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Torn between extremes: the ups and downs of phytoplankton

Received: 31 May 2004/Accepted: 6 September 2004
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Abstract We present a model to investigate the success and resulting patterns of phytoplankton migration, based on motility which depends exclusively on the internal energy and nutrient state of the cells. The model consists of migrating and non-migrating sub compartments for phytoplankton, and migration is a function of the prescribed threshold values for internal quotas. The different modes of phytoplankton behavior are evaluated in the framework of a coupled physical–biological model that includes wind-driven up- and downwelling. The results show that (1) migration is almost always advantageous with respect to biomass, (2) a wide variety of migration patterns (e.g., subsurface maxima, surface-avoidance behavior) can be reproduced by a relatively simple treatment of motility, (3) multiple deep chlorophyll maxima can be explained as the result of certain threshold values in combination with negligible vertical movement of the water, and (4) descending tongues of high phytoplankton concentration may be caused by migratory behavior and not necessarily by subduction due to frontal convergence. Thus, our model offers explanations for a large variety of observed phytoplankton distributions and migration patterns.

Keywords Vertical migration · Phytoplankton · Upwelling · Downwelling · Internal quotas · Multiple deep maxima

Responsible Editor Andreas Oschlies

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1 Introduction

Dependent on both light and nutrients, phytoplankton cells face a fundamental dilemma, since only seldom are they lucky enough to find both in the same location. Instead of remaining passive and relying on the advective and turbulent exchange of nutrients from below (upwelling) or deeper (winter) mixing to restore the nutrient levels, they may “choose” to actively seek their fortune by migration.

Indeed, vertical migration achieved either through adjustment of buoyancy or by means of flagella has been observed for many primary producers in limnic and oceanic waters. The former is used by several cyanobacteria species (e.g., Oliver 1994; Villareal and Carpenter 2003) and some of the larger diatoms (e.g., Richardson and Cullen 1995; Moore and Villareal 1996) the latter is common for most dinoflagellates (e.g., Eppley et al. 1968; Jones 1991; Figueroa et al. 1998), which represent a large fraction of the phytoplankton and are thus subject of most migration studies. During periods of nutrient exhaustion in the upper layers of stratified environment, motility enables the species to access the higher nutrient concentrations in deeper layers (e.g., Eppley et al. 1968; Raven and Richardson 1984). Frequently, a nocturnal downward migration to the nutricline has been found (e.g., MacIntyre et al. 1997, and further references therein). However, both field and laboratory observations have revealed a large variety of different migration patterns, which have been connected to a similar number of corresponding strategies (see Fig. 1). In particular, it has been assumed that migration follows external factors, i.e., temporal and spatial changes in (1) the light environment and (2) the nutrient field (called photochemotaxis). For example, it has been shown that variations in the light regime can provoke changes in the swimming direction of the species (Clegg et al. 2003); similarly, surface avoidance in cases of high irradiance has been reported for

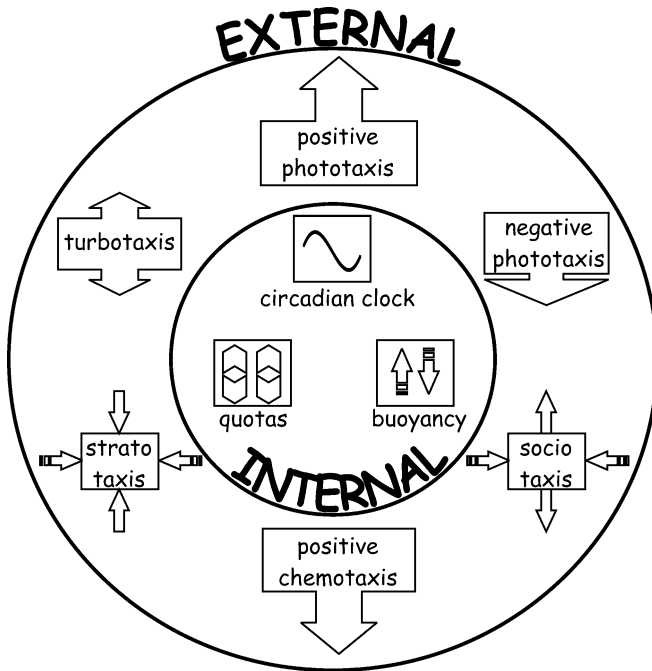


Fig. 1 Overview of proposed vertical migration strategies for phytoplankton. Among the external factors, *positive phototaxis* and *chemotaxis* are most often applied, *negative phototaxis* corresponds to surface avoidance due to excessive light levels. *Turbotaxis* summarizes responses to gradients in turbulence and current shear. *Stratotaxis* refers to gradients in temperature, salinity, density, or pressure, which the phytoplankton may use to find its preferred environment. *Sociotaxis* includes gradients in biological interactions like grazing, crowding, and the production of harmful exudation substances (i.e., negative chemotaxis). Internal factors are *circadian* rhythms, density-regulated motility and the state of internal (nutrient and energy) quotas. Depth-keeping behavior is part of either stratotaxis or buoyancy. *Geotaxis* does not appear in this diagram because it does not refer to a causing mechanism but is merely a description of the migration direction. Comprehensive descriptions of the migration behavior of a species are often accomplished by prescribing threshold values, target depths, gradient detection limits, and/or time periods for a combination of these mechanisms

phytoplankton in coastal areas (Anderson and Stolzenbach 1985).

Closer examination of the different factors leading to a certain migration behavior indicate that (1) species with the ability to migrate may or may not use this capability, and (2) not necessarily all individual organisms of a population carry out the same vertical movements. The history (or internal state) of the individual cell seems to be equally important for migration as the instantaneous nutritional or light environmental conditions (Cullen and MacIntyre 1998; Kamykowski et al., 1998; Clegg et al., 2003). This may or may not include migration as a circadian rhythm induced by an endogenous clock as proposed by Suzuki and Johnson (2001), which, however, alone is often insufficient to explain the observed complex migration behavior (Yamazaki and Kamykowski 2000).

Motility of phytoplankton has been the target of several modeling studies. Models treating phytoplankton migration as an externally controlled process have

been applied successfully in some cases (e.g., Yamazaki and Kamykowski 1991). More recently, motility as a function of the internal physiological state has been considered. The “natural” framework for such studies is the Lagrangian approach. Models of this kind have been applied, for example, to quantify the success of internal and external based migration behavior of a phytoplankton cell (Kamykowski and Yamazaki 1997) or to quantify the success of migrating dinoflagellates compared to “passive” diatoms (Broekhuizen 1997). Eulerian methods have been employed to investigate the bloom of certain harmful algae (Liu et al. 2001, 2002). There are, however, still some open questions: (1) cases where only part of the population is found to migrate require a more quantitative explanation, (2) the development of multiple deep chlorophyll maxima (e.g., Kononen et al. 2003) has not been investigated and (3) the adaptation of migrating phytoplankton populations to various physicochemical environments has not been taken into account with sufficient detail.

To improve our understanding of phytoplankton migratory behavior and its consequences, we present a biological model which treats vertical migration as exclusively dependent on the internal state of the cells. One goal was to minimize the number of empirical parameters (threshold values for the internal biochemical status of the cells and the external fields) that have previously been used to describe the behavior of migrating phytoplankton species (Kamykowski and Yamazaki 1997; Liu et al. 2001). This model will be coupled to a twodimensional ocean circulation model to investigate the migration behavior of phytoplankton under different environmental conditions (up- and downwelling).

After a detailed model description and the presentation of the experimental configuration in Section 2, we show the results of a parameter study that highlights the sensitivity of migration patterns relative to internal quotas and under varying physical conditions (Section 3). A summary is presented in Section 4, followed by conclusions and an outlook (Section 5).

2 The modeling approach

2.1 State of the art of migration modeling

Coupled physical-biological models are usually of the Eulerian type. In the widely used NPZD-type models the growth of phytoplankton is described as directly proportional to light and external nutrient availability. These have been used successfully to simulate passive phytoplankton dynamics under a wide variety of circumstances. Migration can be included, either by prescription and/or dependent on external light and nutrient fields.

A relatively recent development is the consideration of internal quotas (Droop 1973). In this new generation of mechanistic models (e.g., Geider et al. 1998; Baird

et al. 2004, metabolism aspects are taken into account by adding more compartments for the internal nutrient and energy status of the cells. While this is straightforward for Lagrangian models, it presents a problem for Eulerian models, because different values of internally stored energy or nutrients *cannot* be mixed or advected. Consequently, one has to resort to more elaborated ways of treating the internal quotas: for example, Janowitz and Kamykowski (1999) have proposed an expanded Eulerian model, which considers a spectrum of internal states. Such a model was used by Liu et al. (2001), who then prescribe a large number of threshold values and other parameters for the internal and external state of one particular phytoplankton species. We believe that significant progress in understanding of phytoplankton migration can be made with an alternative approach, using a model that is simple enough to explore the full parameter space without loss of generality.

2.2 The EQN model for phytoplankton

Our goal here is to develop a conceptually simple, yet flexible (i.e., universally applicable) tool to study vertical migration patterns of phytoplankton in a comprehensive way. We chose the Eulerian framework to facilitate its coupling to OGCMs.

Our model uses three compartments to describe phytoplankton: the phytoplanktonic organic cell compounds P , the intracellular stored inorganic nitrogen S and the gross stored energy G . This allows us to consider nutrient uptake and growth (following ideas by Droop 1973) as well as light capture (e.g., Baird et al. 2004) as separate processes, determined by the internal quotas for nutrient $Q = S/P$ and energy $E = G/P$. External nitrogen N completes our system.

Within this framework, the resulting **EQN** (Energy–Quota–Nutrient) phytoplankton model reads:

$$\frac{\partial G}{\partial t} = \underbrace{\omega_{lc}\sigma_L(1 - (E/E_{\max})^n)P}_{\text{light capture}} - \underbrace{\omega_{up}(1 - \sigma_Q)\sigma_N\sigma_E P}_{\text{nutrient uptake}} - \underbrace{\omega_{gr}\sigma_Q\sigma_E P}_{\text{growth}} - \underbrace{\mu(1 - \sigma_E)G - \mu^*PG}_{\text{mortality}} \quad (1)$$

$$\frac{\partial S}{\partial t} = \omega_{up}(1 - \sigma_Q)\sigma_N\sigma_E P - \omega_{gr}\sigma_Q\sigma_E P - \mu(1 - \sigma_E)S - \mu^*PS \quad (2)$$

$$\frac{\partial P}{\partial t} = \omega_{gr}\sigma_Q\sigma_E P - \mu(1 - \sigma_E)P - \mu^*P^2 \quad (3)$$

$$\frac{\partial N}{\partial t} = -\omega_{up}(1 - \sigma_Q)\sigma_N\sigma_E P. \quad (4)$$

The first equation describes energy gain through light capture, energy consumption due to uptake and growth, as well as energy loss, through phytoplankton mortality. For convenience, the gross energy G like phytoplankton P is given in nutrient units (mmol N m^{-3}), so that no further conversion factors need to be applied. According

to Raven and Richardson (1984), the energetic cost for using the flagella is usually negligible, therefore we do not specify an energy sink due to migration. The energetic costs of cell maintenance are also not included in our system of equations, because conceptually we are considering only the energy exceeding this maintenance. Note, however, that both can be easily added, if found necessary for a specific study.

We assume a temperature-dependent maximum growth rate of

$$\omega_{gr} = \ln(2) \cdot 0.851 \cdot 1.066^T$$

and, to remain close to the traditional two-equation system with only N and P (see also the Appendix), we specify that maximum growth and uptake rates are identical and that the maximum light capture rate is the sum of both:

$$\omega_{lc} = (\omega_{gr} + \omega_{up}) = 2\omega_{gr}.$$

These maximum rates are reduced by several processes:

– The external light limitation factor is defined as

$$\sigma_L = \frac{\alpha I(z)}{\sqrt{\omega_{lc}^2 + \alpha^2 I(z)^2}},$$

where α is the initial slope of the PI curve, and the photosynthetically active radiation is computed including self-shading as

$$I(z) = I_s \exp [k_w z + k_c \int_0^z P(z') dz'],$$

with z negative downward.

– For internal light capture limitation we have chosen the term $(1 - (E/E_{\max})^n)$ (n large and even) instead of the often used $(1 - E/E_{\max})$ because we find it implausible to assume that the light capture will be reduced well before the maximum value E_{\max} is reached. Following Baird et al. (2004), we use $E_{\max} = 1$, i.e., the internal energy storage can be as large as the energy stored in the organic material.

– Both uptake and growth are limited by the internally available energy (σ_E), the former also by the external availability of nutrients (σ_N). Again, the form of σ_E assumes that uptake and growth do not slow down before the energy reserves are almost exhausted. The partitioning between growth and uptake is regulated by σ_Q ; below a critical value of nutrient quota Q_c more energy is used for uptake than for growth and vice versa. The partitioning and limiting functions are thus

$$\sigma_E = 1 - \left(\frac{E}{E_{\max}} - 1\right)^n,$$

$$\sigma_N = \frac{N}{k_N + N}, \text{ and}$$

$$\sigma_Q = \frac{Q}{Q_c + Q}.$$

The mortality is decomposed into two parts: a linear term is weakly dependent on the internal energy level, to

include, e.g., genetic defects and based on the idea that a too-low energy level will increase mortality and a non-linear term that takes into account a higher (nonlinear) grazing pressure during periods of high phytoplankton concentrations. The details of the sink terms, however, do not affect the qualitative structure of the solutions.

A complete listing of model parameters is given in Table 1. Although most model parameters are taken to represent motile dinoflagellates, many of the results may also be applicable to buoyant diatoms and cyanobacteria.

In this system of equations, nutrient assimilation is not directly proportional to the light availability. Although this could be easily changed for species with light-dependent nitrogen uptake, we find that the chosen energy limitation factor σ_E causes nutrient uptake and growth to cease shortly after dusk and to begin shortly after dawn, without prescribing a strict relationship. We also acknowledge that energy storage might be reduced when phosphorus and iron are the limiting nutrients. It should be noted, though, that our goal in this study is not to represent the complexity of all physiologically relevant quantities of a specific phytoplankton species, but to highlight the multitude of migration patterns that

can be derived from internal quotas alone. Obviously, the model can be adapted to a multitude of species and regions.

2.2.1 Sub-compartments

While these equations can be directly used in a Lagrangian approach, they are not applicable to an Eulerian model without further consideration. The reason is that the internal quota and energy levels are not subject to mixing and advection like continuous concentrations like nutrients or phytoplankton itself, because they do not represent a continuous field of indistinguishable particles. The continuum hypothesis, which forms the basis for coupled Eulerian hydrodynamic-ecosystem models is no longer valid, if the particles are not identical. Internal quotas cannot be treated as a generally accessible pool of resources, like the external nutrients. In particular, a mixing process that homogenizes two populations of phytoplankton with different internal nutrient quota does not lead to a uniform population with the average internal quota; in other words, the history of sub-populations is important.

An alternative is to use Eulerian methods, which include distribution functions (as used in sea-ice models and water droplet models in the atmosphere). Here, a variable (e.g., phytoplankton) will be decomposed into several classes which are representative for different ranges of internal nutrient level. One such approach has been used by Janowitz and Kamykowski (1999) and Liu et al. (2001) under the name expanded Eulerian method. In this sense, models like the one by Baird et al. (2004), can be described as a zero-order approach to internal quotas.

A prerequisite for coupling this EQN model to a multidimensional ocean circulation model is the restriction to a minimum number of categories. Therefore, we have subdivided the phytoplankton, internal energy, and internal nutrient compartments into only four subcompartments: one for low energy quota – low nutrient quota (LL), one for high energy quota–low nutrient quota (HL), one for low energy quota–high nutrient quota (LH) and one for high energy quota–high nutrient quota (HH), henceforth called categories. The boundaries between these categories are determined by the threshold values θ_E and θ_Q for internal energy quota and internal nutrient quota, respectively. This 2×2 matrix enables us to consider the history of the individual organisms, the evolution of their nutritional and energetic status.

To implement phytoplankton motility, we assume that members of the HL (LH) category migrate downward (*upward*) with a constant speed. Thus, the only assumption we make for the implementation of migration is fixed migration velocities and the fundamental dependence on internal quotas. For the two remaining categories (HH and LL) we assume passive behavior, based on the assumption that cells with either high or

Table 1 Variables and constants for the EQN model

Prognostic variables	
Nutrient (here Nitrogen)	N (mmol N m ⁻³)
Gross stored energy	G (mmol N m ⁻³)
Internally Stored nitrogen	S (mmol N m ⁻³)
Organic Phytoplanktonic nitrogen	P (mmol N m ⁻³)
Ratios and factors	
Internal Energy level	E (G/P) (nondimensional)
Nitrogen Quota	Q (S/P) (nondimensional)
Limitation factor for Energy	σ_E (nondimensional)
Partitioning factor for internal nitrogen Quota	σ_Q (nondimensional)
Limitation factor for Nitrogen uptake	σ_N (nondimensional)
Limitation factor for Light	σ_L (nondimensional)
Critical value for internal Quota	$Q_c = 0.25$ (nondimensional)
Exponent for the energy limitation factor	$n = 20$ (nondimensional)
Value for maximum internal Energy quota	$E_{\max} = 1$ (nondimensional)
Constants	
Initial slope of the PI-curve	$\alpha = 2.9 \times 10^{-7} \text{ m}^2 \text{ W}^{-1} \text{ s}^{-1}$
Half saturation constant for Nitrogen	$k_N = 0.3 \text{ mmol m}^{-3}$
Linear mortality rate	$\mu = 2 \times 10^{-7} \text{ s}^{-1}$
Quadratic mortality rate	$\mu^* = 1 \times 10^{-7} \text{ m}^3 (\text{mmol N})^{-1}$
Self shading parameter	$k_c = 0.07 \text{ m}^2 (\text{mmol N})^{-1}$
Attenuation coefficient for coastal seawater	$k_w = 0.1 \text{ m}^{-1}$
Other variables	
Maximum light capture rate	$\omega_{lc} \text{ (s}^{-1}\text{)}$
Maximum nitrogen uptake rate	$\omega_{up} \text{ (s}^{-1}\text{)}$
Maximum growth rate	$\omega_{gr} \text{ (s}^{-1}\text{)}$
Temperature	$T \text{ (}^\circ\text{C)}$
Depth	$z \text{ (m)}$
Irradiance (PAR)	$I \text{ (W m}^{-2} \text{ s}^{-1}\text{)}$
Surface Irradiance (PAR)	$I_s \text{ (W m}^{-2} \text{ s}^{-1}\text{)}$

low nutrient and energy levels do not gain much by migration; the former is self-sufficient, the latter will not benefit immediately from either higher external nutrient concentrations because of the lack of energy to take them up or from higher light levels because it does not have sufficient nutrients to grow¹.

Of course, more refined assumptions could be made (migration speed proportional to internal quotas, or even external concentrations or daytime), but that would weaken our approach, as it would require the specification of a number of parameters that are generally not known and thereby reduce the fundamental nature of the results.

2.2.2 Transfer of phytoplankton between categories

Additional assumptions have to be made about the redistribution of biomass between different categories. Again, we resort to a relatively simple approach, assuming that the computed internal quota \bar{q} (denoting either E or Q) represents a mean value and that the actually occurring values lie in the range $(\bar{q} - \delta q \leq q \leq \bar{q} + \delta q)$ with uniform distribution. If the quota in any category approaches the threshold value θ_q , an increasingly large fraction of the phytoplankton biomass (and their quotas) will be transferred to the adjacent category. Simultaneously, the internal quota of the remaining phytoplankton decreases, since those individuals with the most extreme quota have left the subcompartment. The transfer velocity v_q is assumed to be proportional to the proximity to the threshold value.

The redistribution terms in the prognostic equations (for phytoplankton P , gross internal energy G , and stored internal nutrient S , here represented as Ψ) reads:

$$\frac{\partial \Psi}{\partial t} = -\frac{\partial \Psi}{\partial E} (v_E^\Psi \Psi) - \frac{\partial \Psi}{\partial Q} (v_Q^\Psi \Psi),$$

where v_E^Ψ and v_Q^Ψ are the generalized velocities in E and Q direction. For the exchange between HH and HL they are

$$\begin{aligned} v_q^P &= v_{q_{HH}}^P - v_{q_{HL}}^P \\ v_{q_{HH}}^P &= \lambda \{1 + \max[(\theta_q - q_{HH})/\delta q, -1]\} \\ v_{q_{HL}}^P &= \lambda \{1 - \min[(\theta_q - q_{HL})/\delta q, 1]\} \\ v_{q_{HH}}^Q &= v_{q_{HH}}^E = 0.5v_{q_{HH}}^P \\ v_{q_{HL}}^Q &= v_{q_{HL}}^E = 1.5v_{q_{HL}}^P, \end{aligned}$$

with $\delta q = 0.05$ and a transfer timescale of $\lambda^{-1} = 7200$ s. The factors for quota transfer result from the assumption of uniform distribution of quotas. Analogous expressions hold for the transfer between the other categories. It turns out that the model is rather insensitive

to reasonable changes in any of the parameters, as rapid transfer into a neighboring category changes the mean quota there sufficiently to initiate partial return transfer.

This model, called **EQN2x2**, is coupled to the physical OGCM, as described next.

2.3. The physical model

The physical component is represented by a fully prognostic primitive equation ocean circulation model (Haidvogel et al. 1991), with a vertical mixing parameterization that determines the vertical mixing coefficient $A_v(x, z, t)$ by taking into account the local stratification and vertical current shear (Pacanowski and Philander 1981).

The experimental configuration features a two-dimensional ($x - z$) domain, with a flat bottom at 50 m depth. The horizontal resolution is 1 km, the vertical grid has 50 degrees of freedom and is slightly stretched, with 0.75 m at the surface and 1.5 m at the bottom.

Initially, the fluid is horizontally uniformly stratified, with a thermocline in 15 m depth. A nutricline is located in 30 m depth (Fig. 2a). Wind stress normal to the model plane, increasing gradually for the first 7 model days, induces upwelling at the right and downwelling at the left boundary. Solar radiation is assumed to vary strictly sinusoidally with a period of 24 h (thus giving 12 h of daylight) and a maximum photosynthetic active radiation of 200 W m^{-2} .

The biological model is coupled to the physical model by considering the usual advection–diffusion equation:

$$\begin{aligned} \frac{\partial \Psi}{\partial t} &= -\frac{\partial}{\partial x} (u\Psi) - \frac{\partial}{\partial z} [w\Psi] + A_H \nabla^2 \Psi \\ &+ \frac{\partial}{\partial z} \left[A_v(x, z, t) \frac{\partial \Psi}{\partial z} \right] + \text{biology}. \end{aligned} \quad (5)$$

Migration is included through an upstream advection scheme, which for our vertical grid has a maximum implicit diffusion of $A_v = 3 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$, a value not causing excessive diffusivity.

3 Results

3.1 Reference experiment

To obtain a basic understanding of the features produced by the model, we have conducted a reference experiment, that uses our model in a purely passive mode (no vertical migration). The results after 14 days of integration are displayed in Fig. 2b,c. During the first 7 days (before the full wind forcing) the phytoplankton population grows and finally extends down uniformly to the thermocline (pycnocline).

The wind forcing induces an overturning motion, characterized by narrow lateral boundary layers and a general flow above the thermocline towards the downwelling coast (left) and a relatively broad return flow at

¹One might argue that it is advantageous for LL cells to migrate upward to start a new cycle with an increased energy level, but this would require a two-step strategy (ascent first to make later descent reasonable), something we do not consider here.

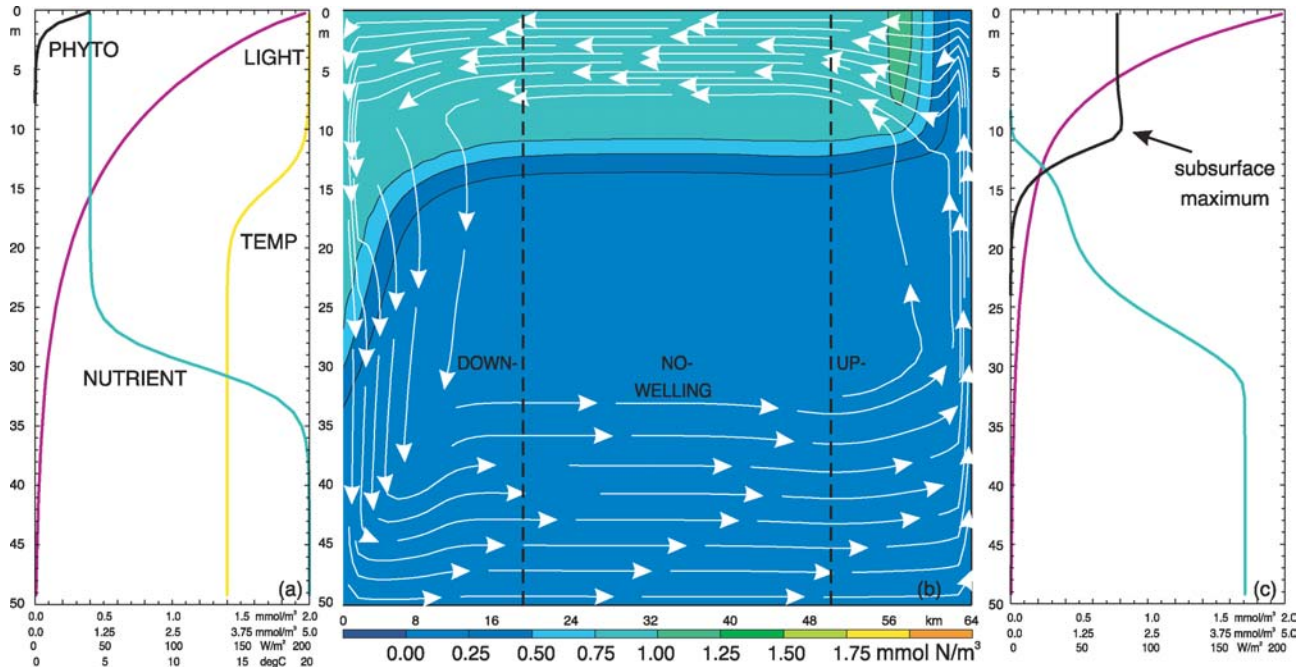


Fig. 2 The reference experiment. **a** initial profiles of temperature (yellow), nutrient (green), photosynthetically active radiation (PAR) (purple) and phytoplankton (black). Note the different scales for each variable. **b** phytoplankton distribution after 14 days of integration,

overlaid is the fully developed up- and down-welling circulation. **c** vertical profiles after 14 days in the center of the model domain (no-welling area)

depth. The final surface velocity reaches about 2 cm s^{-1} , while the maximum vertical velocities are about 8 m day^{-1} directly at the boundary. This leads to a tilted surface mixed layer, with a twofold deepening near the downwelling coast and a vanishing thermocline on the upwelling coast. After day 8, the nutrients above the thermocline are almost exhausted and limit further growth. After 2 weeks, the phytoplankton distribution shows a nearly homogeneous top layer with values exceeding 1 mmol N m^{-3} only in the area slightly downstream of the upwelling center, i.e., in the surface nutrient front (Fig. 2b). Such a pattern is typical not only for coastal upwelling situations but has been observed and simulated in frontal upwelling systems as well (Strass et al. 2002 Hense et al. 2003). A weak subsurface maximum is found above the midbasin secondary nutricline which coincides with the thermocline (Fig. 2c), at the base of the mixed layer. Due to the passive behavior of the phytoplankton in this experiment, there is no accumulation (advectively caused higher concentrations) but only growth-related local maxima. The vertically integrated phytoplankton biomass is highest along the downwelling coast, while a minimum is found directly at the upwelling coast, because the upwelled water is low in phytoplankton. There are only small differences between night and day.

3.2 Migration experiments

As explained in the model description section, each phytoplankton subcategory is characterized by a

specific migration behavior. For LL and HH, we assume no motility, HL descends, LH ascends with a speed of 2 m h^{-1} (a medium value from the range of $0.03\text{--}6.5 \text{ m h}^{-1}$ reported for dinoflagellates by Levandowsky and Kaneta 1987). Within this framework, it is possible to examine the evolution and patterns of a sample phytoplankton population as a function of their threshold values for the onset of migratory behavior. The experiments are labeled by their threshold values (θ_E, θ_Q) .

High values of θ_E indicate a reduced tendency to migrate downward (i.e., the organism migrates downward only if the internal energy storage is quite high). High values of θ_Q indicate a reduced tendency to migrate upward (i.e., the organism migrates upward only if the internal nutrient storage is quite high). For example, case (0.1,0.9) represents a species that is especially light-sensitive and migrates downward with relatively small amounts of internal energy, while it required high nutrient storage before migrating upward again. On the other hand, (0.9,0.1) represents a species that is very nutrient-sensitive. Species (0.1,0.1) is highly active, as the threshold values for migration are low.

3.2.1 Biomass

We have chosen the spatially averaged biomass as the main diagnostic quantity. Its sensitivity to different threshold values is summarized in Fig. 3, showing the ratio of area-averaged biomass between the migrating and the reference experiment after 14 days, for different

threshold values θ_E and θ_Q . A suite of 81 experiments was carried out, at increments of 0.1 in both parameter directions.

First of all, it should be noted that the total biomass for migrating cases can be significantly larger than for the passive case (typically from about 20% in the downwelling up to 50% in the upwelling zone, Fig. 3). This is due to the fact that migration generally deepens the euphotic zone (defined as the layer above the compensation depth, where production equals respiration) significantly. The apparent dilemma of being torn between the extremes of opposite poles (light and nutrients) may therefore be seen as the prerequisite for generally increased growth. Only very large θ_Q values combined with very small θ_E values may result in lower biomass, because these organisms leave the sunlit surface layer too quickly and suffer from a permanent energy deficit.

The results of the full parameter study (Fig. 3) reveal further differences in the resulting biomass for the three different physical regimes (downwelling, nowelling, upwelling; see Fig. 2 for the definition of the three regimes). In all regimes, we find areas in the parameter space where the biomass is increased by more than 50%; even higher rates of increase are found in nowelling (65%) and upwelling (more than 100%) areas.

Thus, the net success of a species does depend critically on its threshold values. It turns out that the highest

domain-wide biomass values are found for medium values of θ_E and small values of θ_Q . Apparently, a moderately quick response to internal nutrient changes is the optimal strategy with respect to primary production and biomass, while extremely quick migration onsets are less favorable. We find different locations of the maximum for different physical regimes; in particular the upwelling areas have their own parametric dependence: the maximum biomass is found at the smallest θ_E with moderate θ_Q , indicating that it is advantageous in upwelling areas to be downward-motile. It needs to be emphasized, however, that the upwelling area is characterized by a generally smaller vertically averaged biomass than in down- and nowelling areas. Finally, we note that extreme nutrient sensitivity combined with low energy sensitivity [i.e., case (0.9,0.1), representative of a buoyant species] does not lead to the highest biomass values in any physical regime.

3.2.2 Spatial distribution patterns

Figure 4 shows the distribution of phytoplankton in four selected cases (marked by dots in Fig. 3) after 14 days of integration. The first, (0.1,0.9), represents a species that descends with even small amounts of internal energy, but tries to accumulate a substantial amount of nutrients before migrating upward again. Correspondingly, a subsurface maximum is formed, however, with relatively small amplitudes due to the lack of energy. This behavior resembles a surface avoidance strategy, where organisms leave layers of highest irradiance quickly. The absolute maximum is found slightly downstream of the upwelling center, where slightly higher levels of nutrients are made available by advection.

The second example, (0.1,0.3), is a case where the maximum biomass in the upwelling area is found. This specific behavior is best suited to make use of the upward motion. Consequently, the surface maximum is found closest to the coast. Observations in upwelling regimes will probably simply detect a single near-surface maximum, without any indications of migration, although the species has and uses this capability (cf. Fig. 2 for the passive patterns). Yet, even in this case, the biomass in the nowelling area is significantly higher, with a pronounced maximum below the thermocline. Spatial patterns like this are occasionally observed (e.g., Pavelson et al. 1999), and usually interpreted as a result of physical downwelling (subduction) that carries biomass downward (Franks 1992). It is therefore interesting to note that, in our case, no downward frontal advection is responsible for this pattern (see the overturning motion in Fig. 2b), just a migrating species with a certain combination of θ_E and θ_Q threshold values will lead to such distribution.

The third (0.5,0.1) and fourth (0.2,0.1) examples were chosen to show the effects of moderate sensibility to internal energy storage. In both cases, two very dis-

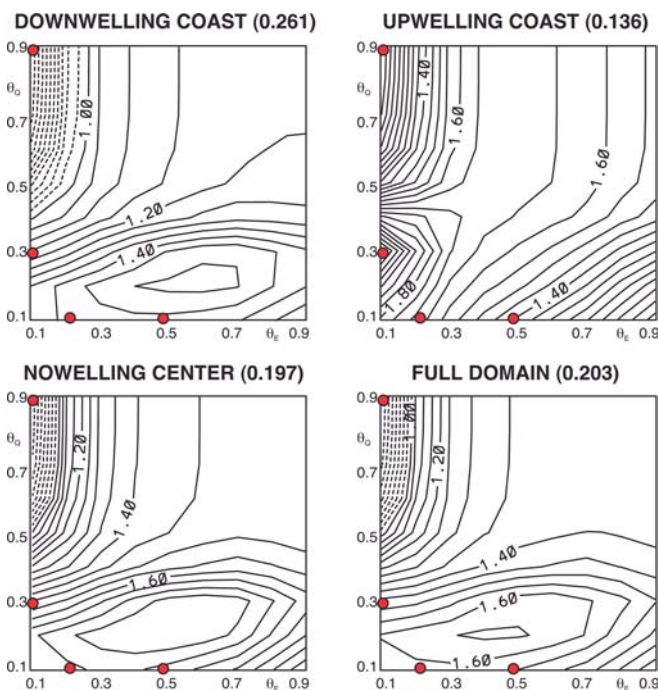
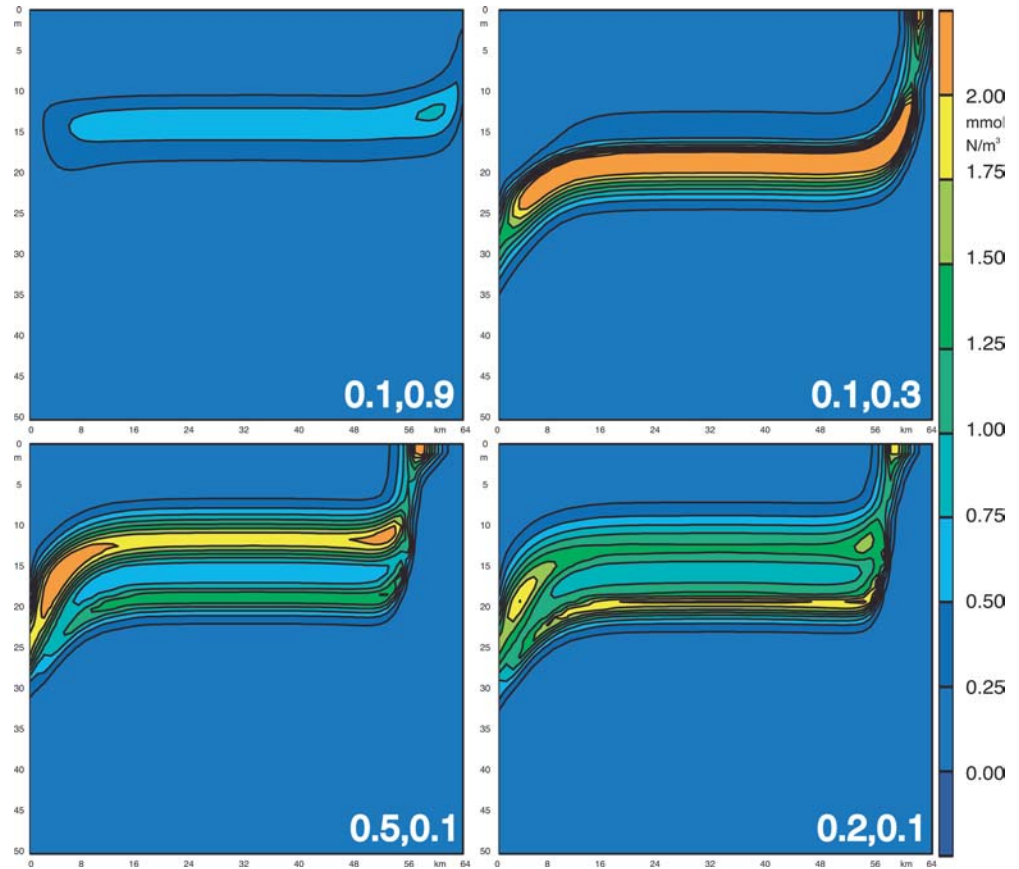


Fig. 3 Parametric dependence of the area-averaged biomass (obtained from 81 experiments) after 14 days for different threshold values θ_E and θ_Q . The mean biomass of the passive reference experiment (in mmol N m^{-3}) is given in parentheses. The values in each panel are normalized with respect to this mean. The contour interval is 0.05. Dashed lines indicate values smaller than 1. The red dots show the location of the experiments presented in Fig. 4

Fig. 4 Four selected spatial distributions of phytoplankton, for different values of (θ_E, θ_Q) ; each panel shows a midnight snapshot after 14 days of integration. (0.1,0.3): maximum biomass in upwelling region; (0.1,0.9): surface avoidance, (0.5,0.1) and (0.2,0.1): maximum biomass in down- and nowelling regions, with formation of double subsurface/deep phytoplankton maxima



tinctive subsurface/deep maxima develop, depending on the exact choice of values more or less deep, with either the upper or lower being more pronounced. Local maxima occur at the surface (downstream the upwelling coast) and deeper at the boundaries of the central nowelling region. Such patterns have been found in observations (e.g. Pavelson et al. 1999; Kononen et al. 2003) of *Heterocapsa triquetra* Ehrenb., indicating that these model results represent a realistic migration mode.

In summary, the inspection of the corresponding spatial distributions reveals interesting differences between the cases. High θ_Q values typically show one subsurface maximum, located at the depth of optimum growth conditions. Lower θ_Q values tend to lead to more or less pronounced double maxima at depth in the nowelling regime. Such multiple deep maxima do not exist in regions with even the slightest vertical motion.

3.2.3 Temporal evolution

An example of the temporal evolution of the biomass is shown in Fig. 5 for the case (0.5,0.1). With increasing time and nutrient depletion, the phytoplankton population penetrates deeper and deeper into the water column and even exceeds the depth of the pycnocline. The distribution is highly nonuniform and characterized by a distinctive diurnal cycle in both near-surface and deep layers. This is all the more noteworthy, as the model does not explicitly prescribe a diurnal migration pattern (through specified

migration times, or as a function of light availability). Instead, while present in the radiation-forcing function and therefore in the energy input, the time scale depends on external and internal nutrient availability along the trajectory of the organisms and just happens to be synchronous to a diel rhythm.

It is also obvious that maxima occur in different depths at different times. There are times with one (sub-surface) maximum, alternating shallow and deep maxima (depending on the time of day), and temporary occurrences of multiple maxima. The time of observations during the day may be therefore quite important in correctly categorizing the migration behavior of a species.

This is also evident from the profiles in Fig. 5b,c, where noon and midnight differences are shown for the last day of integration. The amplitude of subsurface and deep phytoplankton maxima varies, according to daytime, as do the relative contributions of each subcategory for the two maxima. The lower maximum is always located at the optimum depth, where the combination of light and nutrient is optimal. The exact location of the upper maximum depends on the vertical migration velocity, and is closer to the surface for higher migration speeds.

4 Summary

Phytoplankton migration is an aspect of marine ecosystems that is still not fully understood. The complexity

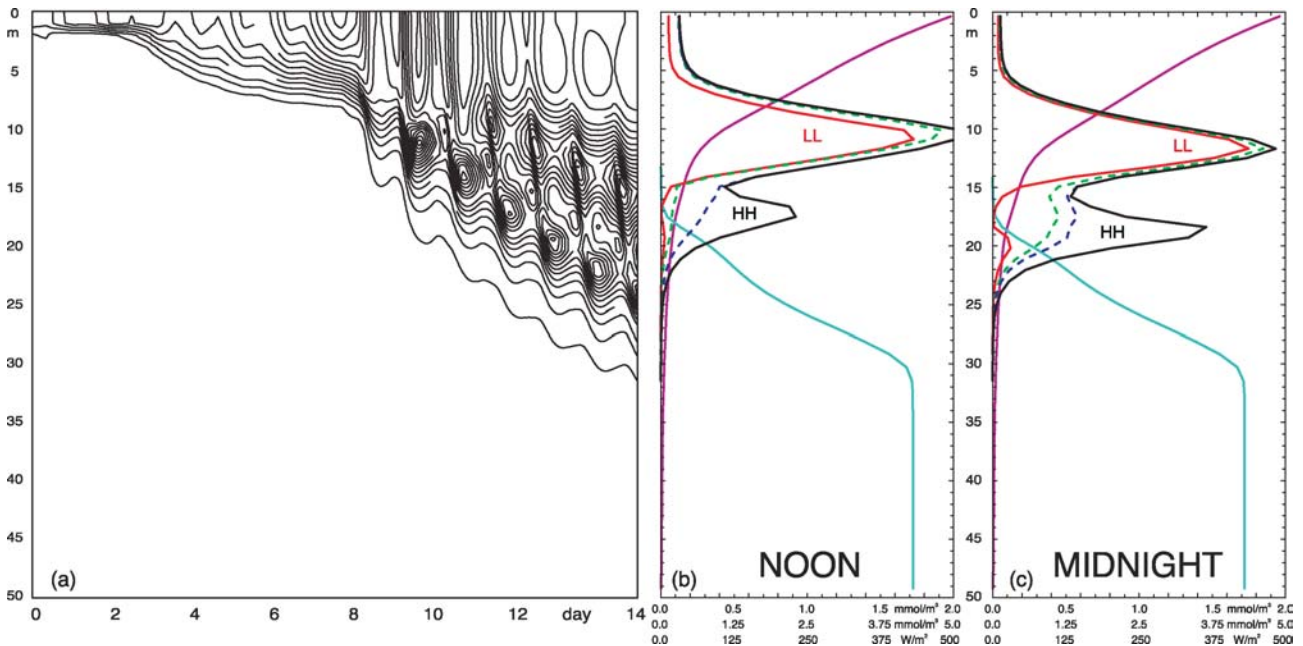


Fig. 5a–c Time dependence of phytoplankton distribution for case (0.5,0.1): **a** time series of vertical profile of horizontally averaged phytoplankton concentration (contour interval 0.1); **b,c** vertical profiles of the cumulative contribution of subcategories LL (*red*),

LH (*dashed green*), HL (*dashed blue*) and HH (*black*) to the total biomass in the nowelling region: **b** noon of day 14, **c** midnight of day 14. Light and nutrient profiles have been added to illustrate the depth of the maxima

of the underlying system, incomplete observations, and various a priori assumptions prohibit definite answers to the questions of why (and how) patterns can and do vary in time, why only part of the population takes part in a migratory response, and under which circumstances multiple high-concentration layers develop.

We have presented a model for migrating phytoplankton taking into account the evolution of the internal energy and nutrient levels to investigate the development of phytoplankton layers, and in particular of subsurface (deep) maxima. The model can easily be related to the traditional two-equation model (phytoplankton, external nutrients, see Appendix). Motility is assumed to take place with a constant upward and downward speed and depend only on internal energy and nutrient quota. This model thus significantly differs from all other models, where migration is at least partly parameterized to depend on external factors (e.g., Kamykowski and Yamazaki 1997; Liu et al. 2001). The history of the energy and nutrient status is included by decomposing the phytoplankton compartment into several categories with different properties. The distinction between high energy–high nutrient (HH), high energy–low nutrient (HL), low energy–high nutrient (LH) and low energy–low nutrient (LL) phytoplankton enables them to respond differently to environmental changes, whereas only phytoplankton which is characterized by high energy–low nutrient or low energy–high nutrient quota carry out motility. A typical pathway through the physical and parameter space is summarized in Fig. 6.

First, we find a distinctive dependence on the sensitivity to internal quota of energy and nutrient; secondly, during the evolution of a phytoplankton bloom under growing nutrient limitation, we find high concentration layers in different depths at different times. Day and night differences occur. We have shown that the success of each set of threshold values (thought to be species-dependent characteristics) varies with different environmental conditions. It is therefore plausible to expect that different species dominate in different physical regimes.

Our results show that migration always leads to higher biomass in upwelling regions, and that the relative gain can be more than in other regimes. This may seem surprising, because the traditional view is that migration is of advantage mainly in oligotrophic stratified regions. However, small-amplitude migration is beneficial under upwelling conditions due to the large vertical nutrient gradients near the surface. Hence, marine ecosystem models neglecting phytoplankton migration may suffer from a systematic underestimation of primary production².

Observations of multiple deep chlorophyll maxima are scarce. Our model results show that they are formed exclusively in regions without any appreciable vertical motion, which makes their rare occurrence in nature plausible. Further experiments (not shown here) confirm our expectation that the separation of the two maxima depends mainly on the migration velocity of the species:

²Models that include sinking of phytoplankton may not suffer from this deficiency in upwelling regions.

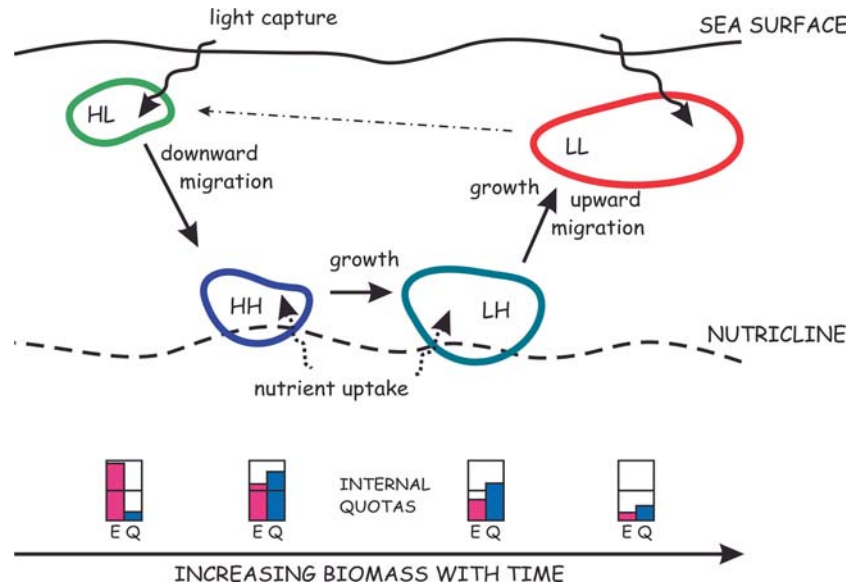


Fig. 6 Idealized pathway of a population through the model categories. Consider an LL population initially near the surface, which takes up energy, until it belongs to the HL category. It will then migrate downward. Close to the nutricline it will have acquired enough nutrients to switch to the HH category, where it grows and continues to take up nutrients until the energy drops sufficiently low and the population belongs to the LH category. Then it moves upward, and growth continues under improving light conditions until the internal nutrients are exhausted and the population finally belongs to the LL category. This cycle may then be repeated, starting from the already increased biomass, possibly down to a deeper level, unless the physical environment has changed. Of course, other closed loops are also possible, in which a population alternates between two or three categories. The complex interactions between organism sensitivity and its physical environment is illustrated by the widely varying patterns in Fig. 4

higher velocities lead to more separated maxima, up to the occurrence of a near-surface maximum. The deeper maximum moves downward with time and may be finally found below the pycnocline. We emphasize that these results are in no way limited to the special case with different depths of thermo- and nutriclines (which was chosen to represent the most common situation in oligotrophic systems). Additional experiments have shown qualitatively very similar results.

In areas with vertical up-(down-)ward transport, high (low) internal quotas of energy and nutrients prevent the phytoplankton from descending (ascending). In these cases, almost the entire phytoplankton population remains in the passive categories HH and LL. The first case is in agreement with observations that phytoplankton stops to migrate when sufficient nutrients are available (MacIntyre et al. 1997). The second is consistent with observations that phytoplankton can be trapped in nutrient depleted environments (Eppley et al. 1968).

5 Conclusions

We have used a relatively simple approach, exclusively relying on a metabolism-dependent migration scheme in

an Eulerian framework. The model can be used in several ways:

- To explain the occurrence of various phytoplankton distribution patterns as the result of the interplay between migration behavior based on internal quotas and the physical environment.
- To compare the success of different strategies for one specific environmental situation, and to determine the optimal (in terms of maximum biomass or primary productivity) strategy.
- To assess the success of one particular strategy in several physical situations.

Our conclusions can be summarized as follows:

- Migration increases the biomass/primary production in several typical environmental regimes and enhances the overall productivity of the ecosystem by increased food for higher trophic levels.
- No taxis-related migration is required to obtain a wide variety of migration patterns, including multiple deep phytoplankton (chlorophyll) maxima; the physical environment plays a crucial role in this respect.
- No explicit assumptions regarding circadian rhythms are necessary to obtain quasi-diel migration patterns.
- Multiple subsurface/deep phytoplankton maxima are exclusively found in regions without any appreciable vertical motion (other than the possible periodic movements of isopycnals due to internal waves). Hence it is not surprising that observations of this phenomenon are very sparse.
- Our model results offer an alternative explanation for offshore tongues of phytoplankton that extend downward into the water column. While these can be caused by physically induced subduction, they may also be the result of migratory behavior in the transition zone between up- and no-welling regions.
- We propose that the migration behavior of almost any phytoplankton species can be described entirely by a

set of two threshold values for internal quotas and one migration velocity. Observed patterns like daily cycles, surface avoidance, buoyancy, depth-keeping, and even multiple subsurface maxima may result, depending on the physical environment.

- EQN can be easily related to the traditional two-equation model. It therefore represents a straightforward extension of state-of-the-art marine ecosystem models and is well suited to simulate a wide range of situations, at moderate cost. Coupling to three-dimensional regional ocean circulation models seems possible in the near future.

It needs to be pointed out that the goal of this study was not to reproduce a specific observed feature, but to show that various phytoplankton migration schemes can be described by the EQN2x2 model, without explicitly prescribing migration times, target depths and detection limits for external gradients. Thus, our model represents a simple, yet versatile and universal approach³. While our experiments have been carried out with only one parameter set, they nevertheless form a comprehensive set of cases. Different growth rates, a different temperature dependence, modifications in the energy consumption for uptake and growth, additional nutrient dependencies, and different grazing scenarios will lead to quantitatively different solutions, but the fundamental patterns are likely to remain similar.

We also believe that the biological part of the model has the ingredients which are necessary to address biological processes involved in the formation of harmful algal blooms. The ability to migrate has been proposed to be crucial for the growth of harmful algae (Smayda 2002).

Finally, we note that the model results presented here only are valid for monospecific blooms. The co-evolution of several phytoplankton species with different migration behavior might result in quite complex distribution patterns. The same may be true for different ascent and descent velocities, which have been described for several dinoflagellates (Smayda 2002). More detailed and extensive observations are needed on motile phytoplankton populations in different environmental (physical and nutrient) conditions to fully determine the strengths and weaknesses of this modeling approach.

Appendix

The correspondence of the four-equation system to the two-equation approximation for phytoplankton dynamics can be demonstrated as follows: ignoring the losses and assuming that the explicit time dependence of both internal quotas is zero, we can write:

$$\sigma_Q \sigma_E = \sigma_N$$

$$\sigma_N \sigma_E (1 - \sigma_Q) = \sigma_N$$

such that

$$\sigma_E = 1 + \sigma_N$$

$$\sigma_Q = \frac{\sigma_N}{(1 + \sigma_N)}.$$

In other words, two-equation systems implicitly assume that the internal quotas change instantly with the exterior nutrient concentration. The four-equation EQN model does not use these constraints and offers the possibility to examine the effects of (1) behavior depending on internal quotas as presented in this paper, and (2) differences between light capture, uptake, and growth.

Acknowledgements The comments of two anonymous reviewers are gratefully acknowledged.

References

- Anderson DM, Stolzenbach KD (1985) Selective retention of two dinoflagellates in a well-mixed estuarine embayment: The importance of diel vertical migration and surface avoidance. *Mar Ecol Progr Ser* 25:39–50
- Baird ME, Oke PR, Suthers IM, Middleton JH (2004) A plankton population model with biomechanical descriptions of biological processes in an idealised 2D ocean basin. *J Mar Sys* (In press)
- Broekhuizen N (1999) Simulating motile algae using a mixed Eulerian-Lagrangian approach: does motility promote dinoflagellate persistence or co-existence with diatoms?, *J Plankt Res* 21/7: 1191–1216
- Clegg MR, Maberly SC, Jones RI (2003) The effect of photon irradiance on the behavioral ecology and potential niche separation of freshwater phytoplanktonic flagellates. *J Phycol* 39: 650–662
- Cullen JJ, Eppley RW (1981) Chlorophyll maximum layers of the Southern California Bight and possible mechanisms of their formation and maintenance *Oceanolog Acta*, 4/1: 23–32
- Cullen JJ, MacIntyre JG (1998) Behavior, physiology and the niche of depth-regulating phytoplankton. In Anderson DM, Cembella AD, Hallegraeff GM (eds) *Physiological ecology of harmful algal blooms*. NATO ASI Series, G41 organization Springer Berlin Heidelberg, New York pp 559–579
- Droop MR (1973) Some thoughts on nutrient limitation in algae. *J Phycol* 9: 264–272
- Eppley RW, Holm-Hansen O, Strickland JDH (1968) Some observations on the vertical migration of dinoflagellates. *J. Phycol* 4: 333–340
- Fennel K, Boss E (2003) Subsurface maxima of phytoplankton and chlorophyll: steady-state solutions from a simple model. *Limnol Oceanogr* 48/4: 1521–1534
- Figuerola FL, Niell FX, Figueiras FG, Villarino ML (1998) Diel migration of phytoplankton and spectral light field in the Ría de Vigo NW Spain. *Mar Biol* 130: 491–499
- Franks PJS (1992) Sink or swim: accumulation of biomass at fronts. *Mar Ecol Progr Ser* 82: 1–12
- Geider RJ, MacIntyre HL, Kana TM (1998) A dynamic regulatory model of phytoplankton acclimation to light, nutrients, and temperature. *Limnol Oceanogr* 43/4: 679–694
- Haidvogel DB, Wilkin JL, Young RE (1991) A semi-spectral primitive equation ocean circulation model using vertical sigma and orthogonal curvilinear horizontal coordinates. *J. Computational Phys* 94: 151–185
- Hense I, Timmermann R, Beckmann A, Bathmann U (2003) Regional ecosystem dynamics in the ACC: Simulations with a three-dimensional ocean-plankton model. *J Mar Syst* 42: 31–51

³Note, however, that our model cannot represent subsurface chlorophyll maxima based on physiological changes of the carbon-to-chlorophyll ratio (Cullen and Eppley 1981; Fennel and Boss 2003).

- Janowitz GS, Kamykowski D (1999) An expanded Eulerian model of phytoplankton environmental response. *J Ecol Modell* 118: 237–247
- Jones RI (1991) Advantages of diurnal vertical migration to phytoplankton in sharply stratified, humic forest lakes. *Arch Hydrobiol* 120: 75–87
- Kamykowski D, Yamazaki H (1997) A study of metabolism-influenced orientation in the diel vertical migration of marine dinoflagellates. *Limnol Oceanogr* 42/5: 1189–1202
- Kamykowski D, Milligan EJ, Reed RE (1998) Biochemical relationships with the orientation of the autotrophic dinoflagellate *Gymnodinium breve* under nutrient replete conditions. *Mar Ecol Progr Ser* 167: 105–117
- Kononen K, Huttunen M, Hällfors S, Gentien P, Lunven M, Huttula T, Laanemets J, Lilover M, Pavelson J, Stips A (2003) Development of a deep chlorophyll maximum of *Heterocapsa triquetra* Ehrenb. at the entrance of the Gulf of Finland. *Limnol Oceanogr* 48(2): 594–607
- Levandowsky M, Kaneta P (1987) Behaviour in dinoflagellates. In Taylor FJR (ed) *The biology of dinoflagellates*. Blackwell, Oxford, pp 360–398
- Liu G, Janowitz G, Kamykowski D (2001) Influence of environmental nutrient conditions on *Gymnodinium breve* Dinophyceae population dynamics: a numerical study. *Mar Ecol Progr Ser* 213: 13–37
- Liu G, Janowitz G, Kamykowski D (2002) Influence of current shear on *Gymnodinium breve* (Dinophyceae) population dynamics: a numerical study *Mar Ecol Progr Ser* 231: 47–66
- MacIntyre JG, Cullen JJ, Cembella AD (1997) Vertical migration, nutrition and toxicity in the dinoflagellate *Alexandrium tamarense*. *Mar Ecol Progr Ser* 148: 201–216
- Moore JK, Villareal TA (1996) Buoyancy and growth characteristics of three positively buoyant marine diatoms. *Mar Ecol Progr Ser* 132: 203–213
- Oliver RL (1994) Floating and sinking in gas-vacuolate cyanobacteria. *J Phycol* 30: 161–173
- Pacanowski RC, Philander SGH (1981) Parametrization of vertical mixing in numerical models of tropical oceans. *J Phys Oceanogr* 11: 1443–1451
- Pavelson J, Kononen K, Laanemets J (1999) Chlorophyll distribution patchiness caused by hydrodynamical processes: a case study in the Baltic Sea. *ICES J Mar Sci* 56: 87–99
- Raven JA, Richardson K (1984) Dinophyte flagella — a cost-benefit analysis. *New Phytol* 98: 259–276
- Richardson TL, Cullen JJ (1995) Changes in buoyancy and chemical composition during growth of a coastal marine diatom: ecological and biogeochemical consequences. *Mar Ecol Progr Ser* 128: 77–90
- Smayda TJ (2002) Turbulence, watermass stratification and harmful algal blooms: an alternative view and frontal zones as “pelagic seed banks”. *Harmful Algae* 1: 95–112
- Strass VH, Garabato AN, Pollard R, Fischer H, Hense I, Allen J, Read J, Leach H, Smetacek V (2002) Mesoscale frontal dynamics: shaping the environment of primary production in the Antarctic Circumpolar Current. *Deep-Sea Res Part II*, 49/18: 3735–3769
- Suzuki L, Johnson CH (2001) Algae know the time of day: circadian and photoperiodic programs. *J Phycol* 37: 933–942
- Villareal TA, Carpenter EJ (2003) Buoyancy regulation and the potential for vertical migration in the oceanic cyanobacterium *Trichodesmium*. *Microb Ecol* 45/1: 1–10
- Yamazaki AK, Kamykowski D (2000) A dinoflagellate adaptive behavior model: response to internal biochemical cues. *Ecol Modell* 134: 59–72
- Yamazaki H, Kamykowski D (1991) The vertical trajectories of motile phytoplankton in a wind-mixed water column. *Deep-Sea Res* 38: 219–241