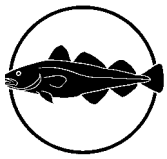
The Faroese Fisheries Laboratory

Fiskirannsóknarstovan



A Mathematical Model of the Lowest Trophical Levels on the Faroese Shelf

by

Sólvá Káradóttir Eliasen, Eilif Gaard and Bogi Hansen

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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 1-1) 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).

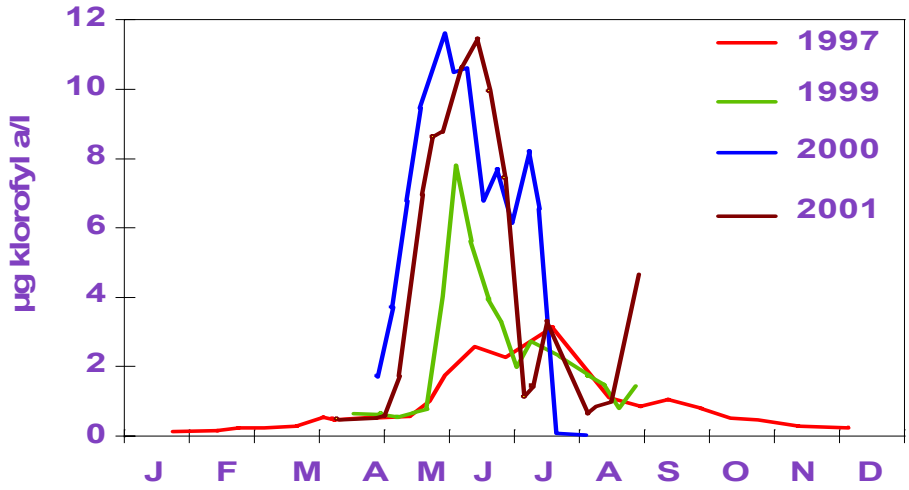

Figure 1-1. Observed annual variations in phytoplankton concentration on the Faroese shelf (Unpublished data, FFL)

The initial modeling effort was therefore aimed at illuminating this process and the living organisms in the model have been limited to a homogeneous phytoplankton population and a *Calanus* population that is imported into the system in spring. Except for this import, the system is assumed to be closed and without any spatial variation. This approximation is justified from the experience that the inner Faroe shelf is a rather homogeneous body that is kept well mixed by the strong tidal currents.

The possibility to initiate the modeling activity was given by a grant to the FFL from The Faroes Partnership. The money was granted for a period over several years and the FFL decided to use the financing for the first year to establish a project to implement the basic model. Since there was no experience with ecosystem modeling in Faroese waters, a number of fundamental questions had to be addressed. A main aim was also to clarify which further physical and biological investigations need to be conducted to establish a model.

This technical report describes the basic features of the implemented model and discusses the results in relation to observations. Suggestions are made for how to proceed in adapting the model and a number of questions are raised that need to be solved by further observations.

2 The Model Ecosystem

The model ecosystem has four components, nutrients, phytoplankton, zooplankton, and detritus, see Figure 2-1.

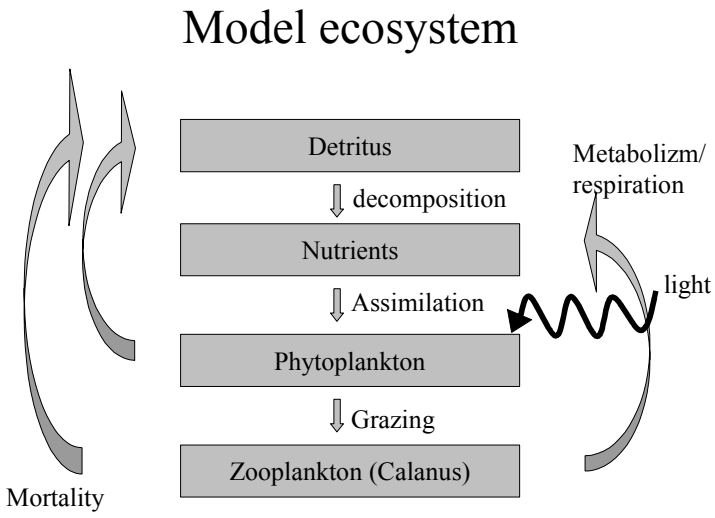

Figure 2-1. Ecosystem used in the model.

Usually there are three basic nutrients: Nitrate, silicate and phosphate, but as a simplification only nitrate is modeled, since nitrate usually is the limiting factor. Nutrients are used by phytoplankton and regenerated from phytoplankton respiration, zooplankton metabolism, and decomposition of detritus. The phytoplankton respiration is neglected in this system, since it is assumed that it can be included in the growth, because the phytoplankton absorbs nitrate in the growth and excrete nitrogen in the respiration. During the winter there is an almost constant high concentration of nutrients, which starts to decrease in the spring bloom, when the light intensity is sufficient for the growth.

Phytoplankton is modeled as an organism with growth depending on the light intensity and nutrient concentration. Phytoplankton is grazed by zooplankton and has mortality, depending on the nutrients. Dead phytoplankton becomes detritus before decomposing to nutrients again.

The growth of zooplankton depends on phytoplankton concentration, temperature and somatic weight. In order to calculate the weight of zooplankton, a zooplankton life cycle is constructed, where the zooplankton develops through 13 stages from eggs to adult copepods. The mortality, which includes zooplankton eaten by other higher organisms, varies depending on zooplankton stage, and generates new detritus. Zooplankton metabolism generates new nutrients.

Detritus is a pool where dead phytoplankton, zooplankton and phaeces are accumulated before decomposed into nutrients. In the model, the higher trophical levels have been included into the detritus pool also. During the winter all detritus is decomposed into nutrients, and the initial detritus concentration in the beginning of the spring is zero. Detritus is calculated in nitrogen content.

3 Equations

Formulas concerning zooplankton growth are from: Miller & Tande, 1993 and Carlotti & Fiksen, 1998. Furthermore, other publications are used, see section 7. In this section the formulas used in the program and the considerations behind the formulas are presented

3.1 Basic Equation system

Detritus differential equation:

$$\frac{dD}{dt} = Mort_P + Mort_Z - Decomp_N$$

Equation 3-1

Nutrient differential equation:

$$\frac{dN}{dt} = -G_P + M_Z + Decomp_N$$

Equation 3-2

Phytoplankton differential equation:

$$\frac{dP}{dt} = G_P - G_Z - Mort_P .$$

Equation 3-3

Here D, N, and P respectively are concentrations of detritus, nutrients, and phytoplankton. All quantities are given in $\frac{\mu molN}{kg}$.

$Mort_P$ is the daily phytoplankton mortality:

$$Mort_P = \left(d_{\min} + \left(d_{\max} - d_{\min}\right)e^{-N/\kappa_N}\right)P$$

Equation 3-4

$Decomp_N$ is the daily rate of nutrients, decomposed from detritus:

$$Decomp_N = \frac{\log 2}{T_{½}} D$$

Equation 3-5

G_P is the daily phytoplankton assimilation:

$$G_P = \gamma_P \frac{N}{\kappa_N + N} P$$

Equation 3-6

M_Z is the zooplankton metabolism:

$$M_Z = \mu_Z \cdot Z$$

Equation 3-7

G_Z is the zooplankton grazing:

$$G_Z = p_1 k_1 p_4 p_5^{\,T} \left(10^3 mgC\_mymol \cdot W\right)^{p_6} \begin{cases} 0 & if \quad P < p_2 \\ \dfrac{P - p_2}{p_3 - p_2} & if \quad p_3 > P \geq p_2 \\ 1 & if \quad P \geq p_3 \end{cases}$$

where W is the weight of C4 – C6 biomass in $\frac{\mu molN}{kg}$ and *mgC_mymol* is a conversion factor given in Table 8-1.

Equation 3-8

(Carlotti & Fiksen, 1998)

$Mort_Z$ is the daily zooplankton mortality. It is given as constant daily mortality rates, only dependent on the various stages of zooplankton. Equation 3-15 gives the number of zooplankton organisms dying in every time step. To calculate the $Mort_Z$ biomass we use Equation 3-9. The other constants are given in section 8, Appendix.

Growth of zooplankton is divided into stages of zooplankton development, from eggs to C6. In each stage, the organisms have an age, determining its weight. The maturation from each stage to the next and also the internal development is independent of phytoplankton concentration. Only the spawning is dependent on the phytoplankton concentration.

The concentration of zooplankton is measured in number of zooplankton organisms. Each stage of zooplankton has a specific duration, depending on the water temperature, which we assume constant. Through these stages every zooplankton organism develops by the system described below.

The weight of zooplankton is determined for each stage *j*, and thereafter added:

$$B_j = \sum_i W_{10,j}(1 + R_j Duration_{j,i}) A_{j,i} \; ; \quad B_\Sigma = \sum B_j$$

Equation 3-9

Here, $W_{10,j}$ is a vector with lowest stage weights, R_j is a regression vector, both given in Table 8-2, *Duration* is a matrix with durations of the individual stages, given as:

$D_{j,i+1} = D_{j,i} + \frac{1}{stage\ duration}$, and A is a matrix with zooplankton abundances.

The equations for zooplankton calculate changes in number of zooplankton organisms. These values are stored in the abundance matrix mentioned above.

Number of eggs:

$$\frac{d(Egg)}{dt} = egg_{prod}(P, C6) - hatched\ \ eggs - mortality$$

Equation 3-10

Abundance of stages N1 – C5:

$$\frac{d(N1-C5)}{dt} = molting\ \ from\ \ stage\ \ below - molting\ \ to\ \ next\ \ stage - mortality + import(C5)$$

Equation 3-11

Abundance of C6:

$$\frac{d(C6\ \ male)}{dt} = 0.5 \cdot molting\ \ from\ \ C5 - mortality(C6\ \ male)$$

Equation 3-12

$$\frac{d(C6\ \ female)}{dt} =$$

$$0.5 \cdot molting\ \ from\ \ C5 - mortality(C6\ \ female, total\ \ number\ \ of\ \ eggs) + import(C6)$$

Equation 3-13

(Miller & Tande, 1993)

Import(C5,C6) is the Calanus import in the early spring period. A typical import is $1\frac{C6}{m^3 day}$ during 2 months and the *C5*:*C6* ratio is 1:4. It is assumed that the C6 import is exclusively females. The Calanus import is typed in by the user when entering the program, see also section 8.

C6 females begin to spawn when they reach the spawning age, provided that the phytoplankton concentration is above P_{spawn}. Egg_{prod} is calculated daily and is given as:

$$Egg_{prod}(JD+1) = C6(age \geq Spawn_{age}) \begin{cases} 0 & if \quad P_{ave}(JD) \leq P_{Spawn} \\ Egg_{\max} \dfrac{P_{ave}(JD) - P_{Spawn}}{\kappa_E + \left(P_{ave}(JD) - P_{Spawn}\right)} & if \quad P_{ave}(JD) > P_{Spawn} \end{cases}$$

where $C6(age \geq Spawn_{age})$ is the number of C6 females that have reached spawning age and $P_{ave}(JD)$ is the average phytoplankton concentration on day *JD*.

Equation 3-14

Mortality is given as a vector with survivor rates for each stage (see Appendix Table 8-2), and is applied for each time step. For each stage *j* it is given as:

$$A_j(t+dt) = A_j(t) \cdot (1 - S_j)^{dt}.$$

Equation 3-15

(Miller & Tande, 1993)

The mortality of *C6* females is as for the other stages dependent on the survivor rate, but in addition *C6* females die when they have spawned Egg_{total} number of eggs.

3.2 Conversion of units

When calculating changes in concentrations it is necessary to measure all concentrations in the same units. In the program the basic unit is $\frac{\mu molN}{kg}$. Detritus and nutrients are measured either in weight of nitrogen or number of nitrogen molecules. Phytoplankton is usually measured in $\frac{mgC}{m^3}$ or $\frac{mg\ \ Chl\ \ a}{m^3}$, and zooplankton is usually measured in dry weight $\frac{mgZ}{m^3}$.

In Table 8-1 the conversion factors *mgN_mymol*, *mgC_mymol* and *mgZ_mymol* are shown.

3.3 Light in the Faroe Islands

To calculate the growth rate of phytoplankton, it is necessary to know the solar light intensity. This is to a large extent determined by the angular height of the sun (Sakshaug *et.al.*, 1992)

The incident light is dependent on latitude φ. The Earth is tilted 23.45°=Φ *rad* which means that the sunlight comes in with a maximum angle varying between 90°−φ–23.45° at winter solstice and 90°−φ+23.45° at summer solstice at our latitudes.

The maximum angle as a function of *JD* (Julian day number) is given as:

$$I_{\max} = 90° - \varphi + 23.45° \cos\left(2\pi \tfrac{JD+193}{365}\right); \varphi \geq 23.45°$$

Equation 3-16

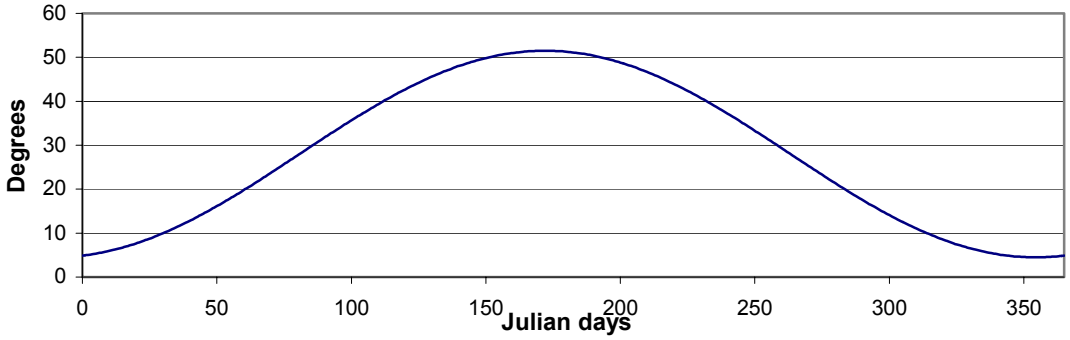

Figure 3-1. Maximum solar angle at 62 degrees north.

The sun angle *v* over the horizon as a function of time (*JD*) is given by the formula:

$$\sin v = \sin(\varphi)\sin\left(\Phi \sin(\tfrac{JD-81}{365} \cdot 2\pi)\right) - \cos(\varphi)\cos\left(\Phi \sin(\tfrac{JD-81}{365} \cdot 2\pi)\right)\cos(\tau \cdot 2\pi)$$

where τ represents the time of day, going from midnight to next midnight local time.

Equation 3-17

The day-length *D* (the time the sun is above the horizon) is given as [*hours*]:

$$D = 0.133 \cdot \arccos\left[-\tan\varphi \tan\left(\Phi \cos\left(2\pi \tfrac{JD+193}{365}\right)\right)\right]$$

Equation 3-18

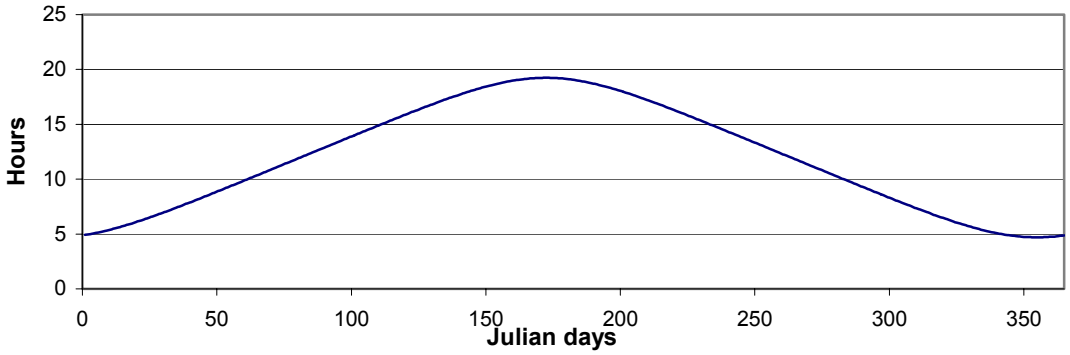

Figure 3-2. Day length at 62 degrees north

Without an atmosphere, the total irradiance reaching the earth at a locality would be:

$$E = 1360 \frac{W}{m^2} \cdot \sin \nu$$

where *v* is the sun angle over the horizon

Equation 3-19

This value is different at the earth surface, since the atmosphere absorbs part of the radiation and also there is diffuse and scattered light.

Phytoplankton photosynthesis uses light with wavelength 350-700nm. Light in this interval is called Photosynthetically Active Radiation (PAR). Approximately 43% of the irradiance energy is in the PAR interval (Jerlov, 1976):

$$E(350nm - 700nm) = 0.43 \cdot 1360 \frac{W}{m^2 \mu m}.$$

Equation 3-20

In order to measure the photosynthesis, it is necessary to know how many light quanta the irradiance contains. In the PAR interval this is done by the formula:

$$Q(350nm - 700nm) = 2.75 \cdot 10^{18} \cdot E(350nm - 700nm) = 1.2 \cdot 10^{18} \cdot E(350nm - 3000nm)$$

Equation 3-21

Usually numbers of quanta are measured in numbers of mol, which is achieved by division with Avogadros' number:

$$\mathrm{N_a} = 6.022 \times 10^{23} mol^{-1}.$$

Thereby the light intensity at the sea surface as a function of the sun angle above the horizon is given as:

$$Q(350nm-700nm)=1.99\times10^{-6}\cdot E(350nm-700nm)\cdot\sin v\frac{mol}{m^2 s}$$

(1 mol photons=1 Einstein).

Equation 3-22

3.4 Observations from Landsverkfrøðingurin (LV)

LV has carried out light observations during 10 years on 8 different locations on the Faroe Islands (Heinesen, 1997). The irradiance is observed in the spectral interval 300nm – 2500nm. The observations are compared with the calculated theoretical light radiation (Jerlov, 1976)

$$Q(350nm-700nm)=2.75\cdot10^{18}\cdot E(350nm-700nm)=1.2\cdot10^{18}\cdot E(350nm-3000nm)$$

Equation 3-23

This formula is valid in the interval 350nm – 3000nm. By looking at the complete spectrum of the downward irradiance, it is seen that only about 1% of the irradiance is received in the interval 300nm – 350nm and less in the interval 2500nm – 3000nm. Therefore this formula is used to convert the observations from LV [W/ m^2] to [quanta/m^2/s] in PAR.

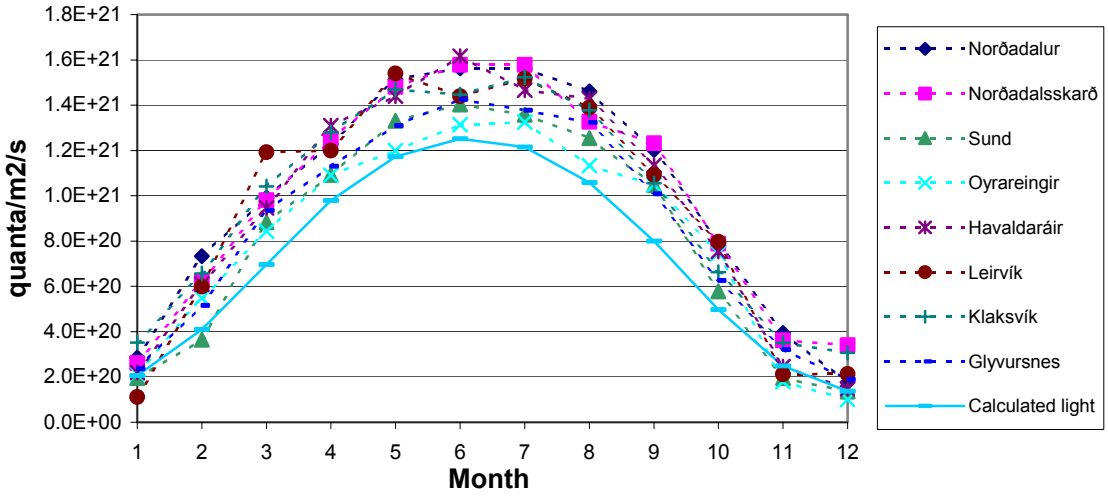

Figure 3-3. Maximum observations from LV converted to quanta/m2/s in PAR and calculated maximum light.

By comparing the calculated maximum light radiation and the observed maximum value during 10 years it can be seen that the observed light can be up to 40% higher than the theoretical value. This is probably because no scattered light is included in the calculated light.

The observations contain an average value for each month, which is used in the calculation of the photosynthesis. The average light is up to a factor ten times less than the maximum light. This is because the average is calculated over the complete day, i.e. the night included. The observations are performed on land, which generally is cloudier than on open sea. There is not yet performed any compensation for this.

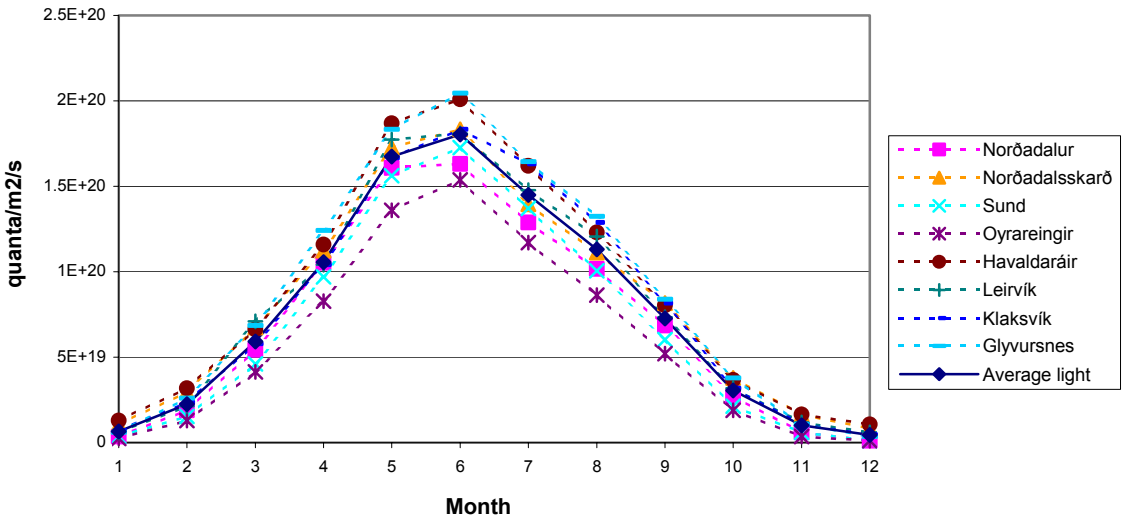

Figure 3-4. Average LV light observations during 10 years. The solid line is the average from all stations.

In order to simulate the real light during a month, the average light is interpolated by a general Lagrange interpolation polynomial. This way it is possible to calculate the average light every day.

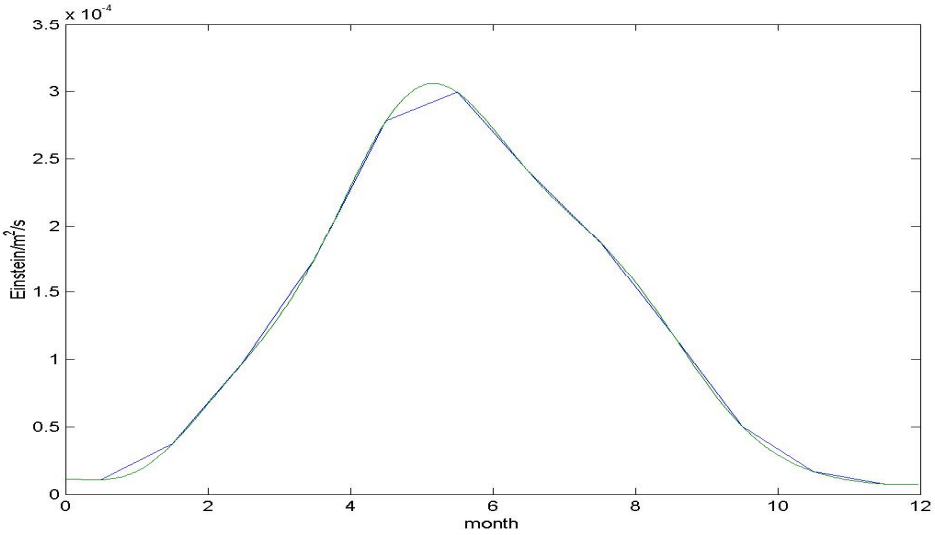

Figure 3-5. The average light above the sea surface in the Faroes, based on interpolated observations from the LV.

The light varies from year to year. Therefore the year with the least average irradiance is used as a lowest value for light and the largest observed values are used as a highest value.

3.5 Light attenuation and photosynthesis

3.5.1 Calculation of Photosynthesis - method one

The light attenuates when it penetrates the sea. The average light intensity in a water column with depth D is given as:

$$\bar{I}_D = \frac{I_0}{kD}\left(1 - e^{kD}\right) \approx \frac{I_0}{kD}$$

Equation 3-24

where I_0 is the light intensity at the sea surface and k is an extinction coefficient, given as:

$$k = \frac{\ln\left(\frac{I_0}{I(d)}\right)}{d}.$$

Equation 3-25

Investigations have indicated a typical k on the order of $0.144 m^{-1}$ (Hansen, 2000). In our case we operate with an average depth of 75 meters, which gives:

$$\begin{aligned}\bar{I}_D &= \frac{1.99 \times 10^{-6} \cdot E(350nm - 700nm) \cdot \sin v}{0.144 m^{-1} \cdot 75m} \frac{Einstein}{m^2 s} \\ &= 1.85 \times 10^{-7} \cdot E(350nm - 700nm) \cdot \sin v \frac{Einstein}{m^2 s}\end{aligned}$$

Equation 3-26

(Lalli & Parsons, 1997)

The light radiation is responsible for the phytoplankton photosynthesis, i.e. growth. In order to determine the photosynthesis, γ_P, a Michaelis-Menten function is used:

$$\gamma_P = P_{\max} \frac{I}{\kappa_i + I}$$

Equation 3-27

Here P_{max} is the maximum photosynthesis and κ_i is a half saturation constant.

As constants are used:

$$P_{\max} = 2.4 \frac{mgC}{mgC \cdot day} \qquad \text{and}$$

$$\kappa_i = 20 \cdot 10^{-6} \frac{Einstein}{m^2 s}.$$

This function neglects light inhibition since it only reaches a maximum value when $\gamma_P \to P_{\max}$ (Lalli & Parsons, 1997).

The photosynthesis is a nonlinear function of the light I (See Equation 3-27). Therefore it is necessary to use the light as a function of depth calculating the photosynthesis, and thereafter calculate the average photosynthesis in the water column. This procedure has been attempted in section 3.5.2.

3.5.2 Calculation of Photosynthesis - method two

To calculate the average photosynthesis in the water column it is assumed that the light is exponentially dependent on the depth, and that the average photosynthesis is calculated by integrating the photosynthesis in the whole water column, and thereafter dividing by the depth:

$$<\gamma_P>=\frac{1}{-D}\int_D^0 P_{\max}\frac{I(z)}{\kappa_i+I(z)}dz=\frac{P_{\max}}{-D}\int_D^0\frac{1}{\frac{\kappa_i}{I(z)}+1}dz=\frac{P_{\max}}{-D}\int_D^0\frac{1}{\frac{\kappa_i e^{-kz}}{I_0}+1}dz$$

Equation 3-28

Integrating this gives:

$$<\gamma_P>=\frac{P_{\max}}{-D}\left[z-\frac{1}{-k}\ln\left(1+\frac{\kappa_i}{I_0}e^{-kz}\right)\right]_D^0=\frac{P_{\max}}{-D}\left[\frac{\ln\left(1+\frac{\kappa_i}{I_0}\right)}{k}-D-\frac{\ln\left(1+\frac{\kappa_i}{I_0}e^{-kD}\right)}{k}\right]$$

$$=\frac{P_{\max}}{kD}\left[kD-\ln\left(\frac{I_0+\kappa_i}{I_0+\kappa_i e^{-kD}}\right)\right].$$

Equation 3-29

This equation is used in the modeling for calculating the average photosynthesis in the water column, since it gives more realistic growth rate values. The daily rate of photosynthesis is given in $\frac{1}{day}$. The difference in growth rate between the two methods mentioned can be seen in Figure 3-6. The growth rate *Photosynthesis*=$<\gamma_P\ (I(z))>$ is the growth rate most similar to the observed growth rate.

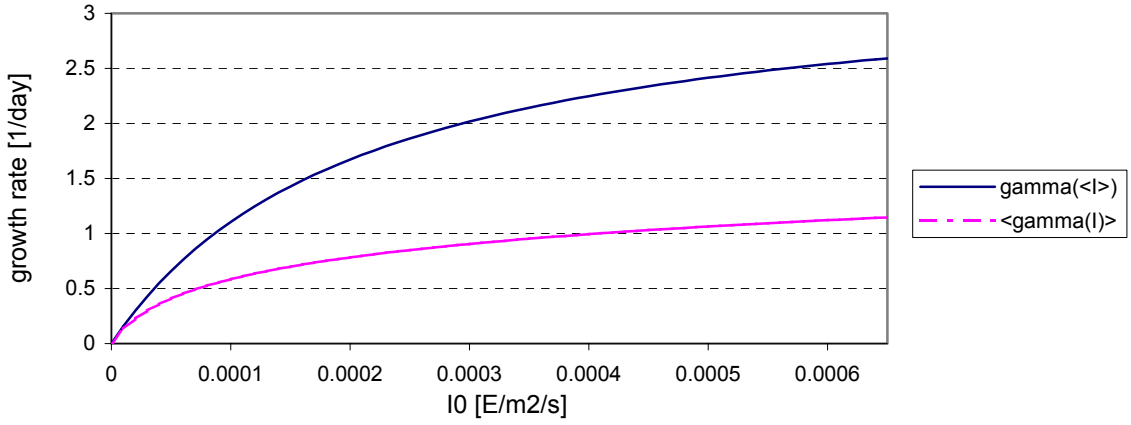

Figure 3-6.

Growth rate calculated by method one and two.

In order to reach a more correct value for the extinction coefficient, a linear function is used for *k*, depending on the phytoplankton concentration:

$$k = 0.1 + \alpha_{ext} P$$

Equation 3-30

$$\alpha_{ext} = 8.1 \cdot 10^{-2} \frac{kg}{\mu molN \cdot m} \quad , \qquad P = \left[\frac{\mu molN}{kg} \right];$$

This function gives k=0.35 m^{-1} when $P = 245 \frac{mgC}{m^3} \sim 7 \frac{mgChla}{m^3} \sim 3.1 \frac{\mu molN}{kg}$, which are values seen in observations from R/V Magnus Heinason. With this method a shading effect is achieved.

4 Numerical solution

In the model, the differential equations presented in section 3.1 are discretized and solved. In this modeling, forward differencing has been used:

$$f(t+\Delta t) \approx f(t) + \left.\frac{df}{dt}\right|_t \Delta t \,.$$

Equation 4-1

The program is written in Matlab. A diagram of the program can be seen in Table 4-1.

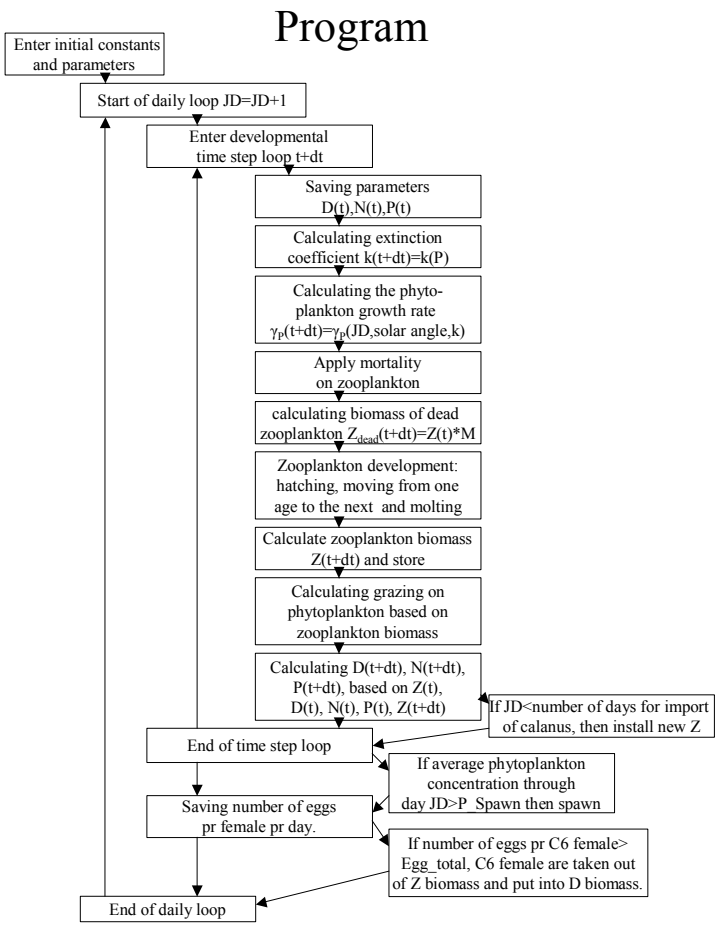

Table 4-1. Diagram of the program.

5 Results

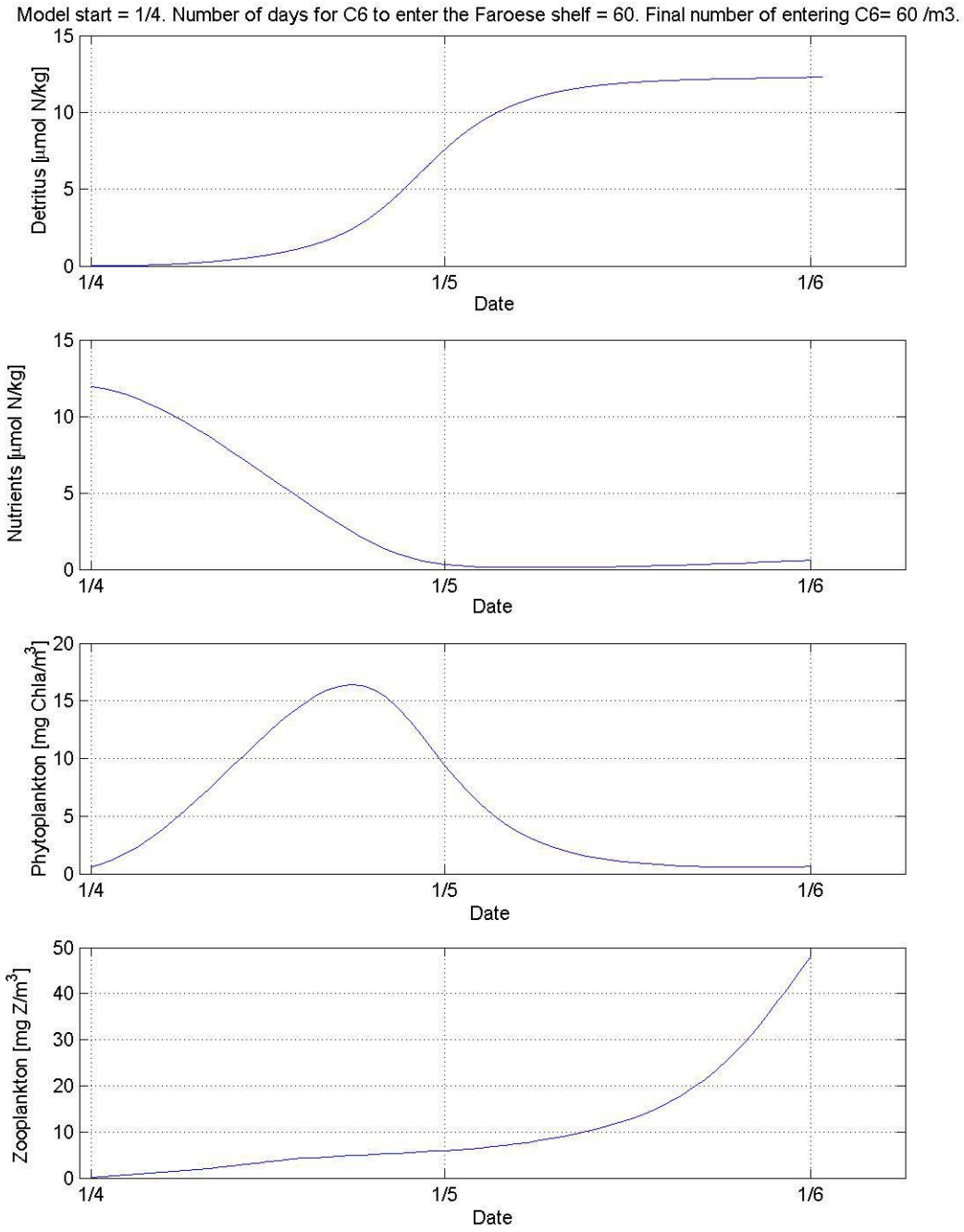

Figure 5-1. Modeled detritus, nutrients, phytoplankton and zooplankton concentrations. The import of Calanus has been set to a typical value of 1 C6/day/m3 during 60 days. The light used is average light in the Faroe Islands.

Figure 5-1 shows a typical run of the model, with typical light values and typical zooplankton import. These model results can be compared to observed phytoplankton development (Figure 1-1) and nutrient variation (Figure 5-2). The

nutrients and phytoplankton concentrations behave as expected from the observations, except that the decrease in nutrient concentration is steeper than in the observations, and also it appears too early which also is the case with the phytoplankton maximum.

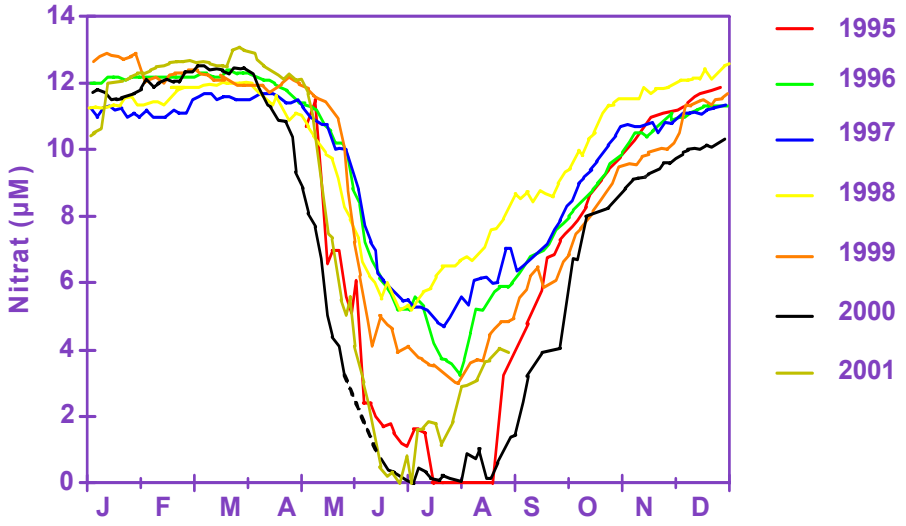

Figure 5-2. Observed annual nitrate concentrations on the Faroese shelf [µmol N/kg] (Unpublished data, FFL)

The grazing from zooplankton on phytoplankton computed by the model is very small and indicates an ecological efficiency from the first to the second trophical level much smaller than generally observed in nature.

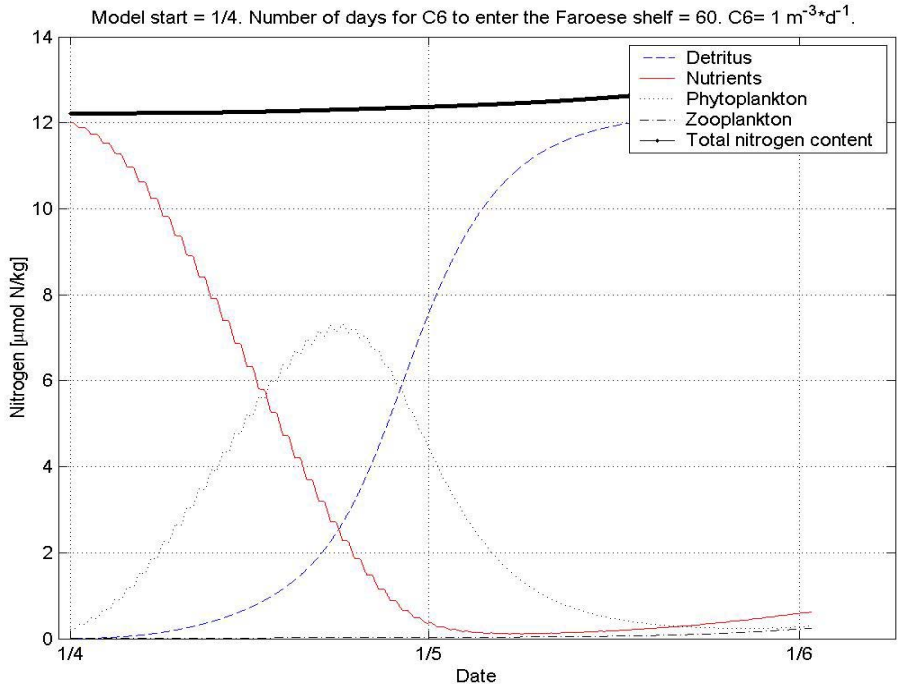

Figure 5-3. Modeled detritus, nutrient, phytoplankton and zooplankton all measured in µmol N/kg. The import of Calanus is subtracted from the total nitrogen content.

Assuming system is isolated there is a demand of constant total nitrogen content. This requirement is not perfectly fulfilled as can be seen in Figure 5-3.

In the nature zooplankton can allocate surplus gain to lipids, which are not included in the weight calculations used in the program. Therefore the increase in nitrogen can be ascribed to consumption of additional zooplankton fat storages during spawning.

6 Discussion

A mathematical model of the phyto- and zooplankton dynamics on the inner Faroe shelf has been developed from basic principles and the literature. The model results show the gross features of the spring bloom on the Faroe shelf as observed, but discrepancies are seen in details. In the model, the peak in phytoplankton biomass occurs too early and is too high. Nutrient depletion, therefore, also occurs too early, and is steeper than usually observed.

Some of the discrepancies may be due to inappropriate representation of light intensity in the model. Much effort was spent in determining appropriate functions for typical light variation in Faroese waters in spring, but the available information on light conditions in the Faroes is very sparse. In the model, the representation of light variation was based mainly on measurements of solar radiation on land, adapted to oceanic conditions; but direct light measurements from FFL's research vessel R/V Magnus Heinason indicate that light in the model perhaps has been too intensive. The direct in-situ light measurements have been too few to allow typical values to be determined, but additional instrumentation has been acquired for R/V Magnus Heinason and in future, light measurements will be performed more regularly.

Modeling of grazing by zooplankton on phytoplankton also needs to be adapted. The algorithms for zooplankton development and grazing include a number of empirical relationships with parameters acquired from literature. Their applicability in Faroese waters and the consistency within the model need to be explored in more detail.

Future development of the model will first focus on clarification of the problems with light and grazing to reach better agreement with nature. When that goal has been reached, horizontal variation will be implemented into the model to study the change from the shallow to the deeper parts of the shelf and into the surrounding water.

7 References

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8 Appendix

In this appendix a list with all constants used in the program is listed.

Constant	Meaning	Value	Unit
T	Average temperature	6.5	$^{\circ}C$
Lat (φ)	Latitude	62	$^{\circ}$
dt	Time step	1/48	*day*
Depth	Average depth of water column	75	*m*
Alfa_ext (α_{ext})	Gradient in attenuation equation	8.1e-2	$\frac{kg}{\mu molN \cdot m}$
P_max (P_{max})	Maximum photosynthesis	2.4	$\frac{1}{day}$
Kappa_1 (κ_1)	Half saturation for photosynthesis	$20e10^{-6}$	$\frac{E}{m^2 s}$
Kappa_N (κ_N)	Half-saturation constant for phytoplankton growth on nutrients and in the mortality of P	1.8	$\frac{\mu molN}{kg}$
Kappa_E (κ_E)	Half-saturation constant for zooplankton egg production	0.88	$\frac{\mu molN}{kg \cdot day}$
My_P (μ_P)	Phytoplankton metabolism	0	day^{-1}
My_Z (μ_Z)	Zooplankton metabolism	0.272	day^{-1}
mgN_mymol	Converting [mg N/m3] to [my_mol N/kg]	$\frac{1}{14.35} = 0.07$	$\frac{\mu molN \cdot m^3}{mgN \cdot kg}$
mgC_mymol	Converting [mg C/m3] to [my_mol N/kg]	$\frac{16}{106 \cdot 12} = 0.013$	$\frac{\mu molC \cdot m^3}{mgN \cdot kg}$
mgZ_mymol	Converting [mg Z/m3] to [my_mol N/kg]	$\frac{16 \cdot 0.4}{106 \cdot 12} = 0.005$	$\frac{\mu molN \cdot m^3}{mgZ \cdot kg}$
d_min (d_{min})	Parameter sedimentation rate	0.0192	day^{-1}
d_max (d_{max})	Parameter sedimentation rate	0.192	day^{-1}
T2 ($T_{½}$)	Half-life period for detritus	300	day
p2 (p_2)	Lower limit of zooplankton feeding	0.63	$\frac{\mu molN}{kg}$
p3 (p_3)	Food is unlimited above p3	2.52	$\frac{\mu molN}{kg}$
p4 (p_4)	Temperature coefficient	0.4	*(dimensionless)*
p5 (p_5)	Temperature coefficient	1.096	*(dimensionless)*
p6 (p_6)	Exponent in allometric relationship	0.7	*(dimensionless)*
k1 (k_1)	Correction for lack of molting	0.75	*(dimensionless)*
Spawn_age ($Spawn_{age}$)	Minimum C6 female age when hatching can start	8	*day*

P_Spawn (P_{Spawn})	Phytoplankton concentration necessary for hatching	0.44	$\frac{\mu molN}{kg}$
Egg_total (Egg_{total})	Total content of eggs pr C6 female	800	
Egg_max (Egg_{max})	Maximum number of eggs hatched pr day pr C6 female	80	

Table 8-1. Constants used in the program.

	Lowest stage weight W_{10} (used in Equation 3-9, should be given in $\frac{\mu molN}{ind}$)		Regression coefficient R (used in Equation 3-9)	Finite daily survivorship S	Stage duration with T=6.5°C	Maximum ingestion rate for C4, C5 and C6, p_1
	$\frac{\mu g}{ind}$	$\frac{\mu molN}{ind}$			*day*	day^{-1}
Egg	0.7	3.5e-3	0	0.85	2.0504	
N1	0.7	3.5e-3	0	0.92	3.172	
N2	0.7	3.5e-3	0	0.92	3.172	
N3	0.7	3.5e-3	0.1	0.92	3.172	
N4	0.8	4.0e-3	0.1	0.92	3.172	
N5	0.9	4.5e-3	0.1	0.92	3.172	
N6	1	5.0e-3	0.1	0.92	3.172	
C1	2.317	11.7e-3	1.077	0.95	4.7328	
C2	4.81	24.2e-3	1.077	0.96	5.347	
C3	9.99	50.3e-3	1.077	0.97	5.2966	
C4	20.75	104.4e-3	1.077	0.98	5.712	1.5
C5	34.12	171.7e-3	2.33	0.99	11.724	1.3
Male C6	138	694.3e-3	0	0.25		1
Female C6	149	749.7e-3	0	0.95		1

Table 8-2. Zooplankton constants

In addition to this, some constants are typed in when entering the program.
Parameters determined by the user when starting the program:

- Type of light: minimum, average or maximum
- Date of start of model
- Date of end of model
- Size and duration of zooplankton import. The import is exclusively C5 and C6, and it is assumed that the import of C6 is four times larger than the import of C5 and that the import of C6 only is C6 females.
- File to store selected parameters in.

As start values of detritus, nutrients and phytoplankton are used:

- Initial Detritus content D=0 $\frac{\mu molN}{kg}$.
- Initial Nitrogen content N=172.2 $\frac{mgN}{m^3}$ =12 $\frac{\mu molN}{kg}$
- Initial phytoplankton content P=17.5 $\frac{mgC}{m^3}$ =0.22 $\frac{\mu molN}{kg}$.