Modelling the life cycle of cold-water dinoflagellates and diatoms—dynamics on seasonal and interannual time scales

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Zusammenfassung

In gemäßigten Küstenregionen werden Frühjahrsblüten von Phytoplankton in der Regel von Diatomeen dominiert. In den letzen Jahrzehnten waren in einigen Gebieten der Nord- und Ostsee allerdings Kaltwasser-Dinoflagellaten dominant, obwohl sie eine geringere Wachstumsrate als Diatomeen aufweisen. Die Ursachen dafür sind zur Zeit noch nicht vollständig verstanden. Man vermutet, dass die Lebenszyklen der Diatomeen und Dinoflagellaten eine entscheidende Rolle für die Zusammensetzung der Phytoplanktongemeinschaft spielen. Zum Beispiel bilden viele Arten zum Ende der Wachstumsphase Ruhestadien aus, die als Saatpopulation zukünftiger Blüten dienen.

Die vorliegende Arbeit untersucht die Zystenbildung der Dinoflagellaten, die Rolle ihrer Lebenszyklen auf saisonale Dynamiken und die zwischenjährlich variierenden Dominanzen von Dinoflagellaten und Diatomeen. Dazu wurde ein numerisches Ökosystemmodell entwickelt und evaluiert, das die Lebenszyklen beider Phytoplanktongruppen, die physikalischen Bedingungen und die Konkurrenz beider Gruppen um Nährstoffe und Licht berücksichtigt. Insbesondere wurden mit dem Modell funktionale Abhängigkeiten zwischen Wachstum, der Ausbildung von Ruhestadien und Umweltfaktoren identifiziert und formalisiert.

Das Lebenszyklusmodell der Dinoflagellaten berücksichtigt vier Kompartimente: wachsende vegetative Zellen, Gameten, sinkende Ruhezysten und aufsteigende germinierende Zellen. Die Übergänge zwischen diesen Kompartimenten werden als Funktionen von externen Faktoren (z.B. Nährstoffe, Temperatur und Licht) und endogenen Faktoren (z.B. Reifeperioden) definiert.

Das Modell des Diatomeen-Lebenszyklus enthält zwei Kompartimente: ein wachsendes Stadium (mit einer im Vergleich zu den Dinoflagellaten mehr als doppelt so hohen Wachstumsrate) und ein ruhendes Stadium. Die Übergänge zwischen diesen Kompartimenten hängen von den Wachstumsbedingungen der vegetativen Diatomeen ab, die wiederum von externen Umweltbedingungen abhängen.

Als Modellregion wurde der Finnische Meerbusen in der Ostsee gewählt, da er als sehr gut untersuchte Region umfangreiche Modellevaluierungen erlaubt. Die Parametrisierung des Modells und die Abschätzung von Raten erfolgten für die Kaltwasser-Dinoflagellate *Biecheleria baltica* und die Diatomee *Thalassiosira baltica*, die den Hauptteil der Frühjahrsblüten im Finnischen Meerbusen bilden. Das entwickelte Ökosystemmodell ist allgemein für Dinoflagellaten und Diatomeen anwendbar und wurde an das eindimensionale Wassersäulenmodell GOTM (General Ocean Turbulence Model) gekoppelt, das die physikalische Umgebung mit einem realistischen atmosphärischen Antrieb für die Ostsee liefert.

Evaluationen zeigen, dass das Modell Beobachtungsdaten angemessen widerspiegelt. In Übereinstimmung mit Daten aus der Ostsee simuliert das Dinoflagellaten-Lebenszyklusmodell zwei Maxima von motilen Zellen. Das erste Maximum im späten Winter kann auf die Germinierung von Zysten zurückgeführt werden, das zweite Maximum auf das Wachstum von vegetativen Zellen.

Die Lebenszyklusmodelle von Diatomeen und Dinoflagellaten spiegeln zwischenjährlich variierende Dominanzen wieder, obwohl Dinoflagellaten im Vergleich zu den Diatomeen die unterlegenen Wettbewerber sind. Die Variabilität der Dominanz resultiert aus den Lebenszyklusprozessen, den physikalischen Bedingungen und dem Wettbewerb der Arten um Nährstoffe und Licht. Insbesondere kann die dominierende Art auf die Abundanz der Ruhestadien und die Temperatur im Frühjahr zurückgeführt werden. Eine relativ hohe Abundanz von Diatomeensporen führt zu einer Dominanz von Diatomeen. Eine hohe Abundanz von Zysten der Dinoflagellaten führt zu einer Dominanz von Dinoflagellaten, wenn langsam steigende Temperaturen eine Frühjahrsblüte von vegetativen Dinoflagellaten begünstigen bevor es zu einer Zystenbildung kommt. Andernfalls, wenn die Temperaturen schnell ansteigen, dominieren die Diatomeen trotz einer hohen Abundanz von Dinoflagellaten. In diesem Fall beginnt die Zystenbildung bevor eine ausgeprägte Blüte entstehen kann.

Insgesamt erweitert diese Arbeit das Verständnis zu Lebenszyklusprozessen von Kaltwasser-Dinoflagellaten und Diatomeen und ihrer Rolle für saisonale und zwischenjährliche Dynamiken.

Abstract

Phytoplankton spring blooms in temperate coastal waters have been generally dominated by diatoms. In some areas of the Baltic and North Sea, however, cold-water dinoflagellates have become dominant in spring during the past decades despite their low growth rates. Although the factors responsible for the interannually varying dominances are not fully understood, the life cycles of dinoflagellates and diatoms have been proposed to play an important role in governing the phytoplankton composition. For example, many species form resting cysts at the end of the growth period that act as a seed population for future blooms.

This thesis addresses the encystment of dinoflagellates, the role of life cycles for their seasonal dynamics, and the interannually varying dominances between dinoflagellates and diatoms. A numerical ecosystem model was incrementally developed and evaluated taking into account the life cycles of both phytoplankton groups, physical conditions, and inter-species competition for nutrients and light. This model allows to identify and formalise the functional dependence among growth, formation of resting stages, and environmental factors.

For the dinoflagellate life cycle, four life cycle compartments are considered with different growth and motility properties: growing vegetative cells, gametes, sinking resting cysts, and rising germinating cells. The transitions among these life cycle compartments are defined as functions of external (e.g., nutrients, temperature, and light) and endogenous factors (e.g., maturation periods). The diatom life cycle model is composed of two life cycle compartments: resting cells and growing vegetative cells with a maximal growth rate more than twice the maximal dinoflagellate growth rate. The transitions between these compartments rely on the growth conditions of the vegetative cells, which in turn depend on external factors.

The Gulf of Finland in the Baltic Sea was chosen as a model region allowing comprehensive model evaluations. While the model is generally applicable to diatoms and dinoflagellates, value estimations and parameterisations were performed based on observation data for the diatom *Thalassiosira baltica* and the cold-water dinoflagellate *Biecheleria baltica*, two of the most abundant and, therefore, relevant phytoplankton species in the Gulf of Finland. The resulting ecosystem model is coupled to the one-dimensional water column model GOTM (General Ocean Turbulence Model), which provides the physical environment with a realistic atmospheric forcing for the Baltic Sea.

Evaluations show that the model adequately represents observation data. The dinoflagellate life cycle model simulates two peaks of motile cells in late winter and

in early spring, which is in agreement with observations from the Baltic Sea. The early peak in late winter can be attributed to excystment, the second peak to growth of vegetative cells. The life cycle models of diatoms and dinoflagellates are able to reproduce interannually varying dominances, although dinoflagellates are inferior competitors to diatoms. This variability results from life cycle interactions, physical conditions, and inter-species competition for nutrients and light. In particular, the overall dominant species of the year can be linked to the abundances of the resting stages and the temperature in spring. Relatively high abundances of diatom spores lead to a dominance of diatoms. High abundances of dinoflagellate cysts lead to a dominance of dinoflagellates if slowly increasing temperature favours a spring bloom of vegetative dinoflagellates before encystment begins. Otherwise, if temperature rapidly increases, diatoms become dominant despite high abundances of dinoflagellate cysts. In this case, encystment starts before a pronounced spring bloom is built.

Overall, the thesis extends the understanding of cold-water dinoflagellate and diatom life cycle processes and their role on seasonal and interannual dynamics.

Contents

1 Introduction

1.1 Variability in phytoplankton abundances and composition

Dinoflagellates and diatoms are key groups of marine phytoplankton. They generate most of the earth's atmospheric oxygen, form the basis of marine food webs, and are responsible for a major part of the global primary production. Changes in their abundances may have profound consequences on ecosystems and biogeochemical cycles. Despite propagating to higher trophic levels, shifts in the species composition may significantly impact the carbon export due to different sedimentation rates of different species.

In temperate and coastal waters, phytoplankton species generally show seasonal dynamics with spring blooms yielding a major part of the annual new production. During winter, the abundances of phytoplankton are generally low. Wind stress and low atmospheric temperature cause a mixing of the water column, which enriches the surface layers with nutrients. In spring, increasing solar radiation and decreasing wind stress raise the surface temperature leading to enhanced stratification and to a rapid increase in biomass, the phytoplankton spring bloom.

The conditions in spring, particularly repleted nutrients, favour fast-growing species. As diatoms are able to quickly assimilate nutrients and build up biomass, they usually dominate this period (e.g., Margalef, 1978; Smayda and Reynolds, 2001, 2003). Dinoflagellates are also abundant in this period, but usually have significantly less biomass.

In the past decades, however, observations have indicated an increasing number of years whose spring blooms are dominated by cold-water dinoflagellates. Wasmund et al. (1998) were among the first, who have shown a decrease in diatoms in favour of dinoflagellates in regions of the Baltic Sea from 1979–1993. Wasmund and Uhlig (2003) have extended this analysis with more comprehensive datasets and correspondingly found a decreasing long-term trend for diatoms in spring. The resulting gap is filled by dinoflagellates, whose biomass may even have exceeded former diatom biomasses. Klais et al. (2011) recently confirmed these observations; they have found a significant variability in the species composition and a substantial shift towards dinoflagellates

over four decades.

The reasons underlying the shift of dominance are not well understood yet. Dinoflagellates are generally considered to be an inferior competitor to diatoms. For instance, dinoflagellates have a lower maximal growth rate (e.g., Chan, 1978; Furnas, 1990; Spilling, 2007) and a higher demand for energy (due to more frequent sexual reproduction). Given such physiological disadvantages, a dominance of dinoflagellates is particularly surprising.

1.2 Phytoplankton life cycles

Both, coastal diatoms and dinoflagellates, form resting stages (e.g., McQuoid et al., 2002) as a common survival strategy. Resting stages are means of protection for a survival during periods when conditions are not favourable for vegetative cells. In particular, they are used as a mechanism for distribution over time and space; they spread the species to new areas and form the inoculum for subsequent blooms (e.g., Wall, 1971; Lewis et al., 1999; McQuoid et al., 2002).

Besides environmental factors, changes in the timing and size of the inoculum (i.e., the cells that initialise a bloom) have been proposed as relevant factors for changes in phytoplankton species composition (Kremp et al., 2008). As life cycle processes regulate the inoculum, they can be considered to drive the composition.

The life cycle of dinoflagellates is relatively complex involving several (sexual and asexual) phases and transitions. The excystment (cyst germination) of different dinoflagellate species is primarily determined by a maturation period and, thereafter, assumed to be regulated by environmental factors like temperature, light, and oxygen conditions. Encystment often involves sexual differentiation; vegetative cells transform into gametes, sometimes by depauperating division, where multiple small sized gametes are formed within a short period of time. The fusion of gametes results in a planozygote, a motile cell that typically possesses two longitudinal flagella. The planozygote may immediately transform into a resting cyst or continue to photosynthesise for some time (before resting cyst formation) to ensure production of sufficient storage products for the resting period. Planozygotes shed their flagella and develop a complex multilayered cyst wall. Resting cysts can remain viable for several decades (McQuoid et al., 2002). Additionally, a species may have different encystment strategies and use both, direct and indirect factors, to ensure formation of long-term survival stages (Kremp et al., 2009).

The life cycle of diatoms is less complex with less phases and transitions. In contrast to dinoflagellates, the formation of resting stages, called “resting spores”, is asexual and associated with unfavourable environmental conditions (e.g., depleted nutrients, insufficient light, and improper temperature, see e.g., Drebes, 1966; Durbin, 1978; Hargraves and French, 1983). Resting spores can remain viable for long periods in cool and dark conditions and rapidly transform into vegetative stages (e.g., Mann,

2002).

Sexual reproduction also occurs in diatoms, however, less frequent than in dinoflagellates. Vegetative growth reduces the diatoms cell size and changes their characteristic shape (e.g., Round et al., 1990). Both are restored by auxosporulation (i.e., the formation of an auxospore involving sex, e.g., D'Alelio et al., 2010). Lewis Jr (1984) argues that reductions in cell size act as triggers for sexual reproduction, preventing it from occurring too frequently. With reproduction intervals greater than one year, environmental cues can be considered ineffective. Moreover, such reproduction has been hardly observed to date (Mann, 1988; Jewson, 1992).

1.3 Modelling phytoplankton life cycles

Besides field and laboratory studies, numerical ecosystem models are viable means to investigate ecosystem dynamics in general and, particularly, interactions between diatoms and dinoflagellates. Different model studies have addressed the coexistence of diatoms and dinoflagellates. Aksnes et al. (1995) have developed an ecosystem model to examine the coexistence of diatoms and warm-water flagellates in coastal waters. Broekhuzien (1999) followed a mixed Eulerian-Lagrangian model approach identifying motility as an essential factor for the persistence of dinoflagellates. Using a similar approach, Ross and Sharples (2007) have found that severe physiological disadvantages cannot be compensated by motility alone, but require further factors for a coexistence of competing motile and non-motile species.

While none of these model studies has included the life cycle of both phytoplankton groups, recent studies have considered the life cycle of individual phytoplankton groups in ecosystem models. Hense (2010) gives an overview and examples of how to model life cycles of planktonic organisms.

Surprisingly, diatoms have hardly been studied by life cycle models at all. As an exception D'Alelio et al. (2010) have used a matrix model to investigate the sexual reproduction cycle of a diatom. In contrast, the life cycle processes of dinoflagellates have been a prominent object of model studies. McGillicuddy et al. (2003) have developed an excystment model and subsequently shown that realistic temporal and spatial distribution patterns of dinoflagellates are only obtained if the observed cyst distribution and excystment are included in the model (McGillicuddy et al., 2005; He et al., 2008; Li et al., 2009). Estrada et al. (2010) have additionally considered encystment using two different approaches. In a matrix population model, the dinoflagellate life cycle is described by a chain of life cycle processes. In a population model, cyst concentrations are assumed to be proportional to vegetative cells. The life cycle transitions are either probability functions or only depend on thresholds of cell concentrations, but not on any environmental factors (e.g., temperature or light) or internal factors (e.g., dormancy). Peperzak (2006) has developed a time-discrete model for dinoflagellates with life cycle aspects focusing on the probabilities of encystment

and the time-dependent excystment, but has not addressed the underlying factors and mechanisms that cause them. None of these models, however, has dynamically described the full life cycle of dinoflagellates.

Certain aspects of life cycle processes have also been considered for other phytoplankton groups such as the *Phaeocystis* (e.g., Lancelot et al., 2005). Models of complete life cycles have been developed, for example, for cyanobacteria (Hense and Beckmann, 2006; Hellweger et al., 2008; Jöhnk et al., 2011). Such models have been successfully applied to lakes (Hellweger et al., 2008; Jöhnk et al., 2011) and coastal regions (e.g., 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 summary, there are a number of models that include certain life cycle aspects of phytoplankton groups (dinoflagellates, diatoms, *Phaeocystis*) or the entire life cycle (cyanobacteria). Despite the relevance of species interactions, there are hardly any model studies considering life cycle aspects of more than one phytoplankton group. In particular, hardly any model addresses both, diatoms and dinoflagellates. Yamamoto et al. (2002) have focused on the life cycle of a dinoflagellate but only consider sinking dynamics of diatoms. While Eilertsen and Wyatt (2000) have proposed a life cycle model for diatoms and dinoflagellates, the life cycle transitions and interspecies dynamics depend on external processes that are fixed in time and quantity. None of these models has addressed the interannually varying dominances of diatoms and dinoflagellates.

1.4 Objectives

The overall objectives of this thesis are to investigate the encystment of dinoflagellates, the role of life cycles for their seasonal dynamics, and the interactions of the two phytoplankton key groups, dinoflagellates and diatoms. To achieve these objectives, we incrementally develop and evaluate an ecosystem model of nutrients, detritus, and two life cycles, one for dinoflagellates and one for diatoms. Specific questions that the thesis aims to answer include:

What are the main mechanisms behind the encystment process of dinoflagellates? How can the process be described in an ecosystem model? Answers to these questions are crucial to understand under which conditions dinoflagellates produce cysts. While the excystment is rather well studied (e.g., described by Anderson, 1998; Nuzzo and Montresor, 1999; Bravo et al., 2010), the mechanisms underlying encystment are an open question.

How can the seasonal cycle of cold-water dinoflagellates be explained? Observations indicate that cold-water dinoflagellates that dominate spring blooms show

very often two distinct spring bloom peaks. In particular, the formation of the first bloom is not well understood yet. It is unclear, whether these peaks are a result of certain environmental conditions or of specific physiological properties of cold-water dinoflagellates.

Does a persistent increase in temperature lead to enhanced dinoflagellate concentrations and cyst formation? The observed trend of increasing dinoflagellate abundances in the past years (e.g., Klais et al., 2011) raises the question whether an increase in sea surface temperature is favourable for dinoflagellate growth and cyst formation.

What factors trigger the alternation between dominances of dinoflagellates and diatoms in spring blooms on interannual time scales? Both, diatoms and dinoflagellates, can dominate the spring bloom. It is unclear under which conditions which group dominates. Based on insights of a mesocosm study, initial concentrations seem to be decisive while environmental conditions seem to play a rather minor role (Kremp et al., 2008).

1.5 Outline

The Chapters 1.5, 2.5, and 4 of this thesis are written as journal publications. With their own abstracts, introductions, and conclusions, they are self-contained and can be read independently from each other.

Chapter 1.5 "Encystment of a cold-water dinoflagellate—from in vitro to in sillico" has been published in the Journal of Marine Systems (Warns et al., 2012). Based on a reanalysis of a previously published laboratory data set for *B. baltica*, a numerical model is developed to study the dinoflagellates cyst formation (encystment). With the model, we identify and formalise the functional dependence among growth, cyst formation, and environmental factors. We have found two mechanisms in the model that are essential to accurately reproduce the laboratory data: a time lag in cyst formation and a reduction in the growth rate of vegetative cells as soon as cysts are formed.

Chapter 2.5 "Modelling the life cycle of dinoflagellates: a case study with Biecheleria baltica" has been published in the Journal of Plankton Research (Warns et al., 2013). This chapter describes how the dinoflagellate encystment model was complemented by additionally covering excystment. The resulting model dynamically describes the full life cycle of the dinoflagellate *B. baltica*. In particular, the model is able to adequately represent the seasonal cycle and succession of *B. baltica's* life cycle

stages with two blooms in spring when coupled to the water column model GOTM. Additional sensitivity experiments indicate that temperature is an important factor regulating the succession of *B. baltica* life cycle stages. A varying temperature leads to less growing cells and more resting cysts during spring.

Chapter 4 "Modelling spring bloom dynamics in the Baltic Sea—interactions between dinoflagellates and diatoms" remains to be published and will be submitted soon. In this chapter, we investigate the interactions of two key phytoplankton species, *T. baltica* and *B. baltica*, in the Baltic Sea. To study the interactions, the dinoflagellate life cycle model is complemented by a diatom life cycle model newly developed based on data from literature. Both life cycle models are jointly coupled to GOTM, which is set up for the Baltic Sea. With the resulting model, we study the relationships of both life cycles, the seasonal succession of life cycle stages, and the interannually varying dominances resulting from physical conditions and inter-species competition for nutrients and light. In particular, the model is able to represent interannually varying dominances of dinoflagellates and diatoms despite differences in growth rates. Analyses indicate that the extent of species abundances in winter and temperature conditions in spring determine which species dominate the spring bloom.

Chapter 5 concludes the thesis with a summary of our main findings and proposed directions for future research.

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2 Encystment of a cold-water dinoflagellate—from in vitro to in sillico

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Abstract

Blooms of dinoflagellates are frequently observed in coastal regions. The dynamics of these blooms are strongly affected by life cycle transitions. For example, many species form resting cysts at the end of the growth period that act as a seed population. Despite considerable efforts, one major process of the dinoflagellate life cycle—the encystment—is not fully understood. In this study, we reanalyse a published laboratory data set for the cold-water dinoflagellate *Biecheleria baltica* and develop a numerical model to study cyst formation. We find significant differences between cell counts and biomass, leading to different conclusions about the encystment process. To accurately reproduce the laboratory data, two mechanisms have to be taken into account in the model: a time lag in cyst formation and a reduction in the growth rate of vegetative cells as soon as cysts are formed. Using this model we are able to identify and formalise the functional dependence among growth, cyst formation, and environmental factors. Our model can serve as a prerequisite for dinoflagellate life cycle models to study the dynamics of bloom formations.

2.1 Introduction

Dinoflagellates are an important group of marine phytoplankton. In coastal waters they often form blooms that can be toxic or have other harmful effects. In some parts of the world, dinoflagellates increasingly play a role as primary producers (Klais et al., 2011). Many dinoflagellates have complex life cycles and alternate between a growing and a resting stage. The transitions between these stages (i.e., encystment and excystment) are important in regulating the bloom dynamics of dinoflagellates. These transitions may determine the timing, duration, and even the magnitude of the seasonal appearance of dinoflagellates in the phytoplankton community.

While the mechanisms of excystment (cyst germination) are well known for most species (e.g., described by Anderson, 1998; Nuzzo and Montresor, 1999; Bravo et al., 2010), the regulation and implications of encystment (cyst formation) are far less understood despite considerable efforts. Such lack of understanding is attributed to the complexity of the encystment process. In many dinoflagellate species encystment involves sexual differentiation (see Fig. 2.1): vegetative cells differentiate into gametes, sometimes by depauperating division, where multiple small sized gametes are formed within a short period of time. The fusion of two gametes results in a planozygote, a motile cell that typically possesses two longitudinal flagella. The planozygote may immediately transform into a resting cyst or continue to photosynthesise for some time (before resting cyst formation) to ensure production of sufficient storage products for the resting period. Planozygotes shed their flagella and develop a complex multilayered cyst wall. For a detailed description about encystment or generally the life cycle of dinoflagellates the reader is referred to the review by Kremp (2012). Since sexual cyst formation is a multi-stage process, several factors may be involved. Additionally, a species may have different encystment strategies and use both direct and indirect factors, to ensure formation of long-term survival stages (Kremp et al., 2009).

A variety of factors have been related to the induction of encystment. Laboratory studies have repeatedly indicated that resting cysts are formed when nutrients are limiting (e.g., Von Stosch, 1973; Anderson and Lindquist, 1985; Figueroa et al., 2005). However, in nature, resting cyst formation is commonly observed under nutrient replete conditions (e.g., Wall et al., 1970; Kremp and Heiskanen, 1999; Probert, 2002). Besides nutrients, changes in light (Sgrosso et al., 2001) and temperature (Rengefors, 1998; Meier et al., 2004; Kremp and Parrow, 2006) have been proposed to induce sexual reproduction and cyst formation. Indirect evidence exists for a role of other factors, such as a certain number of cell divisions (Olli and Anderson, 2002), cell densities increasing the chance for contact among sexual cells (Uchida, 2001), and the presence of allelochemicals (Fistarol et al., 2004) or pheromones (e.g., Darden Jr, 1966; Wyatt and Jenkinson, 1997; Persson et al., 2008).

The Baltic Sea has experienced a shift towards dinoflagellate dominance in the past decades (Klais et al., 2011). In the northern parts, *Biecheleria baltica* Moestrup, Lindberg et Daugbjerg [Moestrup et al. (2009) = *Woloszynskia halophila* sensu

Kremp et al. (2005)] is one of the most abundant species of the spring phytoplankton community. As a cold-water species with a narrow temperature window for growth (Kremp et al., 2005) *B. baltica* spends much of the seasonal cycle as benthic resting cysts (Kremp and Anderson, 2000). Large cyst deposits have been documented in the Gulf of Finland, where high cell concentrations of *B. baltica* are frequently observed during the spring bloom (Olli and Trunov, 2010). The strategy of massive cyst formation and the spreading of cyst beds are considered important reasons for the recent expansion and increasing dominance of this species (Klais et al., 2011). Due to the importance of the species in the spring bloom community, the life cycle of *B. baltica* has been studied extensively and the results of these studies emphasise the role of cysts in their bloom dynamics. Cyst formation may not only terminate the bloom, but also facilitate the export of a large fraction of newly produced phytoplankton biomass to the benthic system (Kremp and Heiskanen, 1999). The regulation of *B. baltica* cyst formation is, like in most dinoflagellates, complex. Involved sexual processes and the dependence on variable triggering conditions impede the understanding of cyst formation and, thus, the quantification of sedimentation, and export of biomass.

The goal of the present study is to identify and formalise the factors that influence the encystment of the dinoflagellate *B. baltica*. Therefore, we reanalyse the experimental data set of Kremp et al. (2009) for the cyst formation of *B. baltica* by converting the data from cell counts into biomass and by using a numerical model to describe the functional dependence between growth, cyst formation, and the triggering factors. Modelling encystment is a necessary prerequisite to construct a complete dinoflagellate life cycle model that can be coupled to a water column or an ocean circulation model to study dinoflagellate bloom dynamics.

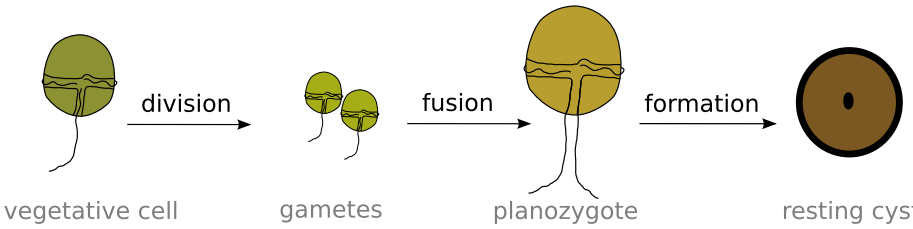

Figure 2.1: Conceptual overview of the encystment in *Biecheleria baltica*. One vegetative cell transforms into multiple gametes by depauperating divisions leading to small cell size. The fusion of two gametes leads to a planozygote that transforms into a resting cyst.

2.2 Laboratory data

The cold-water dinoflagellate *B. baltica* is a well studied organism in terms of its growth and life cycle characteristics. The major knowledge that we use to investigate encystment and to implement a model is based on the laboratory experiments by Kremp et al. (2009). They investigated cyst formation of *B. baltica* (= *Woloszynskia halophila* in their study) at different temperatures (3°C and 6°C) and nutrient conditions (deplete and replete) using a "multivessel" approach to monitor encystment and nutrient dynamics. In such a set up, one independent vessel is available for analysis at each sampling point and treatment.

B. baltica only formed significant amounts of cysts in the treatment with 6°C (and replete nutrients). Kremp et al. (2009) concluded that temperature was the major trigger of cyst formation in this species, and not nutrient depletion. Therefore, we analyse the data for the 3°C and the 6°C treatment with replete nutrients, but not those with deplete nutrient conditions.

Data conversion All life cycle stages differ in size and biomass (see also Fig. 2.1). To quantify the biomass changes during the stage succession we convert of all cell types into the same biomass unit, i.e., $\mathrm{mmol\,N\,m^{-3}}$.

During the experiments different variables were recorded; the most relevant ones for our study are: (1) the number of motile cells—i.e., the sum of vegetative cells, gametes, and planozygotes—per volume X_m, (2) the number of cysts per volume X_c, (3) the total amount of particulate organic nitrogen (PON) per volume in $\mathrm{g\,N\,ml^{-1}}$, and (4) nutrient concentrations.

We obtain Z_c the nitrogen concentration of cysts as follows: the nitrogen concentration of cysts Z_c are derived from the cyst concentration X_c and the nitrogen content of single cysts Y_c. As the nitrogen content of single cysts Y_c was not recorded during the experiment, we calculate it as follows: first, the volume of a cyst is calculated using observed cell dimensions (Kremp et al., 2008) and formulas for standard geometric shapes of phytoplankton taxa (Sun and Liu, 2003). Second, these volumes are converted into carbon units according to Menden-Deuer and Lessard (2000) and afterwards into nitrogen units using the Redfield ratio (Redfield, 1958). Using these conversion factors we derive a nitrogen content per cyst Y_c of (16.95 ± 0.03) $\mathrm{pmol\,N\,cyst^{-1}}$. The nitrogen concentration of the motile cells Z_m are obtained from the particulate organic nitrogen concentration of the whole sample minus the nitrogen concentration of the cysts Z_c. In that way, we accounted for the variable N cell content of motile cells, which consisted of variable biomasses of vegetative cells, gametes, and planozygotes. The cell counts of the laboratory experiments are illustrated in Fig. 2.2 and the converted biomass data (Z_m and Z_c) in Fig. 2.3.

As we calculate the concentration of motile cells Z_m by subtracting the estimated cyst mass from the measured total PON, Z_m in principle includes any organic detritus beside motile cells. Detritus has not been regarded separately by Kremp et al. (2009)

and is assumed to be negligible.

Data re-evaluation The consideration of biomass instead of cell counts may generally lead to different conclusions. Next, we present the data based on both cell counts (published in Kremp et al., 2009) and biomass and explain the differences.

The cell counts of motile cells at 3°C show a strictly monotonic increase throughout the experiment (Fig. 2.2). Cysts are not formed at 3°C during the 52 days. At the higher temperature (6°C), motile cells increase until day 22 and remain almost constant for the rest of the experiment. This increase of motile cells in the beginning at 6°C is higher compared to the increase at 3°C. Cysts are formed from day 26 onwards.

In the biomass data, the motile cells in both temperature treatments start to grow and take up dissolved inorganic nitrogen (Fig. 2.3). Between days 30 and 40, at 3°C, low nutrient concentration limits growth. Thus, the concentration of motile cells does not increase after day 35. Similar to the 3°C experiment, the nutrient concentration decreases strongly in the beginning of the 6°C experiment (until day 21), but is not depleted during the 52 days. Since cysts are abundant from day 26 onwards at nutrient replete conditions, it is obvious that nutrient depletion does not act as a trigger for cyst formation in the experiment at 6°C. The biomass of motile cells is similar at both temperatures until the onset of cyst formation around day 26. Thereafter, the biomass of motile cells in the 6°C treatment stays substantially below the biomass in the 3°C treatment.

Since gametes are comparatively small and have less biomass, the data set based on cell counts shows differences to the data set based on biomass. These differences are: (1) an increasing number of motile cells throughout the experiment (Fig. 2.2), but unchanged or even decreasing biomass after day 35 (Fig. 2.3) at 3°C and (2) a higher amount of motile cells at 6°C than at 3°C, but similar biomass in both treatments until the onset of cyst formation. Both differences can be explained by a reduction in cell size due to gamete formation that leads to a simultaneous increase in cell number and a decrease in biomass. This is supported by (1) the observed reduction in cell size in the 3°C experiment over time (Kremp et al., 2009) and (2) the higher proportion of motile cells, which are gametes, from the beginning onwards in the 6°C compared to the 3°C experiment (Kremp et al., 2009).

The delay of cyst formation in relation to the onset of gametes needs to be accommodated in the model and raises some questions about additional factors involved, besides temperature. As mentioned above, a number of hypotheses address triggers for encystment. For example, formation of cysts could be induced by pheromones (Darden Jr, 1966; Starr, 1970; Uchida et al., 1996; Persson et al., 2008). Wyatt and Jenkinson (1997) argue that, when a threshold concentration of gametes is reached, the gametes sense each other. If the density of gametes is above a specific threshold, the gametes start to fuse and form resting cysts. Thus, the density of gametes is

directly (by cell contact) or indirectly (by pheromones) involved in cyst formation, which is taken into account in the model (see Section 2.3).

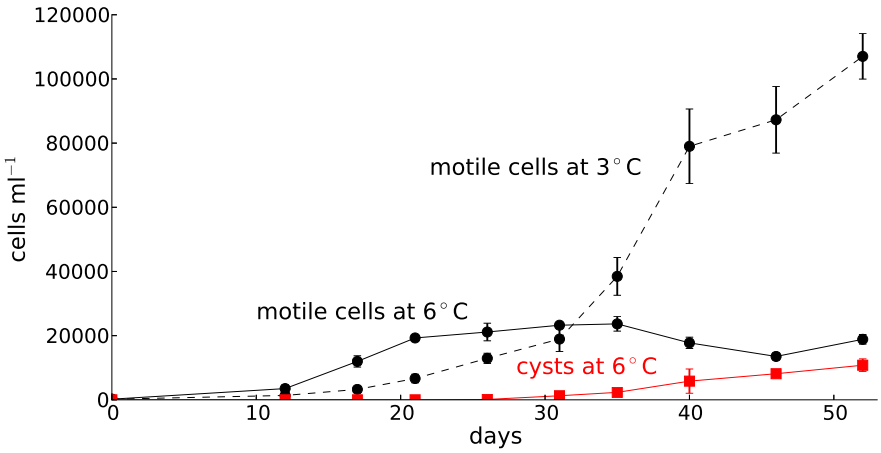

Figure 2.2: Time series of cell and cyst counts over 52 days. The data are from laboratory experiments with *Biecheleria baltica* (Kremp et al., 2009) with corresponding standard deviations at 3°C (dashed) and at 6°C (solid).

2.3 Model setup

We present a numerical model, which is based on laboratory experiments described above, to study the encystment process. In analogy to the cell types observed in the laboratory experiments, we consider motile cells—i.e., the sum of vegetative cells, gametes, and planozygotes—as well as cysts. While vegetative cells are modelled explicitly, we have combined gametes and planozygotes into a single compartment, because planozygotes undergo rapid encystment (Olli and Anderson, 2002; Figueroa et al., 2005, 2006), making this cell type an ephemeral life cycle stage. We also conducted numerical sensitivity experiments that considered planozygotes explicitly; the results indicate that the differences are negligible compared to the model results presented here.

Although our focus is on life cycle stages and the transition from vegetative cells to cysts, we additionally consider nutrients and dead organic matter (detritus) in order to describe the batch conditions realistically and conserve mass. Therefore, our model considers five compartments: V vegetative cells, G gametes, C cysts, nutrients N, and detritus D. Their changes in time are given by

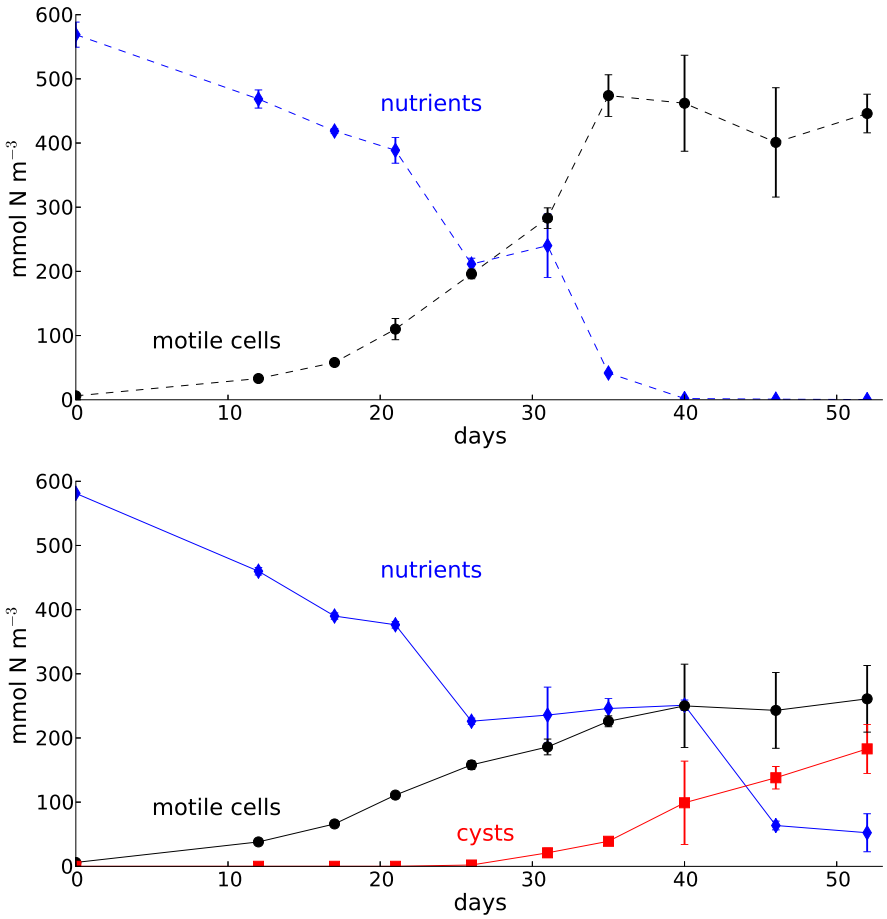

Figure 2.3: Concentrations of nutrient, cells, and cysts over 52 days. The data from laboratory experiments with *Biecheleria baltica* (Kremp et al., 2009) are converted into biomass units with corresponding standard deviations at 3°C (top) and at 6°C (bottom).

$$\frac{\partial V}{\partial t} = \underbrace{\mu_{NV}\, V}_{\text{growth}} - \underbrace{\tau_{VG}\, V}_{\text{transition}} - \underbrace{\lambda_{VD}\, V}_{\text{loss}}, \tag{2.1}$$

$$\frac{\partial G}{\partial t} = \underbrace{\tau_{VG}\, V - \tau_{GC}\, G}_{\text{transition}} - \underbrace{\lambda_{GD}\, G}_{\text{loss}}, \tag{2.2}$$

$$\frac{\partial C}{\partial t} = \underbrace{\tau_{GC}\, G}_{\text{transition}}, \tag{2.3}$$

$$\frac{\partial N}{\partial t} = \underbrace{\rho_{DN}\, D}_{\text{remineralisation}} - \underbrace{\mu_{NV}\, V}_{\text{growth}}, \tag{2.4}$$

$$\frac{\partial D}{\partial t} = \underbrace{\lambda_{VD}\, V + \lambda_{GD}\, G}_{\text{losses}} - \underbrace{\rho_{DN}\, D}_{\text{remineralisation}}, \tag{2.5}$$

where the transitions among life cycle compartments (τ), loss terms (λ), and the growth of vegetative cells (μ) are indexed indicating the direction of the change. For example, τ_{VG} is the transition from vegetative cells V to gametes G. See Tab. 2.1 for specific values of all constants.

We assume that only vegetative cells grow due to photosynthesis and nutrient uptake. We do not consider internal nutrient quotas, because they do not appear to play a major role in life cycle processes (see Kremp et al., 2009). The actual growth rate μ_{NV} depends on the availability of nutrients, irradiance, and temperature:

$$\mu_{NV}(N, I, T) := \mu_{\max}\, l_N\, l_I\, l_T, \tag{2.6}$$

where $\mu_{\max}$ is the maximal growth rate and l_N, l_I, and l_T are limitation functions of nutrients, irradiance, and temperature as described next.

Following Monod (1949), we define the nutrient limitation function by

$$l_N := \frac{N}{k_N + N}, \tag{2.7}$$

where k_N is the half-saturation constant for nutrients.

Light limitation is based on the functional relationship of Webb et al. (1974) and on observations indicating that growth is already maximal at low irradiance around 10 $\mathrm{W\,m^{-2}}$ (Spilling and Markager, 2008):

Table 2.1: Parameters for the encystment model. Values that have been visually adjusted are indicated by "*", k_N from Fasham (1993), and ρ_{DN} from Enriquez et al. (1993).

Symbol	*Parameter*	*Value*	*Unit*
k_N	half-saturation constant for N	0.5	$\mathrm{mmol\,N\,m^{-3}}$
ρ_{DN}	remineralisation rate	0.1	$\mathrm{d^{-1}}$
$\mu^*_{\max}$	maximal growth rate of V	0.39	$\mathrm{d^{-1}}$
α^*	initial slope used in limiting function l_I	0.18	$\mathrm{m^2\,W^{-1}\,d^{-1}}$
c^*_1	constant of limiting function l_I	0.4	$\mathrm{d^{-1}}$
c^*_2	constant of limiting function l_T	0.8	$\mathrm{°C^{-1}}$
c^*_3	constant of limiting function l_T	2.3	°C
c^*_4	constant of limiting function l_T	3	$\mathrm{°C^{-1}}$
c^*_5	constant of limiting function l_T	8.5	°C
τ^*_1	minimal transition rate from V to G	0.015	$\mathrm{d^{-1}}$
τ^*_2	maximal transition rate from G to C	0.06	$\mathrm{d^{-1}}$
GQ^*_1	threshold for transition from G to C	0.58	-
c^*_6	constant of transition function f_1	4.5	-
c^*_7	constant of transition function f_1 and f_2	2	$\mathrm{°C^{-1}}$
c^*_8	constant of transition function f_1 and f_2	4.5	°C
c^*_9	constant of limiting function l_G	0.27	-
c^*_{10}	constant of limiting function l_G	2.7	-
c^*_{11}	constant of limiting function l_G	100	-
λ^*_{VD}	loss rate of V	0.008	$\mathrm{d^{-1}}$
λ^*_{GD}	loss rate of G	0.008	$\mathrm{d^{-1}}$

$$l_I := 1 - \exp\left(\frac{-\alpha\, I_{\mathrm{PAR}}}{c_1}\right), \tag{2.8}$$

where I_{PAR} is the incoming irradiance and c_1 is a constant.

The temperature limitation function is based on data obtained from two laboratory studies. The experiment from Kremp et al. (2009) shows that growth takes place at 3°C and 6°C. Furthermore, Kremp et al. (2005) has observed that *B. baltica* does not grow at 10°C and growth ceases below 0°C. Thus, we formulated a temperature-dependent growth limiting function l_T:

$$l_T := 0.5\ \left(\tanh\left(c_2\ \left(T - c_3\right)\right)\ -\ \tanh\ \left(c_4\ \left(T\ -\ c_5\right)\right)\right), \tag{2.9}$$

where T is temperature and c_2 - c_5 are constants (see Tab. 2.1 for specific values).

Please note that we deliberately do not make use of the functional relationship between growth and temperature in Kremp et al. (2005). Firstly, their growth rate is based on cell counts and not on biomass (Kremp et al., 2005). Our reanalysis presented above shows that the differences are significant. Second, in the experiment by Kremp et al. (2005) the cells have been acclimated over several weeks (ca. 4 weeks) to the respective temperature, which is not the case in the experiments used here. The not acclimated conditions are representative for a fluctuating natural environment.

We assume that gametes are formed with a minimal rate at low temperature (below 3°C) and the formation of gametes increases with increasing temperature reaching a maximal rate at 6°C (Kremp et al., 2009). The transition rate from vegetative cells to gametes τ_{VG} is given by

$$\tau_{VG} := \tau_1\, f_1(T) \text{ with} \tag{2.10}$$

$$f_1(T) := 1 + c_6\ \left(0.5\ \left(1 + \tanh\left(c_7\left(T - c_8\right)\right)\right)\right), \tag{2.11}$$

where T is temperature and c_6 - c_8 are constants, τ_1 describes the minimal rate of transfer from vegetative cells to gametes, and f_1 is 1 below 3°C and about 6 above 6°C.

For the transition rate τ_{GC} from gametes to resting cysts, we consider temperature and the density of gametes. Using a constant concentration of gametes as a threshold of cyst formation in a model is not appropriate, because the threshold value may be vary depending on environmental factors like turbulence. Instead, we use the ratio of gametes to vegetative cells GQ for the transfer from gametes to cysts. Including a gamete quota threshold GQ_1 in the transition from gametes to cysts parameterises the hypotheses mentioned in Section 2.2. We use a running mean $\overline{GQ}$ over 5 days. If the quota $\overline{GQ}$ is greater than a constant threshold GQ_1 and the temperature T is

high enough (above 3°C), the gametes transform into resting cysts. Thus, we define

$$\tau_{GC} := \begin{cases} \tau_2 \, f_2(T) & \text{for } \overline{GQ} > GQ_1, \\ 0 & \text{otherwise} \end{cases} \tag{2.12}$$

$$\text{with } f_2(T) := 0.5 \ \left(1 + \tanh\left(c_7 \left(T - c_8\right)\right)\right), \tag{2.13}$$

where T is temperature and c_7 and c_8 are constants, τ_2 describes the maximal rate of transfer from gametes to cysts, and f_2 is 0 at temperatures below 3°C and 1 at temperatures above 6°C.

For the compartments of vegetative cells and gametes constant loss processes are considered (see Eq. 2.1 and 2.2). The losses are transferred into detritus that is remineralised and transferred back to nutrients (see Eq. 2.5 and 2.4), which can be taken up by vegetative cells.

We use a non-stiff 4th order Runge-Kutta numerical scheme (MATLAB solver ode45) to solve our equations. We initialise the nutrient field ($N_i = 569$ mmol N m^{-3} for 3°C experiment and $N_i = 581$ mmol N m^{-3} for 6°C) and life cycle stages ($V_i = 6$ mmol N m^{-3}, $G_i = C_i = D_i = 0$ mmol N m^{-3} for both experiments) on the basis of the laboratory experiments of Kremp et al. (2009). Similar to the experiments we assume a 14 h:10 h light-dark cycle with constant irradiance of 22 W m^{-2} during day and 0 W m^{-2} during night. The model is run for the whole time period of the experiment, that is 52 days.

2.4 Model calibration and evaluation

Since vegetative cells, gametes, planozygotes, and detritus have not been regarded separately by Kremp et al. (2009) we evaluate the model compartments vegetative cells, gametes, and detritus as one compartment. Further, we call this compartment motile cells, because the modelled concentration of detritus is very low. As explained above, Kremp et al. (2009) used a "multivessel" approach to monitor encystment and nutrient dynamics. Because each vessel has different initial conditions we have normalised the laboratory data and the model data to compensate for the different (initial) concentrations among the vessels.

We have adjusted most of the parameter values by visually fitting the model to the observed data. The results of this calibration are shown in Table 2.1. The resulting growth at 3°C is slightly lower than at 6°C yielding the temperature-dependent growth rate illustrated in Fig. 2.4. In the 3°C experiment, the development of motile cells over the course of the 52 days is very well represented by the model (Fig. 2.5a). The steps in the concentrations of motile cells and nutrients are due to the light-dark cycle.

In the 6°C experiment, the simulated concentration of motile cells is well represented

until cyst formation takes place. The model suggests that the concentration of motile cells further increases until day 35 before it decreases strongly (Fig. 2.5b). This is in contrast to the observations that indicate only a slight increase of motile cells from day 26 onwards (Fig. 2.2). Furthermore, the model does not represent the nutrient concentration well, because the modelled nutrients are depleted around day 32, while the observed nutrients do not deplete at all. Obviously, the model overestimates growth of the vegetative cells resulting in an exponential increase of motile cells before nutrients become limiting (Fig. 2.5b). Adjustments of parameters in both temperature experiments do not lead to satisfactory results. Additional sensitivity experiments that consider planozygotes explicitly or that regard *growing* gametes did not change the model behaviour significantly. It is unclear what kind of processes or factors lead to the reduced growth rate in the laboratory experiments as soon as cysts are formed. For instance, it cannot be excluded that allelochemical substances (i.e., interspecific messengers that can have positive or negative effects) are involved. In order to include such effects in our model, we have introduced a growth limiting function that considers a reduced growth rate in dependence of gamete concentrations. For the sake of simplicity, we use again (for the transition rate τ_{GC}) the ratio of gametes to vegetative cells GQ as:

$$l_G := c_9 \left(c_{10} - \tanh \left(c_{11} \left(\overline{GQ} - GQ_1 \right) \right) \right), \tag{2.14}$$

where $\overline{GQ}$ is the running mean of the gamete quota GQ over 5 days, GQ_1 is the gamete quota threshold, and c_9 - c_{11} are constants (see Tab. 2.1 for the specific values).

Introducing the limitation function l_G has significantly improved the model behaviour. The modelled concentrations of nutrients, motile cells, and cysts are in agreement with the experimental data at both temperatures (Fig. 2.5c).

Our model allows to distinguish the temporal development of vegetative cells and gametes. At 3°C, the model shows higher concentrations of vegetative cells than gametes during the whole period. At 6°C, the proportion of gametes increases over the course of the experiment (Fig. 2.6), which is in agreement with the observations. Although, Kremp et al. (2009) did not quantitatively determine the cell concentrations of vegetative cells and gametes they found that the proportion of gametes, at 6°C was larger than in the 3°C experiment.

2.5 Discussion

We have reanalysed a published laboratory data set and present an encystment model that includes vegetative cells, the sexual stages (gametes and planozygotes), as well as cysts. The encystment as part of the life cycle of dinoflagellates is currently not fully understood. In previous studies, cyst formation has often been associated

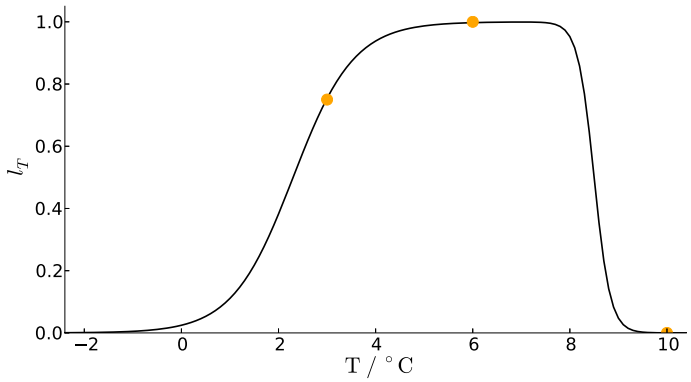

Figure 2.4: The temperature-dependent growth rate. The dots represent data derived from observations (Kremp et al., 2005, 2009).

with unfavourable conditions (e.g., Von Stosch, 1973; Anderson and Lindquist, 1985; Figueroa et al., 2005). However, cyst formation is also observed under seemingly favourable conditions (e.g., Wall et al., 1970; Kremp and Heiskanen, 1999; Probert, 2002). This is in line with our findings: both, the re-calculated laboratory data (based on biomass) and model results show that cyst formation starts to occur during the phase of increasing motile cells when nutrients are still available. Nevertheless, temperature plays an important role in regulating cyst formation, because cysts are only observed in the 6°C experiment and not at 3°C (Kremp et al., 2009). Our model results further indicate that at the beginning of the phase of exponential increase of motile cells, the growth rate of vegetative cells must be even higher at 6°C compared to 3°C. Otherwise, the same biomass in the 6°C experiment compared to 3°C cannot be explained due to a higher proportion of non-growing gametes. We derived overlapping temperature ranges for growth and sex of *B. baltica* from the data. The model suggests that during the entire sex phase (encompassing gamete and cyst formation) vegetative cells and gametes are present. This is a counter indication for the hypothesis that cyst formation occurs under unfavourable conditions and is in agreement with the conclusions by Kremp et al. (2009).

Our model, which includes vegetative and sexual stages, allows to quantify the growth rate of *B. baltica*. This is not possible from the observed data itself, because simultaneously to the growth of vegetative cells, gametes are formed and cysts may be formed. Determining the growth rate only from the exponential phase of the vegetative cells underestimates the actual growth rate, because the biomass "loss" due to transitions from vegetative cells to gametes is not considered.

There are two aspects of the encystment process that cannot be easily explained from reanalyses of the laboratory data: (1) the late formation of cysts and (2) the reduced growth rate when cysts are formed. A number of possibilities might explain these two phenomena. For instance, the cyst formation may be induced by pheromones

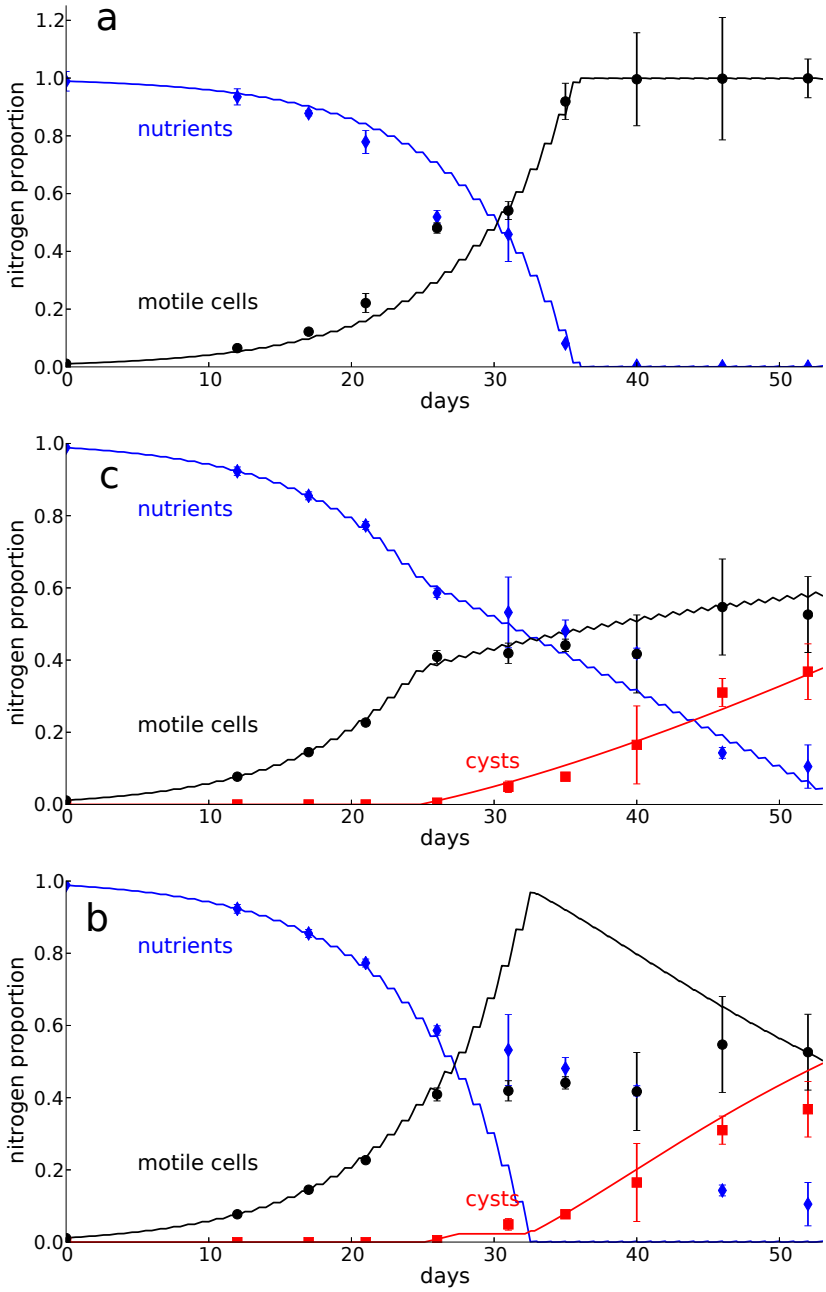

Figure 2.5: Normalised concentrations of observed (dots) and simulated (lines) nutrients, motile cells, and cysts over 52 days at 3°C (a) and 6°C (b, c). The observed concentrations (see Fig. 2.3) have been normalised on the basis of DIN (for the nutrients) or PON (for the cells and cysts) at each time, taking into account the multivessel approach. The simulated concentrations have been normalised using the maximal concentration of the specific compartment (nutrients, motile cells, or cysts), which is the same for the whole time period. The results of the two simulation experiments at 6°C are shown in b (not limited by l_G) and c (limited by l_G).

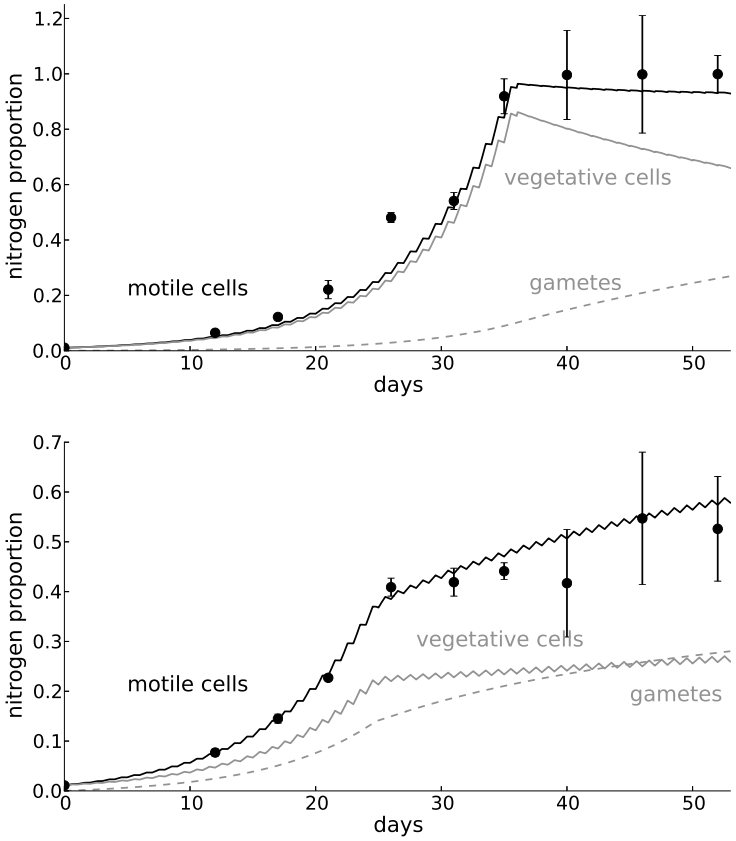

Figure 2.6: Similar legend as in Fig. 2.5, but in addition the simulated cells are split into vegetative cells and gametes.

or a threshold of gamete density (Darden Jr, 1966; Starr, 1970; Uchida et al., 1996; Wyatt and Jenkinson, 1997). The growth may be reduced by allelochemicals released by gametes. However, no quantitative observations are available. Therefore, we have introduced for our model study (1) a threshold of a quota that presents the density of gametes to reproduce a time lag in cyst formation and (2) a growth limiting function that describes the relationship between gamete concentration and growth. The growth limiting function is in contrast to observations by Olli and Anderson (2002) who have noticed an increasing growth rate when cysts are formed. However, they have exclusively considered cell counts instead of biomass.

In our model setup we have not explicitly taken into account planozygotes. So far, the role of planozygotes is not clear. Observations indicate that the planozygote phase is long in *B. baltica* (Kremp and Heiskanen, 1999; Kremp et al., 2009); during this phase they grow in size. Sensitivity experiments that include planozygotes explicitly or that consider growing gametes have not improved the model results unless additional assumptions similar to those above are made (i.e., a time lag in cyst formation and a reduced growth rate when cysts are formed). Nevertheless, it cannot be excluded that other processes might come into play that are not known yet. Our assumptions were necessary to represent the data, but are not based on physiological mechanisms. Future laboratory studies may focus on these aspects to gain a more detailed understanding of the processes involved. From an ecosystem modelling (and ecological) perspective, we urge to investigate life cycle dynamics on the basis of biomass and not solely on cell counts in future laboratory experiments. As shown in our study, the differences are not negligible.

Our encystment model is based on laboratory experiments with *B. baltica*. The model can be extended to describe the entire life cycle by including excystment (germination of cysts). In addition the model can be adjusted to describe encystment of other dinoflagellate species by changing, for instance, the temperature dependencies of growth if warm-water dinoflagellates are considered (e.g., *Alexandrium fundyense*, see Etheridge and Roesler, 2005). For other dinoflagellate species, nutrient limitation might be considered to adequately describe the encystment process (e.g., Pfiester, 1975; Anderson and Lindquist, 1985; Figueroa et al., 2005).

The mathematical description of encystment helps to advance current life cycle modelling activities. In contrast to our model, other models that consider the encystment of dinoflagellates are based on cell counts (e.g., Yamamoto et al., 2002; Olli et al., 2004; Peperzak, 2006; Estrada et al., 2010). As we have shown, different conclusions can be drawn depending on whether a study is based on cell counts or on biomass. Besides that, the models by Olli et al. (2004), Peperzak (2006), and Estrada et al. (2010) present simplified models that do not explicitly consider any dependence of the encystment on external or internal factors (e.g., nutrients, temperature, or light). In the model by Yamamoto et al. (2002), it is assumed that the encystment of the dinoflagellate *Alexandrium tamarense* depends on nutrient depletion. This approach might be plausible for this specific species, but, as mentioned earlier, encystment

has been observed under nutrient repleted conditions. In a number of ecosystem modelling studies (e.g., McGillicuddy et al., 2003, 2005; He et al., 2008; Li et al., 2009) encystment has been neglected and only excystment has been taken into account. Hence, by finding a mathematical formulation for the encystment, we are now able to develop a complete life cycle model for dinoflagellates to study the dynamics of bloom formation.

Acknowledgements

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

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Journal of Plankton Research (2013) 35(2): 379–392

Abstract

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 *B. 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 *B. baltica* with two blooms in spring. The first bloom can be explained by germination of resting cysts in winter, the second bloom by growth of vegetative cells. Sensitivity experiments indicate that temperature is an important factor regulating the composition of *B. baltica* life cycle stages; increased or decreased temperature leads to less 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.

3.1 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 generally spring blooms are 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. (2005), see references therein for details on the complex taxonomic history]. Particularly in the Gulf of Finland, *B. 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 initialise a bloom) is regulated by life cycle processes of *B. baltica*. The species produces large amounts 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 *B. 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 massive amounts 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 arise 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 few dinoflagellate models consider life cycle processes. The excystment model by 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., 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. (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 produced cysts can germinate again) is not taken into account. Estrada et al. (2010) studied the role of resting cysts on bloom formation using two different approaches. In the first one, 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 is applied by 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., Hense and Burchard, 2010; Moll and Stegert, 2007) 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 *B. baltica* to study the succession of life cycle stages within the seasonal cycle. We consider the case that 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 *B. baltica*. However, we do not consider interannual variability and shifts in the species composition. In order to study the effects of climate variability on bloom and cyst formation, we have conducted different temperature scenarios.

3.2 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 idea of 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, remineralisation is a sink for detritus and a source for nutrients.

In order 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). 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 *B. 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 (en- and excystment, Fig. 3.1). The growth and encystment processes are modelled according to Warns et al. (2012), which has previously been evaluated for *B. 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 *B. 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 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 regard 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.

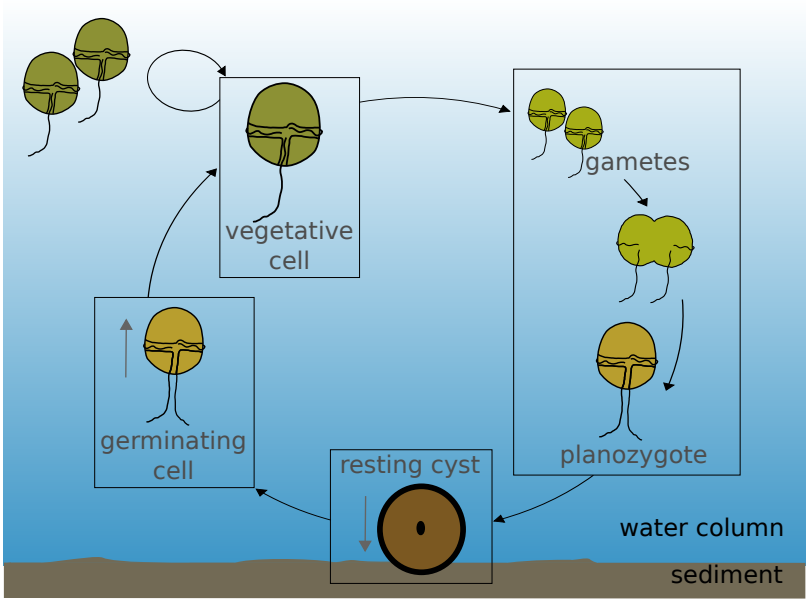

Figure 3.1: Conceptual overview of the dinoflagellate life cycle, the four model compartments (vegetative cells, gametes, cysts, and germinating cells), and the transitions among the compartments.

3.3 Model description

Our life cycle model considers four life cycle compartments: vegetative cells V, gametes G, cysts C, and germinating cells R. In order to realistically describe the ecosystem and conserve mass, the model has additional ecosystem compartments for nutrients N and detritus D (Fig. 3.2). The life cycle is circular and unidirectional, from vegetative cells to gametes to cysts to germinating cells, and back to vegetative cells.

The changes of the life cycle compartments are given by transition functions τ, loss terms λ, vertical motility ω, and a function for the growth of vegetative cells μ. The variables are indexed describing the direction of the change. For example, τ_{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

$$\frac{\partial V}{\partial t} = \underbrace{\mu_{NV}\, V}_{\text{growth}} + \underbrace{\tau_{RV} R - \tau_{VG}\, V}_{\text{transition}} - \underbrace{\lambda_{VD}\, V}_{\text{loss}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial V}{\partial z}\right)}_{\text{diffusion}}, \tag{3.1}$$

$$\frac{\partial G}{\partial t} = \underbrace{\tau_{VG}\, V - \tau_{GC}\, G}_{\text{transition}} - \underbrace{\lambda_{GD}\, G}_{\text{loss}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial G}{\partial z}\right)}_{\text{diffusion}}, \tag{3.2}$$

$$\frac{\partial C}{\partial t} = \underbrace{\tau_{GC}\, G - \tau_{CR}\, C}_{\text{transition}} - \underbrace{\lambda_{CD}\, C}_{\text{loss}} - \underbrace{\omega_C \frac{\partial C}{\partial z}}_{\text{sinking}} - \underbrace{\delta_C\, C^2|_{z=-H}}_{\text{burial}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial C}{\partial z}\right)}_{\text{diffusion}}, \tag{3.3}$$

$$\frac{\partial R}{\partial t} = \underbrace{\tau_{CR}\, C - \tau_{RV}\, R}_{\text{transition}} - \underbrace{\lambda_{RD}\, R}_{\text{loss}} - \underbrace{\omega_R \frac{\partial R}{\partial z}}_{\text{rising}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial R}{\partial z}\right)}_{\text{diffusion}}, \tag{3.4}$$

$$\frac{\partial N}{\partial t} = \underbrace{\rho_{DN}\, D}_{\text{remineral.}} - \underbrace{\mu_{NV}\, V}_{\text{growth}} + \underbrace{F^N|_{z=0}}_{\text{atm. deposition}} - \underbrace{\frac{1}{\theta}\,(N_0 - N)|_{z=-H}}_{\text{restoring}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial N}{\partial z}\right)}_{\text{diffusion}}, \tag{3.5}$$

$$\frac{\partial D}{\partial t} = \underbrace{\lambda_{VD}\, V + \lambda_{GD}\, G + \lambda_{CD}\, C + \lambda_{RD}\, R}_{\text{losses}} - \underbrace{\rho_{DN}\, D}_{\text{remineral.}} - \underbrace{\omega_D \frac{\partial D}{\partial z}}_{\text{sinking}} + \underbrace{\frac{\partial}{\partial z}\left(A_{\text{v}} \frac{\partial D}{\partial z}\right)}_{\text{diffusion}}. \tag{3.6}$$

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,

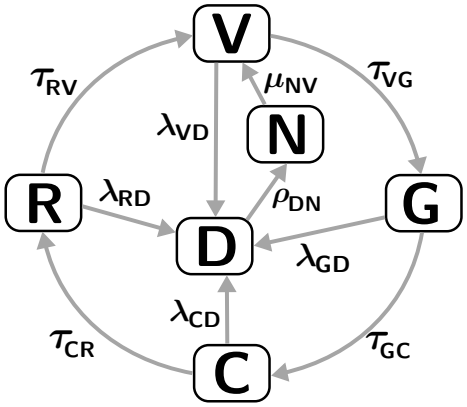

Figure 3.2: Conceptual overview of the life cycle model compartments (vegetative cells V, gametes G, cysts C, and germinating cells R) as well as of the compartments for nutrients N, and detritus D and the transitions among these compartments. The rates are Greek letters indexed describing the direction of the change.

which represent, for example, cell lysis and grazing. The losses go into the detritus, which is remineralised 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 Tab. 3.1.

The mathematical formulation of growth and encystment is taken from our previous model described in detail by 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:

1. we consider vertical attenuation of irradiance by

$$I_{\mathrm{PAR}} := I_0 \exp\left(k_{\mathrm{w}}\, z - k_{\mathrm{c}} \int_z^0 \left(V\left(z'\right) + G\left(z'\right) + C\left(z'\right) + R\left(z'\right) + D\left(z'\right)\right) dz'\right) \quad (3.7)$$

with z negative downward, where I_{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 $\overline{T}$ 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 parameterised based on observations on *B. baltica*. According to 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 τ_{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 between t_{m1} and t_{m2}. Quiescent cysts transform into germinating cells if the temperature at the bottom T_{bot} is between 0 and 9 °C. The values for t_{m1} and t_{m2} are adjusted that the cysts germinate in late winter, which is in agreement with observations. That is, we define

$$\tau_{CR} := \begin{cases} \tau_3 \, f_3(T_{\mathrm{bot}}) & \text{for } t_{\mathrm{mat}} \in [t_{\mathrm{m1}}, t_{\mathrm{m2}}] \\ 0 & \text{otherwise} \end{cases} \text{ with} \tag{3.8}$$

$$f_3(T_{\mathrm{bot}}) := (0.5 \tanh(c_1 (T_{\mathrm{bot}} + c_2)) + 0.5) - (0.5 \tanh(c_3 (T_{\mathrm{bot}} - c_4)) + 0.5), \tag{3.9}$$

where τ_3 is maximum of the transition rate τ_{CR} and f_3 is a function being greater than 0 at bottom temperature between 0 and 9 °C and 0 otherwise (Fig. 3.3 and Tab. 3.1).

The maturation time t_{mat} is calculated from a concentration-weighted integral over time following the approach of 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_{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 τ_{RV} as

$$\tau_{RV} := \tau_4 \; f_4(I_{\mathrm{PAR}}) \tag{3.10}$$

$$\text{with } f_4(I_{\mathrm{PAR}}) := 1 - \exp\left(-0.5 \; I_{\mathrm{PAR}}\right), \tag{3.11}$$

where τ_4 is the maximum of the transition rate τ_{RV} and I_{PAR} is the photosynthetic active radiation.

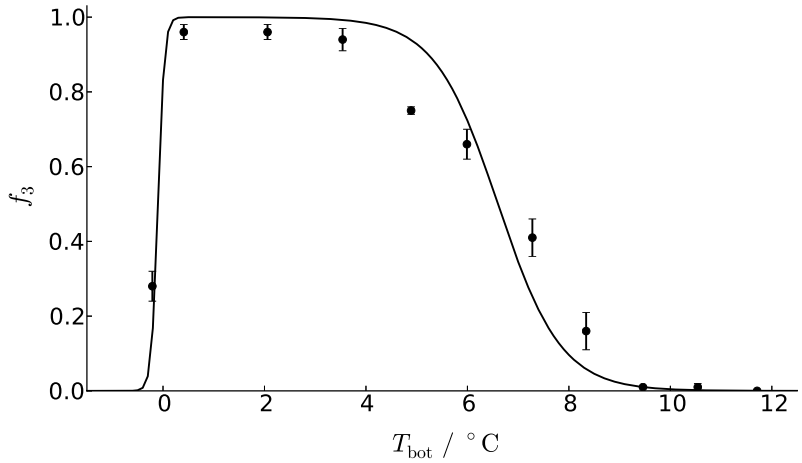

Figure 3.3: The function f_3 determines the transition rate τ_{CR} and depends on the temperature in the bottom layer T_{bot}. The dots with standard deviations show observational data from experiments conducted by Kremp and Anderson (2000).

3.4 Model application

The model is coupled to the one-dimensional 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 (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.

Table 3.1: Parameters and constants for the life cycle model.

Symbol	Parameter	Value	Unit
k_c	self-shading parameter	0.03	$\mathrm{m}^2(\mathrm{mmol\,N})^{-1}$
k_w	attenuation coefficient	0.13	m^{-1}
τ_3	maximal transition rate from C to R	0.05	d^{-1}
τ_4	maximal transition rate from R to V	0.3	d^{-1}
t_m1	start of "quiescence" for C	210	d
t_m2	end of "quiescence" for C	300	d
$\overline{l_I}_\mathrm{crit}$	critical value for setting maturation time to 0	0.64	–
λ_{VD}	loss rate of V	0.03	d^{-1}
λ_{GD}	loss rate of G	0.03	d^{-1}
λ_{RD}	loss rate of R	0.03	d^{-1}
δ_C	deposition coefficient of C	0.0029	$\mathrm{m}^3(\mathrm{mmol\,N})^{-1}\mathrm{a}^{-1}$
ω_C	sinking of C	-8	md^{-1}
ω_R	rinsing of R	8	md^{-1}
ω_D	sinking of D	-10	md^{-1}
c_1	constant used in transition function f_3	8	–
c_2	constant used in transition function f_3	0.1	$^\circ\mathrm{C}^{-1}$
c_3	constant used in transition function f_3	0.8	–
c_4	constant used in transition function f_3	6.6	$^\circ\mathrm{C}^{-1}$
F^N	atmospheric nitrogen deposition	-0.2	$\mathrm{mmol\,N\,m}^{-2}\,\mathrm{d}^{-1}$
N_0	restoring value of nutrients at the bottom	10	$\mathrm{mmol\,N\,m}^{-3}$
θ	restoring time of nutrients at the bottom	7200	s

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 Eq. 3.5). 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 $10\,\mathrm{mmol\,N\,m^{-3}}$ every 2 hours (N_0 and θ see also Eq. 3.5). All other boundary conditions are "no flux". The numerical scheme for the discretisation 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.

3.5 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. 3.4a). 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. 3.4b). In autumn, remineralised 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. 3.5, blue line). The germinating cells rise from the bottom to the light-flooded upper layers of the water column, where they transform into vegetative cells. The excystment process results in a first peak of the motile cells (i.e., the sum of germinating cells, vegetative cells, and gametes) in February. The relatively cold temperature limits the growth in February and March. When the temperature rises in April, the concentration of vegetative cells rapidly increases (Fig. 3.5, grey line). This increase in vegetative cells results in a second peak of motile cells at the beginning of May (Fig. 3.6). The decrease in vegetative cells at the end of May is partly caused by the beginning of the encystment process when the biomass is transfered into the gametes (Fig. 3.5). This transition is driven by temperature; a temperature rise to $> 3\,^{\circ}\mathrm{C}$ induces a rapid increase in gametes (Fig. 3.5, 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. 3.6), where they mature until the next year, when the cycle begins anew.

3.6 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. (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 (2000). The field data comprises the vegetative population of *Scrippsiella hangoei* nearby the Gulf of Finland from May 1995 to June 1996. Please note that *B. baltica* and *Scrippsiella hangoei* were regarded as one species until 2005; see 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 formulas 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 (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. 3.7), since the information about the proportions is missing. For the field data, monthly 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 ($7.9\,\mathrm{pmol\,N\,cell^{-1}}$), gametes ($2.5\,\mathrm{pmol\,N\,cell^{-1}}$), and planozygotes ($17.4\,\mathrm{pmol\,N\,cell^{-1}}$).

The comparison between model and observations show a similar seasonal pattern with two biomass peaks in spring, one in January/February and a second one in May (Fig. 3.7). This is in line with observations by Kremp (2000); Spilling (2007) who recognised 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. (2010) confirmed that both peaks are caused by *B. baltica*.

The model and the converted field data show similar maximal peak concentrations (Fig. 3.7). The maximal concentration of the converted field data is between 0.59

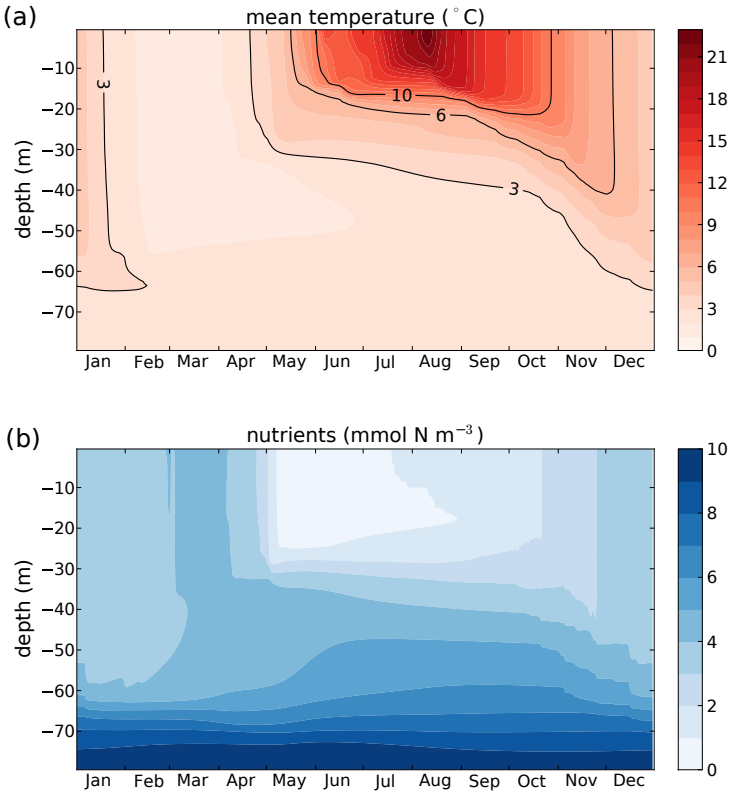

Figure 3.4: The seasonal distribution of (a) the mean temperature $\overline{T}$ and (b) the nutrients N. The contour lines in temperature indicate the critical thresholds for the different life cycle transitions.

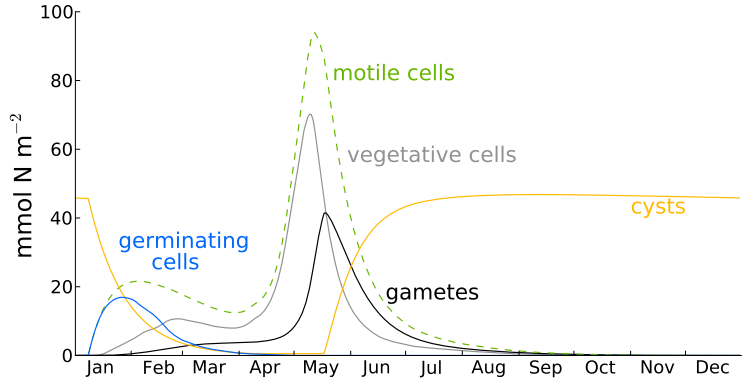

Figure 3.5: The seasonal distribution of the integrated concentrations of germinating cells, vegetative cells, gametes, resting cysts, and motile cells (sum of the total concentrations of germinating cells, vegetative cells, and gametes).

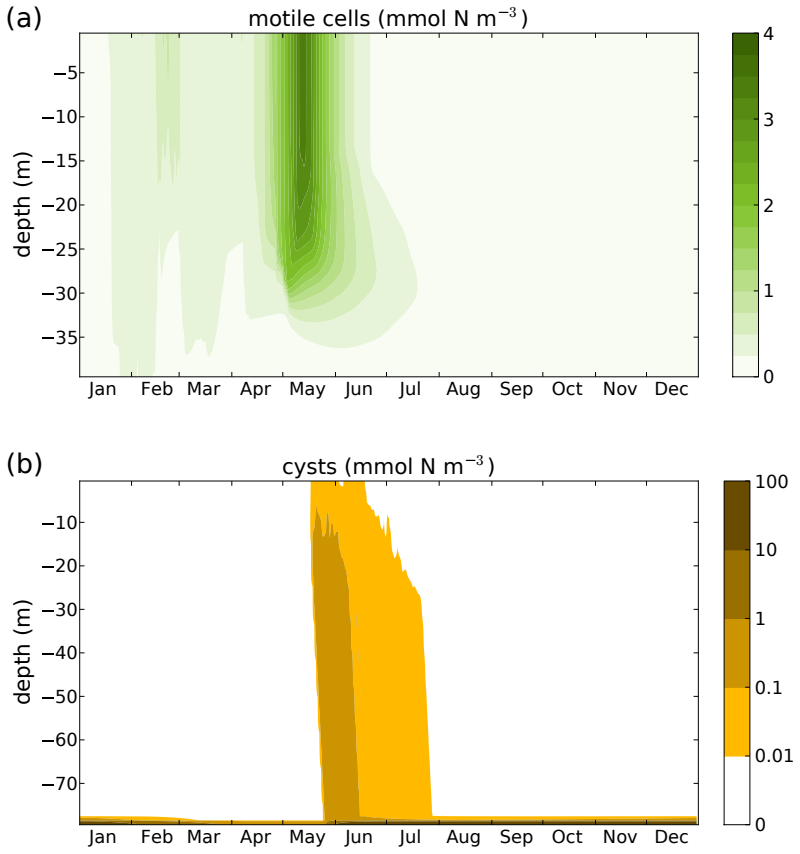

Figure 3.6: The seasonal distribution of different life cycle compartments (a) motile cells (sum of the total concentrations of vegetative cells, gametes, and germinating cells) in the upper 40 m and (b) cysts over depth.

and 4.05 mmol N m^{-3} depending on which of the different cell types is assumed to dominate (Fig. 3.7a). Please note that the values in Fig. 3.7a 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, remineralisation, and sinking of detritus. We use the same functions and parameters as in the life cycle model for describing these processes. The only exception is mortality, which we increased slightly (from 0.03 d^{-1} to 0.04 d^{-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. 3.8). In the

model without a life cycle, the bloom maximum occurs around 4 weeks later and there is only one peak, which is also in contrast to 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 the surface where temperature for growth is optimal, which is in contrast to observations. Olli et al. (1998) show that cells are typically concentrated in surface layers. If the life cycle is not considered also 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 ($0.8\,\mathrm{d}^{-1}$ instead of $0.4\,\mathrm{d}^{-1}$) 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 (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 ($17.0\,\mathrm{pmol\,N\,cyst}^{-1}$, Warns et al., 2012), in the Gulf of Finland, the theoretical seed pool is between $19.0\,\mathrm{mmol\,N\,m}^{-2}$ (for a germination potential of 10%) and $190.1\,\mathrm{mmol\,N\,m}^{-2}$ (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 $45.4\,\mathrm{mmol\,N\,m}^{-2}$ lies 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 (1999) reported the maximum cyst flux for *Scrippsiella hangoei* at the end of May with $\sim 2.8\,\mathrm{mmol\,N\,m}^{-2}\,\mathrm{d}^{-1}$. The life cycle model shows a slightly earlier maximal cyst flux (mid May) of $\sim 2.1\,\mathrm{mmol\,N\,m}^{-2}\,\mathrm{d}^{-1}$, which is quite close to observations.

3.7 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 *B. 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

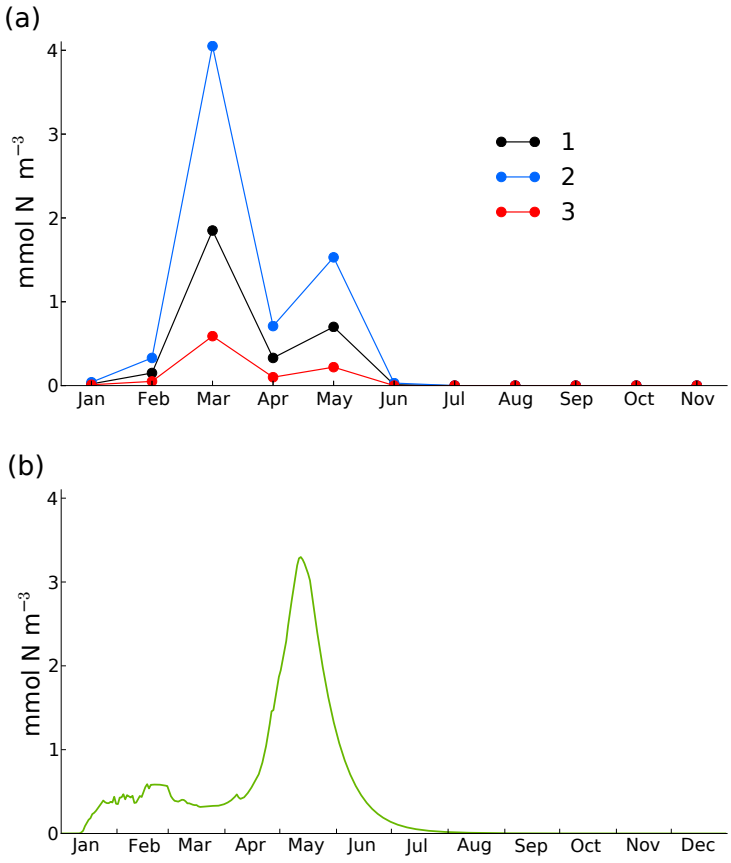

Figure 3.7: The mean biomass concentrations of motile cells in the upper 20 m over time (a) from observations and (b) from model results. The observations are based on cell counts (Kremp and Anderson, 2000) and are converted into biomass concentrations. Different lines show different *nitrogen per cell* 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).

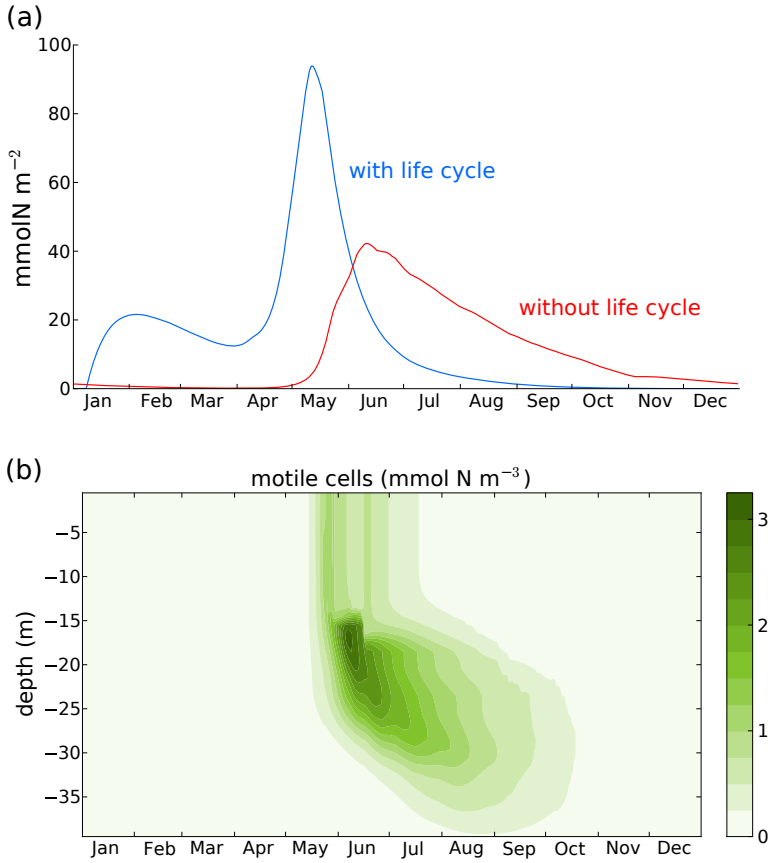

Figure 3.8: The seasonal distribution of (a) the integrated concentrations of motile cells in the reference run (considering the life cycle) and the sensitivity experiment (not considering the life cycle) and (b) motile cells (vegetative cells) in the upper 40 m (not considering the life cycle).

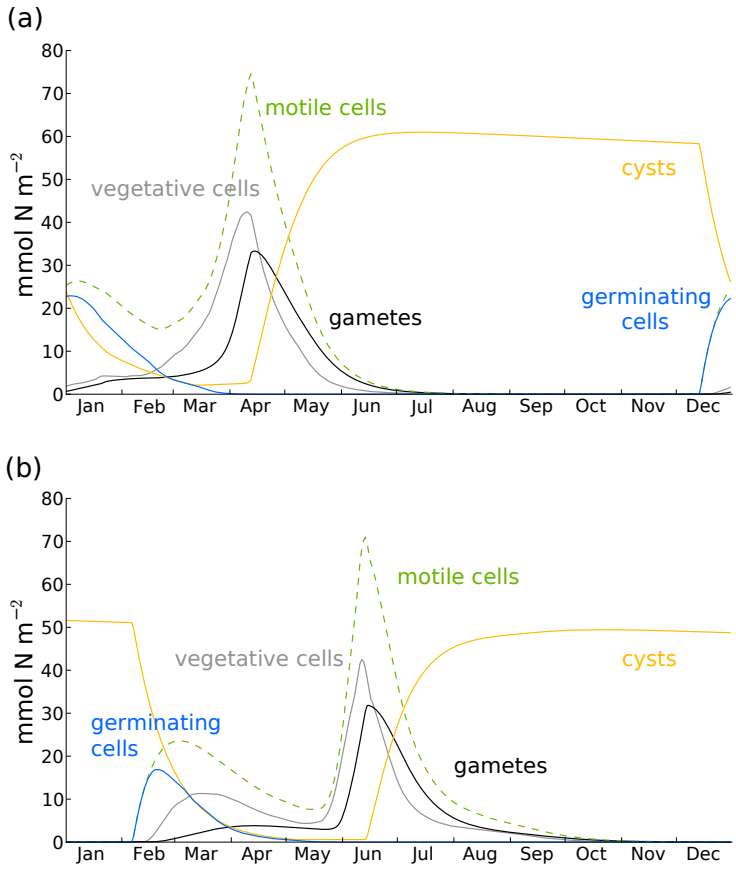

Figure 3.9: The seasonal distribution of the integrated concentrations of the life cycle compartments in (a) the warming and (b) the cooling scenario.

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. 3.9a) 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 (Tab. 3.2). 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. 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 built 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. 3.9b). 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 (Tab. 3.2), 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 $> 2\,^{\circ}\mathrm{C}$) 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 concentration of the first bloom is related to the amount of the seed pool; the larger the seed pool, the larger the first bloom. The magnitude 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.

3.8 Discussion

We have developed a numerical life cycle model of a Baltic key phytoplankton species, the cold-water dinoflagellate *B. baltica*. To the best of our knowledge, our model is the first that describes the dynamics of the complete life cycle of dinoflagellates including the growing, sexual, resting, and germinating phases. The model includes the mathematical formulation of the encystment model of Warns et al. (2012), which has been calibrated using data from laboratory studies with *B. baltica*. In the current study, we have additionally described the excystment process and have coupled the

Table 3.2: 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

resulting life cycle model to a one-dimensional water column model to investigate the seasonal cycle of *B. 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 is in agreement with observations in the Baltic Sea (e.g., Kremp and Anderson, 2000; Kremp, 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 has raised questions about the causes. Certain characteristics like 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 *B. baltica* is too low to explain the 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 is in contrast to 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. (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 encyst 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 prevent 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 *B. 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 the 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 to productivity of dinoflagellates or phytoplankton (Radi and de Vernal, 2008). However, our model results show that this correlation does not exist. 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. In order 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 at 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 *B. 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 daylength (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 en- 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 stages 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 produce only 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.

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4 Modelling spring bloom dynamics in the Baltic Sea—interactions between dinoflagellates and diatoms

Alexandra Warns and Inga Hense

Abstract

Generally, phytoplankton spring blooms are dominated by diatoms in temperate coastal waters. In recent years, however, cold-water dinoflagellates have become dominant in some areas of the Baltic and North Sea during spring. Such interannually varying dominances are particularly surprising given that the maximal growth rate is considered to be significantly lower for dinoflagellates than for diatoms. While the reasons for the interannual variability are not fully understood yet, the species life cycles have been proposed as a major factor in governing the phytoplankton spring bloom composition. For studying the relationships among life cycles and the interannual variability, we have developed a numerical model for the life cycles of dinoflagellates and diatoms. For the dinoflagellate life cycle, four life cycle stages are considered: growing vegetative cells, gametes, sinking resting cysts, and rising germinating cells. The transitions between these life cycle stages are assumed to be functions of external and endogenous factors. The diatom life cycle is composed of two life cycle stages, growing and resting stages, with a maximal growth rate more than twice the maximal dinoflagellate growth rate. Its transitions are assumed to depend on external factors only. The overall life cycle model is coupled to a water column model, which is set up for the Gulf of Finland in the Baltic Sea. Results obtained with the model show interannually varying dominances of dinoflagellates and diatoms despite differences in growth rates. Analyses indicate that relatively high abundances of diatoms in winter lead to a diatom-dominated spring bloom. High abundances of dinoflagellates in winter lead to a dinoflagellate-dominated year if the spring temperature favour a spring bloom of dinoflagellates before encystment begins.

4.1 Introduction

Dinoflagellates and diatoms are key groups of marine phytoplankton and, as primary producers, are of particular relevance for biogeochemical cycles and the food web. In the Baltic and North Sea, phytoplankton spring blooms used to be dominated by diatoms. However, observations have indicated an increasing number of years whose spring blooms are dominated by cold-water dinoflagellates (e.g., Edwards et al., 2006; Klais et al., 2011; Wasmund et al., 2011). The dominances of both phytoplankton groups and their relative abundances may have specific consequences for the nutrient cycling in the pelagic system (Kremp et al., 2008).

The reasons for the interannually varying dominances are not fully understood yet. In general, dinoflagellates can be considered as an inferior competitor to diatoms, as they have, for instance, a lower photosynthetic rate than diatoms (e.g., Chan, 1978; Furnas, 1990; Spilling, 2007b). Given such physiological disadvantages, their dominance is particularly surprising. Both, coastal diatoms and dinoflagellates, form resting stages (e.g., McQuoid et al., 2002) as a common survival strategy for (i) protection (survival during periods when conditions are not favourable for vegetative cells), (ii) propagation (acting as seed populations), and (iii) dispersion (spreading species to new areas) (e.g., Wall, 1971; Lewis et al., 1999; McQuoid et al., 2002). Changes in the timing and size of the dinoflagellate inoculum have been proposed as factors supporting dinoflagellates (Kremp et al., 2008). The inoculum (i.e., the cells that initialise a bloom) is regulated by life cycle processes, which are relatively complex for dinoflagellates, involving several (sexual and asexual) stages and transitions (e.g., Figueroa et al., 2006; Kremp, 2012). In contrast, the life cycle of diatoms is less complex with less phases and transitions (Fig. 4.1).

Many diatoms are known to form resting stages, which are referred to as "resting spores" (e.g., McQuoid and Hobson, 1996). Generally, the formation of resting spores is asexual (e.g., von Stosch and Drebes, 1964; Drebes, 1966; McQuoid and Hobson, 1996) and associated to unfavourable environmental conditions (e.g., depleted nutrients, insufficient light, and unsuitable temperature see e.g., Drebes, 1966; Durbin, 1978; Hargraves and French, 1983). Resting spores can remain viable for long periods in cool and dark conditions and rapidly transform into vegetative stages (e.g., Mann, 2002). Vegetative growth reduces the diatoms cell size and changes their characteristic shape (e.g., Round et al., 1990). Both are restored by auxosporulation (e.g., D'Alelio et al., 2010) (i.e., the formation of an auxospore involving sex). Lewis Jr (1984) argue that reductions in cell size act as triggers for sexual reproduction, preventing it from occurring too frequently. With reproduction intervals greater than one year, environmental cues can be considered ineffective for a sexual reproduction. With assumed periods between 2 and 40 years, the sexual reproduction of diatoms has been hardly observed to date (Mann, 1988; Jewson, 1992).

Two key groups involved in varying dominances are the diatom *Thalassiosira baltica* and the dinoflagellate *Biecheleria baltica* (Kremp et al., 2008). In particular, *B. baltica*

has become a dominant component of the spring bloom in the Gulf of Finland (Klais et al., 2011). The success of *B. baltica*—despite a lower maximal growth rate—is linked to a specific life cycle strategy. It produces large amounts of resting cysts at the end of each bloom (Heiskanen, 1993; Kremp and Heiskanen, 1999). Growing cyst deposits resulting from mass sedimentation have been proposed to promote the expansion of the species in the Gulf of Finland (Klais et al., 2011).

So far, few model studies address the life cycle processes of diatoms and dinoflagellates and their interannually varying dominances. Yamamoto et al. (2002) focus on the life cycle of dinoflagellates and for diatoms they consider only their sinking dynamics. The authors study seasonal dynamics, but do not address varying dominances. While Eilertsen and Wyatt (2000) propose a life cycle model for both, diatoms and dinoflagellates, the life cycle transitions and interspecific dynamics are assumed to depend on external processes that are fixed in time and quantity.

The goal of the present study is to identify and formalise the processes that influence the interannually varying dominances between two phytoplankton groups. We combine our previous life cycle model for *B. baltica* (Warns et al., 2013) and a newly developed diatom life cycle model for *T. baltica*. The combined model is used to study the seasonal succession of life cycle stages and the interannually varying dominances resulting from physical conditions and inter-species competition for nutrients and light.

4.2 Model description

Ecosystem model parameterisation

The model considers two different phytoplankton groups, dinoflagellates P^1 and diatoms P^2. The dinoflagellate life cycle is modelled by four compartments, vegetative cells P_1^1 ("vegetative dinoflagellates"), gametes P_2^1, resting cells P_3^1 ("cysts"), and germinating cells P_4^1. The life cycle of diatoms is modelled by two compartments, vegetative cells P_1^2 ("vegetative diatoms") and resting cells P_2^2 ("spores"). The model does not consider the sexual reproduction of diatoms, assuming that sexual reproduction is not relevant for a seasonal succession in terms of forming blooms and resting stages. To realistically describe the ecosystem and conserve mass, the model has two additional ecosystem compartments one for nutrients N and one for detritus D (Fig. 4.1).

In the dinoflagellate life cycle model, the mass circulates unidirectionally, from vegetative cells to gametes to cysts to germinating cells, back to vegetative cells. In the diatom life cycle model, the mass circulates between the vegetative and the resting cells. The changes of the life cycle compartments are given by transition functions τ, loss terms λ, vertical motilities ω, and functions for the growth of vegetative cells μ. The variables are indexed describing the respective directions of change (Fig. 4.2).

For example, $\tau_{P_1^1 P_2^1}$ describes the transition from vegetative cells P_1^1 to gametes P_2^1.

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

$$\frac{\partial P_1^1}{\partial t} = \underbrace{\mu_{N P_1^1}\, P_1^1}_{\text{growth}} + \underbrace{\tau_{P_4^1 P_1^1}\, P_4^1 - \tau_{P_1^1 P_2^1}\, P_1^1}_{\text{transition}} - \underbrace{\lambda_{P_1^1 D}\, P_1^1}_{\text{loss}}, \tag{4.1}$$

$$\frac{\partial P_2^1}{\partial t} = \underbrace{\tau_{P_1^1 P_2^1}\, P_1^1 - \tau_{P_2^1 P_3^1}\, P_2^1}_{\text{transition}} - \underbrace{\lambda_{P_2^1 D}\, P_2^1}_{\text{loss}}, \tag{4.2}$$

$$\frac{\partial P_3^1}{\partial t} = \underbrace{\tau_{P_2^1 P_3^1}\, P_2^1 - \tau_{P_3^1 P_4^1}\, P_3^1}_{\text{transition}} - \underbrace{\lambda_{P_3^1 D}\, P_3^1}_{\text{loss}} - \underbrace{\omega_{P_3^1} \frac{\partial P_3^1}{\partial z}}_{\text{sinking}}, \tag{4.3}$$

$$\frac{\partial P_4^1}{\partial t} = \underbrace{\tau_{P_3^1 P_4^1}\, P_3^1 - \tau_{P_4^1 P_1^1}\, P_4^1}_{\text{transition}} - \underbrace{\lambda_{P_4^1 D}\, P_4^1}_{\text{loss}} - \underbrace{\omega_{P_4^1} \frac{\partial P_4^1}{\partial z}}_{\text{rising}}, \tag{4.4}$$

$$\frac{\partial P_1^2}{\partial t} = \underbrace{\mu_{N P_1^2}\, P_1^2}_{\text{growth}} + \underbrace{\tau_{P_2^2 P_1^2}\, P_2^2 - \tau_{P_1^2 P_2^2}\, P_1^2}_{\text{transition}} - \underbrace{\lambda_{P_1^2 D}\, P_1^2}_{\text{loss}} - \underbrace{\omega_{P_1^2} \frac{\partial P_1^2}{\partial z}}_{\text{sinking}}, \tag{4.5}$$

$$\frac{\partial P_2^2}{\partial t} = \underbrace{\tau_{P_1^2 P_2^2}\, P_1^2 - \tau_{P_2^2 P_1^2}\, P_2^2}_{\text{transition}} - \underbrace{\lambda_{P_2^2 D}\, P_2^2}_{\text{loss}} - \underbrace{\omega_{P_2^2} \frac{\partial P_2^2}{\partial z}}_{\text{sinking}}, \tag{4.6}$$

$$\frac{\partial N}{\partial t} = \underbrace{\rho_{DN}\, D}_{\text{remineralisation}} - \underbrace{\mu_{N P_1^1}\, P_1^1 + \mu_{N P_1^2}\, P_1^2}_{\text{growth}}, \tag{4.7}$$

$$\frac{\partial D}{\partial t} = \underbrace{\sum_{i=1}^{4} \lambda_{P_i^1 D}\, P_i^1 + \sum_{i=1}^{2} \lambda_{P_i^2 D}\, P_i^2}_{\text{losses}} - \underbrace{\rho_{DN}\, D}_{\text{remineralisation}} - \underbrace{\omega_D \frac{\partial D}{\partial z}}_{\text{sinking}}. \tag{4.8}$$

In addition, the term $\frac{\partial}{\partial z}\left(A_{\mathrm{v}} \frac{\partial \Phi}{\partial z}\right)$ is added to the right hand side of all of the above changes, where A_{v} denotes the time- and depth-dependent vertical turbulent diffusivity of momentum and Φ the corresponding notations of the changes (P_j^i, N, and D).

Vertical velocities are applied to cysts, vegetative diatoms, and spores, which sink, and to germinating cells, which rise in the water column. The vegetative dinoflagellates and the gametes are assumed to be neutrally buoyant. Since we are only interested in the seasonal cycle and their interannual variability, we do not consider the diurnal

vertical migration of vegetative dinoflagellate cells.

For all compartments we assume constant loss rates that represent, for example, cell lysis and grazing. The losses go into the detritus, which is remineralised and transferred back to the nutrients. The nutrients can be taken up by both vegetative phytoplankton stages.

Dinoflagellate life cycle parameterisation

The parameterisation of the dinoflagellate life cycle are based on experiments with the cold-water dinoflagellate *B. baltica* and are described in Warns et al. (2012, 2013). In summary, the main assumptions for growth, en- and excystment are: (1) The growth of vegetative cells is limited by nutrients, irradiance, temperature, and gamete density. (2) Gamete production is low at low temperature (below 3 °C) and increases with increasing temperature, reaching a maximal rate at 6 °C. (3) Cyst production depends on temperature and the density of gametes. If temperature is sufficiently high (> 3 °C) and the density reaches a specific threshold, gametes transform into cysts. (4) The transition from resting cysts into germinating cells takes place after a mandatory dormancy period (210 days) if the mean temperature over 5 days $\overline{T}$ is adequate (between 0 and 9 °C). (5) Germinating cells migrate upwards into the euphotic zone and transform into vegetative cells depending on light conditions.

Diatom life cycle parameterisation

The parameterisation of the diatom life cycle is based on studies with the cold-water diatom *T. baltica*. We assume that vegetative diatoms grow due to photosynthesis and nutrient uptake. The actual growth rate $\mu_{NP_1^2}$ depends on the availability of nutrients, irradiance, and temperature:

$$\mu_{NP_1^2}(T, N, I) := \mu_{\max P_1^2}\, l_5\, l_6\, l_7, \tag{4.9}$$

where $\mu_{\max P_1^2}$ is the maximal growth rate and l_5, l_6, and l_7 are limitation functions of nutrients, irradiance, and temperature. Note that the maximal growth rate of diatoms is chosen more than twice as high as the one of dinoflagellates, which is a relation well-known in literature (e.g., Lalli and Parsons, 1997). More precisely, $\mu_{\max P_1^2} = 0.9\,\mathrm{d}^{-1}$ while $\mu_{\max P_1^1} = 0.4\,\mathrm{d}^{-1}$.

Following Monod (1949), we define the nutrient limitation function by

$$l_5 := \frac{N}{k_{NP_1^2} + N}, \tag{4.10}$$

where $k_{NP_1^2}$ is the half-saturation constant for nutrients (see Tab. 4.1 for the specific values).

The irradiance limitation is based on the functional relationship of Webb et al. (1974) and on growth experiments with *T. baltica* under varying irradiance conditions (Spilling and Markager, 2008):

$$l_6 := 1 - \exp\left(\frac{-\alpha_{P_1^2}\, I_{\mathrm{PAR}}}{\mu_{\max P_1^2}}\right), \tag{4.11}$$

where I_{PAR} is the incoming irradiance and $\alpha_{P_1^2}$ is the initial slope of the PI curve. The function l_6 has almost reached its maximum value at 25 $\mathrm{W\,m^{-2}}$.

The temperature limitation function l_7 is based on observations by Spilling (2011) that show highest growth rates of *T. baltica* at 12°C:

$$l_7 := 0.5\ \left(\tanh\left(c_{16}\ \left(T - c_{17}\right)\right)\ -\ \tanh\left(c_{18}\ \left(T\ -\ c_{19}\right)\right)\right), \tag{4.12}$$

where T is the temperature and c_{16}, c_{17}, c_{18}, and c_{19} are constants.

The formation of spores is associated with conditions that are unfavourable for growth (e.g., Drebes, 1966; Durbin, 1978; McQuoid and Hobson, 1996). Thus, we assume that the transfer from vegetative diatoms into spores and vice versa depends on growth conditions of vegetative diatoms. To avoid perpetual switches between the stages, we consider the mean growth rate over 5 days ($\bar{\mu}_{NP_1^2}$) for both transitions. If the growth rate $\bar{\mu}_{NP_1^2}$ is below the critical value $\mu_{P_1^2\mathrm{crit}}$, vegetative diatoms start to transfer into spores; if the growth rate is above the critical value, spores transform into the vegetative state (see Fig. 4.3). Thus, we define the transition rate from vegetative diatoms to spores $\tau_{P_1^2P_2^2}$ and the transition rate from spores to vegetative diatoms $\tau_{P_2^2P_1^2}$ as

$$\tau_{P_1^2P_2^2} := \tau_5\, 0.5\, \left(1 - \tanh\left(c_{20}\, \left(\bar{\mu}_{NP_1^2} - \mu_{P_1^2\mathrm{crit}}\right)\right)\right) \tag{4.13}$$

$$\tau_{P_2^2P_1^2} := \tau_6\, \left(-0.5\, \left(1 - \tanh\left(c_{21}\, \left(\bar{\mu}_{NP_1^2} - \mu_{P_1^2\mathrm{crit}}\right)\right)\right) + 1\right) \tag{4.14}$$

where c_{20} and c_{21} are constants.

4.3 Model configuration

The ecosystem model described above is coupled to the one-dimensional water column model GOTM (General Ocean Turbulence Model, Umlauf et al., 2005) that provides the physical environment (i.e., vertical turbulent mixing, temperature, salinity, and

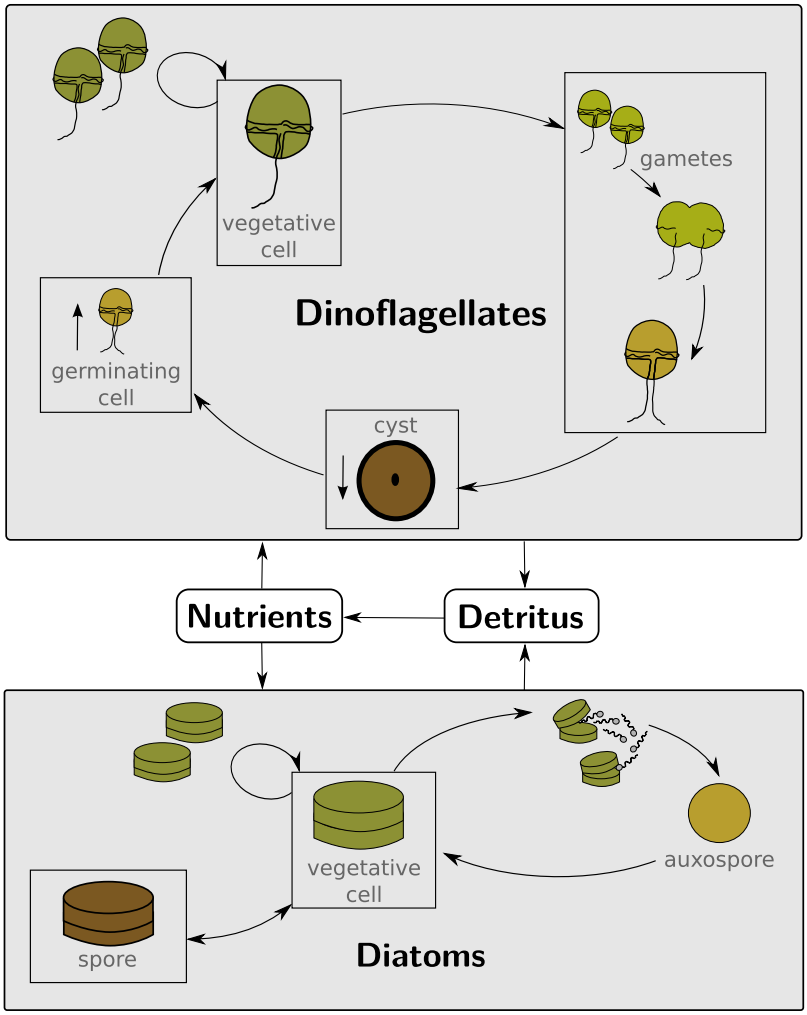

Figure 4.1: Conceptual overview of the entire ecosystem model including the life cycle compartments and the transitions among the compartments.

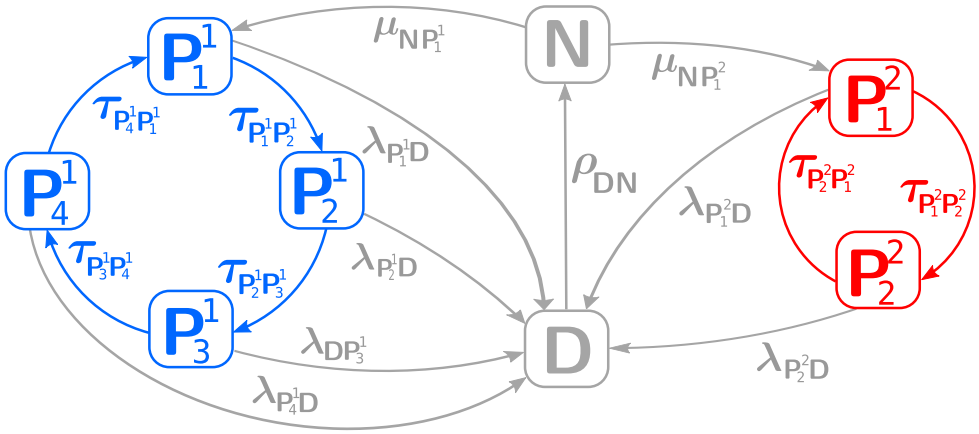

Figure 4.2: Conceptual overview of the dinoflagellates (P^1) life cycle compartments (blue) and the diatoms (P^2) life cycle compartments (red), compartments of nutrients (N) and detritus (D) (grey), and the transitions among the compartments. The rates are denoted by Greek letters indexed with the names of the connected compartments describing the respective directions of change.

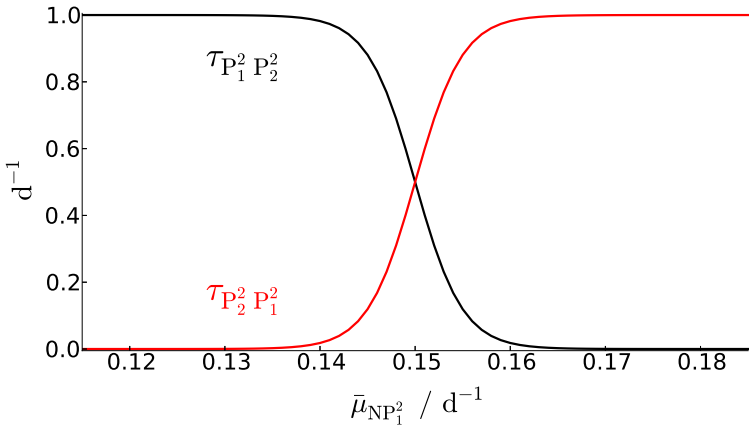

Figure 4.3: The transition functions $\tau_{P_1^2P_2^2}$ from vegetative diatoms into resting diatoms and vice versa ($\tau_{P_2^2P_1^2}$ from resting diatoms into vegetative diatoms).

irradiance fields) using realistic atmospheric forcing from the Gulf of Finland in the Baltic Sea (59.8°N, 25°E). The forcing data are composed of 2 m-atmospheric temperature, air pressure, relative humidity, 10 m-wind velocities, and short wave radiation (calculated from cloud cover and albedo) based on NCEP/NCAR Reanalysis from 1958 to 2012 (Kalnay et al., 1996). For initialising the water column, we use temperature and salinity profiles from the HELCOM Station LL7 (ICES database, `http://www.ices.dk/`). The model is restored to the salinity profile every 5 days. The modelled water column is 80 m deep with a vertical resolution of 1 m. A time step of 900 s is used. The model is applied for the time period 1958-2010 and the first 22 years are considered as spin-up. Thus, all analyses are based on the time period 1980-2010.

At the surface, a nitrogen flux is considered from the atmosphere into the water column using a typical value for the Baltic Sea ($0.2\,\mathrm{mmol\,N\,m^{-2}\,d^{-1}}$, Larsson et al., 2001). This flux is balanced by restoring nutrients in the bottom layer to a "typical" value of $10\,\mathrm{mmol\,N\,m^{-3}}$ every two hours. Additionally, we assume a burial of cysts and diatoms in the bottom layer, which depends quadratically on their concentrations. For all other boundary conditions "no flux conditions" are applied. The numerical scheme for the discretisation of the model equations is a 2nd order modified Patankar-Runge-Kutta scheme (Burchard et al., 2003), which is positive definite and mass conserving.

4.4 Results

Seasonal cycles in different years

The analysis of the model focusses on the time period from 1980 to 2010. The model results show a realistic seasonal cycle of mean temperature $\overline{T}$ (over 5 days) and nutrients for the Gulf of Finland. The seasonal dynamics of solar radiation and wind stress lead to an increase in surface temperature and stratification from April/May to September/October (Fig. 4.4a and Fig. 4.5a), which is in agreement with observations (Heiskanen and Leppänen, 1995). Nutrient concentrations are relatively high in winter until the growth of vegetative dinoflagellates and diatoms leads to a nutrient depletion at the surface from May to July (Fig. 4.4b and Fig. 4.5b). The maximum temperature can be seen in July/August before the radiation decreases. Increasing wind stress and decreasing atmospheric temperature in autumn result in a mixing and cooling of the water column ("autumn mixing"). Remineralised dead organic matter and the autumn mixing refill the nutrient pool at the surface in autumn.

The temperature, light, and nutrient conditions lead to different seasonal distributions of dinoflagellates and diatoms. These distributions are exemplarily described below for the years 1997 and 2009, which show different dominances. In 1997, the spring bloom is dominated by dinoflagellates, in 2009, by diatoms.

In February 1997, the cysts begin to excyst, which results in a first bloom of dinoflagellates in March (Fig. 4.4c). However, growth in March and April is limited due to relatively low temperature; the abundance of dinoflagellates decreases. With higher temperature in May, the concentration of vegetative dinoflagellates rapidly increases resulting in a second bloom of dinoflagellates at the end of May. In June, encystment starts (due to increasing temperature) and causes a decrease in the dinoflagellate bloom and an increase in cyst abundance. The cysts sink to the sediment at the bottom of the water column, where they mature until the next year. The abundance of vegetative diatoms and spores is very low (below 1 mmol N m^{-3}) during the whole year. The seasonal distribution of the dinoflagellate stages is similar to the one described in our previous study (Warns et al., 2013).

In contrast, the diatoms are dominating in the year 2009. The year begins with higher abundances of cysts than spores (Fig. 4.5c). In January, the cysts excyst, which causes a dinoflagellate bloom in February. However, the abundance of dinoflagellates decreases due to relatively cold temperature. With a rapid temperature increase in May, the concentration of vegetative dinoflagellates slightly increases, but also the encystment starts due to further increasing temperature and causes a decrease in the dinoflagellate abundance before even a pronounced bloom is built. From January to May, the growth conditions are not favourable for diatoms (Fig. 4.6). Therefore, the spores do not transform into vegetative diatoms. In May, light and temperature become favourable for growth in the upper layers (around 20 m), the mean growth rate for diatoms $\bar{\mu}_{NP_1^2}$ reaches the critical value $\mu_{P_1^2\text{crit}}$, and spores start to transform into vegetative diatoms. The vegetative diatoms grow and, in late May, form a bloom ranging from the surface to ca. 20 m depth, which is shown in Figure 4.7. The concentrations are significantly higher compared with dinoflagellates who have already started to encyst. In early June, the mean growth rate $\bar{\mu}_{NP_1^2}$ decreases due to depleted nutrient conditions. Hence, the transition is reversed, and the vegetative diatoms start to transform into spores. In the upper 15 m, all vegetative diatoms transform into spores resulting in a decrease of vegetative diatom concentration and an increase in spore concentration with a maximum in mid of June. In summer, the temperature further increases in the upper layers as shown in Figure 4.5, and vegetative diatoms continue to transform into spores. In parallel, as nutrients and temperature are favourable for growth subsurface (around 20 m, Fig. 4.6) and for three short periods (late June, late July, and mid of September), spores transform into vegetative diatoms. In autumn (from late September until early November), increasing nutrients and decreasing temperature are favourable for an enhanced transition from spores to vegetative diatoms in the upper 12 m. In mid of November, the transition is reversed due to decreasing light and temperature in the whole water column; only spores are formed for the rest of the year causing a minor increase in the concentrations of spores.

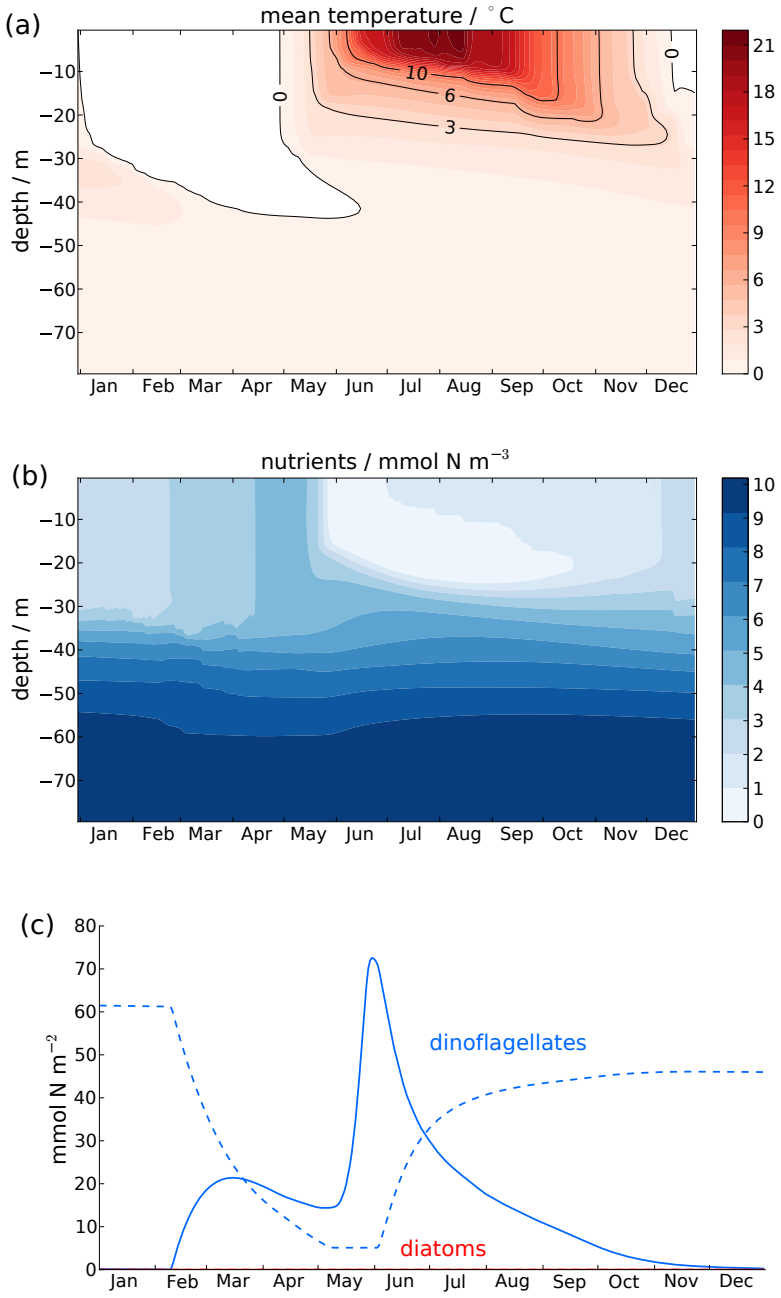

Figure 4.4: Seasonal distribution of (a) the mean temperature $\overline{T}$, (b) the nutrients N, and (c) dinoflagellates and diatoms (solid lines) and their respective resting stages (dashed lines) integrated over 80 m depth for the year 1997. Diatom abundances are very low (below 1 mmol N m^{-3}) during the whole year.

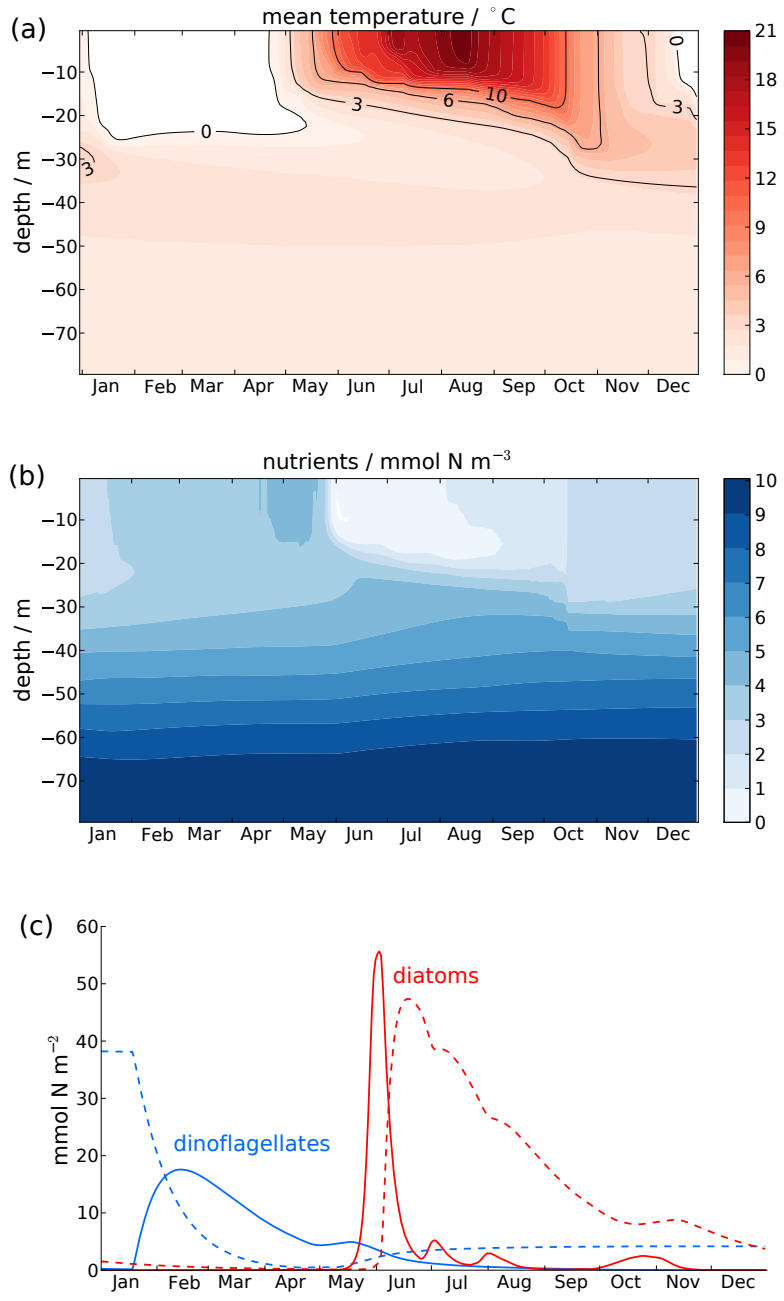

Figure 4.5: Seasonal distribution of (a) the mean temperature $\overline{T}$ and (b) the nutrients N, and (c) dinoflagellates and diatoms (solid lines) and their respective resting stages (dashed lines) integrated over 80 m depth for the year 2009.

Table 4.1: Parameters for the diatom life cycle model.

Symbol	*Parameter*	*Value*	*Unit*
$\mu_{\max P_1^2}$	maximal growth rate of P_1^2	0.9	d^{-1}
$k_{NP_1^2}$	half-saturation constant for N	1.0	mmol N m^{-3}
$\alpha_{P_1^2}$	initial slope used in limiting function l_6	0.15	$\mathrm{m}^2\mathrm{W}^{-1}\mathrm{d}^{-1}$
τ_5	maximal transition rate from P_1^2 to P_2^2	0.2	d^{-1}
τ_6	maximal transition rate from P_2^2 to P_1^2	0.2	d^{-1}
$\mu_{P_1^2\mathrm{crit}}$	critical value for transition	0.15	d^{-1}
$\lambda_{P_1^2 D}$	loss rate of P_1^2	0.02	d^{-1}
$\lambda_{P_2^2 D}$	loss rate of P_2^2	0.02	d^{-1}
$\delta_{P_2^2 D}$	deposition coefficient of P_2^2	0.0029	$\mathrm{m}^3(\mathrm{mmol\,N})^{-1}\mathrm{a}^{-1}$
$\omega_{P_1^2}$	sinking of P_1^2	-0.25	md^{-1}
$\omega_{P_2^2}$	sinking of P_2^2	-0.25	md^{-1}
ρ_{DN}	remineralisation rate	0.1	d^{-1}
ω_D	sinking of D	-10	md^{-1}
k_c	self-shading parameter	0.03	$\mathrm{m}^2(\mathrm{mmol\,N})^{-1}$
k_w	attenuation coefficient	0.13	m^{-1}

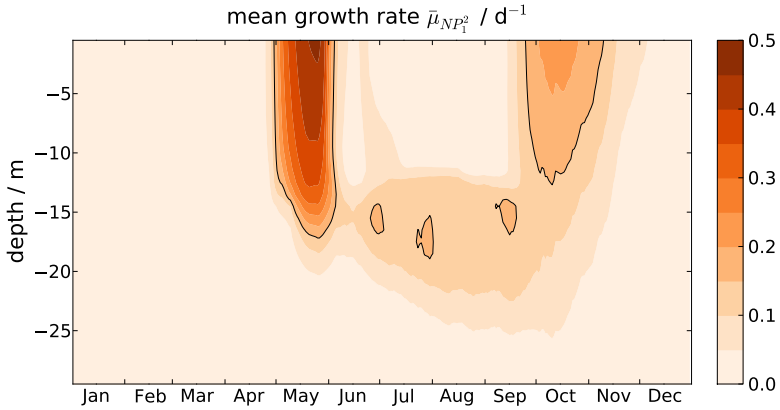

Figure 4.6: Seasonal distribution of the mean growth rate $\bar{\mu}_{NP_1^2}$ of the year 2009. If the growth rate $\bar{\mu}_{NP_1^2}$ is below the critical value $\mu_{P_1^2\mathrm{crit}}$ (black line) vegetative diatoms start to transfer into resting diatoms; if the growth rate is above the critical value resting diatoms transform into the vegetative stage.

Interannual variability

On interannual time scales, the model results show varying dominances of dinoflagellates and diatoms as illustrated in Figure 4.8. If the diatoms are dominating the spring bloom, the abundance of dinoflagellates is low throughout the whole year (1980-83 and 1989) and vice versa (1994-2000 and 2007-2008). For some years, both groups have approximately equal abundances (1984, 1988, 1992, 2004).

In general, the dominance of either dinoflagellates or diatoms results from the winter concentration of resting stages. Winter conditions with more spores than cysts or equal cyst and spore abundances lead to diatom dominance. Years in which spring blooms are dominated by dinoflagellates have higher cyst than spore concentrations in winter. However, while multiple years (1980-84 and 1989, 1990, 2003, 2006, 2009) show spring blooms dominated by diatoms, only in two years (1980 and 1989) higher spore than cyst concentrations occur in winter. The other years show significantly higher cyst than spore concentration in winter, but a spring blooms dominated by diatoms. In these years, the cysts germinate relatively early (i.e., in December of the preceding year until early February) and, consequently, a dinoflagellate bloom appears in winter/early spring. In contrast, in dinoflagellate-dominated years, cysts germinate relatively late (i.e., in March or April) and, therefore, no dinoflagellate bloom appears in winter/early spring.

The underlying reason for a spring bloom dominated by diatoms despite high cyst concentrations in winter is a rapid increase in temperature during spring. The growth of vegetative dinoflagellates starts at lower temperature than their encystment. By a rapid temperature increase, encystment starts relatively early before the vegetative dinoflagellates are able to build up a pronounced spring bloom. Hence, there is only a short time window for dinoflagellate growth leading to a diatom-dominated spring bloom. In contrast, a slow increase in temperature during spring allows vegetative growth, but delays encystment. Hence, vegetative dinoflagellates build up a pronounced bloom in spring before encystments starts leading to dinoflagellate-dominated years. Hence, the temperature gradient during spring is the driving factor for the resulting dominant phytoplankton group in our model.

Comparison to observations

For evaluation, we compare the model results to observation data from the Gulf of Finland in the Baltic Sea. The data are obtained from monitoring datasets by national monitoring agencies around the Baltic Sea (Klais et al., 2011). The data set comprises abundances of spring dinoflagellates and diatoms from 1966 until 2008.

To allow direct comparison, the observation data is converted into the same unit as used for the model (i.e., from $\mu g\,ww\,l^{-1}$ into $mmol\,N\,m^{-3}$). The wet weight concentrations (in $\mu g\,l^{-1}$) are converted into carbon concentrations (in $mg\,C\,m^{-3}$) using a factor of 0.11 (Edler, 1979). The carbon concentrations are converted into

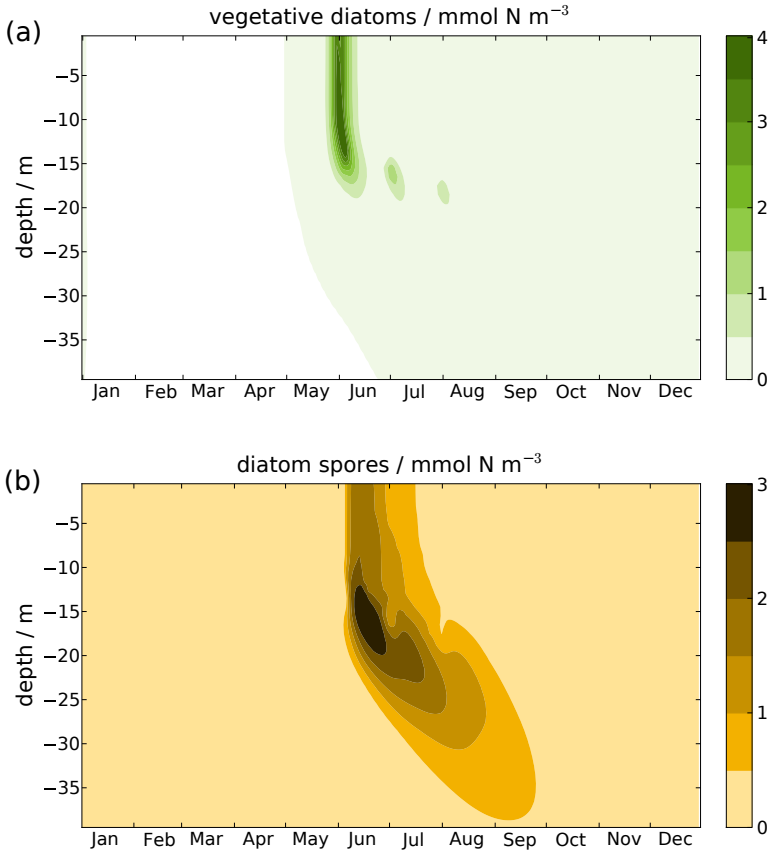

Figure 4.7: Seasonal distribution of (a) vegetative diatoms and (b) spores for the year 2009.

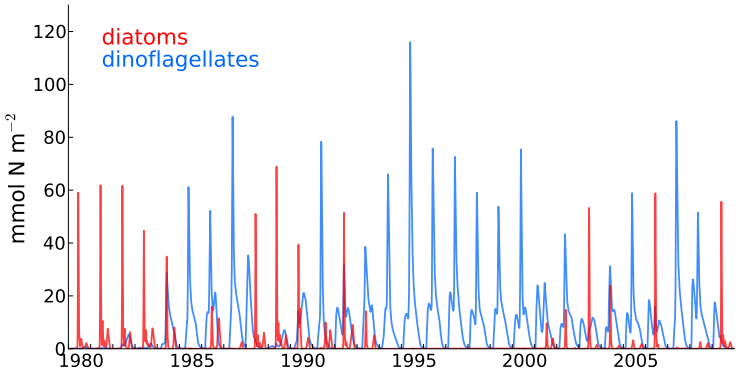

Figure 4.8: Model results of dinoflagellate (blue) and diatom concentrations (red) in mmol N m^{-2} integrated over 80 m depth from 1980 to 2009.

nitrogen concentrations (in mmol N m^{-3}) with a factor of 1/79.5 (resulting from the Redfield ratio and the conversion from g into mol). The resulting data are shown in Figure 4.9.

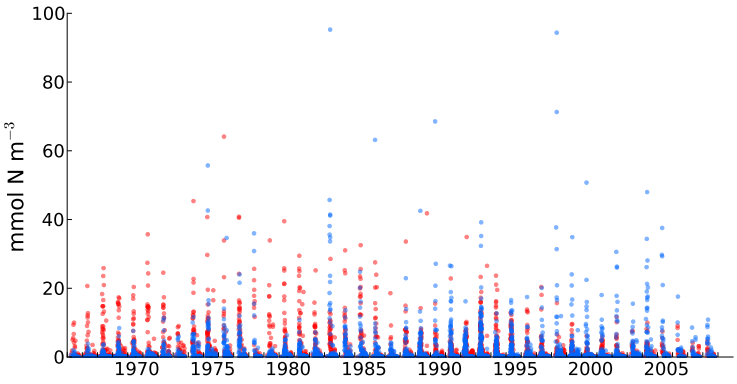

Figure 4.9: Observations of dinoflagellates (blue) and diatoms (red) over time.

The observations were mostly taken within the upper 10 m. The comparison to model results, therefore, also focusses on the upper 10 m of the water column. The observations are widely spread. For further analysis, we have removed very extreme outliers from the observation data. An observation sample s is considered a very extreme outlier if it is more distant than six times the interquartile range below the first quartile Q_1 or above the third quartile Q_3, that is, if

$$s \notin [Q_1 - 6(Q_3 - Q_1), Q_3 + 6(Q_3 - Q_1)]\,. \tag{4.15}$$

With this criterion ca. 8% of all samples have been removed as very extreme outliers. Without these very extreme outliers, the maximal concentration in the observations is approximately 6 mmol N m^{-3} representing an average concentration within the upper 10 m. This value seems reasonable, because, for example, Spilling et al. (2006) have observed a maximal concentration of inorganic nitrogen of approximately 7 mmol N m^{-3} in the Gulf of Finland at surface layers in April.

Additionally, a running mean (over 10 days) has been applied to both, the observations and the model results after linearly interpolating the observations between data points. If there are multiple data points for a day, the interpolation considers the mean of these data points for the day.

The model results represent the observation data adequately in term of the overall maximal biomass. Moreover, both model results and observations show varying dominances of dinoflagellates and diatoms (see Fig. 4.10) although the model uses a maximal diatom growth rate more than twice the maximal dinoflagellate growth.

In some years, the model results show dominating diatoms, while the observed abundance of dinoflagellate is very low throughout the whole year (Fig. 4.8 and 4.9;

1980-1982) and vice versa (1994-2000 and 2007). In contrast, the observed data show abundances of both groups every spring. Likewise, the model suggests that diatoms are dominant, while, in the observed data, the dinoflagellates are dominant (Fig. 4.8 and 4.9; 1983, 1989, 1990, 2003, and 2006) and vice versa (1985, 1987, 1994, and 1996).

Generally, the model adequately represents the timing of the blooms (Fig. 4.11). For some years (e.g., 1987), the model represents the exact timing of the bloom within the seasonal distribution of dinoflagellates. However, in other years, the bloom starts earlier (1988) or slightly later (1984-86) than in the observations (Fig. 4.11a). For the diatoms, the model represents blooms comparable to the observations in spring and in autumn (1989, 1990, 1992, 1993). If the model shows two blooms in a year (in spring and in autumn), the abundances in spring are higher than in autumn (1989, 1990, 1992, 1993) in accordance with the observations. In some years (e.g., 1991), the model only shows an autumn bloom, while only a spring bloom was observed. Overall, the model is able to adequately represent observations and does not systematically mismatch the maximal abundances or the timing of dinoflagellate and diatom blooms.

4.5 Discussion and conclusion

We have newly developed a life cycle model for diatoms and coupled it to an existing dinoflagellate life cycle model (Warns et al., 2013) to identify and investigate the factors that influence the seasonal and interannual variability of phytoplankton groups in the Baltic Sea. To the best of our knowledge, our model is the first describing the dynamics of the complete life cycles of dinoflagellates and diatoms.

In agreement with observations (Laamanen, 1997), the model results show low primary production in winter, a spring bloom, low primary production in summer, and an occasional bloom in autumn. Similar to our previous study (Warns et al., 2013), the model results show realistic seasonal dynamics of the dinoflagellate life cycle stages. In particular, the model simulates two peaks of vegetative dinoflagellates, one in late winter and one in spring, which is in agreement with observations of the Baltic Sea (e.g., Kremp and Anderson, 2000; Kremp, 2000; Spilling, 2007a). For the diatoms, the model suggests two peaks of vegetative diatoms, one in spring and one in autumn, which is also in agreement with observations of the Baltic Sea (e.g., Laamanen, 1997; Commission, 1996; Olli and Heiskanen, 1999).

Our model results show interannually varying dominances of dinoflagellates and diatoms although the maximal growth rate of diatoms is more than twice the maximal dinoflagellate growth rate. The interannual variability results from life cycle interactions, physical conditions, and inter-species competition for nutrients and light. The overall dominant species of the year is linked to the abundances of the resting stages and the temperature in spring. Relatively high abundances of diatom spores lead to a dominance of diatoms. High abundances of dinoflagellate cysts lead to a dominance

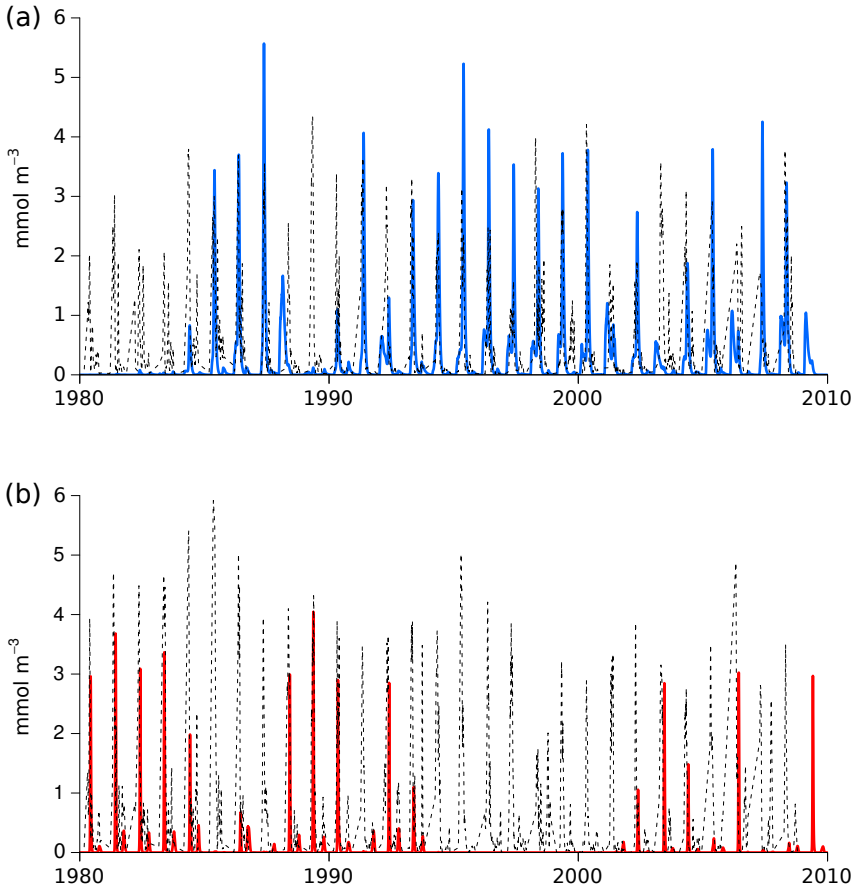

Figure 4.10: Average concentrations of dinoflagellates (a) and diatoms (b) within the upper 10 m for model results (solid line) and for observation data (dashed line) over time. A running mean (over 10 days) has been applied to both, model results and observations.

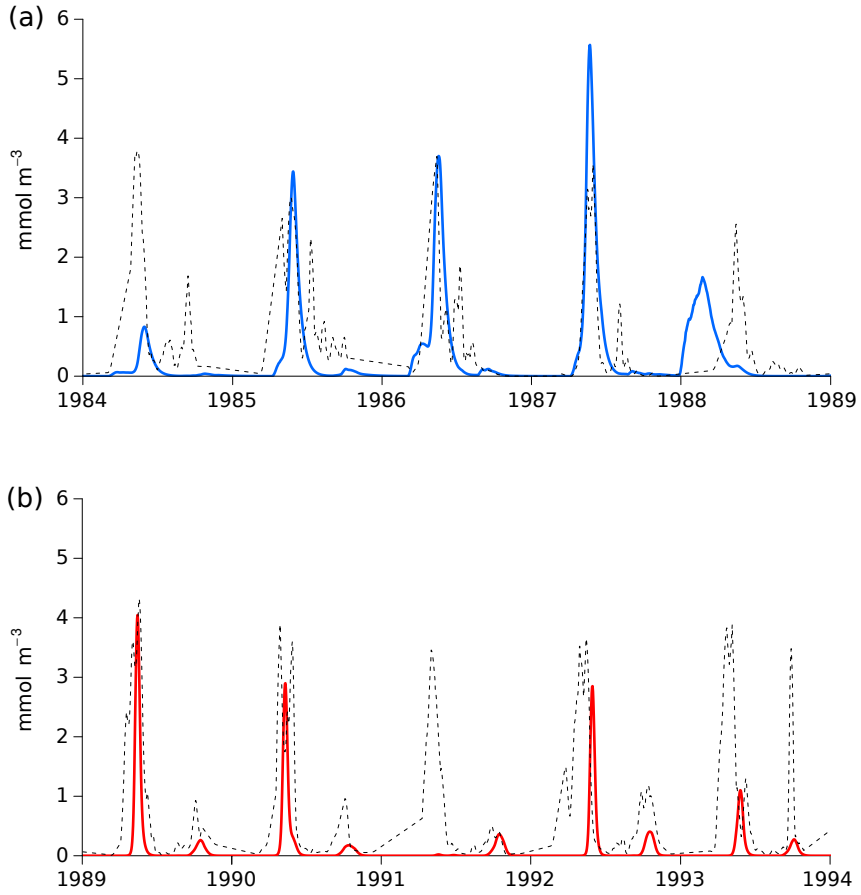

Figure 4.11: Average concentrations of dinoflagellates (a) and diatoms (b) within the upper 10 m for model results (solid line) and for observation data (dashed line) over time. A running mean (over 10 days) has been applied to both, model results and observations.

of dinoflagellates if slowly increasing temperature favours a spring bloom of vegetative dinoflagellates before encystment begins. Otherwise, if temperature rapidly increases, high abundances of dinoflagellate cysts lead to a dominance of diatoms. In this case, encystment starts before a pronounced spring bloom is built.

In comparison to observation data, the model results, unfortunately, show two shortcomings. In some years, the model results show dominating diatoms, while the abundance of dinoflagellates is very low throughout the whole year and vice versa. In contrast, the observed data show abundances of both groups every spring. For some years, the model suggests that diatoms are dominant, while, in the observed data, the dinoflagellates are dominant and vice versa. Both issues could be addressed by additionally considering accumulation of viable cysts that can germinate in later years. In the current model, we assume that cysts are partially deposited and buried at the sea floor. The remaining cysts germinate after a dormancy period if the conditions are favourable. Hence, there is no accumulation of viable cysts that can germinate in later years. Technically, this can be taken into account by introducing an additional model compartment for remaining dinoflagellate cysts. Considering another compartment could change relative abundances and interannually varying dominances. In addition, advection might play a role in the Gulf of Finland which is not considered in this water column model setup. The coupling of the life cycle models with a three-dimensional Baltic Sea circulation model might further improve the model results.

With our newly developed model system, we are able to show interannually varying dominances of spring bloom dinoflagellates and diatoms although diatoms are superior competitors to cold-water dinoflagellates; diatoms have a higher maximal growth rate, a faster transition between life cycle stages, and much less frequent (and energy consuming) sexual reproduction. The model is able to adequately represent seasonal and interannual patterns in the observations and can be relatively easily adjusted to represent other dinoflagellate and/or diatom species.

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5 Conclusions and outlook

The aim of this thesis was to investigate the encystment of dinoflagellates, the role of life cycles for their seasonal dynamics, and the interannually varying dominances between diatoms and dinoflagellates. We have incrementally developed an ecosystem model for both phytoplankton groups taking their life cycles, physical conditions, and inter-species competition for nutrients and light into account. Our basic approach on modelling the life cycles was to describe a self-contained mass-conserving systems, where all sources and sinks balance.

The ecosystem model is formalised as a numerical model considering four dinoflagellate and two diatom life cycle compartments with different properties of growth and motility. The transitions among the life cycle compartments are defined as functions of external and endogenous factors. The resulting ecosystem model was coupled to the one-dimensional water column model General Ocean Turbulence Model (GOTM, Umlauf et al., 2005), which provides a physical environment with a realistic atmospheric forcing.

For evaluation, the model results were compared to data from different field, laboratory, and statistical studies, that are independent from the data taken into account for the model development. Being particularly well studied, the Gulf of Finland was chosen as the model region allowing comprehensive model evaluations. While the model is generally applicable to diatoms and dinoflagellates, value estimations and parameterisations were performed for the diatom *T. baltica* and the dinoflagellate *B. baltica*, two of the most abundant and, therefore, relevant phytoplankton species in the Gulf of Finland.

The model results show a realistic seasonal cycle of temperature, nutrients, and phytoplankton species. For example, nutrient concentrations are relatively high in winter until the growth of vegetative dinoflagellates and diatoms leads to a nutrient depletion at the surface from May to July. In agreement with observations, the model results show low primary production in winter, a spring bloom, low primary production in summer, and an occasional bloom in autumn. In particular, the model realistically represents a pronounced spring bloom of dinoflagellates with two distinct peaks and two blooms for diatoms, one in spring and one in autumn.

Our model studies allow to derive conclusions beyond what can be directly determined from the observation data itself. For example, we have identified significant

differences between the development of cell counts and biomass, allowing more differentiated conclusions about the encystment process. Our studies have indicated monotonically increasing cell counts despite constant biomass for a laboratory experiment, which highlights the need to investigate life cycle dynamics on the basis of biomass and not solely on cell counts. Furthermore, our encystment model allows to quantify the growth rate of *B. baltica*, which would be challenging without a model; determining the growth rate only based on the observation data may underestimate the actual growth rate, because the biomass "loss" due to transitions from vegetative cells to gametes could be missed.

Encystment of dinoflagellates

For investigating the relevant mechanisms underlying the encystment process, we have reanalysed the laboratory data set of Kremp et al. (2009) for *B. baltica* and have developed a numerical model of encystment formalising the functional dependence among growth, cyst formation, and environmental factors.

The reanalysis has revealed that cyst formation starts to occur during the phase of increasing motile cells. As nutrients are still available during this period, nutrients do not seem to affect cyst formation. In contrast, temperature plays an important role in regulating cyst formation; cysts are only observed in 6°C experiments, but not at 3°C.

The model results indicate that, at the beginning of the phase of motile cells' exponential increase, the growth rate of vegetative cells must be higher at 6°C than at 3°C. This is necessary to compensate a higher proportion of non-growing gametes. Otherwise, there is hardly an explanation for the same biomass in the 6°C experiment compared to 3°C.

Moreover, the model suggests that, during the entire sex phase, vegetative cells and gametes are present. This is a counter indication for the hypothesis that cyst formation occurs under unfavourable conditions and is in agreement with the conclusions by Kremp et al. (2009).

There are two issues of the encystment process that could not be easily explained from reanalyses of the laboratory data: (i) a late formation of cysts and (ii) a reduced growth rate when cysts are formed. Our evaluations have shown that these issues can be covered by (i) a threshold of a quota that presents the density of gametes and (ii) a growth limiting function that describes the relationship between gamete concentration and growth. Introducing these aspects into the model allows to adequately represent observation data.

Seasonal dynamics of dinoflagellates

To investigate the seasonal dynamics, we have developed and evaluated a complete life cycle model for dinoflagellates. Results obtained using the model show a realistic

seasonal succession of life cycle stages with a pronounced spring bloom.

The evaluations indicate that considering life cycles is essential for adequately reproducing observation data. When using a simplified version of the dinoflagellate model, without considering the life cycle, the observed seasonal patterns cannot be reproduced. For example, the maximum abundance appears too late, because the growth rate of *B. baltica* is too small for an early bloom formation within a year.

The life cycle model simulates two peaks of motile cells in late winter and in early spring, which is in agreement with observations from the Baltic Sea. The late peak in spring can be attributed to growth of vegetative cells while the early peak in late winter is a result of germinating cells. After a mandatory dormancy, the cysts transform into germinating cells that rise from the bottom to the upper layers of the water column, where they transform into vegetative cells. This excystment process results in a first peak of the motile cells in February. However, the relatively low temperature limits the growth in February and March. When the temperature rises in April, the concentration of vegetative cells rapidly increases resulting in a second peak of motile cells at the beginning of May.

Temperature sensitivity of dinoflagellate abundances

Kremp et al. (2009) have observed that an increase in temperature induces an increase in gamete differentiation and subsequent cyst formation. They suggest that a temperature increase is taken as a signal by the species to complete sexual reproduction. We have performed temperature sensitivity experiments showing that, in warming scenarios, nutrient concentrations are indeed higher in spring when compared with reference runs. Higher encystment under warm conditions prevent high abundances of vegetative growing cells, which would take up the nutrients.

Enhanced cyst formation earlier in spring and subsequent cyst accumulation may further increase the seed pool. We have 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 to productivity of dinoflagellates or phytoplankton (Radi and de Vernal, 2008). As mentioned above, our model results indicate that this relationship may be more complex. While cysts biomass drives a first bloom, temperature conditions in spring are decisive for a second bloom.

Interannually varying dominances between diatoms and dinoflagellates

We have developed and combined numerical models for the life cycles of diatoms and dinoflagellates to study the seasonal succession of the life cycle stages of both groups and, in particular, their interannually varying dominances.

Our evaluations have shown that combined life cycle models are able to reproduce interannually varying dominances although dinoflagellates are inferior competitors to diatoms. The variability results from life cycle interactions, physical conditions, and inter-species competition for nutrients and light.

In particular, the overall dominant species of the year can be linked to the abundances of the resting stages and the temperature in spring. Relatively high abundances of diatom spores lead to a dominance of diatoms. High abundances of dinoflagellate cysts lead to a dominance of dinoflagellates if slowly increasing temperature favours a spring bloom of vegetative dinoflagellates before encystment begins. Otherwise, if temperature rapidly increases, diatoms become dominant despite high abundances of dinoflagellate cysts. In this case, encystment starts before a pronounced spring bloom is built.

Directions for future research

Multiple directions for future research arise from the thesis. Such directions include model enhancements, improvements of the model system, and applications to other species and regions.

Model enhancements allow to better reproduce some aspects of observations. For example, while reproducing interannually varying dominances, the model does not precisely reproduce the dominant species for a given year. In some years, the model suggests that diatoms are dominant, while observations indicate a dominance of dinoflagellates and vice versa. Furthermore, the model results show very low dinoflagellate biomasses throughout a year when the spring bloom is dominated by diatoms. In contrast, observations show significant biomasses for both species every spring. Both aspects could be addressed by introducing a model compartment for viable cysts that can germinate in later years. In particular, an additional compartment may allow to reproduce the gradual shift of dominances observed in the Baltic Sea in recent years.

Improvements of the model system allow to include relevant aspects that have not been addressed yet. For example, advection may play a central role in the Gulf of Finland, which is not considered in our current water column model setup. For an improved representation of spatial variability, our life cycle models could be coupled to a three-dimensional circulation model.

Applying our model concepts to other species and regions will likely reveal further insights into phytoplankton dynamics. For example, studies of harmful algae blooms benefit from model applications. While we focussed on *T. baltica* and *B. baltica*, our model is generally applicable to other phytoplankton groups and species. Necessary modifications may include changes in the nutrient uptake behaviour and in the temperature dependencies of growth, for example, if warm-water dinoflagellates are considered. Additionally, other factors influencing life cycle transitions like daylength

or specific nutrients might be required to represent other groups adequately. More comprehensive changes are required if additional life cycle stages and transitions are needed. Dinoflagellate species that produce only temporary cysts, however, can be relatively easily described by omitting the maturation time.

Besides other model species, further model regions may be considered as well. An application of our models to the North Sea promises particularly interesting insights because of different trends in dominance. Hinder et al. (2012) have investigated long-term spatial variability of phytoplankton species in the North Sea using data from the Continuous Plankton Recorder and have found pronounced variations in diatom and dinoflagellate abundances. Comparable to the Baltic Sea, dinoflagellates have become relatively more abundant than diatoms from the 1960s to the 1980s. In contrast, however, this trend has switched afterwards. The dinoflagellate abundances have been found to decline since 2006, which led to a marked increase in the relative abundance of diatoms over dinoflagellates.

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List of publications and declaration of contributions

Warns, A., Hense, I., and Kremp, A., (2012) Encystment of a cold-water dinoflagellate—from *in vitro* to *in silico*. Journal of Marine Systems, doi:10.1016/j.jmarsys.2012.10.003, (in press)

I have prepared the observational data, developed the model, performed the model runs, analysed and discussed the model results, as well as structured and written the article. Inga Hense had the original idea, gave support regarding analyses and discussion of model results, and gave assistance in structuring and writing the article. Anke Kremp provided the observational data set, gave support regarding the observational data, and gave assistance in writing the article.

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I have prepared the observational data, developed the model, performed the model runs, analysed and discussed the model results, as well as structured and written the article. Inga Hense had the original idea, gave support regarding analyses and discussion of model results, and gave assistance in structuring and writing the article. Anke Kremp helped in discussions of the model results and the comparison between model results and observations and gave assistance in writing the article.

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I have prepared the observational data, developed the model, performed the model runs, analysed and discussed the model results, as well as structured and written the article. Inga Hense had the original idea and gave assistance in writing individual sections of the article.

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