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Impacts of Physical Transport on Estuarine Phytoplankton Dynamics and Harmful Algal Blooms

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Impacts of Physical Transport on Estuarine Phytoplankton Dynamics and Harmful Algal Blooms

A Dissertation

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Doctor of Philosophy

by

Qubin Qin

January 2019
This dissertation is submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

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ABSTRACT

The spatial and temporal variability of phytoplankton biomass in estuaries is determined by both local processes and transport processes. Local processes include biological processes (e.g., photosynthesis, respiration/excretion, and grazing) and settling, whereas transport processes include advective and diffusive transports. Transport processes have been demonstrated to regulate phytoplankton dynamics significantly by distributing both phytoplankton and other dissolved and particulate substances (e.g., nutrients, salts, sediments, and chromophoric dissolved organic matter). Yet, these transport properties lack a framework that unifies the pieced description of their various effects, and quantification of their importance under various environmental conditions. This dissertation highlights the role of horizontal transport processes on phytoplankton dynamics in estuaries, including the initiation of harmful algal blooms (HABs).

In Chapter 2, the flushing effect of transport processes and its interaction with local processes are exclusively examined, and its relative importance on the variability of phytoplankton biomass is quantified and compared to that of the local processes over timescales from hours to years, using an introduced concept of transport rate that can be numerically computed.

In Chapter 3, a simple yet inclusive mathematical model is developed to examine the temporal and spatial variabilities in phytoplankton biomass in response to the various effects of physical transport, under nutrient and light limiting conditions. For estuaries whose dominant nutrient loading is from river input, three basic patterns are revealed for the relationships between phytoplankton biomass and flushing time under various environmental conditions.

In Chapters 4 and 5, the flushing effect of transport processes on the initiation of harmful algal blooms (HABs) in estuaries is investigated, which is then applied to examine the location and timing of the initiation of an annual Cochlodinium (recently renamed Margalefidinium) polykrikoides bloom in the lower James River. Theoretical analysis shows that the flushing is the key factor that affects HAB initiation in multiple interconnected systems, and a relatively long period of time (weeks) is required for a successful bloom. A HAB tends to be observed first in locations with relatively long residence time, such as tributaries or areas with large eddies. Multiple unconnected originating locations can co-exist within an estuary that highly depends on hydrodynamics and salinity. A numerical module for C. polykrikoides bloom is developed and built into a 3D numerical model - EFDC, which considers the competitive advantages of C. polykrikoides such as mixotrophic growth, swimming, grazing suppression, and resting cyst germination. Numerical model results show that the flushing effect determines the origins of C. polykrikoides blooms in the lower James River, and the sub-tributary of Lafayette River, which is characterized by relatively long residence time, is favorable for the first bloom to occur, regardless of the cyst distribution. A further investigation of various environmental conditions for the C. polykrikoides bloom reveals that temperature and physical transport control the interannual variability in the timing of its initiation, and individual perturbations by southerly wind, heavy rainfall, and spring tide can cause strong flushing capable of interrupting, or even terminating, initiation of a HAB event in the lower James River.
Impacts of Physical Transport on Estuarine Phytoplankton Dynamics and Harmful Algal Blooms
Chapter 1. Introduction
Phytoplankton is one major primary producer in estuaries, and they contribute greatly to the organic matter input into the ecosystem and higher trophic levels in the food web. On the other hand, however, the proliferation of phytoplankton can also be harmful to the health status of estuarine ecosystems. As a result of anthropogenic nutrient enrichment, large increases in phytoplankton biomass have occurred in many estuarine and coastal aquatic environments worldwide over the past half-century, causing the deterioration of water quality including the increase in the frequency of hypoxia and harmful algal blooms, loss of benthic macrophytes like submersed aquatic vegetation (SAV) (e.g. Cloern, 2001; Kemp et al., 2005). In recent decades, the nutrient reduction has been implemented in some estuarine and coastal systems, which has been shown to be an effective management strategy to reduce the phytoplankton biomass and to restore degraded ecosystems (Duarte et al., 2015). Because of the importance of phytoplankton in ecosystem production and health, it is essential to examine the temporal and spatial variability in estuarine phytoplankton biomass and understand how various environmental conditions affect phytoplankton dynamics.

Phytoplankton dynamics are influenced by many processes. In an estuary, as illustrated in Figure 1.1, the variability of phytoplankton biomass at a location is controlled by both local processes and transport processes. Local processes include biological processes (such as photosynthesis, respiration/excretion, and grazing) and settling, while physical transport processes (or simply referred to as transport processes) include advective and diffusive transports. The local processes can be affected directly by many environmental factors, including temperature, light, nutrients, grazing pressure, pH, stratification, and so forth. The effect of transport processes can be divided into direct and
indirect effects, as they affect distribution of both phytoplankton and other dissolved and particulate substances (e.g., nutrients, salts, sediments, chromophoric dissolved organic matter, and grazers).

**Flushing effect of transport processes**

The effects of transport processes on phytoplankton dynamics are well-recognized concepts. For quite a long time, the direct effect of flushing phytoplankton out of the system has been highlighted as the primary effect by estuarine ecologists. The mechanism of this effect is related to water retention in the system, and the concept, therefore, is straightforward to understand: a shorter time of water retention flushes more phytoplankton out. This flushing effect can alter phytoplankton community abundance and composition (Ferreira et al., 2005; Paerl et al., 2006; Costa et al., 2009). A variety of concepts of transport time, such as residence time, flushing time, and age, are commonly used to investigate the impact of physical transport over large spatial and long temporal scales (Monsen et al., 2002). A region with long transport time is recognized as a stable aquatic environment with a slow exchange of water and its carrying substances between inside and outside of a region. Therefore, it is indicative of a suitable condition for accumulations of substances like phytoplankton. Hence, a positive phytoplankton-transport time relationship is suggested as a result of this flushing effect and has been observed in many estuaries (Lucas et al., 2009). For example, the phytoplankton biomass is typically higher with longer residence times. While this flushing effect of physical transport on the variability of phytoplankton biomass has been emphasized, their relative importance compared to local processes has not been well-addressed. Although it is well-known that episodic events, such as storm surges and large discharge events, may
dramatically increase the contribution of transport processes on relatively short timescales (e.g., a few days), and may have greater impact on phytoplankton dynamics than local processes, few studies discuss how the contributions may change over a range of timescales from days to years under normal conditions. Lucas et al. (2009) suggest that the variability of phytoplankton biomass can be described by a steady-state balance between local biological processes and transport processes described by residence time, i.e., it is assumed that the short-term variability of phytoplankton biomass is negligible and local and transport processes are equal but counterbalanced in contribution. While this steady-state balance assumption may hold for long-term timescales, it is questionable for short-term timescales, such as daily and weekly timescales. A relevant discussion on the comparison of the relative importance of the two processes would be helpful to answer what range of timescales the assumption may be valid.

The flushing effect of transport processes depends on the non-zero horizontal gradients of phytoplankton biomass. They may increase the local concentration of a property if the incoming water has higher biomass, or decrease it if the incoming water has lower biomass. Thus, the impact of transport processes not only depends on hydrodynamic fields but also depends on the horizontal gradients of phytoplankton biomass. When studying their flushing effect of transport processes on phytoplankton dynamics, the transport of phytoplankton is caused by both physical transport and non-physical transport (Figure 1.1). The mechanisms of these two types of transport are different. For conservative substances such as salinity, the non-zero horizontal gradients are caused by the difference of concentrations in the incoming flows and the estuary, and also by the interactions between forcings (i.e., flow, tide, and wind) and geometry, and
the corresponding transport is the physical transport that can be described by various concepts of transport time. For non-conservative substances, like phytoplankton, while the physical transport may still be the dominant component, an additional mechanism that can induce non-zero gradients may come from the spatially inhomogeneous local processes (growth or decay), and the corresponding process is the non-physical transport. Most studies considering the flushing effect of transport processes on phytoplankton dynamics only take account for the physical transport, while ignoring the non-physical transport or being unaware of its existence.

**Indirect effects of transport processes**

Though the concept of the direct flushing effect of transport processes is straightforward, it is not the only way to regulate the variability of phytoplankton biomass. Lucas et al. (2009) compile relationships across systems, and show that longer transport time does not always result in higher phytoplankton biomass, and lower or nearly the same biomass has also been widely found in nature. This inconsistency indicates that transport processes may also have other effects that may play an important role in regulating phytoplankton dynamics. Indeed, the indirect effects of transport processes on algal growth through its effect on nutrient delivery has been recently suggested (e.g. Borsuk et al., 2004). Interestingly, the effect of transport processes on nutrient delivery and hence on phytoplankton dynamics is developed separately to the flushing effect on phytoplankton in history, and like the flushing effect, studies suggest that shorter residence time results in larger exporting rate of nutrients out of an estuary (Nixon et al., 1996). Hence, with the same nutrient loading, longer transport time retains more nutrients within the system. This effect of transport processes that flush nutrients
out, however, may not be as important as their effect on nutrient input, especially in the riverine nutrient-dominated systems. Higher river inflow, corresponding to shorter transport time, stimulates more nutrient loading into the system, and the net result of nutrient delivery, therefore, increases bioavailable nutrients in the system (Paerl et al., 2014). The resultant indirect effect of transport processes on phytoplankton dynamics is that shorter transport time corresponds to enhanced photosynthesis and higher phytoplankton biomass through bottom-up control when the growth of phytoplankton in the system is under nutrient limitation. Consequently, the direct and indirect effects of physical transport may lead to opposite results of phytoplankton biomass variability, and this dual role in regulating algal biomass has been linked to transport time. Peierls et al. (2012) found that the relationship between phytoplankton biomass and transport time is non-monotonic and unimodal in two small estuaries, and also suggested that the peak biomass occurs when freshwater flushing time is about 7-10 days by fitting the observational data with an empirical function.

Even though the conceptual model has been established, many questions remain unanswered for the effects of transport processes. Does the relative importance of these two effects vary with time and space? Does this non-monotonic relationship hold for every estuary? Is the transport time leading to the peak biomass always 7-10 days? How do the environmental factors and ecophysiology affect the peak of phytoplankton biomass for an estuary? To answer these questions, the underlying mechanisms and general patterns of this relationship need to be examined.
Initiation of *Cochlodinium polykrikoides* blooms

Of the water quality issues related to phytoplankton, harmful algal blooms (HABs) receive more and more attention due to their impact on ecosystems and their cause of significant loss in economy. HABs with a variety of species have been observed widely throughout the world (Granéli and Turner, 2006), and eutrophication is thought to be one important reason for their expansion in the U.S. and other nations (Heisler et al., 2008). The general interests lie in understanding the environmental conditions promoting blooms and also in developing the policies and techniques for the prevention, control, and mitigation (Kudela and Gobler, 2012).

Estuarine HABs can originate either from adjacent coastal areas or within estuaries. The HABs initiated and developed in adjacent coastal areas are transported into the estuaries, and the process can be impacted by upwelling-downwelling cycle and onshore-offshore transport (e.g., Fermin et al., 1996). Conversely, annual occurrences of HABs in many estuaries have been suggested to originate within estuaries independently although the bloom can be also found in adjacent coastal areas (Anderson, 1997; Mulholland et al., 2009).

In Virginia rivers and the lower Chesapeake Bay, for example, the assemblage of HAB species includes *Cochlodinium polykrikoides* (recently proposed to be renamed to *Margalefidinium polykrikoides* by Gómez et al., 2017), *Alexandrium monilatum*, *Microcystis aeruginosa*, *Prorocentrum minimum*, *Karlodinium veneficum*, and *Chattonella subsalsa* (Marshall and Egerton, 2013). The monitoring shows that the *C. polykrikoides* bloom occurs almost every year in the lower Chesapeake Bay and its tributaries in late summers over the past two decades (Morse et al., 2013). Although the
precise toxins leading to its toxicity have not yet to be confirmed, it has been widely found that *C. polykrikoides* could kill most marine organisms including other algae, copepod, bivalves, coral reefs, and fish during bloom events (e.g. Jiang et al., 2009, 2010; Tang and Gobler, 2009a, 2009b, 2010; Richlen et al., 2010). Extensive studies on *C. polykrikoides* suggest that this species has competitive advantages in growth over other phytoplankton species through a variety of strategies (Kudela and Gobler, 2012), and the processes that affect *C. polykrikoides* blooms can be grouped into: 1) the ecophysiology of *C. polykrikoides*, such as the effects of temperature, salinity, light on the growth rates, the ability to have mixotrophic growth, and swimming behaviors; 2) food-web interactions including ecological impacts of *C. polykrikoides* bloom, its grazing suppression and allelopathy effects on competitors; 3) transport processes; and 4) the formation of cysts in its life cycle to avoid the unfavorable environmental conditions and the germination of cysts to vegetative cells when conditions become suitable.

However, the underlying mechanisms of the initiation, growth, and die-off of *C. polykrikoides* blooms are not fully known due to the complex processes they involve, which prevents scientists predicting when, where, and how large they will bloom, and thus makes it difficult to find an effective strategy to control the bloom. Many related scientific questions for which answers remain unclear include: Where are the originating locations of *C. polykrikoides* blooms in the James River? Why is the Lafayette River, a sub-tributary of the James River, one of the important initiation places for the bloom (e.g., Mulholland et al., 2009)? More specifically, what are the characteristics of this sub-tributary and the environmental conditions that make it favorable for the initiation of
HABs in the lower James River? In addition, what environmental conditions control the interannual variability in the timing of HAB initiation?

While no consensus on the cause of HABs in the James River has been reached, possible impacts of transport processes have been considered in addition to local processes (e.g., Morse et al., 2013). Recent studies in Nauset Estuary on Cape Cod, USA, also suggest that water temperature and water retention are the two dominant factors in controlling the *Alexandrium fundyense* bloom that originates from three salt ponds within the estuary (Ralston et al., 2014; 2015). This suggests that a full examination of the effects of transport processes on triggering estuarine HAB events and its interaction with local processes is needed. Particularly, due to the complex interaction between physical forcings and geometry, the flushing effect may not be uniform throughout an estuary, making the role of flushing effect of transport processes more than a simple loss term that prevents the accumulation of algae and delays the occurrence of HABs in estuaries.

**Dissertation structure and objectives**

This dissertation focuses on the various effects of transport processes on phytoplankton dynamics in estuaries. Four chapters present the original research conducted as part of this dissertation. A quantitative understanding of various effects of transport processes is presented in Chapters 2 and 3, and their impacts on the initiation of estuarine HABs are highlighted in Chapters 4 and 5, in which a realistic case of annual *C. polykrikoides* blooms in the James River, a tributary of Chesapeake Bay, USA, is examined.

Chapter 2 examines the relative importance of local and transport processes (flushing effect) on the local variability of phytoplankton biomass over a range of
timescales from hours to years, in the upper James River, using the 1990–2013 monthly time series data of surface chlorophyll a from two Chesapeake Bay Program long-term monitoring stations and three-year high-frequency time series data of chlorophyll a collected at a continuous monitoring station. The concept of transport rate is introduced to quantify the flushing effect of transport processes, and its values are computed numerically using a tracer method. The validation of steady-state assumptions on phytoplankton dynamics is also examined.

Chapter 3 develops a simple yet inclusive mathematical model to study the impacts of transport processes on the phytoplankton dynamics in estuaries under various environmental conditions and variations of ecophysiology of phytoplankton. The patterns of relationships between phytoplankton biomass and flushing time under both nutrient and light limitation are revealed. The location of the zone of maximum phytoplankton biomass in estuaries is also discussed.

Chapter 4 quantitatively examines the flushing effect of transport processes on the location of HAB (C. polykrikoides) initiation, and compares its contribution to that of biological processes. A mathematical model is developed to study the HAB initiation in estuary-subestuary systems, and a numerical model for C. polykrikoides bloom based on EFDC is used to confirm the theoretical analysis for its initiation over the lower James River. For this chapter, as the focus is to examine effects of flushing and net biological processes rather than simulating C. polykrikoides to match the observations, some processes are not included such as nutrient and light limitation, uptake of DOC, and grazing. The swimming behavior of C. polykrikoides is considered by forcing the algae to
stay at the surface layer during the daytime, and the crucial effects of temperature and salinity on the specific growth rate of C. polykrikoides are explicitly accounted for.

Chapter 5 builds more processes into the numerical module for *C. polykrikoides* bloom in EFDC, including nutrient and light limitation on its growth, the abilities of mixotrophic growth, swimming behavior, grazing suppression, and formation and germination of resting cysts. The contribution of environmental conditions and competitive advantages of *C. polykrikoides* to the initiation of their bloom is studied. Particularly, the dominant factors on the timing of *C. polykrikoides* bloom are identified.
References


and Margalefidinium gen. nov. for C. polykrikoides and allied species (Gymnodiniales, Dinophyceae). Harmful Algae 63, 32-44.


Lucas, L.V., Thompson, J.K., Brown, L.R., 2009. Why are diverse relationships observed between phytoplankton biomass and transport time. Limnol. Oceanogr. 54(1), 381-390.


the identification and phylogeny of the fish-killing dinoflagellate *Cochlodinium polykrikoides*. Harmful Algae 9, 163–172.


## Description of some terms used in this dissertation.

<table>
<thead>
<tr>
<th>Terminology</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Phytoplankton dynamics</strong></td>
<td>The variability in phytoplankton biomass in this dissertation.</td>
</tr>
<tr>
<td><strong>Local processes</strong></td>
<td>Processes only defined for phytoplankton dynamics in this dissertation, regulating the growth and accumulation of phytoplankton at a location, including biological processes (such as photosynthesis, respiration/excretion, and grazing) and settling.</td>
</tr>
<tr>
<td><strong>(Physical) transport processes</strong></td>
<td>Processes including advective and diffusive transports, contributing to the dynamics of all kinds of dissolved and particulate substances (e.g., phytoplankton) in aquatic systems. For the phytoplankton dynamics, the processes regulate the accumulation of phytoplankton at a location through both direct and indirect effects.</td>
</tr>
<tr>
<td><strong>Flushing effect of transport processes</strong></td>
<td>The direct effect of transport processes that affects the dynamics of all kinds of dissolved and particulate substances (e.g., phytoplankton) in aquatic systems. The flushing effect on a specific substance is through transporting this substance, dependent on both hydrodynamics and spatial gradients of concentrations of the substance. The flushing effect is mainly referred to that on phytoplankton dynamics in this dissertation.</td>
</tr>
<tr>
<td><strong>Indirect effects of transport processes</strong></td>
<td>Other effects of transport processes besides flushing on phytoplankton dynamics by affecting local processes, through the distribution of heat energy and other dissolved and particulate substances (e.g., nutrients, salts, sediments, chromophoric dissolved organic matter, and grazers). The indirect effects are only referred to that on phytoplankton dynamics in this dissertation.</td>
</tr>
<tr>
<td><strong>Physical transport</strong></td>
<td>A type of transport processes that exists for the dynamics of all kinds of dissolved and particulate substances (e.g., phytoplankton) in aquatic systems. This dissertation mainly focuses on its contribution to phytoplankton dynamics. For physical transport, the spatial gradients of concentrations of the substance that generate the flushing effect are caused by the difference of concentrations in the incoming flows and that in the estuary, and also by the interactions between forcings (i.e., flow, tide, and wind) and geometry.</td>
</tr>
<tr>
<td><strong>Non-physical transport</strong></td>
<td>A type of transport processes that exists only for the dynamics of non-conservative substances such as phytoplankton. This dissertation mainly focuses on its contribution to phytoplankton dynamics. For non-physical transport, the spatial gradients of phytoplankton dynamics that generate the flushing effect are caused by the spatially inhomogeneous local processes.</td>
</tr>
<tr>
<td><strong>“Transport in” process/effect</strong></td>
<td>A term referred to transport processes or their flushing effect when the incoming water causing an increase in local phytoplankton biomass.</td>
</tr>
<tr>
<td><strong>“Transport out” process/effect</strong></td>
<td>A term referred to transport processes or their flushing effect when the incoming water causing a decrease in local phytoplankton biomass.</td>
</tr>
</tbody>
</table>
Figure 1.1. Schematic of the impact of local and transport processes on the variability of phytoplankton biomass. Flushing is the direct effect of transport processes, which can be caused by both physical transport and non-physical transport. In addition, the dotted black line shows that transport processes can also affect local processes through transporting heat energy and other dissolved and particulate substances (e.g., nutrients, salts, sediments, chromophoric dissolved organic matter, and grazers), which results in various indirect effects of transport processes on phytoplankton dynamics.
Chapter 2. The contribution of local and transport processes to phytoplankton biomass variability over different timescales in the Upper James River, Virginia

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Abstract

Although both local processes (photosynthesis, respiration, grazing, and settling), and transport processes (advective transport and diffusive transport) significantly affect local phytoplankton dynamics, it is difficult to separate their contributions and to investigate the relative importance of each process to the local variability of phytoplankton biomass over different timescales. A method of using the transport rate is introduced to quantify the contribution of transport processes. By combining the time-varying transport rate and high-frequency observed chlorophyll a data, we can explicitly examine the impact of local and transport processes on phytoplankton biomass over a range of timescales from hourly to annually. For the Upper James River, results show that the relative importance of local and transport processes differs on different timescales. Local processes dominate phytoplankton variability on daily to weekly timescales, whereas the contribution of transport processes increases on seasonal to annual timescales and reaches equilibrium with local processes. With the use of the transport rate and high-frequency chlorophyll a data, a method similar to the open water oxygen method for metabolism is also presented to estimate phytoplankton primary production.

Keywords: Transport rate; phytoplankton biomass; high-frequency observational data; primary production; timescale; open water method
Introduction

Phytoplankton dynamics, such as the variability of biomass at a location, are controlled by both local processes and physical transport processes. Local environmental conditions, such as temperature, light, nutrient supply, and grazing pressure, strongly regulate phytoplankton growth and primary production through both bottom-up and top-down controls (Kremer and Nixon, 1978). Transport processes in aquatic systems, including advective transport and diffusive transport, affect phytoplankton biomass by redistributing either biomass (direct effect), or dissolved and particulate substances such as nutrients that regulate phytoplankton growth (Lucas et al., 1999; Cloern, 2001; Paerl et al., 2006; Lancelot and Muylaert, 2011).

The interactions between local and transport processes are complex, and their contributions to phytoplankton dynamics can vary under different dynamic conditions. Because each external forcing (e.g., tide, flow, and wind) and environmental factor (light and temperature) has its own periodic fluctuation, the fluctuation will affect these two processes. We hypothesize that the relative importance of local and transport processes varies with timescales, which is also indicated by previous literature. Lucas et al. (2006) suggest that intra-daily variability of phytoplankton biomass is largely controlled by both the diurnal light cycle and the semidiurnal tidal oscillation, which implies the importance of contributions from both local environmental conditions and tide on the hourly timescale. Lake et al (2013) conducted measurements of photosynthetic rates and integrate daily production on summer months in the York River for both the spring and neap tides. They found that daily primary production does not show a clear variation during spring-neap cycle, which suggests that the local biological processes are dominant
for daily primary production rather than transport processes. Shen et al. (2008) show that the high biomasses of macroalgae and phytoplankton are the dominant cause of diurnal variation of dissolved oxygen concentration (DO) resulting from high production during daytime and high respiration at night. It suggests that local biological processes can be the dominant processes for primary production for the daily timescale in estuaries and shallow-water systems. Conversely, changes in freshwater discharge are considered to be a major factor driving strong seasonal and annual patterns of phytoplankton biomass in river-dominated estuaries, which modulate the location and strength of algal blooms through transport and nutrient supply (Valdes-Weaver et al., 2006; Reaugh et al., 2007; Costa et al., 2009; Peierls et al., 2012). Bukaveckas et al. (2011) show that algal blooms vary longitudinally along the Upper James River, and peak at the location where residence time becomes large due to a change of geometry, where about two-thirds of the net primary production is respired locally, and the remaining one-third is transported out of the region by fluvial and tidal advection. It suggests that the variability of phytoplankton biomass can be altered by a dynamic condition resulting from a change of local geometry.

These studies point out the relative importance of transport processes compared to local biological processes on particular timescales. However, due to the difficulty to explicitly separate their contributions, few contributions to the literature discuss how the comparison changes over a range of timescales from days to years. For example, Lucas et al. (2009) suggest that the variability of phytoplankton biomass can be described by a steady-state balance between local biological processes and transport processes described by residence time (i.e., it assumes that the variability of phytoplankton biomass is
negligible, and local and transport processes are equal but counterbalanced in contribution). While this steady-state balance assumption may hold for long-term timescales, it is questionable for short-term timescales, such as daily and weekly timescales. A relevant discussion on the comparison of relative importance of the two processes is helpful to answer on what range of timescales the assumption is valid.

The relative importance of each process on phytoplankton dynamics also needs to be evaluated for studies based on in situ observational data. As the development of instruments, many water quality parameters like DO and chlorophyll-a fluorescence can be measured in situ at 15-min intervals, which is often referred to as high-frequency data (http://web2.vims.edu/vecos/). The easy accessibility of high-frequency DO data has prompted wide applications of the open water method for estimating ecosystem primary production and metabolism (Odum, 1956; Howarth and Michaels, 2000; Cole et al., 2000; Caffrey, 2004; Kemp and Testa, 2011). When applying this method for estimating daily ecosystem primary production and metabolism, the effect of physical transport processes is usually neglected (Staehr et al., 2010). This estimation without considering transport, however, may have large biases when biological metabolism or DO is significantly influenced by transport processes (Kemp and Boynton, 1980). In the discussion section of this study, we applied a similar open water method to estimate phytoplankton primary production using high-frequency chl-a concentration (denoted by chl-a) data. The question as to whether the approach will cause more bias using phytoplankton data is unknown as spatial horizontal gradients of chl-a are often larger than those of DO. To evaluate the approach, the contribution of the transport processes on the daily timescale needs to be addressed.
The objective of this study is to evaluate how the relative importance of local and transport processes to the local variability of phytoplankton biomass vary over a range of timescales from hours to years. Because the transport processes not only affect the phytoplankton biomass but also affect the nutrient transport, when evaluating the relative importance of transport processes to biomass variability, the contribution of transport processes is restricted to the direct effect that redistributes biomass, and therefore other indirect effects that regulate phytoplankton growth, such as temperature, light availability, and nutrient limitation, are attributed to the contribution of local processes. The Upper James River was selected as the study site where both local and transport processes contribute greatly to phytoplankton dynamics (Bukaveckas et al., 2011).

**Methods**

We first indicate how to attribute the variability of phytoplankton biomass to the contributions of local and transport processes separately by decomposing the transport equation. Then we present a detailed procedure to compute each contribution by using *in situ* observational phytoplankton data and dynamic fields. The phytoplankton biomass dynamics and contribution of local processes were estimated using observational data, while the contribution of transport processes was estimated using dynamic fields computed by a dynamic model. Lastly, we statistically analyzed to evaluate the relative importance of local and transport processes, respectively, over a range of timescales.

*Decompose change of biomass*

The observation of phytoplankton data can be described by a three-dimensional transport equation with source and sink terms (Chapra, 1997). For simplicity, the first-
order reaction transport equation for volumetric phytoplankton biomass in the $x$-direction can be expressed as follows:

$$\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} - \frac{\partial}{\partial x} \left(K \frac{\partial C}{\partial x}\right) = gC$$

(2.1)

where $C$ denotes volumetric phytoplankton biomass (g C m$^{-3}$), $x$ and $t$ denote location and time, respectively, $u$ is current velocity (m s$^{-1}$), $K$ is diffusivity (m$^2$ s$^{-1}$), and $g$ denotes the growth rate of phytoplankton (d$^{-1}$) as a result of local processes. We combined growth and loss as a net growth term $g$, as $g = G - R - M$, where $G$ is the gross growth rate, $R$ is the respiration/excretion rate, and $M$ is the mortality rate due to both grazing and settling. The gross growth rate $G$ is a function of available light, nutrients, and temperature (Chapra, 1997). Note that Eq. (2.1) only includes terms in the $x$-direction for making the following derivations clear and all variables vary vertically. The terms on the left-hand side of Eq. (2.1) are the time derivative term, advective transport, and diffusive transport, respectively. Transport processes may increase local concentration of a property if the incoming water has higher concentrations, or decrease it if the incoming water has lower concentrations. Thus, the impact of transport processes does not only depend on hydrodynamic fields ($u$ and $K$) but also on the horizontal gradient of phytoplankton biomass ($\partial C / \partial x$).

Areal phytoplankton biomass (g C m$^{-2}$) can be conventionally obtained by vertical integration of volumetric phytoplankton biomass $C$ from the bottom to the surface, i.e.,

$$B = \int_0^H Cdz,$$

where $z$ is the vertical location, and $H$ is the water depth (m), $B = C \cdot H$ if the water column is well-mixed. As no phytoplankton is transported across the surface or
the bottom, integrating Eq. (2.1) gives the transport equation for areal phytoplankton biomass:

\[
\frac{\partial B}{\partial t} + \int_0^H \left[ u \frac{\partial C}{\partial x} - \frac{\partial}{\partial x} \left( K \frac{\partial C}{\partial x} \right) \right] dz = g_B B
\]  

(2.2)

where \( g_B \) is the vertical mean growth rate that accounts for the growth of areal biomass \( B \).

Analogous to the algal growth for biological process, we express transport processes as a transport rate \( F_B \), which is defined as

\[
F_B = \frac{1}{B} \int_0^H \left[ u \frac{\partial C}{\partial x} - \frac{\partial}{\partial x} \left( K \frac{\partial C}{\partial x} \right) \right] dz,
\]

(2.3)

and the governing equation (2.1) can be transformed into the expression:

\[
\frac{\partial B}{\partial t} = (g_B - F_B) B
\]

(2.4)

Dividing Eq. (2.4) by \( B \) on both sides gives the equation for the rates:

\[
\frac{1}{B} \frac{\partial B}{\partial t} = g_B + (-F_B)
\]

(2.5)

The impact of transport processes, expressed by \( F_B \) in Eq. (2.3), depends on \( \partial C/\partial x \). The non-zero \( \partial C/\partial x \) can be caused by either the change of dynamic conditions due to interaction between forcings (i.e., flow, tide) and geometry, or the spatially inhomogeneous local biological processes. Thus, the contribution of transport processes comes from both the dynamically induced transport (referred to as physical transport) and the non-physical transport. The contribution of non-physical transport can be expected to be relatively small locally as biological processes have less spatial gradient compared to the physical transport. Our aim is to understand the physical transport that contributes the
change of biomass. We introduce transport rate $F$ that only expresses the physical transport and we can now write Eq. (2.5) as follows:

\[
\begin{align*}
\dot{r} &= \frac{g_B}{Local} + \frac{(-F)}{Physical\ Transport} + \frac{(F - F_B)}{Non-physical\ transport} \\
&= \mu + \frac{(-F)}{Physical\ Transport}
\end{align*}
\]

where $r$ is the rate to express the variability of phytoplankton biomass as $r = \frac{1}{B} \frac{dB}{dt}$, and can be estimated from in situ observations of phytoplankton biomass $B$. The physical transport rate $F$ is unknown but it can be estimated by using hydrodynamic field and boundary conditions. $\mu = g_B + (F - F_B)$, which represents the growth rate of biomass that resulted from the combined local contributions. Once we know both values of $r$ and $F$, $\mu$ can be computed as $(r - F)$. When $g_B$ is zero (such as conservative properties) or it is spatially homogenous, $F$ equals $F_B$, and $\mu$ equals $g_B$. We will refer to $r$ as the relative growth rate, and to $\mu$ as the effective growth rate in the following sections. As $F$ only represents the transport contribution, a negative $F$ value corresponds to a “transport in” process that increases biomass, and a positive $F$ value corresponds to a “transport out” process that decreases biomass in accordance with Eq. (2.6), and a zero $F$ means there is no contribution of transport processes on local phytoplankton variability.

Eq. (2.6) demonstrates that the relative change of biomass is a result of competition between local and transport processes, and their contributions could be evaluated by comparing the effective growth rate $\mu$ to the transport rate $F$:

1) $\mu > F$ leads to $r > 0$, biomass increases

2) $\mu < F$ leads to $r < 0$, biomass decreases
3) $\mu = F$ leads to $r = 0$, biomass remains constant

Note that $\mu$ and $F$ could both have negative values. For example, the observed biomass $B$ at a location may increase at night ($r > 0$) when photosynthesis does not occur ($\mu < 0$), but biomass can increase due to a transport of biomass to this location ($F < 0$, “transport in”).

**Study site**

The James River is a tributary of the lower Chesapeake Bay located along the U.S. East Coast (Figure 2.1). The Upper James River is the tidal freshwater region where salinity is between 0 and 0.05. Calibrated time series data (15-min intervals) were collected from Chesapeake Bay Continuous Monitoring Station JMS073.37 at the Virginia Commonwealth University Rice Rivers Center (‘RC’, green triangle, http://web2.vims.edu/vecos/), from March to November 2006, 2007, and 2008. Data were measured using YSI 6600 data sondes with the Clean Sweep Extended Deployment System, include a number of parameters such as $chl$-a, temperature, turbidity, and water depth ($H$). All calibration and maintenances follow the YSI, Inc. operating manual methods. Particularly, $chl$-a data were obtained using laboratory calibrated sensors that converts *in vivo* fluorescence of chlorophyll $a$ to $chl$-a. The sondes were deployed around 0.5 to 0.9 m below the surface of the water during the observational period, while the mean water depth $H$ was about 2.5 m, and the mean tidal range was about 0.76 m at Station RC. Hourly irradiation data were obtained at nearby Richmond Airport. Also, monthly time series data of surface $chl$-a were collected from Chesapeake Bay Program Long-term Monitoring Stations TF5.4 and TF5.5 (blue squares).
The monthly data were used for three long-term timescales (monthly, seasonal, and annual), while the high-frequency data were used to analyze the relative importance of each contribution for continuously increased timescales from hourly to annually.

*Compute relative growth rate*

As the instantaneous relative growth rate is defined as \( r = \frac{\partial \ln B}{\partial t} \), the solution is \( B_{t+dt} = B_t e^{r dt} \) \((dt \to 0)\), which computes biomass measured at time \( t + dt \) \((B_{t+dt})\) from the biomass at time \( t \) \((B_t)\). This indicates that the relative growth rate can be calculated by the change of biomass. Thus, for a time series of *in situ* measured phytoplankton biomass with an observational time interval of \( \Delta t \), a time series of relative growth rate \( r_{\Delta t} \) that reflects the change in biomass from time \( t \) to \( t + \Delta t \) can be calculated as:

\[
r_{\Delta t} = \frac{1}{\Delta t} \left[ \ln(B_{t+\Delta t}) - \ln(B_t) \right] = \frac{1}{\Delta t} \ln \left( \frac{B_{t+\Delta t}}{B_t} \right)
\]

where \( B_t \) and \( B_{t+\Delta t} \) are the biomass measured at times \( t \) and \( t + \Delta t \), respectively. For example, \( r_{\Delta t} \) is the relative growth rate over daily timescale when \( \Delta t = 1 \) day; \( r_{\Delta t} \) is the relative growth rate over monthly timescale when \( \Delta t = 30 \) days.

*chl-a* data were used to obtain phytoplankton biomass. High-frequency *chl-a* data collected at 15-min intervals were first smoothed to 1-h averages. Using hourly mean *chl-a* in the units of \( \text{g m}^{-3} \), the biomass in the water column can be estimated as \( B = C \cdot H = (C: \text{chl-a}) \cdot \text{chl-a} \cdot H \). Here, the assumption of a well-mixed water column was applied. This assumption is reasonable for the shallow Upper James River with no persistent stratification (Bukaveckas et al., 2011), while the mean euphotic depth is about 2-3 m.
For a constant $C$: chl-$a$ ratio (g C/g chl-$a$), the rate can be estimated according to Eq. (2.7):

$$ r_{hr} = \frac{1}{\Delta t} \ln \left[ \frac{(chl-a-H)_{t+\Delta t}}{(chl-a-H)_{t}} \right], \text{ with } \Delta t = 1 \text{ hr}, $$

(2.8)

where the subscript “$hr$” denotes the observed hourly growth rate, and $C$: chl-$a$ ratio was withdrawn since it did not affect rate computation. The $C$: chl-$a$ ratio varies with seasons and species, which can be measured using observations. We applied a constant $C$: chl-$a$ ratio at Stations TF5.5 and RC as the seasonal variation of $C$:chl-$a$ ratio is relatively small and the average $C$: chl-$a$ ratio was $39 \pm 2$ g C/g chl-$a$ (Bukaveckas et al., 2011).

**Compute transport rate**

The transport rate $F$ can be computed based on a conservative tracer using a 3D numerical model. For a conservative tracer $\theta$, it is governed by Eq. (2.1) with zero growth rate (Note that $C$ is replaced by tracer concentration $\theta$ for clarity):

$$ \frac{\partial \theta}{\partial t} + \frac{\partial u \theta}{\partial x} + \frac{\partial v \theta}{\partial y} + \frac{\partial w \theta}{\partial z} = \frac{\partial}{\partial x} \left( K_x \frac{\partial \theta}{\partial x} \right) + \frac{\partial}{\partial y} \left( K_y \frac{\partial \theta}{\partial y} \right) + \frac{\partial}{\partial z} \left( K_z \frac{\partial \theta}{\partial z} \right) $$

(2.9)

where $u$, $v$, $w$ represent velocities in the $x$, $y$, and $z$ directions, respectively; and $K_x$, $K_y$, $K_z$ represent diffusivities in the $x$, $y$, and $z$ directions, respectively. For the modeling domain, no tracer comes from the boundaries at all times, i.e. $\theta_{in} = 0$ at both river and open boundaries. By using this boundary condition, it assumes that phytoplankton in the Upper James River are mainly from autochthonous sources, which is reasonable in James River as the chl-$a$ at the fall-line of the James River is much lower than the chl-$a$ downstream (Bukaveckas et al., 2011). The initial condition, $\theta_0 = 1$, is set everywhere within the domain. The tracer is transported by the dynamic fields, which results in the change of
horizontal tracer gradient due to the change of geometry and dynamic forcing conditions.

Therefore, the transport rate for tracer concentration, $F_\theta$, can be computed as $F_\theta = -\frac{\partial \theta}{\partial t} = -\frac{\partial \ln \theta}{\partial t}$, and the transport rate $F$ used in this paper to represent the contribution of transport processes can be computed as $F = -\frac{1}{\int_0^\infty \theta dz} \frac{\partial}{\partial t} \int_0^\infty \theta dz$. Because the rate of $F$ is normalized by the tracer, the initial condition and the magnitude of the tracer concentration will not affect the model results after a sufficient initial simulation period, and the impact of the initial condition is negligible in the calculation of $F$.

A real-time three-dimensional numerical model for the James River was developed (Shen et al., 2016) using the Environmental Fluid Dynamics Code (EFDC), and it has a good spatial resolution to represent the local variation of complex geometry. The model was forced by hourly tide and salinity at the mouth and hourly wind and heat flux obtained at nearby airport stations, which account for both tidal and meteorological variation. The model was calibrated and verified from 1990–2013 for both hydrodynamics and water quality (Shen et al., 2016). There are a total of 3,066 grid cells in the horizontal and eight layers in the vertical. The model was also used to compute water age in the James River (Shen and Lin, 2006). As the cross-section of the Upper James is narrow and located in the freshwater region without salinity-induced stratification, the volume-controlled freshwater residence time was estimated as the difference of the lateral mean water age at the control section near Stations TF5.4 and TF5.5 along the main channel.
With the use of the numerical model, the transport rate $F$ over the entire time series from 2006 to 2008 was computed based on Eq. (2.9) with specific boundary and initial conditions described above.

**Compute rates for each timescale**

Mean rates for timescales longer than the hourly timescale can be obtained by taking the average of the hourly rate $r_{hr}$ over the given time interval of $\Delta t$ through the following equation:

$$\bar{r} = \frac{1}{\Delta t} \int_{t}^{t+\Delta t} r_{hr} dt = \frac{1}{\Delta t} \int_{t}^{t+\Delta t} \frac{1}{B} \frac{\partial \ln B}{\partial t} dt = \frac{1}{\Delta t} \left[ \ln(B_{t+\Delta t}) - \ln(B_t) \right]$$  \hspace{1cm} (2.10)

It can be seen that the mean rate only depends on the biomass at the beginning and ending time for the interval of $\Delta t$. Therefore, rates for timescales longer than the hourly timescale can be obtained by two equivalent methods, either using Eq. (2.7) with $\Delta t$ equals the particular timescale, or using the average as Eq. (2.10). Here, the two methods Eq. (2.7) and Eq. (2.10) were applied to data at Station TF5.5 and RC, respectively. After we obtain both $\bar{r}$ and $\bar{F}$, the effective growth rate $\bar{\mu}$ on that timescale was calculated using Eq. (2.6), $\bar{\mu} = \bar{r} + \bar{F}$. The overbar will be dropped hereafter when we present results with the understanding that the values are mean values.

**Evaluate contributions of local and transport processes**

Eq. (2.6) provides a way to evaluate the contributions of local processes and transport processes to phytoplankton variability in terms of effective growth rate $\mu$ and transport rate $F$. A statistical method is applied to evaluate the contributions of local and transport processes. Correlation coefficient values, $R^2$, between $F$ and $r$ and between $\mu$ and $r$, are calculated for each timescale to examine the proportions of the variance of $r$
that could be explained by $F$ and $\mu$, respectively. Additionally, the overall relative importance of local and transport processes on each timescale can be quantified by comparing the root-mean-square (rms) of the entire time series of $F$ and $\mu$ on that timescale:

$$Local: \frac{\text{rms}(\mu)}{\text{rms}(F)+\text{rms}(\mu)}; \quad Transport: \frac{\text{rms}(F)}{\text{rms}(F)+\text{rms}(\mu)} \quad (2.11)$$

Note that, on each timescale, the relative importance of each process computed by Eq. (2.11) used the entire time series of data during the observational period (1990-2013 for Station TF5.5 and 2006-2008 for Station RC). The analysis reflects their overall contribution during the entire observational period on this timescale, indicating the averaged relative importance or the contribution under normal conditions. The result of short timescale does not represent their contribution over a shorter period during abnormal conditions. For example, episodic events, such as storm surges and large discharge events, may dramatically increase contribution of transport processes in a few days at Station RC, and have greater impact on phytoplankton dynamics than local processes during those events; however, these signals were filtered out when considering the entire observational period, and it will later be shown below that the change of phytoplankton biomass on daily timescales was overall dominated by local processes.

**Results**

*Evaluation of contribution of transport processes*

By comparing the transport rate to the relative growth rate, the contribution of transport process to phytoplankton biomass variability was evaluated over a sequence of timescales. Note that for long-term timescales (monthly, seasonal, and annual), we only
present results from long-term monitoring data at Station TF5.5, and summarize results from high-frequency data at Station RC at Table 2.1, and the results from two data sources are comparable.

**Short-term timescales**

The correlation of the relative growth rate \( r \) and the transport rate \( F \) for a 3-year period was analyzed using the high-frequency data for timescales shorter than daily (Table 2.1). Overall, their correlations were relatively low, suggesting that transport processes were not the dominant processes to phytoplankton variability for those timescales during the observation period.

The tide in this estuary shows a semidiurnal cycle. From a transport perspective, the net effect of transport on biomass is more important in tidal and daily timescales. However, for an intratidal scale, the tide can have a large influence on biomass during the flood and ebb periods, which will modulate the phytoplankton concentration in the water column. The contribution of tide, therefore, is expected to play an important role in the phytoplankton dynamics during food and ebb periods. An example from October 2008 is shown in Figure 2.2. Rates \( r \) and \( F \) on the timescale of 6 h were significantly linearly correlated \( (R^2 = 0.52, p < 0.001) \). The correlation was even higher when only nighttime data were used (Figure 2.2c, \( R^2 = 0.54, p < 0.001 \)). A strong tidal signal was observed that indicated both rates were modulated by the semidiurnal tide.

The 6-h averaged time series data revealed that increases in phytoplankton biomass occurred during the night \( (r > 0) \) when no photosynthesis occurred (Figure 2.2c), and the mass increase corresponded to a negative transport rate (note that figure plots use \(-F\) ), which suggests that the increases in biomass at night were caused by a “transport in”
process due to the transport induced by tides and freshwater discharge. Although the tide can modulate the intratidal transport processes, the large intratidal variability will be filtered for a tidal or daily period and the influence of net physical transport processes on biomass on tidal and daily timescales is not as important as local processes (Table 2.1).

**Monthly timescale**

The time series of chl-a and local residence time for the period of 2000-2013 at Station TF5.5 are plotted in Figure 2.3a. This figure shows that chl-a and residence time had the same variations. On a monthly timescale, chl-a correlated with the residence time ($R^2 = 0.33, p < 0.001$, Figure 2.3b). Lower chl-a was shown to correspond with shorter residence time, although the correlation was more diverse when residence time was long, which usually occurred in the summer, indicating that the contribution of local processes is more important during summer when the dynamic conditions become favorable for growth.

The transport rate $F$ was correlated to the relative growth rate $r$ at Station TF5.5 for the period from 2000 to 2013 ($R^2 = 0.25, p < 0.001$) as shown in Figure 2.3c and 2.3d. Variations of $r$ and $F$ were in phase, in general, which suggests that the monthly variability of phytoplankton biomass is modulated by hydrodynamics. Note that only 13-year result was presented in Figure 2.3 for making the plot clear, and the correlation between $r$ and $F$ during the entire years of long-term monitoring data (1990-2013) was shown in Table 2.1.

**Seasonal timescale**

For the seasonal timescale, analysis of the time-series data from the years 1990 to 2013 showed that transport rate $F$ was correlated with relative growth rate $r$ ($R^2 = 0.22, p$
The transport rate $F$ remained positive, and transport processes had a net “transport out” effect on phytoplankton biomass throughout the observation period (Figure 2.4a). The relative growth rate $r$ had either positive or negative values, but the corresponding effective growth rate $\mu$ was always positive, suggesting that the contribution of local processes leads to an increase in phytoplankton biomass.

All three rates ($r$, $F$, and $\mu$) showed seasonal variations (Figure 2.5). The transport rate, $F$, appeared to have smaller magnitudes during summer than during other seasons, corresponding to the lowest freshwater discharge into the James River in the summer. The effective growth rate, $\mu$, seemed to be lower during summer and fall than during spring and winter. This seasonal change can be attributed to a change in composition of algal species and an increase in respiration, grazing, and nutrient limitation during the summer (Marshall and Egerton, 2013). As a consequence, the relative growth rate tended to be low during summer and fall, even though $F$ was lower. It shows that $\mu$ was much larger than $r$, after removal of the impact of transport processes (Figure 2.5), indicating the values of $r$ would underestimate the effective growth rate of phytoplankton without considering any effect of the physical transport.

**Annual timescale**

For the annual timescale, the correlation between $F$ and $r$ was significant ($R^2 = 0.48$, $p < 0.001$, Figure 2.4d) and it was higher than the correlation between $\mu$ and $r$ ($R^2 = 0.24$, $p < 0.001$). Similar to the seasonal timescale, both $F$ and $\mu$ remained positive, while the magnitude of the relative growth rate $r$ diminished (Figure 2.4c), indicative of the balance between local and transport processes. The contribution of transport processes showed a net “transport out” effect on interannual phytoplankton biomass variability in
the Upper James River, i.e. more biomass was transported out of this region than was transported in.

**Rate variations**

The daily effective growth rate, $\mu$, may be of the same magnitude as the gross growth rate, $G$, if respiration and grazing pressure are very low. Theoretically, the daily gross growth rate represents photosynthetic production, and it has maximum values ranging from 1 to 5 d$^{-1}$ dependent on the temperature, nutrients, and phytoplankton species (Eppley, 1972; Brush et al., 2002). However, the estimated effective growth rate may be an order of magnitude smaller than the theoretical maximum values, due to suppression of photosynthesis by nutrient and light limitation, respiration, settling, and grazing. The variability of $\mu$ reflects a net response of phytoplankton to the change of local environment conditions.

We used median rates as representative of typical values for each timescale (Figure 2.6a). Positive values of the rates $r$, $\mu$ and $-F$ corresponded to the increase of phytoplankton biomass whereas negative values indicated a decrease. Both medians of positive and negative rates, respectively, are listed in Table 2.1. In general, both the medians of positive and negative rates decreased as the timescale increased.

For seasonal or longer timescales, the medians of transport rates ($-F$) were negative at Station RC (Table 2.1). In fact, $-F$ was always negative on these long-term timescales, suggesting that the net contribution of transport processes flushed biomass downstream (“transport out”). $\mu$ was always positive, suggesting that the net contribution of local processes was to increase the phytoplankton biomass, i.e., phytoplankton primary
production was larger than the loss from respiration, excretion, settling, and grazing. The competition between local and transport processes leads to either an increase or a decrease of phytoplankton biomass, which was reflected by the existence of both positive and negative values of $r$ when the timescale exceeded the monthly timescale.

**Relative importance of local and transport processes**

The increased correlation between rates $F$ and $r$ from a monthly timescale to an annual timescale, based on analysis of long-term monthly monitoring data at Station TF5.5, suggested that the relative importance of the transport processes to phytoplankton variability increases when evaluating it on a longer timescale. This result was consistent with the evaluation using high-frequency data at Station RC during 2006 to 2008 (Figure 2.6c and 2.6d). The coefficient of determination, $R^2$, also showed that the proportions of $r$ variance that could be explained by the transport rate $F$ increased with the increase of timescale, whereas the proportions that could be explained by the effective growth rate, $\mu$, decreased.

The relative importance of contributions of local and transport processes over continuously increasing timescales was compared for the period from 2006 to 2008 (Figure 2.6d). The relative importance of transport processes had an increasing trend with increasing timescale whereas that of local processes had a decreasing trend, and they were equally important in the monthly timescale at Station RC. The relative importance of each contribution was more diverse in timescales shorter than daily; it shows that the contribution of local processes peaked on daily and tidal timescales, whereas the transport processes showed peaked relative importance on timescales around 6 and 18 h (Figure 2.6d). These variations are caused by the intratidal variability and will be
discussed below. It can be seen that tide also modulates the local processes though the net tidal contribution is less.

Discussion

Factors affecting local and transport processes

Similar to the hydrodynamic conditions investigated for many other estuaries (Wang et al., 2004; Barcena et al., 2012; Lemagie and Lerczak, 2015), river inflow and tides are the two primary factors affecting the transport processes in the Upper James River and contribute to phytoplankton biomass dynamics, while other forcings such as wind play less important roles.

River inflow determines the overall net long-term advection characteristics of the Upper James River. The phytoplankton biomass transported from the upstream freshwater is generally found to be smaller than the biomass generated in the tidal freshwater region and estuary (e.g., Bukaveckas et al., 2011; Peierls et al., 2012; Paerl et al., 2014). As the residual current always flows downstream, the biomass is transported downstream, resulting in a net “transport out” effect on phytoplankton biomass when viewing it from a long-term perspective. Consistently, river inflow also had the net “transport out” effect in the Upper James River, reflected by only positive medians of transport rate $F$ found on the annual timescale (Table 2.1).

Tides also have substantial effects on phytoplankton variability. The dominant constituent of tide in the Upper James River is the semi-diurnal $M_2$ tide with a 12.42-h tidal period. Both advective and diffusive transport are enhanced during either flood or ebb tides, which increase the relative importance of transport processes on a timescale of about one-half of the tidal period (around 6 h); whereas the largest relative importance of
local processes is around tidal and daily timescales, because the net impact on transport processes from tides is minimal by averaging over a complete tidal cycle, it is consistent with results in Figure 2.6c and 2.6d.

The local processes are fundamental for phytoplankton variability, regardless of the transport processes. It is found that local processes always have an important contribution to the phytoplankton biomass dynamics in the Upper James River even on the timescales with a large physical contribution (Figure 2.6d). For the monthly timescale, the results are more scattered with an increase of residence time (Figure 2.3b), these large residence times usually occurred in summers when both riverine flows and transport rate were small (Figure 2.5), and the contribution of local processes became relatively more important than that of transport processes. Local processes play critical roles on diurnal timescales, owing to the well-recognized diurnal variation that phytoplankton biomass increases during the day because of photosynthesis, but decreases at night.

The contribution of local processes also showed seasonal variations represented by the effective growth rate \( \mu \) (Figure 2.5). In general, a smaller value of \( \mu \) appeared in summer and fall than during winter and spring. One possible reason for this seasonal change is the phytoplankton species succession. The “transport out” effect by freshwater has been found to be a determining factor on phytoplankton growth and composition in river-dominated estuaries as it tends to select fast-growing species in high-flow conditions (Ferreira et al., 2005; Paerl et al., 2006; Costa et al., 2009). The maximum freshwater discharge occurs in the winter and spring in the James River. The enhanced “transport out” processes along with abundant nutrients favors freshwater diatoms that
have relatively high intrinsic growth rates to become the dominant species in these two seasons. In the summer and fall, when the “transport out” effect is reduced and residence time increases, the percentage contribution of dinoflagellates and cyanobacteria with lower intrinsic growth rates increases (Valdes-Weaver et al., 2006; Marshall and Egerton, 2013). Temperature, nutrients, and grazing may be other factors affecting the seasonal change of the contribution of local biological processes, as respiration and grazing often peak in summer while nutrient limitation is severe though with large benthic flux input of recycled nutrients (Kemp et al., 2005).

**Long-term validation**

Complex phytoplankton dynamics can be described by the balance between local and transport processes under steady-state conditions (Lucas et al., 2009), and it is expected that this balance is acceptable on long-term timescales but may be questionable on shorter timescales. Therefore, it is interesting to examine on which timescales this assumption is valid.

The steady-state assumption is equivalent to assuming that \( r = 0 \), or that the magnitude of \( r \) is negligible compared to the magnitudes of \( \mu \) and \( F \). Direct comparisons of \( r \) to \( \mu \) and \( F \) show that the assumption is valid for seasonal to annual timescales in the region as \( r \) is small. By using the root-mean-square (\( rms \)) of each rate to quantify their magnitudes, it is found that the ratios of \( rms(F) \) to \( rms(r) \) and \( rms(\mu) \) to \( rms(r) \) increased as timescales increased (Figure 2.6b). This suggests that contributions of local and transport processes have the tendency to be balanced only when the timescale is longer than 10 days (Figure 2.6a and 2.6b). Their difference becomes more significant for hourly to daily timescales.
**Phytoplankton primary production**

The open water method using high-frequency dissolved oxygen data has been widely applied to estimate gross primary production, ecosystem respiration, and net ecosystem metabolism (Staehr et al., 2012). Because of the influence of advection processes, high-frequency phytoplankton data have not often been used to estimate these metabolic rates. Here, we used high-frequency chl-\(\alpha\) data to estimate phytoplankton gross primary productivity similar to open water oxygen method and to evaluate the influence of physical transport on estimation of the rate.

For each time interval (e.g. \(\Delta t = 15\) minutes), the change of phytoplankton biomass \((\Delta B)\) is described by the equation below:

\[
\frac{\Delta B}{\Delta t} = GPP - RPP - FPP
\]  

where \(GPP\) is the 15-minute phytoplankton gross primary productivity (g C m\(^{-2}\) 15 min\(^{-1}\)), \(RPP\) is the 15-minute rate of total phytoplankton respiration and consumption (including respiration, grazing, and settling, g C m\(^{-2}\) 15 min\(^{-1}\)), which represents total biological losses. \(FPP\) is the 15-minute rate of transport in or out of phytoplankton by transport processes (g C m\(^{-2}\) 15 min\(^{-1}\)); a positive \(FPP\) (-\(F < 0\)) means that the carbon produced by local biological processes is transported out of this location and benefits the food web in adjacent areas (Cloern, 2007). We also use \(DPP\) to denote the difference between \(GPP\) and \(RPP\),

\[
DPP = GPP - RPP.
\]  

\(FPP\) is estimated from the product of phytoplankton biomass and transport rate, and it was calculated using the transport rate \(F\) computed from the numerical model in
this study \( (FPP = F \cdot B) \). The method for computing \( GPP \) and \( RPP \) is similar to the open water method, and \( DPP \) was first computed by summation of \( \Delta B / \Delta t \) and \( FPP \) for each time interval. Daily \( RPP \) was estimated from the extrapolation of nighttime \( RPP \) (= the sum of nighttime 15-minute \( DPP \)) to one day; and daily \( GPP \) was estimated, according to Eq. (2.13), from daily \( DPP \) (= the sum of 15-minute \( DPP \) over one day) plus daily \( RPP \). Both daily \( GPP \) and \( RPP \) are in units of g C m\(^{-2}\) d\(^{-1}\). Unrealistic negative values of daily \( GPP \) were found for some days (about 24%), and they were excluded from the calculations following the way of the open water method (Caffrey, 2003). Most of the negative daily \( GPP \) values appeared on rainy days when precipitation may enhance the flushing effect from runoff from adjacent watersheds. The results are representative of primary productivity and metabolic rates under normal weather conditions. Note that the transport rate \( F \) used was computed from the numerical model that only represents the physical transport as shown in Eq. (2.6), and the results are only used to quantify the influence of physical transport on the estimation of \( GPP \).

For the Upper James River, the typical \( C: chl-a \) ratio equals 39 g C/g chl-a with small seasonal variability (Bukaveckas et al., 2011). Because we have no winter data, the annual phytoplankton primary production cannot be correctly estimated. Nevertheless, we assumed that gross primary production in winter was lower than or equal to the minimum of seasonal production. The annual phytoplankton gross primary production were estimated to be about 255.90, 685.91, and 486.26 g C m\(^{-2}\) yr\(^{-1}\), respectively, for the years 2006, 2007, and 2008 (Table 2.2). These estimations were comparable to the 12-year averaged (1989-2001) annual phytoplankton gross primary production, around 230 g C m\(^{-2}\) yr\(^{-1}\), measured in the laboratory using \(^{14}\)C method at Station TF5.5 (Nesius et al.,
An example of the seasonal averages of GPP, RPP, and DPP in 2008 are also shown (Figure 2.7), and the seasonal average of GPP during the summer 2008 was 2.31 g C m\(^{-2}\) d\(^{-1}\), close to the seasonal mean rate of 2.11 g C m\(^{-2}\) d\(^{-1}\) using the method of dissolved oxygen incubations for the nearby York River during the same time period (Lake et al., 2013).

The amount of primary production transported out ranges from 7% to 13% (FPP/GPP). It suggests that the net physical transport processes have a minor impact on estimates of GPP and RPP on daily scale under normal weather conditions. This is consistent with the analysis of biomass variability on the daily timescale.

Conclusions

To evaluate the contribution of transport processes to phytoplankton biomass variability using high-frequency observational data, we introduced the transport rate method, which enables us to estimate each contribution exclusively as a first-order approximation. The Upper James River was selected as the study site, and the results support the hypothesis that both local and transport processes contributed significantly to the local variability of phytoplankton biomass, but their relative importance changed on different timescales. On a short-term basis such as daily and weekly timescales, even though the transport processes could modulate phytoplankton biomass variability on an intratidal timescale due to flood and ebb variations, the intratidal variations will be removed over a tidal cycle. The local processes dominated the overall contributions during the observational period; however, the relative importance of transport processes tended to be equivalent to the local processes in the long-term timescales (e.g., seasonal and annual). Another analysis of this study shows that the local processes were almost
balanced by the transport process on the seasonal and annual timescales, and approached a steady-state condition for phytoplankton dynamics, whereas the time derivative term became important for shorter timescales.

Examination of the transport rate revealed that transport processes exhibited a persistent “transport out” effect on long-term timescales to decrease in situ phytoplankton biomass in this region, but it was not the case for timescales shorter than seasonal that transport processes could either increase or decrease the biomass, corresponding to “transport in” and “transport out” processes, respectively.

Transport processes had a small impact on the estimation of daily gross phytoplankton productivity. By applying a method analogous to the open water oxygen method that calculates phytoplankton gross primary production using 15-minute observational data, the percentage of production flushed out was around 7-13% under normal weather conditions.

The use of the transport rate is a first-order approximation for quantifying transport processes. Zero concentrations were applied at the boundaries for this study, and the computed transport rate \( F \) did not account for the possible effects of inputs from boundaries (though these are very low), and therefore the contribution of the transport processes considered was the redistribution of biomass produced within the study area due to the change of dynamics and geometry. The additional bias of the transport rate on the hourly timescale could come from the numerical method and model grid resolution that may not be able to simulate the microscale variability of physical processes, which causes the patchiness of phytoplankton distribution that makes the observed \( chl-a \) data fluctuate highly with a change of dynamic conditions. Besides the use of the numerical
calculation, the transport rate can also be estimated based on field observations of current, salinity and water depth. In addition, the pattern of the relative importance of local and transport processes on different timescales demonstrated in the Upper James River may vary at other locations of the estuary, which would warrant further study.

Acknowledgments

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Table 2.1. Estimated values for each parameter for different timescales based on analysis of three years of high-frequency continuous monitoring data at Station JMS073.37 (RC) and 24 years of long-term monitoring data at Station TF5.5 (1990-2013). Results of transport rate $F$ are computed from the 3D numerical model.

<table>
<thead>
<tr>
<th>Statistical parameters for each timescales</th>
<th>Continuous Monitoring Station (JMS073.37) 2006 – 2008</th>
<th>Long-term Monitoring Station (TF5.5) 1990 – 2013</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medians of (d$^{-1}$)</td>
<td>Hourly (1 h)</td>
<td>Tidal (12.5 h)</td>
</tr>
<tr>
<td>positive $r$</td>
<td>1.3795</td>
<td>0.2437</td>
</tr>
<tr>
<td>negative $r$</td>
<td>-1.2740</td>
<td>-0.2443</td>
</tr>
<tr>
<td>positive $-F$</td>
<td>1.3174</td>
<td>0.1359</td>
</tr>
<tr>
<td>negative $-F$</td>
<td>-1.1343</td>
<td>-0.1481</td>
</tr>
<tr>
<td>positive $\mu$</td>
<td>1.3555</td>
<td>0.2987</td>
</tr>
<tr>
<td>negative $\mu$</td>
<td>-1.3179</td>
<td>-0.2779</td>
</tr>
<tr>
<td>Correlation of determination $R^2$</td>
<td>$F \sim r$</td>
<td>0.0138</td>
</tr>
<tr>
<td></td>
<td>$\mu \sim r$</td>
<td>0.9226</td>
</tr>
<tr>
<td>Relatively Importance</td>
<td>Transport</td>
<td>0.2189</td>
</tr>
<tr>
<td></td>
<td>Local</td>
<td>0.7811</td>
</tr>
</tbody>
</table>
Table 2.2. Estimates of annual phytoplankton gross primary production ($GPP$), total biological losses ($RPP$, including respiration, grazing and settling), $DPP$ ($GPP - RPP$), the amount of production flushed out ($FPP$) at Station RC for the three years 2006 to 2008. $FPP/GPP$ representing the fraction of production flushed out are also presented.

<table>
<thead>
<tr>
<th>Annual phytoplankton metabolic rates</th>
<th>$GPP^1$</th>
<th>$RPP^1$</th>
<th>$DPP^1$</th>
<th>$FPP^2$</th>
<th>$\frac{FPP}{GPP}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(g C m$^{-2}$ yr$^{-1}$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>255.90</td>
<td>274.29</td>
<td>-18.39</td>
<td>32.65</td>
<td>12.76%</td>
</tr>
<tr>
<td>2007</td>
<td>685.91</td>
<td>688.50</td>
<td>-2.59</td>
<td>47.76</td>
<td>6.96%</td>
</tr>
<tr>
<td>2008</td>
<td>486.26</td>
<td>512.42</td>
<td>-26.16</td>
<td>31.87</td>
<td>6.55%</td>
</tr>
</tbody>
</table>

$^1$estimated using 15-minute observational data

$^2$estimated using numerical model
Figure 2.1. Map of the Chesapeake Bay and James River. Locations for the Continuous Monitoring Stations RC, and the Long-term Monitoring Stations TF5.4 and TF5.5 are shown, respectively, by the green triangle and the blue squares. The domain of the James River 3D model is also presented.
Figure 2.2. Comparison of the 6-h moving averages of $r$ and $F$ at Station RC in October 2008. a) time series of relative growth rate $r$ (red line), transport rate $F$ (blue line, here plotted as $-F$), and irradiance (black line); b) the relation between $-F$ and $r$ using all data during the month (daytime + nighttime); c) the relation between $-F$ and $r$ only at nighttime.

$R^2 = 0.525, p < 0.001$

$r = 0.460(F) = 0.001$

$R^2 = 0.544, p < 0.001$

$r = 0.447(F) = 0.194$
Figure 2.3. Contributions of transport processes on monthly timescales at Station TF5.5. 
a) time series of chl-a (black line, $\mu g \text{ L}^{-1}$) and residence time (blue line); b) the relationship between chl-a and residence time; c) time series of relative growth rate $r$ (black line) and transport rate $F$ (blue line, $-F$); d) the relationship between $-F$ and $r$. The data used are from the years 2000 to 2013.
Figure 2.4. Rates $r$, -$F$, and $\mu$ on seasonal and annual timescales during the years 1990 to 2013 at Station TF5.5.
Figure 2.5. Box plot for rates $r$, -$F$, and $\mu$ on seasonal timescale during the years 1990 to 2013 at Station TF5.5. Horizontal lines in the boxes indicate medians, boxes indicate interquartile ranges, whiskers indicate the extremes that are set to be 1.5 times the range from the boxes, notches in boxes indicate the 95% confidence intervals of medians, and circles indicate outliers.
Figure 2.6. a) Medians over different timescales for positive and negative rates, respectively. Transport rate (\(-F\), blue lines), relative growth rate \(r\) (red lines), and growth rate \(\mu\) (green lines); b) Ratios of root-mean-square of rates. Blue line denotes \(\text{rms}(F)\) to \(\text{rms}(r)\), green line denotes \(\text{rms}(\mu)\) to \(\text{rms}(r)\); c) coefficient of determination \(R^2\) between \(F\) and \(r\) (blue line) and between \(\mu\) and \(r\) (green line); and d) estimates of the relative importance of transport processes (blue line) and local processes (green line).
Figure 2.7. Phytoplankton primary production in each season of 2008 at Station RC, by assuming $FPP = F \cdot B$ (winter data are not available). Phytoplankton gross primary productivity ($GPP$), phytoplankton total biological losses ($RPP$, including respiration, grazing and settling), phytoplankton $DPP$ ($GPP - RPP$), error bars represent the 95% confidence intervals.
Chapter 3. Relationships between phytoplankton biomass and transport time in riverine nutrient-dominated estuaries
Abstract

In an estuarine system, physical transport processes can impact phytoplankton dynamics through various mechanisms. The direct effect is through flushing that transports phytoplankton outside of the system, and the indirect effects are through the redistribution of dissolved or particulate constituents (e.g., nutrients, salts, sediments, and chromophoric dissolved organic matter) that can affect biological processes, by regulating light and/or nutrient availabilities. In this study, we developed a simple yet inclusive mathematical model to describe the temporal and spatial variability in phytoplankton biomass in response to various effects of physical transport. The model provides insight into the relationship between phytoplankton biomass and flushing time and its variations with environmental conditions resulting from the combined effects of light and nutrient availabilities and flushing on phytoplankton. This model confirms diverse relationships between phytoplankton biomass and flushing time suggested by observations, which can be either monotonic or non-monotonic in response to the effect of physical transport processes.

The model reveals three distinguished patterns between phytoplankton biomass and flushing time for riverine nutrient-dominated estuaries. If flushing time is sufficiently long (weak flushing), it will cause a nutrient limitation and all three patterns will show a negative relationship between flushing time and phytoplankton biomass. As flushing time decreases (strong flushing), the Pattern-1 system shifts to a positive relationship when the system shifts from nutrient limitation to light limitation, and the Pattern-2 system remains a negative relationship if nutrient limitation remains unchanged until the flushing effect on the export of both phytoplankton and nutrients becomes dominant. For the Pattern-3
system, it shifts from nutrient limitation to light limitation first and then returns to nutrient limitation as flushing time decreases. At an extremely short flushing time, flushing on phytoplankton can be the dominant effect to prevent phytoplankton accumulation in the system. In addition, this model confirms the existing of a zone of maximum phytoplankton biomass in an estuary where biomass is much higher than elsewhere. This zone locates at the transition zone where the light limitation shifts to nutrient limitation for both the Pattern-1 and Pattern-3 systems, but the location moves farther upstream for the Pattern-2 system.
Introduction

Phytoplankton is a major primary producer that provides organic matter to support the food web of aquatic ecosystems. It is estimated that about 60 Pg of organic carbon is produced by phytoplankton globally each year (Behrenfeld et al., 2005). In highly productive estuaries and coasts, the increase of biomass and change in composition of phytoplankton can affect the health status of aquatic ecosystems through the loss of macrophytes and the increase in both harmful algal blooms and hypoxia events (Cloern, 2001; Kemp et al., 2005).

The variability of phytoplankton biomass at a location is controlled by both local processes (photosynthesis, respiration/excretion, grazing, sinking) and transport processes (advective and dispersive transports) (Kremer and Nixon, 1978). The biological processes determine the balance of growth and loss of phytoplankton through bottom-up and top-down controls, which are affected by local environmental conditions (temperature, salinity, light availability, nutrient supply, grazing pressure, and so on).

The effects of physical transport processes can be as important as biological processes on phytoplankton dynamics, particularly over long-term timescales (Qin and Shen, 2017). The unique feature of transport processes in estuaries is their key role in transporting various dissolved and particulate substances along the estuary resulting in generating horizontal gradients from the head to the mouth due to estuarine circulation that is controlled by various physical forcings, including river inflow, tide, and wind. For example, Boynton and Kemp (2000) show that while phytoplankton growth is affected by various environmental factors, the annual flow alone can explain 78% of the temporal variations in biomass and 59% of that in the production at a mainstem station in the upper
Chesapeake Bay. Transport processes can affect phytoplankton biomass in direct and indirect ways (Lucas et al., 1999; Cloern, 2001; Paerl et al., 2006; Lancelot and Muylaert, 2011).

The direct effect of transport processes that moves phytoplankton out of the system has been well-recognized. Generally, a shorter time of water retention flushes more phytoplankton out, and this flushing effect is suggested to be able to alter algal community abundance and composition (e.g., Ferreira et al., 2005; Paerl et al., 2006; Costa et al., 2009). To quantify the flushing effect for a waterbody, a variety of concepts of transport time, such as residence time, flushing time, and age, are commonly used (Monsen et al., 2002). Transport time varies over a wide range from less than 1 day to more than 1 year for estuaries (Nixon et al., 1996; Du and Shen, 2016). A system with long transport time is characterized with a slow exchange of water parcels and their carrying substances between inside and outside of the system, which is a situation favorable for the accumulation of substances like nutrients and phytoplankton. Hence, a positive phytoplankton-transport time relationship is suggested as a result of this flushing effect that has been observed in many estuaries (Lucas et al., 2009). However, longer transport time does not always result in higher biomass, and phytoplankton biomass can be negatively correlated or show no relationship to transport time, as shown by observations across multiple systems compiled by Lucas et al. (2009).

In addition, while transport processes can affect phytoplankton biomass directly through the flushing, they can regulate the biomass indirectly through their mediation on the biological processes by affecting distribution of heat energy and other substances like nutrients, salinity, suspended sediment, and grazers.
One major indirect effect is through nutrient delivery that regulates the nutrient availability in the system (e.g., Borsuk et al., 2004). Like the flushing effect on phytoplankton, studies suggest that shorter residence time results in a larger exporting rate of nutrients out of an estuary (Nixon et al., 1996). Hence, with the same nutrient loading, a waterbody with long transport time retains more nutrients inside the system. For the system where nutrient inputs are usually associated with river discharge, higher river inflow, corresponding to shorter transport time, brings in more nutrient into the system, which can result in a net increase of nutrient delivery by transport processes, therefore, increasing bioavailable nutrients in the system (Paerl et al., 2014). The resultant indirect effect of transport processes can enhance photosynthesis and higher phytoplankton biomass through bottom-up control when the growth of phytoplankton in the system is under nutrient limitation. Consequently, the direct and indirect effects of physical transport may lead to opposite results of algal biomass variability, and this dual role in regulating algal biomass has been linked to transport time. For example, Peierls et al. (2012) found that the relationship between phytoplankton biomass and transport time is non-monotonic and unimodal in two small estuaries, and also suggested that the peak biomass occurs when freshwater flushing time is about 7-10 days by fitting the observational data with an empirical function. Correspondingly, the relationship between phytoplankton biomass and nutrient loading can be either positive in some systems (e.g., Boynton and Kemp 2000) or negative in others (e.g., Hart et al., 2015).

In a system under light limitation, another mode of indirect effects of transport processes is through the control of light availability in the water column, as the loadings
of sediments and CDOM are usually proportional to the river discharge (Sanford et al., 2001).

The effects of physical transport on the variability in phytoplankton biomass have been studied using different approaches, including statistical methods that conduct regressions between in situ observed biomass and river discharge or transport time (e.g., Boynton and Kemp 2000) and numerical models that conduct experiments either using three-dimensional complex models or developing simplified numerical models (e.g., Liu and de Swart, 2015). Nevertheless, these studies usually focus only on one or several pieces of the effects of transport processes and can only examine them descriptively or statistically, and many studies are conducted within one system over a restricted period of time, in which the relationships are described for a limited range of transport conditions, and therefore the relationships found in one estuary may not be applied directly to another estuary. There are also literature studying the phytoplankton dynamics with simple analytical analyses (e.g., O'Brien 1974; Wofsy 1983; Lucas et al., 1999; 2009), but the various effects of transport processes have not been fully examined, either the effects are not considered at all or some pieces are not included (e.g., the indirect effect through regulating nutrient availability). To date, it lacks a simple mathematical framework that unites all the elements of the direct and various indirect effects, which can be used to reveal the relationships between biomass and transport processes under different environmental conditions and to evaluate the existing, previously proposed relationships. In addition, such a framework would also help answer some scientific and management questions, such as: “1. How do the effects of transport processes change the effects of biological processes? 2. On what transport timescale will phytoplankton
biomass reach the peak biomass? 3. How is the maximum biomass affected by the limitations of light and nutrients? and 4. How does the change in transport processes affect phytoplankton assemblage?”

The goal of this study is to develop a simplified mathematical model toward the unified framework, which can describe phytoplankton dynamics in response to the hydrodynamics under nutrient- and light-limiting conditions. We aim the model to be as simple as possible with several assumptions, yet to be used to reveal basic patterns of variations in phytoplankton biomass under light- and nutrient-limiting conditions in response to increase in transport time.

**Relationships between phytoplankton biomass and flushing time**

**Model development**

In developing a simplified physics-based mathematical model to study the relationships between phytoplankton biomass and flushing time, we consider a well-mixed waterbody with a mean depth $H$ and a volume $V$, equivalent to the upper mixed layer of an estuary (Figure 3.1).

**Governing Equation for phytoplankton biomass variability**

When it is assumed that the phytoplankton biomass in the incoming water from both the head and mouth is negligible, the variability of the volumetric phytoplankton biomass (denoted as $C$) in this well-mixed system can be described as

$$\frac{d(cv)}{dt} = GCV - RCV - (1 - b)Q_{out}C,$$  

(3.1)

where $G$ is the gross growth rate, $R$ is the total local loss rate of phytoplankton, such as respiration/excretion, grazing, and settling, $b$ is the returning ratio, indicating the fraction
of water flushed out of the system that reenters the system as inflow, and $Q_{out}$ is the volumetric rate of outflow at the mouth. From the conservation of flow and salt (Knudsen, 1900), we have the equations under steady state condition, $Q_{out} = Q_{in} + Q_R$, and $(1 - b)Q_{out}Sal = Q_{in}Sal_0$, where $Sal$ and $Sal_0$ are average salinities within the system and at the mouth, respectively, $Q_R$ denotes the river inflow, and $Q_{in}$ denotes the inflow at the mouth. Thus, $(1 - b)Q_{out} = \frac{Sal_0}{(Sal_0-Sal)} Q_R = \frac{1}{\theta} Q_R$, and $Q_{in} =$ 

\[ \left[ \frac{1}{\theta(1-b)} - 1 \right] Q_R, \] 

and $Q_{out}$ can be larger than $Q_R$ in estuaries (MacCready and Geyer, 2010). The definitions of all parameters with units are listed in Table 3.1.

Letting the flushing rate $F = \frac{(1-b)Q_{out}}{V}$, Eq. (3.1) becomes:

\[
\frac{d(CV)}{dt} = GCV - RCV - FCV
\]  

(3.2)

Note that the flushing rate is used to describe the flushing effect only when the transport processes show a net “transport-out” effect, and it is identical to the transport rate, introduced in Chapter 2, for this simple model. On relatively long time scales (e.g., monthly, seasonal, and annual timescales), the influences of hydrodynamics and biological processes on the variability of phytoplankton biomass approaches equilibrium (Qin and Shen, 2017), i.e., the phytoplankton dynamics is close to the steady-state conditions ($\frac{d(CV)}{dt} \approx 0$). Apparently, when $F$ is large enough, there is no positive steady-state solution, indicating that phytoplankton are washed out and its biomass keeps decreasing ($\frac{d(CV)}{dt} < 0$) until it becomes zero. The flushing effect of physical transport can also be described by the freshwater flushing time, $\tau$, as $\tau = \frac{\theta V}{Q_R} = \frac{1}{F}$ for a well-mixed
system (Chapra, 1997). In a river-dominated system, the flushing time is inversely proportional to the river inflow.

Light availability and nutrient supply are two important factors controlling biological processes that are considered explicitly in this study. The gross growth rate $G$ is regulated by the maximum gross growth rate at a reference temperature ($G_m$), photosynthetically active radiation (denoted as $I$), and concentration of bioavailable nutrients (denoted as $N$), for the phytoplankton, the bioavailable nutrients, $N$, are dissolved inorganic nutrients. $G$ therefore may be expressed as (Madden and Kemp, 1996):

$$\begin{align*}
G &= G_m \min[f(I), f(N)] \quad (3.3)
\end{align*}$$

where $f(I)$ and $f(N)$ are the growth-limiting functions for light and nutrient, respectively, and both of them are within the range of 0 to 1. Thus, the dynamics in phytoplankton biomass of the entire system needs to be examined under nutrient and light limitations, respectively.

**Light limitation**

Here, we adapt the limitation function by Steele (1965) that accounts for light inhibition, $f(I) = \frac{I}{I_{opt}} e^{-\frac{I}{I_{opt}}}$. According to the Beer-Lambert law, $I(z) = I_0 e^{-k_d z}$, where $k_d$ is the light attenuation, and the depth-averaged daily limitation function can be obtained as $f(I) = \frac{e}{k_d H} \left( e^{-\frac{I_0}{I_{opt}}} e^{-k_d H} - e^{-\frac{I_0}{I_{opt}}} \right)$ in a well-mixed system. Under the cases $H > H_u$ (depth of the photic zone), the irradiance approach zero at the bottom and hence
the first term approaches to 1. Then \( f(I) = \frac{e}{k_d H} \left( 1 - e^{-\frac{I_0}{I_{opt}}} \right) \). Note that the light-dark cycle has been considered by using the daily-averaged \( G_m \).

Then, the dynamics of the phytoplankton biomass under the light limitation, \( C_I \), can be described by:

\[
\frac{d(C_I V)}{dt} = \frac{e}{k_d H} \left( 1 - e^{-\frac{I_0}{I_{opt}}} \right) G_m C_I V - (F + R) C_I V \quad (3.4)
\]

The light attenuation \( k_d \) is determined by substances that absorb, reflect, or scatter light, including phytoplankton, suspended sediment, and water itself. There are two types of suspended sediment that have different effects in magnitude on light attenuation: chromophoric dissolved organic matter (CDOM) and other suspended sediments. The sediment concentration can be divided into two parts, one part unrelated to flushing (base concentrations), and the other that changes with flushing. The effects of base sediment concentration and the effect of particle-free water are lumped into a parameter \( k_w \). The concentration of the remaining part of suspended sediment is denoted by \( S \), and its effect on light attenuation is denoted by \( k_s S \). Thus, with the effect of phytoplankton, light attenuation can be expressed by

\[
k_d = k_w + k_s S + k_c C_I, \quad (3.5)
\]

where \( k_c \) is the light extinction by phytoplankton that equals to the division of light extinction by chl-a to the ratio of carbon to chl-a of phytoplankton, i.e., \( k_c = \frac{k_{chl}}{C:Chl} \).
The part of sediment concentration $S$ can be calculated using the first-order mass-balance equation, by assuming the majority of sediment loading ($L_s$) is proportional to the river inflow, i.e., $L_s = \frac{Q_r S_R}{V} = \theta F S_R$, where $S_R$ denotes the concentration of suspended sediment of this part at the head. Under the steady state,

$$0 = \theta F S_R - FS - \omega_s S,$$

where $\omega_s$ denotes the local loss rate of suspended sediment that can be due to the decay of CDOM and the settling of solid sediment, and its steady-state solution reads

$$S = \frac{\theta F S_R}{F + \omega_s}.$$ 

The steady-state solution for $C_I$ is solved to be

$$C_I = \frac{e^{G_m}}{H k_c} \left( 1 - e^{-\frac{I_0}{t_{opt}}} \right) \frac{1}{(F+R)} \frac{k_s \theta F S_R}{k_c F + \omega_s} - \frac{k_w}{k_c}$$

$F$ in the first and second terms indicates the direct flushing effect of physical transport on biomass and the indirect effects on biomass through regulating the sediment including CDOM, respectively. Eq. (3.7) can be plotted to visualize the relationship of phytoplankton and flushing time. The relationship will vary for different values of parameters while the pattern holds. Using values of an example system listed in Tables 3.1 and 3.2, the pattern can be plotted as shown in Figure 3.2a (chl-a is used to represent the biomass). This solution shows a positive biomass-flushing time relationship, which reflects the combined effects of transport processes and light influence on phytoplankton. At extremely short flushing times, there is no positive steady-state solution, and phytoplankton cannot accumulate in the system. This is because local phytoplankton growth cannot exceed the loss of biomass due to flushing, as a result of both low growth rate (high CDOM or TSS) and high flushing.
Nutrient limitation

By assuming negligible allochthonous phytoplankton, the dynamics of bioavailable nutrient concentration and phytoplankton volumetric biomass only under nutrient limitation, $C_N$, can be described as two coupled equations:

\[
\begin{align*}
\frac{d(NV)}{dt} &= W_N - FNV - \frac{1}{\alpha} f(N)G_mC_NV \\
\frac{d(C_NV)}{dt} &= f(N)G_mC_NV - FC_NV - RC_NV
\end{align*}
\] (3.8)

where $\alpha$ is C:N ratio, and $W_N$ is the nutrient loading rate, which can be divided into two parts, one part that is contributed by nutrients in various forms originally imported from outside the estuary, $W_{in}$, and the other that is only recycled from the loss of the phytoplankton through remineralization, $W_{phyto}$, i.e., $W_N = W_{in} + W_{phyto}$. The sources of $W_{in}$ include allochthonous sources (watershed, coastal water, atmosphere) and nitrogen fixation if it exists. Note that allochthonous sources of $W_{in}$ in the system (upper mixed layer) do not only include the allochthonous bioavailable nutrients (i.e., inorganic nutrients), but also includes bioavailable nutrients transported from the lower water column or sediments that are transformed from allochthonous organic nutrients through remineralization. $W_{phyto}$ is the loading rate including all possible contribution from the loss of phytoplankton, including the direct release of inorganic nutrients, the remineralization of phytoplankton organic nutrients that is within the system, and the portion of remineralized nutrients coming back to the system through the regeneration of phytoplankton that is settled into the lower water column or sediments. Setting the ratio $\beta$ to be the fraction of the total bioavailable nutrients recycled from the loss of phytoplankton, the expression of $W_{phyto}$ becomes $W_{phyto} = \frac{1}{\alpha} \beta RC_NV$. 
Therefore, dividing $V$ in two sides of Eq. (3.1) and setting $F = \frac{Q_R}{\theta V} = \frac{(1-b)Q_{out}}{V}$ and $L_{in} = \frac{w_{in}}{V}$ returns the governing equations at steady state:

\[
\begin{align*}
0 &= L_{in} + \frac{1}{\alpha} \beta R C_N - F N - \frac{1}{\alpha} f(N) G_m C_N \\
0 &= f(N) G_m C_N - R C_N - F C_N
\end{align*}
\]  
(3.9)

Phytoplankton biomass $C_N$ can be expressed as:

\[
C_N = \frac{\alpha}{(1-\beta)R+F} (L_{in} - FN)
\]  
(3.10)

Eq. (3.10) provides the basic form of phytoplankton biomass under nutrient limitation.

$L_{in}$ includes the direct input of N and the portion from allochthonous organic nutrients through remineralization. The direct input of N can be expressed as $\theta F N_R + L_i$, where the nonpoint-source N loading rate equals $\frac{Q_R N_R}{V} = \theta F N_R$. $N_R$ is the N concentration of river discharge, and the remaining portion can be denoted by $L_i$ that is not related to flushing. Similarly, the N loading rate due to allochthonous organic nutrients can be related to the loading rate of allochthonous organic nutrients $(\theta F O_R + L_o)$ times the fraction of allochthonous organic nutrients that contributes to the N loading rate (denoted by $\varepsilon$), i.e., this portion of N loading rate is expressed as $\varepsilon(\theta F O_R + L_o)$. Therefore, $L_{in} = \theta F N_R + L_i + \varepsilon(\theta F O_R + L_o)$.

Transport processes can also affect the two parameters $\varepsilon$ and $\beta$, and their explicit expressions as a function of F are achieved through a detailed examination on phytoplankton dynamics and its interaction with nutrient cycling, as presented in the Appendix. In general, both of them increase with flushing time. By adapting the Monod-type limitation function for gross growth rate under nutrient limitation, i.e., $f(N) =$
\[ \frac{N}{N+N_k} \text{, where } N_k \text{ is the half-saturation coefficient for N uptake, we can explicitly calculate} \]

Eq. (3.9) as a function of F. The steady-state solutions read:

\[
\begin{align*}
C_N &= \frac{\alpha}{(1-\beta)R+F} [\theta FN_R + L_i + \epsilon(\theta FO_R + L_o) - FN] \\
N &= \frac{R+F}{G_{m-R-F}} N_k
\end{align*}
\]

Eq. (3.11) shows explicitly the effects by physical transport on phytoplankton dynamics under nutrient limitation: the flushing effect, denoted by F in the denominator \((1 - \beta)R + F\), and the indirect effects of nutrient supply denoted by F in several terms: direct import, \(\theta FN_R\), and export, \(F \frac{R+F}{G_{m-R-F}} N_k\), and remaining input from the transformation of allochthonous organic nutrients into N and the internal recycling of phytoplankton (terms associated with \(\epsilon\) and \(\beta\)).

Apparently, the relationship between \(C_N\) and flushing depends on the relative contribution of the N loading rate from the portion positively related to F. In the riverine nutrient-dominated estuaries, F is proportional to the river inflow, and the major N loading is, in general, positively related to F.

Figure 3.2b shows the pattern of the biomass distribution in terms of flushing time (using the values of parameters listed in Table 3.1 and 3.2). For different parameters incorporated into the model, the curve will change, but the pattern distribution remains the same. As shown in Figure 3.2b, the solution indicates that the indirect effect dominates the dynamics of biomass when \(\tau\) is large (small F), and as \(\tau\) decreases (F increases), nutrient loading rate increases and more nutrients become available that results in an increase of the biomass, but when \(\tau\) becomes short enough (a large F), the
physical transport dominates and flushes phytoplankton out of the system. Again, at extremely short flushing times, phytoplankton cannot accumulate in the system due to the high flushing even the growth rate is relatively high (high nutrient availability).

It is interesting to note that the steady-state nutrient concentration under a nutrient-limiting condition is not affected by the nutrient loading (Eq. 3.3), indicating the key role of the nutrient uptake by phytoplankton, recycling, and the modulation of dynamics (flushing rate) in the nutrient dynamics.

**Combined solution**

Phytoplankton dynamics can be explained by combining the cases of light limitation and nutrient limitation. For a system, the biomass can only increase when both light and nutrients are available, or maximum biomass is limited by the scarce sources. Thus, phytoplankton biomass under various environmental conditions can be described by the minimum of biomass described by Eqs. (3.6) and (3.9), i.e., \( C = \min(C_I, C_N) \):

\[
C = \begin{cases} 
\frac{e^{G_m}}{HK_c} \left( 1 - e^{-\frac{I_0}{I_{opt}}} \right) \frac{1}{(F+R)} - \frac{k_w}{k_c} \frac{\theta F S_R}{F + \omega_s} - \frac{k_w}{k_c}, & \text{if } C_I < C_N \\
\frac{\alpha}{(1-\beta)R+F} \left[ \theta F (N_R + \varepsilon O_R) + \left( L_i + \varepsilon L_o \right) - F \frac{R+F}{G_m-R-F} N_k \right], & \text{if } C_I \geq C_N 
\end{cases}
\]

(3.12)

In addition, the areal phytoplankton biomass (denoted by \( B \)) can be obtained by the integration over depth, which expressed as the production of biomass \( C \) and water depth \( H \) for the well mixed system, i.e., \( B = CH \).

As a summary, the effects of transport processes considered in the mathematical model include the direct effect (flushing phytoplankton out of the system), and indirect effects (importing bioavailable nutrients and CDOM into the system, flushing the
nutrients and CDOM out of the system, respectively, and acting its roles in the remineralization of allochthonous organic nutrients and the internal recycling of phytoplankton).

**Patterns and the maximum mean biomass**

A system with a specific combination of environmental conditions and phytoplankton ecophysiology can have a specific phytoplankton biomass curve in terms of flushing time. Nevertheless, their relationships with flushing time can be grouped into 3 patterns, as illustrated in Figure 3.3. Note that the flushing time of an estuary can only vary within a confined range. All 3 patterns show a flushing-dominant regime at extremely short flushing times, and no positive equilibrium in phytoplankton biomass exists, indicating that phytoplankton cannot accumulate in this regime.

The first pattern shows that the light is limiting when flushing is large (flushing time is short), and the biomass increases with flushing time, while nutrients are limiting when flushing is small (flushing time is long) and the biomass decreases with increasing flushing time. Note that some estuaries, either with a relatively short length or a large flushing rate, may only experience the light limitation if their flushing times vary only within the light limitation regime, in which the corresponding phytoplankton biomass always shows a positive correlation to flushing time.

The second pattern shows the nutrient-limiting condition. The environmental conditions for this pattern are either with high light irradiance or low nutrient loading. In this case, the system is only under nutrient limitation, the biomass increases with flushing time when the flushing time is small, but it keeps decreasing after the flushing time reaches a certain value.
The third pattern may be rare in the nature, but it can happen theoretically. Compared to the first pattern, the system can be under nutrient limitation again when flushing is extremely high indicating the flushing rate is higher than the uptake rate.

As \( \tau \) becomes large, the biomass increases with \( \tau \) first and then decreases, and therefore the maximum biomass occurs when \( \tau = \tau_m \). Apparently, \( \tau_m \) varies with the change in environmental conditions.

For a system that is under the nutrient limitation with a small flushing effect but under light limitation with a large flushing effect, the maximum biomass occurs when the system shifts from light limitation into nutrient limitation, i.e., at \( \tau_m \) leading to \( C_I = C_N \). In this example system, the maximum in mean phytoplankton biomass occurs at \( \tau_m \) of around 8.6 days (Figure 3.3a).

For a system that is under nutrient limitation even with a large flushing effect (small flushing time), the maximum mean phytoplankton biomass occurs with a relatively small flushing time. Typically, the flushing time \( \tau_m \) equals less than a few days, and it equals around 3 days for \( C_N \) shown in the example system (Figure 3.3b).

**Impacts of environmental conditions and ecophysiology of phytoplankton**

While there are three patterns of the relationship between biomass and flushing, the detailed curve can vary with different combinations of environmental conditions and ecophysiology of phytoplankton, and the change in relationship can be diagnosed using this mathematical model by tuning the parameters.

Apparently, since the relationship is related to both nutrient limitation and light limitation, the relationship will change for any changes in environmental conditions that
affect light and nutrient availabilities. A decrease in $I_0$ and/or an increase in $S_R$ increases the biomass under light limitation (Figure 3.4a), and a system with biomass close to the maximum can switch from under nutrient limitation to under light limitation. Change in light extinction coefficients, $k_w$ and $k_s$ due to CDOM or TSS, also affect the light availability (e.g., Figure 3.3). Similarly, a decrease in N loading ($N_R, L_I$) and/or in allochthonous organic nutrient loading ($O_R, L_o$) lowers the biomass under nutrient limitation (Figure 3.4b) and can let a system switch from under light limitation to under nutrient limitation. The relationship is also affected by the contribution from the remineralization of organic nutrients (denoted by $\varepsilon$) and the recycle of phytoplankton (denoted by $\beta$) (Figure 3.4c), a higher $\varepsilon$ or $\beta$ alleviates the nutrient limitation.

Changes in $G_m$ and $R$ also vary the relationship (Figure 3.4d). A system with a higher $G_m$ has a higher biomass C, while that with a higher R has a lower biomass. Although the response of C to G or R is clear, the relative importance of the change of G and R on the change of the magnitude of C, however, depends on $\tau$. For example, when $\tau$ is large and the system is under nutrient limitation, it is more likely that the change in C caused by the relative change in R is larger than that in G. When $\tau$ is small, especially when the system is under light limitation, G is as important as R. Since different phytoplankton species have different combinations of $G_m$ and $R$, the mathematical model can also be helpful to diagnose the difference response for different species.

The temperature is a major factor affecting the phytoplankton growth in the estuaries, and its impacts have been implicitly included in the mathematical model through temperature-sensitive parameters, including $\varepsilon, \beta, G_m$, and $R$. In general, higher
temperature leads to higher rates of bacterial activities and hence higher rates of remineralization (larger $\varepsilon$) and recycle (larger $\beta$), and also leads to higher $G_m$ and $R$.

**Biomass at locally spatial scales in river-dominated estuaries**

The relationship of the mean phytoplankton biomass in the system to the flushing time can be extended to diagnose the biomass at a local scale. Here, we only consider the river-dominated estuary with one major source of water and nutrients from the head.

**Spatial distribution of biomass**

Following the way in Peierls et al., (2012), an estuary can be divided into a series of segments, and each segment has the domain from the head of the estuary to a location (Figure 3.5). Since $\tau = \frac{\theta V}{Q R}$, with the same river inflow, the flushing time of each segment is proportional to the size of the segment, which can be used as a spatial coordinate. Then the mean phytoplankton biomass of each segment, $C^{seg}$, can be estimated using the mathematical model, as shown in Figure 3.6 for the example system.

**Local biomass variability**

Since only phytoplankton biomass at fixed stations along an estuary, rather than the mean biomass of an estuary, is measured in the field, it is worthwhile to study how the local variability in biomass at one fixed station is affected by the transport processes.

For a fixed station, its biomass is represented by the mean phytoplankton biomass of the waterbody around this station. For example, for the station located downstream of the segment $j-1$ but within segment $j$, the biomass can be estimated by the mean biomass of the local waterbody $j$, $C_{j}^{local}$, which equals the ratio of the difference in total biomass to the volumes difference of the two segments,
\[ C_{local}^{j} = \frac{v_{seg}^{j} c_{seg}^{j} - v_{seg}^{j-1} c_{seg}^{j-1}}{v_{seg}^{j} - v_{seg}^{j-1}} = C_{seg}^{j} + \frac{v_{seg}^{j-1}}{v_{seg}^{j} - v_{seg}^{j-1}} (C_{seg}^{j} - C_{seg}^{j-1}). \] (3.13)

For \( j = 1 \), \( C_{local}^{1} = C_{1}^{seg} \). Note that the value of \( \frac{v_{seg}^{j-1}}{v_{seg}^{j} - v_{seg}^{j-1}} \) increases with location, but it is independent of time, \( t \). For a series of segments with a constant increment in volume, \( \frac{v_{seg}^{j-1}}{v_{seg}^{j} - v_{seg}^{j-1}} \) equals \( j - 1 \) for the segment \( j \) with \( j > 1 \). Because each segment corresponds to the same river inflow at each time, the spatial change in volume of each segment can be estimated by \( V_{seg} = \frac{Q_{R} T_{seg}}{\theta} \), and therefore, The spatial distribution of \( C_{local}^{j} \) can be related to the spatial variations in flushing time of each segment, using mean \( \theta \) in both \( j \) and \( j-1 \) segment:

\[ C_{local}^{j} = C_{seg}^{j} + \frac{T_{seg}^{j-1}}{T_{seg}^{j} - T_{seg}^{j-1}} (C_{seg}^{j} - C_{seg}^{j-1}). \] (3.14)

Eq. (3.14) can describe the spatial distribution of phytoplankton biomass at a specific time. Compared to the spatial distribution of segment-averaged biomass \( C_{seg}^{j} \), the local biomass \( C_{local}^{j} \) is higher than \( C_{seg}^{j} \) when \( C_{seg}^{j} > C_{seg}^{j-1} \), but lower when \( C_{seg}^{j} < C_{seg}^{j-1} \) (Figure 3.6), and therefore the distribution of \( C_{local}^{j} \) shows a sharper peak than \( C_{seg}^{j} \).

There exists a zone of maximum phytoplankton biomass in the estuary (referred to as the estuarine phytoplankton maximum or EPM hereafter), located between the segment with the flushing time of \( \tau_{m}^{seg} \) and its landward segment. The location of the EPM zone shifts toward the head with a longer flushing time of the system (Figure 3.7). In those systems that the entire locations are under light limitation, the biomass tends to be monotonically higher seaward, and the EPM zone exists at the seaward end of the system. If all
conditions including the hydrology are similar, biomass in the EPM zone for Pattern-1 estuaries is in general higher than Pattern-2 estuaries that is due to a lower biomass taking up less nutrients in the upper region in Pattern-1 estuaries and hence a higher nutrient availability in the EPM zone.

At a fixed station, the temporal variations in local biomass $C_{j, local}$, described by Eq. (3.13), mainly follows the relationship between $C_{j, seg}$ and flushing time of that segment, and it is higher than $C_{j, seg}$ when $C_{j, seg} > C_{j-1, seg}$, but lower when $C_{j, seg} < C_{j-1, seg}$. Therefore, $C_{j, local}$ also shows a monotonic relationship to flushing time of the segment $j$ (Figure 3.8). When the growth of phytoplankton is under nutrient limitation for a long flushing time, an increase in river inflow can result in an increase in biomass; but when the flushing becomes large enough, it can result in a reduced biomass, because the flushing effect of transport processes surpasses its effect on nutrient supply or the limiting factor on the growth at the station is switched to light limitation. The biomass of a local waterbody reaches high at the time when it becomes the ETM zone of the system.

The model is expected to resemble the spatial distribution of both the segment-averaged biomass and local biomass well if the variability in other parameters is much smaller than that in flushing time. In some estuaries, nevertheless, the distribution can deviate significantly from the model prediction at some locations where parameters show large spatial gradients even though the general pattern may still hold, like in the estuarine turbidity maximum (ETM) zone where the suspended sediment concentration may be largely elevated. In the ETM zone, the low clarity can decline the light availability and push the condition of the zone toward light limitation, and this dampening effect on light
can be large in some estuaries but small in others. The biomass, correspondingly, in the ETM zone can be low and deviate from the mathematical model if the dampening effect is significant. In extreme cases, the ETM zone may cause the biomass to be near zero that separates the entire estuary into distinct two regions, and biomass distribution along the main channel of each region can be described, respectively, by the mathematical model with a specific environmental condition combination. In the James River, the biomass is significantly low in the ETM zone that exists in the middle of the estuary, and the biomass distribution can be studied separately for the upper tidal freshwater region and the lower saline water region (Bukaveckas et al., 2018).

**Zone of maximum phytoplankton biomass**

A zone of maximum phytoplankton biomass (EPM) in an estuary has been widely observed. When every location in the system is under the nutrient limitation for phytoplankton growth, the EPM zone is near the head where both the flushing effect on phytoplankton and nutrient limitation are alleviated, and in the condition that the phytoplankton in the upper estuary experience the light limitation in growth, the EPM zone can locate further downstream. Due to the effects of transport processes, the location of EPM zone varies with hydrology, such as the change in river inflow (Figure 3.7).

The EPM zone is sometimes suggested to be associated with the ETM zone (Azhikodan and Yokoyama, 2016), and it is observed to locate landward (e.g., Bukaveckas et al., 2018), seaward (e.g., Fisher et al., 1988), or within the ETM zone (e.g., Cloern et al., 1983; Cole et al., 1992; Kocum et al., 2002) across various systems. Nevertheless, as indicated by this study, the formation of the EPM zone is associated with
the interaction between transport processes and various environmental conditions, and this mechanism is different to that forming the ETM zone. Therefore, though they may be geographically tied nearby, the EPM zone does not necessarily associated with the ETM zone and their location relations can vary with hydrology.

**Revealing of relationships in natural systems**

According to the mathematical model, under one combination of environmental conditions and ecophysiology of phytoplankton, the relationship between biomass and flushing time corresponds to one curve. In nature, however, no idealized data set exists, every parameter has its spatial and temporal variability. Nevertheless, if the variability in biomass is regulated dominantly by transport processes, the biomass-flushing time relationship should follow one curve with a narrow deviation range, and the non-monotonic relationship of increasing first but decreasing later is evident. Here, we diagnose the relationships in some natural estuaries and compare them to the patterns described by the model.

**Annual timescale**

For phytoplankton dynamics in a specific system, the annual timescale is good to reveal the biomass-flushing time relationship. On the timescales longer than monthly, variations in parameters caused by episodic perturbations or short-term oscillations with periods less than a month in the environmental conditions and ecophysiology of phytoplankton are smoothed out and much reduced. When considering the annual timescale, the interannual variations in temperature and light irradiance are no longer as large as their monthly and seasonal variations, resulting in relatively small interannual variations in those temperature-related and light-related parameters and, hence, a
relatively large variation in $F$ compared to that of shorter timescales. For example, Qin and Shen (2017) show that even without considering the indirect effects of transport processes, the direct flushing effect increases with timescale and can be as important as the effect of local processes on the phytoplankton dynamics on the annual timescale. In addition, variations in parameters caused by climate change or human activity on the annual timescale may not be as large as that on longer timescales (e.g. decades), such as the variations in the nonpoint-source nutrient concentration and sediment concentration. Thus, effects of transport processes, represented by $F$ or $\tau$ in the mathematical model, are relatively important on the annual timescale and can be the dominant regulation on phytoplankton dynamics in many estuaries. In fact, most studies clearly showing the effects of transport processes are based on the annual timescale (e.g., Boynton and Kemp, 2000).

**Seasonal timescale**

We can also compare the summer biomass to the spring biomass in a system, i.e., compare the relationships on the seasonal timescale. On the seasonal timescale, the flushing time can vary significantly, e.g., in the temperate estuaries, the variations in environmental conditions temperature and $I_0$, and that in remineralization coefficients $\varepsilon$ and $\beta$ also show strong seasonality. Corresponding to the change in temperature, the ecophysiology of phytoplankton $G_m$ and $R$ also reach a maximum in the summer and a minimum in the winter. Note that $R$ is a combination of respiration/excretion, grazing, settling, and net vertical transport, and the high grazing usually coincides with high temperature in the summer. Thus, the relationships between biomass and flushing time for different seasons follow different trajectories and even different patterns.
In temperate estuaries, from the spring to the summer, both surface light and temperature increase while the input of CDOM and solid sediments decreases due to the reduced river inflow, the gross growth rate also increases, and therefore all the changes in the environmental conditions and ecophysiological coefficients increases the biomass under light limitation, and the $C_I$ curve is higher, indicating an alleviation in light limitation. On the other hand, while the riverine nutrient loading is relatively low in the summer, the recycled nutrient loading can be elevated largely, and the loss term also increases which tends to lower biomass. Therefore, the change in the $C_N$ curve is case specific. Correspondingly, the flushing time associated with maximum biomass is shifted. For example, in one estuary, if the limiting factor changes from light availability in the spring to nutrient availability in the summer, the location of maximum biomass zone shifts toward the head.

**Case studies: The tidal freshwater region of James River**

A realistic case was provided in the tidal freshwater region of James River, a partially-mixed tributary of Chesapeake Bay. In this region, the dominant nutrient input is from the river discharge at the head, and phytoplankton growth is suggested to be mainly under light limitation (Bukaveckas et al., 2011). Diatoms and chlorophytes dominate the phytoplankton assemblage (Bukaveckas et al., 2018). Monthly chl-a data over 1990-2013 were collected from the long-term monitoring stations by the Chesapeake Bay Program (http://www.chesapeakebay.net/). The river discharge data at the fall-line were collected by the United States Geological Survey (USGS).

The entire mainstem of the tidal freshwater region of the James River was divided into 49 local waterbodies with similar volumes of about $5.557 \times 10^6$ m$^3$, with volumes
determined using the James River EFDC model (Shen et al., 2016). The six main-channel monitoring stations (TF5.2, TF5.2A, TF5.3, TF5.5, TF5.5A, and TF5.6) located at the 1st, 2nd, 3rd, 11th, 19th, and 40th local waterbodies, respectively. The volume of a specific segment \( j \) \((j = 1, 2 \ldots 49)\) was calculated by summarizing the volumes from the 1st local waterbody to the \( j \)th local waterbody.

Date-specific flushing times for each station and for the entire region were calculated based on the method described in Alber and Sheldon (1999). Because this region is dominated by freshwater with salinity less than 0.5, the fraction of freshwater, \( \theta \), is close to 1. At one station located at \( j \)th local waterbody, the date-specific flushing time for the \( j \)th segment at a specific observational date was computed by dividing the volume of the \( j \)th segment by date-specific average river discharge over a certain period between the chosen date and some antecedent days, while the period was determined by iteratively adding the river discharge at an additional antecedent day into the average until the period equals the flushing time.

Overall, phytoplankton chl-a shows non-monotonic relationships to date-specific flushing time at these stations (Figure 3.9a). Due to the variations in local condition, both specific curves of relationship and \( \tau_m \) to reach the maximum biomass can vary with the station. At Station TF5.5, \( \tau_m \) was close to 12 d in the summer and 18 d in the winter (Figure 3.9b).

Wintertime and summertime averages of chl-a at each local waterbody were computed for each year by extrapolating the averages of chl-a at 6 stations linearly to the entire region. The mean chl-a for the entire tidal freshwater James River was then computed by averaging the chl-a over the entire region, which shows a non-monotonic
relationship to date-specific flushing time for the entire region (Figure 3.9c). The maximum mean chl-a occurred around 22-25 d, suggesting that the region was the Pattern-1 or Pattern-3 system over the majority of time, and the maximum phytoplankton biomass occurred when it shifts from light limitation to nutrient limitation.

The spatial variabilities in phytoplankton biomass varied with time, and the location of maximum chl-a among the 6 stations switched at different observational date (Figure 3.10a and 3.10b). In the summer, the zone of EPM shifts toward the downstream with shorter flushing time (Figure 3.10b).

Overall, the wintertime and summertime averages of chl-a over 1990-2013 resemble spatial variabilities as described in the mathematical model (Figure 3.10c). The maximum value located at Station TF5.5 in the summer, farther upstream than the winter location at Station TF5.5A.

Discussion

Other relationships between variables

While this study focuses on how the physical transport affects biomass, the model can be used to diagnose other relationships between phytoplankton biomass and other variables explicitly under steady-state conditions, which helps to examine relationships between measured variables including those already known from statistical regression models or those not yet revealed.

Productivity vs. biomass vs. flushing time

Under steady state, the areal phytoplankton gross primary productivity (GPP) can be estimated as $GPP = (F + R)B$, either under nutrient limitation or light limitation.
Therefore, primary productivity is correlated positively to the biomass, and the $GPP:B$ ratio is dependent on both the flushing effect and loss term. Unless with a sufficiently large $F$, the ratio can be relatively constant to flushing time, on the annual timescale (Figure 3.11a), e.g., the correlation between mean production and chl-a in the Chesapeake Bay (Harding et al. 2002). On the seasonal timescale, both $F$ and $R$ can vary significantly with time, and the seasonal variations in the $GPP:B$ ratio need to be considered in two cases. In the systems or locations of one system where flushing time is relatively long resulting in a comparable smaller seasonality in $F$ than that in $R$, such as the lower estuary where phytoplankton growth is under nutrient limitation all year around, the $GPP:B$ is expected to be low in the summer as $R$ is temperature related; while in the systems with large seasonal variations in $F$, such as the upper estuary, the hydrological cycle that large $F$ in the winter/spring time but low $F$ in the summer can counterbalance the seasonality in $R$, which indicates that the ratio is not necessarily small in the summer.

In a system where the flushing time is relatively large and phytoplankton growth is under nutrient limitation, the interannual variability in biomass is dependent largely on the transport processes, and therefore the primary productivity also decreases with flushing time (Figure 3.11a). For example, the interannual variability of phytoplankton primary productivity in the main-stem of Chesapeake Bay is suggested to be correlated highly to annual river inflow and nutrient loading (Boynton et al. 1982; Harding et al. 2002).
**Nutrient concentration vs. flushing time**

Eq. (3.7) can be used to study the relationship between nutrient concentration and flushing time, and it can be transformed into:

\[
N = \frac{1}{\frac{G_m}{R+F} + 1} N_k
\]  

(3.15)

In the system under nutrient limitation, according to Eq. (3.15), the steady-state nutrient concentration decreases with the increase in the flushing time (dashed line in Figure 3.11b), which confirms the relationships in observations (e.g., Peierls et al., 2012).

Because the biomass decreases with shorter flushing time when the system experiences light limitation, this negative relationship between \(N\) and \(\tau\) still holds (solid line in Figure 3.9b).

When temperature increases, biological parameters \(G_m\) and \(R\) also increase, and it results in the decrease in nutrient concentration. If the \(F\) also decreases, \(N\) becomes even smaller. Thus, in the temperate estuaries, summertime \(N\) with high temperature and low flushing is generally much lower than the wintertime \(N\) (e.g., Peierls et al., 2012). When the flushing time is sufficiently long, the steady-state \(N\) response in small variations with the changes in temperature.

Because of the direct uptake by phytoplankton, the decreasing rate of \(N\) with increasing flushing time is expected to be higher than that in exporting organic nutrients and total nutrient.
Biomass/productivity vs. nutrient loading rate vs. nutrient concentration

As shown using the example system, the phytoplankton biomass increases with the nutrient loading rate, when a system is under nutrient limitation (Figure 3.11c).

According to Eq. (3.6), the biomass under nutrient limitation is a function of $L_{in}$:

$$\ln C = \ln(L_{in} - FN) + \ln \alpha - \ln[(1 - \beta)R + F]$$  \hspace{1cm} (3.16)

Correspondingly, the expression for primary productivity is:

$$\ln GPP = \ln(L_{in} - FN) + \ln(\alpha H) + \ln(R + F) - \ln[(1 - \beta)R + F]$$  \hspace{1cm} (3.17)

When the flushing time is relatively long (small $F$ and $N$), Eqs. (3.16) and (3.17) suggest that the relationships of biomass/productivity to nutrient loading rate can be roughly fitted by a positive natural log-transformed linear regression, i.e., $\ln C \sim \ln L_{in}$, $\ln GPP \sim \ln L_{in}$, which has been shown using cross-system data on the annual timescale in Nixon (1992) and Nixon et al. (1996) though their correlations may be damped by variations in other biological parameters. Note that the linear relationships do not require the separation of nutrient loadings into different sources, therefore a high nutrient loading can be either from a high non-point source input or from a high point-source input, and the relationships exist not only for river-dominated systems but also for other types of estuaries as long as the flushing effect on exporting nutrient is not extremely strong. For a system that the major nutrient loading is proportional to $F$, the relationship deviates from the linear regression when $L_{in}$ becomes large, corresponding to a large $F$. For example, in river-dominated estuaries, the biomass shows such a natural log-transformed linear relationship to riverine nutrient loading when the riverine nutrient loading rate is low, but
tends to approach flat as the loading rate increases, such as the observations by Peierls et al., (2012).

When F is extremely large, the high flushing reverses the relationship, as also suggested by Peierls et al., (2012) where they find one observation does not follow the linear positive relationship during a low flushing time period in the New River estuary. In addition, the system does not have to be in extremely high flushing condition because a system becomes more likely to be under light limitation as F increases, large flow results in large nutrient loading rate, which also generates large flushing effect and high sediment loading input, which in turn reduces the biomass as indicated by Eq. (3.11), and biomass does not exhibit a positive correlation to nutrient loading rate.

The biomass/productivity is positively correlated to the concentration of the limiting nutrient at long flushing times, when the system is under nutrient limitation. However, the nutrient concentration is not the determining factor on biomass/productivity, and higher biomass/productivity does not necessarily correspond to higher nutrient concentration. The analysis here supports that phytoplankton biomass has a good relationship with the nutrient loading rate rather than the nutrient concentration, as suggested by Boynton et al., (1982).

*Biomass deposition vs. flushing time*

Transport of organic matter produced by phytoplankton from the upper layer to the lower layer or the bottom sediment can contribute significantly to the oxygen consumption and the associated hypoxia issues in an estuary. Biomass deposition is one loss term in the mathematical model, and its rate equals \( \omega_c B \). Therefore, the deposition at one location is proportional to the areal biomass B on the annual timescale, which is
expected to increase with river inflow when it is under nutrient limitation, but decreases at large river inflow. Spatially, the maximum biomass deposition location is near the EPM zone. This agrees with the finding at a fixed station in Chesapeake Bay by Boynton and Kemp (2000) that shows a non-monotonic relationship between chl-a deposition and river flow, and supports their explanation that the decline in biomass in the year with the extreme strong flow is due to the shift of the EPM zone toward father downstream.

**Model accuracy and limitation**

Some assumptions are used to develop the mathematical model, because the purpose of this study is not to use the model to simulate the phytoplankton biomass accurately, which can be achieved by numerical models, but to provide a frame that can analytically study the variability of biomass under the effects of transport processes with various environmental conditions. The model is developed by assuming a complete mixing, which cannot accurately resemble the relationship in a natural system on short-term timescales or local fine scales. The temporal variations in biological processes always exist, and may become large enough compared to the variations in physical transport, especially when flushing time becomes large (F becomes small). This dampens the accuracy of this model in revealing the relationship between biomass and flushing effect in downstream estuary if the system has a long flushing time. In addition, due to the simplicity of this model, the effect of stratification and mixing of water column by tide or wind on the vertical transport is not explicitly included in the model, but it has been included implicitly in the parameter $R$ for phytoplankton dynamics and in the parameters $\epsilon$ and $\beta$ for nutrient dynamics. This is another source of variations for the relationships between biomass and flushing time for a realistic study.
This mathematical model may not be applied for the very shallow systems but with low turbidity, in those systems, light can penetrate to the bottom, and the irradiance at the bottom is not vanished. In addition, phytoplankton may not be the dominant primary producer (McLusky and Elliott, 2004), and the interactions with other primary producers (e.g., SAVs, benthic microalgae, macroalgae, marsh) may play an important role in phytoplankton dynamics.

The mathematical model is developed with a focus on the bottom-up control, while the grazing of phytoplankton by secondary producers (e.g., zooplankton, benthic bivalves) is implicitly included for the model closure using a grazing rate as a part of $R$ that is independent to flushing. The grazing term in the governing equation Eq. (3.1) may be expressed explicitly as $G_z \frac{C}{C+C_k} Z$ for an individual secondary producer, where $G_z$ is the gross growth rate of secondary producer, $C_k$ is the half-saturation coefficient for taking up phytoplankton, and $Z$ is the biomass of secondary producer. In many estuarine systems, the grazing rate can be assumed reasonably to be a rate relatively independent to both phytoplankton biomass and flushing. For example, in systems where zooplankton is the main component of secondary producers, the total zooplankton biomass may be roughly assumed to be constantly proportional to phytoplankton biomass in many cases (Park et al., 2005), especially when the phytoplankton is not a limiting resource to the growth of zooplankton. In Chesapeake Bay, the spatial distribution of zooplankton abundance does in general agree with that of phytoplankton biomass, showing their maximum abundance located near the maximum phytoplankton biomass zone (Kemp et al., 2005). The elevated zooplankton abundance is also widely found in the ETM zone of other estuaries (e.g., Morgan et al., 1997; Kimmerer et al., 1998). In some other estuaries,
however, this assumption may not hold, and the grazing rate cannot be assumed as an independent parameter when studying phytoplankton-transport time relationship. Nevertheless, if the grazing overall is a small term, deviations from the model curves may be expected to be small and the non-monotonic relationship is still hold. But if the grazing pressure is significantly large, the grazing rate may vary largely with transport time, and the relationship between phytoplankton biomass and transport time can either follow or not follow the non-monotonic relationship shown in this study.

This model does not separate nutrients into nitrogen or phosphate. In an estuary, the upstream region is usually suggested to suffer phosphate limitation, whereas the downstream region is under nitrogen limitation (Kemp et al., 2005), and the limiting resource can also vary seasonally from phosphate to nitrogen at one location.

The discussed spatial distribution of the biomass requires the major input of nutrients from the head of the system, and it may be off the model curves for the systems having the major input of nutrients from the coastal seas.

**Conclusions**

A mathematical model is developed to diagnose the effects of transport processes on the variability of phytoplankton biomass over long-term timescales, including the direct flushing effect, and indirect effects by importing and exporting nutrients and sediments. When the system is under light limitation, the flushing effect and the effect through regulating sediments dominate the biomass variability that tend to induce a positive phytoplankton-flushing time relationship; when the system is under nutrient limitation, the flushing effect acts against the effect through regulating nutrients that tend to induce a negative relationship, and the biomass only increases with flushing time at
short flushing times but decreases afterward. For the system that can switch between light limitation and nutrient limitation, it tends to be under light limitation at small flushing times but under nutrient limitation at long flushing times, with the maximum biomass occurring at a middle flushing time. The variability in biomass at a local station also shows a similar non-monotonic pattern with flushing time. The spatial distribution of biomass along a river-dominated estuary can also be shown by the model, and the upper estuary at short flushing times generally shows an increase in biomass downstream while the lower estuary shows a decrease if there is under nutrient limitation.

In addition, the mathematical model can be used to verify and mechanically explain various relationships between variables obtained in observations. Many variables show monotonic relationships to flushing time; others, however, can exhibit non-monotonic relationships. This study suggests that when relationships between variables are examined, the effects of transport processes need to be considered.

**Appendix. Expressions for \( \varepsilon \) and \( \beta \)**

The full calculation of phytoplankton biomass under nutrient limitation requires an examination on phytoplankton dynamics and its interaction with nutrient cycling, including the dynamics of both inorganic nutrients and organic nutrients.

The total loss rate of phytoplankton, \( R \), can be divided into a biologically-related part (respiration/excretion, grazing, and natural death, denoted by \( R_p \)) and a physically-related part (sinking and vertical transport, denoted by \( \omega_c \)), and the dynamics of phytoplankton biomass Eq. (3.2) becomes:

\[
\frac{dc}{dt} = GC - FC - (R_p + \omega_c)C \tag{A1}
\]
The gain (+) of the organic nutrients in the system include the import from outside of the system (allochthonous sources), and the transformation of inorganic nutrients to organic nutrients in the system (autochthonous sources). In river-dominated estuaries, the nonpoint-source loading rate of allochthonous organic nutrients from the watershed is proportional to the flushing $\theta F O_R$, where $O_R$ is the organic nutrient concentration of the water from the watershed, and the remaining portion of allochthonous organic nutrient loading rate is denoted by $L_o$. The transformation of inorganic nutrients to organic nutrients is primary through phytoplankton uptake. Bioavailable nutrients are assimilated to become organic nutrients by phytoplankton, and they are released into the water column through the biologically-related loss of phytoplankton. Set $\beta_i$ to be the fraction of dissolved nutrients in the total nutrients that are directly released into the water from the recycled phytoplankton, the portion of organic nutrients is $(1 - \beta_i)$.

The loss (-) of organic nutrients includes the flushing-out by physical transport and the transformation of organic nutrients to inorganic nutrients. The loss to fish landings is neglected here as it generally accounts for a very small percent (Nixon et al., 1996). For simplicity, the remineralization rate in the system, $k$, and loss rate due to settling and vertical transport, $\omega_o$, for organic nutrients from two sources are assumed the same in the derivation.

The equations for dynamics of organic nutrient concentration are developed for allochthonous sources (denoted by $O_1$) and autochthonous sources (denoted by $O_2$), respectively:
\[
\frac{dO_1}{dt} = \theta F O_R + L_o - F O_1 - (k + \omega_o)O_1 \quad (A2)
\]
\[
\frac{dO_2}{dt} = \frac{1}{\alpha} R_p C (1 - \beta_i) - F O_2 - (k + \omega_o)O_2 \quad (A3)
\]

Under the steady-state condition, the concentrations of \(O_1\) and \(O_2\) can be calculated:

\[
O_1 = \frac{\theta F O_R + L_o}{F + k + \omega_o} \quad (A4)
\]
\[
O_2 = \frac{1}{\alpha} \frac{R_p C (1 - \beta_i)}{F + k + \omega_o} \quad (A5)
\]

With respect to the dynamics of dissolved nutrients, the gain processes (+) include the loading, \(W_{in}\), and the loading from the recycled phytoplankton, \(W_{phyto}\), i.e., \(W_N = W_{in} + W_{phyto}\). The loss processes (-) include the uptake via phytoplankton (- \(\frac{1}{\alpha} GCV\)) and flushing by physical transport (-\(FNV\)).

Set \(L_{in} = \frac{W_{in}}{v}\) and \(L_{phyto} = \frac{W_{phyto}}{v}\), the Eq. (3.4) for N becomes:

\[
\frac{dN}{dt} = L_{in} + L_{phyto} - \frac{1}{\alpha} G C - F N \quad (A6)
\]

\(L_{in}\) includes the inputs of dissolved nutrients originally from the outside of the estuary through a variety of sources (Nonpoint-source input of N from the watershed, input from coastal areas, atmospheric deposition, underground water input, and point-source input from sewage treatment plants), the transform of allochthonous organic nutrients into inorganic nutrients, and nitrogen fixation if it exists. Similarly to the assumption used for organic nutrients, in river-dominated estuaries, the nonpoint-source loading rate of allochthonous N from the watershed is proportional to the flushing \(\theta FN_{R}\), where \(N_R\) is the N concentration of the water from the watershed, and the remaining portion of
allochthonous N loading rate is denoted by \( L_i \). \( L_{phyto} \) includes all the recycling ways of phytoplankton (directly into inorganic nutrients with an expression of \( \frac{1}{\alpha} R_p C \beta_i \), and the regeneration of autochthonous organic nutrients and the settled phytoplankton). The transformation of organic nutrients to inorganic nutrients is through remineralization, which can happen in the system or in the lower layer or the bottom sediments after their sinking.

The dynamics of inorganic and organic nutrients and settled phytoplankton in the lower water column or the sediment are not explicitly formulated here. For those settled organic nutrients and phytoplankton, only a portion of them can be remineralized into inorganic nutrients and recycled back to system, the remaining portion (the fraction is denoted by \( \gamma \)) leaves the system permanently, e.g., through bury or denitrification (only for nitrogen). Therefore, the expressions for the transformations of allochthonous and autochthonous organic nutrients are \( [k + (1 - \gamma) \omega_o]O_1 \) and \( [k + (1 - \gamma) \omega_o]O_2 \), respectively, and the expression for the transformations of settled phytoplankton is \( \frac{1}{\alpha} (1 - \gamma) \omega_c C \). Note that the nutrients in organic form settled into the lower layer and bottom sediment may not be fully recycled during some periods, and it results in an accumulative effect that in one period, both the nutrients current settled and previously settled provide the recycled N flux. This accumulative effect that provides extra recycled N loading rate from the previous settled organic nutrients to nutrient dynamics at the current state may not be significant when the annual timescale is considered, but it may be neglected on the seasonal timescale. For example, a large amount of organic nutrients and phytoplankton are either imported or produced in the spring, and the amount of nutrients in organic form settled into the bottom sediment also significantly enhanced.
These organic nutrients may not be fully recycled in the spring, and the uncycled part is remineralized in the summer along with the newly settled organic nutrients when the high temperature enhances the microbial activity. In the model, the extra recycled N loading rate in some periods caused by the accumulative effect is implicitly included in $L_i$. In summary,

\[
L_{\text{in}} = \theta FN_R + L_i + [k + (1 - \gamma)\omega_o]O_1
\]
\[
L_{\text{phyto}} = \frac{1}{a} R_p C \beta_i + \frac{1}{a} (1 - \gamma)\omega_c C + [k + (1 - \gamma)\omega_o]O_2
\]

Substituting Eqs. (A4) and (A5) into Eq. (A7), and set the expressions for $L_{\text{in}}$ and $L_{\text{phyto}}$ read:

\[
L_{\text{in}} = \theta FN_R + L_i + \varepsilon(\theta FO_R + L_o)
\]
\[
L_{\text{phyto}} = \frac{1}{a} [R_p C \beta_i + (1 - \gamma)\omega_c C + \varepsilon R_p C (1 - \beta_i)]
\]

where $\varepsilon = \frac{k+\gamma\omega_o}{F+k+\omega_o}$, is the fraction of allochthonous organic nutrients that contributes to the N loading rate. The value of $\varepsilon$, therefore, approaches to 0 with a large F (short flushing time $\tau$), and approaches to $\left(1 - \frac{\gamma\omega_o}{k+\omega_o}\right)$ with a small F (long flushing time $\tau$), indicating that the input N loading from the remineralization of organic nutrients, from both allochthonous and autochthonous sources, becomes smaller with a larger flushing effect because a larger portion is flushed out.

Substituting Eqs. (A8) and (A1) into (A6), under the steady-state conditions, the equation for N becomes

\[
0 = \theta FN_R (1 + \varepsilon \varphi) + L_i + \varepsilon L_o - FN - \frac{1}{a} R_p C (1 - \beta_i) (1 - \varepsilon) - \frac{1}{a} (F + \gamma \omega_c) C
\]
where \( \varphi = \frac{O_R}{N_R} \), and the associated solution for biomass \( C \) is

\[
C = \frac{\alpha}{[(1-\beta)(1-\epsilon)R_p+\gamma \omega_c]+F} \left[ (1 + \epsilon \alpha) \theta F N_R + L_i + \epsilon L_o - FN \right].
\]  

(A10)

Compared to the basic form for biomass Eq. (3.6),

\[
\beta = 1 - \frac{(1-\beta)(1-\epsilon)R_p+\gamma \omega_c}{R}.
\]  

(A11)

\( \beta \) is the parameter describing the recycling nutrient loading from the phytoplankton, which is associated with \( L_{phyto} \). As \( \beta \) varies positively with \( \epsilon \), any change of conditions that alters the value of \( \epsilon \) also change the value of \( \beta \), including the flushing rate \( F \). \( \beta \) decreases with a larger \( F \) (shorter \( \tau \)), indicating that the recycled portion of phytoplankton becomes smaller with a larger flushing effect.

The total nutrient \( (T_N) \) includes the inorganic nutrients (\( N \)), organic nutrients in the water (\( O_1 \) and \( O_2 \)), and the assimilated portion within living phytoplankton \( \left( \frac{C}{\alpha} \right) \), i.e.,

\[
T_N = N + O_1 + O_2 + \frac{C}{\alpha},
\]

and the equation for \( T_N \) dynamics sums Eqs. (A1-A3) and (A6):

\[
\frac{dT_N}{dt} = L_{TN} - F T_N - \gamma \left( \frac{1}{\alpha} \omega_c C + \omega_o O_1 + \omega_o O_2 \right)
\]  

(A12)

where \( L_{TN} = \theta F N_R + L_i + \theta F O_R + L_o \) is the volumetric \( T_N \) loading rate.
References


Lucas, L.V., Thompson, J.K., Brown, L.R., 2009. Why are diverse relationships observed between phytoplankton biomass and transport time. Limnol. Oceanogr. 54(1), 381-390.


Table 3.1. The list of parameters required in the mathematical model, Eq. (3.12), and their values on the annual timescale used in the example Pattern-1 system. Note that ε and β are two parameters that vary with flushing time, and their explicit expressions using additional parameters are presented in the Appendix, with values listed in Table 3.2.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Physical settings</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$H$</td>
<td>Depth of system</td>
<td>$m$</td>
<td>3</td>
</tr>
<tr>
<td>$\theta$</td>
<td>$Q_R/[(1-b)Q_{out}]$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nutrient related</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$N_R$</td>
<td>N of the water from the watershed</td>
<td>$g \text{ N m}^{-3}$</td>
<td>0.5</td>
</tr>
<tr>
<td>$O_R$</td>
<td>O of the water from the watershed</td>
<td>$g \text{ N m}^{-3}$</td>
<td>0.3</td>
</tr>
<tr>
<td>$L_i$</td>
<td>Volumetric N loading rate from the direct allochthonous N input except for nonpoint source</td>
<td>$g \text{ N m}^{-3} \text{ d}^{-1}$</td>
<td>0.001</td>
</tr>
<tr>
<td>$L_o$</td>
<td>Volumetric O loading rate from the direct allochthonous O input except for nonpoint source</td>
<td>$g \text{ N m}^{-3} \text{ d}^{-1}$</td>
<td>0.0006</td>
</tr>
<tr>
<td>$\varepsilon$</td>
<td>Fraction of allochthonous organic nutrients that contributes to the N loading rate</td>
<td></td>
<td>Varying</td>
</tr>
<tr>
<td>$\beta$</td>
<td>Fraction of the total bioavailable nutrients recycled from the loss of phytoplankton</td>
<td></td>
<td>Varying</td>
</tr>
<tr>
<td>Light related</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$I_0$</td>
<td>PAR at the surface</td>
<td>$\mu\text{E m}^{-2} \text{s}^{-1}$</td>
<td>300</td>
</tr>
<tr>
<td>$k_w$</td>
<td>Light attenuation by particle-free water and by partial contribution from suspended sediment including CDOM that is assumed to be constant</td>
<td>$m^{-1}$</td>
<td>0.96</td>
</tr>
<tr>
<td>$k_s$</td>
<td>Light attenuation by suspended sediments and by partial contribution from suspended sediment including CDOM that varies with flushing</td>
<td>$(g \text{ S})^{-1} \text{ m}^2$</td>
<td>0.06</td>
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<tr>
<td>$k_{chl}$</td>
<td>Light extinction by chlorophyll-a</td>
<td>$(g \text{ chl-a})^{-1} \text{ m}^2$</td>
<td>16.7</td>
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<tr>
<td>Sediment related</td>
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<td></td>
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<td>$S_R$</td>
<td>S of the water from the watershed</td>
<td>$g \text{ S m}^{-3}$</td>
<td>14</td>
</tr>
<tr>
<td>$\omega_s$</td>
<td>Loss rate for suspended sediments due to settling and vertical transport</td>
<td>$d^{-1}$</td>
<td>0.33</td>
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<td>Phytoplankton related</td>
<td></td>
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<tr>
<td>$G_m$</td>
<td>Maximum G as a function of temperature</td>
<td>$d^{-1}$</td>
<td>1.0</td>
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<td>$R$</td>
<td>Total local loss rate due to respiration/excretion, grazing, settling, and vertical transport</td>
<td>$d^{-1}$</td>
<td>0.3</td>
</tr>
<tr>
<td>$\alpha$</td>
<td>C:N ratio</td>
<td>$g \text{ C }/\text{ g N}$</td>
<td>5.68</td>
</tr>
<tr>
<td>$C:Chl$</td>
<td>Carbon to chlorophyll-a ratio of phytoplankton</td>
<td>$g \text{ C }/\text{ g chl-a}$</td>
<td>45</td>
</tr>
<tr>
<td>$N_k$</td>
<td>Half-saturation coefficient for N uptake</td>
<td>$g \text{ N m}^{-3}$</td>
<td>0.2</td>
</tr>
<tr>
<td>$I_{opt}$</td>
<td>Optimal PAR leading to maximum growth rate</td>
<td>$\mu\text{E m}^{-2} \text{s}^{-1}$</td>
<td>300</td>
</tr>
</tbody>
</table>
Table 3.2. The list of parameters for calculating $\epsilon$ and $\beta$ (Appendix) and their values on the annual timescale used in the example case.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutrient related</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_i$</td>
<td>Fraction of dissolved nutrients in the total nutrients that are directly released into the water from the recycled phytoplankton</td>
<td></td>
<td>0.2</td>
</tr>
<tr>
<td>$\gamma$</td>
<td>Fraction of settled organic nutrients and phytoplankton leaving the system permanently</td>
<td></td>
<td>0.25</td>
</tr>
<tr>
<td>$k$</td>
<td>Remineralization rate of organic nutrients in the waterbody of the system</td>
<td>$d^{-1}$</td>
<td>0.05</td>
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<tr>
<td>$\omega_o$</td>
<td>Loss rate for organic nutrients due to settling and vertical transport</td>
<td>$d^{-1}$</td>
<td>0.033</td>
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<tr>
<td>Phytoplankton related</td>
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<td>$R_p$</td>
<td>Biologically-related loss rate</td>
<td>$d^{-1}$</td>
<td>0.2</td>
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<tr>
<td>$\omega_c$</td>
<td>Physically-related loss rate for phytoplankton due to settling and vertical transport</td>
<td>$d^{-1}$</td>
<td>0.1</td>
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</table>
Notation of all variables and parameters.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
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<tbody>
<tr>
<td>Physical settings</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$t$</td>
<td>Time</td>
<td>$d$</td>
</tr>
<tr>
<td>$V$</td>
<td>Volume of system</td>
<td>$m^3$</td>
</tr>
<tr>
<td>$V_{seg}$</td>
<td>Volume of segment</td>
<td>$m^3$</td>
</tr>
<tr>
<td>$H$</td>
<td>Depth of system</td>
<td>$m$</td>
</tr>
<tr>
<td>$z$</td>
<td>Depth ranged from 0 (surface) to $-H$ (bottom)</td>
<td>$m$</td>
</tr>
<tr>
<td>$H_u$</td>
<td>Depth of photic zone</td>
<td>$m$</td>
</tr>
<tr>
<td>$Q_R$</td>
<td>Water input from the watershed</td>
<td>$m^3 d^{-1}$</td>
</tr>
<tr>
<td>$Q_{in}$</td>
<td>Inflow rate</td>
<td>$m^3 d^{-1}$</td>
</tr>
<tr>
<td>$Q_{out}$</td>
<td>Outflow rate</td>
<td>$m^3 d^{-1}$</td>
</tr>
<tr>
<td>$b$</td>
<td>Returning ratio</td>
<td></td>
</tr>
<tr>
<td>$Sal$</td>
<td>Mean salinity of the system</td>
<td>ppt</td>
</tr>
<tr>
<td>$Sal_0$</td>
<td>Salinity at the mouth</td>
<td>ppt</td>
</tr>
<tr>
<td>$\theta$</td>
<td>The ratio of $Q_R$ to $Q_{out}$</td>
<td></td>
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<tr>
<td>$F$</td>
<td>Flushing rate</td>
<td>$d^{-1}$</td>
</tr>
<tr>
<td>$\tau$</td>
<td>Flushing time, $1/F$</td>
<td>$d$</td>
</tr>
<tr>
<td>$\tau_{seg}$</td>
<td>Flushing time for segment</td>
<td>$d$</td>
</tr>
<tr>
<td>$\tau_m$</td>
<td>Flushing time of mean biomass maximum</td>
<td>$d$</td>
</tr>
<tr>
<td>$\tau_{seg}^m$</td>
<td>Flushing time of segment-averaged biomass maximum</td>
<td>$d$</td>
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<td>Nutrient related</td>
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<tr>
<td>$N$</td>
<td>Bioavailable nutrient concentration</td>
<td>$g N m^{-3}$</td>
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<tr>
<td>$O_1$</td>
<td>Allochthonous organic nutrient concentration</td>
<td>$g N m^{-3}$</td>
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<tr>
<td>$O_2$</td>
<td>Autochthonous organic nutrient concentration</td>
<td>$g N m^{-3}$</td>
</tr>
<tr>
<td>$T_N$</td>
<td>Total nutrient concentration, $T_N = N + O_1 + O_2 + C/\alpha$</td>
<td>$g N m^{-3}$</td>
</tr>
<tr>
<td>$N_R$</td>
<td>N of the water from the watershed</td>
<td>$g N m^{-3}$</td>
</tr>
<tr>
<td>$O_R$</td>
<td>O of the water from the watershed</td>
<td>$g N m^{-3}$</td>
</tr>
<tr>
<td>$\varphi$</td>
<td>$N_R/O_R$</td>
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</tr>
<tr>
<td>$W_N$</td>
<td>Total N loading rate</td>
<td>$g N d^{-1}$</td>
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<td>$W_{in}$</td>
<td>N loading rate with sources originally from outside system</td>
<td>$g N d^{-1}$</td>
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<td>$W_{phyto}$</td>
<td>N loading rate from the recycled phytoplankton</td>
<td>$g N d^{-1}$</td>
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<tr>
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<td>$W_{in}/V$</td>
<td>$g N m^{-3} d^{-1}$</td>
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<tr>
<td>$L_{phyto}$</td>
<td>$W_{phyto}/V$</td>
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<td>$L_i$</td>
<td>Volumetric N loading rate from the direct allochthonous N input except for nonpoint source</td>
<td>$g N m^{-3} d^{-1}$</td>
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<td>$L_o$</td>
<td>Volumetric O loading rate from the direct allochthonous O input except for nonpoint source</td>
<td>$g N m^{-3} d^{-1}$</td>
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<td>$L_{T_N}$</td>
<td>Volumetric $T_N$ loading rate</td>
<td>$g N m^{-3} d^{-1}$</td>
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<tr>
<td>$\varepsilon$</td>
<td>Fraction of allochthonous organic nutrients that contributes to the N loading rate</td>
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</tr>
<tr>
<td>$\beta$</td>
<td>Fraction of the total bioavailable nutrients recycled from the loss of phytoplankton</td>
<td></td>
</tr>
<tr>
<td>$\beta_i$</td>
<td>Fraction of dissolved nutrients in the total nutrients that are directly released into the water from the recycled phytoplankton</td>
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</tr>
<tr>
<td>Symbol</td>
<td>Description</td>
<td></td>
</tr>
<tr>
<td>--------</td>
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<td></td>
</tr>
<tr>
<td>( \gamma )</td>
<td>Fraction of settled organic nutrients and phytoplankton leaving the system permanently</td>
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</tr>
<tr>
<td>( k )</td>
<td>Remineralization rate of organic nutrients in the waterbody of the system</td>
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<tr>
<td>( \omega_o )</td>
<td>Loss rate for organic nutrients due to settling and vertical transport</td>
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**Light related**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tbody>
<tr>
<td>( I )</td>
<td>Photosynthetically active radiation (PAR) ( \mu )E ( m^2 \ s^{-1} )</td>
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<tr>
<td>( I_0 )</td>
<td>PAR at the surface ( \mu )E ( m^2 \ s^{-1} )</td>
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<tr>
<td>( k_d )</td>
<td>Light attenuation ( m^{-1} )</td>
</tr>
<tr>
<td>( k_w )</td>
<td>Light attenuation by particle-free water and by partial contribution from suspended sediment including CDOM that is assumed to be constant ( m^{-1} )</td>
</tr>
<tr>
<td>( k_s )</td>
<td>Light attenuation by suspended sediments and by partial contribution from suspended sediment including CDOM that varies with flushing ( (g \ S)^{-1} \ m^2 )</td>
</tr>
<tr>
<td>( k_{chl} )</td>
<td>Light attenuation by chlorophyll-a ( (g \ chl-a)^{-1} \ m^2 )</td>
</tr>
<tr>
<td>( k_C )</td>
<td>( k_{chl}/C : Chl ) ( (g \ C)^{-1} \ m^2 )</td>
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**Sediment and CDOM related**

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<tr>
<td>( S )</td>
<td>Suspended sediment concentration ( g \ S \ \ m^{-3} )</td>
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<tr>
<td>( S_R )</td>
<td>( S ) of the water from the watershed ( g \ S \ \ m^{-3} )</td>
</tr>
<tr>
<td>( L_s )</td>
<td>Volumetric suspended sediment loading rate ( g \ S \ \ m^{-3} \ \ d^{-1} )</td>
</tr>
<tr>
<td>( \omega_s )</td>
<td>Loss rate for suspended sediments due to settling and vertical transport ( d^{-1} )</td>
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**Phytoplankton related**

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tbody>
<tr>
<td>( C )</td>
<td>Volumetric biomass ( g \ C \ \ m^{-3} )</td>
</tr>
<tr>
<td>( C_N )</td>
<td>Volumetric biomass under nutrient limitation only ( g \ C \ \ m^{-3} )</td>
</tr>
<tr>
<td>( C_l )</td>
<td>Volumetric biomass under light limitation only ( g \ C \ \ m^{-3} )</td>
</tr>
<tr>
<td>( B )</td>
<td>Areal phytoplankton biomass ( g \ C \ \ m^{-2} )</td>
</tr>
<tr>
<td>( C^{seg} )</td>
<td>Segment-averaged volumetric biomass ( g \ C \ \ m^{-3} )</td>
</tr>
<tr>
<td>( C_{local} )</td>
<td>Mean volumetric biomass for local waterbody ( g \ C \ \ m^{-3} )</td>
</tr>
<tr>
<td>( GPP )</td>
<td>Phytoplankton gross primary productivity ( g \ C \ \ m^{-2} \ \ d^{-1} )</td>
</tr>
<tr>
<td>( G )</td>
<td>Gross growth rate ( d^{-1} )</td>
</tr>
<tr>
<td>( G_m )</td>
<td>Maximum ( G ) as a function of temperature ( d^{-1} )</td>
</tr>
<tr>
<td>( R )</td>
<td>Total local loss rate due to respiration/excretion, grazing, settling, and vertical transport ( d^{-1} )</td>
</tr>
<tr>
<td>( R_p )</td>
<td>Biologically related loss rate ( d^{-1} )</td>
</tr>
<tr>
<td>( \omega_c )</td>
<td>Physically related loss rate for phytoplankton due to settling and vertical transport ( d^{-1} )</td>
</tr>
<tr>
<td>( \alpha )</td>
<td>C:N ratio ( g \ C / g \ N )</td>
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<tr>
<td>( C : Chl )</td>
<td>Carbon to chlorophyll-a ratio of phytoplankton ( g \ C / g \ chl-a )</td>
</tr>
<tr>
<td>( f(N) )</td>
<td>Growth limiting function for light</td>
</tr>
<tr>
<td>( f(I) )</td>
<td>Growth limiting function for nutrient</td>
</tr>
<tr>
<td>( N_k )</td>
<td>Half-saturation coefficient for N uptake ( g \ N \ \ m^{-3} )</td>
</tr>
<tr>
<td>( I_{opt} )</td>
<td>Optimal PAR leading to maximum growth rate ( \mu )E ( m^2 \ s^{-1} )</td>
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**Secondary producer related**
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<th>Unit</th>
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<tr>
<td>$Z$</td>
<td>Biomass of secondary producer</td>
<td>$g \ C \ m^3$</td>
</tr>
<tr>
<td>$G_Z$</td>
<td>Gross growth rate as a function of temperature</td>
<td>$d^1$</td>
</tr>
<tr>
<td>$C_k$</td>
<td>Half-saturation coefficient for C uptake</td>
<td>$g \ C \ m^3$</td>
</tr>
</tbody>
</table>
Figure 3.1. Illustration of physical settings and hydrodynamics in an estuary. The system considered in this study is the upper mixed layer (light-grey layer).
Figure 3.2. Relationship between volumetric phytoplankton biomass (represented by chl-a) and flushing time, $\tau$. a) under light limitation only ($C_I$), and b) nutrient limitation only ($C_N$). The example system uses values of parameters listed in Table 3.1 and 3.2.
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Figure 3.11. Relationships between variables in Pattern-1 system (solid lines) and Pattern-2 system (dashed lines). a) variabilities in areal phytoplankton gross primary productivity (GPP), areal biomass (B), and GPP:B ratio with flushing time, $\tau$. b) variability in bioavailable nutrients concentration (N). c) changes in phytoplankton biomass with volumetric nutrient loading rate ($L_{in}$) and nonpoint-source N input ($\theta FN_R$), respectively.
Chapter 4. Physical transport processes affect the origins of harmful algal blooms in estuaries
Abstract

The effects of physical transport processes on the initiation of harmful algal blooms (HABs) in estuaries were investigated through both mathematical model simulations and numerical experiments. This study highlights the contribution of flushing effect. The model results show that the spatial difference in the flushing effect at different waterbodies due to the geometry complexity is one major factor causing the spatially inhomogeneity of algal density during the HAB initiation, and the ratio of transport time to volume is one of the key variables to determine the differential flushing effect on HAB initiation in multiple interconnected system. As a result, a HAB tends to be observed first in the locations with relatively long residence time, such as tributaries or areas with large eddies; and multiple unconnected originating locations can co-exist within an estuary.

Two numerical experiments were conducted for studying the contribution of flushing effect to the annual Cochlodinium (recently renamed Margalefidinium) polykrikoides bloom in the lower James River. The results show that the flushing effect can be the major factor driving the spatial difference in the density of C. polykrikoides during the bloom initiation, and the relatively small waterbody with the long residence time of Lafayette River, a subtributary, is favorable for the first bloom occurrence, which explains the observations that the Lafayette River is one originating location for this bloom. The impact of cyst distribution is suggested to be comparably small to the flushing effect on the spatial gradients of algal density in this system, and the C. polykrikoides bloom in the lower James River provides an example showing that the HAB originating locations do not have to be the beds with abundant cysts.
Keywords: Harmful algal blooms; initiation; Transport; Residence time; Estuary;

Cochlodinium polykrikoides
Introduction

Over the past half century, human activities have been contributing greatly to facilitate the deterioration of water quality in many estuarine and coastal aquatic environments (Cloern, 2001; Kemp et al., 2005). Of various water quality issues, harmful algal blooms (HABs) receive more and more attention due to their impact on ecosystems and economic loss. HABs of a variety of different species have been observed widely in estuaries throughout the world (Granéli and Turner, 2006; Lewitus et al., 2012), and eutrophication through nutrient enrichment is thought to be an important reason for their expansion in the U.S. and other nations (e.g., Smayda, 1990; Anderson et al., 2002; Glibert et al., 2005; Heisler et al., 2008; O’Neil et al., 2012). The general interests lie in understanding the environmental conditions promoting blooms and also in developing the policies and techniques for the prevention, control, and mitigation (Kudela and Gobler, 2012), which requires examinations of fundamental processes that affect algal growth and accumulation in estuaries.

Both local processes (e.g., photosynthesis, respiration, grazing, settling, and possible vertical migration) and physical transport processes through advection and dispersion affect the development of HABs (Donaghay and Osborn, 1997). Like other non-HAB algal species, while local biological processes determine the local growth of phytoplankton, transport processes also show great impacts on the variability of phytoplankton over a wide range of timescales (Lucas et al., 1999; Pitcher et al., 2010; Qin and Shen, 2017). The latter can be as important as the former in regulating HABs in estuarine and coastal systems, such as altering the relationship between anthropogenic nutrient enrichment and HABs at local scales (Davidson et al., 2014). The local processes
can be affected directly by many environmental factors, including temperature, light, nutrients, grazing pressure, pH, stratification, and so forth, and their impacts on HABs have been investigated intensively for a variety of HAB species (e.g., Wells et al., 2015). The effect of transport processes can be divided into direct and indirect effects. Because the flow redistributes the algal biomass within the system and exchange with adjacent waterbodies, transport processes can affect HABs directly in a variety of ways from the beginning and throughout each stage of initiation, development, and termination. The effect of flushing algae out of the system has been highlighted as the primary effect of physical transport on dynamics of phytoplankton including HAB species, which can alter local algal community abundance and composition (Ferreira et al., 2005; Paerl et al., 2006; Costa et al., 2009). The changes in flushing effect can cause changes in the frequency and timing of the HAB occurrence (e.g., Alvarez-Salgado et al., 2008; Paerl et al., 2011). In addition, horizontal transport processes by circulation can transport initial population to the habitats where HABs favored (e.g., Tyler and Seliger, 1978; Li et al., 2000; McGillicuddy et al., 2003; Hall et al., 2008; Kim et al., 2016); can transport the developed HABs from its origins to other areas to induce a bloom there (e.g., MacFadyen et al., 2005; Giddings et al., 2014); can concentrate cells in local areas (e.g., Hall et al., 2008; Escalera et al., 2010); and can act as a barrier to inhibit the shoreward transport of HABs from offshore coastal waterbodies (e.g., Hickey et al., 2005). Studies also reveal that the flushing effect interacts with algal behaviors, such as the swimming behavior that changes the vertical position of algae in the water column (e.g., Anderson and Stolzenbach, 1985; Donaghay and Osborn, 1997; Ralston et al., 2015). Besides the flushing effect, transport processes can impact the local phytoplankton growth indirectly.
through their mediation on the biological processes, since the flow can distribute heat energy that influences local temperature and other substances like nutrients, salinity, suspended sediment, grazers, and co-occurring algae.

While the impacts of transport processes on HABs in coastal upwelling systems, largely induced by the atmospheric oscillations through its influence on both the upper-layer water stratification and retention (Pitcher et al., 2010), have been investigated, the effects of transport processes on estuarine HABs are much less discussed. Though the initiation and development of some estuarine HABs are strongly impacted by physical conditions in the adjacent coastal areas through upwelling-downwelling cycle and onshore-offshore transport (e.g., Fermin et al., 1996), annual occurrences of HABs in many estuaries have been suggested to originate within the estuaries (Anderson, 1997; Mulholland et al., 2009). It then would be important to understand the mechanisms and the associated environmental conditions leading to the local initiation of the estuarine blooms and their retention within the system. Recent studies in Nauset Estuary on Cape Cod, USA, suggest that water temperature and water retention are the two dominant factors in controlling the *Alexandrium fundyense* bloom that originates from three salt ponds within the estuary (Ralston et al., 2014, 2015).

Due to the complex interaction between physical forcings and geometry, the flushing effect may not be uniform throughout an estuary, making the role of flushing effect of transport processes more than a simple loss term that prevents the accumulation of algae and delays the occurrence of HABs in estuaries. In this study, we used both mathematical and numerical models to demonstrate that this spatial difference in flushing
can affect and even determine spatial gradients in algal density and locations of estuarine HAB initiation.

Specifically, the bloom of *Cochlodinium polykrikoides* in the lower James River, USA, is used as an example. *C. polykrikoides*, recently proposed to be renamed *Margalefidinium polykrikoides* (Gómez et al., 2017), is a primary dinoflagellate species that regularly forms HABs in the coastal waters of Southeast Asia, Europe and North America for many decades, and has been shown to expand across the globe (Kudela and Gobler, 2012). Although the precise toxins leading to its toxicity have not yet to be confirmed, it has been widely found that the blooms of *C. polykrikoides* (generally characterized by densities > 1000 cells ml\(^{-1}\) in the lower James River, according to Morse et al., 2013) are strongly toxic and could kill most marine organisms including other algae, copepod, bivalves, coral reefs, and fish during bloom events (e.g. Jiang et al., 2009; 2010; Tang and Gobler, 2009a; 2009b; 2010; Richlen et al., 2010).

The underlying mechanisms of the initiation, growth, and die-off of *C. polykrikoides* blooms, however, are not fully known due to the complex processes they involve. *C. polykrikoides* are suggested to have a variety of strategies for growing well in estuaries (Kudela and Gobler, 2012), such as vertical migration behavior, uptake of organic nitrogen, grazing suppression, mixotrophic consumption, allelopathic effects, and the formation of both temporary and resting cysts. This prevents scientists from accurately predicting when and where these blooms will occur, and how large they will be, thus resulting in a challenge to find an effective strategy to control the bloom. Virginia, for example, is one of the locations on the East Coast of the US that have been reported to have *C. polykrikoides* blooms for over 40 years (Mackiernan, 1968; Ho and
Zubkoff, 1979). While monitoring programs demonstrate that blooms occur almost annually in the lower Chesapeake Bay and its tributaries in late summers over the past two decades (Morse et al., 2013), many questions on the initiation of C. polykrikoides blooms remain unanswered. Within the scope of this study, we examined one question by highlighting the flushing effect of transport processes: Why the tributaries of the lower James River, Lafayette River and its adjacent Elizabeth River, are the major originating locations of the bloom (Mulholland et al., 2009; Morse et al., 2011).

**Dynamics of HAB algal density**

**Governing equation**

In the estuarine systems, the dynamics of harmful algal (HA) density in the water column at a given location and time can be described by the first-order reaction transport equation, including both the local processes and transport processes:

\[
\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} - \frac{\partial}{\partial x} \left( K \frac{\partial C}{\partial x} \right) = gC + S
\]  

(4.1)

where \(C\) denotes algal density (cell ml\(^{-1}\)), \(x\) and \(t\) denote location and time, respectively, \(u\) is current velocity (m s\(^{-1}\)), \(K\) is diffusivity (m\(^2\) s\(^{-1}\)), and \(g\) denotes the net growth rate of the algae (d\(^{-1}\)) as a result of local processes including photosynthesis, respiration, mortality, and settling. \(S\) denotes external sources or sinks of algae. For those HA species that can produce cysts, the germination of cysts from the bottom sediments can be treated as external loading as well.

Using the approach of Qin and Shen (2017), the transport processes can be represented by a transport rate (denoted as \(F\)) that describes the variability of flushing effect, the dynamics of algal density at a location can be described as:
\[
\frac{\partial C}{\partial t} = gC - FC + S, \quad (4.2)
\]

where the impacts of local biological processes and transport processes are decomposed as the first and second terms on the right hand side, which we hereafter refer to as local and transport processes. Define relative growth rate as \( r = \frac{\partial C}{c\partial t} \) (i.e., \( C = C_{init}e^{rt} \)), where \( C_{init} \) is the initial density, the equation for the rates can be obtained by dividing \( C \) on both sides of Eq. (4.2), which gives:

\[
r = g - F + S/C. \quad (4.3)
\]

**Flush effect on time required for HAB initiation**

A HAB initiation in this study is referred to as the process of HA growing from its presence in the water column to the level of bloom density, and its time duration is affected by both the initial algal density and the relative growth rate. The relative growth rate, \( r \), is controlled by ecophysiology of the specific HA species and environmental conditions, which varies in time and location, and it can be either positive (increase in density) or negative (decrease in density). Therefore, a presence of harmful algae in the water column does not necessarily result in a HAB at that location. A successful initiation of a HAB requires 1) a sufficient period of time for harmful algae to grow to the level of bloom density, and 2) a positive mean relative growth rate during that period. The time required for its initiation, \( t_B \), is a function of the positive mean relative growth rate, \( \langle r \rangle \):

\[
t_B = \frac{1}{\langle r \rangle} \ln(C_{bloom}/C_{init}) \quad (4.4)
\]

where \( C_{bloom} \) is the bloom density. Definition of algal density as an indicative presence and bloom varies with algal species and cases. Specifically for the initiation of \( C \).
**polykrikoides** bloom in the lower James River, we use 1 cell ml\(^{-1}\) to indicate the presence and 1000 cells ml\(^{-1}\) or higher as the level of HAB (Morse et al., 2013). The time required for the algal growing to the bloom level is given by:

\[ t_B = \frac{1}{\langle r \rangle} \ln(1000) \text{ days}, \quad \text{or} \quad t_B \approx \frac{1}{\langle r \rangle} \text{ weeks.} \quad (4.5) \]

For example, for the Japanese strain of *C. polykrikoides* with the net maximum daily growth rate of about 0.41 d\(^{-1}\) (Kim et al., 2004), Eq. (4.5) suggests that it would still require over 2 weeks to lead to a HAB even under the optimal growth condition (Figure 4.1).

Thus, according to Eq. (4.4), any environmental factor that can alter the value of relative growth rate can affect the time required for a HAB initiation, and the flushing by transport processes therefore is one critical factor in regulating the initiation time. The flushing effect can be either “transport out” that delays the initiation or “transport in” that shortens the required time, indicating by a positive or a negative transport rate, respectively.

**Spatial distribution of algal density**

In an estuary, the complex geometry and the incompletely mixing of estuaries results in the large spatial variability in both the flushing effect and local processes, which creates various segments with different environmental conditions for HAB initiation. During the initiation of a HAB event, the bloom density can be reached earlier in the areas with persistently higher algal density, therefore, the spatial difference in algal density and the associated environmental conditions need to be examined to better understand the existence and characteristics of the originating locations for HABs in a
system. To understand the underlying mechanism, a mathematical model for examining the spatial distribution of algal density is developed.

**Mathematical model**

We consider a system consisting of two connected waterbodies 1 and 2 (Figure 4.2). In an estuary, these two waterbodies can represent the mainstem of the estuary and an adjoining tributary, respectively, which is very common in many estuaries. The analysis of HAB initiation in this system requires the comparison of algal density between these two waterbodies. Assume that both waterbodies 1 and 2 are completely mixed for simplicity. Under steady state, conservation requires $V = V_1 + V_2$ and $Q = Q_{R1} + Q_{R2}$, where $V$ and $Q$ denote the volume and outflow of the system, respectively; $V_1$ and $V_2$ denote the volumes and $Q_{R1}$ and $Q_{R2}$ denote the inflow into the two waterbodies, respectively.

The dynamics of algal density in these two waterbodies can be described by mass-balance equations, with the assumption of no input of algae from inflows:

\[
V_1 \frac{dC_1}{dt} = g_1 C_1 V_1 - Q e C_1 - (Q_e - Q_{R2}) C_1 + Q_e C_2, \quad (4.6.1)
\]

\[
V_2 \frac{dC_2}{dt} = g_2 C_2 V_2 - Q e C_2 + (Q_e - Q_{R2}) C_1, \quad (4.6.2)
\]

with initial conditions $C_1 = C_{1,ini}$ and $C_2 = C_{2,ini}$, at $t = 0$, where $C_1$ and $C_2$ denote the mean density in the two waterbodies, respectively, $g_1$ and $g_2$ denote the mean net growth rate, respectively, and $Q_e$ denotes the exchange flow between the two waterbodies. Note that the external loading by germination ($S$ in Eq. 4.1) is not included in the mathematical model. While the initial contribution can be implicitly included in the initial density, no
additional germination is considered occurs as its relative contribution to density
variation (last terms in Eqs. 4.2 and 4.3) during the initiation becomes small, particularly
with increasing algal density, compared to that due to the local growth or horizontal
transport (Crespo et al., 2011).

We further used residence time for each waterbody to represent the flushing effect
of physical transport. Residence time indicates the mean time required for substance to
leave the system, which is a good indicator of the flushing effect that integrates all the
impacts from physical forcings, such as freshwater advection, tidal mixing, and wind-
induced circulation (Monsen et al., 2002), and it can be used to diagnose the flushing
effect of transport processes on the algal growth over large scales (Lucas et al., 2009). A
region with long residence time is recognized as a stable aquatic environment with a slow
exchange between water parcels and their carrying substances inside and outside of a
region. The general formula for residence time (denoted by \( \tau \)) can be computed using the
remnant function \( R \) (Takeoka, 1984). For a completely mixing system, the remnant
function is \( R = C_0 e^{-t/\tau} \) and the residence time equals the e-folding time (Prandle, 1984).
This can be equivalently expressed as \( \frac{dC}{dt} = -\frac{1}{\tau} C \). For a system of Figure 4.2, the
expressions for local residence time, \( \tau_1 \) and \( \tau_2 \), for waterbody 1 and 2, respectively, can
be mathematically derived by assuming that concentrations of input flow are zero.

\[
V_1 \frac{dC_1}{dt} = -(Q + Q_e - Q_{R2})C_1 \quad (4.7.1)
\]

\[
V_2 \frac{dC_2}{dt} = -Q_e C_2 \quad (4.7.2)
\]
Therefore, the partial residence time for waterbody 1 and 2 are expressed as 
\[ \tau_1 = \frac{V_1}{Q + Q_e - Q_{R2}}, \] and 
\[ \tau_2 = \frac{V_2}{Q_e}, \] respectively. One advantage of using residence time to quantify
the flushing effect is because the residence time for any system (either completely or
incompletely mixed) can be computed using numerical modeling approaches (e.g.,
Delhez et al., 2004; Du and Shen, 2016).

The dynamics of algal density can be derived by dividing \( V_1 \) and \( V_2 \) for the two
equations, respectively. Set \( \theta = \frac{V_2}{V_1} \), and \( \eta = \frac{Q - Q_{R2}}{Q_e} \) that indicates the information of
exchange between the two waterbodies, and apply the Eq. (4.7) of residence time, we can
get

\[
\frac{dC_1}{dt} = g_1 C_1 - \frac{1}{\tau_1} C_1 + \frac{\theta}{\tau_2} C_2 \tag{4.8.1}
\]

\[
\frac{dC_2}{dt} = g_2 C_2 - \frac{1}{\tau_2} C_2 + \frac{\eta}{\tau_2} C_1 \tag{4.8.2}
\]

Since \( Q_e \gg Q_{R2} \) for a typical estuary, \( \eta \) is positive and close to 1.

**Spatial gradients in density**

Set \( \phi \) to be the ratio of algal density in waterbody 2 to that in waterbody 1, i.e.,
\[ \phi = \frac{C_2}{C_1}, \] we can get the first-order equation \( \frac{d\phi}{dt} = f(\phi) \) for \( \phi \) from Eqs. (4.8.1) and
(4.8.2):

\[
\frac{d\phi}{dt} = f(\phi) = a\phi^2 + b\phi + c \tag{4.9}
\]

where
\[ a = -\frac{\theta}{\tau_2} < 0 \]
\[ b = (g_2 - g_1) + \left(\frac{1}{\tau_1} - \frac{1}{\tau_2}\right) \]
\[ c = \frac{\eta}{\tau_2} \geq 0 \]

The time-dependent solution for \( \phi \) in Eq. (4.9) can be calculated explicitly, but it is easier to understand the pattern of \( \phi \) by interpreting Eq. (4.9) into a vector field. An example of the vector field for Eq. (4.9) assuming \( g_2 = g_1 \) is shown in Figure 4.3, in which only the flushing effect is considered. Specifically, the typical parameters of this example system are \( \tau_1 = 6.66 \) days, \( \tau_2 = 9.31 \) days, \( \theta = 0.0085 \), \( \eta = 1 \). It can be shown that there is one positive stable fixed point \( \phi^* \) that makes \( \frac{d\phi}{dt} = 0 \) for Eq. (4.9), which means that \( \phi \) keeps increasing toward \( \phi^* \) when it is smaller than \( \phi^* \) but decreases when it is larger. Thus, \( \phi^* \) is the equilibrium ratio of \( C_2 \) to \( C_1 \), indicating that it is the ratio of algal density, rather than their difference, that approaches a constant under a steady hydrodynamic condition.

Apparently, as \( a < 0 \), \( \phi^* = \frac{-b - \sqrt{b^2 - 4ac}}{2a} \), which is always larger than 1 as long as \( \tau_2 / \tau_1 > (1 - \eta + \theta) \). In addition, since an estuary usually has a stronger exchange flow than riverine flow by a factor of 2-34 at the head (MacCready and Geyer, 2010), \( \eta \) is close to 1. Therefore, from the extreme case assuming that \( \eta = 1 \), the necessary condition for having a \( \phi^* \) larger than 1 in estuarine systems requires \( \tau_2 / \tau_1 > \theta \), or

\[ \frac{\tau_2}{\nu_2} > \frac{\tau_1}{\nu_1}. \]
Eq. (4.10) suggests that, for such a system with two connected waterbodies, the gradients of algal density between waterbodies are not determined by residence time only, but by residence time normalized to volume, and the waterbody with a relatively long residence time and small volume has high algal density when equilibrium is reached. In an estuary, tributaries or areas with large eddies are usually areas with high algal density because of their long residence time as well as small volumes resulting a $\phi^*$ much larger than 1.

The value of $\phi^*$ can be used to compare the algal density between the waterbodies, which varies in different systems and greatly depends on the ratios of both residence time, $\tau_2/\tau_1$, and volume, $\theta$, and $\eta$ (Figure 4.4). For a system with a large value of $\phi^*$, a simple expression for $\phi^*$ can be approximated as $\phi^* \approx \frac{-b}{a} = \frac{1}{\theta} \left( \frac{\tau_2}{\tau_1} - 1 \right)$, which requires $b^2 \gg |4ac|$ or an equivalent condition that $(\phi^*)^2 \gg \frac{4\eta}{\theta}$. For the system in Figure 4.3, the value of $\phi^*$ calculated by this simple expression is 48.87, close to its accurate value of 51.18.

The time required to reach equilibrium also varies, which depends not only on $\tau_2/\tau_1$ and $\theta$, but also on the absolute values of residence time. A smaller residence time or a higher flushing effect can shorten the time required to reach equilibrium. As shown in Figure 4.3b, with an initial $\phi$ equal zero, it requires about 158.7 days for such an example system of Figure 4.3a to reach the density ratio above 99% of the equilibrium $\phi^*$ of 51.18, but only 79.4 days is needed if both residence times are shortened by half.

In a natural system with an equilibrium $\phi^*$ above 1, as the HAB event can occur without fully reaching equilibrium, it is very likely that the time required for the initiation
of a HAB is shorter than the time required for \( \phi \) reaching equilibrium \( \phi^* \), and hence the value of \( \phi \) can be smaller than \( \phi^* \) when a HAB appears. However, while \( \phi \) above 1 is required for the waterbody 2 to have an earlier HAB occurrence, \( \phi \) does not have to reach the value of the equilibrium \( \phi^* \). Also, the time required for \( \phi \) to reach 1 is quite short compared to the total time for reaching the equilibrium if \( \phi \) begins with a value lower than 1; and for this example system, even with an initial \( \phi \) that equals zero, the time required to reach \( \phi > 1 \) only takes about 7.8 days, while it takes an additional 31 days to get \( \phi > 10 \). While most HAB species usually grow relatively slow (Smayda, 1997; Jeong et al., 2015) and hence the time of HAB initiation usually longer than weeks (Eq. 4.5), the values of \( \phi \) are usually above 1 during the initiation and the ratios become large when a HAB first appears in the system.

Thus, a hypothesis is proposed that when the flushing effect of transport processes is the dominant factor in regulating the spatial gradients of algal density, a HAB tends to first appear in the areas with a relatively large ratio of residence time to volume in estuaries.

**Contributions of local and transport processes to density distribution**

According to Eq. (4.9), the impact of local processes on the density ratio \( \phi \) is through the coefficient \( b \), and the relative contributions of local and transport processes on the spatial difference can be compared through the values of \( (g_2 - g_1) \) and \( \left( \frac{1}{\tau_1} - \frac{1}{\tau_2} \right) \). Particularly, if \( (g_2 - g_1) \) is much smaller than \( \left( \frac{1}{\tau_1} - \frac{1}{\tau_2} \right) \), the contribution of local processes to \( \phi \) is negligible.
Temperature is a primary factor in regulating algal growth, and there is an optimal temperature range for the growth of a specific HAB algal species (Wells et al., 2015). Since temperature of a year shows a cycle that is high in the summer but low in the winter, the growth rate of a HAB species, $g$, always shows an increase during the initiation. When a HAB species first appears in the system, the environmental conditions usually have not reached the optimal conditions in this early stage, and their growth rate, $g$, at each waterbody is low in magnitude, and therefore the difference $(g_2 - g_1)$ is much smaller than $(\frac{1}{\tau_1} - \frac{1}{\tau_2})$ and the contribution of local processes is negligible. During the initiation of HABs, environmental conditions become more favorable for algal growth, and the growth rate increases correspondingly. The values of difference $(g_2 - g_1)$ and the contribution of local processes to the spatial difference in algal density can also increase, which, in fact, is largely affected by the indirect effects of transport processes that can generate horizontal gradients in heat, salinity, nutrient concentrations, suspended sediment concentrations, grazing pressure and co-occurring non-HAB algal concentrations. Nevertheless, the difference in the flushing effect of the two waterbodies, dependent on the hydrodynamics, does not decreases during the initiation, and their relative contribution to the spatial difference in algal density is still important, and it can be always larger than the contribution of local processes in many systems. An example of comparing the relative contribution of local and transport processes to the algal density distribution during $C.\ polykrikoides$ bloom initiation in the lower James River is discussed later.
Flush effect in the lower James River

To understand the dynamic effects on the coupled lower James River and its subestuary of Elizabeth River and Lafayette River, we can examine and compare residence time associated with each waterbody.

We applied a calibrated and verified real-time 3-D numerical model (Shen et al., 2016) to compute the local residence time following the method proposed by Delhez et al. (2004). The model was forced by hourly tide and salinity at the mouth and hourly wind and heat flux, with 3,066 grid cells in the horizontal and 8 layers in the vertical. We focused on 4 segments in the lower James River, including the Lafayette River, the Elizabeth River, the Nansemond River, and the Mainstem connected to the Elizabeth River and the Nansemond River with mean summer salinity larger than 10 because *C. polykrikoides* cannot grow well with low salinity (Figure 4.5). The volume-averaged local residence time was calculated from 2006-2013 for each segments (Table 4.1).

The results show that the Nansemond River had the longest mean residence time of about 25.53 d during May-July for the years 2005-2013, followed by the Lafayette River of about 9.31 d and the mainstem of about 6.66 d, and the Elizabeth River had the shortest residence time of around 5.24 d (Table 4.1). After normalized by the respective volumes, the Lafayette River had the largest value of the ratio of residence time to volume (∇/V), while the mainstem had the smallest value. Therefore, according to Eq. (4.10), for summertime HABs including *C. polykrikoides* blooms in the lower James River, it is expected that the Lafayette River will reach the bloom density first, followed by Nansemond River and Elizabeth River and the mainstem be the last one to reach bloom density based on the flushing effect due to transport processes.
**C. polykrikoides bloom initiation**

In this section, we examined the initiation of *C. polykrikoides* bloom in the lower James River using numerical model experiments. According to the analysis above, we hypothesized that 1) the flushing effect of transport processes is the dominant factor regulating the spatial variability of growth of *C. polykrikoides* between the mainstem and tributaries (e.g., the Lafayette River) in the lower James River if biological process is same in each waterbody, and HABs will occur in the waterbody with relatively long residence time; 2) the flushing effect can be the determinant factor in determining the location of the first bloom appearance even when the effect of local processes is different among those waterbodies.

To test the hypotheses, we conducted two numerical HAB experiments with realistic hydrodynamic fields of the year 2009. The purpose of the experiments is to examine effects of flushing and net biological process rather than simulating *C. polykrikoides* to match the real cases, some processes were not included such as nutrient and light limitation, uptake of DOC, and grazing.

**Experiment with constant growth rate**

Scenario 1 is to examine the flushing effect of transport processes only, and we set the growth rate, \( g \), to be a constant of 0.41 \( \text{d}^{-1} \), which is about the maximum growth rate measured in the laboratory under optimal conditions (Kim et al., 2004; Gobler et al., 2012). The swimming behavior of *C. polykrikoides* is considered by forcing the algae to stay at the surface layer during the daytime.

The laboratory cultures by Tang and Gobler (2012) showed that 2-40% of resting cysts can germinate successfully at 18-21°C within 12-31 days.
River, the water temperature had exceeded 18°C and salinity was above 16 by April 22, 2009, according to the hydrodynamics model results, and the environment conditions can have a growth rate, \( g \), higher than 0.1 d\(^{-1}\) according to the experimental results reported by Kim et al. (2004). Temperature went up to above 22°C by April 29, 2009. In addition to resting cysts, temporal cysts produced by *C. polykrikoides* may also exist in the lower James River, which have been shown to be able to overwinter (Kim et al., 2002) and revert to vegetative cells within 1 day to 1 week (Tang and Gobler, 2012; Shin et al., 2017). Thus, the germination and release processes can start from April and last into May. According to Morse et al. (2013), in the end of May to early June of 2009, *C. polykrikoides* with a density larger than 1 cell ml\(^{-1}\) were found to be present in water samples collected from the Lafayette River and Elizabeth River. Thus, in the numerical experiments, *C. polykrikoides* were released initially from the bottom layer at the mainstem of the James with a density of 1 cell ml\(^{-1}\), and the release date was chosen to be June 1, 2009. The release at the mainstem of the James is on purpose to show the transport processes to induce HABs initially in the region with long residence time. No “new” algae were input from the mouth of the James River or the upper James River, and cells could be transported out during ebb tide while some fraction could re-enter the estuary on the following flood tide. Additionally, to demonstrate the process of the increase in \( \phi \) to an equilibrium, the release area in Scenario 1 was restricted over the mainstem (Figure 4.6a). After the first release in the mainstem, the algae soon spread over the lower James River including both the mainstem and its tributaries by estuarine circulation (Figure 4.6b).
The mean algal density for each segment was obtained as volumetric averages at each time step. The result shows that *C. polykrikoides* in the Lafayette River first reached the bloom density near the surface after 24.29 d after the release (Figures 4.6c and 4.7a), followed by the Nansemond River after 26.25 d and the Elizabeth River after 29.29 d (Figure 4.7a), and lastly in the mainstem of the lower James River near the mouth after 33.54 d (Figures 4.6d and 4.7a). Under this growth condition, the bloom occurred in the mainstem about 9.25 days later than that in the tributaries.

The increase of $\phi$ during the initiation of *C. polykrikoides* bloom is also clearly illustrated in Figure 4.7b. Since the algae were only released in the mainstem at the beginning, the ratios of algal density in the three tributaries to that in the mainstem, $\phi$, started with initial values of zero, and it only took about a few days for the average density in tributaries to be higher than that in the mainstem ($\phi > 1$) under the tidal oscillation. $\phi$ then varied with the changes in the hydrodynamic field but increased to values on the orders larger than 1, and the magnitude of the values of $\phi$ is consistent to the results of analytical analysis using the calculated residence time.

Although we only focus on comparison of the mean algal density of each segment, algal density at different locations within one segment did not increase in the same pace due to the local changes of geometry and the inhomogeneity of the hydrodynamic field, which resulted in the inhomogeneous spatial distribution. Apparently, *C. polykrikoides* in some areas of the western branch of the Elizabeth River and the eastern shoal of the Nansemond River also reached the bloom density (Figure 4.7c) although the Lafayette River became the first tributary having the mean surface density over the bloom density among the tributaries and mainstem,
The results of Scenario 1 support the hypothesis that the bloom occurs earlier in tributaries with relatively longer residence time than the mainstem in the lower James River.

**Experiment with varying growth rate**

In Scenario 2, we examined the relative importance of the flushing effect of transport processes when the local processes are also included. For the purpose of this experiment, we neglected settling and grazing and therefore assumed \( g \) equals the specific growth rate. We further neglected the nutrient limitation and light limitation because these two limiting factors may not be as important as temperature and salinity during the initiation (Morse et al., 2013). Thus, the growth rate, \( g \), varying spatially only as a function of temperature and salinity in this Scenario, i.e., \( g = g_0 f(\text{temperature, salinity}) \), where \( g_0 \) is the maximum specific growth rate and \( f \) is the function between 0-1.

In the lower James River, both the impacts of temperature and salinity on the growth of *C. polykrikoides* are significant. The optimal temperature for *C. polykrikoides* growth is between 24-27 °C, while salinity is generally lower than the optimal salinity for growth (25-40). The values of specific growth rate were then calculated in the model as a function of temperature and salinity using the culture results presented in Kim et al. (2004). However, calculations suggested that there was a gap between the calculated specific growth rate and the observed specific growth rate. According to the values reported by Morse et al. (2013), *C. polykrikoides* was detected at concentrations of 7-8 cells ml\(^{-1}\) on June 4 in the upper Lafayette River, and its abundance increased to 437 cells ml\(^{-1}\) by June 27, and reached 1515 cells ml\(^{-1}\) by June 30 as an indication of the bloom.
Therefore, during the bloom initiation, the estimated relative growth rate from June 4 to June 27 was 0.173 d\(^{-1}\), and from June 4 to June 30 was 0.202 d\(^{-1}\). These were already close to the value of specific growth rate calculated using the culture results according to Kim et al. (2004), which was approximately 0.19 d\(^{-1}\) under the conditions of temperature and salinity during that period. The calculated relative growth rate would be lower than the calculated specific growth rate (0.19 d\(^{-1}\)) because of the flushing effect, and it would be also lower than the observed relative growth rate, 0.173-0.202 d\(^{-1}\). This suggests that the real specific growth rate in nature should have a higher value than that calculated one using culture results in Kim et al. (2004). This gap between observed and calculated values may be due to two possible reasons. The first one is that the results by Kim et al. (2004) are obtained from culture experiments of a Japanese strain of \textit{C. polykrikoides} in culture, and may underestimate the growth rate of American/Malaysian ribotype at the same salinity region, since the American/Malaysian ribotype is suggested to have a wider salinity tolerance (Kudela and Gobler, 2012). A 14:10 (day: night) culture experiment for \textit{C. polykrikoides} collected in the lower Chesapeake Bay suggests that their growth rate with the salinity of approximately 21 is about 0.5-0.7 d\(^{-1}\) (personal communication with Kim Reece, unpublished data). The second one is mixotrophic growth. \textit{C. polykrikoides} can prey on algae with a size smaller than 12 \(\mu m\) and maintain a high growth rate (Jeong et al., 2004), and also take up a variety of organic carbons (Mulholland et al., 2009; 2018). Mulholland et al. (2018) indicates that uptake of organic carbon may be an important source of carbon for dinoflagellate including \textit{C. polykrikoides} in the Lafayette River. For our model experiment, we used locally estimated growth rate, the value was 2.3 times the reported cultural value \(g_0\), and the value of 2.3 is close to the ratio of
mixotrophic to autotrophic growth rate (Jeong et al., 2004; 2015). A detailed analysis of the contribution of mixotrophic growth to *C. polykrikoides* growth is discussed in Chapter 5.

Both release time and algal density of the initial release were the same as Scenario 1, but the releasing areas included the mesohaline and polyhaline regions of the lower James River and its tributaries (Figure 4.8a). Therefore the initial ratios of the algal density in the tributaries to that in the mainstem equaled 1.

For Scenario 2, the growth rate, $g$, varies across the estuary (Figure 4.9b) due to the spatial variations in temperature and salinity. The results show that the algal density was still higher in the tributaries with a relatively longer residence time than that in the main-stem (Figure 4.8b). The mean algal density in the Lafayette River during the initiation was also the highest among the tributaries and mainstem, and therefore the Lafayette River was the tributary where the system-wide HAB occurred first. Compared to Scenario 1, however, the Nansemond River had lower algal density than that in the Elizabeth River during the initiation period, which is due to the low salinity. In fact, though the temperature and salinity were similar to the Lafayette River, *C. polykrikoides* did not develop well in the upper Elizabeth River throughout the modeling period. This pattern of *C. polykrikoides* distribution that appeared in the Lafayette River but not in the upper Elizabeth River in the year 2009 is consistent to the observation by Mores et al. (2013). This difference in the HAB locations between Scenarios 1 and 2 exhibits the effect of local processes contributing to the HAB.

The effects of local processes and the flushing effect of transport processes on the spatial difference in algal density can be evaluated using Eq. (4.3) for Scenario 2. For the
entire water column at each waterbody in the lower James River, the mean growth rate $\langle g \rangle$ was estimated by averaging the vertically averaged $g$ during the initiation from the release time $t_0$ to first bloom time $t_B$, and the mean relative growth rate was computed as

$$\langle r \rangle = \frac{1}{t_B} \ln(C_{t_B} / C_{t_0}),$$

where $C_{t_0}$ and $C_{t_B}$ are the vertically averaged algal density at $t_0$ and $t_B$, respectively. The associated mean transport rates, $\langle F \rangle$, are calculated by the subtraction of the mean $\langle g \rangle$ from the mean relative growth rate ($\langle F \rangle = \langle r \rangle - \langle g \rangle$). To study the difference in the rates between two segments, the spatially averaged rates for each segment were also obtained by taking volumetric averages.

The impacts of flushing and local processes on the algal distribution between two waterbodies are reflected by the difference in spatially-averaged transport rates, $F$, and growth rate, $g$, of the two waterbodies, respectively. Results of Scenario 2 show that the spatially averaged $g$ was about 0.422 d$^{-1}$ and 0.460 d$^{-1}$ for algae in Lafayette River and the mainstem of the lower James River, respectively, and their difference, 0.038 d$^{-1}$, was much smaller than that of the difference in the spatially-averaged $F$, 0.189 d$^{-1}$. This suggests that the impact of flushing was larger than that of local processes causing the $C. polykrikoides$ bloom to initially appear in the tributaries rather than in the mainstem of the lower James River.

The local processes are more important in regulating the density difference between the tributaries because the difference in the transport rate between two tributaries is smaller than that between a tributary and the mainstem. For example, the initiation of $C. polykrikoides$ bloom in the Nansemond River and the Elizabeth River is determined by both local and transport processes. Without considering the local processes, both the algal
density and the equilibrium $\phi$ in the Nansemond River was higher than that in the Elizabeth River as shown in Scenario 1 (Figure 4.7). But in Scenario 2, the relatively low salinity in the Nansemond River led to a comparably lower local growth and algal density than that the Elizabeth River (Figure 4.8b). The difference in the spatially averaged effect growth rate between the Elizabeth River and the Nansemond River is 0.131 d$^{-1}$, which is higher than the difference in the spatially averaged transport rate of 0.119 d$^{-1}$ for the modeling period, suggesting that both the flushing effect and the effect of local processes are important in the distribution of algal density between these two tributaries.

The results of two scenarios support the hypothesis that the flushing effect of transport processes is one of the dominant factors in regulating the spatial gradient in algal density in the lower James River, while the local processes can shape the density distribution among those tributaries.

**Discussion**

*Flushing effect in each waterbody*

While transport processes wash algae out of the system during HAB initiation, the flushing effect varies with time and location, which can be evaluated using the mathematical model. Using the ratio of algal density, $\phi$, the relative growth rate for each waterbody, respectively, is expressed as:

\[
\frac{dc_1}{c_1 dt} = g_1 - \frac{1}{\tau_1} \left( 1 - \frac{\phi \theta \tau_1}{\tau_2} \right) \quad (4.11.1)
\]

\[
\frac{dc_2}{c_2 dt} = g_2 - \frac{1}{\tau_2} \left( 1 - \frac{\eta}{\phi} \right) \quad (4.11.2)
\]
Eq. (4.11) provides the explicitly expressions for the transport rates, $F$, in Eq. (4.3) for the two waterbodies, respectively. Apparently, the flushing effect in the two waterbodies depends on the values of $\phi$, and its net effect can be either "transport out", or "transport in" for an embayment. Particularly, for a system with a large equilibrium $\phi^*$ expressed by $\phi^* \approx \frac{1}{\theta} \left( \frac{t_2}{t_1} - 1 \right)$, $F$ in the two waterbodies are both close to $\frac{1}{t_2}$ when $\phi$ reaches the equilibrium $\phi^*$, indicating equilibrium between the two waterbodies is eventually determined by the flushing in waterbody 2.

When $\phi$ is much smaller than 1 (i.e., $C_2 < C_1$) that gives $\phi < \eta$, such as during the beginning period of Scenario 1, the net flushing effect for the waterbody 2 leads to a "transport in" process, represented by the negative term of $\frac{1}{t_2} \left( 1 - \frac{\eta}{\phi} \right)$, indicating that the exchange flow between the two waterbodies results in a net transport of algae from the waterbody 1 to the waterbody 2. But the flushing effect for waterbody 2 becomes a net "transport out" after $\phi$ becomes larger than $\eta$. The net flushing effect for the waterbody 1 is "transport out" first, represented by the positive $\frac{1}{t_1} \left( 1 - \frac{\phi_1 t_1}{t_2} \right)$, but becomes much smaller as $\phi$ becomes sufficiently large as a result of receiving water with algae in high density from the waterbody 2. During most of the time, both waterbodies show net "transport out" processes. For the coupled system of Figure 4.3, for example, when the value of $\phi$ is larger than 1.0, net flushing effect of both waterbodies shows net "transport out" processes during the process toward the equilibrium (Figure 4.10a). Only when the value of $\phi$ is smaller than 1.0, the waterbody 2 shows a net "transport in" process, and the maximum time for this period is about 10 days, regardless of the initial values of $\phi$. This is also demonstrated by the results of Scenario 1 (Figure 4.10b).
Multiple origins in an estuary

An originating location is where the HAB can initiate independently during the early period of the event, and it is more likely to locate in an area with a relatively long residence time such as tributaries or areas associated with local eddies, which reduce flushing effect according to this study. As multiple locations of HAB initiation can coexist in an estuary-subestuary system, an initiation location can exist as either a single or as multiple origins in an estuary. In the lower James River, for example, while the Lafayette River is shown to be an origin for *C. polykrikoides* bloom, the Elizabeth River also has the relatively long residence time compared to the mainstem during the summer while the salinity there is also high enough to sustain a relatively high growth rate of *C. polykrikoides*, indicating that the Elizabeth River can also be another originating location besides the Lafayette River. Indeed, it is evident that a *C. polykrikoides* bloom can initiate in the Elizabeth River independently from that initiated in the Lafayette River (e.g., Morse et al., 2011). As shown by the model results, though the mean *C. polykrikoides* density of the entire Elizabeth River was not comparable to that of the Lafayette River, the western branch of the Elizabeth River showed high density during the initiation. Observations show that many other dinoflagellates (e.g. *Akashiwo sanguinea*, *Gymnodinium uncatenum*, *Scrippsiella trochoidea*) also bloom in these tributaries (Morse et al., 2013; Egerton et al., 2014; Mulholland et al., 2018), suggesting that these locations have suitable environments for the growth and accumulation of a variety of algae due to their relatively long residence time. Besides the tributaries, originating locations are also suggested to exist in some areas of the main-stem of the lower James River. During 2008, Morse et al. (2011) observed that high chl-a
concentrations patched in the northern shoreline in the main stem during the bloom period in the Lafayette and Elizabeth River before the heavy bloom was transported into the main stem, indicating that there may exist the high density of *C. polykrikoides* formed locally.

The local processes also regulate the algal growth and hence influence the distribution of the origins in an estuary. As shown by the different results of the two scenarios for algal growth in the Nansemond River, low salinity can be one reason that prevents this tributary to be an originating location though it has a relatively long residence time. While HABs can initiate much earlier in these origins than other areas, the time required for a HAB appearance in these origins has smaller difference. Therefore, among those origins, the location that has the first appearance of HAB across the entire system can vary interannually, which is also influenced by the local processes or indirect effects of transport processes that generate spatial gradients in temperature, salinity, nutrients, or grazing pressure.

The model simulation shows that the mainstem of the lower James and tributaries are strongly coupled and transport processes can quickly transport algae to these sub-systems regardless of where it is initiated, while it requires sufficient time for algae to grow to the level of bloom density. For this study, while we focus on the transport processes and local environmental impact on HAB, the origination of the HAB can also depend on the distribution of cysts. Because there are insufficient data for the distribution of cysts, we are not able to address the impact of cysts realistically. Nevertheless, in the lower James River, after cysts are germinated to vegetative cells, they are transported quickly by circulation and tide to spread throughout the entire area. The results of
Scenario 1 with an initial zero density in the tributaries in this study suggested that the originating locations of *C. polykrikoides* bloom do not need to have high-cyst abundances or even the existence of cysts, because the germinated vegetative cells can be imported from adjunct areas (e.g., Tyler and Seliger, 1978). This indicates that, in the lower James River, the distribution of cysts may not be the major factor in determining originating locations of *C. polykrikoides* bloom, and this insensitivity has been also suggested in HABs in others estuarine systems. For example, observations by Crespo et al. (2011) suggested that germination of cysts of *A. fundyense* only accounted for a small percentage of the peak density during the blooms in the Nauset Marsh System of Cape Cod, and the algal density in a location were likely to be influenced more by the growth rather than the initial cyst abundance, which is supported by Ralston et al. (2015) through modeling efforts.

**Conclusions**

While the environmental conditions, such as temperature, light, nutrient supply, grazing pressure, salinity, stratification, and others, are all important in affecting the location and timing of a HAB, in this study, we highlighted the role of transport processes, which plays a critical role for HAB and cannot be neglected. We showed how the flushing effect of transport processes affects the spatial distribution of harmful algae and the origins of HAB initiation in estuaries, which tends to cause a HAB to first appear in areas with relatively long residence time. We also demonstrated that this flushing effect of transport processes can be one of the key environmental factors in determining the originating locations of HABs in many aquatic systems, like *C. polykrikoides* bloom in the lower James River. Thus, the impact of transport processes can play a critical role
in mediating estuarine HABs, and it needs to be taken into consideration when studying the spatial distribution and the timing of a HAB occurrence in estuaries.

Both the analytical analysis using the mathematical model and the numerical case study in the lower James River support our hypotheses that a HAB tends to first appear in the originating locations with relatively long residence time, and multiple originating locations can co-exist in an estuary. While the analytical analysis is conducted for a simplified system, it provides general underlying processes that modulate initiation of HABs, which is applicable to other systems. Additionally, it is also demonstrated that while the formation and germination of cysts can be critical to cause annual occurrence of HABs in many estuarine systems, the originating locations of these blooms do not necessarily coincide to the seed beds with abundant cysts and the role of physical transport processes should be analyzed in conjunction with analysis of observations.

**Acknowledgements**

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toxic dinoflagellate (*Karlodinium veneficum*) bloom in a shallow, eutrophic, lagoonal estuary. Estuaries Coasts 31(2), 402-418.


Lucas, L.V., Thompson, J.K., Brown, L.R., 2009. Why are diverse relationships observed between phytoplankton biomass and transport time. Limnol. Oceanogr. 54(1), 381-390.


Table 4.1. Residence time, volume, and their ratio for each segment of the lower James River for May-July over 2006-2013.

<table>
<thead>
<tr>
<th></th>
<th>Main Stem</th>
<th>Lafayette River</th>
<th>Elizabeth River</th>
<th>Nansemond River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Residence time, $\tau$ (d)</td>
<td>6.66</td>
<td>9.31</td>
<td>5.24</td>
<td>25.53</td>
</tr>
<tr>
<td>Volume, $V \times 10^7$ m$^3$</td>
<td>89.53</td>
<td>0.76</td>
<td>14.97</td>
<td>5.68</td>
</tr>
<tr>
<td>$\tau/V \times 10^7$ d m$^{-3}$</td>
<td>0.07</td>
<td>12.24</td>
<td>0.35</td>
<td>4.50</td>
</tr>
</tbody>
</table>
Figure 4.1. The inverse relationship between the time (weeks) required for the initiation of *C. polykrikoides* bloom from the detection limit of 1 cell ml\(^{-1}\) to the bloom density of 1000 cells ml\(^{-1}\) and the mean relative growth rate (d\(^{-1}\)), \(\langle r \rangle\), during this time period.
Figure 4.2. Schematic of the system with two waterbodies for the mathematical model.
Figure 4.3. a) The vector field for the Eq. (4.9) of the density ratio between the two waterbodies, $\phi$, in an example system with $\tau_1 = 6.66$ d, $\tau_2 = 9.31$ d, $\theta = 0.0085$, $\eta = 1$, b) the changes in values of $\phi$ in the process of approaching the equilibrium (from $\phi = 0$ to $0.99\phi^*$). The 3 curves have the same values of $\tau_2/\tau_1$, $\theta$ and $\eta$ as the example system above, and hence the same value of $\phi^*$, but they are different in the values of residence time of the two waterbodies and therefore in its time length to reach the equilibrium. The solid line shows the process with $\tau_1 = 6.66$ d, $\tau_2 = 9.31$ d, while the dashed line and dotted line show the processes with half the values and doubled the values.
Figure 4.4. The equilibrium values $\phi^*$ representing the spatial difference in algal density caused by the flushing effect of transport processes, with different combinations of the ratio of volume ($\theta = V_2/V_1$) and the ratio of residence time ($\tau_2/\tau_1$).
Figure 4.5. The map of the lower James River and the 4 segments separated by the dashed lines, including the main stem, Lafayette River, Elizabeth River (western, eastern, and southern branches), and Nansemond River.
Figure 4.6. The results of Scenario 1 of the initiation of *C. polykrikoides* bloom in the lower James River since the initial release. The daytime and nighttime growth rates, $g$, are set to be constants of 0.82 and 0 d$^{-1}$, respectively. a) The initial release at the bottom with a density of 1 cell ml$^{-1}$, b) the spread of cells over the lower James River after 0.75 days, c) the time when the averaged surface density of the entire Lafayette River first reached the bloom density (1000 cells ml$^{-1}$), and d) the time when the averaged surface density of the main stem first reached the bloom density. Note that the algal density is in units of cells ml$^{-1}$ and the color bars are different for each subplot, and the maximum values in d) is set to be 1000 cells ml$^{-1}$ to give a better presentation even the density of the model results is higher.
Figure 4.7. The time series of a) the spatially-averaged surface algal density in each segment of the lower James River, and b) the ratios of algal density in three tributaries to the main stem. The thick and thin lines denote the daily and hourly algal density, respectively, while the dashed black line indicates the bloom density (1000 cells ml\(^{-1}\)).
Figure 4.8. The result of Scenario 2 of the initiation of *C. polykrikoides* bloom in the lower James River. The growth rate, $g$, varies with temperature and salinity. a) The initial release at the bottom with a density of 1 cell ml$^{-1}$, b) the time when the averaged surface density of the entire Lafayette River first reached the bloom density (1000 cells ml$^{-1}$).
Figure 4.9. The mean of vertically averaged relative growth rate, gross growth rate, and transport rate (d⁻¹) in the lower James River during the initiation in Scenario 2.
Figure 4.10. a) The changes in the flushing effect denoted by the transport rate in the two waterbodies, respectively, during the process of $\phi$ approaching to the equilibrium, b) Scenario 1 results showing the 14.75-day moving averages of the transport rate in the mainstem of the lower James River and the Lafayette River, respectively, with the spring-neap oscillation removed.
Chapter 5. Physical processes regulate the timing of *Cochlodinium polykrikoides* bloom occurrence in the Lafayette River, USA
Abstract

While *Cochlodinium* (recently renamed *Margalefidinium*) *polykrikoides* blooms almost annually occur in the Chesapeake Bay and its tributaries in the summer, the timing of its first appearance in the Lafayette River, one primary originating location in the lower James River, varies interannually from late June to late July. This study examines the critical environmental factors controlling this interannual variability through both data analysis and numerical modeling. The numerical model for simulating *C. polykrikoides* bloom has been developed including the strategies used by *C. polykrikoides* such as mixotrophic growth, swimming behavior, cyst germination, and grazing suppression. Results show that temperature and the flushing effect of physical transport processes are the two dominant factors controlling the interannual variability in the timing of *C. polykrikoides* bloom occurrence in the Lafayette River. Physical transport processes can delay the bloom occurrence by weeks. On the subtidal timescale, southerly wind and heavy rainfall interacting with spring-neap tide can significantly affect the estuarine circulation and flushing in the Lafayette River, which can cause interrupting, or even terminating, bloom initiation. In contrast, stratification or rainfall along may not be a necessary condition to trigger the bloom.
Introduction

Harmful algal blooms (HABs) have been observed over many estuarine and coastal systems, and anthropogenic nutrient enrichment has been suggested to its worldwide expansion (Heisler et al., 2008). *Cochlodinium polykrikoides* (*Margalefidinium polykrikoides*) is one HAB species that annually blooms in the lower Chesapeake Bay and its tributaries such as the James and York Rivers (Morse et al., 2013).

The *C. polykrikoides* bloom always occurs in the summer, as a result of the temperature-sensitive specific growth rate of *C. polykrikoides* that reaches the maximum at the optimal condition of about 25 °C (Kudela and Gobler, 2012). However, monitoring observes that the timing of the density first reaching the bloom density (> 1000 cells ml\(^{-1}\)) varies interannually, swinging from late June to late July with a range of several weeks. In addition, the duration of the developed *C. polykrikoides* bloom also varies interannually from several days to several weeks. To explain these variabilities and find the possible dominant environmental factors controlling the interannual variability in the timing of *C. polykrikoides* bloom occurrence, a detailed examination is needed on both the *C. polykrikoides* dynamics and the contribution of each environmental factor.

*C. polykrikoides* blooms can be affected by many processes (Kudela and Gobler, 2012) that are related to 1) the ecophysiology of *C. polykrikoides*, such as the effects of temperature, salinity, light and nutrient availabilities on the growth rates, the ability to have mixotrophic growth, and swimming behaviors, 2) food-web interactions including ecological impacts of *C. polykrikoides* blooms, its grazing suppression and allelopathy effects on competitors, 3) transport processes, and 4) the formation of cysts in its life.
cycle to avoid the unfavorable environmental conditions and the germination of cysts to vegetative cells when conditions become suitable.

It has been suggested that the *C. polykrikoides* bloom is able to initiate within the lower James River, and the Lafayette River, a sub-tributary of the lower James River, is one primary originating location (Mulholland et al., 2009; Morse et al., 2011). This suggests that the timing of this bloom occurrence is determined by local growth and accumulation, rather than bloom conditions in adjacent coastal areas.

The objectives of this study are to analyze possible controlling environmental factors as well as growth strategies controlling the interannual variability in the timing of *C. polykrikoides* bloom occurrence in the lower James River and its tributaries, and also to examine possible roles of physical transport processes through the flushing effect. The Lafayette River is the focus of this study since it is one primary originating location that always has the first bloom occurrence, and the possible important physical forcings are discussed. To quantify the contribution of each factor, we developed a numerical model for *C. polykrikoides* bloom and applied it to the entire James River.

**Methods**

*Site description*

James River is a tributary of the lower Chesapeake Bay, USA, and the Lafayette River is a sub-tributary of the lower James River, one of the originating locations for *C. polykrikoides* blooms in the lower James River (Figure 5.1).

Time series of monthly environmental data including chlorophyll-a concentration (chl-a) at long-monitoring Stations LFA01, LFB01, LE5.6, and LE5.4 over 2005-2013
were collected by the Chesapeake Bay Program, and weekly data-flow data of chl-a were collected and then averaged daily at Stations LE5.6 and LE5.4. Also, high-frequency (15-min) data of chl-a fluorescence at Stations NYCC over 2012-2014 in the Lafayette River were collected from Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA) and are available through the Virginia Estuarine and Coastal Observing System (VECOS, http://web2.vims.edu/vecos/). Wind speed and direction data collected at Yorktown USCG Training Center were measured at 15-min intervals by NOAA. Measured 15-min light irradiance data were also collected at Taskinas Creek, a tributary of York River, by the CBNERRVA. Hourly precipitation data were collected at the nearby Newport News airport. Hourly water level data were collected at Sewells Point by NOAA to compute the tidal range in this area. In addition, the times when *C. polykrikoides* density reached the bloom density for each year from 2007-2016, except for 2010, were collected from literature and reports.

**A HAB Model for *C. polykrikoides* bloom in James River**

A HAB model was developed by extending the simplified model in Chapter 4, and it was built into the *EFDC* model. This model focused on the stage of the life cycle as the vegetative cell, and includes many strategies for growing used by *C. polykrikoides*, such as swimming behavior, mixotrophic growth, resting cyst formation and germination. The transformation of vegetative cells into temporary cysts is largely affected by the light availability, and it has been shown that the formation and germination of temporary cysts may be within 12 hours due to the light-dark cycle of a day (Shin et al., 2017). Thus, while the formation and germination of temporary cysts can cause a significant variability in the density of vegetative cells in the diurnal cycle, they may not be important when the
timescale considered is daily. Rather than adding the complexity and uncertainty to the model. The current model does not consider the dynamics of temporary cysts.

**Governing equation**

This is a carbon-based HAB model, consistent with the eutrophication model in EFDC, and the biomass of *C. polykrikoides* is simulated. The results are compared to observational data reported as *C. polykrikoides* density or abundance, in units of cells ml$^{-1}$, using a conversion factor. The conversion from density units to carbon units is $550 \text{ cells ml}^{-1} \approx 1000 \mu g \text{ C} l^{-1} = 1 g \text{ C m}^{-3}$ (Jiang et al., 2010), i.e., $1 \text{ cell ml}^{-1} \approx 1.818 \times 10^{-3} g \text{ C m}^{-3}$.

At a given location, the governing equation for *C. polykrikoides* dynamics can be described as:

$$
\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} + v \frac{\partial C}{\partial y} + w \frac{\partial C}{\partial z} - \left[ \frac{\partial}{\partial x} \left( K \frac{\partial C}{\partial x} \right) + \frac{\partial}{\partial y} \left( K \frac{\partial C}{\partial y} \right) + \frac{\partial}{\partial z} \left( K \frac{\partial C}{\partial z} \right) \right] = (G - R - M)C + wc \frac{\partial C}{\partial z} + germ - encyst + S
$$

(5.1)

where $G$ is the gross growth rate, $R$ is the respiration/excretion rate, and $M$ is the mortality rate due to natural death, grazing, and parasitism. The respiratory loss due to photosynthesis is also included in this model as the term proportional to the phototrophic growth rate ($rG^p$), where $G^p$ is phototrophic growth rate. $germ$ denotes the input rate from the germination of resting cysts, $encyst$ is a sink term denoting the loss rate of vegetative cells due to cyst formation, and $S$ denotes other external sources.
Mixotrophic growth

Without considering interactions between phototrophic growth and heterotrophic growth, the gross growth rate for mixotrophic growth can be expressed as a combination of phototrophic growth and heterotrophic growth, which cannot exceed the optimal growth rate $G_{opt}$ (Ghyoot et al., 2017):

$$G = \min (G^p + G^h, G_{opt})$$  \hspace{1cm} (5.2)

There are many limiting factors for $C. polykrikoides$ growth, and temperature, salinity, light irradiance, and nutrients are considered in the model. The current model does not simulate the effect of Vitamin B, a possible limiting factor under natural conditions that is suggested in the literature (Tang et al., 2010; Koch et al., 2014).

Phototrophic growth

The gross growth rate for phototrophic growth is expressed as a function of temperature, salinity, light irradiance, and dissolved nutrient concentrations:

$$G^p = G^p_{opt} f(T)f(Sal)\min[f(I), f(DIN), f(DIP)]$$  \hspace{1cm} (5.3)

where $f(T)$, $f(Sal)$, $f(I)$, $f(DIN)$, $f(DIP)$ are the growth-limiting functions for temperature ($T$), salinity ($Sal$), irradiance ($I$), dissolved inorganic nitrogen ($DIN$), and dissolved inorganic phosphate ($DIP$), respectively, and their expressions are listed in Table 5.1. The Monod type equation was adopted for both nutrients and light limitations.

Heterotrophic growth

$C. polykrikoides$ can take up organic matter (OM) to maintain a high heterotrophic growth rate (Jeong et al., 2004), and the sources include DOM, a fraction of
POM and organisms with size smaller than 12 μm, such as cryptophyte (Jeong et al., 2004) and bacteria (Seong et al., 2006). Thus, the formulation for $G^h$ is

$$G^h = G_{opt}^h f(T) f(Sal) f(OM_{12}),$$  \hspace{1cm} (5.4)$$

where $f(T)$ and $f(Sal)$ are the same for phototrophic gross growth rate $G^p$ in Eq. (5.3), and the Monod type equation was adapted for $f(OM_{12})$ following the culture experiment in Jeong et al. (2004). In the numerical model, available organic matter is provided by the two groups of simulated algae besides $C.\ polykrikoides$ and also by the other organic matter. $OM_{12} = \sum_i b_i C_i + OM_{dead}$, where $b$ is the fraction of organisms smaller than 12 μm, with $i = 2$ or 3 indicating the index of algae group, and

$$OM_{dead} = \min \left\{ \frac{DOC + a_{1C} RPOC + a_{2C} LPOC}{(DON + a_{1N} RPON + a_{2N} LPON)/ANC}, \frac{(DOP + a_{1P} RPOP + a_{2P} LPOP)/APC}{(DOP + a_{1P} RPOP + a_{2P} LPOP)/APC} \right\},$$

where $ANC$ and $APC$ are nitrogen to carbon ratio and phosphate to carbon ratio, respectively. Correspondingly, the uptake of organic matter corresponding to mixotrophic growth is $G^h C$, and it contributes to kinetic equations for the other two simulated phytoplankton species, dissolved organic carbon (DOC), refractory particulate organic carbon (RPOC), labile particulate organic carbon (LPOC), dissolved organic nitrogen (DON), refractory particulate organic nitrogen (RPON), labile particulate organic nitrogen (LPON), dissolved organic phosphate (DOP), refractory particulate organic phosphate (RPOP), and labile particulate organic phosphate (LPOP), while coefficient $a$ denotes the fraction of particulate organic matter smaller than 12 μm, and $a_{1C}, a_{2C}, a_{1N}, a_{2N}, a_{1P}$, and $a_{2P}$ are the fraction for each component, respectively.
In the model, the contribution (recycle) to nutrient pool is calculated by adding a sinking term \((-C^h C \chi)\) for each kinetic equation, where \(\chi\) denotes the fractions of each component resembling \(OM_{12}\), respectively. Specifically, the corresponding sinking term for the dynamics of the other two phytoplankton species is expressed as:

\[
Phytoplankton \ i: \chi_i = \frac{b_i C_i}{OM_{12}}, \ i = 2 \ or \ 3
\]

For carbon cycle:

\[
DOC: \chi_{1c} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{DOC}{DOC + a_{1c} RPOC + a_{2c} LPOC}
\]

\[
RPOC: \chi_{2c} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_{1c} RPOC}{DOC + a_{1c} RPOC + a_{2c} LPOC}
\]

\[
LPOC: \chi_{3c} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_{2c} LPOC}{DOC + a_{1c} RPOC + a_{2c} LPOC}
\]

nitrogen cycle:

\[
DON: \chi_{1N} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{DON}{DON + a_{1N} RPON + a_{2N} LPON}^{ANC}
\]

\[
RPON: \chi_{2N} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_{1N} RPON}{DON + a_{1N} RPON + a_{2N} LPON}^{ANC}
\]

\[
LPON: \chi_{3N} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_{2N} LPON}{DON + a_{1N} RPON + a_{2N} LPON}^{ANC}
\]

and phosphate cycle:

\[
DOP: \chi_{1P} = \frac{OM_{\text{dead}}}{OM_{12}} \frac{DOP}{DOP + a_{1P} RPOP + a_{2P} LPOP}^{APC}
\]
\[ RPOP: \chi_2^p = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_1 RPOP}{DOP + a_1 RPOP + a_2 LPOP} APC \]

\[ LPOP: \chi_3^p = \frac{OM_{\text{dead}}}{OM_{12}} \frac{a_2 LPOP}{DOP + a_1 RPOP + a_2 LPOP} APC \]

**Carbon to chl-a ratio**

For *C. polykrikoides*, Noh et al. (2018) reported that the chl-a content of the cultured strain is 30 pg chl-a/cell, i.e., 30 \( \mu g \) chl-a l\(^{-1} \) per 1000 cells/ml. In the numerical model, a constant carbon to chl-a ratio (C: Chl) was used. The chl-a content is assumed to be 30 pg chl-a/cell that was obtained from a laboratory measurement (Noh et al., 2018), and the corresponding C: Chl is 60.6 g C / g chl-a.

**Loss terms**

The sink of *C. polykrikoides* biomass includes the respiration/excretion, grazing, degradation by bacteria (e.g., Park et al., 2015), and resting cysts germination (note that loss to temporary cysts is omitted).

The basic metabolism is a function of temperature. The respiratory loss due to photosynthesis is an additional metabolism to respiration/excretion, and the ratio to phototrophic growth rate, \( f^p \), is estimated from the curve between specific growth rate and light irradiance.

The grazing suppression is included by assuming a grazing rate, \( M \), equals zero in the James River model.

The resting cysts are generally produced in the intense phase of a HAB event. The mechanisms of forming resting cysts are still not clear. Some studies suggest that the resting cyst formation occurs when the environmental conditions are not suitable, such as
scarcity of macronutrients. Other studies suggest that the formation of resting cysts is endogenous or ‘clock’-regulated (e.g., Anderson and Keafer, 1987). In the model, the loss due to the formation of resting cysts is not included.

For the termination of *C. polykrikoides* blooms, observations show that the bloom usually declines after September of the year and eventually disappears. Data analysis shows that within one year, the temperature is suitable for *C. polykrikoides* growth from May to June in this area, and it can be a significant limiting factor during the high-temperature period (e.g., August). However, it becomes suitable again from late September through October. If vegetative cells of *C. polykrikoides* could survive to the second suitable period for temperature, they could grow again with a high growth rate and cause a bloom. This suggests that there must be some unknown mechanisms causing the decline of *C. polykrikoides* blooms and prevent their return. While a mandatory dormancy for resting cysts may prevent the re-initiation of the bloom (Kremp and Anderson, 2000), the mechanisms for the collapse still remain unknown, and hypotheses may include the unsuitable environmental conditions (e.g., shortage of nutrients), resting cyst formation, parasitism, and aggregation. In the numerical modeling, the collapse is implicitly considered. To be consistent with observations, the gross growth rate is assumed to be zero after mid-September every year, and the *C. polykrikoides* biomass is removed from the water column by October 1.

*Swimming*

The swimming ability of dinoflagellates allows the cells to change their vertical position in the water column, and studies suggest that in the daytime, *C. polykrikoides* can swim up to the near surface where the potential to receive high light irradiance is
better (Kudela and Gobler, 2012). The maximum swimming speed of \textit{C. polykrikoides} is reported to be 1445 $\mu m \ s^{-1}$ (Jeong et al., 2015). The swimming behavior is modeled with the measured values of speed in Sohn et al. (2011), where they observe in laboratory that the mean swimming speeds at 22 °C for single cell, two-, four-, and eight-cell chain are 391, 599, 800, 856 $\mu m \ s^{-1}$, respectively. Chain-formation provides them a more competitive advantage in receiving light (Kudela and Gobler, 2012). The corresponding velocities are 34–74 m $d^{-1}$, respectively. In the model, the swimming speed is set to be $w_c = 55 \ m \ d^{-1}$, and the cells are only allowed to swim upward. In addition, it is possible that the upward swimming can stop at those layers where the light irradiance is not a limiting factor.

At night there may not be a specific swimming for swimming, and therefore the vertical swimming speed is set to be zero in the model. The vertical mixing, nevertheless, can transport surface cells to the lower layers.

\textbf{Cyst germination}

The external source of vegetative \textit{C. polykrikoides} is from the germination of resting cysts (input from the germination of temporary cyst is omitted), and its input rate depends on the cyst density and the temperature-dependent success rate of germination that is. Tang and Gobler (2012) observed that 2-40% of cultured resting cysts germinated within 12 to 31 days with a temperature between 18-21 °C.

In this model, this process is simplified by assuming a one-time release of vegetative cells in the bottom layer over the mesohaline and polyhaline James River and its tributaries to avoid the uncertainties in the temporal variability in germination rate.
**Calibration and sensitive tests**

The model for *C. polykrikoides* dynamics was applied to examine *C. polykrikoides* bloom in the James River and its tributaries over 2005-2013, which updated the three-dimensional James River hydrodynamic model and water quality model that have been developed and well-calibrated (Shen et al., 2016). Values of parameters were estimated based on culture experiments and the calibration process. The final values of model parameters are listed in Table 5.2.

The values for optimal gross growth rate were estimated based on the culture experiments in Gobler et al. (2012) where they reported the maximum specific growth rate to be 0.43-0.44 d\(^{-1}\) for growth on *DIN* and 0.53 d\(^{-1}\) for growth on glutamic acid at 21 °C on a 14:10 light:dark cycle. The rate by *C. polykrikoides* on *DIN* is close to that reported by Kim et al. (2004), 0.41 d\(^{-1}\). Note that these daily-averaged growth rates were transformed to instantaneous growth rates that applied to each time step in model experiments. Heterotrophic growth was assumed to occur in both light and dark conditions. The values of parameters for computing \(f(T)\) and \(f(Sal)\) were also determined based on the culture experiment results in Kim et al. (2004) using a least-square fit. The parameter for the effect of light availability on \(G^p\) was based on values reported in Kim et al. (2004) and Oh et al. (2006).

*C. polykrikoides* can take up various forms of nitrogen. It is slightly different between the half-saturation coefficients for nitrite and ammonia based on the single nitrogen substrate experiments, but overall they are similar (Kudela et al., 2008; Gobler et al., 2012). The values of half-saturation coefficients for *DIN* and *DIP* used in the model...
were 0.028 $g N m^{-3} (2 \mu M)$ and 0.0177 $g P m^{-3} (0.57 \mu M)$, respectively, according to the culture experiments in Kim et al. (2001).

For the heterotrophic growth, the half-saturation coefficient for organic matter, $OM_{12k}$, was estimated based on the culture experiment in Jeong et al. (2004), where the mixotrophic growth of $C. polykrikoides$ increases with cryptophyte concentration.

For the release of vegetative cells, the date was chosen to be June 4 of each year, more than 31 days after the water temperature raises up to above 18 °C around mid-April in this area, and the initial density was prescribed to be 1 cell ml$^{-1}$.

Sensitivity tests were conducted for examining the effects of mixotrophic growth, swimming, and cyst germination on the initiation and development of $C. polykrikoides$ blooms in the James River. The year 2012 was used as an example, and the experiments were listed in Table 5.3.

**Examination on contributions of strategies and environmental conditions**

The heterotrophic growth rate, $G^h$, was compared to the phototrophic growth rate, $G^p$, to quantify the contribution of mixotrophic growth for initiating and developing $C. polykrikoides$ blooms. In addition, a switch-off numerical experiment was also conducted to investigate the role of mixotrophic growth, by making $G^h$ equal to zero throughout the entire study period.

Values of each limiting function that regulates the gross growth rate during the bloom were compared to examine the relative contribution of environmental factors to $C. polykrikoides$ blooms. The relative contribution of the flushing effect can be quantified
using the rate equation introduced in Qin and Shen (2017), where the effect of local processes (without considering non-transport processes) on the dynamics of \( C. \) polykrikoides was estimated by effective growth rate and the flushing effect of transport processes (including both physical transport and non-physical transport) was estimated by the difference between relative growth rate and effective growth rate.

Integrating Eq. (5.1) over the water column and applying the assumptions used in the model (e.g., neglect grazing) returns the depth-integrated equation:

\[
\frac{dB}{dt} = (\bar{G} - \bar{R})B - \bar{F}_B B + germ - encyst + S \tag{5.5}
\]

where \( B = \int_0^H Cdz \) is the depth-integrated biomass, \( z \) is the vertical location, and \( H \) is the water depth. \( \bar{G} \) is vertical mean gross growth rate that accounts for the growth of \( B \), and \( \bar{G} = \frac{\int_0^H (GC)dz}{B} \) is the transport rate accounting for the effect of transport processes, and

\[
\bar{F}_B = \frac{1}{B} \int_0^H \left[ u \frac{\partial C}{\partial x} + v \frac{\partial C}{\partial y} + w \frac{\partial C}{\partial z} - \frac{\partial}{\partial x} \left( K \frac{\partial C}{\partial x} \right) - \frac{\partial}{\partial y} \left( K \frac{\partial C}{\partial y} \right) - \frac{\partial}{\partial z} \left( K \frac{\partial C}{\partial z} \right) \right] dz.
\]

Note that the integration of the swimming term equals zero.

Because the experiment in this study used a one-time release of initial density for representing the cyst germination and did not explicitly consider cyst formation, both \( germ \) and \( encyst \) are zero during the bloom event simulated here. Without considering other external sources (i.e., \( S = 0 \)), the rate equation for depth-integrated \( C. \) polykrikoides dynamics reads

\[
\frac{\partial B}{B \partial t} = \bar{G} - \bar{R} - \bar{F}_B \tag{5.6}
\]
With the numerical model, the relative contribution of each term in Eq. (5.6) was examined by comparing their values over each bloom event. Particularly, $F_B$ was computed by the balance of the remaining terms.

**Results**

*Model simulation results*

Model results reasonably simulated the annual *C. polykrikoides* blooms in the James River and its tributaries, agreeing well with observed chl-a at the 4 long-term monitoring stations, with peaks occurring in the summer (Figures 5.2). The results show an interannual variability in magnitude, and the years 2010 and 2011 had relatively small blooms compared to other years. Good comparisons also exist between simulated and observed *C. polykrikoides* density in the Lafayette River (Figure 5.3), and between simulated and observed high-frequency chl-a fluorescence data at Station NYCC (Figure 5.4). The bloom peak occurred from late June to early August in 2012, but the bloom had not been well developed until mid-August in 2013.

Nevertheless, some biases existed in the model results. For example, the peak in the early August, 2012, was not well simulated. Biases between model results and observational data may come from various sources. First, the model resolution (several hundred meters) may not be fine enough to properly simulate the local variability of chl-a in the small tributary, and lateral freshwater input from the watershed may also affect the dynamics. In addition, because the model focused on the *C. polykrikoides* bloom that locally originated within the James River and its tributaries, bloom developed outside of James River had not been taken into account, which may introduce biases if high-density *C. polykrikoides* is transported into the studying area. Second, the uncertainties in values
of parameters (e.g., $P_k$ or the constant C:Chl) or variables (e.g., temperature) of the model or in the observational data may exist. Third, the current structure of model may also introduce biases in the simulation, both for \textit{C. polykrikoides} and for other variables. For example, only the dynamics of \textit{C. polykrikoides} was modeled explicitly as a water-quality variable, other algal species were lumped into two groups simulated by two variables. In nature, however, co-occurring algal species have their own characteristics, and may significantly shape the modeled dynamics of \textit{C. polykrikoides} through direct interactions or a competition for light and nutrient availability, and the impacts may not be well-simulated in the model. Field work by Morse et al. (2013) shows that the dinoflagellates \textit{Gymnodinium uncatenum}, \textit{Scrippsiella trochoidea}, and \textit{Akashiwo sanguinea} were the dominant species during the \textit{C. polykrikoides} bloom initiation in 2009.

\textbf{Contribution of growth strategies to bloom}

The overall mixotrophic growth rates, $\bar{G}$, were about 0.227, 0.126, 0.255, and 0.320 d$^{-1}$, respectively, at the four long-term monitoring stations LFA01, LFB01, LE5.6, and LE5.4 (Table 5.4). The heterotrophic growth was found to be the dominant way for \textit{C. polykrikoides} growth. $\bar{G}^H$ accounted for 75-88% of $\bar{G}$, and this percent can be larger than 90% in some years (Supplementary Table S5.1-S5.4). $\bar{G}^H$ was about 2-11 times of the phototrophic growth rate, $\bar{G}^P$, over different years at the four stations. Thus, the model results suggest the importance of mixotrophic growth as a strategy for \textit{C. polykrikoides} to grow in this area. This is consistent to the experimental results in Mulholland et al. (2018). They found that dissolved inorganic carbon only accounted for a very small fraction of the total carbon uptake by mixotrophic dinoflagellate species including \textit{C. polykrikoides}, during both bloom and non-bloom periods in the Lafayette
River, suggesting that phototrophic growth was low and mixotrophic growth contributed substantially to their growth. When the heterotrophic growth rate was set to be zero, i.e., *C. polykrikoides* had the phototrophic growth only, results show that *C. polykrikoides* blooms cannot show up in either the Lafayette River or the lower James River, indicating that mixotrophic growth ensured the occurrence of the bloom (Supplementary Figure S5.1). The sensitivity test also shows that both phagotrophic growth (engulfing particulate organic matter) and osmotrophic growth (taking up dissolved inorganic matter) contribute to the bloom magnitude. Without including phagotrophic growth (*a = b = 0*), *C. polykrikoides* blooms can still occur and the variability in density is similar, though the bloom magnitude is much reduced.

In addition, there was no significant change in bloom magnitude when swimming speed was decreased from 55 $m \, d^{-1}$ to 20 $m \, d^{-1}$ (Supplementary Figure S5.2). However, when the swimming speed was set to be zero, the bloom could not occur (results were not shown), and it may be due to the vertical positions of initially released cells that are concentrated within the bottom layer in the numerical experiments. Nevertheless, this indicates that the swimming behavior is an important strategy, and the variability in density may be sensitive to swimming only when the speed of *C. polykrikoides* is lower than a certain value (the value is lower than 20 $m \, d^{-1}$ according to the sensitivity test). Since the swimming speed of *C. polykrikoides* is in general greater than 34 $m \, d^{-1}$ (Sohn et al., 2011), the variability in density is expected to not be sensitive to the changes in swimming speed in the sensitivity test, neither.
The 10-fold decreased or increased initial density of released vegetative cells did not induce a large change in the variations or the overall magnitude of blooms, but the change varies the timing of the bloom occurrence, yet within 10 days (Figure 5.5).

**Contribution of each environmental factor to bloom**

The contribution of each environmental factor was investigated by examining its limiting function on gross growth rate (Table 5.5). At the surface layer, overall, the growth-limiting function for inorganic nutrients (DIN and DIP) had the lowest values when *C. polykrikoides* presented in the water column, and the function for OM\textsubscript{12} had the highest values. Model results show that both DIP and DIN can be the limiting factor on phototrophic growth in the blooms (Figure 5.6). Note that the values of limiting functions are reported as daily-averaged values, and \( f(I) \) was zero at night but was much higher than that reported in the daytime. In addition, the limiting function of DIP depends on the half-saturation coefficient for DIP, \( P_k \), and the value of \( P_k \) was assigned using the result of a culture experiment in Kim et al. (2001) that may contain a large uncertainty. If \( P_k \) had a lower value, the phosphate limitation would be alleviated.

Flushing also played a critical role in *C. polykrikoides* blooms. The transport rates, \( \overline{F_B} \), had the mean values of 0.113, -0.033, 0.149, and 0.219 d\(^{-1}\), respectively, at the four long-term monitoring stations LFA01, LFB01, LE5.6, and LE5.4. These values are not trivial compared to the mean gross growth rates, \( \overline{G} \) (Table 5.4), and the absolute values of mean \( \overline{F_B}/\overline{G} \) were about 50%, 26%, 58%, and 68%, respectively. Specifically, though \( \overline{F_B} \) shows an interannual variability with both negative and positive values at Station LFB01 in the upper Lafayette River (Supplementary Table S5.2), its overall negative mean value (-0.033 d\(^{-1}\)) indicates that this station experienced a net “transport-
in” process. All the other three stations had positive values of $\overline{F_B}$ for every year, showing net “transport-out” processes. Without flushing effect, *C. polykrikoides* at these stations would reach much higher density.

**Discussion**

**Factors controlling the timing of bloom occurrence**

As discussed in Chapter 4 (Eq. 4.4), the time required for the bloom initiation is computed by:

$$t_B = \frac{1}{\langle r \rangle} \ln(C_{\text{bloom}}/C_{\text{ini}})$$  \hspace{1cm} (5.7)

where $C_{\text{bloom}}$ and $C_{\text{ini}}$ are the bloom density and the initial density, respectively, $\langle r \rangle$ is the mean relative growth rate over the initiation period. Thus, the interannual variability of timing of *C. polykrikoides* bloom occurrence is controlled by the initial density and factors that can regulate the relative growth rate.

Cyst germination contributes the timing of bloom occurrence by determining the initial density. The condition for cyst germination can differ across years, and the initial density of vegetative cells may also vary largely for each year. The effect of variance in $C_{\text{ini}}$ can be evaluated. Based on Eq. (5.7), without considering the variability in $\langle r \rangle$, the change in $t_B$ due to change in $C_{\text{ini}}$ is expressed as:

$$\Delta t_B = -\frac{1}{\langle r \rangle} \Delta (\ln C_{\text{ini}})$$  \hspace{1cm} (5.8)

Eq. (5.8) suggests that an increase in $C_{\text{ini}}$ results in a shorter $t_B$, and the change is affected by relative growth rate. Even with a 10-fold increase or decrease in $C_{\text{ini}}$, a mean value of 0.1-0.3 d$^{-1}$ for $\langle r \rangle$ only leads to a change of 3.3-10 days in $t_B$. Model results
show that mean relative growth rate of *C. polykrikoides* can reach to 0.1-0.3 d\(^{-1}\) or even higher over the initiation period (late April to late June or July) in this studying area. Thus, given the large variability in \(t_B\) observed in the Lafayette River (more than 4 weeks), it suggests that the relative growth rate plays a more important role than cyst germination in driving the interannual variability in the timing of *C. polykrikoides* bloom occurrence.

Environmental factors that can regulate the relative growth rate and influence *C. polykrikoides* bloom, described by Eq. (5.1), are examined individually. This species shows grazing deterrence. There is no specific consumption on *C. polykrikoides*, and the loss of biomass of *C. polykrikoides* to grazers are along with other algae. While grazing is low for the James River, grazing pressure is not likely to largely affect the interannual variability of *C. polykrikoides* growth during the initiation. Due to the mobility of *C. polykrikoides*, the impact of settling or stratification is also unimportant. In addition, Tang and Gobler (2012) reported that the cyst formation rate is less than 1 cyst / 1000 cells in the culture experiment. Therefore, the formation rate of cells to resting cysts is not likely to be an important factor to reduce the *C. polykrikoides* biomass/density, especially during the initiation. Thus, the interannual variability of timing of *C. polykrikoides* bloom occurrence is more controlled by flushing and factors that can regulate the mixotrophic gross growth rate.

As shown in Eqs. (5.3) and (5.4), temperature and salinity are two factors that regulate both phototrophic and heterotrophic growth rates, therefore, they can play an important role in affecting the interannual variability in the timing of the bloom. Further analysis reveals that the interannual variability in gross growth rate regulated by
temperature is about 4.6 times that by salinity during the initiation. During summer, the light attenuation is low in this area that provides abundant light in the upper water column, and the swimming behavior of *C. polykrikoides* allows them to stay near the surface of the water column during the daytime while they also receive little impact from self-shading when their density is not high during the HAB initiation. By comparing the measured light to optimal light (Kim et al., 2004; Oh et al., 2006), calculation shows that no light limitation in the daytime for more than 97% of days during the pre-bloom period for *C. polykrikoides*. The supply of dissolved inorganic nutrients is a limiting factor for the phototrophic growth. Though *DIN* and *DIP* in the lower James River are regulated by other dominant phytoplankton during the HAB initiation, as shown in 2012 and 2013 (Figures 5.6e and 5.6f), the concentrations of *DIN* and *DIP* were low for the early-stage *C. polykrikoides* growth since it has relatively large half-saturation coefficients for *DIN* (2-3 µM) and *DIP* (0.57 µM). Nevertheless, the model results show that the heterotrophic growth, in fact, is the major mechanism for *C. polykrikoides* growth during the bloom initiation (e.g, Figures 5.6a and 5.6b). Therefore, the interannual variability in timing of bloom occurrence is greatly affected by environmental factors that can regulate the heterotrophic growth. Organic matter smaller than 12 µm was relatively abundant during the bloom initiation, and its interannual variability in the effect to growth rate was comparably smaller than that in temperature.

The flushing effect of transport processes also affects the required time significantly. It has been shown in Chapter 4 that a successful initiation requires a positive mean relative growth rate over the initiation period, and the time required to
reach the bloom density is affected by the relative growth rate. Thus, flushing can delay the bloom at originating locations by reducing the relative growth rate.

The above discussion suggests that temperature, salinity, and transport processes are the three important factors contributing to the interannual variability in \( t_B \), while the variability in initial density due to cyst germination is not very important. This suggestion, in fact, is also supported by a simple analysis. In this simple analysis, the initiation density of 1 cell ml\(^{-1}\) on June 4 was first assumed for every year. By assuming the variations in growth rate were only induced by that in temperature and salinity, the daily-averaged growth rate was calculated as \( g = 1.8 \times 0.41 \times f(T)f(SaI) \) where the daily-averaged phototrophic specific growth rate by Kim et al. (2004), 0.41 d\(^{-1}\), was applied. The growth rate \( g \) was multiplied by a factor of 1.8 to account for the mixotrophic growth and effects from other limiting environmental factors, because the mixotrophic growth is a combination of phototrophic and heterotrophic growth. The transport rate, \( F \), was estimated using the residence time for the Lafayette River, following Eq. (4.11.2) in Chapter 4. Relative growth rate was then calculated as \( r = g - F \), and it was averaged over the pre-bloom period for each year (from June 4\(^{th}\) to the observed bloom date) to obtain \( \langle r \rangle \). Therefore, the time required for bloom for each year with the calculated \( \langle r \rangle \) was obtained according to Eq. (5.7), which added the first day, June 4\(^{th}\), returned the calculated bloom date. Results show that the calculated bloom date for each year was close to the observed bloom date (Figure 5.7), suggesting that the interannual variability in the timing of \textit{C. polykrikoides} bloom in the Lafayette River can be well derived by the contribution from the three environmental factors only.
In the study years, since the mean temperatures over the initiation were above the optimal temperature (about 25 °C), the mean relative growth rate decreases with increasing temperature, and therefore, the time required for initiation increases with mean temperature. In addition, as shown by the difference between the blue line with considering flushing and the red line without considering flushing, the required time for bloom with including flushing can be delayed from days to weeks. This simple estimation also shows the importance of relative growth rate to induce such a large interannual variability (more than 4 weeks) in the timing of bloom occurrence.

Thus, during the initiation period for each year, while many factors can contribute to the timing of a *C. polykrikoides* bloom in the Lafayette River, temperature and the flushing effect are two critical factors controlling its interannual variability.

*Transport processes affect the impact of temperature*

The temperature varies from late June to late July, which has a large impact on bloom initiation until the bloom occurs. While both temperature and transport processes play determinant roles in the interannual variability in the timing of *C. polykrikoides* bloom in the Lafayette River, transport processes can indirectly affect the timing by shaping the impact of temperature.

Flushing decreases the relative growth rate and therefore delays the initiation of *C. polykrikoides* bloom. As illustrated in Figure 5.6, the delayed initiation makes *C. polykrikoides* grow in days later, which is generally under higher temperatures, before their density reaches the bloom density, and the temperature-dependent specific growth rate also changes significantly. In the Lafayette River, since the temperature always is beyond the optimal range for *C. polykrikoides* growth, the existence of flushing effect
results in a lower mean relative growth rate over the initiation if longer time is required for initiation. For example, the mean mixotrophic growth rate during the initiation (up to late July) in 2013 was lower than that in 2012 (up to late June), mainly through a temperature-limiting effect (Figure 5.6a and 5.6b).

The existence of the flushing effect of transport processes and its variability contribute to the increase in the variability in the timing of *C. polykrikoides* bloom occurrence. Because the temperature shows an annual cycle with the peak in the summer, the interannual variability in temperature for a fixed range of the year (e.g., June), however, is much less than the variability during the entire initiation that may or may not span into July, and correspondingly, the growth rate for each month also shows a less variability. For example, the standard deviations in temperature and the associated mixotrophic growth rate of the time June 1 to June 20 for 2007-2013 are about 1.36 °C and 0.026 d⁻¹, respectively, which are less than those of the entire initiation, 2.08 °C and 0.042 d⁻¹, respectively.

*Effect of wind on interannual variability in bloom timing*

Since a successful initiation of *C. polykrikoides* bloom requires at least several weeks (Chapter 4), the flushing effect of transport processes needs to be considered on the subtidal or longer timescales, which is regulated by the estuarine circulation and can be affected by various physical forcings, including wind, runoff induced by rainfall/precipitation, and tide.

Among these physical forcings, the wind has been recognized to significantly influence both the vertical mixing and horizontal transport in estuaries (Wang and Elliot, 1978; Scully et al., 2005), and play key roles in many water quality issues, such as in
oxygen dynamics (Scully, 2010a; 2010b). Particularly, the changes in direction of the wind can shift estuarine circulation both in direction and magnitude, and hence alter the transport processes in the system. A recent study by Hong et al. (2018) using dye release experiments showed that the southerly wind increased the exchange between the lower James River and its tributary Elizabeth River and enhanced the transport of dissolved substances to the main channel of the James River, whilst the northerly wind reduced the exchange and inhibited the transport.

The changes in the flushing effect by wind may explain the good correlation between the date of first bloom appearance in the Lafayette River and the mean wind speed for the north-south direction during the pre-bloom period of each year (averaged over June 1 to the date of the first bloom appearance) (Figure 5.8).

While the wind in the *C. polykrikoides* bloom initiation in the Lafayette River may be through the flushing, the correlation between the mean Southerly/Northerly wind speed and the time required for bloom may also be partially due to the weather variability and passing frontal system that results in a covariance between Southerly/Northerly wind speed and temperature. This warrants further study.

**Perturbation of flushing during a HAB event**

While the overall flushing over the bloom initiation can affect the interannual variability in bloom occurrence, individual perturbation by the flushing also matters for individual HAB event. In this section, we demonstrate that how the individual perturbations affect the initiation of a HAB event and even affect the further development after it has successfully initiated.
After the algal density reaches the bloom density, the duration of the bloom depends on the environmental conditions, including transport processes. Flushing effect can be the key factor terminating a HAB event for those short-lasting HABs at the originating locations. The mechanism is that a strong flushing effect can wash out algae from the originating location into a much larger area, and decreases the local algal density significantly, and it requires another initiation with a long time period for algae to reach bloom density again, as shown in the idealized illustration (Figure 5.9). Under the normal flushing condition, the algae grow to the bloom density after tens of days, and a HAB event occurs. Shortly after the occurrence of the bloom, it encounters with a strong perturbation and collapses. The bloom enters the second round of initiation that requires other tens of days to build up the density again. This idealized illustration also indicates there may be more than one initiation period for a HAB event. Because the transport-out effect of flushing requires that the incoming water has a lower algal density than the location, this cause of bloom termination by transport processes more often occurs when a HAB is just initialized at the originating locations when algal density at other locations remains under bloom density.

Thus, it is likely that an initiated bloom can only last for several days as a result of the flushing effect. In the Lafayette River, strong southerly wind, heavy rainfall, and spring tide are important environmental conditions in inducing large flushing during a HAB event, and a strong perturbation on the HAB dynamics occurs when there is a combination of these conditions, capable of interrupting, or even terminating, HAB initiation.
The rainfall and the associated run-off have various effects on the algal dynamics at the local scale. The water input contains substances including nutrients and sediments, but no algae (neither HAB species nor non-HAB species). Therefore, the rainfall results in an increase in nutrient concentration but a “transport out” effect of flushing. For the dynamics of HAB algal density, the contribution of the effect of rainfall and the associated run-off on nutrient availability changes in different stages of a HAB event, it may be insignificant during the bloom initiation when the nutrient availability is not a limitation, but it can be significant for sustaining the bloom when the bloom is fully developed and the nutrient concentration is low. The flushing effect by rainfall always exists and increases with the input of water. Therefore, it is small during a light rainfall that is also inhibited by other effects, but it can become the dominant effect during a heavy rainfall at any stage, especially for tributary with small water volume. Large runoff induced by rainfall can increase flushing for tributary. For example, a significantly negative correlation between the relative growth rate and precipitation for summer 2014 is shown in Figure 5.10, which explains 27.6% of the variability in the relative growth rate.

On the subtidal timescale, the spring-neap tidal cycle also plays a role in regulating the flushing effect on the dynamics of HAB algal density at the originating locations. During the initiation, since the algal density outside of the originating locations is lower, the flushing effect is net transport-out, and it increases with the exchange flow. During the spring tide, the strong exchange flow leads to a strong transport-out effect.

The collapse of a short-last *C. polykrikoides* bloom in 2014 in the Lafayette River may be caused by the flushing effect of transport processes. The bloom was observed in
early July. However, it only lasted for several days and collapsed, and there was no persistently intense of *C. polykrikoides* density afterward. The examination on time series of southerly/northerly wind speed, precipitation, tidal range, chl-a, and *C. polykrikoides* density suggests that the bloom collapse was coincided with a combination of southerly wind, heavy rainfall, and spring tide (Figure 5.11), and that the flushing effect may be the main cause. This collapse was followed by the second round of bloom initiation. However, the density of *C. polykrikoides* never reached to the bloom density again, and the density declined after another combination of southerly wind, heavy rainfall, and spring tide, suggesting that the flushing effect may also be the main cause of the termination of the second initiation.

**Model limitation and future work**

The model presents reasonably well results in simulating *C. polykrikoides* blooms in the Lafayette River, and it can help to understand the advantage of strategies used by this algal species such as the mixotrophic growth and the contribution of each environmental factor to the blooms. However, modeling for some processes has been simplified in the current version, and improvement of the model may be needed in the future work.

The harmful effects of *C. polykrikoides* to organisms become significant when their density reaches 330 cells ml\(^{-1}\) (Tang and Gobler, 2009; Gobler et al., 2012). Thus, in the future version of the HAB model, the grazing rate, \(M\), can be assumed to equal zero only when their density exceeds 330 cells ml\(^{-1}\), otherwise, it can be assumed to be proportional to *C. polykrikoides* biomass as a function of temperature, \(M = M_0 \theta_M^{T-20} C\).
The model adopted a constant speed and a fixed direction (upward) for *C. polykrikoides* swimming during the daytime. Swimming speeds, however, are affected by temperature, nutrients, and irradiance (Smayda, 2002), and the swimming speed may need be allowed to vary with temperature or growth rate. In addition, the direction of swimming may also be related to nutrient gradients at night if the nutrient is shown to be a factor beside light for influencing this behavior.

Algae, including dinoflagellates, can photoacclimate their chl-a content according to changes in environmental conditions such as temperature, light irradiance, and nutrient (Geider et al., 1997). Correspondingly, carbon to chl-a ratio (C:Chl) also varies. For *C. polykrikoides*, Noh et al. (2018) measured chl-a content for a survey cruise during a *C. polykrikoides* bloom, which equaled 43.1 ± 15.8 pg chl-a/cell and ranged from 30.1 to 81.2 pg chl-a/cell. In the James River, C:Chl also varies largely during a *C. polykrikoides* bloom, as shown in Marshall and Egerton (2013).

In the future version of the numerical model, the chl-a content can be assumed to vary according to environmental conditions, and a varying C:Chl is used. The chl-a content can be assumed to be 30 pg chl-a/cell that obtained from the laboratory (Noh et al. 2018), when the phototrophic growth is unlimited by light and nutrient, and the corresponding C:Chl is 60.6 g C / g chl-a. When its phototrophic growth is under light limitation, the chl-a content can be assumed to be 81.2 pg chl-a/cell, and the corresponding carbon to chl-a ratio C:Chl is 22.4 g C / g chl-a. When the phototrophic growth is under nutrient limitation, C:Chl varies. This change will result in a higher chl-a when light is limiting and a lower chl-a when nutrient is limiting for the same simulated biomass. The maximum C:Chl may be set to be 333 g C / g chl-a, adopted from the
empirical model in Cloern et al. (1995). A possible expression of C: Chl for C. *polykrikoides* may be proposed as:

\[
C : \text{Chl} = \begin{cases} 
60.6 & \text{if unlimited growth} \\
\max \left\{ \frac{22.4}{f(T)}, 333 \right\} & \text{if under light limitation} \\
\max \left\{ \frac{22.4}{f(T) \min \{f(DIN), f(DIP)\}}, 333 \right\} & \text{if under nutrient limitation}
\end{cases}
\]

The mechanism for the collapse of *C. polykrikoides* at the late stage of a HAB event, and current model used an artificial algorithm to make the collapse consistent to observations, which should be updated in future versions after the mechanism is revealed. Here, a natural mortality hypothesis is proposed. After a cell of *C. polykrikoides* has reached a certain age, its life stage as a vegetative cell ends. The vegetative cells lost due to the natural mortality can be further assumed to become resting cysts. The hypothesis may be tested using a laboratory culture experiment.

The current model cannot simulate the complete life cycle of *C. polykrikoides* because the cyst dynamics was not included. Nevertheless, it is possible to include the stage of resting cyst in future work. The equation for the cyst dynamics that can be coupled with Eq. (5.1) for vegetative cells is:

\[
\frac{\partial C_{\text{Cyst}}}{\partial t} + u \frac{\partial C_{\text{Cyst}}}{\partial x} + v \frac{\partial C_{\text{Cyst}}}{\partial y} + w \frac{\partial C_{\text{Cyst}}}{\partial z} - \left[ \frac{\partial}{\partial x} \left( K \frac{\partial C_{\text{Cyst}}}{\partial x} \right) + \frac{\partial}{\partial y} \left( K \frac{\partial C_{\text{Cyst}}}{\partial y} \right) + \frac{\partial}{\partial z} \left( K \frac{\partial C_{\text{Cyst}}}{\partial z} \right) \right] =
\]

\[
encyst - R_{Cyst} Cyst - M_{Cyst} Cyst + w_{Cyst} \frac{\partial C_{\text{Cyst}}}{\partial z} - germ + S_{Cyst} \tag{5.9}
\]

where \( R_{Cyst} \) is the decay rate, \( M_{Cyst} \) is the grazing rate by benthos, \( w_{Cyst} \) is the settling velocity of the resting cyst. \( germ \) denotes the input rate from the germination of resting cysts, \( encyst \) is a sink term denoting the loss rate of vegetative cells due to cyst
formation, and \( S_{\text{Cyst}} \) denotes other external sources such as those through the ballast water input. The timing of cyst germination can be assumed to be temperature-dependent. For example, a constant cyst input rate can be assumed to last 30 days for each year in the model, after the temperature reaches the suitable temperature range that is larger than 18 °C. Nevertheless, a comprehensive modeling of cyst germination rate may require to consider environmental factors regulating germination such as temperature, irradiance, and oxygen conditions (Kremp and Anderson, 2000).

**Conclusions**

A numerical model for *C. polykrikoides* bloom is developed, which includes competitive advantages such as mixotrophic growth, swimming behavior, and cyst germination. The model results show that during the bloom initiation, the interannual variability in gross growth rate of *C. polykrikoides* in the Lafayette River is influenced more by temperature than other factors, and the flushing by transport processes also significantly lowers relative growth rate that delays the bloom initiation. Results also show that the strategies used by *C. polykrikoides* also contribute greatly to the initiation of this bloom in the Lafayette River. The heterotrophic growth rate by taking up organic matter is higher than the phototrophic growth rate, and the resulted mixotrophic growth (phototrophic + heterotrophic) counterbalanced the flushing and other unsuitable environmental conditions and ensures that *C. polykrikoides* can grow to the bloom density with a high growth rate in the area.

Temperature and physical transport processes are the two dominant factors controlling the interannual variability in the timing of its initiation. For a specific HAB event, the contribution of each perturbation by flushing can effectively delay, interrupt, or
even terminate the bloom initiation. In the Lafayette River, southerly wind, heavy rainfall interacting with spring-neap tide are suggested to be important physical conditions to increase the flushing effect, and a combination of these three conditions can significantly affect the *C. polykrikoides* bloom by preventing their accumulation.
References


Table 5.1. The *C. polykrikoides* model structure.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Expression</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G$</td>
<td>Gross growth rate</td>
<td>$G = \min(G^P + G^R, G_{opt})$</td>
</tr>
<tr>
<td></td>
<td>If $G_{opt} &lt; (G^P + G^h)$, then</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$G^P = \frac{G^P}{G^P+G^h} G_{opt}$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$G^h = \frac{G^h}{G^P+G^h} G_{opt}$</td>
<td></td>
</tr>
<tr>
<td>$f(T)$</td>
<td>Growth-limiting function for temperature</td>
<td>$f(T) = e^{-k_{T1}(T-T_{opt})^2}, T \leq T_{opt}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$f(T) = e^{-k_{T2}(T-T_{opt})^2}, T &gt; T_{opt}$</td>
</tr>
<tr>
<td>$f(Sal)$</td>
<td>Growth-limiting function for salinity</td>
<td>$f(Sal) = e^{-k_{Sal1}(Sal-Sal_{opt})^2}, Sal \leq Sal_{opt}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$f(Sal) = e^{-k_{Sal2}(Sal-Sal_{opt})^2}, Sal &gt; Sal_{opt}$</td>
</tr>
<tr>
<td>$f(DIN)$</td>
<td>Growth-limiting function for DIN</td>
<td>$f(DIN) = \frac{DIN}{DIN+DIN_k}$</td>
</tr>
<tr>
<td>$f(DIP)$</td>
<td>Growth-limiting function for DIP</td>
<td>$f(DIP) = \frac{DIP}{DIP+DIP_k}$</td>
</tr>
<tr>
<td>$f(I)$</td>
<td>Growth-limiting function for light irradiance</td>
<td>$f(I) = \frac{I}{I+l_k}$</td>
</tr>
<tr>
<td>$f(OM_{12})$</td>
<td>Growth-limiting function for organic matter smaller than 12 µm</td>
<td>$f(OM_{12}) = \frac{OM_{12}}{OM_{12}+OM_{12k}}$</td>
</tr>
<tr>
<td>$R$</td>
<td>Respiration/excretion rate</td>
<td>$R = R_0\theta_R^{T-20} + f^P G^P$</td>
</tr>
</tbody>
</table>
Table 5.2. The *C. polykrikoides* model parameters and their values used in the experiment.

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
<th>Unit</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$G_{opt}$</td>
<td>Maximum instantaneous gross growth rate at the optimal condition during daytime</td>
<td>$d^{-1}$</td>
<td>1.06</td>
</tr>
<tr>
<td>$G_{opt}^p$</td>
<td>Phototrophic instantaneous gross growth rate at the optimal condition during daytime</td>
<td>$d^{-1}$</td>
<td>1.06</td>
</tr>
<tr>
<td>$G_{opt}^h$</td>
<td>Heterotrophic instantaneous gross growth rate at the optimal condition</td>
<td>$d^{-1}$</td>
<td>0.62</td>
</tr>
<tr>
<td>$f^p$</td>
<td>Respiratory losses associated with photosynthesis as a ratio to $G_{opt}^p$</td>
<td></td>
<td>0.16</td>
</tr>
<tr>
<td>$R_0$</td>
<td>Basic metabolism rate at 20 °C</td>
<td>$d^{-1}$</td>
<td>0.025</td>
</tr>
<tr>
<td>$w_c$</td>
<td>Swimming velocity of <em>C. polykrikoides</em></td>
<td>$m ; d^{-1}$</td>
<td>55</td>
</tr>
<tr>
<td>$T_{opt}$</td>
<td>Optimal temperature for growth</td>
<td>°C</td>
<td>25</td>
</tr>
<tr>
<td>$k_{T1}$</td>
<td>Temperature effect on growth below $T_{opt}$</td>
<td>°C$^{-2}$</td>
<td>0.0147</td>
</tr>
<tr>
<td>$k_{T2}$</td>
<td>Temperature effect on growth above $T_{opt}$</td>
<td>°C$^{-2}$</td>
<td>0.0530</td>
</tr>
<tr>
<td>$k_{Sat1}$</td>
<td>Salinity effect on growth below $Sal_{opt}$</td>
<td></td>
<td>0.0024</td>
</tr>
<tr>
<td>$k_{Sat2}$</td>
<td>Salinity effect on growth below $Sal_{opt}$</td>
<td></td>
<td>0.0222</td>
</tr>
<tr>
<td>$I_{opt}$</td>
<td>Half-saturation coefficient for light irradiance</td>
<td>$\mu E ; m^{-2} ; s^{-1}$</td>
<td>30</td>
</tr>
<tr>
<td>$N_k$</td>
<td>Half-saturation coefficient for DIN</td>
<td>$g ; N ; m^{-3}$</td>
<td>0.028</td>
</tr>
<tr>
<td>$P_k$</td>
<td>Half-saturation coefficient for DIP</td>
<td>$g ; P ; m^{-3}$</td>
<td>0.0177</td>
</tr>
<tr>
<td>$\theta_R$</td>
<td>Constant for quantifying the temperature effect on respiration rate</td>
<td></td>
<td>1.07</td>
</tr>
<tr>
<td>$OM_{12k}$</td>
<td>Half saturation coefficient for organic matter smaller than 12 µm</td>
<td>$g ; C ; m^{-3}$</td>
<td>0.0263</td>
</tr>
<tr>
<td>$a$</td>
<td>Fraction of particulate organic matter smaller than 12 µm</td>
<td></td>
<td>0.3</td>
</tr>
<tr>
<td>$b$</td>
<td>Fraction of organisms smaller than 12 µm</td>
<td></td>
<td>0.3</td>
</tr>
</tbody>
</table>
Table 5.3. Sensitivity tests for examining the effects of mixotrophic growth, swimming, and cyst germination on the initiation and development of *C. polykrikoides* blooms in the year 2012. The different values of parameters to the control experiment were bolded.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>$G_{opt}^h$ (d$^{-1}$)</th>
<th>$a$</th>
<th>$b$</th>
<th>$w_c$ (m d$^{-1}$)</th>
<th>$C_{ini}$ (cell ml$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>control</td>
<td>0.62</td>
<td>0.3</td>
<td>0.3</td>
<td>55</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>0.62</td>
<td>0.1</td>
<td>0.1</td>
<td>55</td>
<td>1</td>
</tr>
<tr>
<td>2</td>
<td>0.62</td>
<td>0</td>
<td>0</td>
<td>55</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>0</td>
<td>0.3</td>
<td>0.3</td>
<td>55</td>
<td>1</td>
</tr>
<tr>
<td>3</td>
<td>0.62</td>
<td>0.3</td>
<td>0.3</td>
<td>20</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>0.62</td>
<td>0.3</td>
<td>0.3</td>
<td>55</td>
<td>0.1</td>
</tr>
<tr>
<td>5</td>
<td>0.62</td>
<td>0.3</td>
<td>0.3</td>
<td>55</td>
<td>10</td>
</tr>
</tbody>
</table>
Table 5.4. The overall mean of relative growth rate, $\bar{r}$, mixotrophic gross growth rate, $\bar{G}$, phototrophic growth rate, $\bar{G}^p$, heterotrophic growth rate, $\bar{G}^h$, basic metabolism rate, $R_0\theta_{R}^{T-20}$, respiratory losses associated with photosynthesis, $f^p G^p$, and transport rate for the effect of transport processes, $F_B$, during the blooms in 2005-2013, in units of d$^{-1}$. Note that the values are for the depth-integrated biomass described in Eq. (5.6).

<table>
<thead>
<tr>
<th>Station</th>
<th>$\bar{r}$</th>
<th>$\bar{G}$</th>
<th>$\bar{G}^p$</th>
<th>$\bar{G}^h$</th>
<th>$-R_0\theta_{R}^{T-20}$</th>
<th>$-f^p G^p$</th>
<th>$-F_B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LFA01</td>
<td>0.065</td>
<td>0.227</td>
<td>0.052</td>
<td>0.175</td>
<td>-0.042</td>
<td>-0.008</td>
<td>-0.113</td>
</tr>
<tr>
<td>LFB01</td>
<td>0.108</td>
<td>0.126</td>
<td>0.031</td>
<td>0.095</td>
<td>-0.047</td>
<td>-0.005</td>
<td>0.033</td>
</tr>
<tr>
<td>LE5.6</td>
<td>0.061</td>
<td>0.255</td>
<td>0.044</td>
<td>0.211</td>
<td>-0.040</td>
<td>-0.007</td>
<td>-0.149</td>
</tr>
<tr>
<td>LE5.4</td>
<td>0.060</td>
<td>0.320</td>
<td>0.039</td>
<td>0.282</td>
<td>-0.038</td>
<td>-0.006</td>
<td>-0.219</td>
</tr>
</tbody>
</table>
Table 5.5. The overall mean of daily-averaged growth-limiting function for each environmental factor, including temperature ($T$), salinity ($Sal$), irradiance ($I$), dissolved inorganic nitrogen ($DIN$), dissolved inorganic phosphate ($DIP$), and organic matter smaller than 12 μm ($OM_{12}$), during the blooms in 2005-2013. Note that the values are for the surface layer only, and $f(I)$ equals zero at night.

<table>
<thead>
<tr>
<th>Station</th>
<th>$f(T)$</th>
<th>$f(Sal)$</th>
<th>$f(I)$</th>
<th>$f(DIN)$</th>
<th>$f(DIP)$</th>
<th>$f(OM_{12})$</th>
</tr>
</thead>
<tbody>
<tr>
<td>LFA01</td>
<td>0.643</td>
<td>0.652</td>
<td>0.544</td>
<td>0.385</td>
<td>0.267</td>
<td>0.869</td>
</tr>
<tr>
<td>LFB01</td>
<td>0.450</td>
<td>0.574</td>
<td>0.541</td>
<td>0.353</td>
<td>0.447</td>
<td>0.886</td>
</tr>
<tr>
<td>LE5.6</td>
<td>0.737</td>
<td>0.665</td>
<td>0.490</td>
<td>0.269</td>
<td>0.228</td>
<td>0.866</td>
</tr>
<tr>
<td>LE5.4</td>
<td>0.832</td>
<td>0.710</td>
<td>0.524</td>
<td>0.170</td>
<td>0.234</td>
<td>0.928</td>
</tr>
</tbody>
</table>
Figure 5.1. Map of the lower James River and its sub-tributary Lafayette River, USA. The hollow squares denote the locations of long-term monitoring stations LE5.4, LE5.6, LFA01, and LFB01, and the filled circle denotes the location of the continuous monitoring station NYCC.
Figure 5.2. Comparison of model results of daily-averaged chl-a to the monthly chl-a data (black dot) and weekly dataflow chl-a data (red triangles) at long-term monitoring stations in the Lafayette River (LFA01 and LFB01), the Elizabeth River (LE5.6), and the mainstem James River (LE5.4).
Figure 5.3. Comparison of model results of daily-averaged (thick lines) and hourly (thin lines) *C. polykrikoides* density at two Stations LFA01 and LFB01 to the weekly-averaged observational density data in the Lafayette River in 2011-2013.
Figure 5.4. Comparison of model results of chl-a data (blue lines) to high-frequency observational chl-a data (black lines) at continues monitoring Station NYCC for the years 2012 and 2013. Thick lines denote the daily-averaged chl-a and thin lines denote the hourly chl-a. Solid blue lines denote the modeled daily-averaged chl-a for the entire water column, whereas dashed blue lines denote the maximum and minimum values of modeled chl-a.
Figure 5.5. The results of a sensitivity test on the effect of initial density, $C_{ini}$. Modeled density was presented at 6-hour intervals. The red lines indicate the bloom density (1000 cells ml$^{-1}$).
Figure 5.6. The gross growth rate, $G$, phototrophic growth rate, $G^p$, heterotrophic growth rate, $G^h$, growth-limiting functions for temperature, $f(T)$, salinity, $f(Sal)$, irradiance, $f(I)$, dissolved inorganic nitrogen, $f(DIN)$, dissolved inorganic phosphate, $f(DIP)$, and organic matter smaller than 12 $\mu$m, $f(OM_{12})$, in 2012 and 2013, respectively.
Figure 5.7. The timing of first bloom appearance in the Lafayette River. The comparison between observed and the calculated timing using the data of temperature, salinity, and residence time. The blue and red lines show the results with/without including the flushing effect. For the calculation, the initial density is assumed to be 1 cell ml$^{-1}$ on June 4 of each year. Because the data of measured density have relatively low resolutions (several locations) in space and time (water samples were collected every day or every several days), uncertainties exist for the timing of first bloom appearance. Therefore, the error bar having a length of one week is used, indicating the possible likelihood when the mean density of the entire Lafayette River reaches the bloom density.
Figure 5.8. The timing of first bloom occurring in the Lafayette River vs. the mean Southerly/Northerly wind speed (m d⁻¹) during the initiation period, which is assigned a positive (+) / negative (-) sign, respectively. A linear regression shows a $r^2$ of 0.458, and a $p$ value of 0.065. Because the data of measured density have relatively low resolutions (several locations) in space and time (water samples were collected every day or every several days), uncertainties exist for the timing of first bloom appearance. Therefore, the error bar having a length of one week is used, indicating the possible likelihood when the mean density of the entire Lafayette River reaches the bloom density.
Figure 5.9. An idealized illustration of the impact of individual perturbation by flushing on a HAB initiation. Red dashed line denotes the bloom density (assumed to be 1000 cells ml\(^{-1}\) corresponding to \textit{C. polykrikoides} bloom density). The initial density is set to be 1 cell ml\(^{-1}\), the growth rate \(g\) is set to be 0.4 d\(^{-1}\). The transport rate is characterized by a half-sinusoid with an expression of \(F = \max [0.8\sin(\frac{2\pi}{14.5}t), 0.05]\) for representing the flushing effect under normal spring-neap conditions, and a high transport rate is set with an expression of \(F = \max [2\sin(\frac{2\pi}{14.5}t), 0.05]\) for inducing a strong flushing just after \textit{C. polykrikoides} abundance has reached the bloom density. This strong flushing causes the collapse of the bloom, and the initiation restarts, which requires another tens of days for \textit{C. polykrikoides} to reach bloom density again.
Figure 5.10. The correlation between daily relative growth rate (d⁻¹) at Station NYCC and daily-integrated precipitation (inch) in the summer 2014.
Figure 5.11. Time series of hourly southerly/northerly wind, daily tidal range (m), daily-integrated precipitation (inch), daily-averaged chl-a ($\mu g$ l$^{-1}$) and corresponding calculated relative growth rate (d$^{-1}$) at Station NYCC, and weekly-averaged *C. polykrikoides* density (cell ml$^{-1}$) in the Lafayette River in the year of 2014. Grey bars show the two periods of *C. polykrikoides* density decline.
### Supplementary

Table S5.1. The mean of relative growth rate, $\bar{r}$, mixotrophic gross growth rate, $\bar{G}$, phototrophic growth rate, $\bar{G}^p$, heterotrophic growth rate, $\bar{G}^h$, basic metabolism rate, $R_0\theta_R^{\frac{T-20}{R}}$, respiratory losses associated with photosynthesis, $f^pG^p$, and transport rate for the effect of transport processes, $\bar{F}_B$, over each bloom event in units of d$^{-1}$, at Station LFA01.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\bar{r}$</th>
<th>$\bar{G}$</th>
<th>$\bar{G}^p$</th>
<th>$\bar{G}^h$</th>
<th>$-R_0\theta_R^{\frac{T-20}{R}}$</th>
<th>$-f^pG^p$</th>
<th>$-\bar{F}_B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>0.076</td>
<td>0.256</td>
<td>0.029</td>
<td>0.227</td>
<td>-0.035</td>
<td>-0.005</td>
<td>-0.142</td>
</tr>
<tr>
<td>2006</td>
<td>0.057</td>
<td>0.265</td>
<td>0.064</td>
<td>0.202</td>
<td>-0.042</td>
<td>-0.010</td>
<td>-0.159</td>
</tr>
<tr>
<td>2007</td>
<td>0.072</td>
<td>0.204</td>
<td>0.046</td>
<td>0.158</td>
<td>-0.044</td>
<td>-0.007</td>
<td>-0.083</td>
</tr>
<tr>
<td>2008</td>
<td>0.074</td>
<td>0.188</td>
<td>0.045</td>
<td>0.143</td>
<td>-0.044</td>
<td>-0.007</td>
<td>-0.064</td>
</tr>
<tr>
<td>2009</td>
<td>0.051</td>
<td>0.236</td>
<td>0.057</td>
<td>0.180</td>
<td>-0.041</td>
<td>-0.009</td>
<td>-0.137</td>
</tr>
<tr>
<td>2010</td>
<td>0.072</td>
<td>0.185</td>
<td>0.047</td>
<td>0.138</td>
<td>-0.045</td>
<td>-0.008</td>
<td>-0.062</td>
</tr>
<tr>
<td>2011</td>
<td>0.053</td>
<td>0.215</td>
<td>0.067</td>
<td>0.148</td>
<td>-0.043</td>
<td>-0.011</td>
<td>-0.110</td>
</tr>
<tr>
<td>2012</td>
<td>0.067</td>
<td>0.236</td>
<td>0.055</td>
<td>0.180</td>
<td>-0.043</td>
<td>-0.009</td>
<td>-0.119</td>
</tr>
<tr>
<td>2013</td>
<td>0.065</td>
<td>0.252</td>
<td>0.054</td>
<td>0.198</td>
<td>-0.041</td>
<td>-0.009</td>
<td>-0.140</td>
</tr>
<tr>
<td>Overall</td>
<td>0.065</td>
<td>0.227</td>
<td>0.052</td>
<td>0.175</td>
<td>-0.042</td>
<td>-0.008</td>
<td>-0.113</td>
</tr>
</tbody>
</table>
Table S5.2. The mean of relative growth rate, $\bar{r}$, mixotrophic gross growth rate, $\bar{G}$, phototrophic growth rate, $\bar{G}^p$, heterotrophic growth rate, $\bar{G}^h$, basic metabolism rate, $R_0\theta^{-20}_R$, respiratory losses associated with photosynthesis, $f^p\bar{G}^p$, and transport rate for the effect of transport processes, $\bar{F}_B$, over each bloom event in units of d$^{-1}$, at Station LFB01.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\bar{r}$</th>
<th>$\bar{G}$</th>
<th>$\bar{G}^p$</th>
<th>$\bar{G}^h$</th>
<th>$-R_0\theta^{-20}_R$</th>
<th>$-f^p\bar{G}^p$</th>
<th>$-\bar{F}_B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>0.075</td>
<td>0.214</td>
<td>0.019</td>
<td>0.195</td>
<td>-0.037</td>
<td>-0.003</td>
<td>-0.101</td>
</tr>
<tr>
<td>2006</td>
<td>0.212</td>
<td>0.149</td>
<td>0.042</td>
<td>0.107</td>
<td>-0.047</td>
<td>-0.007</td>
<td>0.116</td>
</tr>
<tr>
<td>2007</td>
<td>0.122</td>
<td>0.095</td>
<td>0.027</td>
<td>0.068</td>
<td>-0.050</td>
<td>-0.004</td>
<td>0.081</td>
</tr>
<tr>
<td>2008</td>
<td>0.071</td>
<td>0.070</td>
<td>0.019</td>
<td>0.051</td>
<td>-0.051</td>
<td>-0.003</td>
<td>0.054</td>
</tr>
<tr>
<td>2009</td>
<td>0.056</td>
<td>0.137</td>
<td>0.040</td>
<td>0.098</td>
<td>-0.046</td>
<td>-0.006</td>
<td>-0.030</td>
</tr>
<tr>
<td>2010</td>
<td>0.131</td>
<td>0.084</td>
<td>0.026</td>
<td>0.058</td>
<td>-0.051</td>
<td>-0.004</td>
<td>0.101</td>
</tr>
<tr>
<td>2011</td>
<td>0.157</td>
<td>0.105</td>
<td>0.036</td>
<td>0.070</td>
<td>-0.049</td>
<td>-0.006</td>
<td>0.106</td>
</tr>
<tr>
<td>2012</td>
<td>0.076</td>
<td>0.143</td>
<td>0.039</td>
<td>0.105</td>
<td>-0.048</td>
<td>-0.006</td>
<td>-0.014</td>
</tr>
<tr>
<td>2013</td>
<td>0.068</td>
<td>0.141</td>
<td>0.032</td>
<td>0.109</td>
<td>-0.046</td>
<td>-0.005</td>
<td>-0.022</td>
</tr>
<tr>
<td>Overall</td>
<td>0.108</td>
<td>0.126</td>
<td>0.031</td>
<td>0.095</td>
<td>-0.047</td>
<td>-0.005</td>
<td>0.033</td>
</tr>
</tbody>
</table>
Table S5.3. The mean of relative growth rate, $\bar{r}$, mixotrophic gross growth rate, $\bar{G}$, phototrophic growth rate, $\bar{G}_p$, heterotrophic growth rate, $\bar{G}_h$, basic metabolism rate, $R_0\theta^{T-20}_R$, respiratory losses associated with photosynthesis, $\bar{f}_p\bar{G}_p$, and transport rate for the effect of transport processes, $\bar{F}_B$, over each bloom event in units of $d^{-1}$, at Station LE5.6.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\bar{r}$</th>
<th>$\bar{G}$</th>
<th>$\bar{G}_p$</th>
<th>$\bar{G}_h$</th>
<th>$-R_0\theta^{T-20}_R$</th>
<th>$-\bar{f}_p\bar{G}_p$</th>
<th>$-\bar{F}_B$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>0.068</td>
<td>0.262</td>
<td>0.026</td>
<td>0.236</td>
<td>-0.034</td>
<td>-0.004</td>
<td>-0.158</td>
</tr>
<tr>
<td>2006</td>
<td>0.049</td>
<td>0.296</td>
<td>0.053</td>
<td>0.244</td>
<td>-0.040</td>
<td>-0.008</td>
<td>-0.202</td>
</tr>
<tr>
<td>2007</td>
<td>0.068</td>
<td>0.225</td>
<td>0.029</td>
<td>0.196</td>
<td>-0.041</td>
<td>-0.005</td>
<td>-0.113</td>
</tr>
<tr>
<td>2008</td>
<td>0.069</td>
<td>0.212</td>
<td>0.030</td>
<td>0.182</td>
<td>-0.042</td>
<td>-0.005</td>
<td>-0.099</td>
</tr>
<tr>
<td>2009</td>
<td>0.056</td>
<td>0.260</td>
<td>0.046</td>
<td>0.214</td>
<td>-0.039</td>
<td>-0.007</td>
<td>-0.160</td>
</tr>
<tr>
<td>2010</td>
<td>0.065</td>
<td>0.231</td>
<td>0.050</td>
<td>0.181</td>
<td>-0.043</td>
<td>-0.008</td>
<td>-0.117</td>
</tr>
<tr>
<td>2011</td>
<td>0.053</td>
<td>0.255</td>
<td>0.067</td>
<td>0.189</td>
<td>-0.041</td>
<td>-0.011</td>
<td>-0.153</td>
</tr>
<tr>
<td>2012</td>
<td>0.061</td>
<td>0.254</td>
<td>0.041</td>
<td>0.212</td>
<td>-0.042</td>
<td>-0.007</td>
<td>-0.147</td>
</tr>
<tr>
<td>2013</td>
<td>0.060</td>
<td>0.295</td>
<td>0.051</td>
<td>0.244</td>
<td>-0.039</td>
<td>-0.008</td>
<td>-0.191</td>
</tr>
<tr>
<td>Overall</td>
<td>0.061</td>
<td>0.255</td>
<td>0.044</td>
<td>0.211</td>
<td>-0.040</td>
<td>-0.007</td>
<td>-0.149</td>
</tr>
</tbody>
</table>
Table S5.4. The mean of relative growth rate, $\bar{r}$, mixotrophic gross growth rate, $\bar{G}$, phototrophic growth rate, $\bar{G}^p$, heterotrophic growth rate, $\bar{G}^h$, basic metabolism rate, $R_0\theta^\text{R-T-20}_{\text{R}}$, respiratory losses associated with photosynthesis, $\bar{f}^p\bar{G}^p$, and transport rate for the effect of transport processes, $\bar{F}_B^{-}$, over each bloom event in units of $d^{-1}$, at Station LE5.4.

<table>
<thead>
<tr>
<th>Year</th>
<th>$\bar{r}$</th>
<th>$\bar{G}$</th>
<th>$\bar{G}^p$</th>
<th>$\bar{G}^h$</th>
<th>$-R_0\theta^\text{R-T-20}_{\text{R}}$</th>
<th>$-\bar{f}^p\bar{G}^p$</th>
<th>$-\bar{F}_B^{-}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>2005</td>
<td>0.074</td>
<td>0.303</td>
<td>0.027</td>
<td>0.276</td>
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<td>-0.004</td>
<td>-0.192</td>
</tr>
<tr>
<td>2006</td>
<td>0.043</td>
<td>0.349</td>
<td>0.045</td>
<td>0.304</td>
<td>-0.037</td>
<td>-0.007</td>
<td>-0.264</td>
</tr>
<tr>
<td>2007</td>
<td>0.068</td>
<td>0.308</td>
<td>0.025</td>
<td>0.283</td>
<td>-0.039</td>
<td>-0.004</td>
<td>-0.200</td>
</tr>
<tr>
<td>2008</td>
<td>0.066</td>
<td>0.299</td>
<td>0.025</td>
<td>0.274</td>
<td>-0.038</td>
<td>-0.004</td>
<td>-0.193</td>
</tr>
<tr>
<td>2009</td>
<td>0.060</td>
<td>0.323</td>
<td>0.044</td>
<td>0.279</td>
<td>-0.037</td>
<td>-0.007</td>
<td>-0.221</td>
</tr>
<tr>
<td>2010</td>
<td>0.066</td>
<td>0.308</td>
<td>0.040</td>
<td>0.268</td>
<td>-0.040</td>
<td>-0.006</td>
<td>-0.198</td>
</tr>
<tr>
<td>2011</td>
<td>0.053</td>
<td>0.314</td>
<td>0.048</td>
<td>0.266</td>
<td>-0.038</td>
<td>-0.008</td>
<td>-0.218</td>
</tr>
<tr>
<td>2012</td>
<td>0.057</td>
<td>0.306</td>
<td>0.032</td>
<td>0.275</td>
<td>-0.040</td>
<td>-0.005</td>
<td>-0.207</td>
</tr>
<tr>
<td>2013</td>
<td>0.053</td>
<td>0.374</td>
<td>0.063</td>
<td>0.311</td>
<td>-0.037</td>
<td>-0.010</td>
<td>-0.278</td>
</tr>
<tr>
<td>Overall</td>
<td>0.060</td>
<td>0.320</td>
<td>0.039</td>
<td>0.282</td>
<td>-0.038</td>
<td>-0.006</td>
<td>-0.219</td>
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</tbody>
</table>
Figure S5.1. The results of a sensitivity test on the effect of mixotrophic growth. Modeled density was presented at 6-hour intervals. The red lines indicate the bloom density (1000 cells ml$^{-1}$).
Figure S5.2. The results of a sensitivity test on the effect of swimming speed. Modeled density was presented at 6-hour intervals. The red lines indicate the bloom density (1000 cells ml$^{-1}$).
Chapter 6. Conclusions
This dissertation discusses the effects of transport processes in phytoplankton dynamics and highlights their role, using the combination of data analysis, theoretical analysis, and numerical model simulations.

The relative importance of local processes and transport processes varies with timescales from hours to years. In general, the importance of transport processes tends to be equivalent to that of the local processes over the longer seasonal and annual timescales (Chapter 2). The steady state assumption for studying the variability in phytoplankton biomass is found to be valid only when the long-term timescales are considered.

Two original mathematical models are developed in this dissertation to theoretically examine the effects of transport processes on estuarine phytoplankton dynamics and HAB initiation, which can be applied to many other estuaries.

In Chapter 3, the simple yet inclusive mathematical model for estuarine phytoplankton dynamics under various environmental conditions is developed. This is a steady-state model that solves the phytoplankton biomass over long-term timescales, which is able to explicitly analyze the effect of transport processes on phytoplankton dynamics that is through various ways. Under the combined effect of light availability, nutrient availability, and flushing effect on phytoplankton, three patterns of the relationship between phytoplankton biomass and flushing time are revealed for the riverine-nutrient dominated estuaries. The flushing time associated with maximum biomass shifts with environmental conditions and ecophysiology of phytoplankton, and it, in general, is much shorter in Pattern-2 systems than Pattern-1 or Pattern-3 systems. While this model is derived for examining the effect of transport processes on variability in phytoplankton biomass, it can provide implications, from a theoretical
perspective, in other studies on various aspects of phytoplankton dynamics, such as the
effect of transport processes on phytoplankton assemblage or the phytoplankton biomass
decline in response to nutrient reduction management.

In Chapter 4, the mathematical model for HAB initiation in estuary-subestuary
systems is developed to examine how the differential flushing effect of transport
processes affects the spatial distribution of the density in two connected waterbodies.
Because the initiation of a HAB event can happen within several weeks that involves a
dramatic increase in HA density, this model considers the time derivative of HA density
(i.e., non-steady-state). Results suggest that HABs tend to first appear in locations with
relatively long residence time.

A numerical module in EFDC is developed for the HAB species - *Cochlodinium
polykrikoides* (Chapters 4 and 5), including mixotrophic growth, swimming behavior,
cyst germination, and grazing suppression. This HAB model is applied to *C.
polykrikoides* blooms in the lower James River, and confirmed that the Lafayette River, a
sub-tributary of the James River, is one originating location of the bloom because of its
relatively long residence time. Model results also suggest that the mixotrophic growth is
important to maintain a high growth of *C. polykrikoides* in this area.

Among those various physical factors, physical transport is one determinant factor
along with temperature to control the interannual variability in the timing of its initiation,
and the southerly wind, heavy rainfall, and spring tide are important environmental
conditions capable of interrupting, or even terminating, the initiation of *C. polykrikoides*
bloom in the James River. Contrary to the traditional thoughts, the analysis of
mechanisms of HAB initiation shows that rainfall or stratification may not be a necessary condition to trigger HABs.

The concept of transport rate is introduced and its computation method using numerical models is provided (Chapter 2). Complementary to the various concepts of transport time, transport rate can quantitatively describe the flushing effect of transport processes on phytoplankton dynamics at local and short-term scales, especially the “transport in” effect that the local phytoplankton biomass increases by receiving incoming flow with higher biomass. While the concept of transport rate is first proposed for phytoplankton dynamics, it can be widely used to describe the flushing effect of transport processes on the dynamics of other substances.

In addition, this dissertation introduces an open water chl-a method that can be used to estimate phytoplankton primary production using high-frequency chl-a data (Chapter 2), which is expected to be applied to other ecosystems. Although the estimation may have some biases, these biases are relatively small and systematical, and they do not prohibit the ecological interpretation that requires information on changes in phytoplankton primary production over long-term timescales.
Vita

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Born November 9, 1988 in Wuhu (Nanling County), Anhui, China. Graduated from Nanling No. 1 High School in 2006. Earned a B.S. in Geography from Nanjing University, Nanjing, Jiangsu, China in June 2010. Earned a M.S. in Physical Oceanography at the Virginia Institute of Marine Science, College of William & Mary in January 2013. After graduation from the M.S. program, worked as a research assistant at Sanya Institute of Deep-sea Science and Engineering, Chinese Academy of Sciences. Entered the Ph.D. program at the Virginia Institute of Marine Science, College of William & Mary in August 2014.