is low, there will be loss. This means that in reality the increase in phytoplankton is greater than predicted by the average photosynthesis. The average photosynthesis for the whole water column forces an equally distributed growth through the water column, in extreme cases yielding a lower growth than in the reality. This will probably only be a problem when there is very high growth because the mixing is always very good.

### 2.1.1 The irradiance $I$

We have reliable time series of irradiance observations from 5 years. Data for the years 1996-2000 are derived from satellite observations and downloaded from [www.satel-light.com](http://www.satel-light.com). These have of course a yearly variation, being highest in June-July and lowest in December. For more details see Technical Report 03-01 "Light in Faroese Waters" (Eliassen *et al*, 2003). If we compare the irradiance observed these years with the phytoplankton observations it seems as if variations in light do not affect the timing of the spring bloom, see Figure 2-3. Also the smooth increase in irradiance during the spring is not at all reflected in the sudden phytoplankton spring bloom, indicating that other factors influence the growth more than the light.

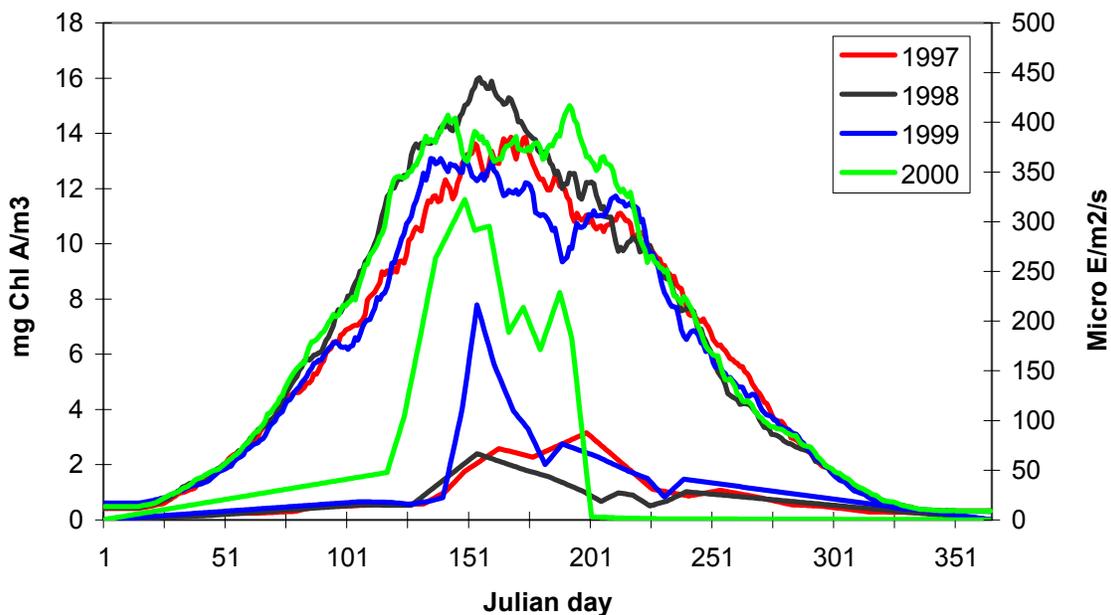


Figure 2-3. Lower curves: Chlorophyll A. Upper curves: 29 days running averages of daily irradiance 1997-2000 ([www.satel-light.com](http://www.satel-light.com)).

We will look closer at the irradiance necessary for the growth to start in section 2.1.3.

### 2.1.2 The attenuation coefficient in water $k$

The attenuation coefficient is known from observations, and is linearly dependent on the phytoplankton concentration (Eliassen *et al.*, 2003). With a phytoplankton concentration of  $0.5 \text{ mgChl A/m}^3$  it is approximately  $0.07\text{m}^{-1}$ , and with this attenuation coefficient, the light is reduced to 1 percent of the original at 65m depth. The equation for the attenuation is given as:

$$k = 0.0644 \frac{1}{m} + \alpha_{ext} \cdot P\left(\frac{\text{mgChlA}}{m^3}\right); \quad \alpha_{ext} = 0.0188 \frac{m^3}{\text{mgChlA} \cdot m}$$

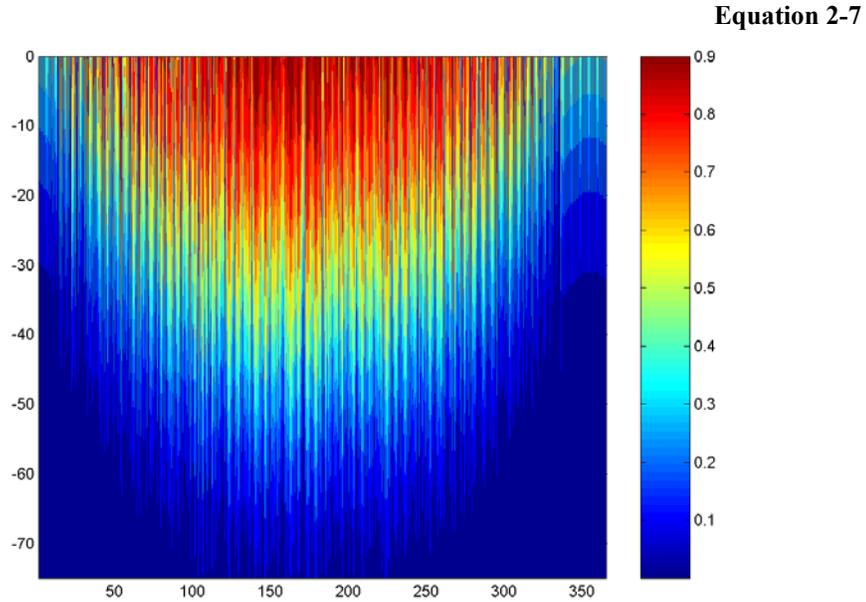


Figure 2-4. Photosynthesis in water column during 1997, Equation 2-8,  $\kappa_I = 60 \mu \text{ E/m}^2/\text{s}$ ,  $k=0.07\text{m}^{-1}$ ,  $P_{max}=1\text{d}^{-1}$ , no nutrient limitation is assumed. In reality  $k$  increases in the bloom period due to high concentrations of phytoplankton in the water, and this implies that the photosynthesis in the bloom period in reality would be lower than shown here. The computations shown here are based on half hourly irradiance values ([www.satel-light.com](http://www.satel-light.com)).

### 2.1.3 The half saturation constant for light absorption $\kappa_I$

The half saturation constant is doubtful. It depends on the temperature, the algal type and photo adaptation, i.e. the algae are better to absorb light in the dark time and therefore it is lower in the winter than in the summer. Since we know little about this variation, it is ignored and a constant value is used. In the literature  $\kappa_I$  varies between  $46\text{-}63 \mu \text{ E/m}^2/\text{s}$  (Sakshaug *et al.* 1992),  $5\text{-}25 \mu \text{ E/m}^2/\text{s}$  (Lalli & Parsons 1997),  $25\text{-}100 \mu \text{ E/m}^2/\text{s}$  (Broström *et al.* 2000). We use  $\kappa_I=40\text{-}60 \mu \text{ E/m}^2/\text{s}$  ( $50 \mu \text{ E/m}^2/\text{s}$  in the computations shown in 2.4 and 3.2).

In Figure 2-4 we have plotted the rate of photosynthesis as a function of depth:

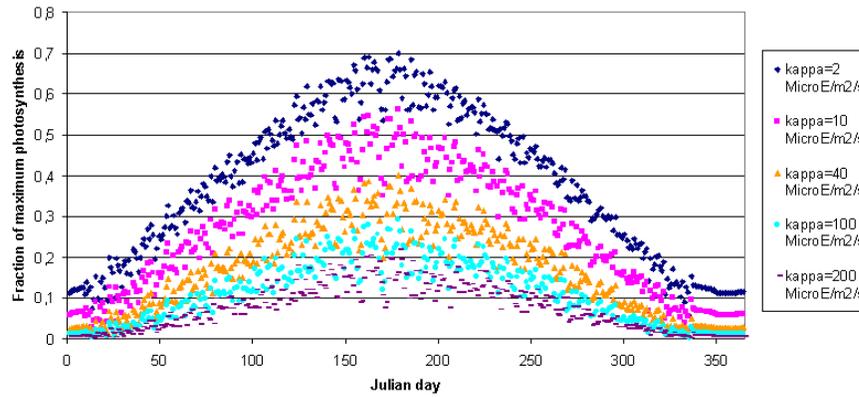
$$g_P(z) = P_{max} \frac{I_0 e^{kz}}{\kappa_I + I_0 e^{kz}}; \quad z \leq 0$$

**Equation 2-8**

It should be mentioned here that the value for  $k$  used in these computations is constant assuming almost no attenuation from algae, which only is correct in the winter time until the bloom starts. In reality  $k$  is higher in the bloom period because of the high algal

concentration, and this implies that the annual variation in growth in the water column is less than shown here.

In the winter photosynthesis is produced to at least 30m depth because of the clear water, but because of the sparse light, it is far from maximum, not even at the surface.



**Figure 2-5. Average photosynthesis in water column during 1997 ([www.satel-light.com](http://www.satel-light.com)) with different  $\kappa_I$ , Equation 2-6,  $P_{max}=1d^{-1}$ ,  $k=0.07m^{-1}$ . No nutrient limitation is assumed, and therefore only the irradiance determines the rate of photosynthesis. The computations shown here are based on average daily irradiance values, and the variation seen is due to varying light intensity from day to day.**

Figure 2-5 shows the average photosynthesis in the water column with different  $\kappa_I$  and no nutrient limitation. It shows that with  $\kappa_I=40 \mu E/m^2/s$ , the average fraction of photosynthesis in the water column is less than 0.05 in January increasing to 0.2 in April. This is probably the same in reality. As in Figure 2-4, the attenuation in the plot is constant, but in the reality it is higher in the bloom period, implying a lower growth than shown here in the bloom period.

Another more detailed way of solving this problem is by assuming that the phytoplankton community changes throughout the year and that the species dominant in the winter are not the same as the species dominant in the spring bloom. This will be considered closer in section 3.3.

#### 2.1.4 The half saturation constant for nutrient uptake $\kappa_N$

The half saturation constant for nutrient uptake is of no importance in the winter-spring time, since nutrients are abundant at this time. In Sakshaug *et al.* (1992) it is  $0.4 \mu molN/kg$  and in Lalli & Parson, (1997)  $2-10 \mu molN/kg$ . We have been using  $1 \mu molN/kg$ , indicating that at these concentrations the algae start to have difficulties absorbing nutrients for photosynthesis. The half saturation constant for nutrient uptake has also been used as a half saturation constant in mortality equations for phytoplankton, since it is assumed that the mortality increases when nutrient absorption starts to be difficult, see section 2.3.

#### 2.1.5 The maximum growth rate $P_{max}$

The maximum growth rate  $P_{max}$  is also a doubtful value. In the literature it varies between  $0.5d^{-1}$  at  $0^\circ C$  (Sakshaug *et al.*, 1992) to  $6d^{-1}$  at  $8^\circ C$  (Lalli & Parsons, 1997).

We see from observations that the net increase in phytoplankton (incl. respiration, mortality and grazing) can be as high as  $0.5d^{-1}$  in the bloom phase (see Figure 2-2) indicating that the

maximum photosynthesis,  $P_{max}$ , can be much higher. Figure 2-2 shows that  $dP/dt$  is positive from February onward. This has been modeled in Figure 2-6, where respiration and mortality are included. If we have a demand that  $dP/dt$  should be positive in winter and that  $dP/dt$  is  $0.5d^{-1}$  in May, it results in a  $P_{max}$  of  $3d^{-1}$ . This gives a very rapid increasing growth rate, resulting in growth already starting in February-March.

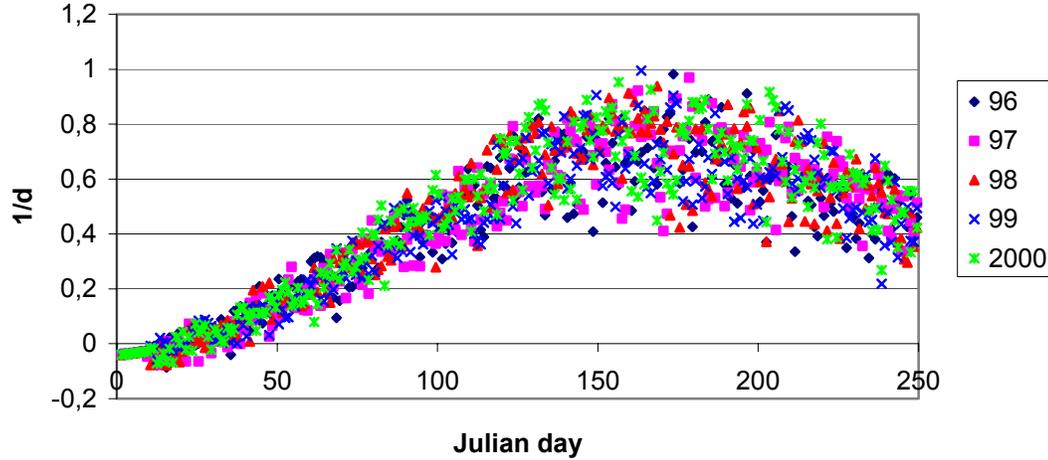


Figure 2-6. Modeled average growth with different irradiances ([www.satel-light.com](http://www.satel-light.com)), i.e.  $g_p - r_p - m_p$ . No grazing, no nutrient depletion and no attenuation due to phytoplankton.  $P_{max}=3d^{-1}$ ,  $r_p=0.05d^{-1}+0.05g_p$ ,  $m_p=0.05d^{-1}$ ,  $\kappa_f=50\mu E/m^2/s$ , depth=75m,  $k=0.07m^{-1}$

Another option is that there are different species, which have different growth rates and half saturation constants, being dominant varying times of the year.

### 2.1.6 Depth $d$

The depth in the model is 75 m, which is the average for the Faroe Shelf. When the depth is increased it delays the spring bloom and reduces its maximum and opposite when it is decreased (see Figure 2-7 and Figure 2-8).

## 2.2 Respiration

The respiration computation is based on the assumption that there is always a basic respiration independent of production, and an additional activity respiration depending on the photosynthesis:

$$R_p = r_p \cdot P + r_{p,A} \cdot G_p \qquad r_p = 0.05 - 0.15 \frac{1}{d} \text{ and } r_{p,A} = 0.05 - 0.15$$

Equation 2-9

The activity respiration is also used in zooplankton modelling, simulating that the algae respire more when they perform photosynthesis.

The respiration coefficient  $r_p$  is typically  $0.05 - 0.15d^{-1}$  (Sakshaug *et al.*, 1992).

## 2.3 Mortality

The mortality rate is dependent on nutrient concentration. With high nutrient concentration there is a relatively low mortality  $d_{min}$ , decreasing to  $d_{max}$  when nutrient concentration decreases.  $\kappa_N$  is a half saturation constant indicating the food limitation when the phytoplankton has difficulties in surviving. It is the same as for nutrient uptake (Sakshaug *et al.*, 1992):

$$M_P = \left( d_{min} + (d_{max} - d_{min}) \cdot \exp\left(-\frac{N}{\kappa_N}\right) \right) P$$

$$d_{min} = 0.05d^{-1}, \quad d_{max} = 0.5d^{-1}, \quad \kappa_N = 1 \frac{\mu\text{molN}}{\text{kg}}.$$

Equation 2-10

In the pre-bloom phase, there is no nutrient limitation, and therefore, the mortality is  $d_{min}$  in this phase.

## 2.4 Conclusion on phytoplankton

The model is run with the above assumptions. Note that all equations used in the computations below are found in section 5. Figure 2-7 and Figure 2-8 show the result. We see that the phytoplankton bloom can start already in the end of February - end of March, and has a maximum in April-May, when nutrient depletion limits the bloom.

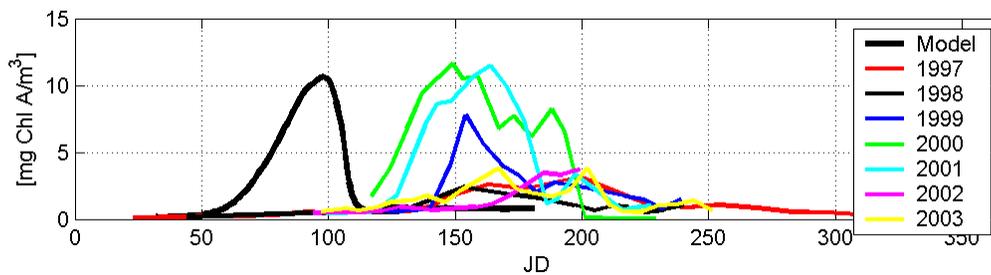


Figure 2-7. Phytoplankton modeled with  $d=75\text{m}$ . No grazing, average irradiance 1996-2000 ([www.satel-light.com](http://www.satel-light.com)), respiration:  $r_p=0.05d^{-1}$ ,  $r_{p,A}=0.05$ ,  $d_{min}=0.05d^{-1}$ ,  $d_{max}=0.5d^{-1}$ ,  $\kappa_I=50\mu\text{E}/\text{m}^2/\text{s}$ ,  $\kappa_N=1\mu\text{molN}/\text{kg}$ ,  $P_{max}=3d^{-1}$ ,

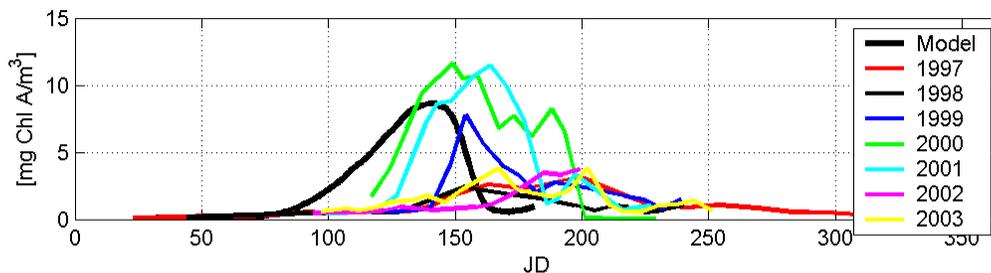


Figure 2-8. Phytoplankton modeled with  $d=150\text{m}$ . All other parameters as in Figure 2-7.

We observe that the bloom does not start before May, even though there is sufficient light in the water for the growth to start in February-April.

It is not clear what postpones the phytoplankton bloom. Probably the phytoplankton community is heterogeneous, as mentioned in section 2. Also there are grazers and at last there are physical properties, which influence the primary production on the Shelf.

### 3 Zooplankton

With no zooplankton present, there is sufficient light for the bloom to start in February-March depending on average depth (see Figure 2-7 and Figure 2-8), while in the reality it starts late April or later. We have added zooplankton in the model in order to see whether zooplankton grazing is able to postpone the spring bloom. We add two different groups: *C.finmarchicus*, which is advected into the system during the spring in one group and benthos and other neritic species in the second group. The latter will in the text be referred to as benthos because the knowledge about other neritic species is limited. The differential equation for zooplankton is given as (Fiksen & Carlotti, 1998):

$$\begin{aligned} C.\textit{finmarchicus}: \quad & \frac{dZ}{dt} = a_z \cdot G_Z - R_Z - M_Z \\ \text{Benthos:} \quad & \frac{dB}{dt} = a_B \cdot G_B - R_B - M_B \end{aligned}$$

**Equation 3-1**

where  $G$  is the grazing,  $R$  is the respiration and  $M$  is the mortality including predation.  $a_Z$  and  $a_B$  are assimilation efficiencies. Grazing will be considered closer in section 3.1.

The respiration is given as (Fiksen & Carlotti, 1998):

$$\begin{aligned} C.\textit{finmarchicus}: \quad & R_Z = r_z \cdot Z + r_{z,A} \cdot a_z \cdot G_Z & r_z &= 0.1d^{-1} \\ & & r_{z,A} &= 0.05 \\ & & a_z &= 0.8d^{-1} \\ \\ \text{Benthos:} \quad & R_B = r_B \cdot B + r_{B,A} \cdot a_B \cdot G_B & r_B &= 0.01d^{-1} \\ & & r_{B,A} &= 0.005 \\ & & a_B &= 0.8d^{-1} \end{aligned}$$

**Equation 3-2**

where  $r_Z$  is a basic respiration, and the second term,  $r_{Z,A}$ , is an additional activity respiration, proportional to the amount grazed.

The mortality, including predation, is given as (Fiksen & Carlotti, 1998):

$$\begin{aligned} C.\textit{finmarchicus}: \quad & M_Z = m_z \cdot Z; & m_z &= 0.05d^{-1} \\ \text{Benthos:} \quad & M_B = m_B \cdot B; & m_B &= 0.001d^{-1} \end{aligned}$$

**Equation 3-3**

The advection of *C.finmarchicus* is modelled as an increase in the *C.finmarchicus* concentration during April and May with 0.2-0.5 mgC/m<sup>3</sup>/d, which corresponds to 1.4-3.5 adult C6/m<sup>3</sup>/d.

### 3.1 Zooplankton grazing

In this section we look at the grazing on phytoplankton. Figure 3-1 shows that the abundance of zooplankton is positively correlated with nitrate. When the biomass of zooplankton is large, the use of nitrate is low. In Figure 2-1 we see that years with small nitrate loss have low abundance of phytoplankton and large nitrate loss coincides with large phytoplankton biomass. So there is a clear correlation connecting the phytoplankton bloom with the abundance of zooplankton, especially *C.finmarchicus*, indicating that it could be this population that controls the phytoplankton in the pre-bloom period.

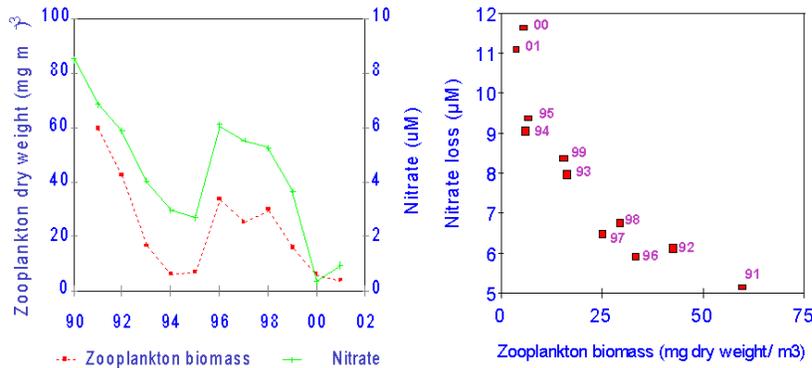


Figure 3-1. Zooplankton and nitrate on the Faroe Shelf. From Gaard (2003).

Let's take a look at what is necessary in order for the *C.finmarchicus* population to suppress the phytoplankton bloom until May.

If we assume a net growth rate (assimilation – mortality) of phytoplankton of 0.05 d<sup>-1</sup> in beginning of April (see Figure 2-2 and Figure 2-5) and a concentration of 0.5 mg chlA/m<sup>3</sup> (see Figure 2-1, upper panel), this implies that the new production of phytoplankton is 0.025 mg chlA/m<sup>3</sup>/d. In order to keep the phytoplankton concentration on a constant level, this is what is to be grazed per day.

By looking at the filtering capacity of *C.finmarchicus*, it can be seen that the task of keeping phytoplankton at a constant low level during April is difficult. Under optimal conditions an adult C6 female can filter 0.5 l/d (Richardson *et al.* 1999), but probably this is lower in April, because with pre-bloom phytoplankton concentrations, zooplankton will not filter effectively. Anyway, if we assume these high filtering capacities during April a *C.finmarchicus* population of:

$$\text{No. C6} = \frac{\text{Amount grazed}}{\text{filtering capacity} \cdot P} = \frac{0.025 \frac{\text{mgChlA}}{\text{m}^3 \text{d}}}{0.5 \cdot 10^{-3} \frac{\text{m}^3}{\text{d}} \cdot 0.5 \frac{\text{mgChlA}}{\text{m}^3}} = 100 \frac{\text{C6}}{\text{m}^3} \sim 14 \frac{\text{mgC}}{\text{m}^3}$$

should be able to suppress the growth. This is an extremely high pre bloom concentration of *C.finmarchicus*. Keeping in mind that this also is a high estimate of what is being filtered by *C.finmarchicus* in April, it is not probable that *C.finmarchicus* alone is able to keep the phytoplankton concentration at a constant low level in the pre-bloom period. Also the net growth rate of phytoplankton is not constant during this period but varies due to the varying

light, and if there is much light one day the production will be much higher, implying a higher production the following days.

Therefore there must also be other factors controlling the bloom in the pre-bloom phase. This could be physical factors such as horizontal and depth variations or other biological factors, not included in the model.

Biological factors are neritic zooplankton species and benthos, which are present on the shelf all year. These could, together with the *C.finmarchicus* population, keep the phytoplankton at a constant low level until May, and this is tried with the so-called benthos component in the model.

When we look at the benthos population on the Faroe Shelf, we see that the benthos biomass is larger than the *C.finmarchicus* biomass. For instance taking the bivalve horse mussel, a rough estimate says that there are 5 horse mussels/m<sup>2</sup> on 400 km<sup>2</sup> having a soft weight of 3 g each (Steingrund and Gaard, personal communication). The Faroe shelf with depths less than 100 m constitutes app. 5.400 km<sup>2</sup>. This gives an approximate biomass of horse mussels of:

$$\frac{5 \frac{\text{bivalves}}{\text{m}^2} \cdot 3 \frac{\text{g}}{\text{bivalve}} \cdot 0.4 \frac{\text{gC}}{\text{g}} \cdot 400 \cdot 10^6 \text{m}^2}{5400 \cdot 10^6 \text{m}^2 \cdot 75 \text{m}} = 6 \frac{\text{mgC}}{\text{m}^3}$$

This corresponds to a *C.finmarchicus* biomass of 43 C6/m<sup>3</sup>. The filtering capacity is higher pr animal, but lower pr weight, since larger animals have a lower metabolism. Also at the bottom the phytoplankton concentrations are probably lower since there always is a bottom boundary layer even though the water column is mixed. So the grazing will be limited in this period. From table 10 in Barker Jørgensen (1990) we can see that horse mussel (*Modiolus modiolus*) with a weight of 3g, which is average on the Faroese Shelf, has an optimal filtering capacity of 342l/d. Pr body weight this corresponds to

$$\frac{\text{Filtering capacity}}{\text{weight in carbon}} = \frac{342 \cdot 10^{-3} \frac{\text{m}^3}{\text{d}}}{3000 \text{mg} \cdot 0.4 \frac{\text{gC}}{\text{g}}} = 0.0003 \frac{\text{m}^3}{\text{mgC} \cdot \text{d}}$$

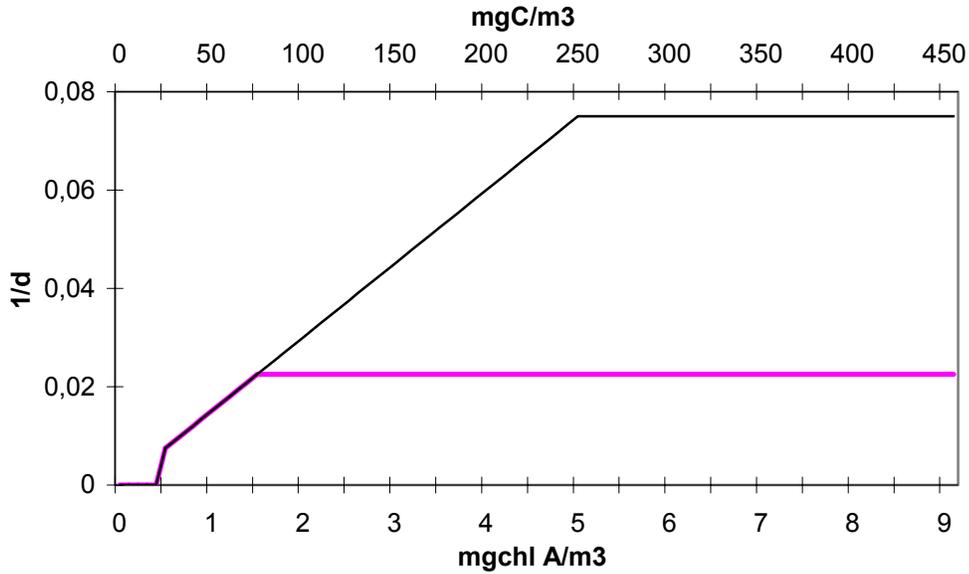
#### Equation 3-4

which is the amount filtered by 1mgC horse mussel pr day, and if we assume the amount of horse mussel as above and a phytoplankton concentration as 1.april, they can maximally graze:

$$\frac{\text{Filtering capacity}}{\text{weight in carbon}} \cdot Z \cdot P = \frac{342 \cdot 10^{-3} \frac{\text{m}^3}{\text{d}}}{3000 \text{mg} \cdot 0.4 \frac{\text{gC}}{\text{g}}} \cdot 6 \frac{\text{mgC}}{\text{m}^3} \cdot 0.5 \frac{\text{mgChLA}}{\text{m}^3} = 0.000855 \frac{\text{mgChLA}}{\text{m}^3 \cdot \text{d}}$$

#### Equation 3-5

which is a high estimate of the amount grazed pr day of the horse mussel population. Remembering that in addition to this we have other benthos species the amount grazed by benthos is probably higher, but still it is much less than the amount grazed by *C.finmarchicus*.



**Figure 3-2. Benthos grazing as a function of the amount of phytoplankton available. ChlA:C=1/50. The black line is the grazing separated in intervals described by H.U.Riisgaard, and the pink line is the grazing when the interval with maximum filtering is decreased to 0.5 – 1.5mgChlA/m<sup>3</sup>.**

The grazing is computed from the filtering capacity of the zooplankton. We consider the grazing as being proportional with the filtering capacity of the animal until it reaches a certain level. Thereafter it is constant and we get a grazing function given as in Figure 3-2. Mussels exploit their filtering capacity while the phytoplankton concentration is in the interval 0.5 - 5 mg ChlA/m<sup>3</sup> and with concentrations above 5 mg ChlA/m<sup>3</sup> they filter with a reduced rate getting a fixed amount of phytoplankton out of the water (Riisgård, 2001), see Figure 3-2, black line. The same is assumed for *C.finmarchicus*. The grazing for benthos is computed as:

$$G_B = \begin{cases} 0 & \text{if } 0 \frac{\text{mgChlA}}{\text{m}^3} \leq P < 0.5 \frac{\text{mgChlA}}{\text{m}^3} \\ g_B \cdot B \cdot P & \text{if } 0.5 \frac{\text{mgChlA}}{\text{m}^3} \leq P < 5 \frac{\text{mgChlA}}{\text{m}^3} \\ 5 \frac{\text{mgChlA}}{\text{m}^3} \cdot \text{Chl} : C \cdot g_B \cdot B & \text{if } 5 \frac{\text{mgChlA}}{\text{m}^3} \leq P \end{cases}$$

$$g_B = 0.0001 - 0.0003 \frac{\text{m}^3}{\text{mgC} \cdot \text{d}}$$

$B$  is the benthos biomass

#### Equation 3-6

The last case in the benthos grazing equation depends on the *chlA:C* ratio. If the *chlA:C* ratio is 1:35, the benthos grazing is maximally 5.25% d<sup>-1</sup> and if the *chlA:C* ratio is 1:50, the benthos grazing is maximally 7.5% d<sup>-1</sup>.  $g_B$  is the filtering capacity deduced in Equation 3-4. In the modelling this seems to be a high value for benthos, because we know from observations that the bodyweight of benthos does not vary much during year, and with this value the benthos can multiply its start weight by 3 or 4 during the bloom period (it is perhaps realistic for small neritic zooplankton species, which filter very effectively).

Therefore it is also plausible to use a lower value, depending on the ratio between neritic species and benthos.

The *C.finmarchicus* grazing is computed with the same limits as for benthos, but with a maximum filtration rate of 0.5l/d/C6 (Richardson *et al.* 1999) assuming an average weight for a C6 of 140µgC/ind (Heath *et al.*, 2000), the animals can filter with optimal conditions:

$$g_z = \frac{0.5 \cdot 10^{-3} \frac{m^3}{d}}{0.140 \frac{mgC}{ind}} = 0.0036 \frac{m^3}{mgC \cdot d}$$

**Equation 3-7**

And the grazing function is given as:

$$G_z = \begin{cases} 0 & \text{if } 0 \frac{mgChLA}{m^3} \leq P < 0.5 \frac{mgChLA}{m^3} \\ g_z \cdot Z \cdot P & \text{if } 0.5 \frac{mgChLA}{m^3} \leq P < 5 \frac{mgChLA}{m^3} \\ 5 \frac{mgChLA}{m^3} \cdot Chl : C \cdot g_z \cdot Z & \text{if } 5 \frac{mgChLA}{m^3} \leq P \end{cases}$$

where Z is the *C.finmarchicus* biomass

**Equation 3-8**

If the *chlA:C* ratio is 1:35, the *C.finmarchicus* grazing is maximally 0.63 d<sup>-1</sup> and if the *chlA:C* ratio is 1:50, the *C.finmarchicus* grazing is maximally 0.9 d<sup>-1</sup>. Here it is assumed that the phytoplankton has a *chlA:C* ratio of 1:35.

There are also neritic zooplankton species. This group constitutes a much smaller biomass than *C.finmarchicus*, because the *C.finmarchicus* population is greater in weight. But these species have a high metabolism, so they could be a significant contributor in keeping phytoplankton at a constant low level. At the moment there is no estimate of this grazing beside the considerations above.

### 3.2 Model run with and without zooplankton

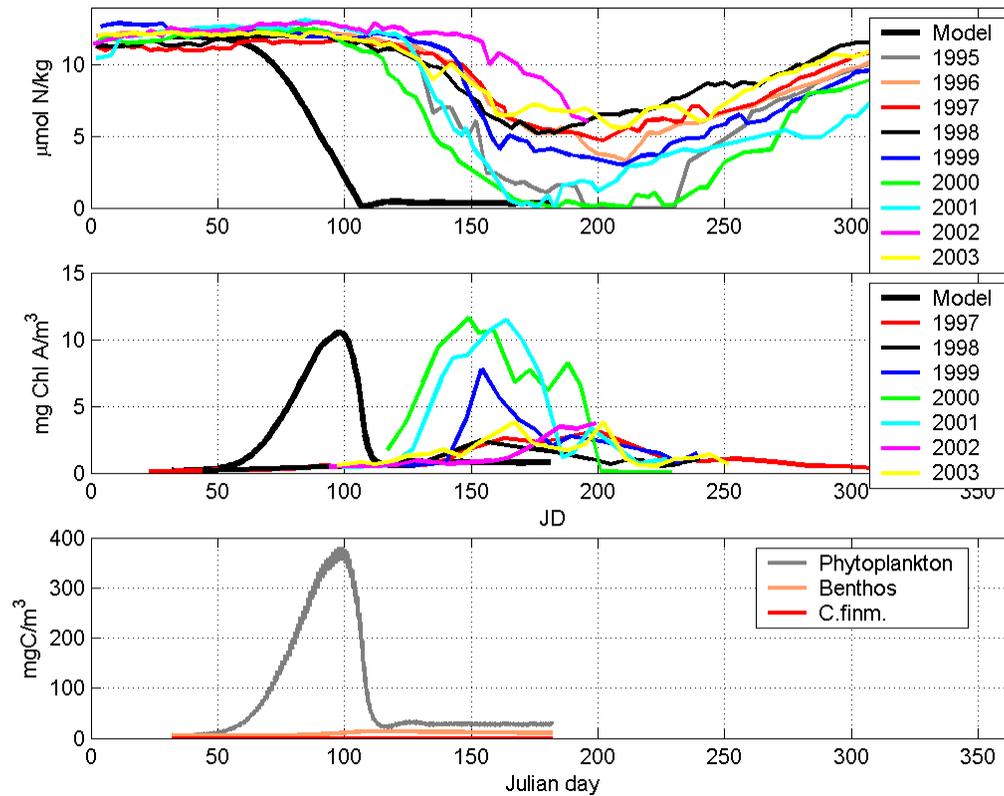


Figure 3-3. Model run with  $d=75\text{m}$ , grazing from horse mussel ( $Z_0=6\text{mgC/m}^3$ ), no *C.finmarchicus* import, average irradiance 1996-2000 ([www.satell-light.com](http://www.satell-light.com)),  $g_B=0.0003 \text{ m}^3/\text{mgC/d}$ ,  $r_P=0.05 \text{ d}^{-1}$ ,  $r_{P,A}=0.05$ , from 1.Feb to 1.July.

In Figure 3-3 we see a model run with only horse mussel present in the ecosystem. We can see that in the end of February the phytoplankton start to bloom, and that the phytoplankton concentration in this period is too low for the zooplankton population to survive at a constant level and therefore the zooplankton biomass is decreasing in this period. It is not until the phytoplankton concentration reaches  $2 \text{ mg Chl A/m}^3$ , that there is sufficient phytoplankton for the zooplankton biomass can start to grow and graze down on phytoplankton. The phytoplankton reaches a maximum in the start of April.

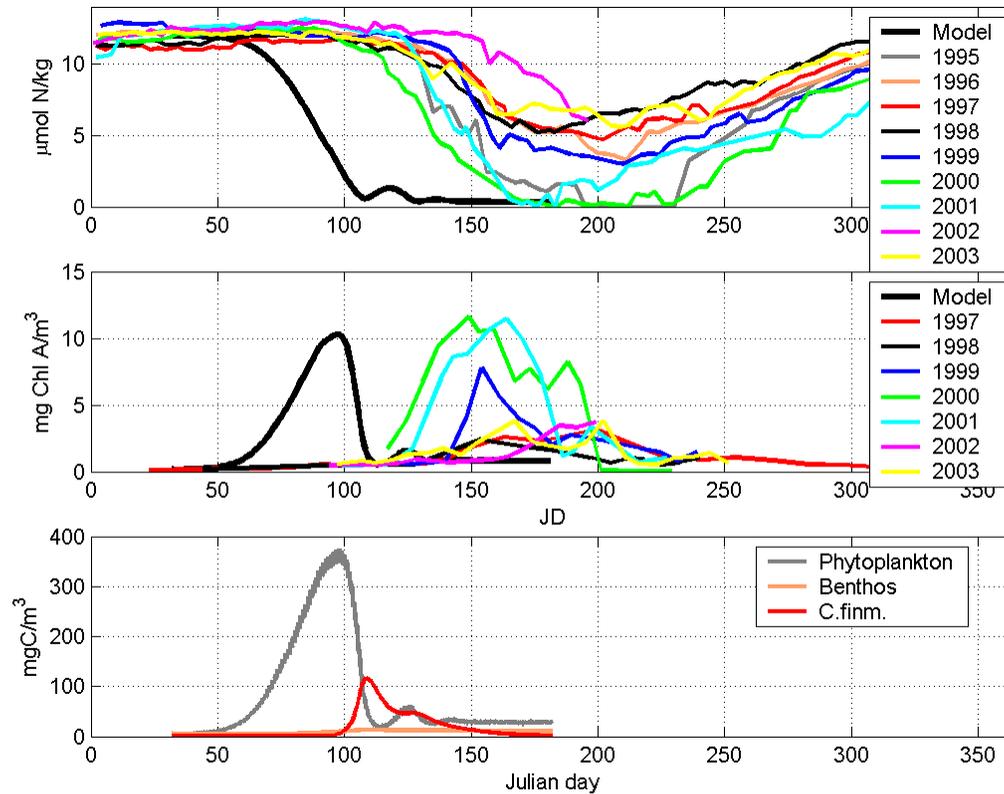
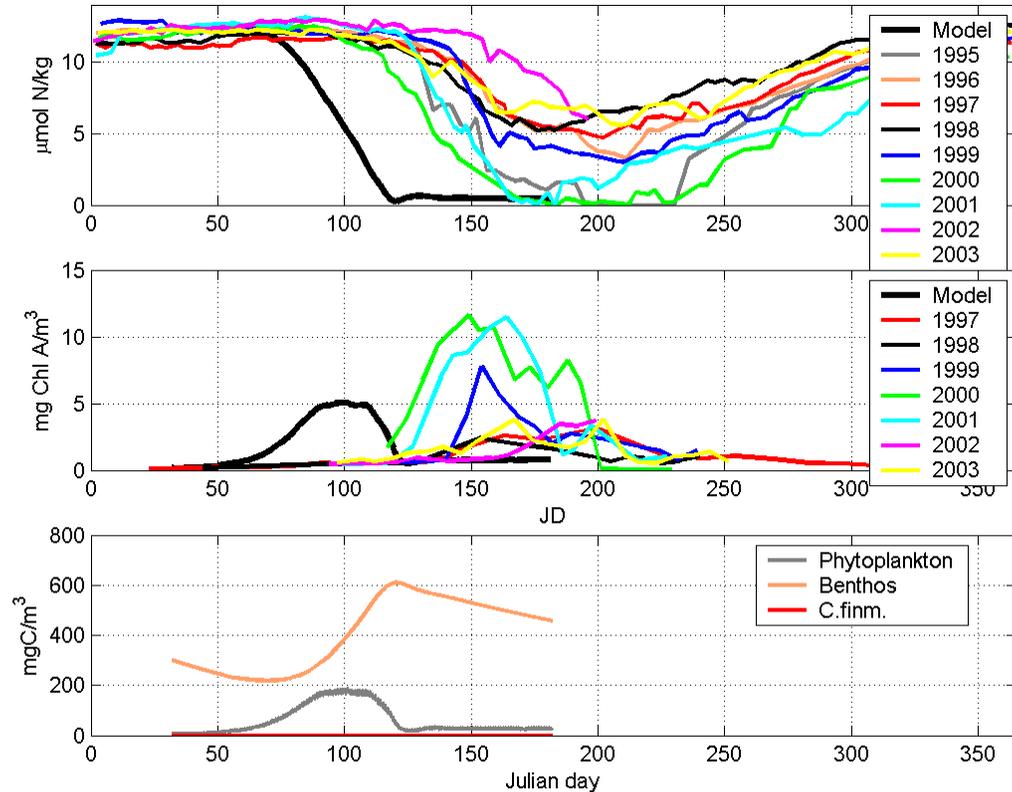


Figure 3-4. Model run with  $d=75\text{m}$ , average irradiance 1996-2000 ([www.satel-ligth.com](http://www.satel-ligth.com)),  $g_B=0.0003 \text{ m}^3/\text{mgC/d}$ ,  $r_P=0.05 \text{ d}^{-1}$ ,  $r_{P,A}=0.05$ , grazing from horsemussel ( $Z_0=6\text{mgC/m}^3$ ) and a *C. finmarchicus* import from 1.April to 1.June of  $0.2 \text{ mgC/m}^3/\text{d}$ . The model runs from 1.Feb to 1.July.

In Figure 3-4 we have both horsemussel and a *C. finmarchicus* import, and we can see that the zooplankton is able to graze down on the phytoplankton bloom earlier than in Figure 3-3. The maximum of the bloom appears earlier, but there is not a significant difference. In the model the phytoplankton bloom is over in April, (cf. Figure 3-3) and therefore the *C. finmarchicus* import starting in April does almost no difference.

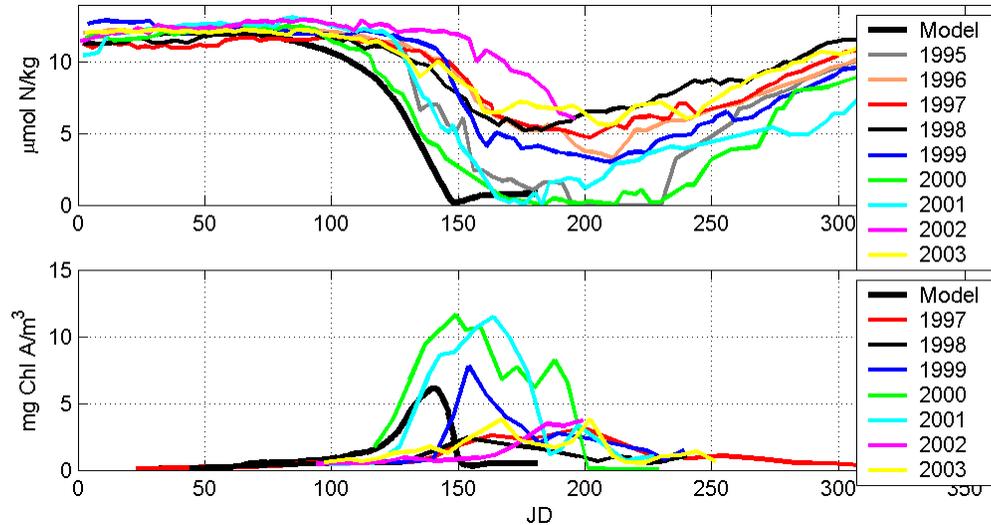
In Figure 3-5 we have assumed that the benthos population is 50 times greater than the horsemussel population, and have run the model with this input. We see that it is not until the phytoplankton concentration is  $1.5\text{-}2 \text{ mg Chl A/m}^3$  that the zooplankton biomass is able to increase.



**Figure 3-5. Model run with a start benthos population of 300 mgC/m<sup>3</sup>, no *C.finmarchicus* import. d=75m, average irradiance 1996-2000 ([www.satell-light.com](http://www.satell-light.com)).  $g_B=0.0003 \text{ m}^3/\text{mgC}/\text{d}$ ,  $r_P=0.05 \text{ d}^{-1}$ ,  $r_{P,A}=0.05$ . The model runs from 1.Feb to 1.July.**

So the conclusion is that when zooplankton is added in the model, the main change is that the maximum of the phytoplankton bloom is lower, while the start of the bloom still is too early, because it is not until the phytoplankton is reaching concentrations above 1.5 mg ChlA/m<sup>3</sup> that the zooplankton population is increasing to abundances being able to graze the phytoplankton down again. If we add sufficiently much benthos in the system to delay the bloom we will not get any bloom, because it is then totally suppressed. Therefore the modelled benthos can't suppress the phytoplankton concentration until May.

With the filtering function showed in Figure 3-2, black line, it is not possible to postpone the spring bloom. In order to postpone the bloom we have to further increase the benthos biomass and demand that when the phytoplankton concentration is below 0.5 mg ChlA/m<sup>3</sup> the animals stop filtering and with a phytoplankton concentration between 0.5-1.5 mg ChlA/m<sup>3</sup>, the animals filter with a constant rate. When the phytoplankton concentration exceeds 1.5 mg ChlA/m<sup>3</sup> the animals can relax and filter with a lower rate, and still get a certain amount of food out of the water, in this case an amount which is 1.5% of their weight pr day (the pink line in Figure 3-2). The result of the modeling is shown in Figure 3-6 and even though this is not a correct assumption we here get a result that reminds of the observations more than before.



**Figure 3-6. Model run with Benthos grazing as in Figure 3-2 (pink curve),  $Z_0=500 \text{ mgC/m}^3$ . No *C.finmarchicus* import,  $P_{\max}=2 \text{ d}^{-1}$ ,  $g_B=0.0003 \text{ m}^3/\text{mgC/d}$ ,  $r_B=0.001 \text{ d}^{-1}$ ,  $r_{B,A}=0.005$  average irradiance 1996-2000 ([www.satel-light.com](http://www.satel-light.com)). The model runs from 1.Feb to 1.July.**

The model developed is a 0-dimensional model with no horizontal or vertical variations and no interaction with the surrounding environment. But if we assume that there is sufficient light for the growth to start in march, and the reason for why there is no bloom is that the zooplankton grazing pressure keeps the phytoplankton concentration on a constant low level, we will see that the nitrate concentration in the model decreases during the spring while there is no bloom, because there is a production, which is being consumed right away. This is not correct according to the reality where the nitrate concentration is at a constant high level until the bloom is observed. This is probably due to exchange of shelf water with off-shelf water which always has a high concentration of nitrate. This has been included in the model by adding the difference between the off-shelf concentration and the shelf concentration of nitrate divided with the flushing rate to the nitrate differential equation, see equation:

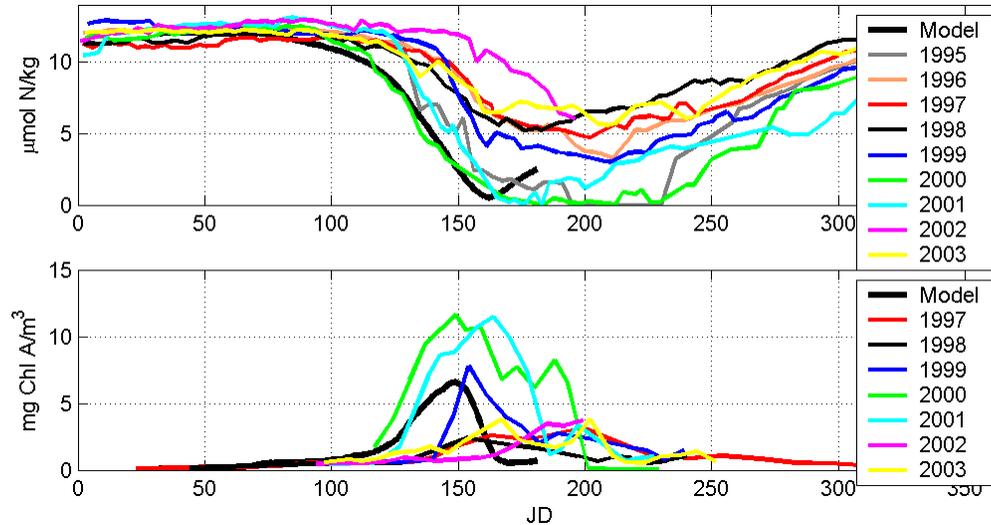
$$\frac{dN}{dt} = -G_P + D_{Decomp} + R_P + R_Z + R_B + \frac{\text{offshelf nitrate concentration} - \text{onshelf nitrate concentration}}{75\text{days}}$$

**Equation 3-9**

where the off-shelf nitrate concentration always is  $12 \text{ } \mu\text{molN/kg}$ .

This way the problem with the nitrate concentration decreasing too early is solved and the result is shown in Figure 3-7, but still the grazing is unrealistic not allowing the animals to filter maximally in the interval  $0.5 - 5 \text{ mgChlA/m}^3$ , but in a much narrower interval.

The additional term in Equation 3-9 is also added to the phytoplankton and detritus differential equations, which all are assumed to have an off shelf concentration of zero.



**Figure 3-7. Model run with same conditions as in Figure 3-6, except that the nitrate exchange between off shelf water is included. Average irradiance 1996-2000 ([www.satel-light.com](http://www.satel-light.com)), benthos grazing as in Figure 3-2 (pink curve),  $Z_0=500 \text{ mgC/m}^3$ ,  $g_B=0.0003 \text{ m}^3/\text{mgC/d}$ ,  $r_B=0.001 \text{ d}^{-1}$ ,  $r_{B,A}=0.005$ . No *C.finmarchicus* import,  $P_{\max}=2\text{d}^{-1}$ . The model runs from 1.Feb to 1.July.**

### 3.3 Model run with two distinct phytoplankton groups

The fact that the phytoplankton community varies during the year has led to another model approach. A model where phytoplankton is separated into two groups has been tried and the results will be shown here.

The hypothesis is, that the chlorophyll observed during the winter time, originates from small flagellates with a low light half saturation constant which makes it possible to survive during winter, but also with a low growth rate, which keeps it at a constant low level during winter. Then there are the diatoms, which in the nature usually are almost absent in the winter, but dominate in the spring bloom. They have a larger light half saturation constant, but also a higher growth rate. Also the diatoms have a higher ChlA content, with the *ChlA:C* ratio being 1:35 whereas the flagellates have a *ChlA:C* ratio of 1:50.

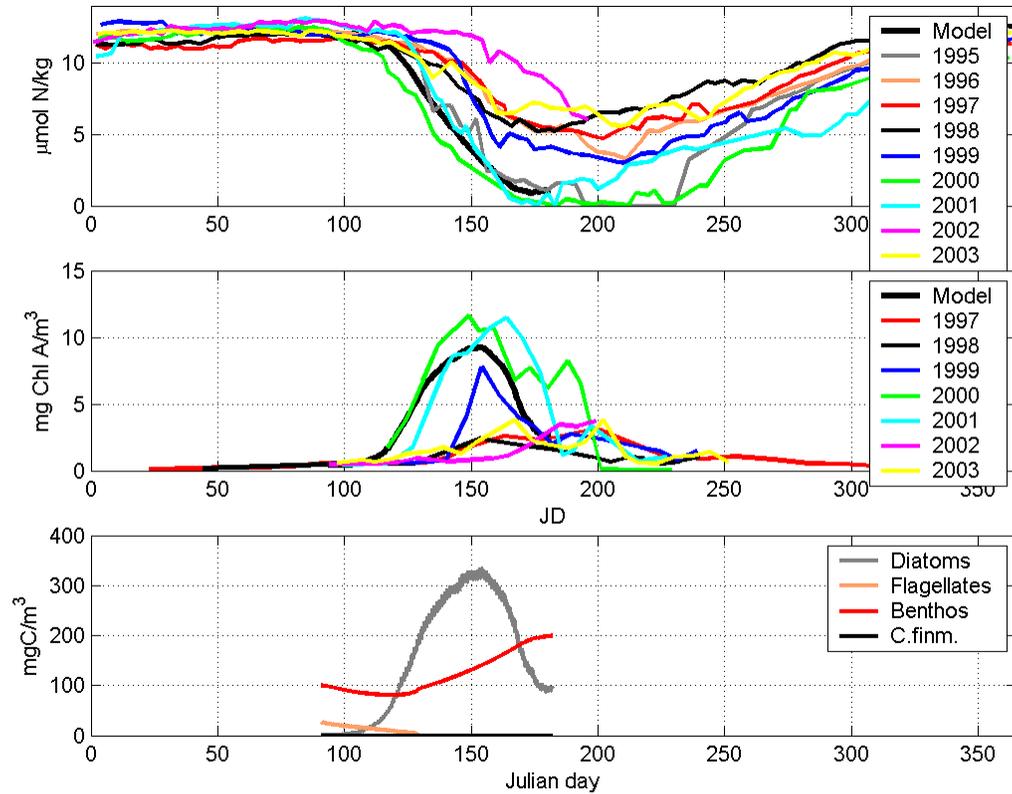
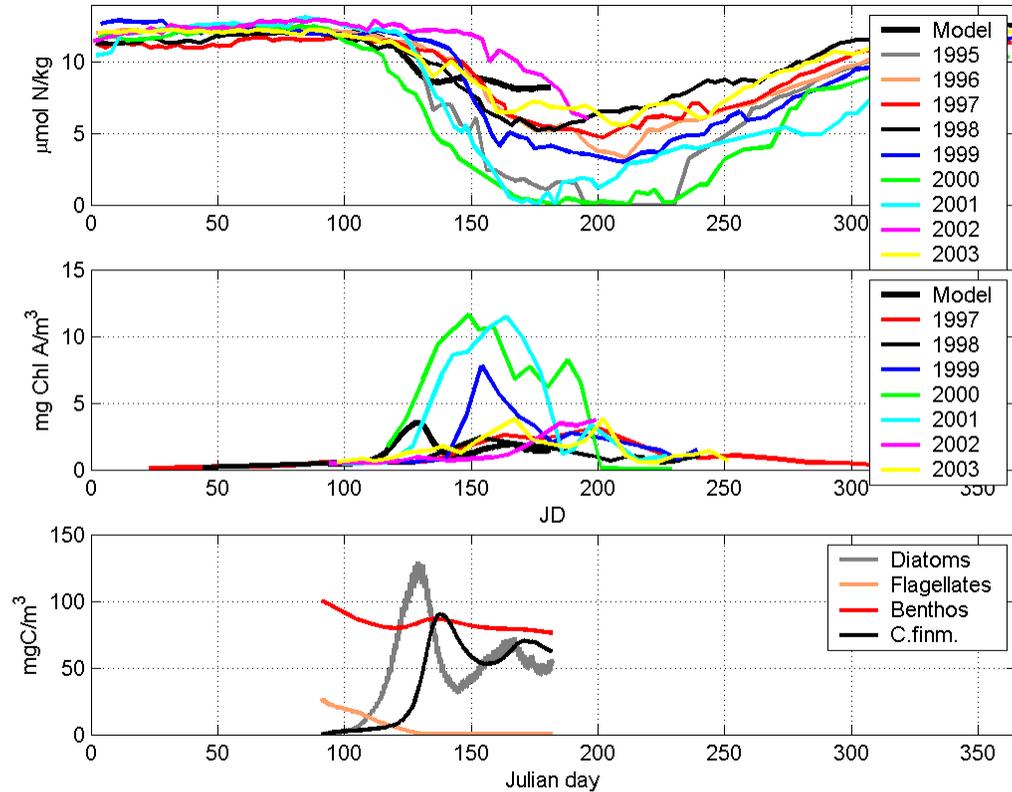


Figure 3-8. Model run with a diatom and a flagellate phytoplankton community. No *C.finmarchicus* present and an initial benthos population of  $100\text{mgC}/\text{m}^3$ . Average irradiance 1996-2000 ([www.satellite-light.com](http://www.satellite-light.com)),  $P_{max,P}=3\text{d}^{-1}$ ,  $\kappa_{I,P}=150\mu\text{E}/\text{m}^2/\text{s}$ ,  $P_{max,F}=0.5\text{d}^{-1}$ ,  $\kappa_{I,F}=10\mu\text{E}/\text{m}^2/\text{s}$ ,  $g_B=0.0002\text{ m}^3/\text{mgC}/\text{d}$ ,  $r_P=0.05\text{ d}^{-1}$ ,  $r_{P,A}=0.05$ ,  $r_F=0.1\text{ d}^{-1}$ ,  $r_{F,A}=0.1$ , F:P is  $\frac{33}{34} : \frac{1}{34}$  ( $P$  indicates diatoms and  $F$  indicates flagellates), the mortality for phytoplankton is unchanged and the same for diatoms and flagellates.  $r_B=0.01$ ,  $r_{B,A}=0.005$ ,  $P_{high}=5\text{mgChlA}/\text{m}^3$ . The model runs from 1.Apr to 1.July.

The result can be seen in Figure 3-8, where the model has been run with an initial benthos concentration of  $100\text{ mgC}/\text{m}^3$  and no *C.finmarchicus* import. The phytoplankton community consists in the beginning of 33/34 flagellates and 1/34 diatoms. This ratio is based on work carried out by Høgni Debes where he has compared the observed fluorescence with the amount of phytoplankton collected by a  $40\mu\text{m}$  net, where of course the small flagellates are eliminated (Debes, pers.communication).

This postpones the spring bloom to start 26.April having a maximum 2.June. Comparing the uppermost panel with the middle panel it can be seen that the modeled phytoplankton concentration coincides with the phytoplankton observed in 2000, but the modeled nitrate concentration is in the bloom phase constantly higher than the observed nitrate concentration in 2000. This indicates that the *ChlA:C* ratio or the mortality of the phytoplankton might be slightly wrong.



**Figure 3-9. Model with diatoms, flagellates, a *C. finmarchicus* import of  $0.5 \text{ mgC/m}^3/\text{d}$  from 1. April to 1. June and a initial benthos population of  $100 \text{ mgC/m}^3$ . All other parameters are the same as in Figure 3-8.**

This model has also been run with a zooplankton inflow, which can be seen in Figure 3-9. An import of  $0.5 \text{ mgC/m}^3/\text{d}$  corresponds to  $3.5 \text{ adult individs/m}^3/\text{d}$ , which is a large but not unrealistic import. As in earlier runs, the *C. finmarchicus* are not able to suppress the bloom, and we observe a small bloom starting at the same time as when there is no *C. finmarchicus*, only with a lower maximum.

## 4 Conclusion

It is possible to delay the spring bloom by separating the phytoplankton community into two species, but still the *C. finmarchicus* can't suppress the bloom as is seen in the nature. This can perhaps be solved by a model with a horizontal variation.

## 5 Appendix: Formulas

Formulas used in the ecosystem model are given below. The phytoplankton can be divided into two distinct groups. Zooplankton is also in two groups where both are assumed to be homogeneous biomasses, without spawning and characterized with growth only by grazing. The references are given in parenthesis above each equation.

Photosynthesis in the whole water column (Eliassen *et al.*, 2003):

$$\begin{aligned} \langle \text{photosynthesis} \rangle &= \frac{1}{-D} \int_D^0 \frac{I(z)}{\kappa_I + I(z)} dz = \frac{1}{-D} \int_D^0 \frac{1}{\frac{\kappa_I}{I(z)} + 1} dz = \frac{1}{-D} \int_D^0 \frac{1}{\frac{\kappa_I e^{-kz}}{I_0} + 1} dz \\ &= 1 + \frac{1}{kD} \ln \left( \frac{I_0 + \kappa_I e^{-kD}}{I_0 + \kappa_I} \right). \end{aligned} \quad \kappa_I = 50 \frac{\mu E}{m^2 s}, D=75,$$

$$k = 0.0644 \frac{1}{m} + \alpha_{ext} \cdot P \left[ \frac{mgChlA}{m^3} \right]; \quad \alpha_{ext} = 0.0188 \frac{m^3}{mgChlA \cdot m}$$

Phytoplankton gross growth (Sakshaug *et al.*, 1994, Lalli & Parsons, 1997):

$$G_P = P_{max} \cdot \min(\langle \text{photosynthesis} \rangle, \frac{N}{\kappa_N + N}) \cdot P$$

$$\kappa_N = 1 \frac{\mu mol N}{kg}, P_{max} = 3 d^{-1}$$

Phytoplankton respiration (Sakshaug *et al.*, 1994 and modified by Solva K. Eliassen):

$$R_P = r_P \cdot P + r_{P,A} \cdot G_P \quad r_P = 0.05 - 0.15 \frac{1}{d} \text{ and } r_{P,A} = 0.15$$

Phytoplankton mortality (Sakshaug *et al.*, 1994 and modified by Bogi Hansen):

$$M_P = \left( d_{min} + (d_{max} - d_{min}) \cdot \exp\left(-\frac{N}{\kappa_N}\right) \right) P$$

$$r_P = 0.05 d^{-1}, d_{max} = 0.5 d^{-1}, \kappa_N = 1 \frac{\mu mol N}{kg}$$

(With a separation of phytoplankton into two groups:  $\kappa_{I,P} = 150 \mu E/m^2/s$ ,  $\kappa_{I,F} = 10 \mu E/m^2/s$ ,

$P_{max,P} = 3 d^{-1}$ ,  $P_{max,F} = 0.5 d^{-1}/s$ ,  $r_P = 0.05 \frac{1}{d}$ ,  $r_{P,A} = 0.05$ ,  $r_F = 0.1 \frac{1}{d}$ ,  $r_{F,A} = 0.05$ )

Grazing: (Richardson *et al.*, 1999, Barker Jørgensen, 1990, Riisgård, 2001):

*C.finmarchicus*:

$$G_Z = \begin{cases} 0 & \text{if } 0 \frac{mgChlA}{m^3} \leq P < P_{low} \\ g_Z \cdot Z \cdot P & \text{if } P_{low} \leq P < P_{high} \\ P_{high} \cdot ChlA : C \cdot g_Z \cdot Z & \text{if } P_{high} \leq P \end{cases}$$

$$g_Z = 0.0036 \frac{m^3}{mgC \cdot d}$$

Same for benthos:

$$G_B = \begin{cases} 0 & \text{if } 0 \frac{\text{mgChlA}}{\text{m}^3} \leq P < P_{low} \\ g_B \cdot B \cdot P & \text{if } P_{low} \leq P < P_{high} \\ P_{high} \cdot \text{ChlA} : C \cdot g_B \cdot B & \text{if } P_{high} \leq P \end{cases}$$

$$g_B = 0.0001 - 0.0003 \frac{\text{m}^3}{\text{mgC} \cdot d}$$

$$P_{low} = 0.5 \frac{\text{mgChlA}}{\text{m}^3}; P_{high} = 5 \frac{\text{mgChlA}}{\text{m}^3}$$

$\text{ChlA} : C = 1 : 35$  for diatoms and  $\text{ChlA} : C = 1 : 50$  for flagellates

In order to increase the survival of *C.finmarchicus* and Benthos when phytoplankton concentrations are low,  $P_{low} = 0.5 \text{ mgChlA/m}^3$  can be lowered to  $P_{low} = 0.2 \text{ mgChlA/m}^3$ . (Gaard, personal communication)

*C.finmarchicus* respiration (Fiksen & Carlotti, 1998):

$$R_Z = r_Z \cdot Z + r_{Z,A} \cdot a_Z \cdot G_Z$$

$$r_Z = 0.01 d^{-1}$$

$$r_{Z,A} = 0.005$$

$$a_Z = 0.8 d^{-1}$$

Benthos:

$$R_B = r_B \cdot B + r_{B,A} \cdot a_B \cdot G_B$$

$$r_B = 0.01 d^{-1}$$

$$r_{B,A} = 0.005$$

$$a_B = 0.8 d^{-1}$$

The mortality, including predation, is given as:

*C.finmarchicus* (Fiksen & Carlotti, 1998):

$$M_Z = m_Z \cdot Z;$$

$$m_Z = 0.05 d^{-1}$$

Benthos:

$$M_B = m_B \cdot B;$$

$$m_B = 0.05 d^{-1}$$

Decomposed detritus material:

$$D_{Decomp} = \frac{\log 2}{T_{1/2}} D$$

$$T_{1/2} = 60 d$$

Differential equations:

Phytoplankton:  $\frac{dP}{dt} = G_P - R_P - M_P - G_Z - G_B$

*C.finmarchicus*:  $\frac{dZ}{dt} = a_Z \cdot G_Z - R_Z - M_Z$

Benthos:  $\frac{dB}{dt} = a_B \cdot G_B - R_B - M_B$

$$\text{Detritus:} \quad \frac{dD}{dt} = M_P + M_Z + M_B + (1 - a_Z)G_Z + (1 - a_B)G_B - D_{Decomp}$$

$$\text{Nutrients:} \quad \frac{dN}{dt} = D_{Decomp} + R_P + R_Z + R_B - G_P$$

When the phytoplankton community is separated into two distinct species, one more differential equation is added for flagellates.

$$\frac{dP}{dt} = G_P - R_P - M_P - G_{Z,P} - G_{B,P};$$

$$\kappa_{I,P} = 150 \frac{\mu E}{m^2 s}, P_{\max,P} = 3d^{-1}, r_P = 0.05d^{-1}, r_{P,A} = 0.05$$

$$\frac{dF}{dt} = G_F - R_F - M_F - G_{Z,F} - G_{B,F};$$

$$\kappa_{I,F} = 10 \frac{\mu E}{m^2 s}, P_{\max,F} = 0.5d^{-1}, r_F = 0.1d^{-1}, r_{F,A} = 0.1$$

$$\frac{dZ}{dt} = a_Z \cdot (G_{Z,P} + G_{Z,F}) - R_Z - M_Z$$

$$\frac{dB}{dt} = a_B \cdot (G_{B,P} + G_{B,F}) - R_B - M_B$$

$$\frac{dD}{dt} = M_Z + M_B + M_P + M_F + (1 - a_Z)(G_{Z,P} + G_{Z,F}) + (1 - a_B)(G_{B,P} + G_{B,F}) - D_{decomp}$$

$$\frac{dN}{dt} = R_Z + R_B + R_P + R_F + D_{decomp} - G_P - G_F$$

In addition to this the exchange parameter is added to the equations for diatoms, nutrients and phytoplankton:

$$\frac{\text{offshelf concentration} - \text{onshelf concentration}}{75\text{days}}$$

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