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The impact of temporal variability in light-climate on time-averaged primary production and a phytoplankton bloom in a well-mixed estuary

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Abstract

Phytoplankton primary production (PP) in turbid estuaries is often limited by light-availability. Two important factors altering light-climate are solar irradiance at the water surface and exponential light-extinction coefficient within the water column. Additionally, the depth of the water body changes the light-climate and corresponding PP by altering the ratio of the euphotic and mixing depth in a well-mixed estuary. These three parameters are highly variable yet are often assumed to be constant by both experimental scientists and modelers because of a lack of data or to reduce complexity. Because assuming constant parameters introduces an error, we utilize an idealized model of depth-integrated primary production to analyze the (individual) impact of temporal variability in these three parameters. We only consider the main tidal and solar constituents in temporal variability of the forcings and apply a second-order moment approximation to analyze the bias introduced to time-averaged PP estimates by neglecting temporal fluctuations. We demonstrate that the sign and magnitude of this bias are system-specific and depend on two non-dimensional parameters that characterize the system. The first is equivalent to the ratio of mixing and photic depth. The second accounts for typical incident irradiance and the photosynthetic parameters of the phytoplankton population present. To demonstrate the applicability of our approach, we apply the model to two cases in the Scheldt estuary (Belgium) in the brackish and freshwater part. In the first application, we study the impact of fluctuations on phytoplankton in dynamic equilibrium, where biomass is assumed to be constant. We show that variability in solar irradiance has the largest impact on time-averaged PP in dynamic equilibrium, resulting in a 30 percent decrease compared to time-invariant forcing. By comparing with a numerical integrator, we show that a second-order moment approximation correctly predicts the order of magnitude of the impact of temporal variability of the individual parameters. In the second application, we study the impact of fluctuations on unbounded exponential phytoplankton growth. Also here, fluctuations in solar irradiance have the largest impact and lead to a significant decrease in exponential growth. In this case study, we show that temporal fluctuations delay the onset of the biomass by two weeks and decrease the biomass by a factor 14 after two weeks compared to time invariant forcing. Additionally, we show that the temporal fluctuations induce low-frequency variability in phytoplankton biomass with similar periodicity as the spring-neap cycle, making it difficult to observe these phenomena in real-world time series.

Keywords: phytoplankton dynamics, light-limited productivity, dynamic model, Scheldt estuary, temporal variability, turbidity

1. Introduction

Primary production (PP) in estuaries and the corresponding phytoplankton biomass dynamics result from a complex interaction of physical and biological processes (Alpine and Cloern, 1992; Dijkstra et al., 2019). Examples of factors that directly impact PP and phytoplankton biomass dynamics are physical-chemical factors such as river flushing (Filardo and Dunstan, 1985; Liu and de Swart, 2015), temperature (Eppley, 1972), salinity (Lucas et al., 1998), nutrients (Tilman et al., 1982; Cira et al., 2016), and light availability (Sverdrup, 1953; Desmit et al., 2005), or biological factors such as grazing

(Lionard et al., 2005). Due to these complex interactions, we expect both strong high-frequency ($\sim \text{hours}^{-1}\text{-days}^{-1}$) and low-frequency ($\sim \text{weeks}^{-1}\text{-months}^{-1}$) dynamics generated by water flow and seasonality in, for example, water temperature, light-availability, and freshwater discharge.

To acquire insight into the complex interacting processes affecting PP and phytoplankton biomass dynamics, both intensive monitoring campaigns (Maris and Meire, 2016) and a broad range of models have been set up, ranging from numerically-costly three-dimensional models (Chen and Mynett, 2006; Chao et al., 2010), idealized two-dimensional models (McSweeney et al., 2017), one-

dimensional models (Brinkman, 1993; Soetaert and Herman, 1995; Vanderborght et al., 2002; Volta et al., 2016; Liu et al., 2018) to zero-dimensional models (Desmit et al., 2005; Cox et al., 2009).

Due to the high complexity of PP and phytoplankton biomass dynamics, idealized models are particularly well suited because they simplify the interpretation of the model results and reduce computational costs, allowing for long-term simulations and extensive sensitivity analyses. More specifically, often model parameters are considered constant to remove nonlinearities and allow for analytical solution procedures (Dijkstra et al., 2017) instead of computational costly iterative solution methods that tidally resolve the phytoplankton dynamics (Arndt et al., 2011). By using constant model parameters, the impact of temporal variability, which is clearly present in factors affecting PP, is neglected. Only a few studies focus on the individual impact of this, sometimes neglected, high-frequency temporal variability in the factors affecting PP and phytoplankton biomass dynamics. The few studies that do exist are limited to specific examples (Desmit et al., 2005).

Therefore, this study aims to construct a generic, idealized model that allows us to study the impact of temporal fluctuations of individual tidal and solar variables of PP and the corresponding phytoplankton dynamics on an hourly-daily timescale.

We focus on well-mixed, turbid- and nutrient-rich estuarine systems, allowing to analytically compute depth-averaged PP and only consider light-limitation, thereby excluding nutrient depletion and temperature dependence. The biological impact of grazing is implicitly included in a constant mortality rate and calibrated to Chlorophyll-a (Chl-a) observations. Moreover, we assume tide-dominated systems and only include periodic temporal variability due to the tides and solar cycle. We focus on the three important factors altering the light-climate on the hourly-daily timescale: solar irradiance at the water surface, exponential light-extinction coefficient within the water column, and depth of the water body, which changes the ratio of euphotic and mixing depth in a well-mixed estuary.

To model the impact of a changing light climate on phytoplankton biomass growth, we use the Platt light-limitation function (Platt et al., 1980). By assuming a well-mixed estuary, we focus on depth-averaged Platt light-limitation (DAP), allowing for an analytical solution approach. Moreover, to explicitly compute the impact of temporal variability of the individual parameters and correct for the usage of averaged parameter values, we use the analytical, second-order up-scaling method often referred to as the moment approximation. This method is based on a second-order Taylor expansion. In the past, the moment approximation has been successfully applied to

terrestrial primary production (Bolker and Pacala, 1997; Wirtz, 2000). However, terrestrial PP significantly differs from estuarine PP because the light climate in estuarine systems also depends on the tidal variability in depth, suspended sediment concentration, and its corresponding complex temporal variability.

To show the applicability of our approach, we work out two applications in the Scheldt estuary (Belgium). Firstly, we apply our framework to a time-averaged production assuming dynamic equilibrium (application 1). This reflects the situation where phytoplankton biomass is top-down controlled by grazing organisms (e.g., zooplankton), which is often the case in real ecosystems, and remains relatively constant during a large part of the season when primary productivity rates are positive. Such dynamic equilibrium is commonly observed after an initial spring-bloom. Secondly, we utilize our idealized model to study phytoplankton dynamics at the onset of a phytoplankton bloom with unbounded biomass growth (application 2).

In this paper, we first introduce the phytoplankton model and DAP function, the corresponding moment approximation, and the two applications in the Scheldt estuary in Section 2. In Section 3, we present the generic results of the moment approximation and apply these results to our two applications in the Scheldt estuary. Finally, we discuss our results in Section 4 and summarize our conclusions in Section 5.

2. Material and methods

In this section, we first present the depth-integrated model for phytoplankton biomass dynamics and corresponding DAP function Λ that includes our three main parameters of interest: the solar irradiance at the water surface E_0 , exponential light-extinction coefficient k_d , and water depth d . Next, we apply a second-order moment approximation to the DAP function Λ , which forms the basis of our subsequent analysis. Finally, we work out applications 1 and 2 in the Scheldt estuary using our framework and present the corresponding observations. To acquire an analytical solution in application 2, we only include sinusoidal (cf. periodic) temporal variability in E_0 , k_d , and d (see Section 2.4). A conceptual diagram of our approach is presented in Fig. 1.

2.1. Phytoplankton model

To describe PP in a tidal, well-mixed system, we start from the following one-dimensional, differential equation for depth-averaged phytoplankton biomass concentration growth rate (units $\text{kg m}^{-3} \text{s}^{-1}$) (Langdon, 1993; Desmit et al., 2005):

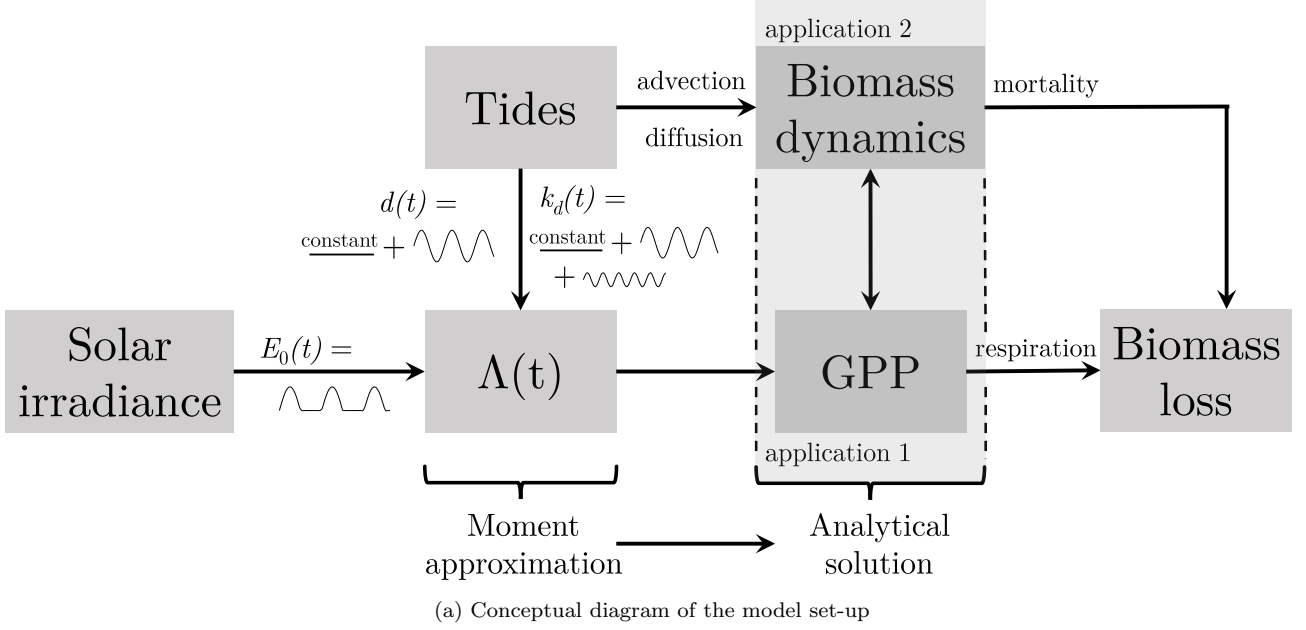


Figure 1: Conceptual diagram of our idealized model. In a well-mixed, light-limited tidal system, gross primary production (GPP) is limited by the DAP function $\Lambda(t)$, which is influenced by solar irradiance and tides. The tides also directly alter biomass dynamics through advection and diffusion in the longitudinal direction. We apply the moment approximation to $\Lambda(t)$ and idealize the temporal variability in E_0 , k_d , and d . This results in an analytical expression that relates temporal variability of GPP and corresponding phytoplankton biomass dynamics to variability in E_0 , k_d , and d . We apply the idealized model to time-averaged GPP in dynamic equilibrium (application 1) and a phytoplankton bloom (application 2) in the Scheldt estuary (Belgium).

$$\begin{aligned}
 & \underbrace{\frac{\partial \tilde{B}(x, t)}{\partial t}}_{\text{phytoplankton biomass growth rate}} \\
 & + \underbrace{\frac{1}{d} \int_0^d \left[\frac{\partial}{\partial x} (\tilde{u} \tilde{B}) + \frac{\partial}{\partial x} \left(K_h \frac{\partial \tilde{B}}{\partial x} \right) \right] dz}_{\text{change in } \tilde{B}(t) \text{ due to advection/diffusion}} \\
 & = \tilde{B} \cdot \left[\underbrace{P_m \cdot \left(\frac{1}{d} \int_0^d \tilde{\Lambda} dz \right)}_{\text{gross primary production (GPP)}} \cdot \underbrace{(1-\rho-m)}_{\substack{\text{respiration} \\ \text{mortality}}} \right], \quad (1)
 \end{aligned}$$

with $\tilde{B}$ the depth-averaged phytoplankton biomass concentration, x the distance from the mouth, z the distance from the water surface in the downward direction, t the time, ρ the respiration and excretion coefficient, m the mortality coefficient, P_m the maximum photosynthetic rate, $\tilde{\Lambda}$ a GPP light-limitation function, $\tilde{u}$ the (vertically homogeneous) water velocities in the longitudinal direction, and K_h the longitudinal eddy diffusivity coefficient.

In Eq. (1), we assume a vertically, well-mixed systems resulting in a depth-independent phytoplankton biomass

concentration $\tilde{B}(x, t)$. Furthermore, we exclude nutrient limitation since we consider primary production in nutrient replete, light-limited systems. Moreover, we also exclude temperature dependence and implicitly included grazing of phytoplankton in the mortality coefficient m . Crucially, we assume balanced-growth conditions: growth and photosynthesis is assumed never to be decoupled on the timescale of our application (i.e., hours-days). All photosynthesis is used for biomass production (Berman-Frank and Dubinsky, 1999). Such decoupling is typical in nutrient limitation situations, which we assume not to occur in the turbid, nutrient replete estuaries under study. Furthermore, we assume that phytoplankton species surviving in turbid conditions are adapted to harvest every photon possible and are thus able to store excess photosynthesized material rather than excrete photosynthetically-derived dissolved organic carbon compounds (PDOC). Consequently, also during the short periods that cells reside in the upper part of the water column where light availability is maximal, growth is balanced.

To model light-limitation, we use the Platt light-limitation function $\tilde{\Lambda}$ (Platt et al., 1980):

$$\tilde{\Lambda} = \left\{ 1 - \exp \left[-\frac{\alpha}{P_m} I \right] \right\}, \quad (2)$$

in which α is the photosynthetic efficiency and I is the

light intensity. Using the Lambert-Beer expression for exponential light attenuation in a water body, Eq. (2) yields:

$$\tilde{\Lambda}(z, t) = \left\{ 1 - \exp \left[-\tilde{\beta} \exp(-\tilde{z}) \right] \right\}, \quad (3)$$

in which $\tilde{\beta}$ and $\tilde{z}$ are dimensionless numbers defined as:

$$\tilde{\beta} = \frac{\alpha E_0}{P_m} \quad \text{and} \quad \tilde{z} = k_d \cdot z. \quad (4)$$

Because the system is assumed to be well-mixed, the total biomass production GPP(t) integrated over the water depth at a fixed location x reads:

$$\text{GPP}(t) = B(t) \cdot P_m \cdot \Lambda(t), \quad (5)$$

with Λ the depth-averaged Platt expression:

$$\Lambda(t) = \frac{1}{d} \int_0^d \tilde{\Lambda}(z, t) dz. \quad (6)$$

For an analytical solution of the DAP, the reader is referred to Appendix A.

In the following section, we apply the moment approximation to $\Lambda(t)$ to study the impact of temporal variability in the individual factors E_0 , k_d , and d and their interactions on PP.

2.2. Moment approximation

Temporal variability in E_0 , k_d , and d impacts phytoplankton dynamics through the time integral of the DAP. This is our starting point to assess the impact of tidal and solar fluctuations on GPP using the moment approximation. In a first step, we add a (further unspecified) time dependence to the variables in the DAP:

$$E_0(t) = \langle E_0 \rangle + E'_0(t), \quad (7)$$

$$k_d(t) = \langle k_d \rangle + k'_d(t), \quad (8)$$

$$d(t) = \langle d \rangle + d'(t), \quad (9)$$

in which the brackets $\langle \rangle$ denote ‘time-averaged value of’. This construction allows us to perform a Taylor expansion

of the DAP. Consequently, we can estimate the impact of temporal variability of the individual parameters on phytoplankton dynamics and their interactions. Also, it is easy to revert to the non-time-dependent result by making $E'_0(t)$, $k'_d(t)$, and $d'(t)$ equal to zero.

Next, we apply a Taylor expansion to the analytic expression of the DAP around the time-averaged values in Eqs. (8) and (9). For a detailed analysis, we refer the reader to Appendix B. Until second-order, this Taylor expansion reads:

$$\begin{aligned} \Lambda(t) \approx \text{mfun}_0(\beta, \lambda) \times \left\{ 1 + \right. \\ + \text{mfun}_\kappa(\beta, \lambda) \cdot [\kappa(t) + \delta(t)] \\ + \text{mfun}_\epsilon(\beta, \lambda) \cdot \epsilon(t) \\ + \text{mfun}_{\kappa^2}(\beta, \lambda) \cdot [\kappa^2(t) + \delta^2(t)] \\ + \text{mfun}_{\epsilon^2}(\beta, \lambda) \cdot \epsilon^2(t) \\ + \text{mfun}_{\epsilon\kappa}(\beta, \lambda) \cdot [\epsilon(t) \cdot \kappa(t) + \epsilon(t) \cdot \delta(t)] \\ \left. + \text{mfun}_{\kappa\delta}(\beta, \lambda) \cdot [\delta(t) \cdot \kappa(t)] \right\}, \end{aligned} \quad (10)$$

in which κ , ϵ , and δ are dimensionless relative fluctuations defined as:

$$\begin{aligned} \epsilon(t) &= \frac{E'_0(t)}{\langle E_0 \rangle}, \quad \kappa(t) = \frac{k'_d(t)}{\langle k_d \rangle}, \\ \delta(t) &= \frac{d'(t)}{\langle d \rangle} \end{aligned} \quad (11)$$

and β and λ are defined as:

$$\beta = \frac{\alpha \langle E_0 \rangle}{P_m} \quad \text{and} \quad \lambda = \langle k_d \rangle \cdot \langle d \rangle. \quad (12)$$

The mfun functions determine the impact of temporal variability in E_0 , k_d , and d on the DAP until second order and are defined in Appendix B (see the R-script *mfun.R* in Supplementary material for an implementation in R). By definition, the function mfun_0 is the DAP without temporal parameter fluctuations. The other terms in Eq. (10) quantify the impact of temporal variability of the individual forcings ($\sim \text{mfun}_\kappa, \text{mfun}_\epsilon, \text{mfun}_{\kappa^2}, \text{mfun}_{\epsilon^2}$) and their interactions ($\sim \text{mfun}_{\epsilon\kappa}, \text{mfun}_{\kappa\delta}$). By construction of Λ , κ and δ come with identical mfun functions:

$$\text{mfun}_\delta = \text{mfun}_\kappa, \quad (13)$$

$$\text{mfun}_{\delta^2} = \text{mfun}_{\kappa^2}, \quad (14)$$

$$\text{mfun}_{\delta\epsilon} = \text{mfun}_{\kappa\epsilon}. \quad (15)$$

The mfun functions are determined by two dimensionless numbers λ and β , which characterize the system under study and have a clear physical interpretation. λ is a measure for the photic properties of the water column. Turbid and deep systems have a large λ , while transparent and shallow systems correspond with a small λ . For fully mixed systems, λ is proportional to the ratio of the mixing depth and euphotic depth, the depth at which the light intensity is one percent of the incident light (Sverdrup, 1953; Kromkamp and Peene, 1995; Desmit et al., 2005). This ratio determines the time phytoplankton spends in the dark and thus affects (vertically integrated) net primary production. Often a critical depth is defined: net positive primary production can only occur when the depth of the mixed layer is less than the critical value (Sverdrup, 1953). Our results confirm that this ratio is an important characteristic of the system, not only controlling the potential for net primary production but also controlling the response of primary production to temporal variability in light climate.

The second dimensionless number β increases with increasing solar irradiance and photosynthetic efficiency. Consequently, for a fixed P_m/α ratio, an equatorial system (more solar irradiance) typically corresponds to a larger β than a system in the northern hemisphere.

In the following, we apply our approach to two case studies in the Scheldt estuary using real observations.

2.3. Application 1: time-averaged GPP

In the first application, we use our idealized model to analyze the impact of temporal fluctuations on time-averaged GPP in case phytoplankton biomass is top-down controlled by grazing organisms (e.g. zooplankton) and can be considered constant, although $\text{GPP} > 0$. Consequently, time-averaged GPP becomes proportional to time-averaged DAP:

$$\langle \text{GPP}(t) \rangle = B \cdot P_m \cdot \langle \Lambda(t) \rangle. \quad (16)$$

We compute $\langle \Lambda(t) \rangle$ using Eq. (10):

$$\begin{aligned} \langle \Lambda(t) \rangle \approx & \text{mfun}_0(\beta, \lambda) \left\{ 1 + \right. \\ & + \text{mfun}_{\kappa^2}(\beta, \lambda) \left[\tilde{\text{Var}}[k_d(t)] + \tilde{\text{Var}}[d(t)] \right] \\ & + \text{mfun}_{\epsilon^2}(\beta, \lambda) \cdot \tilde{\text{Var}}[E_0(t)] \\ & + \text{mfun}_{\epsilon\kappa}(\beta, \lambda) \left[\tilde{\text{Cov}}[E_0(t), k_d(t)] \right. \\ & \quad \left. + \tilde{\text{Cov}}[E_0(t), d(t)] \right] \\ & \left. + \text{mfun}_{\kappa\delta}(\beta, \lambda) \cdot \tilde{\text{Cov}}[k_d(t), d(t)] \right\}, \quad (17) \end{aligned}$$

in which $\tilde{\text{Var}}$ and $\tilde{\text{Cov}}$ are the relative statistical identities variance and covariance, for example:

$$\tilde{\text{Var}}[k_d(t)] = \langle \kappa^2(t) \rangle, \quad (18)$$

$$\tilde{\text{Cov}}[E_0(t), k_d(t)] = \langle \epsilon(t) \cdot \kappa(t) \rangle. \quad (19)$$

As a result of the definitions in Eqs. (8) and (9), the time averages of the $\sim \text{mfun}_\kappa$ - and mfun_ϵ -terms in Eq. (10) disappear in Eq. (17).

Eq. (17) reveals an important interpretation of the second-order mfun functions; variability in k_d , d , and E_0 results in a systematic upward or downward shift in its time-average $\langle \Lambda(t) \rangle$. The second-order mfun functions represent the factors by which the variances and covariances have to be multiplied to calculate the magnitude of this shift. Moreover, the mfun functions define the sign of the shift in $\langle \Lambda(t) \rangle$ and corresponding $\langle \text{GPP} \rangle$. The magnitude is both determined by the average system characteristics (λ , β) and the temporal variability in E_0 , k_d , and d , which define the magnitude of the variance and covariance factors in Eq. (17), and is thus different when considering typical summer or winter conditions.

Therefore, we apply our idealized model to both a summer (10-06-2013 until 02-07-2013) and winter (20-02-2013 until 13-03-2013) case in the Scheldt estuary. Fig. 2 and 3 show the high frequency observations of E_0 , turbidity, and d we use in our first application. The observations were measured in the Scheldt estuary in the brackish region at Kruikebeke (~ 85 km from the mouth). We choose Kruikebeke because here our assumptions (e.g., well-mixed, light-limited) are valid and a long term record of continuous time series of turbidity exists (Cox et al., 2015).

The turbidity time series were obtained using a YSI 6600 multiparameter probe, equipped with an optical turbidity

sensor (YSI6136). Turbidity is expressed in NTU (Nephelometric Turbidity Units). Light from the emitter enters the sample and scatters off particles in the water. The light, scattered at 90 degrees, enters a detector fiber and is measured by a photodiode (YSI, 2017a). The turbidity probe was calibrated in the laboratory using calibration liquid YSI6074 and demineralized water as a zero reference. To compute k_d [m^{-1}] from turbidity [NTU], we used the following expression (Cox et al., 2017):

$$k_d = 0.39(2.1\text{NTU}^{-1} \cdot \text{turb.} - 1.82)^{0.64} \text{ m}^{-1}. \quad (20)$$

Data sets of turbidity and depth at Kruibeke were obtained from waterinfo.be (De Vlaamse Milieumaatschappij; Waterbouwkundig Laboratorium; Maritieme Dienstverlening en Kust, De Vlaamse Waterweg, 2013). We used depth recordings from the tidal gauge at Hemiksem, located approximately 4 km upstream from Kruibeke. Incident irradiance data $E_0(t)$ was obtained from the Royal Meteorological Institute (RMI) of Belgium (RMI, 2013) in Stabroek (~ 25 km from Kruibeke and 50 km from Schellebelle, the other case study site, see below). The sampling interval of E_0 , turbidity, and depth was 10, 15, and 15 min, respectively. A summary of the parameter values corresponding to the data sets is presented in Table 1. Other parameter values used in our calculations are summarized in Table 2. These parameters were based on the literature (Kromkamp and Peene, 1995, 2005; Cox et al., 2010; Maris and Meire, 2016). To assess the accuracy of the moment approximation until second-order terms, we compare the results to the output of a numerical integrator of DAP, making use of the same time series.

2.4. Application 2: phytoplankton bloom

During typically observed phytoplankton spring-blooms we cannot assume dynamic equilibrium of $\tilde{B}(t, x)$ in Eq. (1). In the following, we study the full solution of Eq. (1).

This spatio-temporal differential equation cannot be solved analytically without further assumptions. Therefore, we again focus on a specific location $x = x^*$ and assume that $\tilde{B}(t, x)$ evolves linearly along the estuarine axis near $x = x^*$ and its shape in the longitudinal direction is time-independent on the timescale of our application ($\sim$ days):

$$\tilde{B}(x, t) = B(t)f(x), \quad (21)$$

in which $f(x)$ is a linear function of x . Furthermore, we assume a phase of $-\pi/2$ between the longitudinal velocity

$u(t)$ and the water elevation (cf. d) following van Rijn (2010). For a detailed derivation, the reader is referred to Appendix C. The solution of $B(t)$ yields:

$$B(t) = \tilde{A} e^{-m^* \cdot t + (1-\rho) \cdot P_m \int \Lambda(t) dt} \times e^{\left[\frac{\gamma}{\omega_{M2}} \cdot \cos(\omega_{M2} \cdot t + \Phi_{M2} + \theta) \right]}, \quad (22)$$

with:

$$\tilde{A} = B_0 e^{-(1-\rho) \cdot P_m \int \Lambda(t) dt|_{t=0} - \frac{\gamma}{\omega_{M2}} \cdot \cos(\Phi_{M2} + \theta)}, \quad (23)$$

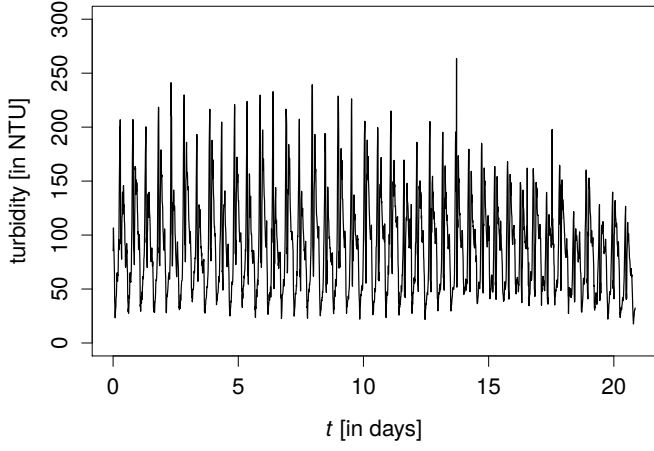
and ω_{M2} the angular frequency corresponding to the semi-diurnal lunar M_2 tide and Φ_{M2} and θ phases corresponding to the idealized time dependence of the water depth d [see below, Eq. (28)]. The coefficients m^* and γ are defined in Appendix C. The integrated loss rate m^* incorporates losses due to grazing, mortality, and residual water currents. γ is a measure of the amplitude of the sinusoidal behavior due to advective transport of phytoplankton biomass [see Eq. (C.1)].

Again, we apply the moment approximation to the solution of $B(t)$ in Eq. (22):

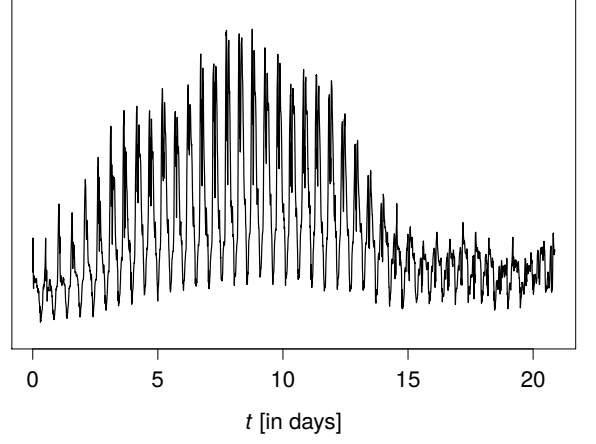
$$\begin{aligned} \int \Lambda(t) dt \approx & \text{mfun}_0 \cdot t \times \left\{ 1 + \right. \\ & + \frac{\text{mfun}_\kappa(\beta, \lambda)}{t} \cdot \int [\kappa(t) + \delta(t)] dt \\ & + \frac{\text{mfun}_\epsilon(\beta, \lambda)}{t} \cdot \int \epsilon(t) \cdot dt \\ & + \frac{\text{mfun}_{\kappa^2}(\beta, \lambda)}{t} \cdot \int [\kappa^2(t) + \delta^2(t)] dt \\ & + \frac{\text{mfun}_{\epsilon^2}(\beta, \lambda)}{t} \cdot \int \epsilon^2(t) dt \\ & + \frac{\text{mfun}_{\epsilon\kappa}(\beta, \lambda)}{t} \cdot \int [\epsilon(t) \cdot \kappa(t) \\ & + \epsilon(t) \cdot \delta(t)] dt \\ & \left. + \frac{\text{mfun}_{\kappa\delta}(\beta, \lambda)}{t} \cdot \int [\delta(t) \cdot \kappa(t)] dt \right\}. \quad (24) \end{aligned}$$

To calculate the integrals in Eq. (24), we use approximate expressions for $\epsilon(t)$, $\kappa(t)$, and $\delta(t)$. We assume that solar irradiance E_0 is given by a truncated sinusoid following Cox et al. (2015):

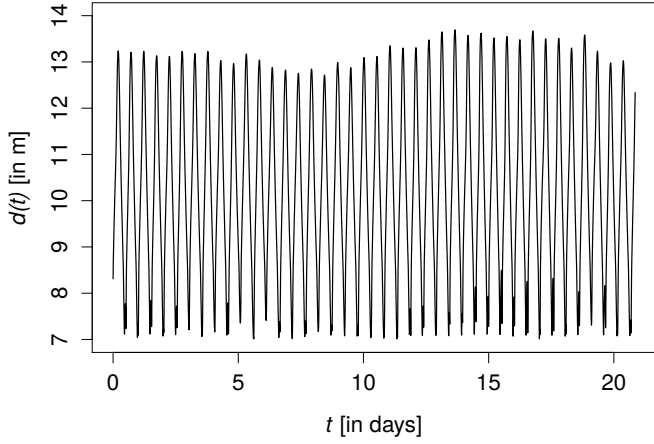
$$E_0(t) = \max(0, a + b \cos(\omega_{S1} t)), \quad (25)$$



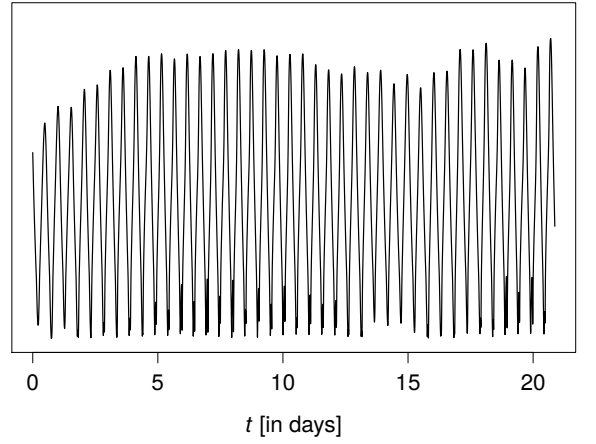
(a) Turbidity in summer



(b) Turbidity in winter



(c) Depth in summer

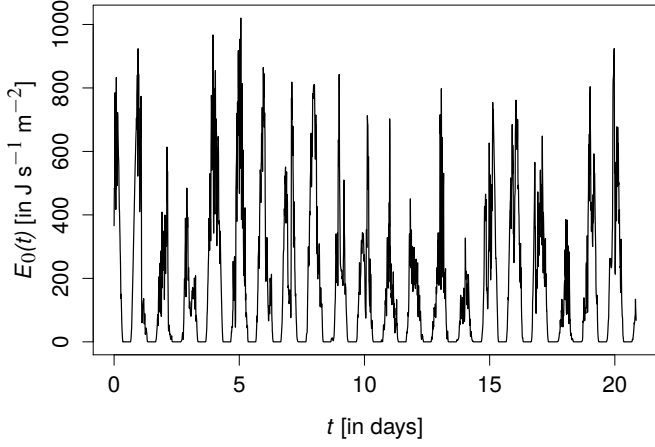


(d) Depth in winter

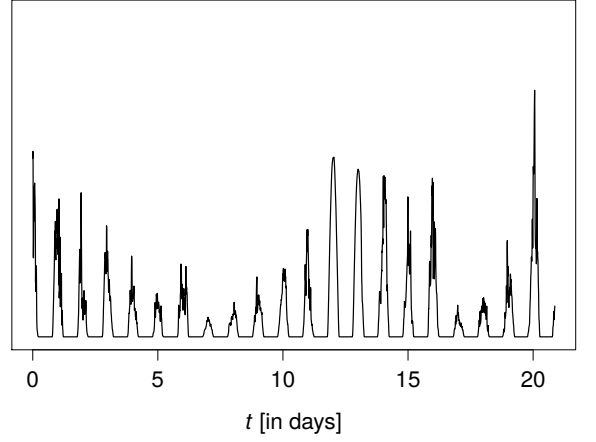
Figure 2: Turbidity and water depth measured in the Scheldt estuary at Kruibeke station (Belgium) in summer and winter. (a)-(b) Turbidity in summer and winter, respectively. (c)-(d) Water depth in summer and winter, respectively.

Table 1: Summarized values corresponding to the time series from Fig. 2 and 3. N is the number of measurements of E_0 , k_d , and d . $\tilde{\text{Var}}$ and $\tilde{\text{Cov}}$ are the relative variance and covariance as defined in Eqs. (18) and (19).

Summer case							
N	3000	$\langle E_0 \rangle$	171 J m ⁻² s ⁻¹	$\tilde{\text{Var}}[E_0]$	1.633	$\tilde{\text{Cov}}[E_0, k_d]$	0.043
λ	92.6	$\langle k_d \rangle$	10.8 m ⁻¹	$\tilde{\text{Var}}[k_d]$	0.099	$\tilde{\text{Cov}}[k_d, d]$	0.036
β	3	$\langle d \rangle$	8.60 m	$\tilde{\text{Var}}[d]$	0.049	$\tilde{\text{Cov}}[E_0, d]$	0.002
Winter case							
N	3000	$\langle E_0 \rangle$	70.0 J m ⁻² s ⁻¹	$\tilde{\text{Var}}[E_0]$	2.704	$\tilde{\text{Cov}}[E_0, k_d]$	-0.021
λ	95.2	$\langle k_d \rangle$	11.1 m ⁻¹	$\tilde{\text{Var}}[k_d]$	0.143	$\tilde{\text{Cov}}[k_d, d]$	0.037
β	1.05	$\langle d \rangle$	8.60 m	$\tilde{\text{Var}}[d]$	0.045	$\tilde{\text{Cov}}[E_0, d]$	-0.013



(a) Solar irradiance in summer



(b) Solar irradiance in winter

Figure 3: Solar irradiance measured at Stabroek (Belgium) in summer and winter. Stabroek is located approximately 25 km from Kruibeke station (a) Solar irradiance in summer. (b) Solar irradiance in winter.

Table 2: Overview of parameter values used in this paper. The values are based on the literature (Kromkamp and Peene, 1995, 2005; Cox et al., 2010; Maris and Meire, 2016).

P_m	5	gC gChl ⁻¹ h ⁻¹	C:Chl	25	gC gChl ⁻¹
α	0.21	gC gChl ⁻¹ h ⁻¹ · (J m ⁻² s ⁻¹) ⁻¹	B_0	775	μg l ⁻¹

in which a and b are further unspecified parameters and ω_{S1} is the diurnal angular frequency. Consequently, we neglect aperiodic temporal variability in E_0 over much more rapid timescales (seconds to minutes, due to, for example, cloud shading) and only include the dominant day-night pattern. We simplify Eq. (25) by only including the first three temporal terms of the Fourier series:

$$E_0(t) = \langle E_0 \rangle + \underbrace{\sum_{n=1}^3 \hat{E}_n \cos(n\omega_{S1}t)}_{E'_0(t)}. \quad (26)$$

Similarly, we only consider the dominant and periodic ω_{M2} and $\omega_{M4} = 2\omega_{M2}$ temporal fluctuations in k_d and d and truncate frequencies larger than M4 (i.e., M6, M8, etc. are neglected) following Chernetsky et al. (2010), Dijkstra et al. (2017), and Horemans et al. (2020):

$$k'_d(t) = \hat{K}_2 \cos(\omega_{M2}t + \Phi_{M2}) + \hat{K}_4 \cos(\omega_{M4}t + \Phi_{M4}), \quad (27)$$

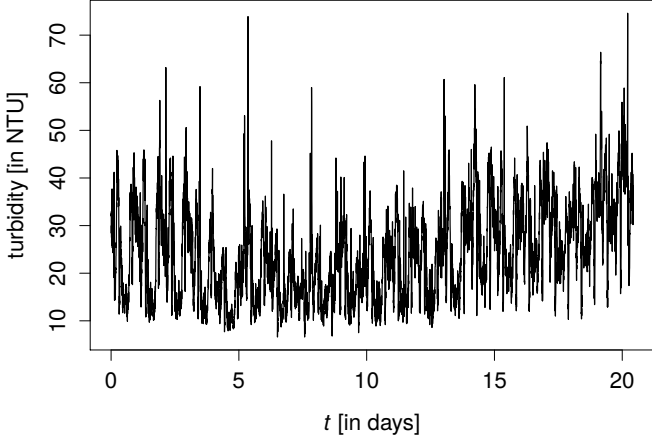
$$d'(t) = \hat{D}_2 \cos(\omega_{M2}t + \Phi_{M2} + \theta), \quad (28)$$

in which Φ_{M2} , Φ_{M4} , θ are the phases and we set $\Phi_{S1} = 0$.

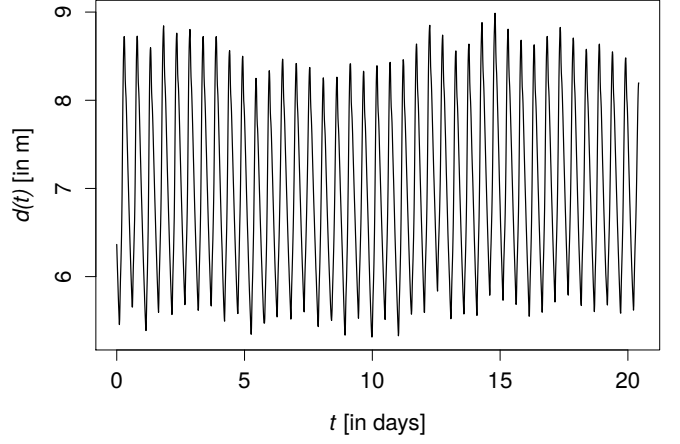
In Appendix D, Eqs. (26)-(28) are fitted to observed time series at our case study site to obtain the amplitudes (i.e., $\hat{E}_n$, $\hat{K}_2$, $\hat{K}_4$, and $\hat{D}_2$) and phases (i.e., Φ_{M2} , Φ_{M4} , and θ). We use time series measured in the Scheldt estuary in the freshwater zone at Schellebelle (~140 km from mouth) during a spring bloom (29-03-2017 until 19-04-2017, Fig. 4). The same methodology and sensors as in application 1 were used. Chl-a concentration was measured using a fluorescence sensor [YSI6025, wavelength 435-470 nm (YSI, 2017b)] with a sampling interval of 5 minutes.

Parameters m^* , γ , and ρ are obtained by fitting Eq. (22) to the observed Chl-a time series. We used a fixed ratio of 25 gC gChl⁻¹ to transform Chl-a concentration to phytoplankton biomass concentration (Maris and Meire, 2016), assuming balanced-growth conditions. Table 3 summarizes the resulting estimated parameters. The order of magnitude of γ and m^* corresponds to the estimated order in Appendix C, i.e., $\mathcal{O}(10^{-1})$ h⁻¹ and $\mathcal{O}(10^{-2})$ h⁻¹, respectively. The order of the fitted value for ρ agrees with values found by Desmit et al. (2005).

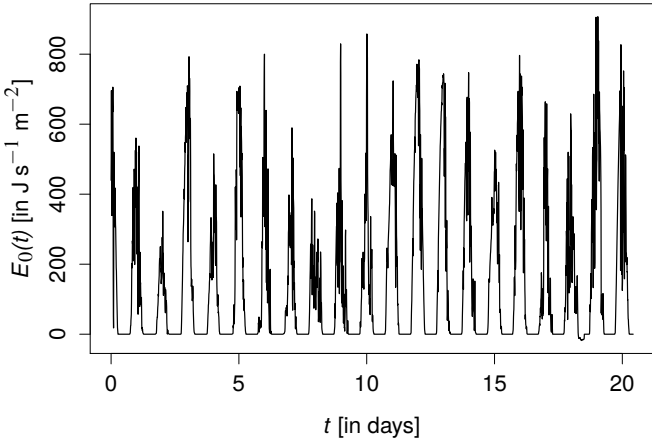
The combination of the moment approximation in Eq. (24) and idealized time-dependence in E_0 , k_d , and d [Eqs. (26)-(28)] allows us to analytically solve the time integral



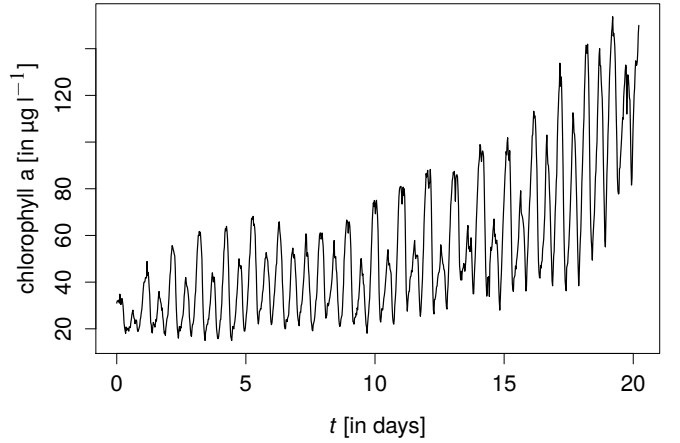
(a) Turbidity in spring



(b) Water depth in spring



(c) Solar irradiance in spring



(d) Chl-a concentration in spring

Figure 4: Turbidity, water depth, and Chl-a concentration measured in the Scheldt estuary at Schellebelle station (Belgium) in spring during a phytoplankton bloom. The solar irradiance is measured at Stabroek (Belgium), located approximately 50 km from Schellebelle. (a) Turbidity in spring. (b) Water depth in spring. (c) Solar irradiance in spring. (d) Chl-a concentration in spring.

Table 3: System parameter estimated by fitting the presumed idealized time dependencies for $E_0(t)$, $k_d(t)$, and $d(t)$ [Eqs. (26)-(28)] and analytical solution of $B(t)$ to the corresponding data sets $k_d(t)$, $E_0(t)$, $d(t)$, and $B(t)$ measured in the Scheldt estuary at Schellebelle (Fig. 4a-4d).

$\text{J m}^{-2} \text{s}^{-1}$		m^{-1}		h^{-1}							
$\hat{E}_1$	142	$\langle k_d \rangle$	4.56	$\langle d \rangle$	4.5 m	ω_{S1}	$\frac{2\pi}{24}$	Φ_{M2}	-3.59	$\langle E_0 \rangle$	$168 \text{ J m}^{-2} \text{s}^{-1}$
$\hat{E}_2$	75.3	$\hat{K}_2$	0.82	$\hat{D}_2$	1.36 m	ω_{M2}	$\frac{2\pi}{12.42}$	Φ_{M4}	-0.253	m^*	0.0834 h^{-1}
$\hat{E}_3$	3.44	$\hat{K}_4$	0.43	ρ	0.837	ω_{M4}	$2 \cdot \omega_{M2}$	θ	-0.30	γ	0.156 h^{-1}

of $\Lambda(t)$ and corresponding analytical solution of $B(t)$ presented in Eq. (22). The main advantage of this approach is that it enables us to directly analyze the propagation of the dominant harmonics in forcings E_0 , k_d , d , and advective water flow into the dynamics of $B(t)$. The analytical solution of $\int \Lambda(t)dt$ is listed in Appendix E. For an implementation of the analytical solution in R, we refer the reader to the R-script *timeIntegrationFunc.R* in Supplementary material.

3. Results

We first show the generic results of the moment approximation by presenting the mfun functions [see Eq. (10)] which translate temporal variability in k_d , E_0 , and d to temporal variability in Λ , GPP, and phytoplankton biomass dynamics. Next, using these mfun functions, we present the results of our two applications in the Scheldt estuary, i.e., time-averaged GPP in dynamic equilibrium (application 1) and a phytoplankton bloom in dynamic non-equilibrium (application 2).

3.1. Moment approximation: the mfun functions

3.1.1. mfun functions of the zeroth- and first-order terms

The zeroth-order mfun₀ function is, by definition, equal to the time-averaged DAP factor $\langle \Lambda \rangle$ in the absence of temporal variability in E_0 , k_d , and d . Fig. 5 shows mfun₀ for various β and λ . mfun₀ ranges from 0 (*maximal light-limitation, no GPP*) to 1 (*no light-limitation, maximal GPP*) and has a simple structure; it increases with increasing β (cf. increasing solar irradiance/ PP efficiency) and decreases with increasing λ (cf. increasing turbidity/depth).

The mfun _{κ} and mfun _{ϵ} functions are plotted in Fig. 6a and 6b, respectively. These first-order functions represent the system-dependent multiplication factors that are required to compute the amplitude of different harmonics in light-climate (cf. Λ), GPP, and corresponding biomass dynamics from the respective amplitudes in E_0 , k_d , and d . mfun _{κ} is negative for every value of λ and β (Fig. 6a), simply reflecting the fact that an increase in k_d (or d) leads to a decrease in $B(t)$. In contrast, mfun _{ϵ} is positive, reflecting the fact that increasing incident irradiance leads to increasing $B(t)$ (Fig. 6b).

3.1.2. mfun functions of the second-order terms

The second-order mfun functions represent the factors by which the variances and covariances have to be multiplied to calculate the magnitude of a systematic upward

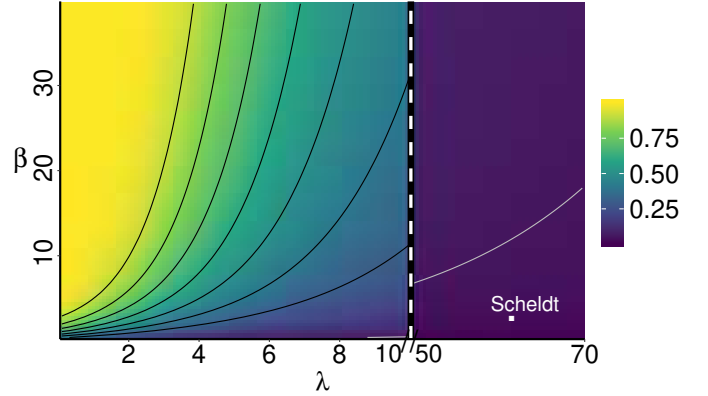


Figure 5: The mfun₀ corresponds to the DAP function Λ in the absence of fluctuations. The averaged positioning of the Scheldt estuary cases described in this paper is also illustrated (i.e. $\lambda \approx 60$, $\beta \approx 3$)

or downward shift in its time-average $\langle \Lambda(t) \rangle$ [Eq. (17)]. They have a more interesting structure (Fig. 7).

Fig. 7b shows that mfun _{ϵ^2} is always negative. In contrast, the sign of the other second-order mfun functions depends on the specific values of λ and β (Fig. 7a, 7c, and 7d). This has a simple interpretation for the time-averaged $\langle \text{GPP} \rangle$ [Eqs. (16) and (17)]. Indeed, temporal variability in E_0 always results in a decrease in $\langle \text{GPP} \rangle$, while variability in light attenuation and depth can lead to both a decrease or an increase in $\langle \text{GPP} \rangle$, depending on the characteristics of the system under study. Here, we assumed that the covariance terms due to E_0 ($\sim \text{mfun}_{\epsilon\kappa}$) are negligible compared to the variance term ($\sim \text{mfun}_{\epsilon^2}$) in Eq. (17). Similarly, for phytoplankton in the exponential growth phase (cf. bloom), second-order temporal variability in E_0 always result in a decrease of the exponential growth, while variability in light attenuation and depth can lead to both a decrease or an increase of the exponential growth. It must be noted that tidal systems for which mfun _{κ^2} is negative ($\lambda \lesssim 5$, Fig. 7a, 7c, and 7d), correspond to shallow and clear systems which can be found in, for example, the Dutch Wadden Sea or the Oosterschelde (Rijkswaterstaat, 2018). These systems often experience nutrient limitation, and thus the results presented here are valid only during periods without nutrient limitation.

The results of the mfun functions show that the propagation of temporal variability in the parameters affecting the light-climate (i.e., E_0 , k_d , and d) to temporal variability in GPP and phytoplankton biomass dynamics may show opposing trends for the different parameters. Moreover, this propagation depends on the time-independent characteristics of the system (i.e., λ and β) and may thus differ for different systems and seasons. In the following sections, we use these results to study our two applications in the Scheldt estuary, covering different seasons.

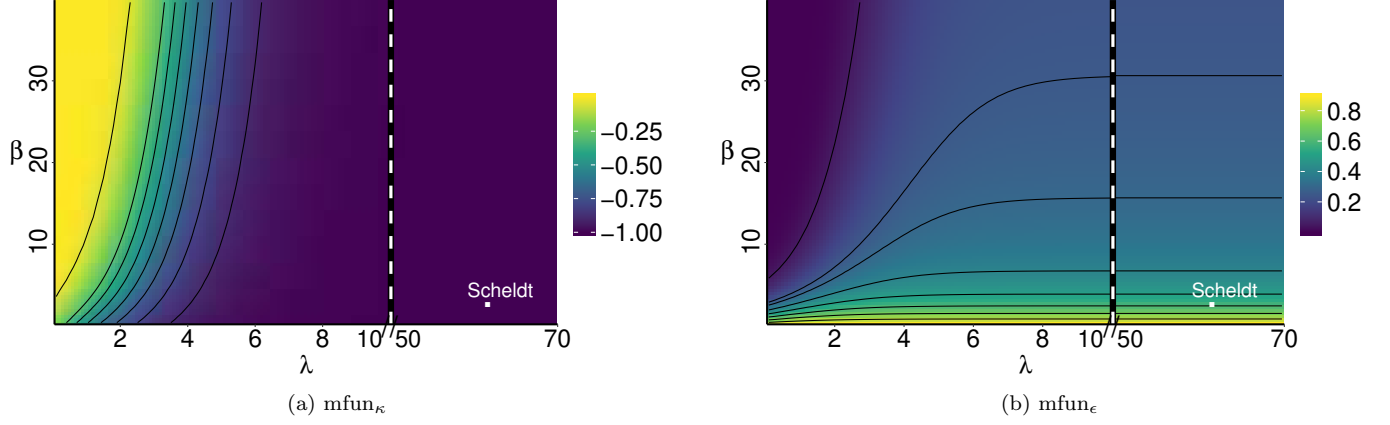


Figure 6: The first-order mfun functions. The averaged positioning of the Scheldt estuary cases described in this paper is also illustrated (i.e., $\lambda \approx 60, \beta \approx 3$). (a) Result of mfun_κ . (b) Result of mfun_ϵ .

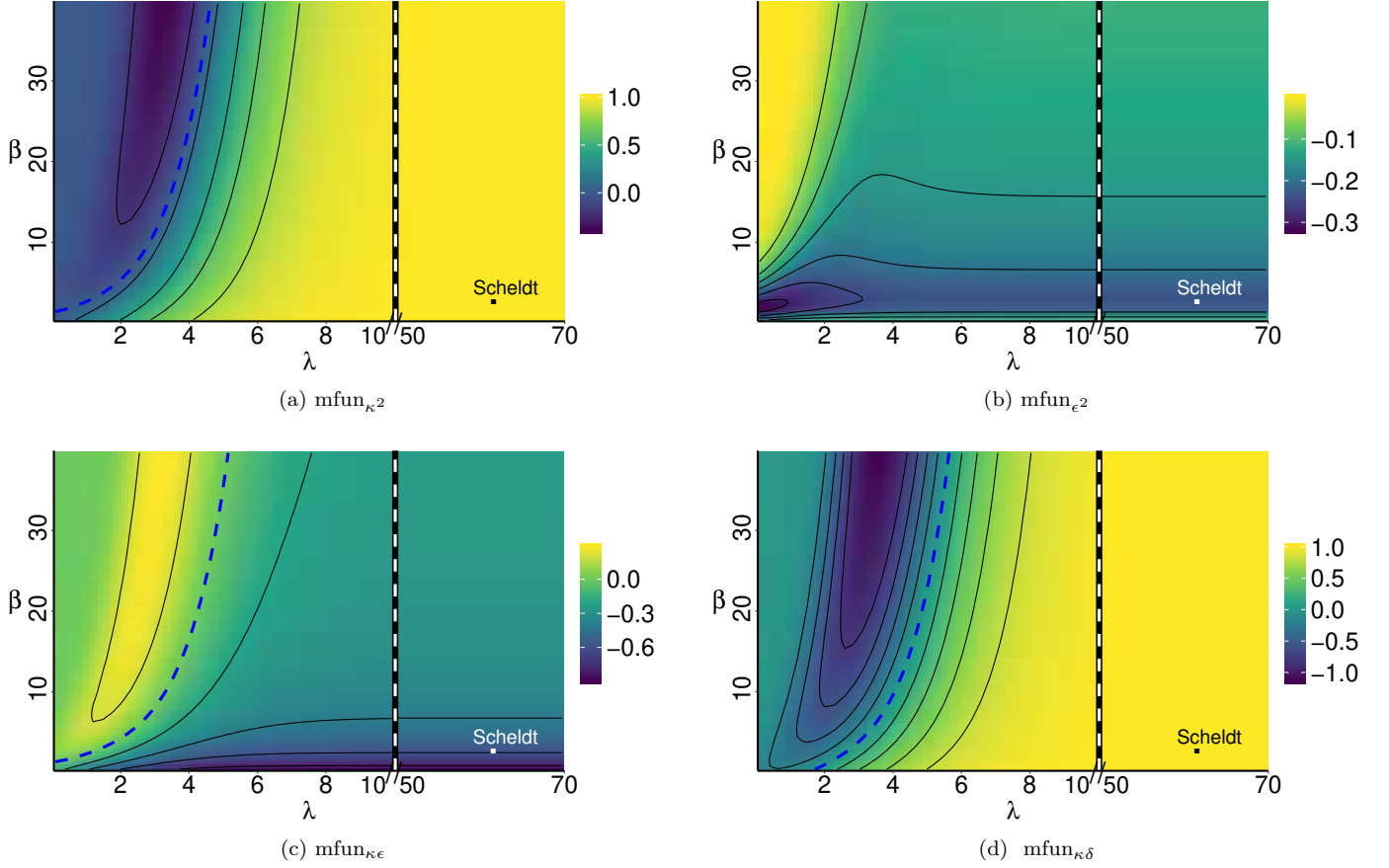


Figure 7: The second-order mfun functions. The averaged positioning of the Scheldt estuary cases described in this paper is also illustrated (i.e., $\lambda \approx 60, \beta \approx 3$). The contour where the mfun function equals zero and changes sign is depicted by a dashed curved line. (a) Result of mfun_{κ^2} . (b) Result of mfun_{ϵ^2} . (c) Result of $\text{mfun}_{\kappa\epsilon}$. (d) Result of $\text{mfun}_{\kappa\delta}$.

3.2. Application 1: time-averaged GPP

In this section, we use the mfun function results from the moment approximation presented in the previous section to study the impact of temporal variability in light-climate (cf. E_0 , k_d , and d) on time-averaged $\langle \text{GPP} \rangle$ in dynamic equilibrium for two cases in the brackish part of the Scheldt estuary. Because we expect different results for different seasons, we analyze both a summer and winter case.

At our relatively deep and turbid case study location, mfun_{κ_2} is always positive (Fig. 7a) and thus temporal variability in k_d and d lead to an increase in $\langle \text{GPP} \rangle$. In contrast, temporal variability in E_0 decreases $\langle \text{GPP} \rangle$ (Fig. 7b).

Fig. 8 shows the results of $\langle \text{GPP} \rangle$ when including temporal variability in all parameters (all var), normalized with $\langle \text{GPP} \rangle$ with time-averaged parameters (i.e., $\langle E_0 \rangle$, $\langle k_d \rangle$, and $\langle d \rangle$) for various integration times T (8.5 h-21 days) using the moment approximation (left) and the numerical integrator (right), applied to a summer (top) and winter (bottom) case. To compute the separate impact of temporal variability in E_0 , k_d , and d on $\langle \text{GPP} \rangle$, we also show the results exclusively including temporal variability in the individual parameters E_0 (E_0 var), k_d (k_d var), and d (d var).

3.2.1. Summer case

In summer, the relative impact of temporal variability on $\langle \text{GPP} \rangle$ is < 10 percent for k_d and d and 10-30 percent for E_0 . Overall, Fig 8 shows good correspondence between the moment approximation and the numerical integrator, even for integration times $T < 24$ h, i.e., the period corresponding to the ω_{S1} angular frequency of temporal variability in E_0 . In this specific summer case study, excluding temporal fluctuations in E_0 , k_d , and d results in an error of approximately 20 percent. Temporal variability in E_0 (E_0 var) has the largest impact on $\langle \text{GPP} \rangle$.

3.2.2. Winter case

Also in the winter case, the moment approximation is in good correspondence with the numerically integrated impact of temporal variability in E_0 , k_d , and d on $\langle \text{GPP} \rangle$, respectively approximately 20-50 percent, 5-20 percent, and < 10 percent. However, we have a slight decrease in accuracy, which is due to the relatively large temporal fluctuations in solar irradiance compared to the averaged solar irradiance in winter. This results in a less accurate approximation by sinusoids of the solar temporal fluctuations [Eq. (26)].

The main difference with the summer case is an increase in the relative importance of fluctuations in k_d . This difference follows from the relative magnitude of temporal variability in k_d (cf. $\text{Var}[k_d(t)]$), which is in winter an order of magnitude larger compared to summer (see Table 1).

Our analysis of the summer and winter case illustrate that the impact of fluctuations in light-climate on $\langle \text{GPP} \rangle$ in dynamic equilibrium may be important, season-dependent, and that a careful analysis based on the observed time series of E_0 , k_d , and d is required.

3.3. Application 2: phytoplankton bloom

In this section, we apply our idealized model to study $B(t)$ in the exponential growth phase. Using our analytical solution of $B(t)$ and corresponding second-order approximation and results of the mfun functions, our approach allows for an extensive analysis by separating the individual impact of temporal variability in E_0 , k_d , and d and their interactions on (exponential) phytoplankton biomass growth. We analyze the time series of the onset of a phytoplankton bloom in spring in the Scheldt estuary in the freshwater region.

Fig. 9 shows both the observed phytoplankton biomass concentration $B(t)$ (cf. Chl-a) and model result using our idealized model [Eq. (22)] with fitted and idealized expressions of temporal fluctuations in E_0 , k_d , and d [Eqs. (26)-(28)]. Our model captures the exponential growth of $B(t)$: both the observed (data) and modeled (all var) $B(t)$ doubles over a time period of approximately two weeks ($\sim 750 \mu\text{g l}^{-1}$ to $\sim 1500 \mu\text{g l}^{-1}$). To study the impact of individual temporal variability on $B(t)$, Fig. 9 shows modeled $B(t)$ in which we only include specific temporal variability. When $B(t)$ is forced by time-invariant $\langle E_0 \rangle$, $\langle k_d \rangle$, and $\langle d \rangle$ (Fig. 9, no fluct.), phytoplankton biomass grows much faster than observed. After two weeks, the phytoplankton biomass when no temporal fluctuations are included is approximately a factor 14 larger than observed. This illustrates the importance of the $\sim t$ terms generated by temporal variability in E_0 , k_d , and d (see Appendix E for a definition of these terms). In particular, this overestimation is due to the absence of temporal variability in E_0 , which again decreases phytoplankton growth. If we solely include temporal variability in E_0 , the modeled phytoplankton biomass is lower than observed (Fig. 9, E_0 var). Including temporal fluctuations in E_0 , but excluding fluctuations in k_d and d , leads to an underestimation of phytoplankton biomass with a factor of 15 after two weeks. In contrast, exclusively including temporal fluctuations in d (Fig. 9, d var) and k_d (Fig. 9, k_d var) results in an overestimation of phytoplankton biomass with respectively a factor of 75 and 34 after two weeks. These results

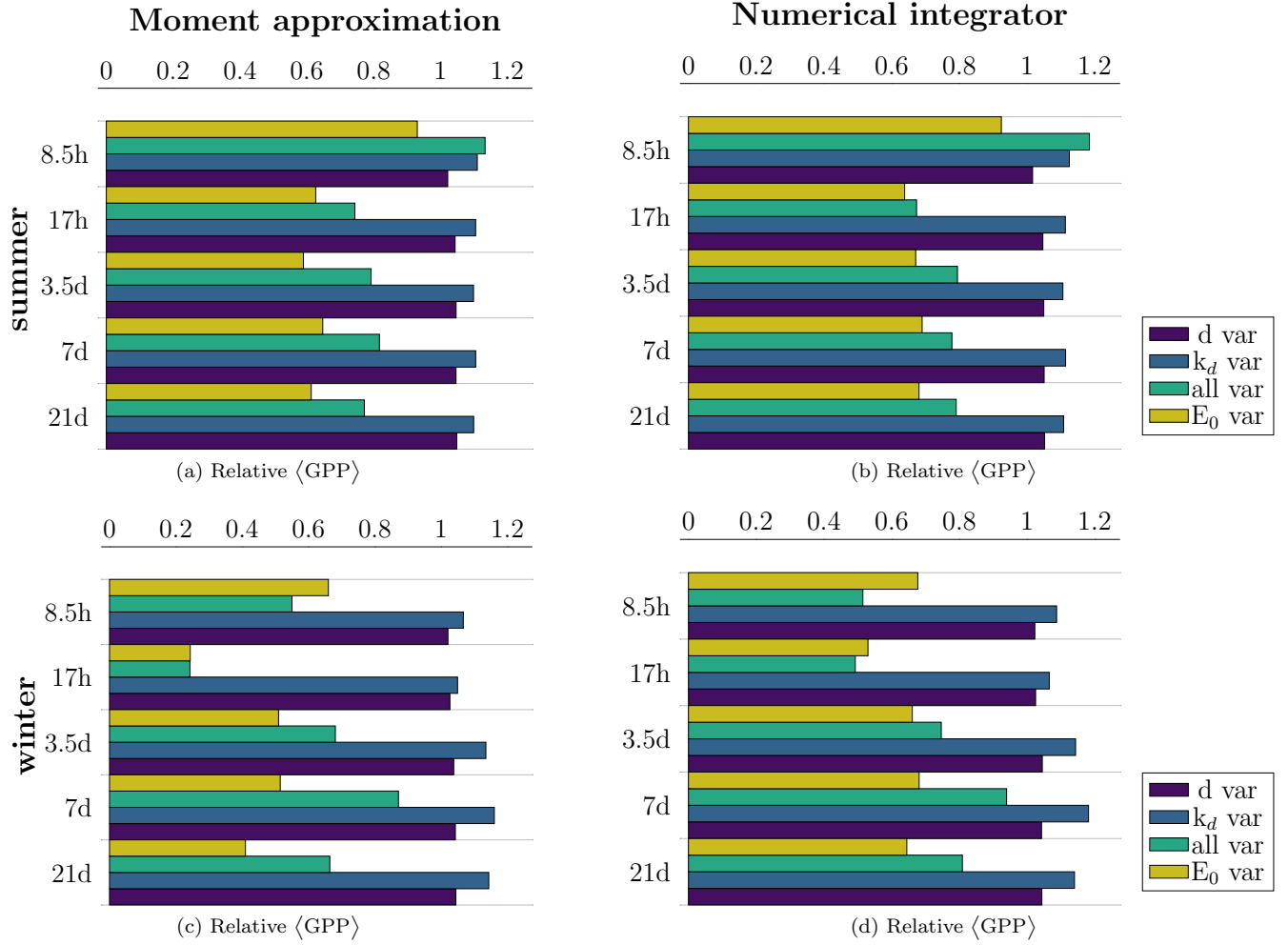


Figure 8: $\langle \text{GPP} \rangle$ in dynamic equilibrium, relative to $\langle \text{GPP} \rangle$ using time-averaged parameters $\langle E_0 \rangle$, $\langle k_d \rangle$, and $\langle d \rangle$ for various integration times (8.5 h-21 days) and seasons (summer and winter) using the moment approximation (left) and a numerical integrator (right). Our framework allows us to compute the impact of temporal variability in an individual parameter on $\langle \text{GPP} \rangle$ (cf. d var, k_d var, and E_0 var) or when temporal variability in all parameters is included (cf. all var). (a) Relative $\langle \text{GPP} \rangle$ in summer for various integration times using the moment approximation. (b) Relative $\langle \text{GPP} \rangle$ in summer for various integration times using a numerical integrator. (c) Relative $\langle \text{GPP} \rangle$ in winter for various integration times using the moment approximation. (d) Relative $\langle \text{GPP} \rangle$ in winter for various integration times using a numerical integrator.

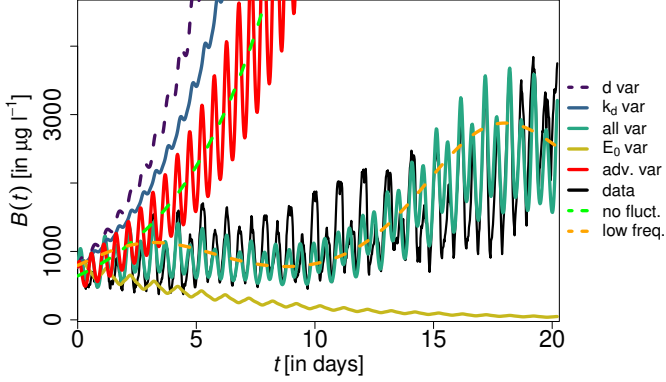


Figure 9: Observed $B(t)$ (data) and model result by including all temporal fluctuations (all var) using our second-order approximation. Our approach allows us to easily identify and exclude individual forcings. The dashed green line (no fluct.) shows the model output for $B(t)$ which is only forced by time-invariant $\langle E_0 \rangle$, $\langle k_d \rangle$, and $\langle d \rangle$. We also show $B(t)$ when we exclusively include temporal fluctuations in d (d var), k_d (k_d var), E_0 (E_0 var), and temporal fluctuations due to advective transport of phytoplankton biomass (adv. var). The orange dashed graph (low freq.) shows $B(t)$ when, on top of the exponential growth, low frequency fluctuations due to interactions between temporal variability in E_0 and k_d and d are included, which results in exponential coefficients $\sim \sin[(\omega_{M2} - 2\omega_{S1})t]$.

are consistent with the results from application 1, but show that the accumulated impact is much larger than expected from the calculations assuming dynamic equilibrium. Finally, temporal fluctuations due to advective transport of phytoplankton biomass do not result in additional exponential growth (Fig. 9, adv. var) when compared to $B(t)$ forced by time-invariant parameters $\langle E_0 \rangle$, $\langle k_d \rangle$, and $\langle d \rangle$ (Fig. 9, no fluct.).

Temporal variability significantly reduces the exponential increase in our case study, which has important consequences, particularly at the onset of phytoplankton blooms. Indeed, during the onset of a phytoplankton bloom, a slight change in growth rate can change the balance with loss terms (e.g., respiration, grazing and flushing), and result in net growth. Thus, other characteristics being equal, a system with fluctuating parameters has an earlier/later onset of the spring phytoplankton bloom than a system without fluctuations. In our case study, temporal fluctuations in E_0 , k_d , and d delay the onset of the bloom by approximately two weeks (see Appendix F for a detailed derivation). Therefore, knowing the magnitude of fluctuations in the forcings E_0 , k_d , and d is at least as important as having a good and realistic estimate of respiration, grazing, and flushing, which in our analysis are included in m^* .

Temporal fluctuations in E_0 , k_d , and d do not only result in additional $\sim t$ terms in the exponential in Eq. (22), but also result in sinusoidal terms. Of particular interest are the non-trivial interaction terms leading to additional low frequency variability in $B(t)$ (Fig. 9, low

freq.). These low frequency fluctuations have a frequency similar to a spring-neap cycle of the horizontal tide (see Appendix E for a definition of these low frequency fluctuations $\sim \sin[(\omega_{M2} - 2\omega_{S1})t]$). This makes it difficult to separate the effects of spring-neap cycles of the horizontal tide from the interaction terms. The model seems to overestimate the impact of interaction terms on $B(t)$. A potential explanation is that the idealized expressions for temporal variability in k_d and d do not include the spring-neap cycle. These results highlight the need for caution when interpreting low-frequency patterns in observed Chl-a time series. As shown, these could both be the result of the spring-neap cycle and interaction terms in the light-limitation factor.

Our analysis of the phytoplankton bloom in spring illustrates that the impact of temporal variability in light-climate and advective water flow on phytoplankton biomass in the exponential growth phase may have crucial consequences: it may result in a 14 times lower phytoplankton biomass after two weeks, delay the onset of the bloom by two weeks, and result in low-frequency temporal variability with similar periodicity as the spring-neap cycle. As in application 1, temporal variability in k_d and d increases, whereas temporal variability in E_0 decreases phytoplankton growth.

4. Discussion

In this section, we first compare our case study results of the impact of temporal variability on time-averaged primary production (application 1) and exponential phytoplankton growth (application 2) to the literature. Next, we discuss the implications of our results for both modelers and experimental scientists. Finally, we discuss the limitations of our approach, focusing on non-local processes and temporal variability in phytoplankton characteristics affecting phytoplankton biomass dynamics.

4.1. The impact of temporal variability on phytoplankton growth

We constructed an idealized model to study the impact of temporal variability in light-climate and advective water flow on time-averaged GPP and phytoplankton biomass dynamics. Our approach allows for an extensive analysis by separating the individual impact of temporal variability in E_0 , k_d , and d and their interactions on time-averaged GPP and (exponential) phytoplankton biomass growth.

In our first application, we found that temporal fluctuations in light-climate impact time-averaged GPP: temporal variability in k_d and d increase, whereas temporal variability in E_0 decrease time-averaged GPP and has a dominant

impact (a decrease up to 50 %, depending on the season). The dominant impact of temporal variability in E_0 complies with the results of Cox et al. (2015). They developed a novel technique to estimate gross primary production using oxygen time series. A core assumption in this method states that gross primary production follows a truncated sinusoidal pattern over time with a 24 h period. Consequently, the method assumes that the main contribution of temporal variability in the forcings is due to temporal variability in E_0 (cf. the 24 h period).

In our second application, we studied the impact of temporal variability in light-climate and advective water flow on phytoplankton biomass dynamics in the exponential growth phase (i.e., phytoplankton bloom). Our results comply with the results of Desmit et al. (2005) who studied the impact of temporal variability in E_0 , k_d , and d within a 40-day time frame for a specific case in the Scheldt estuary. Firstly, the exponential increase in phytoplankton biomass is very sensitive to temporal variability in E_0 , k_d , and d (Fig. 9). Secondly, temporal variability in k_d and d increases the exponential growth, whereas temporal variability in E_0 decreases the exponential growth (Fig. 9). Moreover, the magnitude of the exponential increase is determined by the ratio of time-averaged depth $\langle d \rangle$ and corresponding temporal fluctuations $\langle d'(t) \rangle$, which agrees with our definition of $\delta(t)$ in Eq. (11). Last, a clear link exists between our implementation of advective transport of phytoplankton biomass and the one presented in Desmit et al. (2005). To include advective transport of phytoplankton biomass, Desmit et al. (2005) postulated an additional term in Eq. (1) that is proportional to the derivative of $d(t)$, which agrees with our result in Eq. (C.10) [from Eq. (28) follows that $\partial_t d(t) \sim \sin(t)$]. However, our approach generalizes the work of Desmit et al. (2005) who only studied a specific case in the Scheldt estuary. In contrast to Desmit et al. (2005), our approach is more generic and can be applied to other estuarine well-mixed, light-limited systems. Moreover, our framework allows us to easily compute the impact of temporal fluctuations in the individual parameters and their interactions on phytoplankton growth because we derived an explicit analytical solution for phytoplankton growth and applied a second-order moment approximation.

We thus conclude that our results of the impact of temporal variability on time-averaged GPP and exponential phytoplankton growth comply with results found in the literature and that they allow for a more generic analysis of various well-mixed, light-limited estuaries.

4.2. Implications of our findings for modelers and experimental scientists

Our generic approach may be used to study present-day challenges by both modelers and experimental scientists.

Modelers may use our approach to easily assess the error made by neglecting temporal fluctuations in parameters affecting phytoplankton biomass dynamics. As mentioned in the introduction, various models have been used to model phytoplankton biomass dynamics. Although complex tide-explicit models exist (Arndt et al., 2011), various models often keep certain parameters constant to reduce complexity and allow for fast analytical solution procedures (Dijkstra et al., 2017). Examples are tidally-averaged and/or daily-averaged numerical models to compute estuarine primary production (Brinkman, 1993; Soetaert et al., 1994). The light-extinction coefficient k_d , which is an important parameter in light-limited estuarine systems, is one of the main parameters which contributes to the complexity of PP dynamics because it is affected by suspended particulate matter (SPM) dynamics. Modeling SPM dynamics, even the corresponding large-scale estuarine turbidity maxima, is difficult because it results from a complex concurrence of ETM formation mechanisms [see Burchard et al. (2018) for a recent review]. However, our analysis framework provides a tool to assess the error made by neglecting such complex temporal variability in parameters affecting PP dynamics. As such it can help assess whether a given model with given accuracy and performance is sufficient to realistically simulate and study phytoplankton dynamics. This is particularly important when strong spatial and seasonal gradients in temporal variability in E_0 , k_d (cf. SPM), and d exist. After all, this temporal variability can falsely be attributed (cf. calibrated) to spatial and seasonal variations in intrinsic features of phytoplankton dynamics such as P_m , α , and m . Finally, to use our framework for a model assessment, only basic knowledge on time-average parameter values and corresponding S1, M2, and M4 amplitudes is required.

Our results are also particularly useful for experimental scientists who are interested in data-based estimation of GPP. Our results may partly answer the long-standing question of why bottle incubations underestimate in-situ GPP. Often, bottle incubations are used to estimate GPP in estuaries and coasts. This means that the parameters of the Platt equation α and P_m in Eq. (2) are determined by incubating a sample in the lab at different light intensities (Vegter and De Visscher, 1984; Kromkamp and Peene, 1995). Consequently, the Platt equation needs to be numerically integrated over depth and over time. This requires time series of E_0 , k_d , and d . Whereas time series of incident irradiance are often available, k_d is often estimated as an average on a short time interval during sampling, and linearly interpolated between consecutive sampling (Kromkamp and Peene, 2005). Our results show that in systems with large temporal variability in k_d , this approach leads to a systematic underestimation of time-averaged primary production. Indeed, temporal variability in k_d has a positive impact on GPP (Fig. 8). It has often been found that bottle incubations underestimate primary production when compared to in-site methods. The

reason why this occurs is still poorly understood (Westberry et al., 2012). In addition to so-called ‘bottle effects’ (Swaney et al., 1999) and physiological adaptation effects (Halsey et al., 2010), our results show that large variability in light attenuation can additionally result in an underestimation when this variability is not taken into account.

4.3. Non-local processes and temporal variability in phytoplankton characteristics affecting the phytoplankton dynamics

Although our approach is generically applicable to well-mixed, light-limited estuaries, an extrapolation of our findings to other estuarine cases should be taken with care.

As a first step, we approximated the non-local processes caused by advective and diffusive transport of phytoplankton biomass by a term which is proportional to the derivative of the water depth. As mentioned above, this complies with the postulation presented in Desmit et al. (2005). By applying this idealization, we partly neglected the impact of temporal variability caused by complex interactions between the phytoplankton biomass and the water flow. We assumed that phytoplankton biomass growth is mainly caused by local processes, which complies with the model study carried out by Dijkstra et al. (2019), who focused on the phytoplankton dynamics in the Delaware River Estuary. However, we are aware that this may not be valid in the Scheldt estuary. To correct for complex, non-local interactions between the water flow and phytoplankton biomass, our model can still be used by coupling the model to a hydrodynamical model. By doing so, the impact of individual temporal variability in light-climate on the phytoplankton biomass growth can be investigated, including these complex non-local phytoplankton biomass and water flow interactions, as done by Dijkstra et al. (2019).

Additionally, we focused on temporal variability in parameters affecting the light-climate on an hourly-daily timescale E_0 , k_d , and d and kept most other parameters fixed. For example, we assumed balanced growth conditions and the absence of significant temporal variations in the phytoplankton characteristics on this hourly-daily timescale (cf. P_m , α). In further research, the same approach as presented in this study can be applied assuming temporal variability in the latter parameters. This may cause additional (correlation) terms in the second-order approximation of Λ [Eq. (10)] and thus alter time-averaged GPP and phytoplankton biomass dynamics.

5. Conclusion

We constructed an idealized model to analyze the impact of temporal variability in solar irradiance at the water surface E_0 , exponential light-extinction coefficient k_d , and water depth d on $B(t)$ and corresponding $\langle \text{GPP} \rangle$ in light-limited, vertically well-mixed systems. Apart from providing a full theoretical analysis, our approach allows us to quantify the impact of the temporal variability without a numerical model, to separate the impact of different sources of the temporal variability and their covariance, and it does so for a general light-limited, well-mixed tidal system.

To present the applicability of our idealized model, we applied the model to two cases in the Scheldt estuary. Our results showed that temporal variability in E_0 , k_d , and d can have an important impact on $\langle \text{GPP} \rangle$ in dynamic equilibrium and corresponding phytoplankton dynamics. In the first application, we showed that $\langle \text{GPP} \rangle$ in dynamic equilibrium is mainly impacted by temporal variability in E_0 and results in a 30 percent decrease. In contrast, temporal variability in k_d and d increased $\langle \text{GPP} \rangle$. Furthermore, the results showed a seasonality; in winter, temporal variability in k_d had a larger impact on $\langle \text{GPP} \rangle$ than in summer, due to the larger tidal amplitude in k_d in winter. Finally, our idealized model correctly predicted the order of magnitude of the impact of temporal variability of the individual parameters.

In the second application, we showed that during a phytoplankton bloom, temporal variability significantly contributes to the exponential phytoplankton growth and generates additional low-frequency fluctuations similar to the spring-neap cycle. Moreover, we showed that temporal variability can delay the onset of the phytoplankton bloom by two weeks and can decrease the phytoplankton biomass by a factor 14 after two weeks. Again, our approach allowed us to apply an extensive analysis in which we showed that these low-frequency fluctuations in $B(t)$ are due to covariance of temporal variability in E_0 and k_d , and d .

Appendix A. Analytical solution of DAP

Substitution of $q = \tilde{\beta} \cdot \exp(-k_d z)$ in Eq. (6) allows us to analytically solve the DAP:

$$\frac{1}{d} \int_0^d \tilde{\Lambda}(z) dz = 1 + \frac{1}{\tilde{d}} \left[E_1(\tilde{\beta}) - E_1(\tilde{\beta} \exp(-\tilde{d})) \right], \quad (\text{A.1})$$

in which we used the definition of the exponential integral $E_1(x)$ (Bender and Orszag, 2013):

$$E_1(x) = \int_x^\infty \frac{\exp(-q)}{q} dq \quad (\text{A.2})$$

and with:

$$\tilde{d} = k_d \cdot d. \quad (\text{A.3})$$

Consequently, the DAP is defined by two dimensionless numbers $\tilde{d}$ and $\tilde{\beta}$.

Appendix B. Application of a Taylor expansion to Λ : definition of the mfun functions

Consider a function f which depend on a set of variables $\mathbf{a} = \{k_d, E_0, d\}$. Furthermore, assume that the variables are constructed as a mean value $\langle k_d \rangle, \langle E_0 \rangle, \langle d \rangle$ plus a (small) variation k'_d, E'_0 , and d' , respectively. Consequently, the Taylor expansion at the mean values $\langle k_d \rangle, \langle E_0 \rangle, \langle d \rangle$ until second-order terms yields:

$$\begin{aligned} f(\langle k_d \rangle + k'_d(t), \langle E_0 \rangle + E'_0(t), \langle d \rangle + d'(t)) &\approx f(\langle \mathbf{a} \rangle) \\ &+ \left. \frac{\partial f}{\partial k_d} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} k'_d(t) + \left. \frac{\partial f}{\partial E_0} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} E'_0(t) + \left. \frac{\partial f}{\partial d} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} d'(t) \\ &+ \frac{1}{2} \left. \frac{\partial^2 f}{\partial k_d^2} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} [k'_d(t)]^2 + \frac{1}{2} \left. \frac{\partial^2 f}{\partial E_0^2} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} [E'_0(t)]^2 \\ &+ \frac{1}{2} \left. \frac{\partial^2 f}{\partial d^2} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} [d'(t)]^2 + \left. \frac{\partial^2 f}{\partial k_d \partial E_0} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} k'_d(t) E'_0(t) \\ &+ \left. \frac{\partial^2 f}{\partial k_d \partial d} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} k'_d(t) d'(t) + \left. \frac{\partial^2 f}{\partial d \partial E_0} \right|_{\mathbf{a}=\langle \mathbf{a} \rangle} d'(t) E'_0(t). \end{aligned} \quad (\text{B.1})$$

Application to the DAP using the following property of the exponential integral E_1 (Bender and Orszag, 2013):

$$\frac{dE_1(x)}{dx} = -\frac{\exp[-x]}{x}, \quad (\text{B.2})$$

yields the definitions of the mfun functions presented in Eqs. (B.3)-(B.9).

In the R programming language, the package *expint* can be used to define the mfun functions (see the *R*-script *mfun.R* in Supplementary material).

Appendix C. Solution of phytoplankton biomass concentration

We rewrite Eq. (1) for depth-averaged phytoplankton biomass concentration $\tilde{B}(t)$:

$$\begin{aligned} \frac{\partial \tilde{B}(t, x)}{\partial t} + \underbrace{\frac{1}{d} \int_0^d \left[\frac{\partial}{\partial x} (\tilde{u} \tilde{B}) + \frac{\partial}{\partial x} \left(K_h \frac{\partial}{\partial x} \tilde{B} \right) \right]}_{\text{change in } B(t) \text{ due to transport}} \\ = \tilde{B}(x, t) \cdot [P_m \cdot \Lambda \cdot (1 - \rho) - m]. \end{aligned} \quad (\text{C.1})$$

Scaling of the longitudinal terms in Eq. (C.1) shows that the longitudinal diffusion term is 10^3 times smaller than the longitudinal advection term. To obtain the latter result, we assumed that typical scales for $\tilde{u}$, x , and K_h are 1 m s^{-1} , 10^5 m , and $10^2 \text{ m}^2 \text{ s}^{-1}$, respectively (de Swart et al., 2009). Consequently:

$$\text{change in } \tilde{B}(t) \text{ due to transport} \approx \frac{\partial}{\partial x} \left[\tilde{u}(x, t) \tilde{B}(x, t) \right], \quad (\text{C.2})$$

with $\tilde{u}$ the depth-averaged velocity in the longitudinal direction. This results in:

$$\begin{aligned} \frac{\partial \tilde{B}(t, x)}{\partial t} &= \tilde{B}(x, t) \cdot [P_m \cdot \Lambda \cdot (1 - \rho) - m] \\ &- \frac{\partial}{\partial x} \left[\tilde{u}(x, t) \tilde{B}(x, t) \right]. \end{aligned} \quad (\text{C.3})$$

We need a further simplification to solve this differential equation analytically. The change in phytoplankton biomass concentration due to advection is given by:

$$\begin{aligned} \left. \frac{dB}{dt} \right|_{\text{advection}} &= -\frac{\partial(\tilde{u} \cdot \tilde{B})}{\partial x} \\ &= -\left[\tilde{u} \frac{\partial \tilde{B}}{\partial x} + \tilde{B} \frac{\partial \tilde{u}}{\partial x} \right]. \end{aligned} \quad (\text{C.4})$$

We assume:

$$\tilde{B}(x, t) = B(t) \cdot f(x). \quad (\text{C.5})$$

$$\text{mfun}_0 = \frac{(E_1(\beta) - E_1(e^{-\lambda}\beta))}{\lambda} + 1, \quad (\text{B.3})$$

$$\text{mfun}_{\kappa/\delta} = \frac{1}{\text{mfun}_0} \cdot \left[-e^{\beta(-e^{-\lambda})} - \text{mfun}_0 + 1 \right], \quad (\text{B.4})$$

$$\text{mfun}_\epsilon = \frac{1}{\text{mfun}_0} \cdot \left[\frac{e^{\beta(-e^{-\lambda})} - e^{-\beta}}{\lambda} \right], \quad (\text{B.5})$$

$$\text{mfun}_{\kappa^2/\delta^2} = \frac{1}{\text{mfun}_0} \cdot \left[\frac{\beta\lambda}{2} \left(-e^{\beta(-e^{-\lambda})-\lambda} \right) + e^{\beta(-e^{-\lambda})} + \text{mfun}_0 - 1 \right], \quad (\text{B.6})$$

$$\text{mfun}_{\epsilon^2} = \frac{1}{\text{mfun}_0} \cdot \frac{1 - \beta e^{\beta(-e^{-\lambda})-\lambda} - e^{\beta(-e^{-\lambda})} + e^{-\beta}\beta + e^{-\beta}}{\lambda}, \quad (\text{B.7})$$

$$\text{mfun}_{\epsilon\kappa/\epsilon\delta} = \frac{1}{\text{mfun}_0} \cdot \left[\beta e^{\beta(-e^{-\lambda})-\lambda} - \frac{e^{\beta(-e^{-\lambda})} - e^{-\beta}}{\lambda} \right], \quad (\text{B.8})$$

$$\text{mfun}_{\kappa\delta} = \frac{1}{\text{mfun}_0} \cdot \left[\beta\lambda \left(-e^{\beta(-e^{-\lambda})-\lambda} \right) + e^{\beta(-e^{-\lambda})} + \text{mfun}_0 - 1 \right]. \quad (\text{B.9})$$

Alternatively put, the phytoplankton biomass concentration $\tilde{B}(x, t)$ only scales to the magnitude of the biomass $B(t)$ in time. Here, $B(t)$ is the local carbon biomass concentration at location $x = x^*$ where the Chl-a sensor is deployed. The assumption states that the spatial distribution $f(x)$ of $\tilde{B}(x, t)$ is time-independent. For example, if $f(x)$ is linear, we assume that it stays linear over time. Because, in this paper, we are interested in high-frequency dynamics ($\sim \text{days}^{-1}$), we argue that this assumption is valid. Furthermore, we state that $f(x)$ can be approximated by a linear function (first-order Taylor expansion); We argue that the impact due to advection is a local phenomenon near the location of the Chl-a sensor x^* :

$$\frac{\partial \tilde{B}(x, t)}{\partial x} \approx B(t) \cdot \left. \frac{df(x)}{dx} \right|_{x=x^*}. \quad (\text{C.6})$$

Similarly, we assume:

$$\frac{\partial \tilde{u}(x, t)}{\partial x} \approx u(t) \cdot \left. \frac{dg(x)}{dx} \right|_{x=x^*}, \quad (\text{C.7})$$

with $u(t)$ the water velocity in the x -direction towards the mouth. Furthermore, we assume that the water velocity $u(t)$ mainly consists of a subtidal and an M2 tidal constituent:

$$u(t) = v_0 + A_v \cdot \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta), \quad (\text{C.8})$$

in which $v_0 > 0$ is the residual velocity and A_v is the amplitude of the M2 tidal constituent. To obtain Eq. (C.8),

we assumed a phase shift between the horizontal tide (current velocity) and vertical tide (water level d) of approximately $-\pi/2$ (van Rijn, 2010). If this is not valid, the results can be generalized using an additional phase shift. This is out of the scope of this paper. In Eq. (C.8), A_v has the same sign as $\hat{D}_2$. If we define A_v as being positive, we have:

$$u(t) = v_0 + |A_v| \cdot \text{sign}(\hat{D}_2) \cdot \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta), \quad (\text{C.9})$$

with $\text{sign}()$ the sign function.

Combining Eqs. (C.4), (C.6), (C.7), and (C.9), the change in phytoplankton biomass concentration due to advection yields:

$$\left. \frac{dB}{dt} \right|_{\text{advection}} = - \left[\tilde{v}_0^* + \tilde{\gamma} \cdot \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta) \right] \cdot B(t), \quad (\text{C.10})$$

in which:

$$\tilde{\gamma} = |A_v| \cdot \text{sign}(\hat{D}_2) \cdot \left[g(x) \left. \frac{df(x)}{dx} \right|_{x=x^*} + f(x) \left. \frac{dg(x)}{dx} \right|_{x=x^*} \right], \quad (\text{C.11})$$

$$\tilde{v}_0^* = v_0 \cdot \left[g(x) \left. \frac{df(x)}{dx} \right|_{x=x^*} + f(x) \left. \frac{dg(x)}{dx} \right|_{x=x^*} \right]. \quad (\text{C.12})$$

Filling in the latter results into the differential equation for change in $B(x, t)$ in Eq. (C.3) at $x = x^*$, we acquire:

$$\begin{aligned} \frac{\partial B(t)}{\partial t} = & B(t) \cdot [P_m \cdot \Lambda \cdot (1 - \rho) - m] + \\ & B(t) \cdot \left[-v_0^* - \gamma \cdot \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta) \right], \end{aligned} \quad (\text{C.13})$$

with:

$$\gamma = |A_v| \text{sign}(\hat{D}_2) \cdot \left[\frac{df(x)}{dx} \Big|_{x=x^*} + \frac{dg(x)}{dx} \Big|_{x=x^*} \right], \quad (\text{C.14})$$

$$v_0^* = v_0 \cdot \left[\frac{df(x)}{dx} \Big|_{x=x^*} + \frac{dg(x)}{dx} \Big|_{x=x^*} \right], \quad (\text{C.15})$$

in which we used $f(x)|_{x=x^*} = 1$ and $g(x)|_{x=x^*} = 1$. The term due to advection in Eq. (C.13) is linear to $B(t)$. Consequently, this differential equation can be solved analytically. Because the v_0^* -term results in an $\exp(v_0^* \cdot t)$ factor, we define the mortality m^* as:

$$m^* = m + v_0^*. \quad (\text{C.16})$$

In the following, we estimate the order of magnitude of γ , v_0^* , and m^* at our case study site. In the Scheldt estuary, the water is pushed several kilometers $\sim \mathcal{O}(1)$ up and down over the longitudinal direction every approximately 12.4 h. So:

$$\begin{aligned} \int_0^{6.2h} A_v \sin(M2 \cdot t) dt & \sim \mathcal{O}(1), \\ \Rightarrow A_v & \sim \mathcal{O}(1) \text{ km h}^{-1}. \end{aligned} \quad (\text{C.17})$$

Furthermore, near our case study site, the phytoplankton biomass concentration increases with a factor 1-10 $\sim \mathcal{O}(1)$ over a longitudinal distance of approximately 10 km (Maris and Meire, 2016). Consequently:

$$\frac{df(x)}{dx} \sim \frac{\mathcal{O}(1)}{10 \text{ km}} \sim \mathcal{O}(10^{-1}) \text{ km}^{-1}. \quad (\text{C.18})$$

Therefore, assuming that the longitudinal gradient in velocity u is negligible ($df/dx \gg dg/dx$), we have:

$$\gamma \approx A_v \cdot \frac{df(x)}{dx} \sim \mathcal{O}(10^{-1}) \text{ h}^{-1}. \quad (\text{C.19})$$

Similarly, if we assume $v_0 \sim \mathcal{O}(10^{-1}) \text{ km h}^{-1}$:

$$v_0^* \sim \mathcal{O}(10^{-2}) \text{ h}^{-1}. \quad (\text{C.20})$$

Consequently, if we assume $m \sim \mathcal{O}(10^{-3}) \text{ h}^{-1}$ (Desmit et al., 2005), we have:

$$m^* \sim \mathcal{O}(10^{-2}) \text{ h}^{-1}. \quad (\text{C.21})$$

Appendix D. Application 2: data fit

Application of data fits using the presumed expressions:

$$E'_0(t) = \sum_{n=1}^3 \hat{E}_n \cos(n\omega_{S1}t), \quad (\text{D.1})$$

$$k'_d(t) = \hat{K}_2 \cos(\omega_{M2}t + \Phi_{M2}) + \hat{K}_4 \cos(\omega_{M4}t + \Phi_{M4}), \quad (\text{D.2})$$

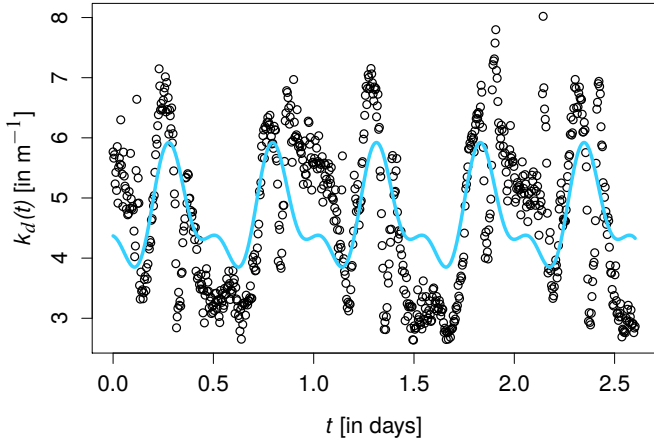
$$d'(t) = \hat{D}_2 \cos(\omega_{M2}t + \Phi_{M2} + \theta), \quad (\text{D.3})$$

to a subset of the data sets of E_0 , k_d , and d at Schellebelle results in Fig. D.10a, D.10b, and D.10c, respectively. We used the *nls()* function of the R programming language to obtain these data fits.

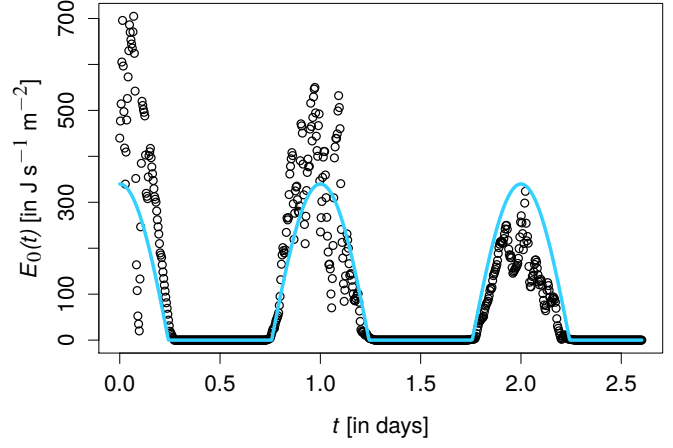
We used subsets to diminish the impact of (low-frequency) temporal variability we did not include in the idealized time dependence in Eqs. (D.1)-(D.3). For example, we excluded long term periodic temporal fluctuations (e.g., spring-neap) and aperiodic temporal fluctuations (e.g., impact of clouds).

Appendix E. Time integration of $\Lambda(t)$

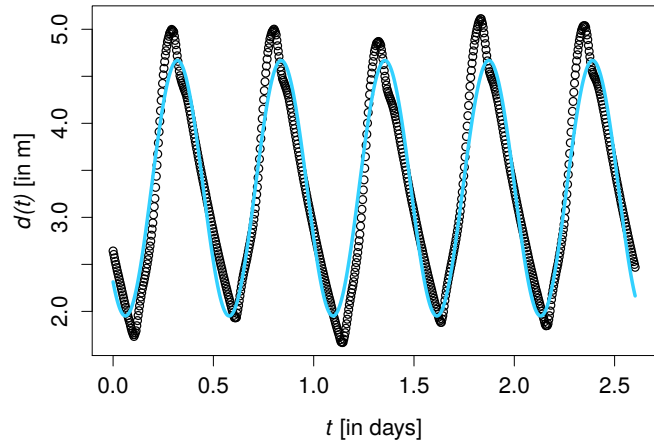
For an implementation in R, we refer the reader to the R-script *timeIntegrationFunc.R* in Supplementary material.



(a) $k_d(t)$ data fit



(b) $E_0(t)$ data fit



(c) $d(t)$ data fit

Figure D.10: The data fit of the postulated time dependencies to the data sets measured in the Scheldt estuary at Schellebelle (Belgium). (a) The subset of $k_d(t)$ and the corresponding data fit. (b) The subset of $E_0(t)$ and the corresponding data fit. (c) The subset of $d(t)$ and the corresponding data fit.

$$\int \kappa(t) dt = \frac{1}{\langle k_d \rangle} \left[\frac{\hat{K}_2 \sin(\omega_{M2} t + \Phi_{M2})}{\omega_{M2}} + \frac{\hat{K}_4 \sin(\omega_{M4} t + \Phi_{M4})}{\omega_{M4}} \right] \quad (E.1)$$

$$\int \epsilon(t) dt = \frac{1}{\langle E_0 \rangle} \left[\frac{\hat{E}_1 \sin(\omega_{S1} t)}{\omega_{S1}} + 1/2 \frac{\hat{E}_2 \sin(2\omega_{S1} t)}{\omega_{S1}} + 1/3 \frac{\hat{E}_3 \sin(3\omega_{S1} t)}{\omega_{S1}} \right] \quad (E.2)$$

$$\int \delta(t) dt = \frac{1}{\langle d \rangle} \left[\frac{\hat{D}_2 \sin(\omega_{M2} t + \Phi_{M2} + \theta)}{\omega_{M2}} \right] \quad (E.3)$$

$$\begin{aligned} \int \epsilon^2(t) dt = & \frac{1}{\langle E_0 \rangle^2} \left[1/2 \hat{E}_1^2 t + 1/2 \hat{E}_2^2 t + 1/2 \hat{E}_3^2 t \right. \\ & + \frac{(\hat{E}_2 \hat{E}_1 + \hat{E}_3 \hat{E}_2) \sin(\omega_{S1} t)}{\omega_{S1}} \\ & + 1/2 \frac{(\hat{E}_2 \hat{E}_1^2 + \hat{E}_3 \hat{E}_1) \sin(2\omega_{S1} t)}{\omega_{S1}} \\ & + 1/3 \frac{\hat{E}_2 \hat{E}_1 \sin(3\omega_{S1} t)}{\omega_{S1}} \\ & + 1/5 \frac{\hat{E}_3 \hat{E}_2 \sin(5\omega_{S1} t)}{\omega_{S1}} \\ & + 1/12 \frac{\hat{E}_3^2 \sin(6\omega_{S1} t)}{\omega_{S1}} \\ & \left. + 1/4 \frac{(\hat{E}_3 \hat{E}_1 + 1/2 \hat{E}_2^2) \sin(4\omega_{S1} t)}{\omega_{S1}} \right] \quad (E.4) \end{aligned}$$

$$\begin{aligned} \int \kappa^2(t) dt = & \frac{1}{\langle k_d \rangle^2} \left[1/4 \frac{\hat{K}_2^2 \sin(2\omega_{M2} t + 2\Phi_{M2})}{\omega_{M2}} \right. \\ & + 1/2 \hat{K}_2^2 t \\ & + \frac{\hat{K}_2 \hat{K}_4 \sin((\omega_{M2} - \omega_{M4}) t + \Phi_{M2} - \Phi_{M4})}{\omega_{M2} - \omega_{M4}} \\ & + \frac{\hat{K}_2 \hat{K}_4 \sin((\omega_{M2} + \omega_{M4}) t + \Phi_{M2} + \Phi_{M4})}{\omega_{M2} + \omega_{M4}} \\ & + 1/4 \frac{\hat{K}_4^2 \sin(2\omega_{M4} t + 2\Phi_{M4})}{\omega_{M4}} \\ & \left. + 1/2 \hat{K}_4^2 t \right] \quad (E.5) \end{aligned}$$

$$\begin{aligned} \int \delta^2(t) dt = & \frac{1}{\langle d \rangle^2} \left[\frac{\hat{D}_2^2 1/2 \cos(\omega_{M2} t + \Phi_{M2} + \theta)}{\omega_{M2}} \right. \\ & \times \sin(\omega_{M2} t + \Phi_{M2} + \theta) \\ & \left. + \hat{D}_2^2 \frac{\omega_{M2} t + \Phi_{M2} + \theta}{2\omega_{M2}} \right] \quad (E.6) \end{aligned}$$

$$\begin{aligned} \int \delta(t) \epsilon(t) dt = & \frac{\hat{D}_2}{\langle E_0 \rangle \langle d \rangle} \left[\right. \\ & 1/2 \frac{\hat{E}_1 \sin((\omega_{M2} - \omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} - \omega_{S1}} \\ & + 1/2 \frac{\hat{E}_1 \sin((\omega_{M2} + \omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} + \omega_{S1}} \\ & + 1/2 \frac{\hat{E}_2 \sin((\omega_{M2} - 2\omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} - 2\omega_{S1}} \\ & + 1/2 \frac{\hat{E}_2 \sin((\omega_{M2} + 2\omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} + 2\omega_{S1}} \\ & + 1/2 \frac{\hat{E}_3 \sin((\omega_{M2} - 3\omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} - 3\omega_{S1}} \\ & \left. + 1/2 \frac{\hat{E}_3 \sin((\omega_{M2} + 3\omega_{S1}) t + \Phi_{M2} + \theta)}{\omega_{M2} + 3\omega_{S1}} \right] \quad (E.7) \end{aligned}$$

$$\begin{aligned} \int \kappa(t) \delta(t) dt = & \frac{1}{\langle k_d \rangle \langle d \rangle} \left[\hat{D}_2 \left(1/2 \hat{K}_2 \cos(\theta) t \right. \right. \\ & + 1/4 \frac{\hat{K}_2 \sin(2\omega_{M2} t + 2\Phi_{M2} + \theta)}{\omega_{M2}} \\ & + 1/2 \frac{\hat{K}_4 \sin((\omega_{M2} - \omega_{M4}) t + \Phi_{M2} - \Phi_{M4} + \theta)}{\omega_{M2} - \omega_{M4}} \\ & \left. \left. + 1/2 \frac{\hat{K}_4 \sin((\omega_{M2} + \omega_{M4}) t + \Phi_{M2} + \Phi_{M4} + \theta)}{\omega_{M2} + \omega_{M4}} \right) \right] \quad (E.8) \end{aligned}$$

$$\begin{aligned}
\int \kappa(t) \epsilon(t) dt &= \frac{1}{\langle E_0 \rangle \langle k_d \rangle} \left[\right. \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_1 \sin((\omega_{M2} - \omega_{S1})t + \Phi_{M2})}{\omega_{M2} - \omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_1 \sin((\omega_{M2} + \omega_{S1})t + \Phi_{M2})}{\omega_{M2} + \omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_2 \sin((\omega_{M2} - 2\omega_{S1})t + \Phi_{M2})}{\omega_{M2} - 2\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_2 \sin((\omega_{M2} + 2\omega_{S1})t + \Phi_{M2})}{\omega_{M2} + 2\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_3 \sin((\omega_{M2} - 3\omega_{S1})t + \Phi_{M2})}{\omega_{M2} - 3\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_2 \hat{E}_3 \sin((\omega_{M2} + 3\omega_{S1})t + \Phi_{M2})}{\omega_{M2} + 3\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_4 \hat{E}_1 \sin((\omega_{M4} - \omega_{S1})t + \Phi_{M4})}{\omega_{M4} - \omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_4 \hat{E}_1 \sin((\omega_{M4} + \omega_{S1})t + \Phi_{M4})}{\omega_{M4} + \omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_4 \hat{E}_2 \sin((\omega_{M4} - 2\omega_{S1})t + \Phi_{M4})}{\omega_{M4} - 2\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_4 \hat{E}_2 \sin((\omega_{M4} + 2\omega_{S1})t + \Phi_{M4})}{\omega_{M4} + 2\omega_{S1}} \\
&+ 1/2 \frac{\hat{K}_4 \hat{E}_3 \sin((\omega_{M4} - 3\omega_{S1})t + \Phi_{M4})}{\omega_{M4} - 3\omega_{S1}} \\
&\left. + 1/2 \frac{\hat{K}_4 \hat{E}_3 \sin((\omega_{M4} + 3\omega_{S1})t + \Phi_{M4})}{\omega_{M4} + 3\omega_{S1}} \right] \quad (E.9)
\end{aligned}$$

Appendix F. The impact of temporal variability in light-climate on the onset of a phytoplankton bloom

We estimate the impact of temporal fluctuations in E_0 , k_d , and d on the onset of a phytoplankton bloom using our idealized model. After two weeks, the modeled phytoplankton biomass when no fluctuations would be present is approximately a factor 14 larger than observed.

Using Eqs. (22) and (24), we estimate the difference in β which is required to obtain the same difference in phytoplankton biomass after 14 days:

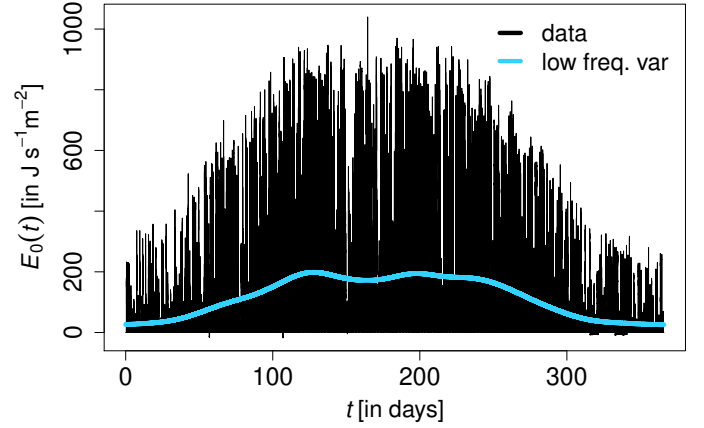


Figure F.11: Observed solar irradiance in 2016 at Stabroek (data) and corresponding low frequency temporal variation (low freq. var).

$$\begin{aligned}
\frac{B_{\text{no fluct.}}(t = 14 \text{ days}, \beta + \Delta\beta)}{B_{\text{no fluct.}}(t = 14 \text{ days}, \beta)} &= 14, \\
\Rightarrow \text{mfun}_0(\lambda, \beta + \Delta\beta) - \text{mfun}_0(\lambda, \beta) &= \\
&= \frac{1}{(1 - \rho)P_m} \frac{\log 14}{14 \text{ days}}, \\
\Rightarrow \Delta\beta &\approx 1.3. \quad (F.1)
\end{aligned}$$

Using Eq. (12), we compute the corresponding difference in solar irradiance $\Delta \langle E_0 \rangle \approx 31 \text{ J s}^{-1} \text{ m}^{-2}$. We use time series of E_0 observed in 2016 at Stabroek (Fig. F.11) to compute the number of days required to increase the (daily-averaged) solar irradiance E_0 (low freq. var in Fig. F.11) by $31 \text{ J s}^{-1} \text{ m}^{-2}$ in April, which equals approximately two weeks. Consequently, temporal variability in light-climate can delay the onset of a phytoplankton bloom by approximately two weeks.

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References

- Alpine, A.E., Cloern, J.E., 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography* 37, 946–955. URL: <http://doi.wiley.com/10.4319/lo.1992.37.5.0946>, doi:10.4319/lo.1992.37.5.0946.
- Arndt, S., Lacroix, G., Gypens, N., Regnier, P., Lancelot, C., 2011. Nutrient dynamics and phytoplankton development along an estuary-coastal zone continuum: A model study. *Journal of Marine Systems* 84, 49–66. doi:10.1016/j.jmarsys.2010.08.005.
- Bender, C.M., Orszag, S.A., 2013. Advanced mathematical methods for scientists and engineers I: Asymptotic methods and perturbation theory. Springer Science & Business Media.
- Berman-Frank, I., Dubinsky, Z., 1999. Balanced growth in aquatic plants: Myth or reality? Phytoplankton use the imbalance between carbon assimilation and biomass production to their strategic advantage. *BIOSCIENCE* 49, 29–37. URL: www.jstor.org/stable/10.1525/bisi.1999.49.1.29?seq=1, doi:10.2307/1313491.
- Bolker, B., Pacala, S.W., 1997. Using Moment Equations to Understand Stochastically Driven Spatial Pattern Formation in Ecological Systems. *Theoretical Population Biology* 52, 179–197. URL: <https://www.sciencedirect.com/science/article/pii/S0040580997913319>, doi:10.1006/TPBI.1997.1331.
- Brinkman, A.G., 1993. Biological processes in the EcoWasp ecosystem model. Technical Report. Institute for Forestry and Nature Research. Wageningen. URL: <https://library.wur.nl/WebQuery/wurpubs/494560>.
- Burchard, H., Schuttelaars, H.M., Ralston, D.K., 2018. Sediment Trapping in Estuaries. *Annual Review of Marine Science* 10, 371–395. URL: <http://www.annualreviews.org/doi/10.1146/annurev-marine-010816-060535>, doi:10.1146/annurev-marine-010816-060535.
- Chao, X., Jia, Y., Shields, F.D., Wang, S.S.Y., Cooper, C.M., 2010. Three-dimensional numerical simulation of water quality and sediment-associated processes with application to a Mississippi Delta lake. *Journal of Environmental Management* 91, 1456–1466. URL: <https://www.sciencedirect.com/science/article/pii/S030147971000037X>, doi:10.1016/J.JENVMAN.2010.02.009.
- Chen, Q., Mynett, A.E., 2006. Modelling algal blooms in the Dutch coastal waters by integrated numerical and fuzzy cellular automata approaches. *Ecological Modelling* 199, 73–81. URL: <https://www.sciencedirect.com/science/article/pii/S030438000600281X>, doi:10.1016/J.ECOLMODEL.2006.06.014.
- Chernetsky, A.S., Schuttelaars, H.M., Talke, S.A., 2010. The effect of tidal asymmetry and temporal settling lag on sediment trapping in tidal estuaries. *Ocean Dynamics* 60, 1219–1241. URL: <http://link.springer.com/10.1007/s10236-010-0329-8>, doi:10.1007/s10236-010-0329-8.
- Cira, E.K., Paerl, H.W., Wetz, M.S., 2016. Effects of Nitrogen Availability and Form on Phytoplankton Growth in a Eutrophied Estuary (Neuse River Estuary, NC, USA). *PLOS ONE* 11. URL: <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0160663>, doi:10.1371/journal.pone.0160663.
- Cox, T., Soetaert, K., Vanderborcht, J.P., Kromkamp, J., Meire, P., 2010. Modelling photosynthesis-irradiance curves: effects of temperature, dissolved silica depletion and changing community assemblage on community photosynthesis. *Limnology and Oceanography - Methods* 8, 424–440. URL: <http://www.aslo.org/lomethods/free/2010/0424.html>, doi:10.4319/lom.2010.8.424.
- Cox, T.J.S., Horemans, D.M.L., De Mulder, T., Meire, P., 2017. Hoogfrequente in-situ metingen van de interactie tussen SPM-en zuurstofdynamiek in het Schelde-estuarium. Deelrapport 1. Metingen nabij het oppervlak. Report ECOBE 018-R215. University of Antwerp, Ecosystem Management Group and University of Ghent, Hydraulics Laboratory.
- Cox, T.J.S., Maris, T., Soetaert, K., Conley, D.J., Van Damme, S., Meire, P., Middelburg, J.J., Vos, M., Struyf, E., 2009. A macro-tidal freshwater ecosystem recovering from hypereutrophication: the Schelde case study. *Biogeosciences* 6, 2935–2948. URL: www.biogeosciences.net/6/2935/2009/, doi:10.5194/bg-6-2935-2009.
- Cox, T.J.S., Maris, T., Soetaert, K., Kromkamp, J.C., Meire, P., Meysman, F., 2015. Estimating primary production from oxygen time series: A novel approach in the frequency domain. *Limnology and Oceanography-Methods* 13, 529–552. URL: <https://aslopubs.onlinelibrary.wiley.com/doi/full/10.1002/lom3.10046>, doi:10.1002/lom3.10046.
- De Vlaamse Milieumaatschappij; Waterbouwkundig Laboratorium; Maritieme Dienstverlening en Kust, De Vlaamse Waterweg, 2013. Metingen en voorspellingen afkomstig van waterinfo.be [data]. <https://www.waterinfo.be/>. Accessed: 2017-06-08.
- Desmit, X., Vanderborcht, J.P., Regnier, P., Wollast, R., 2005. Control of phytoplankton production by physical forcing in a strongly tidal, well-mixed estuary. *Biogeosciences* 2, 205–218. URL: <https://hal.archives-ouvertes.fr/hal-00297523/>, doi:10.5194/bg-2-205-2005.
- Dijkstra, Y.M., Brouwer, R.L., Schuttelaars, H.M., Schramkowski, G.P., 2017. The iFlow modelling framework v2.4: a modular idealized process-based model for flow and transport in estuaries. *Geoscientific Model Development* 10, 2691–2713. URL: <https://www.geosci-model-dev.net/10/2691/2017/gmd-10-2691-2017.pdf>, doi:10.5194/gmd-10-2691-2017.
- Dijkstra, Y.M., Chant, R.J., Reinfelder, J.R., 2019. Factors Controlling Seasonal Phytoplankton Dynamics in the Delaware River Estuary: an Idealized Model Study. *Estuaries and Coasts* 42, 1839–1857. URL: <https://link.springer.com/article/10.1007/s12237-019-00612-3>, doi:10.1007/s12237-019-00612-3.
- Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. *Fishery Bulletin* 70, 1063–1085. URL: <https://spo.nmfs.noaa.gov/sites/default/files/pdf-content/1972/704/eppley.pdf>.
- Filardo, M.J., Dunstan, W.M., 1985. Hydrodynamic control of phytoplankton in low salinity waters of the James River estuary, Virginia, U.S.A. *Estuarine, Coastal and Shelf Science* 21, 653–667. URL: <https://www.sciencedirect.com/science/article/pii/0272771485900642>, doi:10.1016/0272-7714(85)90064-2.
- Halsey, K.H., Milligan, A.J., Behrenfeld, M.J., 2010. Physiological optimization underlies growth rate-independent chlorophyll-specific gross and net primary production. *Photosynthesis Research* 103, 125–137. URL: <http://link.springer.com/10.1007/s11120-009-9526-z>, doi:10.1007/s11120-009-9526-z.
- Horemans, D.M.L., Dijkstra, Y.M., Schuttelaars, H.M., Meire, P., Cox, T.J.S., 2020. Unraveling the essential effects of flocculation on large-scale sediment transport patterns in a tide-dominated estuary. *Journal of Physical Oceanography* 50, 1957–1981. URL: www.ametsoc.org/PUBSReuseLicenses, doi:10.1175/jpo-d-19-0232.1.
- Kromkamp, J., Peene, J., 1995. Possibility of net phytoplankton primary production in the turbid Schelde Estuary (SW Netherlands). *Mar Ecol-Prog Ser* 121, 249–259. URL: <https://www.int-res.com/abstracts/meps/v121/p249-259/>, doi:10.3354/meps121249.
- Kromkamp, J.C., Peene, J., 2005. Changes in phytoplankton biomass and primary production between 1991 and 2001 in the Westerschelde estuary (Belgium/The Netherlands). *Hydrobiologia* 540, 117–126. URL: <https://link.springer.com/article/10.1007/s10750-004-7124-9>, doi:10.1007/s10750-004-7124-9.
- Langdon, C., 1993. The significance of respiration in production measurements based on oxygen. *ICES Marine Science Symposia*

- 197, 69–78. URL: https://www.researchgate.net/profile/Chris_Langdon/publication/230889097_The_significance_of_respiration_in_production_measurements_based_on_oxygen/links/0c960529fb3533df9d000000.pdf.
- Lionard, M., Azémar, F., Boulêtreau, S., Muylaert, K., Tackx, M., Vyverman, W., 2005. Grazing by meso- and microzooplankton on phytoplankton in the upper reaches of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal and Shelf Science* 64, 764–774. URL: <https://www.sciencedirect.com/science/article/pii/S0272771405001460>, doi:10.1016/J.ECSS.2005.04.011.
- Liu, B., de Swart, H.E., 2015. Impact of river discharge on phytoplankton bloom dynamics in eutrophic estuaries: A model study. *Journal of Marine Systems* 152, 64–74. URL: <https://www.sciencedirect.com/science/article/pii/S0924796315001311>, doi:10.1016/j.jmarsys.2015.07.007.
- Liu, B., de Swart, H.E., de Jonge, V.N., 2018. Phytoplankton bloom dynamics in turbid, well-mixed estuaries: A model study. *Estuarine, Coastal and Shelf Science* 211, 137–151. URL: <https://www.sciencedirect.com/science/article/pii/S0272771417302998>, doi:10.1016/j.ecss.2018.01.010.
- Lucas, L.V., Cloern, J.E., Koseff, J.R., Monismith, S.G., Thompson, J.K., 1998. Does the Sverdrup critical depth model explain bloom dynamics in estuaries? *Journal of Marine Research* 56, 375–415. URL: <https://www.ingentaconnect.com/content/jmr/jmr/1998/00000056/00000002/art00004>, doi:10.1357/002224098321822357.
- Maris, T., Meire, P., 2016. OMES rapport 2015. Onderzoek naar de gevolgen van het Sigmaplan, baggeractiviteiten en havenuitbreiding in de Zeeschelde op het milieu. Technical Report. University of Antwerp.
- McSweeney, J.M., Chant, R.J., Wilkin, J.L., Sommerfield, C.K., 2017. Suspended-Sediment Impacts on Light-Limited Productivity in the Delaware Estuary. *Estuaries and Coasts* 40, 977–993. URL: <http://link.springer.com/10.1007/s12237-016-0200-3>, doi:10.1007/s12237-016-0200-3.
- Platt, T., Gallegos, C.L., Harrison, W.G., 1980. Photoinhibition of Photosynthesis in Natural Assemblages of Marine-Phytoplankton. *Journal of Marine Research* 38, 687–701. URL: <http://biblioimarpe.imarpe.gob.pe:8080/bitstream/handle/123456789/1357/BOL%20EXTR.%20Investigaci%C3%B3n%20....-18.pdf?sequence=1>.
- Rijkswaterstaat, 2018. Extinctiecoefficient in m in oppervlaktewater. <http://opendap.deltares.nl/thredds/catalog/opendap/catalog.html>. Accessed: 2018-02-14.
- RMI, 2013. Global solar radiation in stabroek for the year 2013. <https://www.meteo.be>. Accessed: 2017-06-08.
- Soetaert, K., Herman, P., Kromkamp, J., 1994. Living in the Twilight - Estimating Net Phytoplankton Growth in the Westerschelde Estuary (the Netherlands) by Means of an Ecosystem Model (moses). *Journal of Plankton Research* 16, 1277–1301. doi:10.1093/plankt/16.10.1277. wOS:A1994PP53500001.
- Soetaert, K., Herman, P.M.J., 1995. Carbon flows in the westerschelde estuary (the netherlands) evaluated by means of an ecosystem model (moses). *Hydrobiologia* 311, 247–266. URL: <https://dx.doi.org/10.1007/BF00008584>, doi:10.1007/BF00008584.
- Sverdrup, H.U., 1953. On Conditions for the Vernal Blooming of Phytoplankton. *ICES Journal of Marine Science* 18, 287–295. URL: <https://academic.oup.com/icesjms/article/18/3/287/695418>, doi:10.1093/icesjms/18.3.287.
- Swaney, D.P., Howarth, R.W., Butler, T.J., 1999. A novel approach for estimating ecosystem production and respiration in estuaries: Application to the oligohaline and mesohaline Hudson River. *Limnology and Oceanography* 44, 1509–1521. URL: <https://aslopubs.onlinelibrary.wiley.com/doi/abs/10.4319/lo.1999.44.6.1509>, doi:10.4319/lo.1999.44.6.1509.
- de Swart, H.E., Schuttelaars, H.M., Talke, S.A., 2009. Initial growth of phytoplankton in turbid estuaries: {A} simple model. *Continental Shelf Research* 29, 136–147. doi:10.1016/j.csr.2007.09.006.
- Tilman, D., Kilham, S.S., Kilham, P., 1982. Phytoplankton Community Ecology: The Role of Limiting Nutrients. *Annual Review of Ecology and Systematics* 13, 349–372. URL: <https://www.annualreviews.org/doi/pdf/10.1146/annurev.es.13.110182.002025#article-denial>, doi:10.1146/annurev.es.13.110182.002025.
- van Rijn, L.C., 2010. Tidal phenomena in the Scheldt Estuary. Report 1202016-000. Deltares. URL: <http://www.vliz.be/imisdocs/publications/214759.pdf>.
- Vanderborght, J.P., Wollast, R., Loijens, M., Regnier, P., 2002. Application of a transport-reaction model to the estimation of biogas fluxes in the Scheldt estuary. *Biogeochemistry* 59, 207–237. URL: <https://link.springer.com/article/10.1023/A:1015573131561>, doi:10.1023/A:1015573131561.
- Vegter, F., De Visscher, P.R.M., 1984. Phytoplankton primary production in Brackish Lake Grevelingen (SW Netherlands) during 1976–1981. *Netherlands Journal of Sea Research* 18, 246–259. doi:10.1016/0077-7579(84)90004-8.
- Volta, C., Laruelle, G.G., Arndt, S., Regnier, P., 2016. Linking biogeochemistry to hydro-geometrical variability in tidal estuaries: a generic modeling approach. *Hydrology and Earth System Sciences* 20, 991–1030. URL: <https://www.hydrol-earth-syst-sci.net/20/991/2016/hess-20-991-2016-discussion.html>, doi:10.5194/hess-20-991-2016.
- Westberry, T.K., Williams, P.J.L., Behrenfeld, M.J., 2012. Global net community production and the putative net heterotrophy of the oligotrophic oceans. *Global Biogeochemical Cycles* 26. URL: <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2011GB004094>, doi:10.1029/2011GB004094.
- Wirtz, K.W., 2000. Second order up-scaling: theory and an exercise with a complex photosynthesis model. *Ecological Modelling* 126, 59–71. URL: <https://www.sciencedirect.com/science/article/pii/S030438009900174X>, doi:10.1016/S0304-3800(99)00174-X.
- YSI, 2017a. Chlorophyll a measurement. <https://www.ysi.com/parameters/chlorophyll>. Accessed: 2018-01-23.
- YSI, 2017b. Turbidity measurement. <https://www.ysi.com/parameters/turbidity>. Accessed: 2018-01-23.