Journal of
Plankton Research

plankt.oxfordjournals.org

*J. Plankton Res.* (2013) 35(2): 379–392. First published online December 23, 2012 doi:10.1093/plankt/fbs095



# Modelling the life cycle of dinoflagellates: a case study with *Biecheleria baltica*

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Received August 29, 2012; accepted November 17, 2012

Corresponding editor: John Dolan

The cold-water dinoflagellate *Biecheleria baltica* has increasingly dominated the phytoplankton spring bloom in the Baltic Sea during the past years. Life cycle transitions between bloom forming cells and resting cysts are assumed to regulate the bloom dynamics of this species. We investigate the seasonal cycle and succession of *Biecheleria baltica's* life cycle stages using a numerical model with four different stages, vegetative cells, gametes, resting cysts and germinating cells. The transitions among the stages are functions of environmental conditions and endogenous factors. Coupled to a water column model, the model is able to represent the seasonal cycle of *Biecheleria baltica* with two blooms in spring. The first bloom can be explained by germination of resting cysts in winter, the second by growth of vegetative cells. Sensitivity experiments indicate that temperature is an important factor regulating the composition of *Biecheleria baltica* life cycle stages; increased or decreased temperature leads to fewer growing cells and more resting cysts during spring. Our newly developed life cycle model can be used to study in more detail cyst formation, cyst distribution and consequences for biogeochemical cycling in the past and future.

KEYWORDS: life cycle; encystment; excystment; seed pool; spring bloom; dinoflagellate

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## INTRODUCTION

Dinoflagellates are a key group of marine phytoplankton and are important primary producers. Several species can form dense blooms and produce toxic substances with harmful effects on humans and on co-occurring biota (Garcés *et al.*, 2002). In some areas, cold-water dinoflagellates dominate the phytoplankton spring bloom (Klais *et al.*, 2011) and, thereby, can account for a large part of the annual new production.

While spring blooms are generally dominated by diatoms, dominance has been gradually shifting from diatoms to dinoflagellates (i.e. a shift in dominance) in the Baltic Sea and North Sea in recent years (e.g. Edwards *et al.*, 2006; Klais *et al.*, 2011; Wasmund *et al.*, 2011). One of the species that has become dominant is *Biecheleria baltica* [=*Woloszynskia halophila* sensu Kremp *et al.* (Kremp *et al.*, 2005), see references therein for details on the complex taxonomic history]. Particularly in the Gulf of Finland, *Biecheleria baltica* has become a dominant component of the phytoplankton spring bloom (Klais *et al.*, 2011).

The reasons for the shift in dominance are not completely understood. Among other factors, the size of the dinoflagellate inoculum had been considered relevant (Kremp *et al.*, 2008). The inoculum (i.e. the cells that initialize a bloom) is regulated by life cycle processes of *Biecheleria baltica*. The species produces large numbers of resting cysts at the end of each bloom (Heiskanen, 1993; Kremp and Heiskanen, 1999). Growing cyst deposits resulting from mass sedimentation events have been suggested to promote the expansion of the species in the Gulf of Finland (Klais *et al.*, 2011). Despite indications from empirical data, the direct causal relationship among life cycle processes, physical conditions and *Biecheleria baltica* blooms has remained hypothetical.

The transitions between planktonic growing cells and benthic resting cysts regulate bloom dynamics for a number of bloom forming dinoflagellate species (e.g. Anderson *et al.*, 1983; Rengefors, 1998; Bravo *et al.*, 2010). The formation of cysts (encystment) is important in regulating the termination of dinoflagellate blooms (e.g. Anderson, 1984; Kremp and Heiskanen, 1999; Garcés *et al.*, 2004). The subsequent sedimentation and accumulation of cysts after encystment in the sediment leads to the formation of seed banks with large numbers of cysts. The germination of resting cysts (excystment) takes place under specific environmental conditions and contributes to a sudden increase in vegetative cells, representing an inoculum that initiates the bloom (Nehring, 1996; Kremp and Anderson, 2000; Genovesi-Giunti *et al.*, 2006). Indeed, the formation of blooms cannot be explained by vegetative growth alone (McQuoid, 2005) and a large part of the winter population of vegetative cells arises from excystment (Ishikawa and Taniguchi, 1996). As a secondary effect, resting cysts have the potential to reintroduce species (or strains) that have remained absent for a period of time (McQuoid *et al.*, 2002).

So far, only a few dinoflagellate models have considered life cycle processes. The excystment model by McGillicuddy *et al.* (McGillicuddy *et al.*, 2003) focusses on a toxic dinoflagellate species. The model results show that realistic temporal and spatial distribution patterns are obtained only if the observed cyst distribution is included in the model (McGillicuddy *et al.*, 2003, 2005; He *et al.*, 2008; Li *et al.*, 2009). However, their approach is restricted to space and time where data from observations are available (see discussion in Hense, 2010). A similar approach has been applied by Yamamoto *et al.* (Yamamoto *et al.*, 2002), who additionally included encystment. However, the authors only consider a "chain" of life cycle processes, i.e. from germination of a prescribed cyst pool to cyst formation. The complete cycle (in which the cysts produced can germinate again) is not taken into account. Estrada *et al.* (Estrada *et al.*, 2010) studied the role of resting cysts on bloom formation using two different approaches. In the first, the dinoflagellate life cycle is also described only by a chain of life cycle processes instead of a complete cycle. In the second approach, cyst concentrations are assumed to be proportional to vegetative cells. The processes encystment and excystment that lead to either a sink of vegetative cells (source of cysts) or a sink of cysts (source of vegetative cells) are not adequately represented. A different concept to consider the life cycle of dinoflagellates was applied by Peperzak (Peperzak, 2006), who has developed a time-discrete model in which a constant part of a life cycle stage is transferred to another one. Thus, none of these models has dynamically described the full-life cycle of dinoflagellates including the underlying factors and mechanisms that cause them. Studies for other planktonic organisms, however, have shown that this is feasible. For instance, models with a complete life cycle have been developed for cyanobacteria (e.g. Hense and Beckmann, 2006; Hellweger *et al.*, 2008; Jöhnk *et al.*, 2011) and copepods (Fennel, 2001). They have been successfully applied to lakes (Hellweger *et al.*, 2008; Jöhnk *et al.*, 2011) and coastal regions (e.g. Moll and Stegert, 2007; Hense and Burchard, 2010) demonstrating the need to include life cycle processes in ecosystem models to explain, for example, bloom patterns or generation cycles.

In this paper, we present a numerical model of the life cycle of *Biecheleria baltica* to study the succession of life cycle stages within the seasonal cycle. We consider

the case when this dinoflagellate is dominant, a situation that occurs regularly in the Baltic Sea. We aim to understand the relationships among life cycle transitions (en- and excystment), physical conditions, as well as bloom formation and decline of *Biecheleria baltica*. However, we do not consider interannual variability and shifts in the species composition. To study the effects of climate variability on bloom and cyst formation, we have conducted different temperature scenarios.

## MAIN MODEL ASSUMPTIONS

Heteromorphic life cycles containing functionally different stages have been identified for several dinoflagellates (e.g. Von Stosch, 1973; Pfiester and Anderson, 1987; Figueroa *et al.*, 2008). Different dinoflagellate species have different life cycles. For instance, in some species, the formation of resting cysts is coupled to sexual reproduction while other species produce cysts asexually or no resting cells at all (e.g. Kremp, 2012).

Mass conservation is not specifically linked to life cycle (or any specific kind of) models, but our approach to modelling the life cycle is to describe a self-contained, mass-conserving system, where all sources and sinks balance. For example, the nutrient uptake is a source for phytoplankton and a sink for nutrients. Mortality is a sink for phytoplankton, while it is a source for detritus. Further, remineralization is a sink for detritus and a source for nutrients.

To couple life cycle models to ecosystem models, it is necessary to have a common unit for all ecosystem variables. Ecosystem variables are usually expressed in terms of the biomass (e.g. in carbon or nitrogen units).

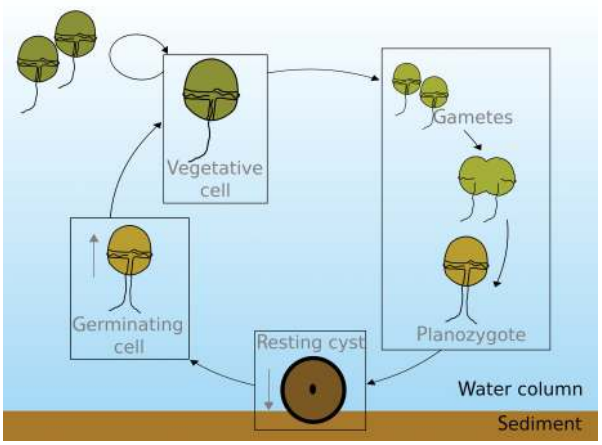


**Fig. 1.** Conceptual overview of the dinoflagellate life cycle, the four model compartments (vegetative cells, gametes, cysts and germinating cells), and the transitions among the compartments.

In this case, it does not matter whether a small number of large cells or a large number of small cells with the same biomass take up the nutrients.

While ecosystem model studies focus on the development of biomass, laboratory and field studies usually focus on the development of cell numbers. Dinoflagellate cells decrease in size (and biomass) during the growth phase, while at the same time their abundance (i.e. numbers) increases (e.g. Kremp *et al.*, 2009). Thus, the same data set can show an increase in cell numbers with a decrease in the cell biomass (e.g. Warns *et al.*, 2012).

We model the life cycle of the Baltic Sea dinoflagellate *Biecheleria baltica* in terms of the biomass (in nitrogen units). On the basis of insights from laboratory experiments (e.g. Kremp *et al.*, 2009) and the literature (e.g. Garcés *et al.*, 2002), we consider the four life cycle compartments vegetative cells, gametes, resting cysts and germinating cells as well as the transitions among these compartments (encystment and excystment, Fig. 1). The growth and encystment processes are modelled according to Warns *et al.* (Warns *et al.*, 2012), which has previously been evaluated for *Biecheleria baltica*. For the current study, we additionally consider the maturation and excystment processes as well as life cycle-related vertical migration.

Cysts sink, because they are immotile and denser than water (Heiskanen, 1993). At the sea floor, some cysts are buried in the sediment (Anderson *et al.*, 1985). The cysts enter a mandatory dormancy period, during which they mature and excystment is physiologically impossible (e.g. Dale, 1983; Binder and Anderson, 1987; Pfiester and Anderson, 1987). In the model, we consider sinking of cysts and losses at the sea floor by applying a burial rate at the bottom, and a maturation time.

Excystment of *Biecheleria baltica* is primarily determined by the specific length of the maturation period and, thereafter, assumed to be regulated by environmental factors such as temperature, light and oxygen conditions (e.g. Anderson *et al.*, 1987; Bravo and Anderson, 1994; Anderson and Rengefors, 2006). The cysts remain quiescent until the environmental conditions become favourable again.

Several studies have identified temperature as the main regulating factor for germination (e.g. Pfiester and Anderson, 1987; Bravo and Anderson, 1994; Kremp and Anderson, 2000). Therefore, we consider temperature for the transition from cysts into germinating cells.

Although studies have found that light increases excystment rates (e.g. Anderson *et al.*, 1987; Kremp and Anderson, 2000; Kremp, 2001), it is also observed that cyst are able to excyst in darkness albeit at a lower rate (e.g. Bravo and Anderson, 1994; Kremp, 2001; Anderson and Rengefors, 2006). Since we could not

deduce a functional relationship between light and encystment, we refrain from introducing light as a factor for the transition from cysts into germinating cells.

There is some evidence that anoxic conditions inhibit germination (e.g. Anderson *et al.*, 1987; Kremp and Anderson, 2000). Oxygen concentrations are not homogeneous in the Baltic Sea; occurrences of low oxygen concentrations are observed at certain times and some locations. We consider a region with oxygenated bottom layers and, therefore, do not consider oxygen as a factor for the transition from cysts into germinating cells.

Overall, excystment is considered as a two-fold process in this study. It consists of the transitions from cysts to germinating cells and from germinating cells to vegetative cells. Germinating cells are typically zygotic and go through meiosis after excystment before vegetative growth can be resumed. In the life cycle model, we assume that germinating cells move upwards to repopulate the upper water column and that light is the main factor triggering transition from germinating to vegetative cells.

In a three-dimensional model simulation in which horizontal gradients in environmental variables are described other factors (e.g. oxygen and light), as triggers for excystment might be added.

## MODEL DESCRIPTION

Our life cycle model considers four life cycle compartments: vegetative cells $V$, gametes $G$, cysts $C$ and germinating cells $R$. To realistically describe the ecosystem and conserve mass, the model has additional ecosystem compartments for nutrients $N$ and detritus $D$ (Fig. 2). The life cycle is circular and unidirectional, from vegetative cells to gametes to cysts to germinating cells, and back to vegetative cells.

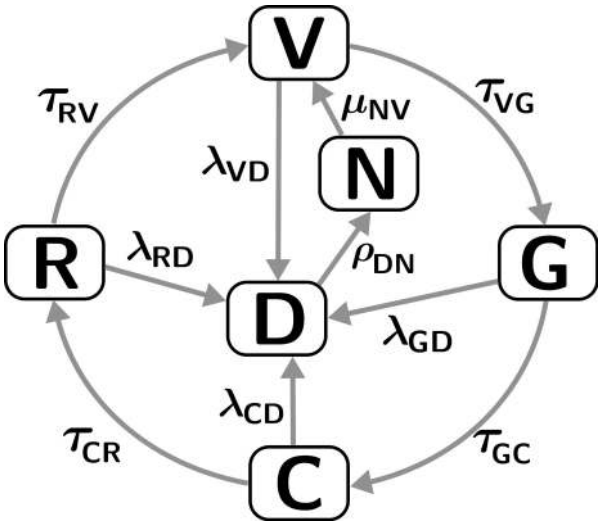


**Fig. 2.** Conceptual overview of the life cycle model compartments (vegetative cells $V$, gametes $G$, cysts $C$ and germinating cells $R$) as well as of the compartments for nutrients $N$, and detritus $D$ and the transitions among these compartments. The rates are Greek letters indexed describing the direction of the change.

The changes of the life cycle compartments are given by transition functions $\tau$, loss terms $\lambda$, vertical motility $\omega$ and a function for the growth of vegetative cells $\mu$. The variables are indexed describing the direction of the change. For example, $\tau_{RV}$ is the transition from germinating cells $R$ to vegetative cells $V$.

The changes of the life cycle and ecosystem compartments over space and time are given by

$$\frac{\partial V}{\partial t} = \mu_{NV} V + \tau_{RV} R - \tau_{VG} V - \lambda_{VD} V + \frac{\partial}{\partial z}\left(A_v \frac{\partial V}{\partial z}\right), \quad (1)$$

$$\frac{\partial G}{\partial t} = \tau_{VG} V - \tau_{GC} G - \lambda_{GD} G + \frac{\partial}{\partial z}\left(A_v \frac{\partial G}{\partial z}\right) \quad (2)$$

$$\frac{\partial C}{\partial t} = \tau_{GC} G - \tau_{CR} C - \lambda_{CD} C - \omega_C \frac{\partial C}{\partial z} - \delta_C C^2|_{z=-H} + \frac{\partial}{\partial z}\left(A_v \frac{\partial C}{\partial z}\right), \quad (3)$$

$$\frac{\partial R}{\partial t} = \tau_{CR} C - \tau_{RV} R - \lambda_{RD} R - \omega_R \frac{\partial R}{\partial z} + \frac{\partial}{\partial z}\left(A_v \frac{\partial R}{\partial z}\right), \quad (4)$$

$$\frac{\partial N}{\partial t} = \rho_{DN} D - \mu_{NV} V + F^N|_{z=0} - \frac{1}{\theta}(N_0 - N)|_{z=-H} + \frac{\partial}{\partial z}\left(A_v \frac{\partial N}{\partial z}\right), \quad (5)$$

$$\frac{\partial D}{\partial t} = \lambda_{VD} V + \lambda_{GD} G + \lambda_{CD} C + \lambda_{RD} R - \rho_{DN} D - \omega_D \frac{\partial D}{\partial z} + \frac{\partial}{\partial z}\left(A_v \frac{\partial D}{\partial z}\right). \quad (6)$$

All variables are subject to diffusion. Vertical velocities are applied to cysts, which sink, and to germinating cells, which rise in the water column. The vegetative cells and the gametes are assumed to be neutrally buoyant. Since we are only interested in the seasonal cycle, we do not consider the diurnal vertical migration of vegetative cells.

We assume constant loss rates for vegetative cells, gametes and germinating cells, which represent, for example, cell lysis and grazing. The losses go into the

detritus, which is re-mineralized and transferred back to the nutrients. The nutrients can be taken up by vegetative cells. For the cysts, we assume burial at the bottom of the water column, but no loss during the relatively short period of sinking down the water column. The burial at the bottom depends quadratically on the cyst concentration. For specific values see Table I.

The mathematical formulation of growth and encystment is taken from our previous model described in detail by Warns *et al.* (Warns *et al.*, 2012). In summary, the main assumptions are: the growth of vegetative cells is limited by the availability of nutrients, irradiance, temperature and gamete concentrations. Gamete production is low at low temperature (below 3°C) and increases with increasing temperature, reaching a maximal rate at 6°C. Cyst production depends on temperature and the concentration of gametes. If temperature is sufficiently high (>3 °C) and the concentration reaches a specific threshold, gametes transform into cysts.

In contrast to our previous zero-dimensional study, light and temperature in our one-dimensional model are obtained as follows:

*Table I: Parameters and constants for the life cycle model.*

| Symbol | Parameter | Value | Unit |
|---|---|---|---|
| $k_C$ | Self-shading parameter | 0.03 | $m^2$ (mmol N)$^{-1}$ |
| $k_W$ | Attenuation coefficient | 0.13 | $m^{-1}$ |
| $\tau_3$ | Maximal transition rate from C to R | 0.05 | day$^{-1}$ |
| $\tau_4$ | Maximal transition rate from R to V | 0.3 | day$^{-1}$ |
| $t_{m1}$ | Start of "quiescence" for C | 210 | day |
| $t_{m2}$ | End of "quiescence" for C | 300 | day |
| $\lambda_{VD}$ | Loss rate of V | 0.03 | day$^{-1}$ |
| $\lambda_{GD}$ | Loss rate of G | 0.03 | day$^{-1}$ |
| $\lambda_{RD}$ | Loss rate of R | 0.03 | day$^{-1}$ |
| $\delta_C$ | Deposition coefficient of C | 0.0029 | $m^3$ (mmol N)$^{-1}$ $a^{-1}$ |
| $\omega_C$ | Sinking of C | −8 | m day$^{-1}$ |
| $\omega_R$ | Rinsing of R | 8 | m day$^{-1}$ |
| $\omega_D$ | Sinking of D | −10 | m day$^{-1}$ |
| $c_1$ | Constant used in transition function $f_3$ | 8 | — |
| $c_2$ | Constant used in transition function $f_3$ | 0.1 | °C$^{-1}$ |
| $c_3$ | Constant used in transition function $f_3$ | 0.8 | — |
| $c_4$ | Constant used in transition function $f_3$ | 6.6 | °C$^{-1}$ |
| $F^N$ | Atmospheric nitrogen deposition | −0.2 | mmol N m$^{-2}$ day$^{-1}$ |
| $N_0$ | Restoring value of nutrients at the bottom | 10 | mmol N m$^{-3}$ |
| $\theta$ | Restoring time of nutrients at the bottom | 7200 | sec |
| $\bar{l}_l$ | critical value for setting maturation time to 0 | 0.64 | — |

(1) we consider vertical attenuation of irradiance by

$$I_{\mathrm{par}} = I_0\, e^{(k_w z - k_c \int_z^0 (V(z')+G(z')+C(z')+R(z')+D(z'))dz')}$$

with $z$ negative downward, where $I_{\mathrm{par}}$ is the photosynthetic active radiation, $I_0$ is the irradiance at the surface, $k_c$ is the self-shading and $k_w$ is the seawater attenuation coefficient.

(2) we use a 5-day running mean of temperature $\bar{T}$ for gamete and cyst production to avoid effects of short-lived temperature variations on growth (e.g. due to day-night cycles or sudden cloud cover changes). In principle, a number of additional state variables, so-called subcompartments (Janowitz and Kamykowski, 1999; Beckmann and Hense, 2004), are needed in a Eulerian framework to distinguish populations with a different temperature history. However, since both vegetative cells and gametes reside mainly in the quasi-homogeneous mixed layer, this simplified approach seems reasonable.

The excystment process is parameterized based on observations on *Biecheleria baltica*. According to Kremp and Anderson (Kremp and Anderson, 2000), resting cysts mature for a period of time (a mandatory dormancy period), before they are physiologically capable of excystment. When the maturation is completed, the cysts enter a state termed "quiescence". Quiescent cysts transform into germinating cells as soon as the temperature is favourable for excystment.

On the basis of these findings, in the model, we define a transition rate from resting cysts into germinating cells $\tau_{CR}$ that depends on a mandatory dormancy period and a temperature interval. More precisely, the cysts are "quiescent" if their maturation time $t_{mat}$ is

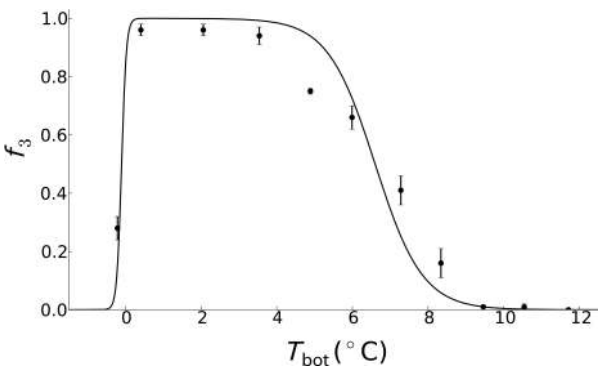


**Fig. 3.** The function $f_3$ determines the transition rate $\tau_{CR}$ and depends on the temperature in the bottom layer $T_{bot}$. The dots with standard deviations show observational data from experiments conducted by Kremp and Anderson (Kremp and Anderson, 2000).

between $t_{m1}$ and $t_{m2}$. Quiescent cysts transform into germinating cells if the temperature at the bottom $T_{\mathrm{bot}}$ is between 0 and 9 °C. The values for $t_{m1}$ and $t_{m2}$ are adjusted so that the cysts germinate in late winter, which is in agreement with observations. That is, we define

$$\tau_{\mathrm{CR}} = \begin{cases} \tau_3 f_3(T_{\mathrm{bot}}) & \text{for } t_{\mathrm{mat}} \in [t_{m1},\ t_{m2}] \\ 0 & \text{otherwise} \end{cases} \quad (8)$$

$$\text{with } f_3(T_{\mathrm{bot}}) = (0.5 \tanh(c_1(T_{\mathrm{bot}} + c_2)) + 0.5) - (0.5 \tanh(c_3(T_{\mathrm{bot}} - c_4)) + 0.5), \quad (9)$$

where $\tau_3$ is maximum of the transition rate $\tau_{\mathrm{CR}}$ and $f_3$ is a function being greater than 0 at bottom temperature between 0 and 9 °C and 0 otherwise (Fig. 3 and Table I).

The maturation time $t_{\mathrm{mat}}$ is calculated from a concentration-weighted integral over time following the approach of Hense and Beckmann (Hense and Beckmann, 2010). We set the maturation time to 0 as soon as the mean (5-day running mean) irradiance limitation function $\overline{l}_I$ at the surface is greater than a critical value $\overline{l}_{I_{\mathrm{crit}}}$ for the first time in the seasonal cycle, and the maturation time $t_{\mathrm{mat}}$ is >200 days.

The characteristics of germinating cells have not been studied in detail in the field or laboratory. However, it is reasonable to assume that germinating cells migrate upwards into the euphotic zone and transform into vegetative cells. We assume that the transition rate of germinating cells to vegetative cells increases with increasing irradiance. As the germinating cells rise in the water column and as the irradiance is higher in upper layers of the water column, the transition primarily takes place in upper layers. We define the transition rate of germinating cells to vegetative cells $\tau_{\mathrm{RV}}$ as

$$\tau_{\mathrm{RV}} := \tau_4 f_4(I_{\mathrm{par}}) \quad (10)$$

$$\text{with } f_4 := 1 - \mathrm{e}^{(-0.5 I_{\mathrm{par}})}, \quad (11)$$

where $\tau_4$ is the maximum of the transition rate $\tau_{\mathrm{RV}}$ and $I_{\mathrm{par}}$ is the photosynthetically active radiation.

## MODEL APPLICATION

The model is coupled to the 1D water column model General Ocean Turbulence Model (GOTM , Umlauf *et al.*, 2005) that provides the physical environment—turbulent mixing, temperature, salinity and irradiance fields. This model allows us to investigate the life cycle dynamics using realistic atmospheric forcing from the Baltic Sea. We use a similar model setup as in Hense and Beckmann (Hense and Beckmann, 2010). The atmospheric forcing data stem from the ECMWF ERA40 reanalysis (Uppala *et al.*, 2005). We use the year 1982, which is a "typical" year (i.e. a year with moderate magnitude of temperature, wind and cloud cover) within the period from 1958 to 2005. The modelled water column has a depth of 80 m with a vertical resolution of 1 m. A time step of 900 s is applied.

At the surface, a nitrogen flux is prescribed from the atmosphere into the water column using a typical value for the Baltic Sea (Larsson *et al.*, 2001) [$F^N$ see also equation (5)]. This flux is balanced by a loss term of cysts in the bottom layer due to burial and restoring of nutrients in the bottom layer to a "typical" value of 10 mmol N $\mathrm{m}^{-3}$ every 2 h [$N_0$ and $\theta$ see also equation (5)]. All other boundary conditions are "no flux". The numerical scheme for the discretization of the ecosystem processes is a second-order modified Patankar-Runge-Kutta scheme (Burchard *et al.*, 2003), which is positive definite and mass conserving. The model is run for 13 years using the perpetual forcing from 1982 to reach a quasi steady state.

## RESULTS

We use the last year (that is in quasi steady state) of our simulation for our analysis. The model results show a realistic seasonal cycle of temperature and nutrients in the Baltic Sea, similar to previous model studies (e.g. Hense and Burchard, 2010). The increase in solar radiation and decrease in wind stress lead to an increase in surface temperature and stronger stratification from April to August (Fig. 4a). Maximum temperature occurs in August before the radiation decreases. Autumn mixing leads to cooling and gradual deepening of the mixed layer. Nutrient concentrations are relatively high in winter until growth of the vegetative cells leads to nutrient depletion at the surface from May to July (Fig. 4b). In autumn, re-mineralized dead organic matter and autumn mixing fill the nutrient pool at the surface again.

In January, the dormancy period of the cysts is completed and the temperature is favourable for excystment, thus, the cysts transform into germinating cells (Fig. 5, blue line). The germinating cells rise from the bottom to the well-illuminated upper layers of the water column, where they transform into vegetative cells. The excystment process results in a first peak of motile cells (i.e. the sum of germinating cells, vegetative cells and gametes) in February. The relatively cold temperature limits growth in February and March. When the temperature rises in April, the concentration of vegetative cells rapidly increases (Fig. 5, grey line). This increase in

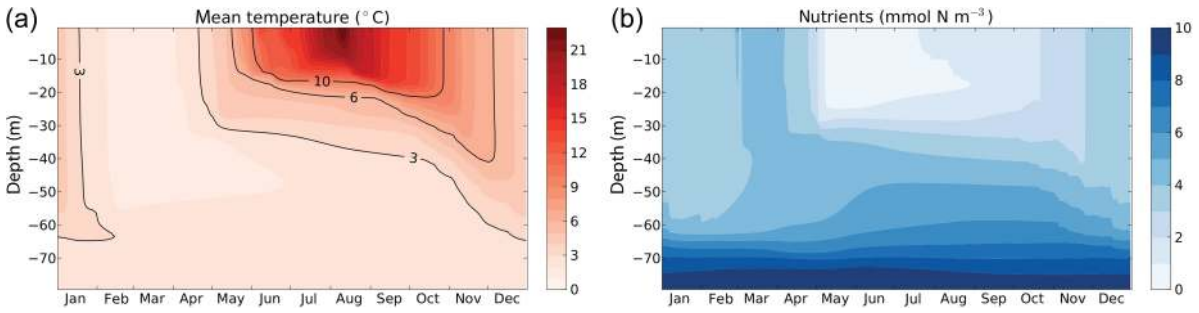


**Fig. 4.** The seasonal distribution of (**a**) the mean temperature $\bar{T}$ and (**b**) the nutrients $N$. The contour lines in temperature indicate the critical thresholds for the different life cycle transitions.

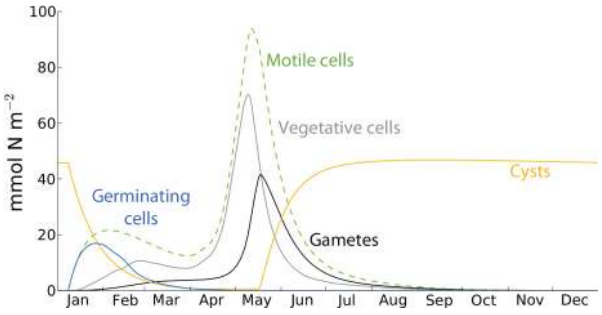


**Fig. 5.** The seasonal distribution of the integrated concentrations of germinating cells, vegetative cells, gametes, resting cysts and motile cells (sum of the total concentrations of germinating cells, vegetative cells and gametes).

vegetative cells results in a second peak of motile cells at the beginning of May (Fig. 6). The decrease in vegetative cells at the end of May is partly caused by the beginning of the encystment process when the biomass is transferred into the gametes (Fig. 5). This transition is driven by temperature; a temperature rise to $>3^{\circ}C$ induces a rapid increase in gametes (Fig. 5, black line). Hence, highest concentrations of gametes are found shortly after maximum concentrations of vegetative cells. The contribution of vegetative cells to the spring bloom is much larger than the contribution of gametes. In addition to the gamete formation, the biomass of vegetative cells is reduced by high surface temperature, nutrient exhaustion, increasing gamete concentrations and mortality. With decreasing concentrations of vegetative cells and increasing concentrations of gametes, cyst formation takes place. The cysts sink to the sediment at the bottom (Fig. 6), where they mature until the next year, when the cycle begins anew.

## MODEL EVALUATION

For the evaluation of the life cycle model, we compare the model results with observations that have not been taken into account for the model development. Additionally, we compare the results with results from a model that does not consider a life cycle.

### Seasonal cycle of motile cells

An adequate quantitative comparison between model results (given in terms of biomass) and observations is non-trivial, because an accurate conversion from biomass into numbers of motile cells is not possible without further knowledge about the proportion of the life cycle stages. Motile cells include cells of different types (i.e. vegetative cells, gametes and planozygotes) with different biomass. The ratio of the different cell types varies over time and even the biomass within a given cell type varies. Warns *et al.* (Warns *et al.*, 2012) found significant differences in data of motile cells either expressed in cell counts or expressed in the biomass due to the varying proportion of the different cell types.

For a rough comparison of model results and observations, we have converted the field data from Kremp and Anderson (Kremp and Anderson, 2000). The field data comprise the vegetative population of *Scrippsiella hangoei* nearby the Gulf of Finland from May 1995 to June 1996. Please note that *Biecheleria baltica* and *Scrippsiella hangoei* were regarded as one species until 2005; see Kremp *et al.* (Kremp *et al.*, 2005) for a detailed discussion on the taxonomy. We converted the cell counts as follows: Using the cell dimensions (Kremp *et al.*, 2008) and formulae given for standard geometric shapes of phytoplankton taxa (Sun and Liu, 2003), a carbon-to-volume ratio according to the recommendations of Menden-Deuer and Lessard (Menden-Deuer and Lessard, 2000) and the Redfield ratio (Redfield, 1958), we can calculate the total concentrations, assuming that either only vegetative cells or gametes or planozygotes occur (Fig. 7), since the information about the proportions is missing. For the field data, monthly

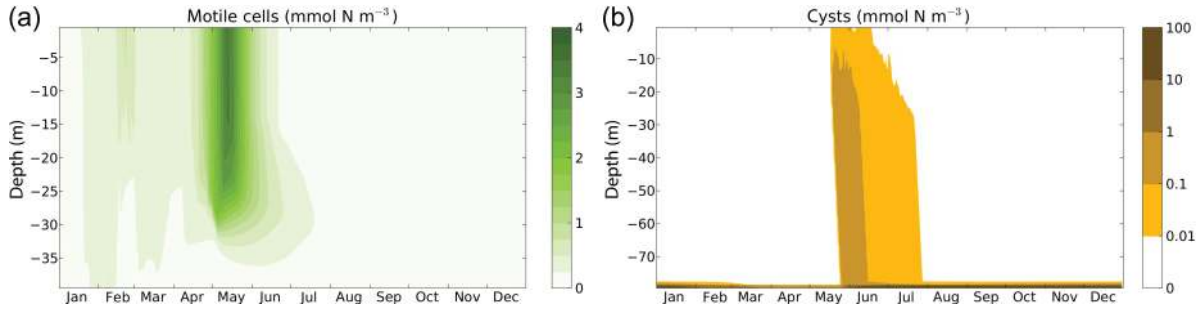


**Fig. 6.** The seasonal distribution of different life cycle compartments (**a**) motile cells (sum of the total concentrations of vegetative cells, gametes and germinating cells) in the upper 40 m and (**b**) cysts over depth.

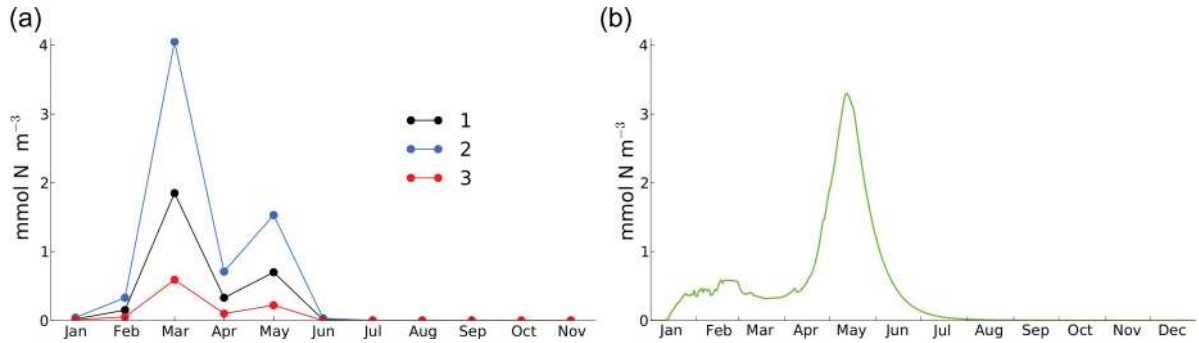


**Fig. 7.** The mean biomass concentrations of motile cells in the upper 20 m over time (**a**) from observations and (**b**) from model results. The observations are based on cell counts (Kremp and Anderson, 2000) and are converted into biomass concentrations. Different lines show different *nitrogen per cell* factors of the different cell types; assuming 100% of the motile cells are vegetative cells (1), gamete (2), or planozygotes (3). Note that the lines span up a range for the actual biomass of motile cells (please see text for detailed informations).

means are considered if more than one value is available per month. The *nitrogen per cell* factor of a motile cell is the mean of the factors for vegetative cells (7.9 pmol N cell$^{-1}$), gametes (2.5 pmol N cell$^{-1}$) and planozygotes (17.4 pmol N cell$^{-1}$).

The comparison between model and observations shows a similar seasonal pattern with two biomass peaks in spring, one in January/February and a second one in May (Fig. 7). This is consistent with observations by Kremp (Kremp, 2000); Spilling (Spilling, 2007) who recognized two peaks of motile dinoflagellate cells in the Gulf of Finland. One is typically found in late winter between the end of January and early March, and another major peak occurs in May. Using molecular detection methods, Sundström *et al.* (Sundström *et al.*, 2010) confirmed that both peaks are caused by *Biecheleria baltica*.

The model and the converted field data show similar maximal peak concentrations (Fig. 7). The maximal concentration of the converted field data is between 0.59 and 4.05 mmol N m$^{-3}$ depending on which of the different cell types is assumed to dominate (Fig. 7a). It should be noted that the values in Fig. 7a are based on a fixed *nitrogen per cell* factor, one for each cell type. However, the ratio of the different cell types varies over time. Depending on the ratio of the different cell types, the biomass of the first peak can be lower or higher than the biomass of the second peak.

To study further the effects of the life cycle on the seasonal development of vegetative cells, we have developed a dinoflagellate model without a life cycle. In this simplified model, we only consider vegetative cells, nutrients and detritus, as well as the processes growth and mortality of vegetative cells, re-mineralization and sinking of detritus. We use the same functions and parameters as in the life cycle model to describe these processes. The only exception is mortality, which we increased slightly (from 0.03 to 0.04 day$^{-1}$) to take into account the losses of all life cycle stages.

The comparison between the model without and with life cycle shows that the life cycle affects the timing, magnitude and duration of the bloom (Fig. 8). In the model without a life cycle, the bloom maximum occurs around 4 weeks later and there is only one peak, which also contrasts with observations. Compared with the results of the life cycle model, the maximal concentration of cells at the surface is less than half. In addition, maximum concentrations occur well below

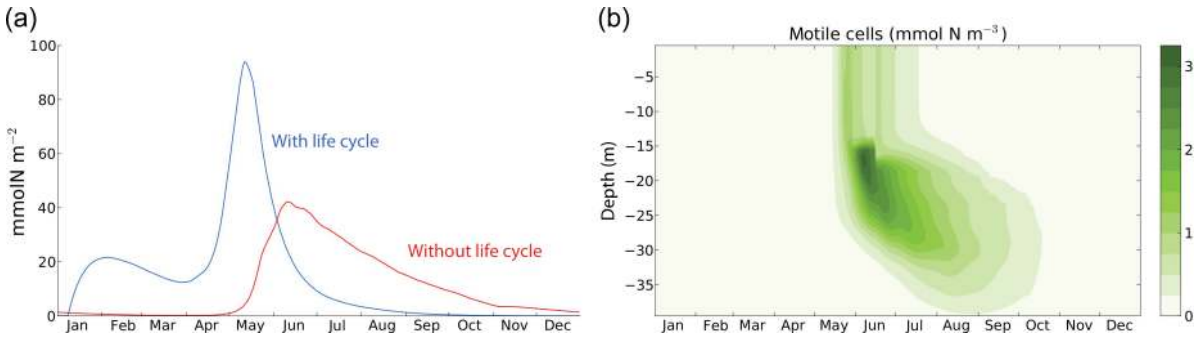


**Fig. 8.** The seasonal distribution of (**a**) the integrated concentrations of motile cells in the reference run (considering the life cycle) and the sensitivity experiment (not considering the life cycle) and (**b**) motile cells (vegetative cells) in the upper 40 m (not considering the life cycle).

the surface where temperature for growth is optimal, which contrasts with observations. Olli *et al.* (Olli *et al.*, 1998) show that cells are typically concentrated in surface layers. If the life cycle is not considered significantly the decline of the bloom after the late spring peak is also delayed.

An earlier and more realistic spring bloom could be represented in such a model by the adjustment of the growth rate. However, in that case the growth rate must be twice as high (0.8 day$^{-1}$ instead of 0.4 day$^{-1}$) as in observations (e.g. Kremp *et al.*, 2005; Spilling and Markager, 2008), which is unrealistic. Even with an increased growth rate the bloom in early spring could not be adequately represented in the model without life cycle, because the bloom period is still prolonged and only one bloom occurs.

### Cyst pool

Kremp (Kremp, 2000) quantified the seeding potential of cyst beds in the Baltic Sea by counting viable cysts in the sediment and investigating their germination potential (i.e. the relative amount of cysts able to germinate). The theoretical seed pool is defined by the total amount of viable cysts in the sediment multiplied by the germination potential. Assuming a fixed nitrogen content of cysts (17.0 pmol N cyst$^{-1}$, Warns *et al.*, 2012), in the Gulf of Finland, the theoretical seed pool is between 19.0 mmol N m$^{-2}$ (for a germination potential of 10%) and 190.1 mmol N m$^{-2}$ (for a germination potential of 100%). The modelled seed pool (i.e. cyst concentration in the model on the day before the excystment starts) of 45.4 mmol N m$^{-2}$ is within this range.

### Cyst flux

Our predicted cyst fluxes agree well with those derived from observations. In the coastal northern Baltic Sea, Kremp and Heiskanen (Kremp and Heiskanen, 1999) reported the maximum cyst flux for *Scrippsiella hangoei* at the end of May with ~2.8 mmol N m$^{-2}$ day$^{-1}$. The life cycle model shows a slightly earlier maximal cyst flux (mid-May) of ~2.1 mmol N m$^{-2}$ day$^{-1}$, which is quite close to observations.

## SENSITIVITY EXPERIMENTS WITH DIFFERENT ATMOSPHERIC TEMPERATURE FORCING

In the previous sections, we have shown that our dinoflagellate life cycle model successfully represents the seasonal cycle of *Biecheleria baltica* with an atmospheric forcing for a typical year (i.e. 1982). To investigate the sensitivity of the life cycle model to temperature changes, we use different forcing sets with modified temperature. Therefore, we changed the temperature of the atmospheric forcing field (dry air temperature and dew point temperature) by ±3°C compared with the reference run to obtain a warming and a cooling scenario.

In the warming scenario, the onset of excystment and both bloom peaks occur 1 month earlier (see Fig. 9a) compared with the reference run. More gametes relative to vegetative cells are formed and more cysts are produced and deposited. The concentration of motile cells during the first bloom is larger than in the reference run, which is caused by a larger seed pool. Nevertheless, the concentration of motile cells during the second bloom is less (Table II). The underlying mechanisms of a relatively small second bloom despite a relatively large seed pool are related to the temperature-dependent growth phase and the temperature-dependent transition from vegetative cells into gametes. High temperature leads to an enhanced transition from vegetative cells into gametes during the growth phase. Thus, the loss of vegetative cells is high.

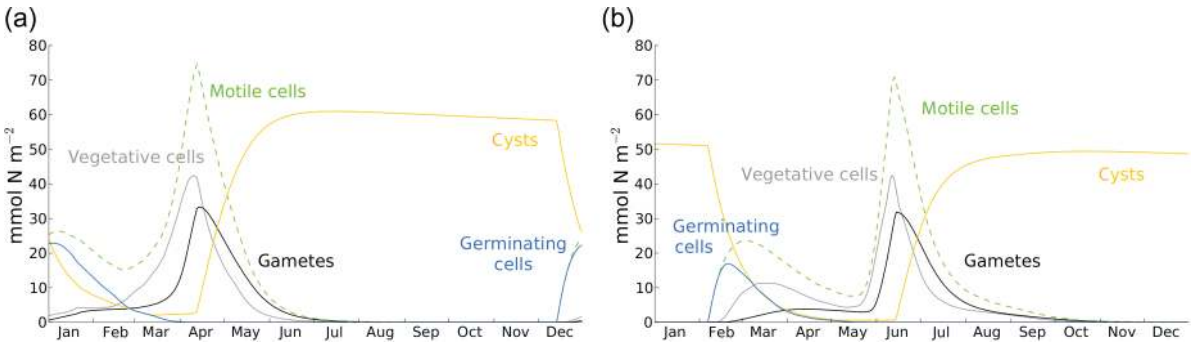


**Fig. 9.** The seasonal distribution of the integrated concentrations of the life cycle compartments in (**a**) the warming and (**b**) the cooling scenario.

*Table II: Results of three different model scenarios with different temperature forcing: the maximal vertically integrated concentrations of germinating cells* R, *vegetative cells* V, *gametes* G *and motile cells* M *as well as the seed pools (cyst concentration in the model on the day before the excystment starts)*

| | +3°C | Reference run | −3°C |
|---|---|---|---|
| $R_{max}$/mmol N m$^{-2}$ | 22.7 | 16.9 | 17.0 |
| $V_{max}$/mmol N m$^{-2}$ | 42.9 | 70.2 | 42.8 |
| $G_{max}$/mmol N m$^{-2}$ | 34.1 | 41.5 | 32.0 |
| $M_{max}$/mmol N m$^{-2}$ | 75.5 | 93.9 | 71.4 |
| Seed pool/mmol N m$^{-2}$ | 57.7 | 45.4 | 50.6 |

In comparison, in the reference run, the transition is relatively low during the growth phase. Hence, the loss of the vegetative cells is lower. Therefore, the vegetative cells can build up more biomass than in the warming scenario.

In the cooling scenario, the excystment and the blooms occur 1 month later than in the reference scenario (see Fig. 9b). More gametes relative to vegetative cells are formed. Compared with the warming scenario, more cysts are produced and deposited. The seed pool is also larger, which leads to a larger first bloom. Similar to the warming scenario, the second bloom is smaller than in the reference run (Table II), which can be explained by the temporal development of the temperature. The temperature is too low for growth until the beginning of May. Afterwards, the temperature rapidly increases (to $>2$ °C) and the vegetative cells increase. However, the continuing increase in temperature leads to an enhanced transition into gametes.

These sensitivity experiments indicate that small changes in temperature have a significant impact on the timing and magnitude of both blooms. The magnitude of the first bloom is related to the amount of the seed pool; the larger the seed pool, the larger the first bloom. The size of the second bloom is driven by a specific temperature pattern during the growth phase. Low gamete production during the growth phase causes a large second bloom, high-gamete production in the beginning of the growth phase causes a small second bloom.

## DISCUSSION

We have developed a numerical life cycle model of a Baltic key phytoplankton species, the cold-water dinoflagellate *Biecheleria baltica*. To the best of our knowledge, our model is the first that describes the dynamics of the complete life cycle of a dinoflagellate including the growing, sexual, resting and germinating phases. The model includes the mathematical formulation of the encystment model of Warns *et al*. (Warns *et al*., 2012), which has been calibrated using data from laboratory studies with *Biecheleria baltica*. In the current study, we have additionally described the excystment process and have coupled the resulting life cycle model to a one-dimensional water column model to investigate the seasonal cycle of *Biecheleria baltica* in the Baltic Sea. Our results show that the model is able to realistically reproduce the development of the different life cycle stages. In particular, the model simulates two peaks of motile cells (the sum of germinating cells, vegetative cells and gametes) in late winter/early spring. This agrees with observations in the Baltic Sea (e.g. Kremp, 2000; Kremp and Anderson, 2000; Spilling, 2007). While the late peak in spring is attributed to growth of the vegetative cells, the early appearance of motile cells in late winter raises questions about the causes. Certain characteristics such as adaptation to low-light conditions, mixotrophy, as well as lack of grazers might explain the sudden appearance. Based on our model results, we suggest that the early peak is a result of

germinating cells. Using a simplified version of the dinoflagellate model, without considering the life cycle, the observed seasonal patterns cannot be reproduced. The maximum abundance appears too late, because the growth rate of *Biecheleria baltica* is too low to explain bloom formation early in the year. In addition, there is only one peak in early summer and the maximum biomass can be found subsurface, which contrasts with observations (Olli *et al.*, 1998).

The sensitivity experiments with different temperature forcings show that changes in temperature have a significant impact on the timing and magnitude of the first and second bloom; more gametes relative to vegetative cells are formed and more cysts are produced. In the warming as well as in the cooling scenario, cyst formation is higher due to a rapid transition of vegetative cells to gametes and cysts. Kremp *et al*. (Kremp *et al.*, 2009) have observed that an increase in temperature from 3 to 6 °C induces an increase in gamete differentiation and subsequent cyst formation. This relationship is considered in our model. They propose that a temperature increase is taken as signal (or token cue) by the species to complete sexual reproduction. Hence, the species encysts before nutrients become limiting. Our life cycle model shows that nutrient concentrations are indeed higher in spring in the warming scenario compared with the reference run. Higher encystment under warm conditions prevents the build up of a large standing stock of vegetative growing cells, which potentially can take up the nutrients.

The assumed temperature increase in the warming scenario corresponds to what is expected for the Baltic Sea area. Since *Biecheleria baltica* constitutes a major part of the spring phytoplankton, a temperature rise will influence the fate of a large fraction of the biomass produced during spring. Enhanced cyst formation earlier in the spring and subsequent cyst accumulation may further increase the seed pool and may lead to a further expansion of the species in the area. This will also have an effect on the nutrient availability for other species and biogeochemical cycling.

We have considered the case that the cold-water dinoflagellate occurs in high abundance in spring in order to study the relationship between life cycle transitions and environmental conditions. On interannual time scales additional processes will determine the dynamics. In particular, competition with diatoms will lead either to the dominance of cold-water dinoflagellates or diatoms. The next step is thus to include diatoms and to study the year-to-year fluctuations in species abundance.

We found that the magnitude of the seed pool is not directly related to the magnitude of the whole motile cell standing stock. This indicates that the accuracy of current geological interpretations is questionable. In the literature, the size of cyst deposits obtained from sediment cores is often used as a proxy of productivity of dinoflagellates or phytoplankton (Radi and de Vernal, 2008). However, our model results show that there is no correlation. Instead environmental conditions control the partition into growth or resting stage biomass.

Our model setup is a first step towards modelling life cycle dynamics and cyst distribution of dinoflagellates. To elucidate the life cycle processes and bloom dynamics, we have chosen seasonal cycles with perpetual atmospheric forcings for the reference and sensitivity runs. We expect additional effects and strong variability in the succession of the life cycle stages and magnitude of the blooms if we use annually varying atmospheric forcing due the nonlinearity of the system. Previous model studies with life cycles of other phytoplankton species (e.g. Hense and Burchard, 2010) show a strong year-to-year fluctuation in the bloom magnitude.

We have assumed that cysts are partially deposited and buried on the sea floor. The remaining cysts germinate after the dormancy period if the conditions are favourable. Hence, there is no accumulation of viable cysts that can germinate in later years. In future model studies using variable forcing or in three-dimensional coupled ocean ecosystem models, this can be taken into account by introducing an additional model compartment.

Our model is based on the life cycle of *Biecheleria baltica*. For this cold-water species, temperature plays an important role in life cycle transition. The model can be relatively easily adjusted to represent other dinoflagellate species. These minor modifications may include changes in the temperature dependencies of growth, for example, if warm-water dinoflagellates are considered (e.g. *Alexandrium fundyense*, see Etheridge and Roesler, 2005). The model description for nutrient uptake behaviour (e.g. for mixotrophy, see Smayda, 1997; Mitra and Flynn, 2010) might also be adjusted. In addition, other factors influencing life cycle transitions like day-length (Sgrosso *et al.*, 2001) or certain nutrients (e.g. Pfiester, 1975; Anderson and Lindquist, 1985; Figueroa *et al.*, 2005) might be needed in order to represent the encystment and excystment of certain species adequately. Major changes in the model concept are necessary if additional life cycle stages are needed and one life cycle stage can transform into more than one stage. For instance, planozygotes of *Alexandrium taylori* follow three different routes: the direct division back to vegetative cells, the short-term encystment (temporary cysts), or the long-term encystment (resting cysts) (Figueroa *et al.*, 2006). Dinoflagellate species that only produce

temporary cysts, however, can be relatively easily described by omitting the maturation time.

Overall, the consideration of the entire life cycle allows us to investigate the role of seed banks in bloom formation in the entire Baltic Sea for hindcasts and projections in three-dimensional-coupled biological-physical models.

## ACKNOWLEDGEMENTS

We thank Markus Pahlow for his valuable comments. The comments of the reviewers are acknowledged.

## FUNDING

This work has been supported by the Cluster of Excellence "CliSAP" (EXC177), University of Hamburg, funded through the German Science Foundation (DFG).

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