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Approaches to model the life cycle of harmful algae

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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:

$$\frac{\partial P}{\partial t} = \mu P - lP \quad (1)$$

$$\frac{\partial x^P}{\partial t} = u \quad (2)$$

$$\frac{\partial y^P}{\partial t} = v \quad (3)$$

$$\frac{\partial z^P}{\partial t} = w + w_P \quad (4)$$

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:

$$\frac{\partial A^P}{\partial t} = 1. \quad (5)$$

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):

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

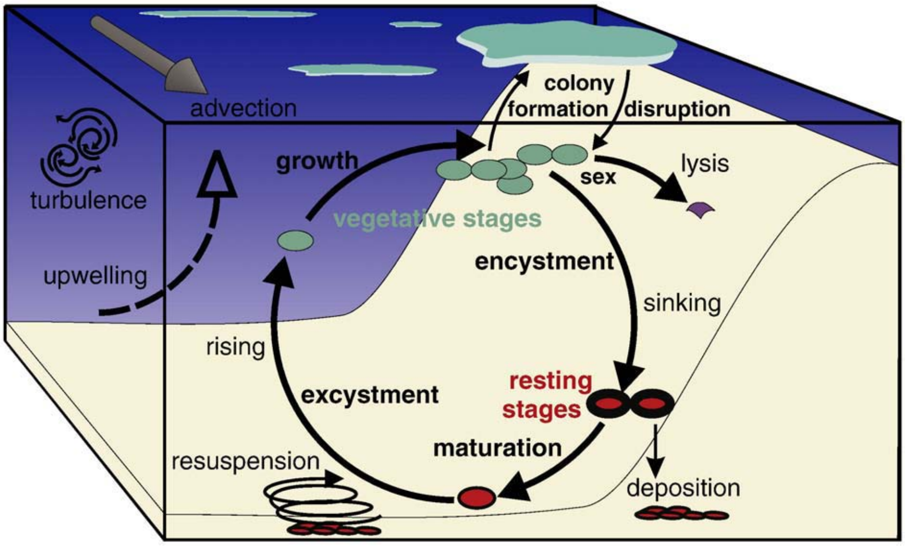

Fig. 1. Overview of major life cycle stages of marine phytoplankton, the main biological and contributing physical processes. Beginning with the vegetative phase, cells grow dependent on endogenous and exogenous factors. For some species this phase may be followed by formation and disruption of colonies. 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.