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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 (\(\sim\)hours\(^{-1}\)-days\(^{-1}\)) and low-frequency (\(\sim\)weeks\(^{-1}\)-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 $E_0$, exponential light-extinction coefficient $k_d$, 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 $\Lambda$ 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 $\Lambda$, 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 kg m$^{-3}$ s$^{-1}$) (Langdon, 1993; Desmit et al., 2005):

$$\frac{dX}{dt} = \nu \cdot X - \mu X,$$
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).

$$\frac{\partial \tilde{B}(x,t)}{\partial t} = \text{phytoplankton biomass growth rate} + \frac{1}{d} \int_0^d \left[ \frac{\partial}{\partial x} (\tilde{u} \tilde{B}) + \frac{\partial}{\partial x} \left( K_h \frac{\partial}{\partial x} \tilde{B} \right) \right] dz$$

$$= \tilde{B} \cdot \left[ P_m \cdot \left( \frac{1}{d} \int_0^d \tilde{\Lambda} dz \right) \cdot (1-\rho)-m \right]$$

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, $\rho$ 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 (PODOC). 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):

$$\tilde{\Lambda} = \left\{ 1 - \exp \left[ -\frac{\alpha}{P_m} I \right] \right\}$$

in which $\alpha$ is the photosynthetic efficiency and $I$ is the

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

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

in which \(\beta\) and \(\bar{z}\) are dimensionless numbers defined as:

\[ \bar{\beta} = \frac{\alpha E_0}{P_m} \quad \text{and} \quad \bar{z} = k_d \cdot z. \quad (4) \]

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:

\[ GPP(t) = B(t) \cdot P_m \cdot \Lambda(t), \quad (5) \]

with \(\Lambda\) the depth-averaged Platt expression:

\[ \Lambda(t) = \frac{1}{d} \int_0^d \bar{\Lambda}(z,t)dz. \quad (6) \]

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:

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

in which \(\kappa, \epsilon,\) and \(\delta\) are dimensionless relative fluctuations defined as:

\[ \epsilon(t) = \frac{E'_0(t)}{\langle E_0 \rangle}, \quad \kappa(t) = \frac{k'_d(t)}{\langle k_d \rangle}, \quad (11) \]
\[ \delta(t) = \frac{d'(t)}{\langle d \rangle} \]

and \(\beta\) and \(\lambda\) 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 \(\sim \text{mfun}_\kappa, \text{mfun}_\epsilon, \text{mfun}_\kappa^2, \text{mfun}_\kappa \epsilon, \) and their interactions \(\sim \text{mfun}_\kappa \epsilon, \text{mfun}_\kappa \delta, \) By construction of \(\Lambda, \kappa\) and \(\delta\) come with identical mfun functions:
The mfun functions are determined by two dimensionless numbers $\lambda$ and $\beta$, which characterize the system under study and have a clear physical interpretation. $\lambda$ is a measure for the photic properties of the water column. Turbid and deep systems have a large $\lambda$, while transparent and shallow systems correspond with a small $\lambda$. For fully mixed systems, $\lambda$ 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 $\beta$ increases with increasing solar irradiance and photosynthetic efficiency. Consequently, for a fixed $P_m/\alpha$ ratio, an equatorial system (more solar irradiance) typically corresponds to a larger $\beta$ 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 $GPP > 0$. Consequently, time-averaged GPP becomes proportional to time-averaged DAP:

$$\langle GPP(t) \rangle = B \cdot P_m \cdot \langle \Lambda(t) \rangle.$$  \hfill (16)

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

$$\langle \Lambda(t) \rangle \approx mfun_0(\beta, \lambda) \left\{ 1+ 
+ mfun_{\kappa^2}(\beta, \lambda) \left[ \bar{\text{Var}}[k_d(t)] + \bar{\text{Var}}[d(t)] \right] \right. 
+ mfun_{\kappa^2}(\beta, \lambda) \cdot \bar{\text{Var}}[E_0(t)] 
+ mfun_{\kappa^2}(\beta, \lambda) \left[ \bar{\text{Cov}}[E_0(t), k_d(t)] 
+ \bar{\text{Cov}}[E_0(t), d(t)] \right] 
+ mfun_{\kappa^2}(\beta, \lambda) \cdot \bar{\text{Cov}}[k_d(t), d(t)] \right\},$$  \hfill (17)

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

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

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

As a result of the definitions in Eqs. (8) and (9), the time averages of the $\sim mfun_{\lambda^2}$ and $mfun_{\kappa^2}$-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 $\langle GPP \rangle$. The magnitude is both determined by the average system characteristics ($\lambda, \beta$) 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 Kruibeke (~85 km from the mouth). We choose Kruibeke 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 (Nepholometric 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\(^{-1}\) turb.] from turbidity [NTU], we used the following expression (Cox et al., 2017):

\[
k_d = 0.39(2.1\text{NTU}^{-1} \cdot \text{turb.} - 1.82)^{0.64} \text{ m}^{-1}.
\] (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 (\( \sim 25 \) 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.

\[ B(t) = B_0 e^{-(\rho - 1) \int_0^t \Lambda(\tau) d\tau} \times e^{\left[ \frac{1}{\omega M_2} \cos(\omega M_2 t + \Phi_{M_2} + \theta) \right]}, \] (22)

with:

\[
\hat{A} = B_0 e^{-(\rho - 1) \int_0^t \Lambda(\tau) d\tau} e^{\left[ \frac{1}{\omega M_2} \cos(\Phi_{M_2} + \theta) \right]},
\] (23)

and \( \omega M_2 \) the angular frequency corresponding to the semi-diurnal lunar M\(_2\) tide and \( \Phi_{M_2} \) and \( \theta \) phases corresponding to the idealized time dependence of the water depth \( d \) [see below, Eq. (28)]. The coefficients \( m^* \) and \( \gamma \) are defined in Appendix C. The integrated loss rate \( m^* \) incorporates losses due to grazing, mortality, and residual water currents. \( \gamma \) 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):

\[
\int \Lambda(t) dt \approx \mu \sum_{\kappa=0}^{\infty} \left[ 1 + \frac{\mu\nu_0(\beta, \lambda)}{t} \int \kappa(t) + \delta(t) dt \right. \\
+ \mu\nu_1(\beta, \lambda) \int \epsilon(t) \cdot \kappa(t) dt \\
+ \mu\nu_2(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_3(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_4(\beta, \lambda) \int \epsilon(t) \cdot \kappa(t) dt \\
+ \mu\nu_5(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_6(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_7(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_8(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_9(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_{10}(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_{11}(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
+ \mu\nu_{12}(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \\
\left. + \mu\nu_{13}(\beta, \lambda) \int \epsilon(t) \cdot \delta(t) dt \right].
\] (24)

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):

\[
E_0(t) = \max(0, a + b \cos(\omega_0 t)),
\] (25)
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 $d$. $\bar{\text{Var}}$ and $\bar{\text{Cov}}$ are the relative variance and covariance as defined in Eqs. (18) and (19).

<table>
<thead>
<tr>
<th></th>
<th>Summer case</th>
<th>Winter case</th>
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<tr>
<td></td>
<td>$N$ 3000</td>
<td>$N$ 3000</td>
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<tr>
<td>$\lambda$</td>
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<td>95.2</td>
</tr>
<tr>
<td>$\beta$</td>
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<td>1.05</td>
</tr>
<tr>
<td>$\langle E_0 \rangle$</td>
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<td>70.0 J m$^{-2}$ s$^{-1}$</td>
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<td>$\langle k_d \rangle$</td>
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<td>11.1 m$^{-1}$</td>
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<tr>
<td>$\langle d \rangle$</td>
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<td>8.60 m</td>
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<tr>
<td>$\bar{\text{Var}}[E_0]$</td>
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</table>
in which $a$ and $b$ are further unspecified parameters and $\omega_S$ 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:

$$E_0(t) = \langle E_0 \rangle + \sum_{n=1}^{3} \hat{E}_n \cos(n\omega_S t). \quad (26)$$

Similarly, we only consider the dominant and periodic $\omega_M = 2\omega_M$ and $\omega_M = 2\omega_M$ temporal fluctuations in $k_d$ and $d$ and truncate frequencies larger than $M_4$ (i.e., $M_6$, $M_8$, etc.) are neglected) following Chernetsky et al. (2010), Dijkstra et al. (2017), and Horemans et al. (2020):

$$k'_d(t) = \hat{K}_2 \cos(\omega_M t + \Phi_M d) + \hat{K}_4 \cos(\omega_M t + \Phi_M d), \quad (27)$$

$$d'(t) = \hat{D}_2 \cos(\omega_M t + \Phi_M d + \theta), \quad (28)$$

in which $\Phi_M$, $\Phi_M$, $\theta$ are the phases and we set $\Phi_S$ = 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., $\Phi_M$, $\Phi_M$, and $\theta$). 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 $m^*$, $\gamma$, and $\rho$ 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 $\gamma$ and $m^*$ corresponds to the estimated order in Appendix C, i.e., $O(10^{-1})$ h$^{-1}$ and $O(10^{-2})$ h$^{-1}$, respectively. The order of the fitted value for $\rho$ 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.
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).

<table>
<thead>
<tr>
<th>$E_1$</th>
<th>$E_2$</th>
<th>$E_3$</th>
<th>$\langle k_d \rangle$</th>
<th>$\langle d \rangle$</th>
<th>$\omega_{S1}$</th>
<th>$\Phi_{M2}$</th>
<th>$\Phi_{M4}$</th>
<th>$\langle E_0 \rangle$</th>
</tr>
</thead>
<tbody>
<tr>
<td>J m$^{-2}$ s$^{-1}$</td>
<td>m$^{-1}$</td>
<td>h$^{-1}$</td>
<td>m$^{-1}$</td>
<td>m$^{-1}$</td>
<td>m$^{-1}$</td>
<td>m$^{-1}$</td>
<td>m$^{-1}$</td>
<td>m$^{-1}$</td>
</tr>
<tr>
<td>142</td>
<td>75.3</td>
<td>3.44</td>
<td>4.56</td>
<td>4.5 m</td>
<td>$\frac{24}{24}$</td>
<td>$-3.59$</td>
<td>$-0.253$</td>
<td>168 J m$^{-2}$ s$^{-1}$</td>
</tr>
<tr>
<td>$\langle k_d \rangle$</td>
<td>$K_3$</td>
<td>$K_4$</td>
<td>$\omega_{M2}$</td>
<td>$\omega_{M4}$</td>
<td>$\rho$</td>
<td>$\theta$</td>
<td>$\gamma$</td>
<td>$m^*$</td>
</tr>
<tr>
<td>$\omega_{S1}$</td>
<td>$\omega_{M2}$</td>
<td>$\omega_{M4}$</td>
<td>$\rho$</td>
<td>$\theta$</td>
<td>$\gamma$</td>
<td>$m^*$</td>
<td>$0.0834 h^{-1}$</td>
<td></td>
</tr>
</tbody>
</table>
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 $\Lambda$, 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 mfun 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 mfun$\lambda$ for various $\beta$ and $\lambda$. mfun$\lambda$ ranges from 0 (maximal light-limitation, no GPP) to 1 (no light-limitation, maximal GPP) and has a simple structure: it increases with increasing $\beta$ (cf. increasing solar irradiance/PP efficiency) and decreases with increasing $\lambda$ (cf. increasing turbidity/depth).

The mfun$_\iota$ and mfun$_k$ 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. $\Lambda$), GPP, and corresponding biomass dynamics from the respective amplitudes in $E_0$, $k_d$, and $d$. mfun$_\iota$ is negative for every value of $\lambda$ and $\beta$ (Fig. 6a), simply reflecting the fact that an increase in $k_d$ (or $d$) leads to a decrease in $B(t)$. In contrast, mfun$_k$ 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 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$_\iota^2$ is always negative. In contrast, the sign of the other second-order mfun functions depends on the specific values of $\lambda$ and $\beta$ (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 $E_0$ ($\sim$ mfun$_\iota$) are negligible compared to the variance term ($\sim$ mfun$_\iota^2$) 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$_\iota^2$ is negative ($\lambda < 5$, 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., $\lambda$ and $\beta$) 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$_{\kappa}$. (b) Result of mfun$_{\epsilon}$.

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$_{\kappa^2}$. (b) Result of mfun$_{\epsilon^2}$. (c) Result of mfun$_{\kappa \epsilon}$. (d) Result of 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. \(E_0, k_d, d\)) on time-averaged \((\langle GPP \rangle)\) 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\(_{a,2}\) is always positive (Fig. 7a) and thus temporal variability in \(k_d\) and \(d\) lead to an increase in \((\langle GPP \rangle)\). In contrast, temporal variability in \(E_0\) decreases \((\langle GPP \rangle)\) (Fig. 7b).

Fig. 8 shows the results of \((\langle GPP \rangle)\) when including temporal variability in all parameters (all var), normalized with \((\langle GPP \rangle)\) with time-averaged parameters (i.e., \((E_0)\), \((k_d)\), and \((d)\)) 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 \((\langle GPP \rangle)\), 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 \((\langle GPP \rangle)\) 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 \(\omega_{\text{S1}}\) 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 \((\langle GPP \rangle)\).

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 \((\langle GPP \rangle)\), 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 \((\langle GPP \rangle)\) 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 (∼750 µg l\(^{-1}\)) and to ∼1500 µg 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 \((E_0),\) \((k_d),\) and \((d)\) (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 over-estimation 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 \text{ var}, k_d \text{ var}, and E_0 \text{ var}) or when temporal variability in all parameters is included (cf. all \text{ 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.
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 $\langle d \rangle$. 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 $\sim \sin(\omega_{M2} - 2\omega_{S1})t$.

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 $n^*$.

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 $E_0$ decreases 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 $P_m$, $\alpha$, 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 $\alpha$ 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-situ 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. $P_m$, $\alpha$). 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 $\Lambda$ [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 $\langle GPP \rangle$ and corresponding $\langle GPP \rangle$ 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 $\langle GPP \rangle$ in dynamic equilibrium and corresponding phytoplankton dynamics. In the first application, we showed that $\langle GPP \rangle$ 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 $\langle GPP \rangle$. Furthermore, the results showed a seasonality; in winter, temporal variability in $k_d$ had a larger impact on $\langle GPP \rangle$ 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 $q = \beta \cdot \exp(-k_d \cdot z)$ in Eq. (6) allows us to analytically solve the DAP:

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

in which we used the definition of the exponential integral $E_1(x)$ (Bender and Orszag, 2013):
Consequently, the Taylor expansion at the mean values \( \bar{E} \) plus a (small) variation \( \tilde{E} \), 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 \( \Lambda \): definition of the mfun functions**

Consider a function \( f \) which depend on a set of variables \( a = \{k_d, E_0, d\} \). 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:

\[
f (\langle k_d \rangle + k_d', \langle E_0 \rangle + E_0', \langle d \rangle + d'(t)) \approx f (\langle a \rangle)
+ \frac{\partial f}{\partial k_d} \bigg|_{a=\langle a \rangle} k_d'(t) + \frac{\partial f}{\partial E_0} \bigg|_{a=\langle a \rangle} E_0'(t) + \frac{\partial f}{\partial d} \bigg|_{a=\langle a \rangle} d'(t)
+ \frac{1}{2} \frac{\partial^2 f}{\partial k_d^2} \bigg|_{a=\langle a \rangle} [k_d'(t)]^2 + \frac{1}{2} \frac{\partial^2 f}{\partial E_0^2} \bigg|_{a=\langle a \rangle} [E_0'(t)]^2
+ \frac{1}{2} \frac{\partial^2 f}{\partial k_d \partial d} \bigg|_{a=\langle a \rangle} [k_d'(t)] [d'(t)] + \frac{\partial^2 f}{\partial d^2} \bigg|_{a=\langle a \rangle} [d'(t)] E_0'(t)
+ \frac{\partial^2 f}{\partial k_d \partial d} \bigg|_{a=\langle a \rangle} [k_d'(t)] d'(t) + \frac{\partial^2 f}{\partial d \partial E_0} \bigg|_{a=\langle a \rangle} d'(t) E_0'(t). \quad \text{(B.1)}
\]

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

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

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 \( \tilde{B}(t) \):

\[
\frac{\partial \tilde{B}(t,x)}{\partial t} + \frac{1}{d} \int_0^d \left[ \frac{\partial}{\partial x}(\tilde{u}\tilde{B}) + \frac{\partial}{\partial x} \left( K_h \frac{\partial}{\partial x} \tilde{B} \right) \right] dx \approx \tilde{B}(x,t) \cdot \left[ P_m \cdot \Lambda \cdot (1 - \rho) - m \right]. \quad \text{(C.1)}
\]

Scaling of the longitudinal terms in Eq. (C.1) shows that the longitudinal diffusion term is \( 10^5 \) 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 \( 1 \text{ m s}^{-1}, 10^5 \text{ m}, \) and \( 10^2 \text{ m}^2 \text{ s}^{-1} \), respectively (de Swart et al., 2009). Consequently:

change in \( \tilde{B}(t) \) due to transport \( \approx \frac{\partial}{\partial x} \left[ \tilde{u}(x,t) \tilde{B}(x,t) \right] \),

\[
\text{(C.2)}
\]

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

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

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

\[
\frac{d\tilde{B}}{dt} \bigg|_{\text{advection}} = - \frac{\partial(\tilde{u} \cdot \tilde{B})}{\partial x}
= - \left[ \tilde{u} \frac{\partial \tilde{B}}{\partial x} + \tilde{B} \frac{\partial \tilde{u}}{\partial x} \right]. \quad \text{(C.4)}
\]

We assume:

\[
\tilde{B}(x,t) = B(t) \cdot f(x). \quad \text{(C.5)}
\]
Alternatively, put, the phytoplankton biomass concentration $B(x,t)$ 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 $B(x,t)$ 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 (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 $x^*$:

\[
\frac{\partial B(x,t)}{\partial x} \approx B(t) \frac{df(x)}{dx} \bigg|_{x=x^*}. \tag{C.6}
\]

Similarly, we assume:

\[
\frac{\partial u(t,x)}{\partial x} \approx u(t) \frac{dg(x)}{dx} \bigg|_{x=x^*}, \tag{C.7}
\]

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:

\[
u(t) = v_0 + A_v \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta), \tag{C.8}
\]

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 $D_2$. If we define $A_v$ as being positive, we have:

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

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:

\[
\frac{dB}{dt} \bigg|_{\text{advection}} = - \left[ v_0^* + \hat{\gamma} \cdot \sin(\omega_{M2} \cdot t + \Phi_{M2} + \theta) \right] \cdot B(t), \tag{C.10}
\]

in which:

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

\[
v_0^* = v_0 \left[ g(x) \frac{df(x)}{dx} \bigg|_{x=x^*} \right. + \left. f(x) \frac{dg(x)}{dx} \bigg|_{x=x^*} \right]. \tag{C.12}
\]
Filling in the latter results into the differential equation for change in $B(x,t)$ in Eq. (C.3) at $x = x^*$, we acquire:

$$\frac{\partial B(t)}{\partial t} = B(t) \cdot \left[ P_m \cdot A \cdot (1 - \rho) - m \right] + B(t) \cdot \left[ - v_0^* - \gamma \cdot \sin(\omega_M t + \Phi_M + \theta) \right],$$

(C.13)

with:

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

(C.14)

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

(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:

$$m^* = m + v_0^*. \tag{C.16}$$

In the following, we estimate the order of magnitude of $\gamma$, $v_0^*$, 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:

$$\int_0^{6.2h} A_v \sin(M2 \cdot t) dt \sim \mathcal{O}(1),$$

$$\Rightarrow A_v \sim \mathcal{O}(1) \text{ km h}^{-1}. \tag{C.17}$$

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:

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

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

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

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

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

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

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

Appendix D. Application 2: data fit

Application of data fits using the presumed expressions:

$$E_n^d(t) = \sum_{n=1}^{3} \hat{E}_n \cos(n\omega_{S1}t), \tag{D.1}$$

$$k_d^d(t) = \hat{K}_2 \cos(\omega_{M2} t + \Phi_{M2}) + \hat{K}_4 \cos(\omega_{M4} t + \Phi_{M4}), \tag{D.2}$$

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

to a subset of the data sets of $E_n^d$, $k_d$, and $d$ at Scheldebelle 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.
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.
\[ \int \kappa(t) dt = \frac{1}{\langle k_d \rangle} \left[ \begin{array}{c} \dot{K}_2 \sin (\omega_M t + \Phi_M) \\ \dot{K}_4 \sin (\omega_M + \Phi_M) \end{array} \right] + \frac{1}{2} \frac{1}{\langle k_d \rangle} \left[ \begin{array}{c} \dot{K}_2 \dot{K}_4 \sin (\omega_M - \omega_M + \Phi_M - \Phi_M) \\ \dot{K}_2 \dot{K}_4 \sin (\omega_M + \omega_M + \Phi_M + \Phi_M) \end{array} \right] + \frac{1}{4} \frac{1}{k_d} \left[ \begin{array}{c} K_2^2 \sin (2 \omega_M t + 2 \Phi_M) \\ 0 \end{array} \right] (E.5) \]

\[ \int \epsilon(t) dt = \frac{1}{E_0} \left[ \begin{array}{c} \dot{E}_1 \sin (\omega_S t) \\ \dot{E}_2 \sin (2 \omega_S t) \\ 1/3 \dot{E}_3 \sin (3 \omega_S t) \end{array} \right] + 1/2 \left( \dot{E}_2 \dot{E}_1 + \dot{E}_3 \dot{E}_2 \right) \sin (\omega_S t) \]

\[ \int \dot{\epsilon}(t) dt = \frac{1}{E_0} \left[ \begin{array}{c} 1/2 \dot{E}_1^2 \sin (\omega_S t) \\ 1/2 \dot{E}_2^2 \sin (\omega_S t) \\ 1/3 \dot{E}_3^2 \sin (3 \omega_S t) \end{array} \right] + 1/2 \left( \dot{E}_2^2 \dot{E}_1 + \dot{E}_3^2 \dot{E}_2 \right) \sin (2 \omega_S t) \]

\[ \int \delta^2(t) dt = \frac{1}{\langle d \rangle^2} \left[ \begin{array}{c} \dot{D}_2 \sin (\omega_M t + \Phi_M) \\ \dot{D}_4 \sin (\omega_M + \Phi_M) \end{array} \right] + \frac{1}{2} \frac{1}{\langle d \rangle} \left[ \begin{array}{c} \dot{D}_2 \dot{D}_4 \sin (\omega_M - \omega_M + \Phi_M - \Phi_M) \\ \dot{D}_2 \dot{D}_4 \sin (\omega_M + \omega_M + \Phi_M + \Phi_M) \end{array} \right] + \frac{1}{4} \frac{1}{d} \left[ \begin{array}{c} D_2^2 \sin (2 \omega_M t + 2 \Phi_M) \\ 0 \end{array} \right] (E.8) \]

\[ \int \delta(t) dt = \frac{1}{E_0} \left[ \begin{array}{c} \dot{D}_2 \sin (\omega_M t + \Phi_M) \\ \dot{D}_4 \sin (\omega_M + \Phi_M) \end{array} \right] + \frac{1}{2} \frac{1}{\langle d \rangle} \left[ \begin{array}{c} \dot{D}_2 \dot{D}_4 \sin (\omega_M - \omega_M + \Phi_M - \Phi_M) \\ \dot{D}_2 \dot{D}_4 \sin (\omega_M + \omega_M + \Phi_M + \Phi_M) \end{array} \right] + \frac{1}{4} \frac{1}{d} \left[ \begin{array}{c} D_2^2 \sin (2 \omega_M t + 2 \Phi_M) \\ 0 \end{array} \right] (E.7) \]
Appendix F. The impact of temporal variability in light-climate on the onset of a phytoplankton bloom

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

\[
\frac{\beta_{\text{no fluct}} (t = 14 \text{ days}, \beta + \Delta \beta)}{\beta_{\text{no fluct}} (t = 14 \text{ days}, \beta)} = 14, \\
\implies \Delta \beta \approx \log_{14} 14 \\
= 1.3.
\]  

(F.1)

Using Eq. (12), we compute the corresponding difference in solar irradiance \( \Delta < E_0 > \approx 31 \text{ J s}^{-1} \text{ m}^{-2} \). 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 J s\(^{-1}\) 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


Langdon, C., 1993. The significance of respiration in production measurements based on oxygen. ICES Marine Science Symposium