A model of phytoplankton growth—effects of vertical mixing and adaptation to light†

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The OCEAN BIO-MODELS Project is a long term research and development programme whose goal is to establish the capability of producing mathematical/numerical models of a marine ecosystem of the Barents Sea, north of Norway. The system is modeled by a set of submodels describing the physical oceanography, chemical oceanography and production and distribution of phytoplankton, zooplankton and fish. In this paper, a phytoplankton model containing light adaptation properties is developed.

The model describes growth of phytoplankton as a function of light intensity, level of adaptation, concentration of nutrients (nitrogen), temperature, grazing and respiration. The level of adaptation is a dynamic function of the past light experience of the algal cells which again depends on the light intensity at the surface and the vertical mixing. Simulation runs have been performed using a one-dimensional (vertical direction) physical model where the turbulent mixing can be specified. The effect on the onset and the dynamics of the spring bloom is discussed for typical vertical mixing profiles found along the Norwegian Coast and in the Barents Sea. The adaptation level is found to have a pronounced effect on the date for the onset of the spring bloom.

1. Introduction

There are a lot of models for predicting rate of photosynthesis as a function of light intensity (Talling 1957, Steele 1962, Platt and Jassby 1976, and others). Common for these models is that they are empirical and describe the short-term variation (hours) in the primary production as a function of light. It has been known for a long time that there are shade and sun adapted plants of the same species which have different photosynthesis–light relationships (Boardman 1977 and references therein).

Light available for photosynthesis is highly variable in aquatic environments. As a result of mixing, the unicellular planktonic algae are potentially exposed to change in light intensity of one to two orders of magnitude within a period of hours. These algae have evolved complex harvesting pigment systems, some of which are capable of adapting to variations in light intensity. Change in intracellular photosynthetic pigments, such as chlorophyll *a*, are often observed within a short time after exposure to a new light regime (Riper *et al.* 1979).

Most models used for predicting the rate of photosynthesis do not seem to take the adaptation properties into account. For an algal population growing in the mixed

layer, we make no serious error by assuming a fixed relationship between photosynthesis and light. However, change in the mixing parameters will affect the dynamic adaptation process and thereby the growth properties of the algae. In a changing environment, these abilities must be taken as a function of the light experience of the cell and not as a function of time and depth. At high latitudes this effect becomes especially important because light changes very much throughout the year and the sea surface may be more or less covered by ice which makes the light available for photosynthesis even more variable.

In this paper, we will present a model of the adaptation process based on a paper of Falkowski (1980) and some unpublished data and ideas from Sakshaug. The model will be tested in an ecosystem consisting of phytoplankton and herbivore zooplankton (copepods). Nutrients (nitrogen) are assumed homogeneously distributed at the start of the simulation and utilized by the phytoplankton. When the nitrogen concentration becomes low, the photosynthetic rate decreases according to a Michaelis–Menten function. At the other end of the ecosystem, the predation on the copepods is a function of time (see Slagstad 1981 for more information).

2. Phytoplankton model

2.1. *Property model of phytoplankton*

Growth of algal cells depends on a great number of cellular characteristics, besides the environmental variables such as light, temperature, and nutrients. These characteristics include internal pool of nutrients, C/N-ratio, ATP-content, chlorophyll-content, size, concentration of various enzymes. A general model of phytoplankton growth should contain features that allows it to calculate growth from the internal state of the algal cells and their environment. This may be performed in the same way as in the copepod model described by Slagstad (1981).

We define a density function $p(t, x)$, where x is a vector of relevant, internal state variables of a cell and t is time. What are the relevant internal state variables? It depends on the questions we ask. For our purpose, we need the chlorophyll content or information about how the light regime affects the ability of the cell to grow. In the literature, data can be found to construct a relationship between the light intensity at which the cells are adapted and their growth rate. The data describing the relationship between chlorophyll, light intensity at which the cells are adapted and growth seem to be more scarce. We, therefore, choose the light intensity at which the algal cells are adapted, I_0, as an internal property to be described in our model. I_0 may be taken to reflect several internal variables such as chlorophyll content, level of enzymes and size of the cells. The vector of internal state variables is now reduced to a scalar, a single property. It can be shown mathematically (Sinco 1969) that a density function of this kind satisfies the partial differential equation

$$\frac{\partial p}{\partial t} = -\frac{\partial}{\partial I_0}(v_{I_0}p) - (w + w_p)\frac{\partial p}{\partial z} + \frac{\partial}{\partial z}\left(D_z \frac{\partial p}{\partial z}\right) + f_{biol} \tag{1}$$

The first term on the r.h.s. of the equation represents the change in adaptation properties of the phytoplankton, whereas the second and the third terms represent the vertical transport and vertical turbulent mixing, respectively. f_{biol} includes the biological processes affecting the production rate of phytoplankton. $v_{I_0}(t, I_0)$ is the rate of change in I_0.

When implementing this model on a digital computer we always have to discretize the water column in sheets or layers of a certain depth. We assume that the plankton in each layer is well mixed and has the same I_0. This value is an average of the degree of adaptation in the cells in the layer. After entering a certain layer the cells are trying to adapt towards an I_0 which is specific for the light conditions in this layer. Using this approximation, we can simplify eqn. (1).

$$\frac{\partial P}{\partial t} = -(w+w_p)\frac{\partial P}{\partial z} + \frac{\partial}{\partial z}\left(D_z \frac{\partial P}{\partial z}\right) + f_{\text{biol}} \tag{2}$$

$$\frac{dI_0^t}{dt} = v_{I_0}(I_{0w}^i, I_0^i, T) \tag{3}$$

where $P(t, z)$ is the concentration of phytoplankton (in nitrogen units) at time t and depth z. I_0^i is the average adaptation light intensity of cells occupying layer no. i in the water column, and I_{0w}^i is the light intensity towards which the cells adapt after arriving at layer no. i. v_{I_0} is the rate of adaptation and T is temperature. The biological term, f_{biol}, describes how respiration, light nutrients and grazing affect the phytoplankton production.

$$f_{\text{biol}} = \mu_{\text{max}}^E f_1(I_z, I_0)G_N P - \phi_r P - q_1(P) \tag{4}$$

The first term on the r.h.s. of the equation represents the phytoplankton growth term, and the second term represents the respiration and mortality of the phytoplankton. The last term gives the effect of the grazing pressure from the zooplankton.

μ_{max}^E is the cell division rate at optimum light and at a given temperature. (The superscript 'E' means maximum division rate when using Eppley's (1972) equation, see eqn. (11).) The relationship between the rate of photosynthesis and light intensity, $f_1(I_z, I_0)$, will be discussed in the next section. The effect of the concentration of nitrogen is assumed to follow the well known Michaelis–Menten expression

$$G^N = \frac{N}{k_N + N} \tag{5}$$

where k_N is the half saturation constant and N is the concentration of nitrogen. The sinking rate of the phytoplankton, w_p, is taken to be a function of nitrogen in the surrounding water masses.

Growth of phytoplankton will remove nutrients from the water. Since we have assumed that nitrogen is the only nutrient to be limiting, we need to have an account for transport, regeneration and uptake of nitrogen. Regeneration takes place partly through excretion from zooplankton and partly through bacterial decomposition of detritus. The equations describing the dynamics of nitrogen and detritus are:

Nitrogen

$$\frac{\partial N}{\partial t} = -w\frac{\partial N}{\partial z} + \frac{\partial}{\partial z}\left(D_z \frac{\partial N}{\partial z}\right) - \mu_{\text{max}}^E f_1(I_z)G_N P + \phi_d D + E^z \tag{6}$$

Detritus

$$\frac{\partial D}{\partial t} = -(w+w_d)\frac{\partial D}{\partial z} + \frac{\partial z}{\partial z}\left(D_z \frac{\partial D}{\partial z}\right) + \phi_r P - \phi_d D \tag{7}$$

The first two terms of the r.h.s. of the equations represent the vertical transport and vertical turbulent mixing, respectively. Growth of phytoplankton is accompanied by a decrease in concentration of nutrients which is accounted for by the third term in eqn. (6). The fourth and the fifth term of eqn. (6) represent the regeneration of nutrients from the detritus and the zooplankton, respectively. Detritus is assumed to originate from dead phytoplankton, term three in eqn. (7).

2.2. *Light–photosynthesis characteristics*

Falkowski and Owens (1980) found that cellular division rate (μ) was best described by an exponential relationship of the form

$$\mu = a_2 + a_1 \log I_0 \tag{9}$$

for adapted cells. I_0 is the light intensity to which the cells are adapted, and a_1 and a_2 are parameters. Sakshaug (pers. comm.) found similar relationship for *Skeletonema costatum*. Using his data, we find the parameter values of a_1 and a_2 equal 0·05 and 0·04, respectively (I_0 is expressed in Wm^{-2}).

In the ocean, the light intensity varies approximately as a sinusoidal function. This variation should be taken into account when calculating phytoplankton growth. At low light intensities (below the adaptation level), the photosynthetic rate may be taken as proportional to the light intensity, independent of temperature. Near or above the adaptation level, the photosynthetic rate will reach saturation. Here we assume the following relationship:

$$\mu_{dyn} = \begin{cases} \dfrac{\mu_0}{I_0} I_z & \text{if } \mu_{dyn} \leqslant \mu_{max} \\[2em] \mu_{max} & \text{if } \mu_{dyn} > \mu_{max} \end{cases} \tag{10}$$

Where μ_{dyn} is the cellular division rate per hour and light unit, μ_0 is the cellular division rate for cells which experience light intensity equal to the adaptation level. μ_0 is calculated by eqn. (9). I_0 is the adaptation level calculated by eqn. (3). μ_{max} is the light-saturated division rate which depends on temperature and adaptation level.

A widely used equation to put an upper bound, $\mu_{max}{}^E(T)$ day^{-1}, on the cell division rate, is one proposed by Eppley (1972). However, the parameter values are modified by data obtained from field studies (Sakshaug 1977) and field dialysis cultures (Hegseth and Sakshaug 1982) of *Skeletonema*.

$$\mu_{max}{}^E = 0 \cdot 74 \exp(0 \cdot 0582T) \tag{11}$$

where T is the temperature.

This equation is valid for optimal light conditions and when nutrients are not limiting the growth. Temperature must also put an upper limit on the division rate when light is sub-optimal. However, data seem to be lacking to construct a relationship. The effect of adaptation on light-saturated photosynthesis is dependent on algal species (Falkowski 1980, Beardall and Morris 1976). Using the data found in Falkowski and Owens (1980), we may estimate the light-saturated division rate to approximately 1·2 to 2·0 times μ_0, for *S. costatum*. The lower value corresponds to shade adapted

cells. For simplicity we keep this upper bound as a constant fraction, 1·5, of μ_0. The upper bound of light-saturated division rate is now given by

$$\mu_{max} = \begin{cases} \mu_{max}{}^E & \text{if } \mu_{max} \geqslant \mu_{max}{}^E \\[2mm] 1\cdot5\mu_0 & \text{if } \mu_{max} < \mu_{max}{}^E \end{cases} \tag{12}$$

2.3. *Chlorophyll and adaptation*

Adaptation affects, among other properties, the intracellular pigment content. Although the chlorophyll content itself is not an important variable in this model, it is important to calculate its amount for the following reasons:

1. Measurements of chlorophyll in the ocean are relatively easy to perform and are often done as a routine. In order to compare the model results with measurements it is, therefore, necessary to have a relationship between the level of adaptation and chlorophyll content.
2. Light is absorbed by the chlorophyll. When calculating attenuation caused by the phytoplankton, the chlorophyll content, in addition to the phytoplankton biomass has to be taken into account.

Over a wide range of light intensities, the pigment content of the unicellular algae can be empirically related to changes in light by a logarithmic function (Falkowski 1980, Falkowski and Owens 1980). At very low light intensities (below approx. $20\mu Em^{-2}sec^{-1}$ or approx. $4\cdot6\,Wm^{-2}$) the cells become slightly bleached, and chlorosis will occur if cells are maintained in the dark for an extended period. Using data from Falkowski (1980, his Fig. 1), we may construct the following relationship between Chl/N-ratio and light intensity at which the cells are adapted:

$$\frac{Chl}{N} = \begin{cases} \left(\dfrac{Chl}{N}\right)_{max} (a_3 + a_4 \log I_0) & \text{if } I_0 > 4\cdot6\ Wm^{-2} \\[4mm] \left(\dfrac{Chl}{N}\right)_{max} a_5 & \text{if } I_0 \leqslant 4\cdot6\ Wm^{-2} \end{cases} \tag{13}$$

where $(Chl/N)_{max}$ is the maximum Chl/N-ratio (i.e. maximum chlorophyll content for shade adapted cells). Sakshaug (1978) found during the spring bloom in the Trondheimsfjord, a maximum Chl/N-ratio equal 0·27 for non-deficient, shade adapted cells. a_3, a_4, and a_5 are equal to 1·32, −0·51, and 0·7, respectively.

2.4. *Time course of adaptation*

Each cell needs some time to adjust its physiological state according to the environmental situation. Data shown by Falkowski (1980) indicate that the rate of adaptation is proportional to the difference between present level of adaptation and the new level of light adaptation towards which the cell is adapting.

$$\frac{dI_0}{dt} = v_{I0}(I_{0w}, I_0) = g_0(I_{0w} - I_0) \tag{14}$$

where g_0 is the rate constant taken to be $0\cdot026\,h^{-1}$ at 15°C during daylight (Falkowski 1980). g_0 is temperature dependent (Q_{10} of approx. 2·0).

When light intensity becomes so low that growth rate becomes only a few percent of its maximum ($\mu_{max}{}^E$) the chlorophyll is reduced when normalizing per carbon or nitrogen unit. This is evident from laboratory investigations of *Skeletonema* (Sakshaug and Andresen, in prep.) and has also been observed in the early spring bloom in the Trondheimsfjord (Sakshaug 1978, Hegseth 1982). The cells approach a dormant stage with very low respiration (Sakshaug, pers. comm.) and may survive for a long time in this stage. At high latitudes, therefore, the cells have a very low level of chlorophyll after the darkest winter. When light intensity increases again, energy is put into biosynthesis of chlorophyll. What is the dynamics of this adaptation process? There are, as far as we know, no data available to construct a relationship between light intensity, chlorophyll content and its rate of biosynthesis at very low light intensities. We, therefore, put forward the following hypothesis for the adaptation process at low light intensities:

> An overwintering algal cell that has become shade adapted during the winter will put the energy obtained by the gradually increasing light into biosynthesis of chlorophyll. Since the chlorophyll level and light intensity are very low, much energy cannot be available for this process. Energy obtained by the cell is probably proportional to both the chlorophyll level and light available and we may assume the following relationship:

$$\frac{d\text{Chl}}{dt} = g_1 \, \text{Chl} \, I_z \qquad (15)$$

> where g_1 is a constant and Chl is the chlorophyll content of the cell. This means that the adaptation process is very slow during the early spring. When the cell reaches a certain level of adaptation, the chlorophyll will probably decrease its importance and other factors such as enzyme level and temperature will dominate in the adaptation process.

The model presented here has the adaptation level expressed as I_0. Equation (15) will, therefore, be on the form

$$\frac{dI_0}{dt} = -g_1(\text{Chl}/\text{N})I_z \qquad (16)$$

Two questions arise when using eqns. (14) and (16). The first one is the transition between low and high light intensity. Low light intensity for a light adapted algae has not the same effect as on a shade adapted one. The energy that the algae can collect is probably of vital importance. We, therefore, take the outcome of the eqns. (14) and (16) that gives the smallest energy input (i.e. lowest rate of adaptation) to the cell.

The second question is the numerical value of the parameter g_1. If g_1 is put equal to 10 the adaptation rate will be almost independent of the energy input. On the other hand, if g_1 is less than 0·1 the adaptation process will not be fast enough to allow the algal cells to become shade adapted before the spring bloom is over. The correct value is between these two extrema. Sakshaug (1978) found that populations of the first spring bloom in the Trondheimsfjord had a Chl/N-ratio of 0·18, although large variations were found. This Chl/N-ratio corresponds, using eqn. (13), to an adaptation level equal 20. To achieve this level of adaptation during the simulation runs, g_1 is chosen equal to 0·5. Figure 1 (*a*) shows the adaptation level (I_0) as a function of time for three different values of g_1. The light conditions at the surface are equal to a latitude of

63·5°N (The Trondheimsfjord, Norway) with no clouds. Depth of vertical mixing is 20 m. Figure 1 (*b*) shows the effect of g_1 on the dynamics of the spring bloom. g_1 seems to be the most important physiological parameter which affects the onset of the spring bloom. Different species of phytoplankton have probably different initial levels of chlorophyll and rate of adaptation when light becomes available after the darkest winter period. This may, among other factors, be important in determining the species' composition during the spring bloom.
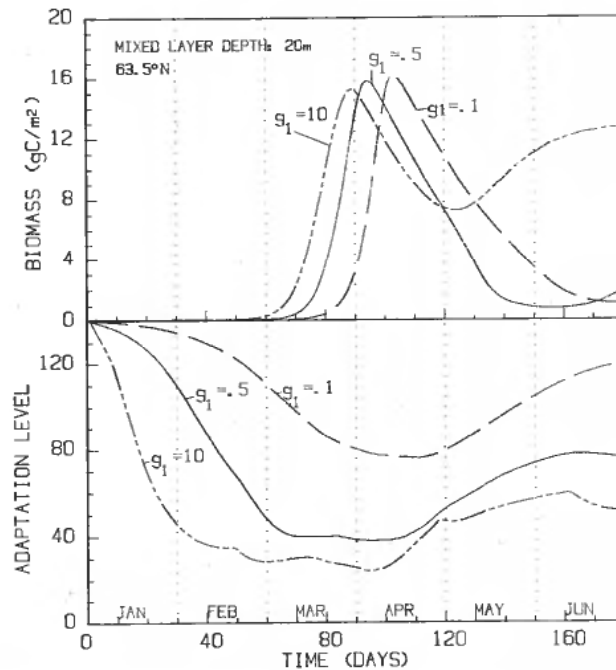
Figure 1. Effect on the depth integrated biomass of phytoplankton and its level of adaptation for three different values of the parameter g_1 (rate of adaptation at low light intensities). The apparently light adapted cells in the beginning of the simulation runs is a result of chlorophyll depression during the winter.

What happens to the chlorophyll during the Arctic winter? We assume here that cells placed in a dark environment lose chlorophyll until they reach a minimum level. The following equation will be applied during complete darkness:

$$\frac{dI_0}{dt} = \begin{cases} g_d(I_{0max} - I_0) & \text{if } I_0 < I_{0max} \\ 0 & \text{else} \end{cases} \qquad (17)$$

where g_d is a constant (equals 0·0004) and I_{0max} is the maximum adaptation level towards which the cells adapt (i.e. minimum level of chlorophyll during the winter) during complete darkness. I_{0max} is put equal to 140 Wm^{-2} which gives a Chl/N-ratio of 0·06 for cells surviving the winter.

2.5. *Physical and biological environment and initial conditions*

We always start our simulation runs with a homogeneous distribution of the limiting nutrient (nitrate) equal $10\,\text{mM Nm}^{-3}$. The vertical water column is divided into layers of depth 5 m. Each layer is assumed to be homogeneous and the vertical mixing coefficient describes the turbulent mixing between the layers. No horizontal movements are assumed. The extinction coefficient is taken equal to $0\cdot08\,\text{m}^{-1}$ for oceanic water (at 76°N) and $0\cdot15\,\text{m}^{-1}$ for coastal water (at 63·5°N and 70°N). Temperature is taken equal to 2·5°C throughout the whole water column and independent of time and latitude. Light is calculated from the theoretical height of the sun. No damping through clouds is usually assumed. This phytoplankton model is coupled to a zooplankton model, described by Slagstad (1981), which exerts a certain grazing pressure upon the algal cells. The parameters used in the phytoplankton model are given in the text and the Table. Phytoplankton is measured in nitrogen units and the initial concentration is taken equal $0\cdot01\,\text{mM Nm}^{-3}$.

Parameter name	Units	Value	Meaning
k_N	mM Nm^{-3}	1·0	Half-saturation constant for nitrate
ϕ_r	h^{-1}	0·002	Respiration rate of phytoplankton
ϕ_d	h^{-1}	0·043	Rate of bacterical decomposition of detritus into nutrients
w_d	mh^{-1}	0·36	Sinking rate of detritus
w_0	mh^{-1}	0·08	Sinking rate of phytoplankton when nutrients are depleted
w_{00}	mh^{-1}	0·02	Sinking rate at high nutrient level
a_1	h^{-1}	0·05	Parameters concerning the effect of adaptation level
a_2	h^{-1}	0·04	on the growth rate
g_0	h^{-1}	0·026	Rate of adaptation at medium and high light intensities
g_1	h^{-1}	0·5	Rate of adaptation per unit Chl/N-ratio
g_d	h^{-1}	0·0004	Rate of adaptation during complete darkness

Parameters used in the simulation runs.

3. Onset of primary production

Sverdrup (1953), in his famous paper, proposed a mathematical model to calculate conditions for blooming of phytoplankton. His conclusions have been widely accepted. Based on information about the light at the sea surface, the extinction coefficient and some value of the compensation light intensity (i.e. light intensity at which the production equals the respiration), he could calculate the critical depth for any water column. If the critical depth was less then the mixed layer, no net production could take place. However, if the critical depth was greater than the depth of mixing, a net positive production would occur in the water column and conditions for the onset of phytoplankton growth would have been established.

The depth of the mixed layer in the sea depends on a number of factors such as bottom topography, latitude, season, fresh water input, storms, temperature at the surface, etc. It is usually deepest in the late winter or early spring, before melt water from land is drained into the sea and solar heating take place. Fjords along the coast of Norway receive more or less fresh water input during the whole winter and, since they are not under the influence of the oceanic waves, the mixed layer is usually a few metres at its maximum.

In the Trondheimsfjord (around 63·5°N) the mixed layer depth is usually about 20 m thick. However, after extremely cold winters the mixing may reach down to more than 100 m (Sakshaug 1972). In the Balsfjord (near 70°N) the fresh water input is relatively small. Strong winds and low temperatures produce a mixed layer which may reach the bottom (180 m) (Eilertsen *et al.* 1981). Near the coast, the vertical mixing often reaches the bottom. This is mainly caused by tidal mixing. Further out, the water from the Coastal current may overlay the heavier Atlantic water, giving a pycnocline which is variable and perhaps a function of the distance from the coast. Off the coast, in the Atlantic water, the vertical mixing may reach several hundred metres and persist until late spring when the solar heating creates a thermocline. Further north, near the ice border, brackish water from the ice melting may create a strong pycnocline at 10–30 m depth. This situation facilitates an early spring bloom at these latitudes. The mixing coefficient within the mixed layer is not infinite. Depending on the conditions at the sea surface (storms, calm, temperature, etc.) the mixing coefficient will vary from day to day and from one year to another. Thus, there is a spectre of situations which gives several possible production conditions.

Definition of the onset of the spring bloom

Measuring winter minimum of phytoplankton in the ocean is not easy because the standing stock is low and does not vary much. Figure 2 shows the dynamics of phytoplankton growth during the winter for two different values of the vertical mixing coefficient, D_z. There are several possibilities for defining when the spring bloom really starts. But here we will take as a definition of the spring bloom the date when the phytoplankton concentration has increased threefold from its initial value.
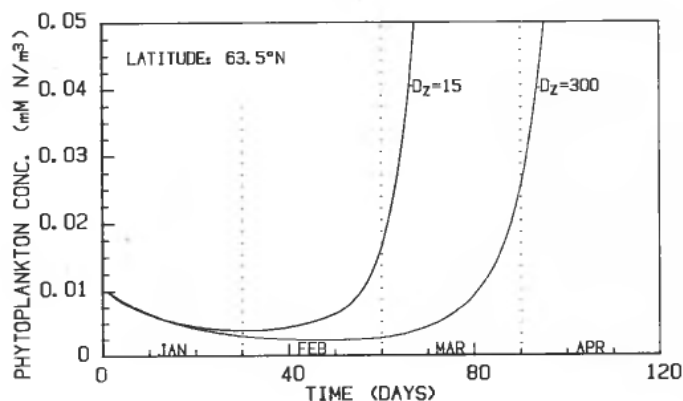

Figure 2. Phytoplankton dynamics during the winter and early spring for two different values of the vertical mixing coefficient. Depth of mixing is 100 m.

3.1. *Effect of the mixed layer depth and latitude*

Increasing the depth of the mixed layer will delay the onset of the spring bloom in a way similar to that found by Sverdrup (1953). Figure 3 shows the start of the spring bloom as a function of the mixed layer depth for three different latitudes. The mixing coefficient within the mixed layer is taken equal 300 cm²s⁻¹ (high enough to ensure the water column well mixed), in the pycnocline: 0·03 cm²s⁻¹, and below the pycnocline: 3 cm²s⁻¹.

When the mixed layer depth becomes less than about 10 m, the sinking rate (0·5 mday⁻¹) will reduce the net growth rate above the pycnocline. We, therefore, observe a delayed onset of primary production when the mixed layer becomes too shallow (Fig. 3). When the mixed layer becomes deeper the sinking rate becomes less important (Fig. 4). At 76°N the water is assumed oceanic and a low extinction coefficient (0·08 m⁻¹) gives a relatively deep euphotic zone during the early spring. The onset of the spring bloom, therefore, becomes less affected by the depth of the vertical mixing.
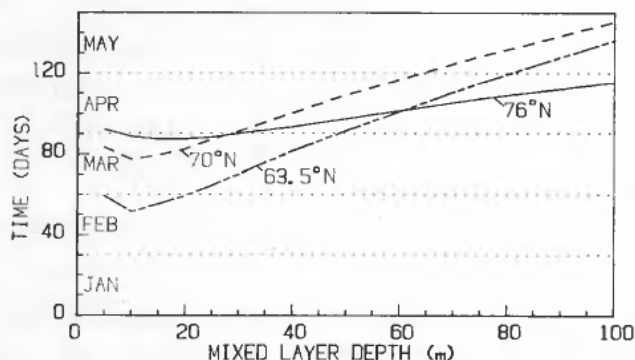
Figure 3. Onset of primary production as a function of the depth of the mixed layer at different latitudes. At the two southernmost latitudes the water is regarded as being coastal and thereby having a higher extinction coefficient.
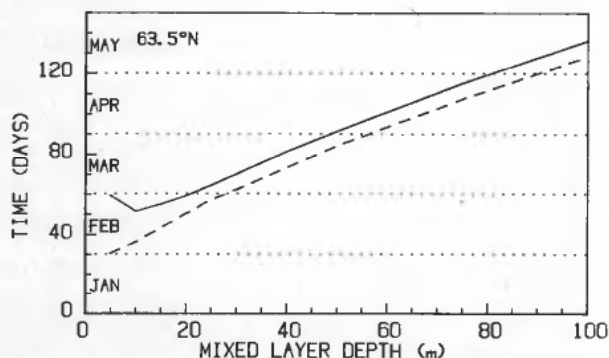
Figure 4. Onset of primary production as a function of the depth of the mixed layer. The solid line indicates the production start in the 'normal' case (all parameters have values according to the Table), whereas the broken line indicates the production start when the sinking rate is put equal zero.

3.2. *Effect of the mixing coefficient*

Start of primary production is plotted in Fig. 5 (solid line) as a function of the mixing coefficient. Depth of the mixed layer is 100 m. If the mixing coefficient is more than about 200 cm²s⁻¹, the water column can be regarded as completely mixed compared with the phytoplankton dynamics. Further increase in this parameter will, therefore, have a minor effect on the onset of the spring bloom. The mixing coefficient above which we can regard the water column well mixed, depends on the depth of the mixed layer. The more shallow the mixed layer is, the smaller the mixing coefficient can be taken to be, whilst still regarding the water column as well mixed (Fig. 5, broken line).

During periods with strong wind and low temperatures at the surface, a high mixing coefficient is likely, and the primary production becomes more dependent on the depth of the mixed layer. In periods with calm surface, the mixing coefficient may well have a sufficient low numerical value to be important for the phytoplankton. Reduction of light intensity by 50% will delay the spring bloom by 2–3 weeks. The start of the copepod production is about 2–3 weeks after the onset of the primary production.
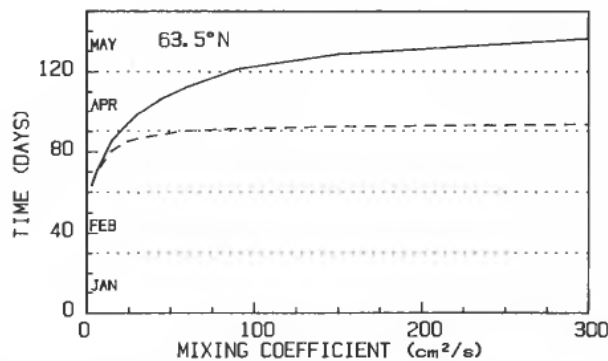

Figure 5. Onset of primary production as a function of the mixing coefficient within the mixed layer (solid line). The depth of the mixed layer is 100 m (solid line) and 50 m broken line).
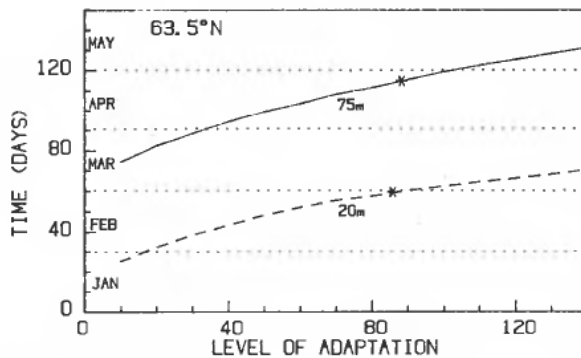

Figure 6. Onset of primary production as a function of the level of adaptation for two different mixed layer depths. The level of adaptation was kept constant during the simulation runs.

3.3. *Effect of adaptation*

Different algal species have different ability to adapt. How this may effect the onset of the spring bloom is indicated in Fig. 6 for two cases of the mixed layer depth. The asterisk marks the date for the onset of the spring bloom when adaptation is dynamic and the parameters are as in the Table. The change in adaptation level has similar effect on the 75 m mixed layer as on the 20 m mixed layer. If the cells were able to keep their chlorophyll content during the darkest winter, the spring bloom could have started 3–4 weeks earlier than in the 'normal' case.

4. Dynamics of the spring bloom

4.1. *Effect of the mixed layer depth and latitude*

In Fig. 7 (*a*) the concentration of phytoplankton (expressed in nitrogen units) in the upper mixed layer is shown as a function of time. A mixing depth of 20 m makes a relatively early spring bloom possible (solid line), despite the turbid water in the two southernmost cases. When the mixing depth becomes deeper, the date of culmination is strongly delayed in the coastal water. In the oceanic water the effect of mixing depth becomes less important. When the mixing depth is 50 m, the simulation runs indicate that the culmination is almost 3 weeks earlier in the oceanic water at 76°N than in the coastal water at 63·5°N.

When the mixing depth is 20 m the culmination is caused by limitation of nutrients. After the first bloom in the upper mixed layer the algal cells are removed by sinking or grazing. In the oceanic water there will be enough light to give a new bloom below this
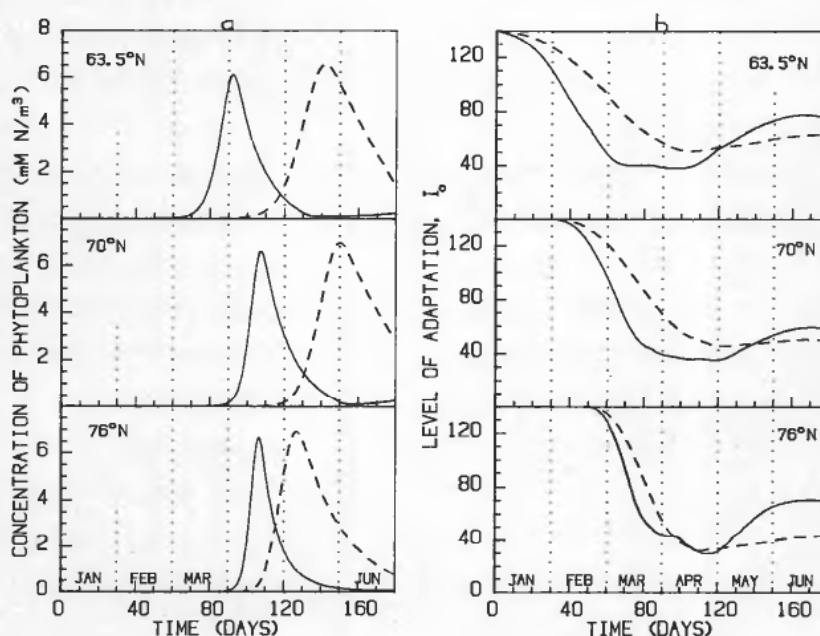

Figure 7.   Phytoplankton concentration and its level of adaptation in the mixed layer during the spring at three different latitudes. Depth of the mixed layer is 20 m (solid line) and 50 m (broken line).

depth. In the coastal water most of the light will be absorbed in the upper 20 m and only a small production can take place. This is indicated in the biomass data in Fig. 8. Production will here depend on regeneration and supply of nutrients through the pycnocline. If the mixed layer depth becomes less than 20 m, a second bloom is possible in the coastal water, too. However, during the spring, melting of snow will release large amounts of fresh water into the sea and change the mixing conditions in the coastal water. A second bloom may, therefore, take place in some of our fjords (Sakshaug and Myklestad 1973) but this case will not be discussed in this work.
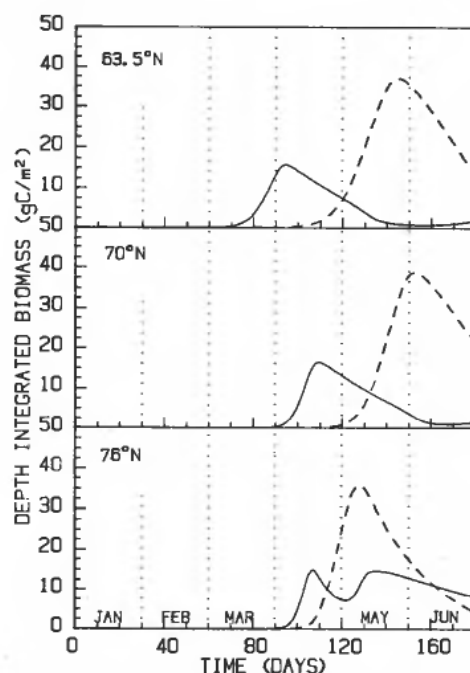

Figure 8. Depth integrated biomass of phytoplankton (gC/m^2) as a function of time at three different latitudes. Depth of the mixed layer is 20 m (solid line) and 50 m (broken line).

If the mixed layer is deeper (50 m), the average light that the algal cells see is low and the adaptation becomes slow (Fig. 7 (*b*)) during the early spring. The growth rate is small until the light intensity has increased and the bloom can start. When the mixing is strong enough, the depth variation of the nutrient and phytoplankton profile is vertical down to the pycnocline. Thus, nutrients from a relatively deep water column are available for phytoplankton growth. This allows a high production rate until the nutrients become limiting.

In the examples shown above, the culmination of the spring bloom was caused by shortage of nutrients. This is in agreement with what is usually found in the sea. However, Eilertsen (pers. comm.) has found that the spring bloom in the Balsfjord is not terminated by the shortage of nutrients (at least not nitrate and silicate). In order to generate some possible hypothesis to explain why this happened, we have made simulation runs using mixed layers down to 200 m. The results of these runs are shown in the Figs. 9 and 10. With the parameters used in these examples, the culmination of
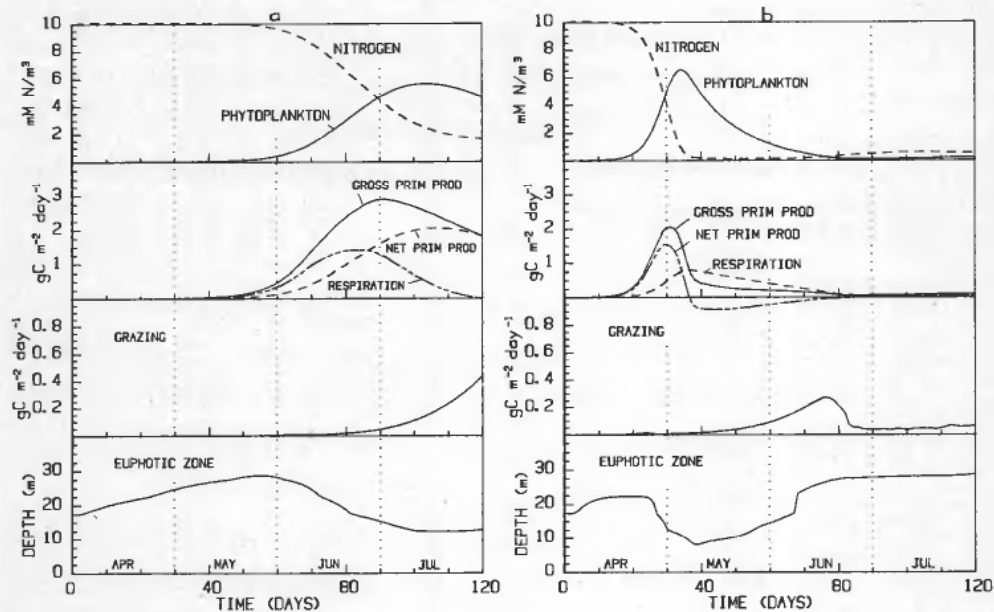
Figure 9. Dynamics of primary production, nitrogen and grazing for a mixed depth of 150 m (*a*) and 20 m (*b*). Latitude: 70°N.
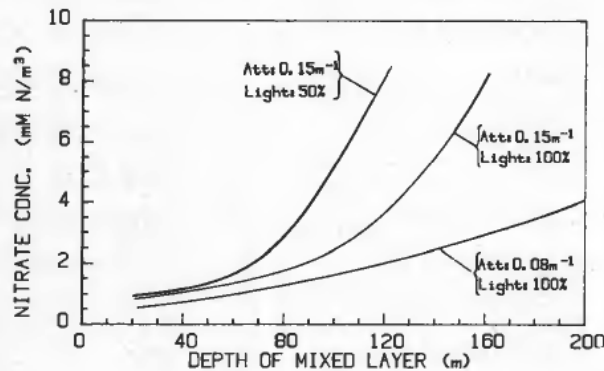

Figure 10. Nitrate in the upper mixed layer at the time of spring bloom culmination as a function of the depth of the mixed layer. Light and attenuation coefficient without phytoplankton (Att:) are given in three combinations.

the spring bloom does not seem to be caused by shortage of nutrients when the depth of the mixed layer is more than approx. 100 m.

A mixed layer has a homogeneous vertical distribution of phytoplankton and nutrients. If the mixed layer is deeper than the euphotic zone, there is one upper part of the water column where light is sufficient to give a net production. The lower part of this zone has the same concentration of phytoplankton but the light intensity is not sufficient to allow any growth. The respiration process will dominate and try to reduce phytoplankton biomass. As the concentration of phytoplankton increases, the depth of the euphotic zone decreases and the respiration process becomes dominating (Fig. 9 (*a*)). Deep mixed layer gives a relatively long period between the onset and

culmination of the spring bloom. The copepods are given more time to become larger and thereby exert a higher grazing pressure on the phytoplankton compared with the shallow mixed case. In addition, there is loss of phytoplankton due to sinking. When the losses equal the production there is no further increase in the phytoplankton biomass. We observe that the grazing pressure is not important in these simulation examples.

If the mixed layer is more shallow (Fig. 9 (*b*)), the depth integrated biomass of phytoplankton becomes less at the same concentration and the total respiration becomes smaller. The regeneration of nutrients through respiration/detritus is reduced and, since the total amount of available nutrients in the mixed layer is less, the culmination of the bloom is more likely to be caused by limitation of nutrients. In Fig. 10 the concentration of nitrate in the mixed layer at the time of spring bloom culmination is plotted against depth of the mixed layer for three combinations of light at the surface and attenuation in the water column. If the production rate is reduced by other factors such as temperature or light, the concentration of nutrients will be higher at the time of culmination.

4.2. *Effect of adaptation*

Shade adapted algal cells are able to collect more light energy than light adapted ones at low light intensity. The average light intensity that the cells see will, besides the latitude and time of the year, depend on the depth of the mixed layer. We may expect, therefore, that the effect of changing adaptation level should depend on the depth of the mixed layer. In Fig. 11 the phytoplankton concentration is plotted as a function of
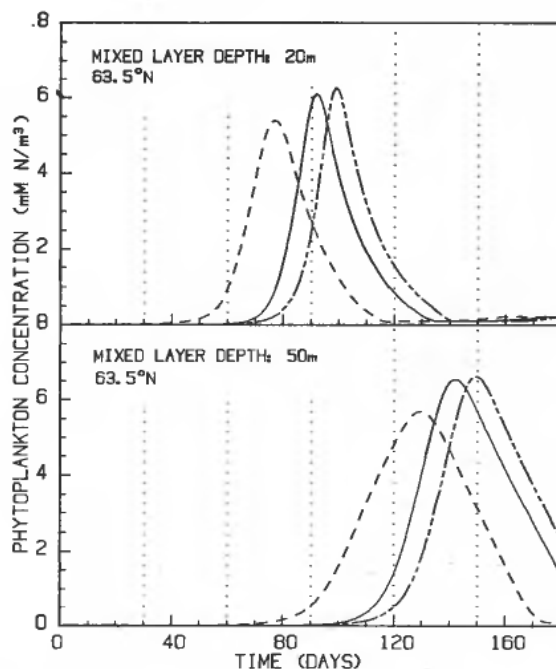

Figure 11. Concentration of phytoplankton in the mixed layer as a function of time for different adaptation conditions. (—————) adaptation is dynamic as in the model; (- - - - - - - -) adaptation level is constant, equal 20; (— - - — - -) adaptation level is constant, equal 100.

time for three different adaptation conditions and mixed layer depths of 20 and 50 m. The solid line shows the 'normal' case where the adaptation process is dynamic as in the model. The broken lines show phytoplankton dynamics when the adaptation level is kept constant during the simulation period.

Keeping the cells shade adapted during the winter and spring will make an early onset of the spring bloom possible (see also Fig. 6). Light inhibition near the surface will, however, reduce the average growth rate and the date of culmination will be less affected by the adaptation level. There is no pronounced difference between shallow and deep mixing cases.

4.3. *Effect of cloud cover*

The cloud cover during the spring may be highly variable from one year to another. The effect on the phytoplankton dynamics of 50% reduction in light intensity is shown in Fig. 12. The solid line is the 'normal' case (100% light), whereas the broken line exhibits the dynamics at reduced light intensity. We observe that this reduction in light intensity leads to a delayed bloom of 2–3 weeks, depending on the mixed layer depth.

It is interesting to see how the adaptation level affects the production when the light intensity is reduced (Fig. 13). Comparing the effect of constant adaptation level under different light conditions (Figs. 11 and 13), it is obvious that the phytoplankton production becomes more sensitive to the level of adaptation when the light conditions are bad. Whereas the variation in the date for spring bloom culmination was about 17 days under 'normal' light conditions, this variation was about 28 days when light intensity was reduced by 50% (mixed layer depth of 20 m). When the mixed layer becomes deeper the variations in the date of spring bloom culmination will increase.
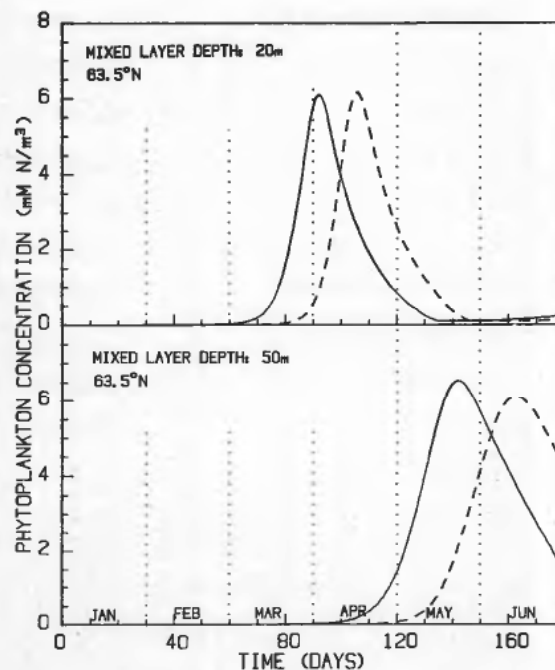

Figure 12.   Comparison between the phytoplankton dynamics under 'normal' light conditions (solid line) and when the light intensity is reduced by 50% (broken line).
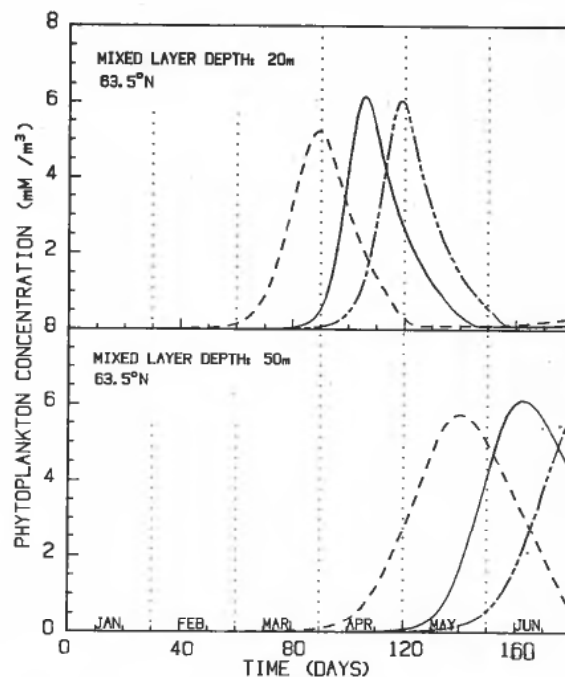
Figure 13. Phytoplankton concentration in the mixed layer as a function of time for different adaptation conditions and reduced light intensity of 50%. (————) adaptation is dynamic as in the model; (- - - - - - - -) adaptation level is constant, equal 20; (— - - — - -) adaptation level is constant, equal 100.

5. Discussion

The purpose of this work was not to calculate the exact dates for the onset and culmination of the spring bloom, but rather to discuss the relative influence of the vertical mixing and adaptation properties on these dates. Data used in the simulation runs are uncertain and some of them are only guesses. We should, therefore, be careful when comparing the simulation results with measurements. In general, the biological data and, especially, the physical data (vertical mixing coefficient and advection) are incomplete, which will add still more uncertainty. However, it is important to find out which parameters would give the most pronounced effect on the result when their numerical values are perturbated.

The respiration rate has been taken as a constant, independent of adaptation level. Falkowski and Owens (1980) found that the respiration rate was reduced when the cells became shade adapted. As mentioned earlier Sakshaug (pers. comm.) have data which indicate a low respiration rate when the cells were in a dormant stage. A lower respiration rate during the early spring than used in the model would have given an earlier spring bloom. Simulation experiments performed indicate that this is especially pronounced when the depth of mixing increases. For example, reducing the respiration rate by 50% will give a spring bloom which is one week earlier when the mixing depth is 20 m, whereas it is 3 weeks earlier when the mixing depth is 75 m.

In the north, near the ice border, the warm Atlantic water will melt the ice and create a mixed layer which is only a few metres thick. This melting is possible during the

winter and the early spring, long before the solar heating has any influence on the stability of the water column. Simulation runs indicate that the spring bloom may start as early as in March/April. There are no data available for this area at this time of the year. However, the Fisheries Research Institute in Bergen took a cruise up to the ice border in the first half of May 1981. They found a very low level of nitrate above the pycnocline (Rey, pers. comm.) which indicated that the primary production must have started in April that year.

Further south, in Balsfjord, vertical mixing reaches almost to the bottom (180 m) during the spring. If the water column is well mixed (i.e. the vertical mixing coefficient approaches infinity), the primary production should not, according to the simulation results, start before June. The data that are available (Eilertsen 1979) show that the onset of primary production may take place as early as in March and culmination occurs in the second half of April. How could this be possible? Although the Balsfjord apparently seems to be well mixed, the mixing coefficient is probably far from infinite. The fjord is not under the influence of oceanic waves and the vertical mixing is probably in the region where small variations may affect the primary production (see Fig. 5). Since the mixing coefficient depends on the meteorological conditions at the surface, we may expect to find relatively large variations in the spring bloom dynamics from year to year.

In the Trondheimsfjord, the mixed layer is usually about 20 m when the spring bloom starts. In such a shallow mixed layer the mixing coefficient will not have any strong effect on the phytoplankton dynamics. Provided that the depth of the mixed layer could be kept at this level, the effect of wind and temperature should be small. Variable light conditions are probably more important. The date for the spring bloom culmination predicted by the model is in good agreement with what was found by Sakshaug (1972) and Sakshaug and Myklestad (1973).

A deep mixed layer will not only delay the bloom but the depth integrated biomass of phytoplankton will be greater and the bloom will persist for a longer period. Bech (1982) has found similar results when sampling in two areas near Tromsø with different turbulence characteristics. A deep mixed layer will usually give a higher total production of phytoplankton (Slagstad 1981). This will facilitate a high production of zooplankton because food is available over a wide range of depths and the animals do not depend upon an optimal behaviour in order to be where the food is present.

By changing parameters in the adaptation part of the model, we can simulate algal species having different responses to various light conditions. Doing this, it is hard to find any combinations of the parameters that produce one algal species which is best adapted to certain mixing conditions and any other combinations which are best adapted to other mixing conditions. In general, the most dark adapted species will grow fastest during the early spring, whether the mixing is deep or shallow. Thus, there must be other, additional factors which interact if the species composition changes when the depth of the mixed layer is changed. Sinking rate and effect of temperature are possible factors here.

We have seen in this report that the vertical stability is the most dominating factor in determining the onset and the dynamics of the spring bloom. It is likely that the stability conditions may effect the species composition as well. How this affects the zooplankton growth and thereby the growth potential for the fish is not known. We must, however, expect that an optimal way exists of controlling the vertical stability, seen from a fish growth rate point of view.

Many fjords along the coast of Norway receive water from hydroelectric power plants during the winter. It may well be that some of these power plants could, in addition to the energy demands, be optimized in order to give the best possible stability conditions for production of fish.

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