REVIEWS

Why are diverse relationships observed between phytoplankton biomass and transport time?

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Abstract

Transport time scales such as flushing time and residence time are often used to explain variability in phytoplankton biomass. In many cases, empirical data are consistent with a positive phytoplankton–transport time relationship (i.e., phytoplankton biomass increases as transport time increases). However, negative relationships, varying relationships, or no significant relationship may also be observed. We present a simple conceptual model, in both mathematical and graphical form, to help explain why phytoplankton may have a range of relationships with transport time, and we apply it to several real systems. The phytoplankton growth–loss balance determines whether phytoplankton biomass increases with, decreases with, or is insensitive to transport time. If algal growth is faster than loss (e.g., grazing, sedimentation), then phytoplankton biomass increases with increasing transport time. If loss is faster than growth, phytoplankton biomass decreases with increasing transport time. If growth and loss are approximately balanced, then phytoplankton biomass is relatively insensitive to transport time. In analyses of several systems, portions of an individual system, or time periods, apparent insensitivity of phytoplankton biomass to changes in transport time could arise due to the superposition of cases with different phytoplankton–transport time relationships. Thus, in order to understand or predict responses of phytoplankton biomass to changes in transport time, the relative rates of algal growth and loss must be known.

Aquatic scientists and resource managers commonly invoke time for transport through a surface water body to help explain variability in phytoplankton biomass, often seeking empirical relationships between phytoplankton and transport time scales such as flushing time and residence time to characterize that variability. A positive phytoplankton–transport time (P–T) relationship suggests that as transport time increases (or decreases), so does phytoplankton biomass or production. Observations consistent with a positive P–T relationship are frequently made in rivers and lakes (Søballe and Kimmel 1987; Reynolds 2000; Allan and Benke 2005), floodplains (Schemel et al. 2004; Ahearn et al. 2006), estuaries (Howarth et al. 2000; Jassby 2008), and lagoons (Torréton et al. 2007), and weak flushing (long transport time) has been identified as a condition favoring harmful algal blooms in aquatic systems across the globe (Paerl and Huisman 2008). High flow (short transport time) has thus been offered as an explanation for low phytoplankton biomass and resistance to eutrophication (Wetzel 2001; Caraco et al. 2006). Despite the prevalence of positive P–T relationships in nature, negative (Søballe and Bachmann 1984), spatially variable (Søballe and Bachmann 1984; Paerl et al. 2006), temporally variable (Alpine and Cloern 1992; Strayer et al. 2008), or non-monotonic (Walz and Welker 1998; Hein

et al. 2003) relationships are also observed within and across aquatic systems. In other cases, no significant relationship may be detected (Basu and Pick 1996).

Here we address the question: Why is this broad range of relationships observed between phytoplankton biomass and transport time? We present a simple conceptual model that includes parameters accounting for algal growth, loss, and advective transport in a generic aquatic system. Despite all of its simplifications and assumptions, the conceptual model offers an explanation of why diverse P–T relationships are observed within and across systems, demonstrating that the relationship is determined by the algal growth–loss balance. We further show how the framework presented extends previous conceptual models of phytoplankton regulation in surface waters.

Methods

Development of the conceptual model—The distribution of suspended algal biomass undergoing growth, loss, and transport in an idealized, advective, steady-state system can be described by

$$B(x) = B_{out} = B_{in}\ \exp\left(\frac{\mu_{growth} - \mu_{loss}}{u}x\right) \qquad (1)$$

B is algal biomass concentration (e.g., as μg chlorophyll a [Chl a] L^{-1} or cells L^{-1}), x is distance downstream from the inlet, B_{in} is algal biomass concentration entering the system at a defined upstream boundary ($x = 0$), μ_{growth} (d^{-1}) is the algal specific growth rate, μ_{loss} (d^{-1}) is the sum of specific loss rates due to biological (e.g., pelagic and benthic grazing, senescence, disease) and physical processes (e.g., sedimentation), and u is the characteristic velocity along the primary flow direction in dimensions of length/time. Here "loss" is meant to include only biomass removal processes operating between the upstream and downstream boundaries, not the loss of biomass from the system due to downstream advection. Equation 1 was derived from a time-varying one-dimensional partial differential equation (PDE) for streamwise advection and first-order growth and loss of phytoplankton.

The PDE on which Eq. 1 is based and its underlying assumptions (uniformity of all properties across the flow cross section, no longitudinal mixing, concentrations can vary in the streamwise direction) are consistent with the well-known "plug flow" model of chemical engineering (Himmelblau and Bischoff 1968; Coulson and Richardson 1971; Perry et al. 1984). To obtain Eq. 1, it was further assumed that at any point in space B does not vary in time (i.e., $\partial B/\partial t = 0$, "steady-state"), and that geometry, velocity, and growth–loss parameters are uniform and constant. Constancy of u implies unidirectional flow. These assumptions may be best satisfied in shallow, narrow, rapidly flowing channel environments. The resulting relationship shown in Eq. 1 is identical to steady-state plug flow relationships derived for chemical reactors (Himmelblau and Bischoff 1968) and similar to expressions previously used in aquatic ecology to describe relationships between phytoplankton biomass concentration, benthic grazing and settling (Coughlan 1969; Søballe and Bach-

mann 1984), and algal growth (de Ruyter van Steveninck et al. 1992; Walz and Welker 1998; Reynolds 2000).

Physical and biological process rates were converted into time scales, which places them in a single, comparable currency. The relationship described by Eq. 1 can be represented as a function of three key time scales: τ_{tran} (the time scale for transport of water and algae through the system), τ_{growth} (the time scale for algal growth), and τ_{loss} (the time scale for combined algal losses). Such time scales represent the inverses of rates, are positive numbers, and are often expressed in units of days. For the idealized plug flow system considered here, $\tau_{tran} = x/u$, the time for a water parcel to travel through a domain of length x. τ_{loss} is the reciprocal of the sum of specific loss rates (μ_{loss}). Here, we define μ_{loss} to include, depending on data availability, the zooplankton grazing rate μ_{zp} (d^{-1}), the depth-averaged effect of grazing by benthic filter feeders expressed as benthic grazing rate BG ($m^3\ m^{-2}\ d^{-1}$) divided by water column height H (m), and the algal sedimentation rate expressed as sinking speed W_s ($m\ d^{-1}$) divided by H. Other loss processes such as senescence and death by parasitism and disease (Suttle 2005; Kagami et al. 2007) could also be incorporated into μ_{loss}. We estimate τ_{growth} as the reciprocal of μ_{growth}, taken as a depth-averaged net growth rate (i.e., proportional to photosynthesis minus respiration); it would, however, be acceptable to use gross growth rate and incorporate respiration losses into τ_{loss}, especially if net growth were negative. Substituting the time scales for transport, growth, and loss into Eq. 1, the conceptual model equation expressed in terms of our three time scales is obtained:

$$B_{out} = B_{in}\ \exp\left(\frac{\tau_{tran}}{\tau_{growth}} - \frac{\tau_{tran}}{\tau_{loss}}\right) \qquad (2)$$

Transformation of Eq. 1 (a function of x) to the equivalent form expressed in terms of time scales (Eq. 2) implicitly converts the relationship from an Eulerian ("field description") perspective to a Lagrangian ("particle-following") perspective (cf. Kundu 1990; Munson et al. 1990). The role of τ_{tran} here is to characterize the time for a water parcel to travel through a defined region (i.e., a "transit time"), thus relating the time phytoplankton within the parcel are exposed to that region's growth–loss conditions. The simple expression $\tau_{tran} = x/u$ (or equivalently volume/flow) may represent well the time of transit for strongly advective systems with unidirectional flow (e.g., rivers), but may not accurately characterize transit time in other (e.g., horizontally inhomogeneous, geometrically complex, strongly tidal, or dispersive) systems that deviate substantially from the plug flow model assumptions. A true time of transit for water parcels from a specified inlet to a specified outlet in such systems may not be easily estimated.

The shorter the time scale, the faster and therefore more dominant the process. Ratios of time scales represent the relative speed or dominance of two processes. For example, the dimensionless ratio $\tau_{loss}^* = \tau_{loss} : \tau_{growth}$ is less than unity when the time scale for losses is shorter than the time scale
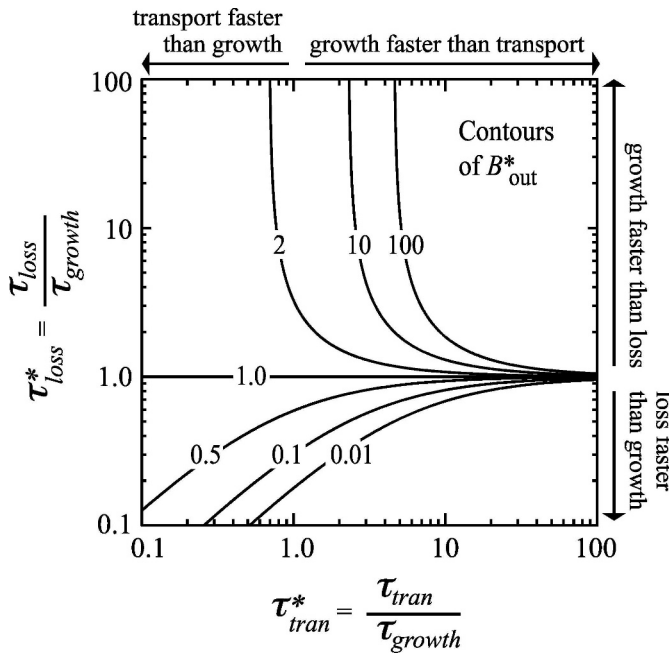
Fig. 1. Contours of B^*_{out}, the ratio of downstream (outgoing) to upstream (incoming) algal biomass, as a function of τ^*_{loss} (time scale for algal loss normalized by the time scale for algal growth) and τ^*_{tran} (time scale for transport normalized by the time scale for algal growth).

for growth. In other words, losses are collectively more rapid than growth. τ^*_{loss} is greater than unity when the time scale for losses is longer than the time scale for growth, i.e., when growth is more rapid than losses. Similarly, the ratio $\tau^*_{tran} = \tau_{tran} : \tau_{growth}$ is less than unity when transport through the system is faster than growth, but greater than unity when growth is faster than transport.

Combining many variables into dimensionless ratios can help one express a mathematical relationship in terms of fewer variables (Munson et al. 1990). If Eq. 2 is divided by B_{in} and the right-hand side is expressed in terms of the two time scale ratios above, a dimensionless expression for algal biomass in our generic system is obtained:

$$B^*_{out} = \frac{B_{out}}{B_{in}} = \exp\left(\left[1 - \frac{1}{\tau^*_{loss}}\right]\tau^*_{tran}\right) \qquad (3)$$

Equation 3 describes B^*_{out}, a nondimensional number representing the algal biomass concentration at some downstream domain boundary or outlet (location x) normalized by the biomass concentration at the upstream boundary or inlet ($x = 0$). From a Lagrangian perspective, B^*_{out} represents the relative change in biomass concentration within a water parcel as it travels through the domain over time τ_{tran}. From an Eulerian perspective, B^*_{out} represents the steady-state ratio of biomass export from the domain to biomass import to the domain. If $B^*_{out} = 1$, the biomass concentrations at the inlet and outlet are the same; if $B^*_{out} < 1$, then biomass at the outlet is less than biomass at the inlet; and if $B^*_{out} > 1$, biomass at the outlet is greater than biomass at the inlet.

In Fig. 1, we present contours of B^*_{out} calculated from Eq. 3 as a function of τ^*_{loss} and τ^*_{tran}, both over the range 0.1–100. This range corresponds to reasonable ranges of τ_{tran}, τ_{loss}, and τ_{growth} for aquatic systems (Strayer et al. 1999; see also Web Appendix 1, www.aslo.org/lo/toc/vol_54/issue_1/0381a1.pdf). The sensitivity of algal biomass to transport time is revealed by whether contours are crossed as the plot is traversed horizontally (i.e., as dimensionless transport time changes).

Interpretation of the conceptual model—Examination of the dimensionless expression above (Eq. 3) and its graphical representation in Fig. 1 reveals a range of relationships between algal growth, loss, transport, and biomass. If $\tau^*_{loss} = 1$ (growth and loss are equally fast), then the expression within the parentheses in Eq. 3 is zero, making $B^*_{out} = 1$, regardless of the value of τ^*_{tran}. In other words, if losses balance growth, algal biomass does not change as it is transported through the system and transport time does not affect algal biomass concentration. This regime is represented by the horizontal $B^*_{out} = 1$ contour located at $\tau^*_{loss} = 1$ in Fig. 1. In this part of the plot, B^*_{out} contours are not crossed as the plot is traversed horizontally; therefore, B^*_{out} does not change as dimensionless transport time, τ^*_{tran}, changes. Thus, if growth and losses are equal, then there is no relationship between phytoplankton biomass and transport time.

If $\tau^*_{loss} > 1$ (growth dominates losses), then the expression within the parentheses in Eq. 3 is positive, making $B^*_{out} > 1$; in this case, if τ^*_{tran} increases, then B^*_{out} increases. Thus, biomass is enhanced during travel through the system, and downstream biomass increases with transport time. This regime is represented by the portion of the plot above the horizontal $\tau^*_{loss} = 1$ line in Fig. 1. Here, all contours of B^*_{out} are greater than 1, and increasing contours are crossed as the plot is traversed toward the right, in the direction of increasing τ^*_{tran}. Therefore, if growth is faster than losses, then an increased transport time will amplify net biomass growth. This case represents the positive P–T relationship.

When losses dominate growth ($\tau^*_{loss} < 1$), then the expression within the parentheses in Eq. 3 is negative; B^*_{out} is less than unity and decreases if τ^*_{tran} increases. Biomass is thus diminished during transit and downstream biomass decreases with increasing transport time. This regime corresponds to the portion of the plot below the horizontal $\tau^*_{loss} = 1$ line, where all contours of B^*_{out} are less than 1. Decreasing contour values are crossed as the plot is traversed toward the right. Therefore, if losses are collectively faster than growth, then an increased transport time amplifies net biomass loss. This case represents the negative P–T relationship.

It is also evident from Eq. 3 that as τ^*_{tran} approaches zero, the term in parentheses approaches zero and B^*_{out} approaches unity. Thus, as transport becomes very fast, algal biomass concentration within a water parcel barely changes as it moves through the system. This case corresponds to the far left side of Fig. 1, where τ^*_{tran} is small and, regardless of τ^*_{loss}, B^*_{out} contours are not significantly different from 1. This fast transport case

Table 1.   Time scales, ratios, and observed and predicted B_{out}^* for nine cases in six aquatic systems. τ_{loss} is the time scale for algal loss; τ_{tran} is the transport time scale; and τ_{growth} is the time scale for algal growth. τ_{loss}^* and τ_{tran}^* are the dimensionless loss and transport time scales, each normalized by τ_{growth}. B_{out}^* is the ratio of outgoing (downstream) algal biomass to incoming (upstream) algal biomass; observed B_{out}^* is based on measurements of streamwise biomass gradients, and predicted B_{out}^* is calculated using Eq. 3. Calculation details and data sources are provided in Web Appendix 1.

System	τ_{loss} (d)	τ_{tran} (d)	τ_{growth} (d)	τ_{loss}^*	τ_{tran}^*	Observed B_{out}^*	Predicted B_{out}^*
Merced River	0.97	1.2	1.1	0.92	1.2	1.1	0.90
Krumme Spree	1.6	1.1	2.2	0.75	0.52	0.32	0.84
Rhine, May 1990	18	1.0	2.6	6.9	0.38	2	1.4
Rhine, Sep 1990	5.3	1.3	2.2	2.4	0.59	2	1.4
Hudson, 1991	50	35	24	2.1	1.5	4.7	2.1
Hudson, 1993	3	31	5	0.60	6.2	1.3	0.02
Mildred Island	4.2	4.8	3.1	1.4	1.5	4.4	1.5
Potomac, Sep 1979	16	3	7.1	2.3	0.42	1.1	1.3
Potomac, Jul 1981	3	3	7.1	0.42	0.42	0.72	0.56

signifies the decreasing importance of growth and loss processes as transport becomes more rapid, i.e., the faster algal biomass is transported through an environment, the less opportunity the biomass has to be modified by growth or loss.

To summarize, the primary lessons from the idealized conceptual model (Eq. 3; Fig. 1) are as follows: (1) The relative rates of growth and loss, not transport time, determine the sign of phytoplankton biomass change (i.e., increase or decrease) within an aquatic system. (2) Transport time modulates the relative magnitude of biomass increase or decrease during transport over a given distance x; therefore, an increased transport time can enhance accumulation or depletion of algal biomass, depending on the growth–loss balance. (3) If growth is balanced by losses, then transport time has no effect on biomass. (4) Through its modulating role, transport time is related to downstream algal biomass concentration relative to the upstream concentration (i.e., $B_{out} : B_{in}$), not to the absolute magnitude of downstream biomass (B_{out}).

Results

The P–T relationship varies between systems—From the conceptual model and lessons discussed above, it is evident that there are three possible relationships between phytoplankton biomass and transport time: positive, negative, and none (i.e., zero slope in a regression of biomass against transport time). The sign of the relationship depends on the growth–loss balance, as represented by τ_{loss}^*. Real aquatic systems display the full range of τ_{loss}^* and thus of P–T relationships (*see* Table 1). For example, values of τ_{loss}^* for the upper Rhine in May (weak benthic grazing) and September (stronger benthic grazing) 1990 are estimated to have been 7 and 2, respectively; this scaling places that system in the upper portion of Fig. 1, where an increase in transport time causes an increase in downstream biomass (*see* Web Appendix 1 for details and data sources for all real-system calculations). τ_{loss}^* for the Merced River, California, during summer 2003 is estimated to have been about 0.9, which places that system near the horizontal $\tau_{loss}^* = 1$ line in Fig. 1, where algal growth and loss are roughly in balance and, consequently, phytoplankton biomass is

relatively insensitive to changes in transport time. In 1981, after dense colonization by the freshwater clam *Corbicula fluminea*, τ_{loss}^* in the freshwater tidal Potomac River is estimated to have been 0.4, placing that system in the lower portion of Fig. 1, where an increase in transport time causes a decrease in downstream biomass and B_{out}^*. This range of τ_{loss}^* observed in nature suggests that a consistent P–T relationship (or even sign) should not be expected among systems.

The possibility of different, even opposite, P–T relationships can explain why in some cases no relationship is detected. The conceptual model suggests that when searching for a single P–T relationship among systems, one must first consider whether those systems may be growth-dominated ($\tau_{loss}^* > 1$) or loss-dominated ($\tau_{loss}^* < 1$). If the growth–loss balance is not considered, then multiple, superimposed P–T relationships may be collectively disguised as ''no relationship.'' For example, Basu and Pick (1996; *see* their table 1) surveyed phytoplankton biomass (as Chl a), total zooplankton biomass (TZ), total phosphorus (TP), total nitrogen (TN), and transport time (as ''age'') in an extensive study of 31 Canadian rivers (the ''age'' of a water parcel is the time that has elapsed since it entered the water body; Bolin and Rodhe 1973; Zimmerman 1976). Basu and Pick (1996) concluded that there was no statistically significant relationship between algal biomass and transport time ($r^2 = 0.03$; *see* Fig. 2A). If their data are subdivided based on possible $\tau_{loss}^* < 1$, $\tau_{loss}^* > 1$, and $\tau_{loss}^* = 1$ regimes, significant relationships appear.

We plotted Chl a vs. age for the subset of Basu and Pick's (1996) rivers most likely to be loss-dominated, i.e., rivers with the highest reported TZ (TZ > 9 μg L^{-1}). Zooplankton grazing rate is proportional to zooplankton biomass (Cloern 2007); therefore, of the total data set, these six rivers appear the most likely, based on the available data, to have losses that dominate growth ($\tau_{loss}^* < 1$). A significant negative relationship exists between Chl a and age for these cases, consistent with the conceptual model for $\tau_{loss}^* < 1$ (Fig. 2B; $r^2 = 0.69$, $p < .05$, $n = 6$; regression performed on log-transformed data). The TZ threshold of 9 μg L^{-1} is used here because it maximizes the Chl a–age correlation for ''high''-TZ systems and is statistically significant. Negative relationships were evident with other
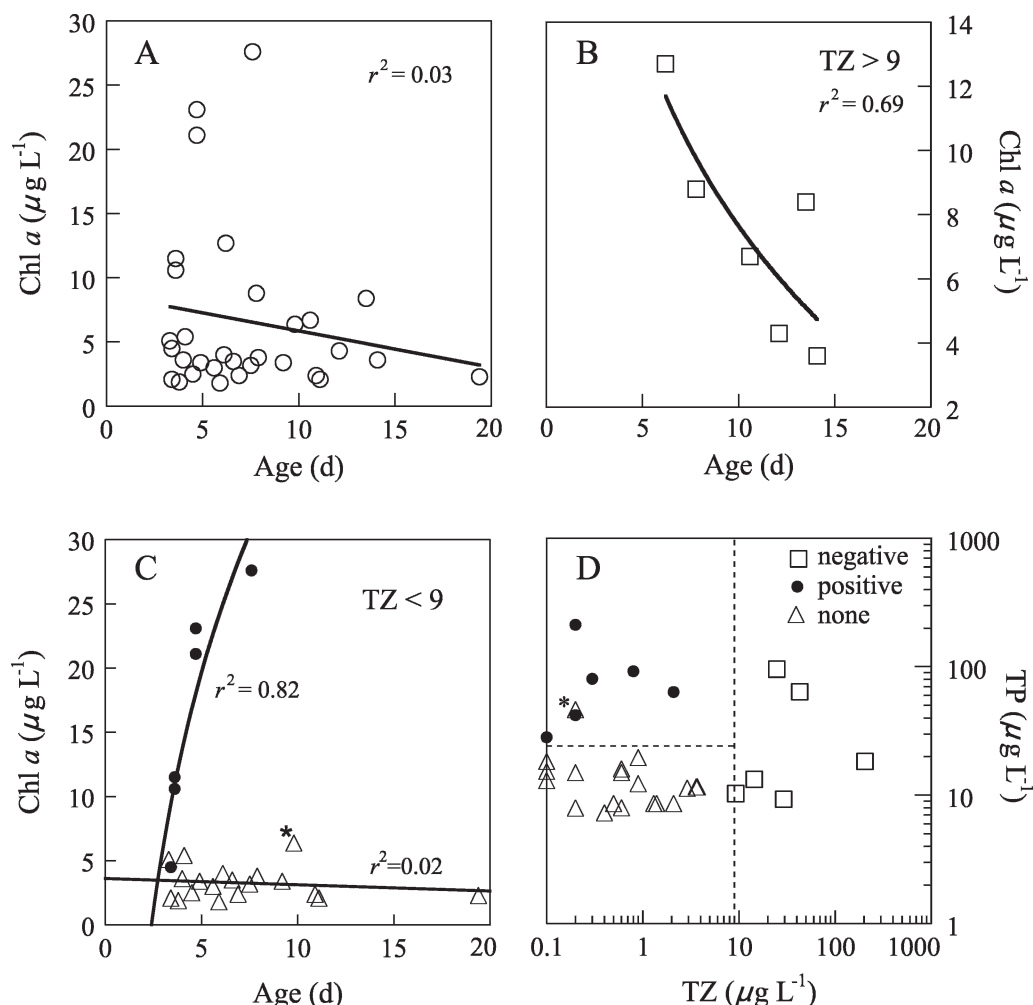
Fig. 2. Data from 31 Canadian rivers previously published by Basu and Pick (1996; *see* their table 1). Chlorophyll *a* vs. water age for (A) all 31 rivers, with no significant relationship between Chl *a* and age, (B) the subset of rivers with total zooplankton biomass (TZ) above 9 μg L^{-1} and with a significant negative relationship between Chl *a* and age, and (C) the subset of rivers with TZ below 9 μg L^{-1} and with two evident relationships: a positive Chl *a*–age relationship (filled circles) and a level response of Chl *a* to age (open triangles). In (D), total phosphorus (TP) vs. TZ for all 31 rivers with symbols coded for positive, negative, and no relationship between Chl *a* and age; symbols are consistent with (B) and (C). *Δ indicates the Grand River.

TZ thresholds, but the variability accounted for by the regression decreased substantially with lower TZ cutoffs (r^2 = 0.44 and 0.41 for cutoff TZ values of 2 and 3 μg L^{-1}, respectively). Our interpretation is that as the "high"-TZ subset of rivers is restricted to higher zooplankton biomass, it becomes more distinctly loss-dominated (i.e., τ^*_{loss} becomes smaller), displaying a stronger negative P–T relationship.

For the remainder of the rivers (those with TZ < 9 μg L^{-1}), a plot of Chl *a* vs. age reveals two more distinct relationships. Basu and Pick (1996) showed that Chl *a* was significantly correlated with TP (R^2 = 0.76, p < 0.001) across their entire data set and argued, based on TN : TP ratios, that P must be the limiting nutrient. We therefore split this subset of rivers using the guideline of 25 μg L^{-1} suggested by Dodds et al. (1998) as the oligotrophic–mesotrophic TP boundary for streams. We found that a significant positive Chl *a*–age relationship exists for all but one of the rivers in the low-TZ subset with TP greater than

25 μg L^{-1} (Fig. 2C, filled circles; r^2 = 0.82, p < 0.05, n = 6; regression performed on log-transformed data). It appears likely that phytoplankton in these rivers with high TP and low TZ were not significantly nutrient-limited and thus had large growth rates and values of τ^*_{loss} greater than 1. The positive Chl *a*–age relationship for these six rivers supports this idea and is consistent with the conceptual model for τ^*_{loss} > 1. The single river with high TP and low TZ that deviated from the positive P–T relationship (the Grand River, denoted by *Δ in Fig. 2C,D) has one of the highest biodiversities of freshwater bivalves in Ontario (Metcalfe-Smith et al. 2000). Based on the data available, estimation of benthic grazing losses for this river was not possible. However, given the much lower Chl *a* measured for this river relative to that predicted from the positive empirical P–T relationship in Fig. 2C and the transport time provided by Basu and Pick (1996), we hypothesize that some significant loss term not accounted for here (e.g., benthic grazing) is responsible for the Grand River's

deviation from the relationship describing the other rivers with high TP and low TZ.

Chl *a* in the remainder of the low-TZ rivers showed no sensitivity to age ($r^2 = 0.02$; Fig. 2C, triangles). Based on the data available, we could not estimate τ_{loss} or τ_{growth} for this or the other subsets of the Basu and Pick (1996) data set. However, given that neither TZ nor TP were particularly high in this subset (except for the Grand River, discussed above) and that Chl *a* had no sensitivity to age, we hypothesize that for these rivers growth and losses were approximately balanced ($\tau^*_{loss} \approx 1$). Therefore, although the Chl *a*–age relationship for this subset is not statistically significant, it is nonetheless meaningful, as we suggest that it arises for a mechanistically understandable reason: growth of algal biomass approximately equaled losses within these rivers.

Figure 2D summarizes graphically how the Chl *a*–age relationship for Basu and Pick's (1996) 31 rivers is tied to TZ (an apparent surrogate for algal loss) and TP (an apparent surrogate for algal growth). For 30 out of 31 rivers, TZ and TP provide delineations between regimes for which Chl *a* increases with, decreases with, and has no sensitivity to age. One cannot expect TZ and TP to delineate these regimes for all aquatic systems, because in other systems other factors may limit or suppress algal growth rate (e.g., other nutrients, turbidity) or dominate losses (e.g., benthic grazing, sedimentation). However, we do expect consideration of the growth–loss balance to help explain the relationship—or relationships—between phytoplankton biomass and transport time for other aquatic systems.

Equations 1–3 suggest that it is not the absolute magnitude of downstream algal biomass, but rather that magnitude normalized by an upstream biomass, that is related to growth, loss, and transport time. Therefore, according to the conceptual model, measurement of the streamwise biomass gradient is required if a relationship is sought between algal biomass and transport time. However, despite the lack of chlorophyll gradient information, the Basu and Pick (1996) data appear to represent strong relationships between un-normalized biomass (B_{out}) and transport time. We hypothesize that the applicability of the conceptual model to un-normalized biomass stems from Basu and Pick's (1996) use of water "age" for transport time; age was calculated based on the watershed area and represents the entire time the water has been in the river system. Suspended algal biomass is generally small at the source of a river (Hilton et al. 2006), so upstream biomass concentration (B_{in}) may not have varied significantly between the rivers studied. We would not expect this situation to necessarily apply in other systems, whose incoming concentrations could vary significantly.

The P–T relationship varies temporally within systems— Just as the growth–loss balance (and P–T relationship) may vary between aquatic systems, that balance can also change over time within an individual system. For example, in the South San Francisco Bay (Thompson et al. 2008) and the Moselle River (Descy et al. 2003), benthic grazing rates have been observed to change significantly over seasonal

scales, potentially causing seasonal shifts between $\tau^*_{loss} < 1$ and $\tau^*_{loss} > 1$ states. Seasonal shifts in τ^*_{loss} can also be driven by changes in solar insolation and nutrient availability. Long-term state changes in algal loss rates and thus τ^*_{loss} may result from invasions by nonindigenous species. For example, we estimate that increased densities of the freshwater clam *C. fluminea* in the Potomac caused a switch from a growth-dominated $\tau^*_{loss} = 2.3$ for September 1979 to a loss-dominated $\tau^*_{loss} = 0.42$ in July 1981 (*see* Table 1 and Web Appendix 1 for calculation details and data sources). Alpine and Cloern (1992) recognized that in northern San Francisco Bay there was one negative Chl *a*–flow relationship (analogous to a positive P–T relationship) when grazers were scarce, but a different regime, characterized by consistently low Chl *a*, following the invasion of the clam *Corbula amurensis*. Similarly, Strayer et al. (2008) observed a shift in the slope of the Hudson's chlorophyll–flow relationship after the zebra mussel invaded; extensive study of this estuary has shown that variations in loss terms might alter the relationship between phytoplankton and flow or transport time (Caraco et al. 2006; Cole and Caraco 2006; Strayer et al. 2008). Thus, although it may be possible for some systems to predominantly inhabit one portion of Fig. 1, thus displaying a single persistent relationship between phytoplankton biomass concentration and transport time, others may shift between the upper, middle or lower portions, thereby potentially switching between regimes with different P–T relationships. For an individual system that shifts between loss-dominated, growth-dominated, or balanced regimes, the search for a single P–T relationship could be confounded by the existence of two or three relationships masquerading collectively as "no relationship."

Can the conceptual model equation predict algal biomass?—Estimating B^*_{out} may be useful for projecting the possible effects of changes in ecosystem parameters controlling algal growth, loss, or transport. To explore the quantitative applicability of the conceptual model equation for estimating biomass in some real systems, we used Eq. 3 to calculate predicted B^*_{out} (based on process time scales estimated from published measurements or models) for comparison with observed B^*_{out} (calculated from observed streamwise algal biomass gradients; *see* Web Appendix 1 for calculation details and data sources and Table 1 for calculation summary). In many cases, predicted B^*_{out} corresponded well with observed B^*_{out} (i.e., within a factor of 2). This was the case for the Rhine in May 1990 and September 1990, the Merced River in summer 2003, and the Potomac in September 1979 and July 1981. We emphasize that because the conceptual model describes relative change in algal biomass during transit, observation of the biomass gradient along the primary flow path is required in order to strictly compare conceptual model biomass predictions with real-system measurements, as we did here.

Although we did not expect the conceptual model to quantitatively predict algal biomass in surface water systems severely violating the basic underlying assumptions (e.g., plug flow, constancy and longitudinal uniformity of

physical and biological conditions), we tested it in such cases to reveal sensitivity of the conceptual model to the assumptions. Two such cases are the summertime tidal freshwater Hudson and the freshwater tidal lake Mildred Island, California. Compared to the Rhine, Merced, and Potomac, correspondence between observed and predicted B_{out}^* was not as good for the Hudson pre–zebra mussel and post–zebra mussel, or for Mildred Island (Table 1).

We believe the lack of coherence between predicted and observed B_{out}^* for these two systems stems from violations of several of the conceptual model's underlying assumptions. Longitudinal tidal dispersion is significant at Mildred Island due to the combination of strong tidal currents and complex geometry (Lucas et al. 2002), thus violating a key plug flow assumption. Given the Hudson's large tidal excursion and large ratio of tidal to river-associated velocity (Geyer and Chant 2006), it is possible that significant tidally generated longitudinal mixing occurred there as well. These systems also violated the plug flow assumption of cross-sectional homogeneity, due to diel density stratification (Baek 2006; Lucas et al. 2006) and lateral hydrodynamic variability (Monsen et al. 2002) in Mildred Island and, in the Hudson, lateral bathymetric heterogeneity, which may be related to cross-stream variations in algal growth (Cole et al. 1992) and benthic grazing rates (Strayer et al. 1996). Oscillatory tidal currents (Geyer and Chant 2006; Lucas et al. 2006), strong longitudinal growth–loss gradients (Cole et al. 1992; Strayer et al. 1996; Lopez et al. 2006), and tributary inlets (Caraco et al. 1997) in these systems underlay divergence from our other assumptions, namely constancy and longitudinal uniformity of physical and biological parameters. Moreover, true transit times were not available for the strongly tidal Hudson or Mildred Island, so we used flushing times (*see* Web Appendix 1), which are intended as integrative measures of an embayment's general exchange characteristics (Monsen et al. 2002) but which may not effectively characterize transit time through regions with complex, oscillatory, tidal flows.

The Krumme Spree is one more system for which the conceptual model did not predict algal biomass well. We hypothesize that errors for this system are related to spatial, temporal, and methodological mismatches between separate, previously published data sets that were not collected for this purpose, but which we patched together to represent this system (*see* Web Appendix 1). Aside from Mildred Island, whose prediction errors likely stem from assumption violations (*see* above), the systems with the most internally consistent data sets (i.e., Potomac, Rhine, Merced) represented the greatest model–measurement coherence.

Although we did not find adequate data to apply the conceptual model to a lake or reservoir, we do expect it to apply to these systems if underlying assumptions are reasonably met. The lessons discussed herein are in fact consistent with observations in lakes and reservoirs where the increase or decrease of phytoplankton biomass with transport time appears related to the dominance of growth or loss terms, respectively (Søballe and Bachmann 1984; Walz and Welker 1998).
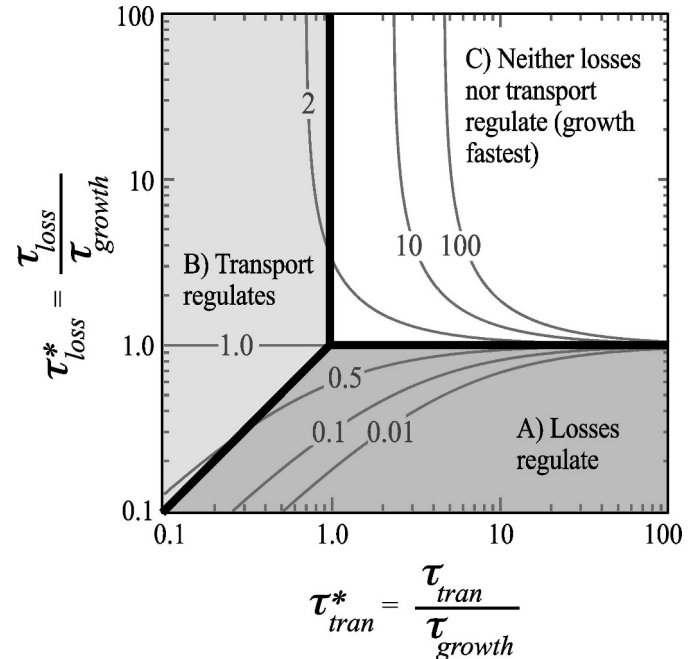

Fig. 3. Reprise of Fig. 1 with superimposed shaded areas describing regimes in the τ_{loss}^*–τ_{tran}^* space where: (A) losses control phytoplankton biomass, which is potentially very low due to depletion during transit (darkest shading), (B) transport controls phytoplankton biomass and biomass does not change significantly while inside the system boundaries (moderate shading), and (C) neither losses nor transport control phytoplankton biomass, which is potentially very large because growth is the fastest process (lightest shading). As in Fig. 1, contours represent B_{out}^*, the ratio of downstream to upstream algal biomass. This nondimensional plot extends the schematic of Strayer et al. (1999).

Discussion

Control of phytoplankton biomass—Up to this point, the conceptual model plot (Fig. 1) has been used to elucidate the *sensitivity* of phytoplankton biomass to changes in transport time, with sensitivity indicated by whether (and which) contours of B_{out}^* are crossed when moving horizontally across the plot. The conceptual model plot can also help clarify regimes of *control*, if a controlling process is defined as the fastest process operating on the phytoplankton.

Time scales (or, inversely, process rates) have previously been used to elucidate control of phytoplankton dynamics in aquatic systems. For example, the growth–loss relationship, sometimes expressed as a "filtration pressure" (Smaal and Prins 1993) or as a ratio of growth and grazing rates or time scales, has been emphasized as an important parameter in determining whether the filter feeding benthos can control the phytoplankton (Officer et al. 1982; Koseff et al. 1993; Cahoon and Owen 1996). The relative time scales for transport and grazing have also been cited as important in determining benthos control regimes (Hily 1991; Dame 1996; Strayer et al. 1999).

Strayer et al. (1999, *see* their fig. 1) described three domains of phytoplankton biomass control in a two-dimensional parameter space defined by hydrologic resi-

dence time (an example of a transport time) on the horizontal axis and bivalve clearance time (a potentially major component of τ_{loss}) on the vertical axis. Those authors acknowledged that the boundaries between domains will vary, depending on phytoplankton growth rates. With a setup similar to that of Strayer et al. (1999) but with transport and loss time scales normalized by the growth time scale, our conceptual model plot shows that those control domain boundaries are defined by $\tau^*_{loss} = 1$, $\tau^*_{tran} = 1$, and $\tau^*_{loss} = \tau^*_{tran}$ (Fig. 3). The distribution of B^*_{out}, our metric indicating the ultimate effect of the combined processes, is consistent with the domains described by Strayer et al. (1999). In the lower Region A, τ_{loss} is less than τ_{tran} and τ_{growth}, and losses are therefore dominant in regulating phytoplankton; B^*_{out} is low due to net depletion of algal biomass during transport through the system. In the left Region B, τ_{tran} is less than τ_{loss} and τ_{growth}, and transport therefore dominates in regulating phytoplankton; B^*_{out} is not extremely different from 1 due to the rapid transport and lack of opportunity for phytoplankton to react substantially to growth or loss. In the upper right Region C, τ_{growth} is less than τ_{loss} and τ_{tran}, and growth is therefore the fastest process; B^*_{out} is potentially large due to positive net accumulation of algal biomass during transport through the system. Thus, by incorporating algal growth and potentially any loss term, the time scale ratios and metric quantity B^*_{out} used in this paper help to extend and generalize the conceptual model of phytoplankton regulation presented by Strayer et al. (1999).

Extending the conceptual model—It has been shown that different phytoplankton taxonomic groups (e.g., cyanobacteria, diatoms) may respond differently to changes in transport time (Paerl et al. 2006). Thus, in addition to explaining variability in total phytoplankton biomass, the conceptual model presented here may also be applied to explore variability among groups with different growth rates, sedimentation rates, and susceptibilities to grazing. Equations 1–3 could also be applied to other reactive, waterborne constituents (e.g., nutrients, contaminants, sediment, or zooplankton) if the major growth and loss processes are estimable in terms of first-order process rates. The conceptual model may serve as a useful tool for exploring phytoplankton dynamics in offshore, near-surface environments in which an advected water parcel may be characterized by limited exchange with adjacent parcels, be tracked through space as a Lagrangian particle, and remain vertically and horizontally well mixed. The same general set of processes affect phytoplankton biomass change in the well-mixed surface layers of deeper marine environments as in the shallower inland environments discussed herein, i.e., growth and loss processes, with benthic grazing and sedimentation losses to the bed for shallower systems replaced by sinking losses through the base of the mixed layer for deeper oceanic systems. Further, the conceptual model provides a basic framework for designing field studies that characterize the full set of processes (growth, loss, and transport) and appropriate measures of system response (i.e., streamwise biomass

gradients) for understanding variability in water quality or suspended biota.

As noted above, fundamental assumptions of the simple conceptual model included invariance of physical and biological parameters in space and time. For a real aquatic system characterized by significant longitudinal or temporal variability, the conceptual model may be applied separately to portions of the system or time periods with distinct and relatively uniform physical–biological properties. For example, if measurements suggested that algal growth rate within a system differed substantially between early and late bloom periods due to self-shading or the development of nutrient limitation, then each of those periods could be treated separately as pseudo–steady state periods. In systems that experience strong seasonal (or spatial) shifts in the abundance of grazers, low-grazing and high-grazing periods (or regions) could be treated separately. Errors associated with dilution or biomass addition by tributaries could be avoided by applying the conceptual model individually to reaches separated by tributaries.

If data were available to characterize spatial variability of algal growth and/or loss rates as integrable (e.g., linear) functions of downstream distance x, then a more general form of the conceptual model equation would be

$$B^*_{out} = \exp\left([1/u] \int_0^x \left[\mu_{growth}(\xi) - \mu_{loss}(\xi) \right] d\xi \right)$$

where all assumptions are as before except for the permitted longitudinal variability of growth and loss (ξ is a dummy variable of integration). This form could be applied, for example, in systems where streamwise variations in grazing rates are associated with spatial gradients in substrate for epibenthic or encrusting benthic grazers (e.g., due to the presence of manmade structures). For cases where longitudinal dispersion is significant, it may be possible to implement established analytical expressions that account for that process (Himmelblau and Bischoff 1968). Reynolds and Descy (1996) described equations similar to our Eq. 1 that add the effect of long transport time "dead zones" on downstream algal concentrations within rivers.

In conclusion, we have presented a conceptual model (Eqs. 1–3; Fig. 1) of phytoplankton biomass as it advects through an aquatic system with interior algal biomass growth and loss processes. Albeit highly idealized, the conceptual model helps clarify and delineate the range of possible relationships between phytoplankton biomass and transport time. Transport time does not determine whether phytoplankton biomass increases or decreases—the growth–loss balance (represented by τ^*_{loss}) does. If growth is faster than loss, then phytoplankton biomass increases with transport time. If loss is faster than growth, then phytoplankton biomass decreases as transport time increases. As growth and loss rates approach each other, phytoplankton biomass sensitivity to transport time diminishes. τ^*_{loss} may vary between aquatic systems and spatially or temporally within individual systems. For that reason, in analyses of several systems, portions of an

individual system, or time periods, phytoplankton biomass may appear insensitive to changes in transport time (e.g., in a linear regression) due to the superposition of cases with very different τ^*_{loss} ratios and thus P–T relationships. In order to understand or project how phytoplankton in an aquatic system will respond to a change in flow or flushing, one needs to know whether the difference between growth and loss is positive, negative, or about zero.

Numerous physical, biological, and geochemical characteristics of surface water systems may covary with transport time, especially if transport time is directly governed by freshwater flow; examples of such characteristics include density stratification and vertical turbulent mixing, nutrient loading, water temperature, turbidity, salinity, and grazing pressure (Kimmerer 2002; Paerl et al. 2006; Strayer et al. 2008). Covariation of these attributes with transport time could confound the search for an empirical P–T relationship because changes in these processes could also directly drive changes in the phytoplankton. Because it incorporates time scales for growth and loss, the conceptual model presented herein allows one to account for concomitant changes in many of those covarying system attributes that may influence algal growth and loss rates, as long as their rates are known and the fundamental assumptions underlying the model are not violated.

If the model's underlying assumptions are reasonably met (e.g., negligible longitudinal mixing and cross-sectional variability) and the transport time scale is appropriately defined, then we would expect the conceptual model to predict algal biomass (B^*_{out}) reasonably well, even within tidal systems. For example, the good predictive performance of the conceptual model for the Potomac relative to the Hudson, another tidal river where the model was less predictive, could be related to the relatively weaker tides in the Potomac (as suggested by a smaller tidal excursion; Schaffranek 1987) and potentially weaker longitudinal dispersion and less severe violation of the model's assumptions. Even if violations of assumptions preclude quantitative use of the conceptual model for algal biomass prediction, an estimate of the growth–loss balance (τ^*_{loss}) is nonetheless informative for any aquatic environment, as it provides an index to help intuit whether phytoplankton biomass within a defined region will tend to increase or decrease with transport time. Regardless of the challenges in applying the conceptual model for quantitative prediction, the primary lesson from the conceptual model applies: there is a range of possible relationships between phytoplankton biomass and transport time, and the nature of the relationship is governed by the algal growth–loss balance.

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