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Approaches to model the life cycle of harmful algae

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ABSTRACT

Models of harmful algal blooms (HABs) need to include autecological characteristics of the HAB species because the bloom dynamics can only be successfully described if relevant life cycle aspects (in particular en- and excystment) are included in some way. This study presents an overview on how the life cycle is considered in current Lagrangian and Eulerian models. Examples of the latter are given, which range from crude parameterizations in one-compartment models, to stage-resolving twelve-compartment models. Advantages and disadvantages of the different approaches are highlighted. A generalized model classification is presented which may be used as a framework for further phytoplankton life cycle modeling studies.

1. Introduction

Harmful algal blooms (HABs)[1] are frequently observed in coastal areas but their causes are often somewhat obscure. Many different species of microalgae with their different requirements for optimal growth can form HABs. Some HABs seem to occur entirely naturally, as part of the seasonal succession of marine organisms, others seem to be triggered by environmental changes introduced by human activities (see, e.g., Anderson et al., 2002).

HABs typically appear – and disappear – quite abruptly. This is surprising because the growth rates of many HAB forming species are comparatively low (see, e.g., Stolte and Garcés, 2006). Similarly, blooms are observed to end even though the environmental conditions that are considered favourable persist (Anderson et al., 1983; Kremp and Heiskanen, 1999). This apparent paradox can be explained as the result of the species life cycle. Transitions between vegetative and resting phases – the formation of resting stages (encystment) and the reverse process excystment (germination) – can be responsible for terminating or initiating blooms (e.g., Anderson, 1998; Anderson and Rengefors, 2006; Garcés et al., 2002). Resting cells from previous blooms settle on the bottom, where they accumulate and form a so-called seed bank. When germinating simultaneously and rising in synchrony with the onset of the bloom of the pelagic population, these upward migrating cells can contribute significantly to the bloom. The number of excysting cells may actually be among the most important factors that determine the magnitude of the bloom. Seed banks and blooms are not necessarily in the same geographic location due to transport of the different life cycle stages by ocean currents: Offshore germinating cells may be advected onshore initiating a coastal bloom (e.g., McGillicuddy et al., 2003). Vice versa, an offshore harmful algal bloom may be generated by germinating cells originating at a coastal seed bank (Donaghay and Osborn, 1997).

The various life history strategies of different HAB species can influence not only the timing, magnitude, duration and location of blooms, but also the dominance and seasonal succession of species (Anderson and Rengefors, 2006; Kremp et al., 2008). For example, different cyst-forming dinoflagellate species have different "temperature windows" for germination explaining the seasonal succession of the respective populations (Anderson and Rengefors, 2006).

In general each species has its own life cycle with very specific energy and nutritional demands and sensitivities to environmental conditions. Life cycle transition can therefore be caused by various factors. These include for example, irradiance (e.g., Sgrosso et al., 2001), extra- or intracellular nutrient concentrations (e.g., Anderson and Lindquist, 1985; McQuoid and Hobson, 1996), increased cell contact (e.g., Uchida, 2001), allelochemicals (e.g., Fistarol et al., 2004) and parasites (e.g., Toth et al., 2004). In general it is assumed that unfavourable conditions for the species under consideration induce encystment while favourable conditions are responsible for excystment.

Large year-to-year fluctuations in the abundance of harmful algae are observed but the primary triggering factors are unclear. Variations in light, temperature and nutrients could be responsible. For example, interannual variability in HAB events is often associated with changes in mixing and advection (e.g., Kudela et al., 2005). However, recent observations (e.g., Kremp et al., 2008) and modeling studies (He et al., 2008; Li et al., 2009; Hense and Burchard, 2010) show that also the size of the seed population can play a decisive role.

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[1] Harmful algal blooms are defined here as all occurrences of "high" biomass with negative consequences for other species (e.g., through toxicity, anoxia, …).

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Although the life cycle appears to be essential, it has long been ignored in ecosystem models with HAB species. The reason may be related to the complexity of the life cycle (Fig. 1) of which we often possess only rudimentary knowledge. First of all, it is unclear how many distinct stages need to be considered. The triggering factors leading to life cycle stage transition are not fully understood. Finally, for each life cycle stage we need to specify parameters with respect to nutrient demands (e.g., uptake of dissolved inorganic nitrogen versus nitrogen fixation), motility (e.g., sinking versus rising), tolerance for physical factors (e.g., salinity, temperature, light, and turbulence), mortality, respiration and growth.

This paper presents an overview of existing strategies to include life cycle aspects in numerical ecosystem models (in the following LCM: life cycle models), in particular for species with growing and resting stages. The advantages and disadvantages are discussed and future directions are outlined.

2. The Lagrangian approach

The most natural way to consider the life cycle of an organism is certainly to use an individual-based (or agent-based) approach, following the organism in time through the fluid (advection) and through the different stages of its development (life cycle succession). In other words, organisms are treated as discrete individuals (or collections of individuals) with certain properties.

2.1. Governing equations

A Lagrangian model for a population of identical organisms involves a set of four equations:

$$\frac{\partial P}{\partial t} = \mu P - lP \tag{1}$$

$$\frac{\partial x^P}{\partial t} = u \tag{2}$$

$$\frac{\partial y^P}{\partial t} = v \tag{3}$$

$$\frac{\partial z^P}{\partial t} = w + w_P \tag{4}$$

where P is the phytoplankton biomass, t is the time, μ is the actual growth rate, and l is the loss rate including natural mortality, lysis due to viral infection and grazing by zooplankton and higher trophic levels. The position of the population in three-dimensional space is given by $\vec{x}^P = (x^P, y^P, z^P)$ and changes according to local fluid velocities $\vec{v} = (u(x,y,z,t),\ v(x,y,z,t),\ w(x,y,z,t))$. The three-dimensional velocity field as well as other variables necessary for Lagrangian LCM such as temperature, salinity and light attenuation can be derived from observations or Eulerian ocean circulation models. Vertical motility of the population can be included through $w_P(x, y, z, t)$.

In a simple model, the actual growth rate μ depends on external factors like temperature, light, nutrient availability and salinity, that is $\mu = \mu(T, I, N, S)$, while the loss rate is a function of grazer and virus concentration. Additional dependencies can be included with relative ease.

2.2. Life cycle processes

Life cycle related changes and transformations of phytoplankton take place during the development of the organism. In the Lagrangian approach both endogenous and exogenous triggering factors can be easily included. An endogenous clock can be considered by integrating an equation for the "age" (A^P) of the population relative to some reference date:

$$\frac{\partial A^P}{\partial t} = 1. \tag{5}$$

Growth, mortality and migration can then be made a function of age, varying either continuously or abruptly. A maturation time or a mandatory dormancy period of a resting stage may also be considered by prescribing specific times or time periods. Hence, a characteristic c of the population is a function of external factors like irradiance (I), temperature (T), salinity (S), nutrient concentrations (N) and age (A^P):

$$c = c\left(I, T, S, N, A^P\right). \tag{6}$$

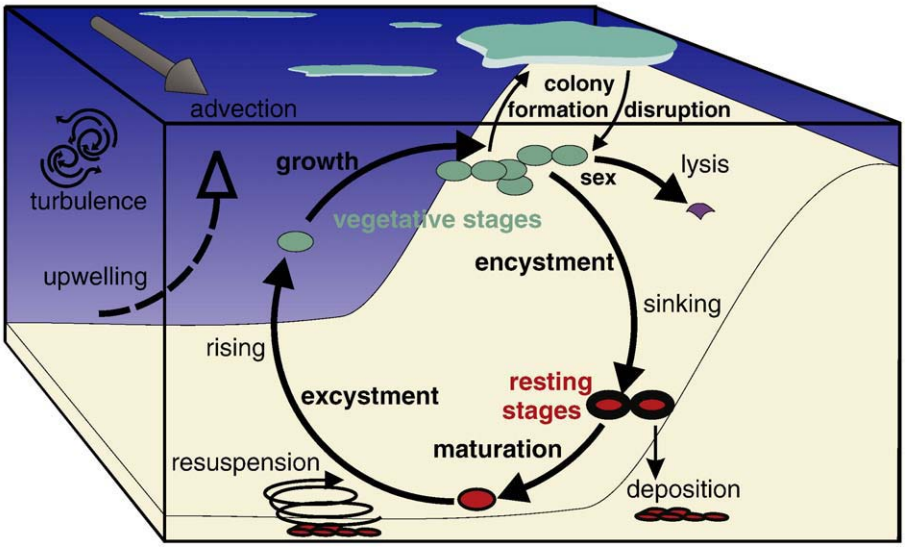

Fig. 1. Overview of major life cycle stages of marine phytoplankton, the main biological and contributing physical processes. Beginning with the vegetative phase, cells grow dependent on endogenous and exogenous factors. For some species this phase may be followed by formation and disruption of colonies. Encystment terminates the vegetative phase and newly formed resting cells settle down to the sediment. After maturation and possibly resuspension, germination takes place. Subsequent rising of the cells (buoyancy induced, by active upward migration and/or due to upwelling) into the euphotic zone closes the loop. For some (e.g., dinoflagellate, diatom) species, sex is involved in life cycle transition (e.g., cyst or colony formation). The spatial distribution of HAB-patches (and fate of the blooms) will depend on the ocean currents and turbulent mixing.

Mechanistic approaches to phytoplankton dynamics emphasize the role of internal factors for the development of organisms. Cell size, as well as the intracellular availability of energy, nutrients, and toxins is probably a better descriptor of phytoplankton properties than external concentrations. This means that for n internal properties $\vec{Q}^P=(Q_1^P,Q_2^P,\ldots,Q_n^P)$ the governing equations are augmented with another set of equations:

$$\frac{\partial \vec{Q}^P}{\partial t} = \vec{\nu}P-\vec{\varphi}P-l\vec{Q}^P \tag{7}$$

where $\vec{\nu}P$ and $\vec{\varphi}P$ are the source and sink terms of the internal pools which in turn depend on external factors and/or the ratios of internal concentration to total biomass (the quotas $\vec{\theta}=\vec{Q}^P/P$). Instead of irradiance and external nutrient concentration in Eq. (6), the internal energy and nutrient quotas ($\vec{\theta}=(\theta_1,\theta_2,\ldots,\theta_n)$) may be used to determine specific characteristics:

$$c = c\left(T,S,\vec{\theta},A^P\right). \tag{8}$$

2.3. Advantages and disadvantages

The advantage of the Lagrangian approach is that populations retain a fixed identity as they move with the fluid. Each population can be unique in its properties; the natural diversity can therefore be easily included and life cycle transitions (e.g., a change in maximum specific growth rate with size) can be represented by linking this property to the age or internal state of the organism.

The obvious disadvantages of Lagrangian modeling are that (i) a very large number of particles needs to be considered for an adequate coverage of any three-dimensional model domain, (ii) the representation of diffusion and vertical convection is not straightforward but requires additional assumptions (e.g., "random walk"), and (iii) the technical overhead for treating the splitting of populations and re-initialization of extinct populations is nontrivial.

2.4. Examples of Lagrangian LCM

Recently, Lagrangian LCMs of harmful algae have been applied to local sites to study the dispersal of a dinoflagellate (Villanoy et al., 2006) or the effect of nutrient reduction on bloom formation of a cyanobacterium (Hellweger et al., 2008).

Villanoy et al. (2006) prescribe the observed cyst distribution on the sea floor as initial values. If a threshold value of bottom velocity is exceeded, the resuspended cysts from the sediment are transformed into the vegetative stage (excystment). The vegetative cells can grow while they are transported with the current field. Encystment is assumed to occur after a specified time period. The model focuses on one bloom period, hence the fate of encysted cells is not considered. The model was successful in representing the spatial distribution patterns of the bloom in Manila Bay.

In a more sophisticated approach, Hellweger et al. (2008) distinguish five life cycle stages comprised of three vegetative stages and two resting stages. Different characteristics (photosynthesis, respiration, division, phosphorus uptake and vertical velocities) are specified to each stage. In addition, the transition between the individual stages is assumed to be a function of internal factors (e.g., maturation time, cell size). In a one-dimensional model application, this LCM has very well represented the seasonal cycle of growing and resting stages.

In these examples the transition between growing and resting stages is a function of either internal or external factors. In a somewhat simpler approach, Woods (2005) sets the timing of en- and excystment at specific days of the year. Overall, these model studies show that Lagrangian methods are well suited to study aspects of bloom formation of cyst-forming species in real world applications.

3. The Eulerian approach

The alternative to the Lagrangian Model approach is to treat a collection of organisms or populations as a continuum and to assign a biomass concentration value at each grid point of the model. This is the traditional way to design for example one-, two-, or three-dimensional NPZD models.

3.1. Governing equations

In this case, the evolution equation for phytoplankton reads

$$\frac{\partial P}{\partial t} = \underbrace{-\vec{v}\cdot\nabla P+\nabla\left(\vec{\kappa}\nabla P\right)}_{\frac{\partial P}{\partial t}|_{\mathrm{PHYS}}} + \mu P - lP - \frac{\partial}{\partial z}(w_P P), \tag{9}$$

where $\vec{v}\cdot\nabla P$ is the advection term and $\nabla(\vec{\kappa}\nabla P)$ represents the turbulent diffusion (with the turbulent diffusivity coefficient $\vec{\kappa}(x,y,z,t)$). Advection and turbulent diffusion are combined into the physical tendency term $\frac{\partial P}{\partial t}|_{PHYS}$. The notation of the biological variables is the same as above.

3.2. Life cycle processes

In an Eulerian model the age information, the average size of the organisms, or any other internal property can only be included through a set of additional equations. Again, let n represent the number of internal pools of phytoplankton. Then the evolution equation for the state vector $\vec{Q}^P=(Q_1^P,Q_2^P,\ldots,Q_n^P)$ reads

$$\frac{\partial \vec{Q}^P}{\partial t} = \frac{\partial \vec{Q}^P}{\partial t}|_{\mathrm{PHYS}} + \vec{\nu}P-\vec{\varphi}P-l\vec{Q}^P-\frac{\partial}{\partial z}\left(w_P\vec{Q}^P\right), \tag{10}$$

where $\vec{\nu}P$ and $\vec{\varphi}P$ are again the source and sink terms of the internal pools or properties.

A particular problem is the diffusion term because mixing assumes that all elements of a compartment are identical. Hence, mixing of populations with different internal quotas will lead to averaged (i.e., erroneous) internal properties. A convenient solution is the introduction of so-called "subcompartments" (e.g., Janowitz and Kamykowski, 1999; Beckmann and Hense, 2004). They represent distinct parameter ranges for internal characteristics which can be identified as individual life cycle stages (Hense and Beckmann, 2006). The remaining task is then to define proper transfer conditions and rates between these subcompartments.

For considering the different life cycle stages, the phytoplankton compartment needs to be divided into M subcompartments. The evolution equation for the state vector $\mathrm{P}=(P_1,P_2,\ldots,P_M)$ then reads

$$\frac{\partial \vec{P}}{\partial t} = \frac{\partial P}{\partial t}|_{\mathrm{PHYS}} + \vec{\mu}\,\vec{P}-\vec{l}\,\vec{P}-\frac{\partial}{\partial z}\left(\vec{w}_{\vec{P}}\,\vec{P}\right) + \mathbb{T}\,\vec{P}, \tag{11}$$

where $\vec{\mu}$, $\vec{l}$ and $\vec{w}_{\vec{P}}$ are vectors of actual growth rate, loss rate and buoyancy velocities for each stage, and $\mathbb{T}=\tau_{i,j}$ is the transfer rate matrix between the individual stages. In principle, the transfer between any two life cycle stages can take place, so the matrix may be dense. However, a closed single loop life cycle in a general multi-compartment Eulerian model is represented by a sparse life cycle succession matrix

$$\mathbb{T} = \begin{pmatrix} -\tau_{1,2} & 0 & \ldots & 0 & \tau_{N,1} \\ \tau_{1,2} & -\tau_{2,3} & 0 & \ldots & 0 \\ 0 & \tau_{2,3} & \ldots & 0 & \ldots \\ \ldots & 0 & \ldots & -\tau_{N-1,N} & 0 \\ 0 & \ldots & 0 & \tau_{N-1,N} & -\tau_{N,1} \end{pmatrix} \tag{12}$$

where the elements $\tau_{i,j}$ denote the transfer from stage i to stage j.

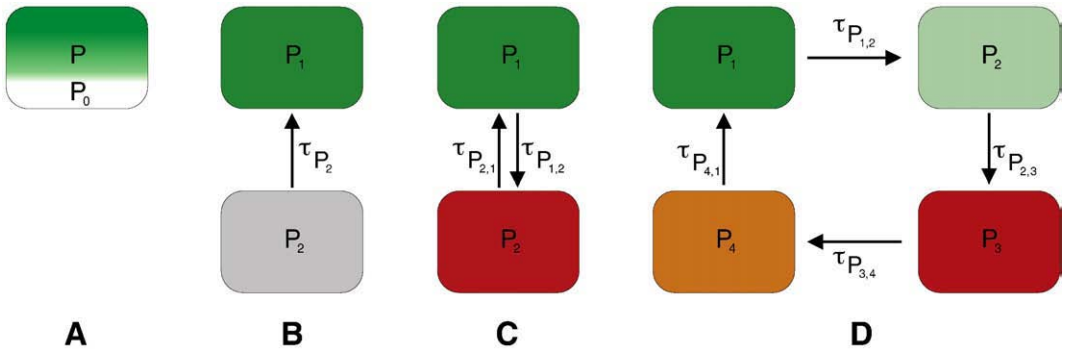

Fig. 2. Schematic diagrams of four different Eulerian life cycle modeling approaches (A–D): A) one-compartment LCM which considers a minimum value of phytoplankton (P_0), B) 1.5-compartment LCM which considers a one-way transfer (τ) from a prescribed pool of a seed population (P_2, obtained, e.g., from observations), C) two-compartment LCM which considers a two-way transfer between the growing (P_1) and the resting stage (P_2), D) four-compartment model which considers two growing and two resting stages which are connected by a unidirectional closed loop.

The transfer rates may be specified as a function of external (environmental) factors (irradiance, temperature, salinity, and nutrients)

$$\tau_{i,j} = \tau_{i,j}(I, T, S, N). \tag{13}$$

Like for the Lagrangian approach, the functional dependence may be modified to rely on internal factors as well

$$\tau_{i,j} = \tau_{i,j}\left(T, S, \vec{\theta}\right). \tag{14}$$

3.3. Advantages and disadvantages

Eulerian models share the advantages of all grid point models: a spatially explicit resolution of the domain under consideration, and the possibility to compute integral quantities and gradients in a straightforward way. In addition, the effects of subgridscale processes (like turbulence) on the biological variables are treated the same way as for the physical variables.

A significant disadvantage is that explicit time information (e.g., of a mandatory dormancy period) cannot be included in the Eulerian approach. Time scales specified for a transfer between compartments merely represent the time after which the source concentration is reduced by a factor of e. As a result, the specification of transfer rates has to rely on ad hoc choices (see, e.g., Beckmann and Hense, 2004).

It should also be noted that the introduction of subcompartments and internal quotas will lead to a significant increase in the number of Eulerian tracers and hence computer resources (memory and computing time).

3.4. Examples of Eulerian LCM

Recent Eulerian models that include phytoplanktonic life cycle dynamics focus on cyanobacteria and dinoflagellates. They range from very simple approaches based on just one compartment to comparatively complex representations of four different stages and two internal quotas.

3.4.1. One-compartment LCM

Models that attempt to represent a species with a pronounced life cycle with only one compartment have to rely heavily on parameterization. As pointed out in the Introduction, an important life cycle aspect is the germination of resting cells in spring. This "seed population" can be represented, very crudely, by a minimum concentration or a minimum production throughout the year (Fig. 2A). Technically, this is realized by prescription of a "minimum value".[2]

The minimum concentration approach (Kiirikki et al., 2001) reads

$$\frac{\partial P}{\partial t} = \frac{\partial P}{\partial t}|_{\mathrm{PHYS}} + \mu P - l(P - P_0) - \frac{\partial}{\partial z}(w_P P), \tag{15}$$

with similar notation as above; P_0 is the constant seed population.

The minimum production approach (Burchard et al., 2006, applying the model of Neumann et al. (2002)) reads

$$\frac{\partial P}{\partial t} = \frac{\partial P}{\partial t}|_{\mathrm{PHYS}} + \mu(P + P_0) - lP - \frac{\partial}{\partial z}(w_P P). \tag{16}$$

The minimum value in both these cases ensures a minimum phytoplankton concentration in the pre-bloom phase. Thus, as desired, the bloom formation can take place relatively rapidly, despite low species specific growth rates (see discussion in Hense and Burchard, 2010). Both approaches yield very similar results, depending of course on the specific choice of P_0; if the same minimum value is used, the former approach leads to higher primary production, i.e. nitrogen fixation in case of cyanobacteria (Hense and Burchard, 2010).

The main advantage of the use of a minimum value is that it is easy to implement and relatively inexpensive to compute. The most obvious disadvantage is, however, that part of the interannual variability is artificially suppressed, because the starting basis for growth is the same each year. This can in principle be remedied by varying the minimum value P_0 with time to account for year-to-year fluctuations (see also next section).

3.4.2. 1.5-compartment LCM

One way to more realistically represent the spatial and temporal distribution of the seed population is to add a separate compartment P_2, which is filled with an (observed) concentration of the seed population (Fig. 2B). A one-way transfer from this fixed pool of biomass to the vegetative stage P_1 will then lead to the desired increase in biomass at rates larger than the maximum specific growth rate.

In our classification of life cycle models, such an approach is called a 1.5-compartment LCM, because there is no two-way exchange between the compartments. The corresponding equations read

$$\frac{\partial P_1}{\partial t} = \frac{\partial P_1}{\partial t}|_{\mathrm{PHYS}} + \mu P_1 - lP + \tau_{2,1} P_2 - \frac{\partial}{\partial z}\left(w_{P_1} P_1\right) \tag{17}$$

[2] It should be noted that the use of such a minimum value has often been regarded as a mere numerical necessity rather than a crude parameterization of the life cycle. Therefore, there is a tendency to "forget" this aspect in the model description.

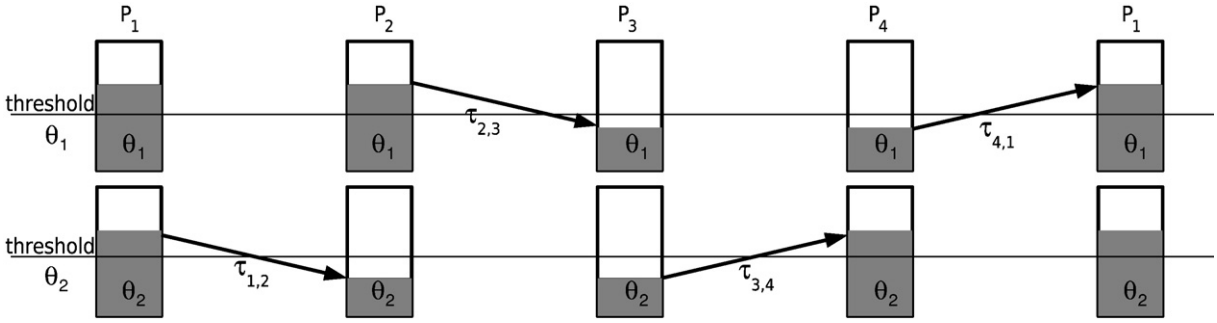

Fig. 3. Schematic illustration of the succession of life cycle stages (P_1–P_4) which are characterized by low/high values of two internal quotas (θ_1, θ_2). The arrows indicate the decrease (or increase) of the respective quota below (or above) a certain threshold leading to a transfer into the next stage.

$$\frac{\partial P_2}{\partial t} = -\tau_{2,1} P_2, \tag{18}$$

where $\tau_{2,1}$ is again the actual transfer rate of biomass (see above). The transfer is occasionally treated as a prescribed (but time-dependent) flux of biomass through the lower boundary of the model (e.g., Eilertsen and Wyatt, 2000), or as piecewise constant with varying values for day and night (Yamamoto et al., 2002). McGillicuddy et al. (2005) consider external factors (temperature, irradiance) as well as a prescribed time-dependent "germination potential" (which can be seen as a measure of internal maturation of the resting cells).

Several models incorporate encystment ε indirectly as a loss term of phytoplankton l (see above): $l = \varepsilon + m$, with m being the mortality. Again, the encystment rate has been determined to depend on internal factors, e.g., phosphorus quota (e.g., Yamamoto et al., 2002) or as a function of external factors using a measure of nutrient limitation (McGillicuddy et al., 2005).

The advantage of this class of models is that a realistic spatially and temporally variable seed population can be taken into account. Even if the knowledge about the actual transfer rate is sparse, the model may still be able to simulate the spatial and temporal variability of the vegetative stage better than assuming a constant (or zero) seed population (see, e.g., McGillicuddy et al., 2005). However, such an approach is restricted to regimes in which information about these resting stages is available and can be used as a "boundary" condition for the model.

3.4.3. A two-compartment LCM

A two-compartment LCM is the most simple version of a model that explicitly resolves a fully closed life cycle with a two-way transfer (Fig. 2C). The cycle succession matrix then becomes

$$\tau_{2\times 2} = \begin{pmatrix} -\tau_{1,2} & \tau_{2,1} \\ \tau 1,2 & -\tau_{2,1} \end{pmatrix}. \tag{19}$$

Assuming that we distinguish between the growing stage P_1 and the resting stage P_2 the corresponding equations read:

$$\frac{\partial P_1}{\partial t} = \frac{\partial P_1}{\partial t}|_{\mathrm{PHYS}} + \mu_1 P_1 - l_1 P_1 + \tau_{2,1} P_2 - \tau_{1,2} P_1 - \frac{\partial}{\partial z}\left(w_{P_1} P_1\right) \tag{20}$$

$$\frac{\partial P_2}{\partial t} = \frac{\partial P_2}{\partial t}|_{\mathrm{PHYS}} + \mu_2 P_2 - l_2 P_2 - \tau_{2,1} P_2 + \tau_{1,2} P_1 - \frac{\partial}{\partial z}\left(w_{P_2} P_2\right) \tag{21}$$

where the growth rate μ_2 is much smaller than μ_1 (or even zero), and the mortality rate l_2 is much smaller than l_1. Without additional equations for internal quotas, the transfer between these two stages has to be specified as a function of external factors (see above).

The corresponding vertical velocities can be chosen in various ways. An obvious choice is to assign a small positive or neutral buoyancy to the vegetative stage w_{P_1} while w_{P_2} represents sinking (after encystment) and rising (after excystment). Using time-integrated quantities of environmental factors to describe the process of motility, the correct timing of the bloom may be reproduced with the ascending or descending resting stage. Alternatively, the motility terms may be replaced by a mechanism that instantaneously transfers all encysting cells into the bottom layer of the model, while excysting cells are analogously transferred to the surface layer.

3.4.4. A four-compartment LCM

Current knowledge on how to adequately subdivide the life cycle of HAB species into distinct stages and how to describe the conditions for stage transitions is sparse. Different species may also require a different number of stages. While the conceptual model of Whipple et al. (2005) identifies 15 life cycle stages for *Phaeocystis*, the life cycle of other species may be captured with sufficient accuracy with fewer stages. For example, Hense and Beckmann (2006) propose a prototype schematic that uses two vegetative and two resting stages to describe the life history of cyanobacteria of the order *Nostocales*. The transfer matrix for such a case is expressed as the following:

$$\tau_{4\times 4} = \begin{pmatrix} -\tau_{1,2} & 0 & 0 & \tau_{4,1} \\ \tau_{1,2} & -\tau_{2,3} & 0 & 0 \\ 0 & \tau_{2,3} & -\tau_{3,4} & 0 \\ 0 & 0 & \tau_{3,4} & -\tau_{4,1} \end{pmatrix}. \tag{22}$$

This four stage model (Fig. 2D) allows for the discrimination of resting cells that sink (akinetes, the resting stage of cyanobacteria) and rise (germinates). It also treats vegetative cells that take up DIN separate from those that fix dinitrogen gas. Although in the life cycle model by Hense and Beckmann (2006) the transfers between the individual stages are a function of internal quotas (see below), it may be possible to describe the transfers by external factors only (e.g., time-integrated quantities).

3.4.5. A twelve-compartment LCM

The consideration of internal quotas is arguably the best way to determine stage transitions.[3]

For the four-stage model described in the previous subsection, Hense and Beckmann (2006) added an energy and a nutrient quota, which led to a total of 12 compartments. This enables the differentiation of the four stages by their internal quotas, thereby, facilitating explicit specification of the transfer among stages (Fig. 3). Thus, if the internal quota of a population approaches a certain (predefined) threshold, a transfer into the neighboring stage is induced.

Discrimination between low and high values of two internal quotas allows us to identify each of the four stages with a unique combination of internal states, and to relate the stage succession to changes in internal quotas: For example (Fig. 3), from P_1 (characterized by a high Q_1 and Q_2-quota) to P_2 (characterized by a high Q_1 and

[3] This is obviously also true for Lagrangian LCM (see Section 2.2).

low Q_2-quota) to P_3 (characterized by a low Q_1 and Q_2-quota) to P_4 (characterized by a low Q_1 and high Q_2-quota) and back to P_1.

A complex multiple compartment LCM has both advantages and disadvantages. Since fully prognostic equations exist for all growing and resting stages, the model can in principle be applied in cases where information about the seed population is sparse. It has to be noted, though, that the description of the life cycle (i) is not "mechanistic", (ii) requires the specification of a relatively large number of (poorly known) parameters and (iii) may be too expensive to be included in three-dimensional ocean general circulation models.

4. Summary and conclusions

The importance of the life cycle of HAB species has been pointed out more than a decade ago in a conceptual paper by Donaghay and Osborn (1997). Since then, a growing number of HAB modeling studies has addressed the role of seed populations and life cycle transition processes. Timing, duration, magnitude and distribution patterns of blooms have been found to critically depend on life cycle related processes, in particular excystment and encystment. For example, McGillicuddy et al. (2005) have shown that the inclusion of germination of the benthic resting stages is a prerequisite for obtaining realistic spatial distribution of the toxic dinoflagellate *Alexandrium fundyense* in the Gulf of Maine. Hense and Burchard (2010) have demonstrated that timing and duration of cyanobacteria blooms in the Baltic Sea are well represented in a full life cycle model, while simpler approaches lead to systematic biases. In addition, interannual variability in external factors, including for instance temperature, irradiance, nutrients, turbulence and flow fields, may not explain observed year-to-year fluctuations in the biomass of harmful algae if a variable seed population is omitted (e.g., Li et al., 2009; Hense and Burchard, 2010).

To streamline the various diverse activities of life cycle related HAB modeling, this overview has presented an inventory of the various approaches and listed their main advantages and disadvantages. The focus has been on the distinction between growing and resting stages; the methodologies may, however, also be adapted to life cycle transitions concerning for instance colony formation and disruption. A few modeling (e.g., Lancelot et al., 2005) and conceptual studies (e.g., Whipple et al., 2005) have already addressed this topic.

The two fundamentally different approaches to the time evolution of marine populations (Lagrangian and Eulerian) are both useful for life cycle modeling. While individual-based methods may seem more natural, fixed grid point (Eulerian) models are equally capable of including life cycle aspects, if subcompartments are introduced to represent distinct life cycle stages. A preference for one approach over the other should be motivated by the specific goals of the study: Lagrangian methods are well suited for studies related to short term events if explicit time information of individual populations is required and/or in regimes where advection and motility is more important than diffusion (see, e.g., Hai et al., 2010). Eulerian methods are advantageous if a larger domain needs to be uniformly covered and/or if integrated (biogeochemical) quantities are to be determined (see, e.g., Roiha et al., 2010).

In the hierarchy of Eulerian HAB models, it seems that one-compartment LCMs are hardly able to represent the observed bloom dynamics (see Hense and Burchard, 2010), while 1.5-compartment models (Yamamoto et al., 2002; McGillicuddy et al., 2005) do better due to the prescription of boundary conditions (abundance and distribution of resting cells). Such models, however, are only semi-prognostic, as the life cycle is not fully closed.

It is not clear at the moment, whether two- or four-compartment models will be a significant step forward (the evaluation is ongoing); but it seems that multi-compartment models (e.g., Hense and Beckmann, 2006) (or a similarly complex Lagrangian model) have the largest potential for capturing the essence of the life cycle dynamics of HABs. Such models, however, have to rely on a large number of (unknown) parameters, which have not yet been determined or confirmed by observations.

Even for key species or key groups we still lack a basic understanding of triggering factors for life cycle transitions, as well as rates for en- and excystment, metabolism for the distinct stages and biomass losses (e.g., during sex). Thus, many open questions need to be resolved to complete our picture of the life cycle of phytoplankton. As the importance of the life cycle in regulating HABs is becoming better recognized, progress in this area is to be expected for the coming years. Modeling activities will certainly play a large part in it (see, e.g., Glibert et al., 2010).

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