

# Changing restoration rules: Exotic bivalves interact with residence time and depth to control phytoplankton productivity

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**Abstract.** Non-native species are a prevalent ecosystem stressor that can interact with other stressors to confound resource management and restoration. We examine how interactions between physical habitat attributes and a particular category of non-native species (invasive bivalves) influence primary production in aquatic ecosystems. Using mathematical models, we show how intuitive relationships between phytoplankton productivity and controllable physical factors (water depth, hydraulic transport time) that hold in the absence of bivalves can be complicated—and even reversed—by rapid bivalve grazing. In light-limited environments without bivalves, shallow, hydrodynamically “slow” habitats should generally have greater phytoplankton biomass and productivity than deeper, “faster” habitats. But shallower, slower environments can be less productive than deeper, faster ones if benthic grazing is strong. Moreover, shallower and slower waters exhibit a particularly broad range of possible productivity outcomes that can depend on whether bivalves are present. Since it is difficult to predict the response of non-native bivalves to habitat restoration, outcomes for new shallow, slow environments can be highly uncertain. Habitat depth and transport time should therefore not be used as indicators of phytoplankton biomass and production where bivalve colonization is possible. This study provides for ecosystem management a particular example of a broad lesson: abiotic ecosystem stressors should be managed with explicit consideration of interactions with other major (including biotic) stressors. We discuss the applicability and management implications of our models and results for a range of aquatic system types, with a case study focused on the Sacramento-San Joaquin Delta (California, USA). Simple mathematical models like those used here can illuminate interactions between ecosystem stressors and provide process-based guidance for resource managers as they develop strategies to augment valued populations, restore habitats, and manipulate ecosystem functions.

**Key words:** benthic; bivalve; clam; *Corbicula fluminea*; exotic; grazing; hydrodynamic; non-native; phytoplankton; productivity; residence time; restoration.

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## INTRODUCTION

Non-native species can complicate ecosystem restoration in several ways. First, non-natives can become integrated into the ecosystem, providing ecological benefits as well as disadvantages. In New Zealand, for example, non-native cats prey

on an endangered flightless parrot, but also provide an ecosystem service as the major predator for introduced rats that also prey on the parrot (Zavaleta et al. 2001). Second, non-natives can interact with other biotic and abiotic stressors, potentially constraining management options (Strayer 2010) and forcing tough deci-

sions. The non-native salt cedar *Tamarix* spp., a prominent invader of arid riparian habitats, thrives where water management has removed natural hydrologic variability (Zavaleta et al. 2001), and it is commonly believed that river management must change if *Tamarix* is to be effectively controlled (Cohn 2005). Interactions between significant biotic and abiotic stressors can result in “novel ecosystems”—new ecosystem configurations that are extremely challenging to restore because they comprise different species, interactions and functions relative to past ecosystems (Hobbs et al. 2009). Third, since environmental disturbance provides expansion opportunities for non-natives (Didham et al. 2005, MacDougall and Turkington 2005), physical habitat restoration can encourage the spread of established non-natives or the introduction of new ones (e.g., a restoration project that removed broom in Marin County, California, resulted in the widespread dominance of European grasses, many of which were associated with low diversity of native species; D’Antonio and Meyerson 2002). Finally, non-natives are generally considered permanent, yet unpredictable. While non-native invasions are frequently irreversible at the ecosystem scale (Mills et al. 2003, Lodge et al. 2006), our ability to forecast the response of those species to restoration at the habitat scale can be severely limited, thus making future states of invaded ecosystems difficult to predict (Strayer et al. 2005).

For novel ecosystems stressed biotically and abiotically, any restoration trajectory back towards the historic state—if it is possible—likely requires management of both biotic and abiotic factors (as with the multi-pronged approach to restoring Australian woodlands; Yates et al. 2000, Hobbs et al. 2009). Thus, even if it were possible to re-create entire physical landscapes from the past, successful restoration of functions and populations could be confounded and limited by biotic factors such as non-native species that can be much more difficult to control. Successful management of interacting stressors requires that controlling abiotic and biotic factors be known, their mechanistic interactions understood, and their ecosystem effects treated by managers as interlinked problems that evolve in time (Hobbs 2007, Strayer 2010).

In this paper, we examine interacting biotic

and abiotic factors controlling primary production in stressed aquatic ecosystems, where the principal biotic stressor considered is grazing by benthic bivalves. Non-native bivalves represent an accelerating global problem expected to intensify with continued globalization of economies (Karatayev et al. 2007). Primary production is also of frequent concern to resource managers. Common goals for aquatic restoration include increasing resources for secondary producers or improvement of water quality for ecological, human health, or recreational purposes. Such goals frequently require either: (1) the maintenance, decrease or increase in appropriate primary producers, or (2) the reduction of specific inappropriate primary producers such as cyanobacteria. Here we apply simple mathematical models that can be used broadly to explore the coupled effects of non-native suspension feeders, habitat depth, and hydrodynamic transport on phytoplankton biomass and production in aquatic systems such as rivers, lakes, and estuaries. In particular, these models help us explore whether and how bivalve grazing changes the relationships between phytoplankton biomass and productivity and potentially the most easily controlled abiotic ecosystem attributes—water depth and hydrodynamic transport rate. Similar models have been developed to examine the effect of sinking (instead of benthic filtration losses) on the relationship between mixing depth and phytoplankton biomass (Diehl 2002) and community composition (Ptacnik et al. 2003). The approaches and lessons presented herein are applicable to aquatic systems anywhere on the spectrum from oligotrophic to eutrophic (sensu Nixon 1995), within model assumptions.

We use *Corbicula fluminea*, one of the world’s most prominent non-native freshwater bivalves (Karatayev et al. 2007), as our representative suspension feeder. We apply our models using the biotic and abiotic characteristics of the Sacramento-San Joaquin Delta (California, USA; hereafter referred to as “Delta”), a stressed freshwater system slated for major water supply and ecosystem management actions in the coming decades. Phytoplankton production has been shown to represent the dominant energy source to the Delta’s pelagic food web (Müller-Solger et al. 2002, Sobczak et al. 2002, 2005), supporting production of zooplankton, the food

resource for critical species and life-stages of declining pelagic fishes (Nobriga 1998, Sommer et al. 2007, MacNally et al. 2010). Over the last few decades, Delta phytoplankton biomass has been low enough to limit the growth of some zooplankton species (Jassby et al. 2002, Müller-Solger et al. 2002), and median chlorophyll *a* concentrations in the early 2000s were less than half of those in the late 1970s, despite chronically high nutrient concentrations (Jassby 2008) and a long-term increase in transparency (Cloern et al. 2011). Along with other factors such as introductions of non-native bivalves, human induced changes in abiotic attributes such as Delta geometry (loss of shallow aquatic habitat, channelization) and hydrology and hydrodynamics (specifically, reductions in residence time) are viewed as having contributed to reduced phytoplankton productivity (ICF International 2012a). Because the Delta's long-term phytoplankton decrease has accompanied declines in herbivorous zooplankton (Kimmerer and Orsi 1996, Winder and Jassby 2011) and fish (Bennett and Moyle 1996, MacNally et al. 2010), low phytoplankton biomass and productivity are considered factors contributing to the multi-decadal decline in fish species. Restoration plans for the Delta therefore include actions expected to enhance primary productivity (California Natural Resources Agency 2010, ICF International 2012c). Two conceptual models, cast here as hypotheses to be tested (Fig. 1), are shaping those plans:

- Hypothesis 1: Shallower habitats are associated with higher phytoplankton biomass and productivity than deeper habitats. (“Shallower is Greener”).
- Hypothesis 2: Habitats with longer transport times (slower hydrodynamics) are associated with higher phytoplankton biomass and productivity than habitats with shorter transport times (faster hydrodynamics). (“Slower is Greener”).

(We use “transport time” as a generic term characterizing the time spent by a water parcel, and the phytoplankton within it, inside a defined region. There are many specific types of transport time scales [e.g., “residence time”, “flushing time”, “age”, and “transit time”], all with their

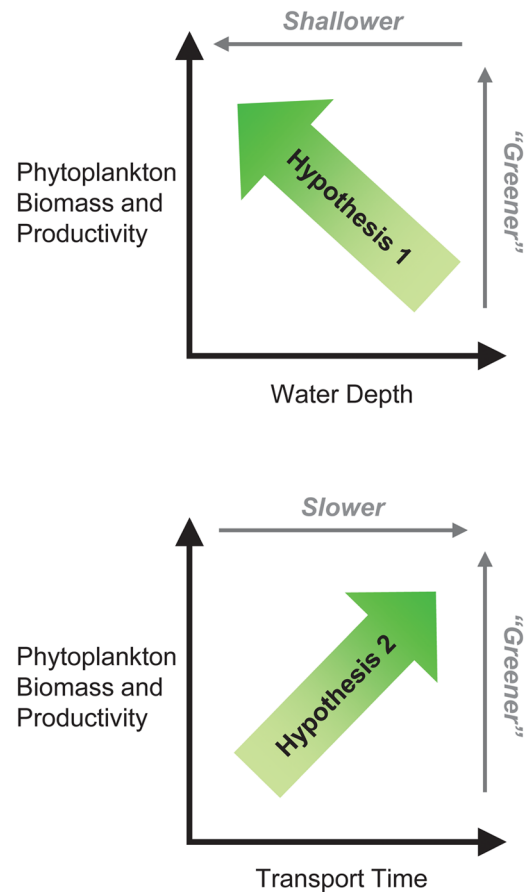


Fig. 1. Schematics of the two hypotheses tested in this study.

own methods of estimation, foundational assumptions, and physical meanings [Monsen et al. 2002, Lucas 2010, de Brauwere et al. 2011, de Brye et al. 2012]. Typically, a faster flow rate or characteristic water velocity results in a shorter transport time.) The above hypotheses seem intuitive and reasonable, given the number of observations within and beyond the Delta that are consistent with the “Slower is Greener” (Howarth et al. 2000, Schemel et al. 2004, Jassby 2005, Ahearn et al. 2006, Paerl and Huisman 2008) and “Shallower is Greener” models (Cole et al. 1992, Sommer et al. 2004, Bukaveckas et al. 2011). In this paper, we test these hypotheses with mathematical models, examining in a process-based way whether water depth and transport time, by themselves, represent (1) useful, generic predictors of phytoplankton biomass and productivity, and (2) effective

management “knobs” for controlling productivity at the food web base. We will illustrate that the relationships between water depth, transport time, and phytoplankton are confounded—and transformed—by the fast removal of phytoplankton by benthic grazers, thus demonstrating that the “Shallower is Greener” and “Slower is Greener” hypotheses are not universally true. We will explain the implications of these findings for restoration of aquatic systems such as the Delta where primary productivity is a management concern.

## DESCRIPTION OF CASE STUDY SITE

The Sacramento-San Joaquin Delta is the tidal, primarily freshwater system at the head of San Francisco Bay (Fig. 2). Today’s Delta is a “novel ecosystem” (Hobbs et al. 2009): a complex network of leveed, interconnected channels and open water habitats that is dramatically changed from the expansive tidal marsh of 150 years ago. Humans have induced these changes, through conversion of original marsh into islands for farming, armoring of tidal channels, manipulation and diversion of freshwater flows, discharge of chemical wastes, and introductions of non-native flora and fauna (Healey et al. 2008). Today, the Delta represents both the hub of California’s freshwater delivery system and an ecosystem in severe decline. As such, State law mandates that multi-billion dollar plans being developed to manage the future Delta address water supply and ecosystem health as “co-equal goals” (California Department of Water Resources 2009).

Low biomass and productivity of phytoplankton in the Delta represent one ecosystem stress likely contributing to long-term declines in zooplankton and native fish. Nutrient limitation of phytoplankton growth in the Delta is extremely rare (Jassby et al. 2002, Lucas et al. 2002, Lopez et al. 2006), due to substantial agricultural and wastewater treatment plant inputs and (interactive) light limitation (turbidity of Delta waters is generally high; Jassby et al. 2002, Jassby 2008). The Delta is relatively shallow, with open water areas  $< \approx 5$  m connected to channels of maximum depth  $\sim 15$  m in most of the Delta, but up to  $\sim 25$  m or more in some locations (F. M. Achete, *personal communication*). The Delta is considered generally vertically well-mixed, based on obser-

vations that vertical density stratification in most of that system is rare (J. R. Burau, *personal communication*) and short-lived (Lucas et al. 2006, Jones et al. 2008).

Non-native bivalves have been shown to strongly influence phytoplankton biomass in the San Francisco Estuary. *C. fluminea* and the “overbite clam” *Potamocorbula amurensis* (formerly *Corbula amurensis*), respectively, are significant sinks for phytoplankton in the freshwater Delta (Lucas et al. 2002, Lopez et al. 2006) and in the brackish parts of the system (Cloern 1982, Alpine and Cloern 1992, Thompson 2005). Grazing by *C. fluminea* is documented as the greatest potential loss process for phytoplankton in much of the Delta, sometimes removing phytoplankton faster than it can grow (Lucas et al. 2002, Lopez et al. 2006). Grazing of phytoplankton by zooplankton has previously been considered to have a relatively unimportant influence on phytoplankton dynamics in the Bay-Delta (Kimmerer 2004). Estimated loss of phytoplankton biomass to zooplankton grazing has been found to be (1) generally too slow to control phytoplankton biomass, and (2) on average only one-eighth of the loss to benthic grazing in habitats colonized by *C. fluminea* (Lopez et al. 2006). However, recent data from the upper San Francisco Bay suggest grazing by microzooplankton could be significant (York et al. 2010).

## METHODS

### *General model description and strategy*

For optimal simplicity and clarity, we examined the influences of water depth and transport time separately. To test Hypothesis 1, we used a simple time-dependent mathematical model of a generic water column describing phytoplankton growth rate, loss rates, biomass, and productivity over a range of water depths ( $H$ , m) and benthic grazing rates ( $BG$ ,  $\text{m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ ; effectively a piston velocity). The objective was to explore quantitatively how water depth influences phytoplankton dynamics in a light-limited system, and how that influence varies with benthic grazing strength. These calculations employed the assumptions that (1) the water column is vertically well-mixed, (2) water depth is constant in time, (3) net horizontal transport of phytoplankton biomass is zero, and (4) only light

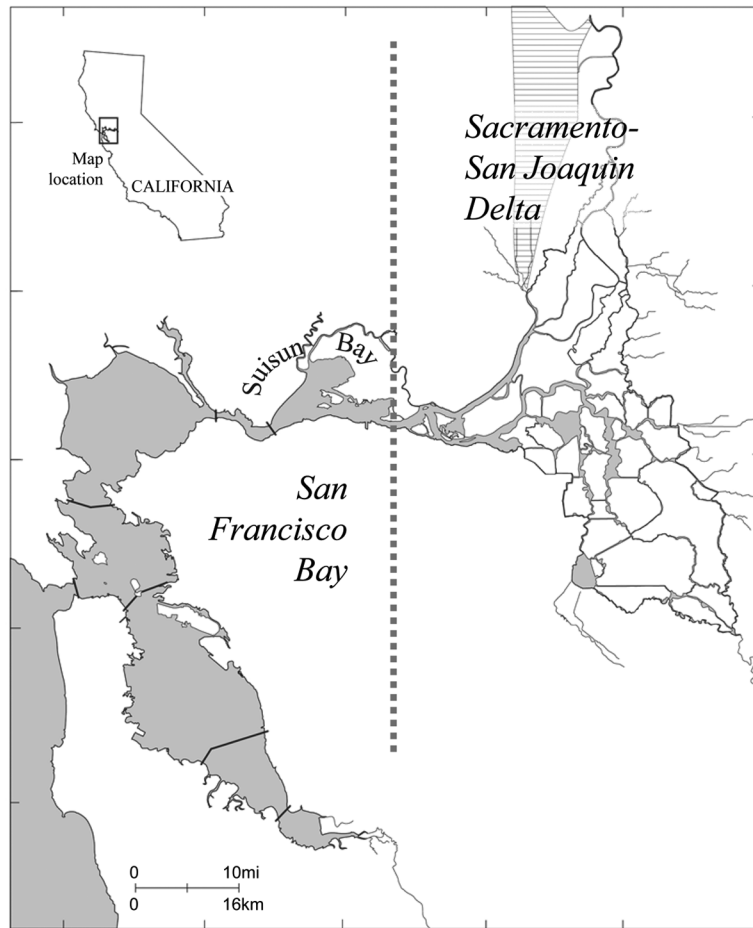


Fig. 2. Map of the San Francisco Bay-Delta.

controls phytoplankton growth rate (i.e., concentrations, forms, and ratios of nutrients are not considered limiting). Depth-averaged rates of phytoplankton net growth ( $\mu_{net}$ , 1/d; gross growth minus respiration) and loss to bivalve grazing ( $BG/H$ , 1/d; Lucas et al. 1999) were first calculated separately, to demonstrate their individual dependencies on  $H$ . Then these rates were combined with zooplankton grazing rate ( $ZP$ , 1/d) to calculate the total “effective” growth rate ( $\mu_{eff}$ , 1/d) of phytoplankton in a given well-mixed water column (Lucas et al. 1999; see Eq. A1 in the Appendix). The form of our depth-averaged benthic grazing loss term is analogous to specific algal sedimentation loss rates (i.e., sinking speed/water depth) implemented in other models of phytoplankton dynamics in vertically well-mixed layers or water columns (Diehl 2002, Descy et al.

2012).  $ZP$  was presumed uniform over the water column. Positive  $\mu_{eff}$  means that growth is faster than combined in situ losses, resulting in a habitat that functions as a net source of phytoplankton biomass. Negative  $\mu_{eff}$  means that local losses are collectively faster than growth, so the habitat functions as a net phytoplankton sink. Effective growth rate was used to calculate phytoplankton biomass  $B$  ( $\text{mg chl } a/\text{m}^3$ ) as a function of time. Calculated indices of habitat function include daily water column net primary productivity ( $NPP$ ,  $\text{mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ; gross productivity minus losses to respiration calculated for day 7 of the simulation) and phytoplankton biomass at 7 days normalized by the initial biomass ( $B_7:B_0$ ). We refer to the latter index as “biomass potential,” since the chosen 7-day simulation length is arbitrary and meant to

convey the relative potential of different habitats to produce phytoplankton biomass. Plots of net productivity and biomass potential versus water depth for different benthic grazing rates are used to evaluate whether Hypothesis 1 should be accepted or rejected. Model details and parameters are described in the Appendix and Table 1. Most parameters are based on measurements from the central Delta (Edmunds et al. 1999, Lucas et al. 2002, Lopez et al. 2006).

To test Hypothesis 2, we used a second simple model describing phytoplankton biomass and productivity as a function of transport time ( $\tau_{\text{tran}}$ , in days) over a range of bivalve grazing rates. The objective was to explore the relationship between phytoplankton and the time it spends in a habitat, and how that relationship is affected by benthic grazing rate. Thus, the role of  $\tau_{\text{tran}}$  here is to characterize the time for a water parcel to travel through a defined habitat, from inlet to exit (i.e., a “transit time”); this quantity thus represents the time phytoplankton within the parcel are exposed to growth-loss conditions within the habitat (Lucas et al. 2009b). (See Lucas [2010] for discussion of how “transit time” is related to commonly referenced terms such as “flushing time” and “residence time.”) For a chosen water depth (3 m), this model calculated phytoplankton effective growth rates for a range of benthic grazing rates, and used those values of  $\mu_{\text{eff}}$  to calculate steady-state habitat-averaged phytoplankton biomass ( $B_{\text{hab}}$ , mg chl *a*/m<sup>3</sup>) and net productivity ( $NPP_{\text{hab}}$ , mg C·m<sup>-2</sup>·d<sup>-1</sup>) as a function of  $\tau_{\text{tran}}$ . Plots of phytoplankton biomass and net productivity versus transport time for different bivalve grazing rates are used to evaluate whether Hypothesis 2 should be accepted or rejected. Model details and parameters are described in the Appendix and Table 1.

#### *Effective growth rate estimates in a real ecosystem*

Benthos and water quality measurements in the Delta over three time periods (August 2001, April–June 2002, May 2003) were combined to estimate phytoplankton effective growth rate over a range of habitats and conditions. The goal was to explore the practical range of  $\mu_{\text{eff}}$  in a real ecosystem, using  $\mu_{\text{eff}}$  as an index of habitat functionality and an indicator of the utility of our theoretical models. Since these results are a

superposition of past  $\mu_{\text{eff}}$  “snapshots”, they should not be presumed to represent the current or future Delta. Calculation details are provided in the Appendix and Table 2.

## RESULTS AND DISCUSSION

### *Model testing of Hypothesis 1: Are shallower habitats greener?*

In turbid, nutrient-rich systems, photosynthesis and gross algal growth are typically greatest and most easily compensate for respiration (i.e.,  $\mu_{\text{net}} > 0$ ) near the water surface, where light is most abundant (Fig. 3A). Deeper in the water column, respiration loss may dominate light-driven growth (i.e.,  $\mu_{\text{net}} < 0$ ). Therefore, in light-limited environments, the depth-averaged net growth rate—the characteristic growth rate for phytoplankton in a vertically well-mixed habitat (Lucas et al. 1999)—increases as the habitat gets shallower (assuming turbidity remains constant). The behavior of  $\langle \mu_{\text{net}} \rangle$  (the day-averaged, depth-averaged net growth rate) therefore roughly parallels that of depth-averaged light as a function of  $H$  (Fig. 3B). If there were no other local loss processes for phytoplankton, then phytoplankton biomass would also be expected to increase with decreasing  $H$ , roughly following net growth rate and depth-averaged light.

The expectation that a shallower habitat will have higher phytoplankton biomass and productivity than a deeper habitat is rooted in the assumption that the “bottom-up” process depicted in Fig. 3A, B (light-limited algal growth) is the only depth-dependent process governing phytoplankton biomass (Lopez et al. 2006). That expectation does not account for the influence of “top-down” or other local loss processes that can vary with  $H$ . In particular, the depth-averaged rate of algal biomass loss to benthic consumers ( $BG/H$ , 1/d) is a strong function of water depth and, like net growth rate, increases in magnitude as  $H$  decreases (Fig. 3C). The intensification of the benthic grazing effect with shallower  $H$  makes intuitive sense: a given population of bivalve feeders pumping at a particular rate will deplete the overlying water column of phytoplankton faster if that water column is shallower (Strayer 1999, Lucas and Cloern 2002). Thus, some of the most important biological processes influencing phytoplankton

Table 1. Parameters specified and variables computed for generic calculations and hypothesis testing (to generate Figs. 3, 4, and 5C, D).

Name	Units	Value/Range	Definition	Description
Definitions				
$\bar{y}$ ( $y$ )			depth-average of variable $y$ day-average of variable $y$	
Parameters				
$a$	$(\text{mg C} \cdot [\text{mg chl } a]^{-1} \cdot \text{h}^{-1})$ $(\mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1})^{-1}$	0.029	photosynthetic efficiency at low irradiance	June 1997 measurements in central Delta (Edmunds et al. 1999; J. Edmunds, <i>personal communication</i> )
$B_0$	$\text{mg chl } a/\text{m}^3$	3.0	initial phytoplankton biomass concentration	Used at beginning of model run. Based on average chlorophyll $a$ measured in Franks Tract and Mildred Island (central Delta) during June 1999 (Lucas et al. 2002)
$B_G$	$\text{m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$	0–10	benthic (clam) grazing rate	Typical values based on measurements in central Delta (Lucas et al. 2002). This is a conservative range, since the maximum value indicated here is less than half the maximum values estimated based on benthic biomass samples from the Delta.
$B_{\text{in}}$	$\text{mg chl } a/\text{m}^3$	3.0	phytoplankton biomass concentration entering habitat through upstream boundary	Used in testing Hypothesis 2.
[C:chl]	$\text{mg C}/\text{mg chl } a$	32	phytoplankton cellular ratio of carbon to chlorophyll $a$	Lopez et al. (2006); estimated for habitats across the Delta following Cloern et al. (1995)
$D$	h	15 (Jun) 12 (Sep) 10 (Dec) 12 (Mar)	photoperiod	National Oceanic and Atmospheric Administration, <i>public communication</i> , <a href="http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html">http://www.srrb.noaa.gov/highlights/sunrise/sunrise.html</a> ; June value used unless otherwise specified.
$H$ $I_0$	$\text{m}$ $\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$	0.05–10.0 59 (Jun) 43 (Sep) 16 (Dec) 36 (Mar)	habitat depth total daily irradiance at water surface (photosynthetically active radiation, PAR)	Represents tidal mean Estimated from month-averaged solar radiation (in $\text{W}/\text{m}^2$ ) for Davis, CA, obtained from California Irrigation Management Information System (Spatial CIMIS), <i>public communication</i> , <a href="http://www.cimis.water.ca.gov/cimis/cimiSatSpatialCimis.jsp">http://www.cimis.water.ca.gov/cimis/cimiSatSpatialCimis.jsp</a> ; Converted to PAR with a factor of 0.18 (Jassby 2008). June value used unless otherwise specified.
$k_{t,0}$	1/m	1.75	light attenuation coefficient	Initial value at beginning of model run. Represents the sum of abiotic and self-shading components. Based on mean values from measurements at Franks Tract and Mildred Island (central Delta) in June 1999 (Lucas et al. 2002).
$p_{\text{max}}$	$\text{mg C} \cdot (\text{mg chl } a)^{-1} \cdot \text{h}^{-1}$	5.0	maximum instantaneous rate of photosynthesis	June 1997 measurements in central Delta (Edmunds et al. 1999; J. Edmunds, <i>personal communication</i> )

Table 1. Continued.

Name	Units	Value/Range	Definition	Description
$\tau_{\text{tran}}$	d	0–7	transport time	Taken herein to represent the time for a water parcel to travel through a defined habitat, from inlet to exit (i.e., a “transit time”). Used in testing of Hypothesis 2.
$ZP$	1/d	0.2	zooplankton grazing rate	Average value based on measurements in Mildred Island and Franks Tract (central Delta) in 2001 and 2002, respectively (Lopez et al. 2006)
<b>Variables</b>				
$B$	mg chl $a/m^3$ (or equivalently $\mu\text{g chl } a/L$ )		phytoplankton biomass concentration	Represents depth-averaged value
$B(x)$	mg chl $a/m^3$		phytoplankton biomass concentration at streamwise location $x$	See Eq. A4. Used for testing Hypothesis 2.
$B_{\text{hab}}$	mg chl $a/m^3$		habitat-averaged phytoplankton biomass concentration	Calculated numerically and using Eq. A5. Used in testing Hypothesis 2.
$B_7:B_0$	...		ratio of calculated phytoplankton biomass at 7 days normalized by initial biomass	Represents the “biomass potential” of a particular modeled habitat. Used in testing Hypothesis 1.
$I_{0t}$	$\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$		instantaneous irradiance (PAR) at water surface	Following Cloern et al. (1995)
$I_{z,t}$	$\mu\text{mol quanta}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$		instantaneous irradiance (PAR) at depth $z$	$I_{z,t} = I_{0t} \exp(-k_t \cdot z)$
$k_t$	1/m		light attenuation coefficient	Dynamically calculated by model used in testing Hypothesis 1. Represents the sum of constant abiotic and dynamic self-shading components. Self-shading component calculated as $0.016 \cdot B$ (Bannister 1974).
$NPP$	mg C $\cdot\text{m}^{-2}\cdot\text{d}^{-1}$		phytoplankton net primary productivity	Day-averaged, depth-averaged value. See Eq. A3. Used in testing Hypothesis 1.
$NPP(x)$	mg C $\cdot\text{m}^{-2}\cdot\text{d}^{-1}$		phytoplankton net primary productivity at streamwise location $x$	$NPP(x) = B(x)[C:chl](\mu_{\text{net}})H$ . Used in testing Hypothesis 2.
$NPP_{\text{hab}}$	mg C $\cdot\text{m}^{-2}\cdot\text{d}^{-1}$		habitat-averaged phytoplankton net primary productivity	Calculated numerically and using Eq. A6. Used in testing Hypothesis 2.
$p$	mg C $\cdot(\text{mg chl } a)^{-1}\cdot\text{h}^{-1}$		instantaneous rate of photosynthesis at depth $z$	$p = p_{\text{max}}[1 - \exp(-I_{z,t}/p_{\text{max}})]$ (Webb et al. 1974)
$resp$	1/d		instantaneous rate of phytoplankton biomass loss to respiration at depth $z$	$resp = 0.015 + 0.15\mu_{\text{gross}}$ (Cloern et al. 1995)
$x$	m		distance downstream of habitat inlet	Relevant to testing of Hypothesis 2.
$\mu_{\text{eff}}$	1/d		effective phytoplankton growth rate	See Eq. A1. The sum of depth-averaged, day-averaged in situ phytoplankton growth and loss terms. Employs assumption that water column is vertically well-mixed.
$\mu_{\text{gross}}$	1/d		instantaneous phytoplankton gross growth rate at depth $z$	$\mu_{\text{gross}} = p \cdot 24.0/[C:chl]$
$\mu_{\text{net}}$	1/d		instantaneous phytoplankton net growth rate at depth $z$	$\mu_{\text{net}} = \mu_{\text{gross}} - resp$ ; gross growth minus respiration

Notes: “Value/Range” cells are blank in the case of dependent variables calculated by models. Equations are found in the Appendix.



Table 2. Parameters specified and variables computed for the calculation of phytoplankton effective growth rate across the Delta (to generate Fig. 6).

Name	Units	Value/Range	Definition	Description
<b>Parameters</b>				
$\psi$	mg C:(mg chl <i>a</i> ) <sup>-1</sup> (mol quanta·m <sup>-2</sup> ) <sup>-1</sup>	0.728	empirical <i>BZI</i> efficiency factor	Calibrated to Delta primary productivity measurements (Jassby et al. 2002).
[ <i>C:chl</i> ]	mg C/mg chl <i>a</i>	32	phytoplankton cellular ratio of carbon to chlorophyll <i>a</i>	Lopez et al. (2006); estimated for habitats across the Delta following Cloern et al. (1995).
<i>I</i> <sub>0</sub>	mol quanta·m <sup>-2</sup> ·d <sup>-1</sup>	38–65	total daily irradiance at water surface (photosynthetically active radiation, PAR)	Estimated from daily solar radiation (in W/m <sup>2</sup> ) obtained for specific sampling dates from California Irrigation Management Information System, <i>public communication</i> , <a href="http://www.cimis.water.ca.gov">http://www.cimis.water.ca.gov</a> . Used average from Brentwood and Twitchell Island, CA. Converted to PAR with a factor of 0.18 (Jassby 2008).
<i>k</i> <sub>t</sub>	1/m	1.1–7.8	light attenuation coefficient	See <i>Notes</i> .
<i>ZP</i>	1/d	0.2	zooplankton grazing rate	Average value based on measurements in Mildred Island and Franks Tract (central Delta) in 2001 and 2002, respectively (Lopez et al. 2006).
<b>Variables</b>				
% <i>P</i> <sub>t</sub>	...	0–100	<i>BZI</i> correction factor for <i>H</i> < photic depth	Brush and Brawley (2009). Implemented single-equation correction.

*Notes:* 2001 and 2002: Light attenuation coefficient was based on measured light profiles where available. Otherwise, it was calculated using  $k_t = 0.76 + 0.076 \cdot \text{SPM} + 0.016 \cdot \text{chl } a$  (SPM = suspended particulate matter [mg/L]; chl *a* in [μg/L]; Lopez et al. 2006). 2003: Light attenuation coefficient was based on Secchi depths (*S*, in cm) measured during benthic sampling (California Department of Water Resources, *personal communication*) and converted to light attenuation using an empirical relationship derived herein:  $k_t = 0.619 + 78.6/S$  ( $R^2 = 0.74$ ). To build that relationship,  $k_t$  was estimated for 2001–2003 at Interagency Ecological Program monitoring sites (<http://www.water.ca.gov/iep/>): (1) in the Sacramento River, western Delta and Suisun Bay (C3, C3A, D4, D7, D8) using  $k_t = 0.892 + 0.0556 \cdot \text{SPM}$  ( $R^2 = 0.71$ ; derived herein from 1999–2001 USGS data at stations 2, 3, 649, and 657; United States Geological Survey, *public communication*; <http://sfbay.wr.usgs.gov/access/wqdata/>); and (2) in the central and eastern Delta (IEP stations D26, D28A, MD10A, P8) using the above expression from Lopez et al. (2006). “Value/Range” cells are blank in the case of dependent variables calculated by models.

biomass in many systems—light driven growth and benthic grazing—are, in the depth-averaged sense, strong functions of water depth and fastest in shallow waters (Lucas et al. 2009a). But because these two processes have opposite signs and different non-linear dependencies on depth, their combined effect on phytoplankton dynamics is not straightforward.

In Fig. 3D, we combine the competing effects of growth and grazing, plotting the effective phytoplankton growth rate as a function of water depth for a realistic range of benthic grazing rate. For  $BG = 0$  (no bivalves), the  $\mu_{\text{eff}}$  curve is the same as the net growth curve in Fig. 3B (shallower *H* leads to faster growth), but with a downward

shift due to inclusion of zooplankton grazing. For large *BG*, benthic grazing dominates the  $\mu_{\text{eff}}-H$  relationship, resulting in negative  $\mu_{\text{eff}}$  for all *H* and a monotonic curve with slope of the opposite sign of the  $BG = 0$  curve. With strong benthic grazing, the increased loss of phytoplankton biomass to bivalve grazers is not compensated for by the increase in light-driven growth as *H* gets shallower. So in this case, shallower *H* leads to increasingly negative  $\mu_{\text{eff}}$  and therefore more adverse conditions for phytoplankton growth. For low to intermediate values of *BG*, the competing processes of growth and benthic grazing can result in a non-monotonic dependence of  $\mu_{\text{eff}}$  on *H*. In these cases, peak  $\mu_{\text{eff}}$  does

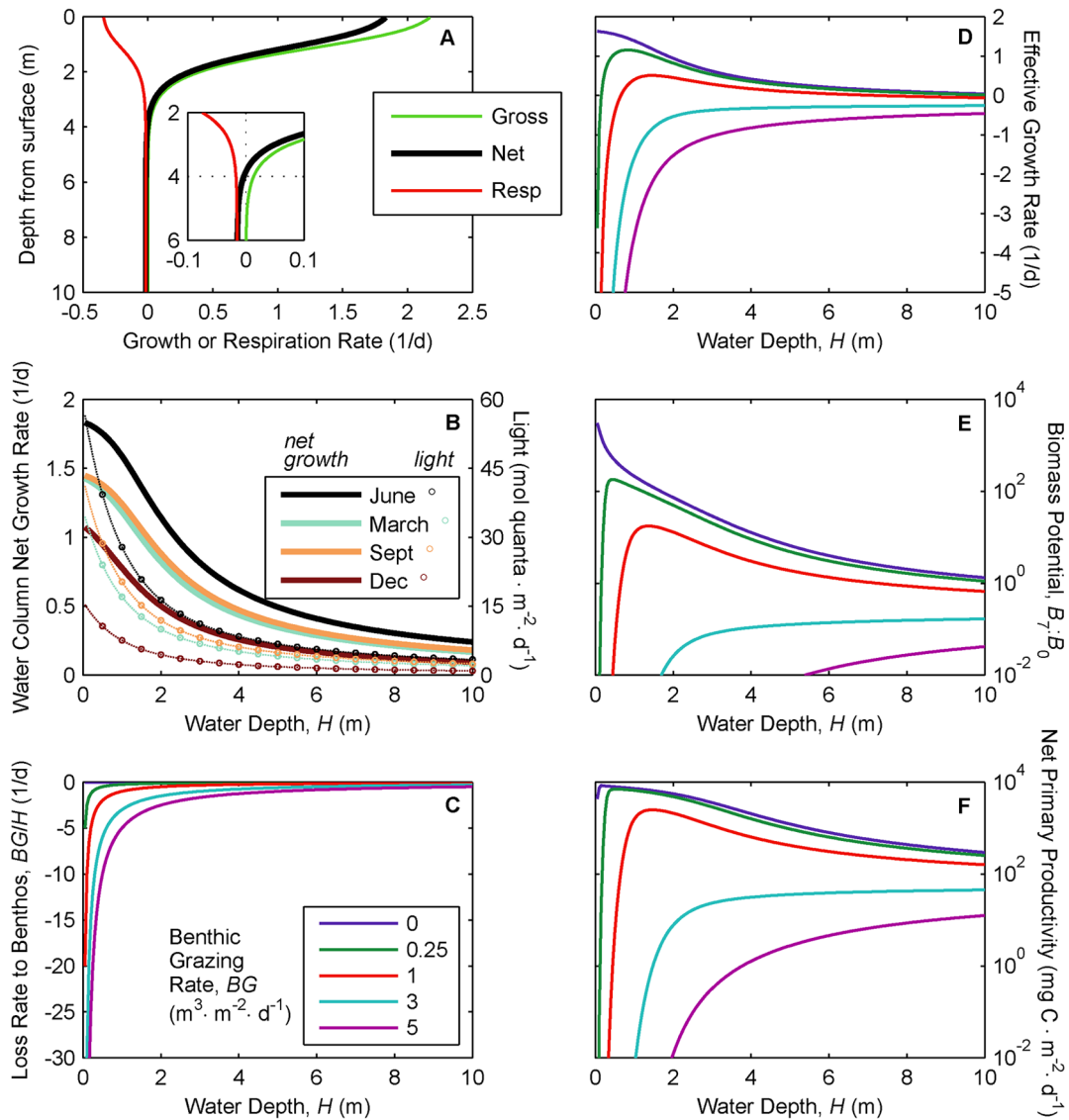


Fig. 3. (A) Vertical profiles of calculated day-averaged phytoplankton gross growth rate, net growth rate, and respiration rate (shown as negative here, since it is a loss process). (B) Calculated day-averaged, depth-averaged phytoplankton net growth rate for day 1 of the simulation (solid curves) and daily depth-averaged irradiance as PAR (dotted curves with circles; calculated following Cloern et al. 1995) as functions of water depth. (C) Calculated depth-averaged rate of phytoplankton biomass loss to benthic grazing versus water depth for five values of benthic grazing rate. (D) Calculated phytoplankton effective growth rate versus water depth for day 1 of the simulation. (E) Phytoplankton biomass potential as represented by  $B_7:B_0$ , the calculated biomass at 7 days normalized by biomass at time = 0, as a function of water depth for five values of benthic grazing rate. (F) Calculated net primary productivity at 7 days versus water depth for five values of benthic grazing rate. (D)–(F) share the same legend as (C). Unless noted otherwise, parameters used in calculations were based on previous measurements in the Delta (Lucas et al. 2002, Lopez et al. 2006; see Table 1).

not occur at the shallowest depths, but at intermediate depths that optimize the balance between light-limited growth and grazing. Since zooplankton grazing is treated as depth-independent, a change in  $ZP$  would result in a vertical shift of the  $\mu_{\text{eff}}-H$  curves in Fig. 3D, with no change in curve shape.

Next, we use  $\mu_{\text{eff}}$  calculations shown in Fig. 3D to advance phytoplankton biomass  $B$  through time and compute  $B_7:B_0$ , our measure of “biomass potential” (Fig. 3E).  $B_7:B_0 > 1$  indicates net biomass increase over time, and  $B_7:B_0 < 1$  indicates net biomass decrease. The  $B_7:B_0$  curves resemble the  $\mu_{\text{eff}}$  curves in Fig. 3D. As habitat depth becomes shallower, biomass potential increases monotonically if  $BG = 0$ , but decreases monotonically if  $BG$  is large. For low to intermediate benthic grazing rates, biomass potential may depend non-monotonically on  $H$ , with peak  $B_7:B_0$  occurring at depths where the growth-grazing balance is optimized, not at the shallowest depth. This non-monotonic behavior is analogous to previous work showing that the competing processes of light-limited algal growth and sedimentation (another depth-dependent loss term) can result in a unimodal relationship between phytoplankton biomass and mixed layer depth (Diehl 2002). Biomass increases over time ( $B_7:B_0 > 1$ ) where  $\mu_{\text{eff}}$  is positive; biomass declines over time ( $B_7:B_0 < 1$ ) where  $\mu_{\text{eff}}$  is negative (compare Fig. 3D and E). Consistent with previous work (Cloern 2007), Fig. 3E demonstrates that shallower habitats might be significantly greener than deeper ones, and they will be if there is no significant depth-dependent loss process such as benthic grazing. However, when benthic grazing is considered, the range of possible bloom outcomes broadens in shallower habitats relative to deeper ones. Therefore, although a shallow habitat has the potential to generate high algal biomass, there is significant uncertainty surrounding whether that potential will be realized. Because net growth and benthic grazing loss are muted in deeper habitats, those environments are more constrained in their range of possible bloom outcomes ( $B_7:B_0 < \approx 1$ ). This suggests that deeper habitats do not have the potential for significant autogenous algal biomass, at least not for the well-mixed, turbid conditions considered here.

Net primary productivity ( $NPP$ ) is an indicator

of a habitat’s capacity to support production at higher trophic levels (Nixon 1988). For shallower habitats, calculated  $NPP$  generally displays a potential for large values but also a broad range of possible values (including low ones), depending in part on benthic grazing rate (Fig. 3F).  $NPP$  in deeper environments is more constrained to a narrow range of relatively low values. This behavior is generally similar to that of biomass potential (Fig. 3E), which is logical since  $NPP$  is proportional to biomass (see Eq. A3 in Appendix). Note that  $NPP$  in areal units, an integral measure of production over the entire water column, also depends directly on  $H$ . This explains why  $NPP$  does not increase monotonically with decreasing  $H$  for the  $BG = 0$  case, as do  $B_7:B_0$  and  $\mu_{\text{eff}}$ . Depth-integrated primary productivity is a non-monotonic function of water depth, even in the absence of benthic grazing or respiration (Cloern 2007). In the loss-free case, maximum productivity is not obtained at the very shallowest depths because a portion of the photons available for photosynthesis hits the bottom sediments instead of chlorophyll molecules (i.e., the lower portion of the photic zone in which photosynthesis could occur is missing in very shallow habitats). The non-monotonic dependence of water column gross productivity on water depth (Cloern 2007) is compounded by the depth-dependent benthic removal of algal biomass, which influences  $NPP$  via  $NPP$ ’s direct dependence on biomass. The combined influences on net productivity result in the collection of  $NPP-H$  curves shown in Fig. 3F, with a much broader range of possible outcomes for shallower habitats than for deeper ones.

Since the 7-day time scale for calculating biomass potential and  $NPP$  is arbitrary and the calculations are based on a particular set of input parameters, the curves in Fig. 3E–F should only be used for habitat inter-comparisons, not for quantitative predictions. The relative relationships between curves in Fig. 3E and F hold for time scales shorter (3 days) and longer (14 days) than the 7-day period employed here (not shown).

In summary, the above modeling analysis has shown that, although shallower nutrient-rich aquatic habitat *might* be associated with higher phytoplankton biomass and productivity, depth-dependent loss processes such as benthic grazing

could cause a reversal of the “shallower is greener” trend, or a non-monotonic relationship between algal biomass and water depth. The range of possible phytoplankton biomass or productivity responses generally increases as the habitat gets shallower. The ultimate function of a shallow habitat (i.e., as either net source or sink of phytoplankton) can be highly uncertain and strongly dependent on the existence and strength of (especially depth-dependent) loss processes such as bivalve grazing. For ecosystems where benthic grazing is prevalent or at least possible, increased shallow aquatic habitat will not necessarily translate into increased algal biomass or productivity. Based on the modeling results, Hypothesis 1 should therefore be rejected.

*Model testing of Hypothesis 2:  
Are slower habitats greener?*

The expectation that longer transport times result in higher phytoplankton biomass and productivity is implicitly rooted in the assumption that the bottom-up process, algal growth, dominates over in situ loss processes. It has been shown with a simple model of a vertically homogeneous advective system that if growth is faster than losses, phytoplankton biomass will indeed increase with time spent in the system (as is commonly expected); on the other hand, if losses dominate over growth, phytoplankton biomass will decrease with time spent in the system (Lucas et al. 2009b). That model (which previously only calculated biomass concentration exiting the habitat) is extended herein to calculate habitat averaged biomass and net primary productivity. We apply that model here for a chosen water depth (3 m) and a realistic range of benthic grazing rates (see the Appendix for calculation details). The grazing rates used result in a broad range of  $\mu_{\text{eff}}$ , from strongly growth-dominated for small  $BG$  ( $\mu_{\text{eff}} > 0$ ) to strongly loss-dominated for larger  $BG$  ( $\mu_{\text{eff}} < 0$ ). We include the specific case of  $BG = 1.8 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , which for these particular conditions results in  $\mu_{\text{eff}}$  of exactly zero.

The green curves in Fig. 4 are those for which  $\mu_{\text{eff}} > 0$  and, consequently, phytoplankton biomass (Fig. 4A) and net productivity (Fig. 4B) rise with increasing transport time. These green curves are cases for which “slower” is indeed

“greener.” The red curves are those for which  $\mu_{\text{eff}} < 0$  and, consequently, phytoplankton biomass and net productivity decrease with increasing transport time. This less intuitive set of loss-dominated cases makes sense nonetheless: the longer a phytoplankton-loaded parcel of water is exposed to net loss conditions, the more phytoplankton biomass will be lost from the parcel by the time it exits the habitat. The red curves thus represent the opposite of the “slower is greener” conceptual model. Consistent with this finding, negative relationships between phytoplankton biomass and transport time have been reported for some aquatic ecosystems with strong algal loss processes (Søballe and Bachmann 1984, Cerco and Noel 2010). The black curves in Fig. 4A, B represent the case where growth is exactly balanced by in situ losses. These  $\mu_{\text{eff}} = 0$  curves are perfectly horizontal, suggesting that transport time is irrelevant to biomass or productivity when loss processes remove phytoplankton at the same rate that it is growing. Thus, biomass will not change within an advecting parcel, regardless of the amount of time spent in that environment.

Additionally, Fig. 4 reveals that the range of possible outcomes is narrow for short transport times and broad for long transport times. The growth-loss conditions within a habitat therefore have little effect on phytoplankton traveling through if transport is very fast and time spent within the habitat is consequently very short. Thus, phytoplankton biomass and productivity appear constrained to modest values under fast transport conditions (assuming modest biomass concentrations enter the habitat in the first place). On the other hand, conditions within the habitat have a dramatic effect on phytoplankton, either positively or negatively, if transport time is long and  $\mu_{\text{eff}} \neq 0$ . The divergence of biomass and productivity curves with increasing transport time (Fig. 4) suggests that slower transport is accompanied by greater uncertainty with respect to realized phytoplankton biomass and productivity.

Given the broad range of modeled outcomes for most values of transport time in Fig. 4, especially for the higher values, transport time should not be expected to serve as a general predictor of phytoplankton biomass or productivity. The relationship between biomass (or

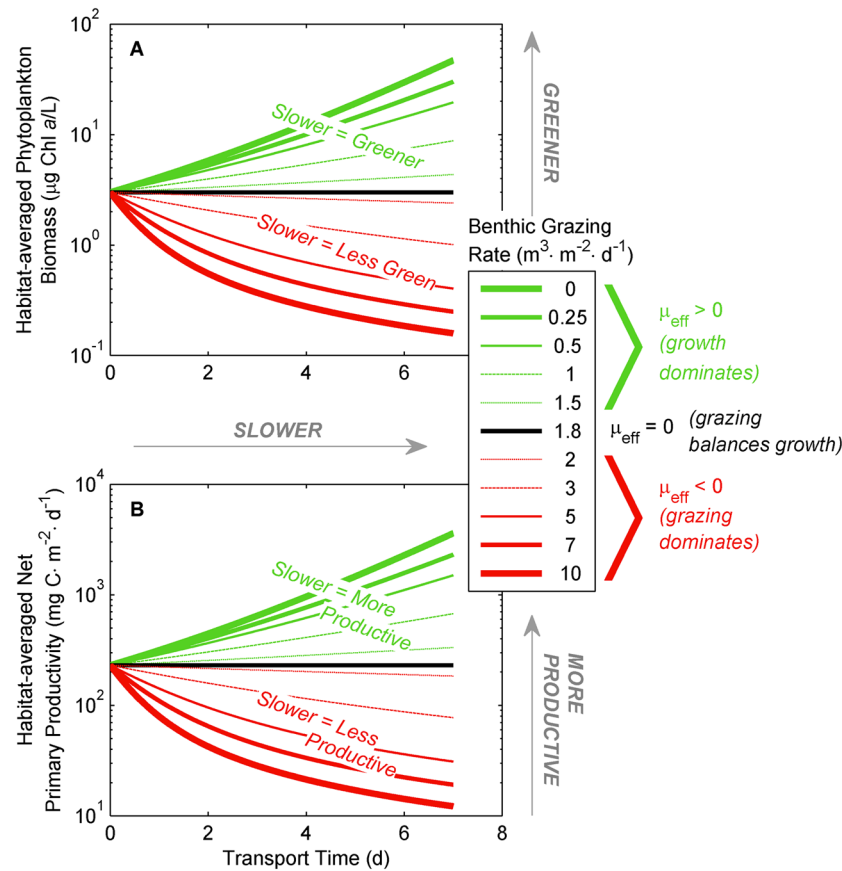


Fig. 4. Model calculations of steady-state average phytoplankton biomass (A) and net phytoplankton primary productivity (B) versus transport time in a flowing habitat for a range of benthic grazing rates typical of the Delta. These calculations were performed for a 3m deep habitat with the characteristic net growth rate shown in Fig. 3B for June conditions.

productivity) and transport time depends on the relative strength of algal growth and in situ loss (Lucas et al. 2009b). Historically observed rates of bivalve grazing (Lucas et al. 2002) can be strong enough to tilt effective growth rate into the negative range, reversing the “slower is greener” trend. Based on these modeling results, Hypothesis 2 should therefore be rejected.

#### Model relevance and utility in a real system:

##### Case study of the Sacramento-San Joaquin Delta

The above analyses are theoretical, though based on widely used mathematical descriptions and reasonable published parameter values. What do observations in an actual aquatic ecosystem indicate about the real-world relevance and applicability of these theoretical

descriptions? Are model-based conclusions consistent with measurements?

*Do measurements suggest shallower habitats are greener? (Hypothesis 1).*—Lopez et al. (2006) used measurements across a range of Delta habitats and seasons to assess whether water depth governs phytoplankton biomass and productivity. As would be expected for a light-limited system, their estimates of algal net growth rate correlated strongly with water depth (consistent with Fig. 3B). However, the more ecologically relevant metrics of algal biomass and net productivity did not correlate with growth rate or depth (Fig. 5A, B herein, modified from Lopez et al. 2006). That study demonstrated that shallow Delta habitats (<5 m) do not necessarily have elevated phytoplankton biomass and pro-

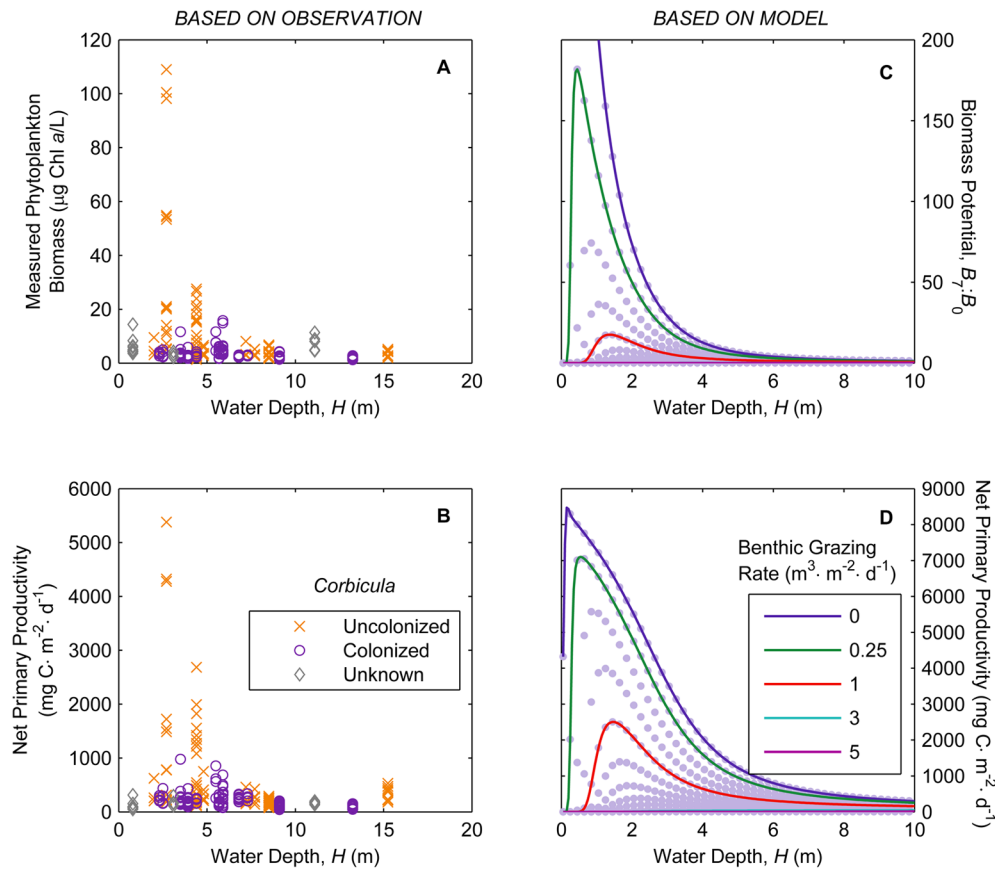


Fig. 5. (A) Measured phytoplankton biomass and (B) calculated measurement-based net primary productivity versus water depth for habitats across the Delta and a range of seasons. Orange x's represent habitats where *Corbicula* was rare or absent ("uncolonized") at the time of sampling. Purple o's represent habitats where *Corbicula* was abundant ("colonized") at the time of sampling. Gray diamonds represent habitats where the clam colonization status at the time of sampling is unknown. Data from Lopez et al. (2006) and Sobczak et al. (2002, 2005). (A) and (B) are an updated and modified version of Fig. 4 in Lopez et al. (2006). (C) Model-calculated phytoplankton biomass potential ( $B_7:B_0$ ) versus water depth. (D) Model-calculated net primary productivity at 7 days versus water depth. (C) and (D) are a reprise of Fig. 3E–F, but plotted on linear scale and with additional dots representing values for 20 different benthic grazing rates between 0 and  $10 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ , a realistic range for the Delta.

ductivity. Lopez et al. (2006) showed that deviations from the bottom-up driven "shallower is greener" relationship were caused by (1) benthic grazing and (2) horizontal transport. Habitats with the highest phytoplankton biomass and productivity were uncolonized by clams (Fig. 5A, B). The shapes of data clouds in Fig. 5A, B may be governed in part by the locations and time periods sampled. Nonetheless, the general behavior is the same as that seen in our model results (replotted in Fig. 5C, D on a linear

scale for the purpose of comparison): (1) well-mixed deep habitats have little chance of being associated with high phytoplankton biomass and productivity; (2) shallow habitats might be associated with high algal biomass and productivity, but they have a broad range of possible values (including low values), with clam presence representing a significant constraint on those variables and a substantial source of uncertainty regarding realized outcomes; (3) if bivalve colonization is possible, then habitat

depth itself is not a good predictor of phytoplankton biomass or productivity, especially in the shallower depth range (less than about 5 m).

The detailed 1999 observations of Lucas et al. (2002) in two Delta open water habitats provide further reason to question the “shallower is greener” assumption. In that study, the shallower habitat (Franks Tract, ~2.5 m deep) had substantially lower phytoplankton biomass than the deeper habitat (Mildred Island, ~5 m deep). This difference was shown to be largely due to differences in benthic grazing rate and, consequently,  $\mu_{\text{eff}}$ . Franks Tract was riddled with clams and operated as a net phytoplankton sink ( $\mu_{\text{eff}} < 0$ ), whereas Mildred Island was nearly clam-free and a phytoplankton net producer ( $\mu_{\text{eff}} > 0$ ).

Observations in the Delta are thus consistent with model results and provide further justification for rejecting Hypothesis 1. In systems like the Delta, where bivalve colonization of individual habitats is possible, the “shallower is greener” expectation should be abandoned.

*Do measurements suggest slower habitats are greener? (Hypothesis 2).*—Results from the phytoplankton-transport time model (Fig. 4) demonstrated that the sign of the phytoplankton effective growth rate controls whether phytoplankton biomass and productivity will increase or decrease with a change in the transport time scale. The modeled range of  $\mu_{\text{eff}}$  resulted in a broad collection of possible algal biomass and productivity responses. How realistic is the range of  $\mu_{\text{eff}}$  implemented in Fig. 4? Does either the growth- or loss-dominated regime predominate in our case study system? Fig. 6A shows estimates of  $\mu_{\text{eff}}$  for 135 cases where measurements of benthic biomass, surface irradiance, and water clarity exist such that benthic grazing rate, algal growth rate, and thus  $\mu_{\text{eff}}$  could be estimated. Capturing spring and summer periods in 2001–2003, Fig. 6A spans the Delta spatially and represents an overlay of effective growth rate “snapshots”. Habitats estimated to be growth-dominated (green symbols, 56 cases), loss-dominated (red symbols, 39 cases), and approximately balanced between growth and loss (yellow symbols, 40 cases) resulted in substantial representation of all three habitat categories within the full dataset. The range of modeled  $\mu_{\text{eff}}$  values underlying Fig. 4 (–2.7 to +0.6 1/d) corresponds well with the measurement

based values underlying Fig. 6A, but with the latter values demonstrating an even broader range (–2.8 to +1.7 1/d). Thus, the full range of functionality depicted in the theoretically derived curves in Fig. 4 appears to be realistic, conservative and relevant to our case study site. Phytoplankton biomass and productivity in Delta habitats should therefore be expected to either increase or decrease in response to slower water movement. Transport time scales such as residence time, flushing time, or transit time should thus not be taken as reliable predictors of phytoplankton biomass or productivity, especially in systems like the Delta, where bivalve grazing can cause habitats to be loss-dominated and the intuitive “slower is greener” conceptual model can consequently fail.

The effective growth rates mapped in Fig. 6A are plotted against habitat depth in Fig. 6B. This provides another view of the distribution of estimated effective growth rate among sampled Delta habitats. Notably, the range of  $\mu_{\text{eff}}$  is narrow (hovering around zero) for deep habitats, but broadens substantially as depth decreases. The model based envelope of  $\mu_{\text{eff}}-H$  curves in Fig. 3D is consistent with the shape of this measurement-based  $\mu_{\text{eff}}-H$  envelope, lending additional credence to the model used to generate the results in Fig. 3. It is important to note the large number of cases in Fig. 6A, B for which  $\mu_{\text{eff}}$  is close to zero, especially in light of the blanket  $ZP$  value that was used, based on the best available information (i.e., the average rate derived from measurements of zooplankton biomass in the central Delta; Lopez et al. 2006). In many cases, higher or lower values of  $ZP$  could tilt estimated  $\mu_{\text{eff}}$  into a different regime. This demonstrates the importance of measuring all components of the algal growth-loss balance for obtaining an accurate, complete picture of aquatic habitat function.

Are observations in the San Francisco Bay-Delta consistent with the dual role depicted for increased transport time in Fig. 4 (i.e., associated with increasing or decreasing phytoplankton biomass and production)? Jassby’s (2008) analysis of long-term chlorophyll records for Suisun Bay (immediately downstream of the Delta; Fig. 2) demonstrated an overall reversal in the direction of the chlorophyll-flow relationship after the 1986 invasion by the estuarine clam *P.*

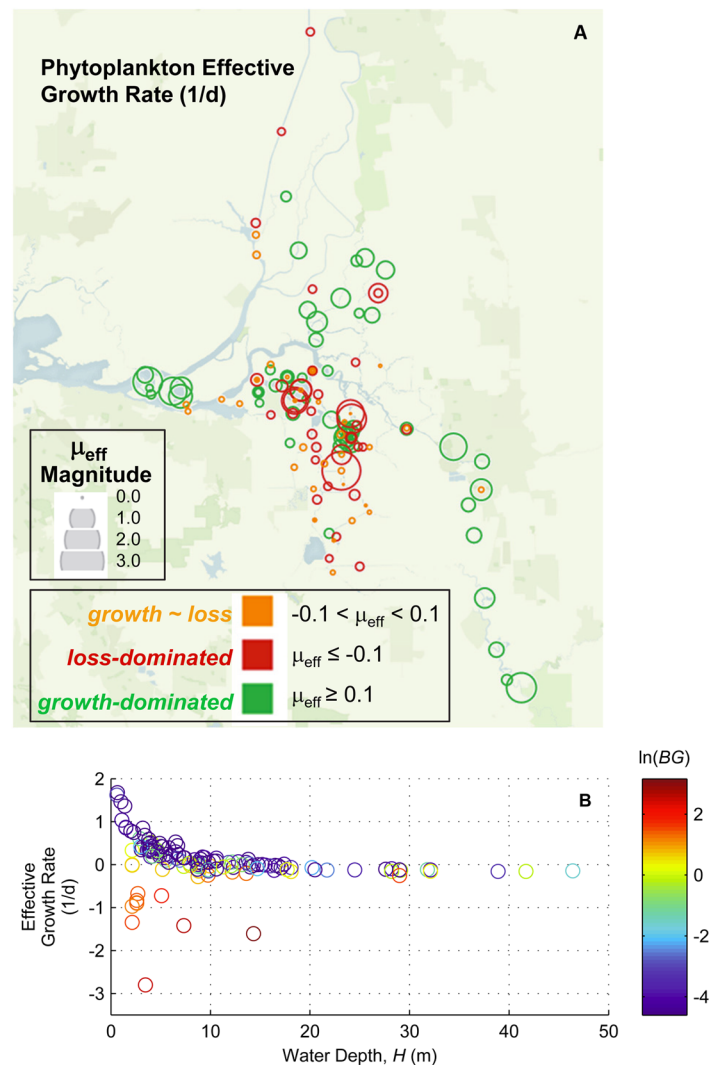


Fig. 6. (A) Map of phytoplankton effective growth rate across the Delta calculated based on parameters measured during field studies in spring-summer 2001–2003. Symbols are color-coded to depict positive (green), negative (red), and approximately zero (yellow) effective growth rate. (B) Phytoplankton effective growth rate versus habitat depth for the cases mapped in panel (A). Color bar is coded to represent  $\ln(BG)$ , where  $BG$  (benthic grazing rate) is in  $\text{m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ . For plotting purposes, minimum  $BG$  was set to  $0.01 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ .

*amurensis*. Before the invasion, Suisun Bay chlorophyll generally decreased with increased freshwater flow to the estuary (and presumably decreased transport time); whereas after the invasion, chlorophyll increased with increased flow. Jassby (2008) posited the *P. amurensis* invasion as the root cause for the change in the chlorophyll-flow relationship, and described an important ecological consequence of the invasion—the enhanced role of allochthonous pro-

duction from the upstream Delta in Suisun's phytoplankton mass balance. Fig. 4 herein, which is generally consistent with Jassby's empirical findings, provides a theoretical basis to help explain the possible mechanisms underlying the observed changes: before the *P. amurensis* invasion, longer residence times in Suisun Bay translated into more time for phytoplankton to experience positive effective growth conditions and thereby accumulate. But after the invasion,



longer residence times meant more time for the non-native clam to graze down the phytoplankton, resulting in intensified biomass depletion. The overall envelope of Jassby's (2008) pre-clam and post-clam chlorophyll-flow curves is also consistent with the envelope of curves in Fig. 4: curves converge at high flow (short transport time) and diverge at low flow (long transport time). We hypothesize that this reflects a higher sensitivity to in situ growth and loss, and thus a broader range of possible bloom outcomes, at longer transport times; whereas, at short transport times, that sensitivity to in situ conditions is diminished and, as Jassby (2008) pointed out, Suisun Bay would be expected to reflect upstream conditions.

Jassby (2008) also explored chlorophyll-flow relationships for the Delta, analyzing long-term chlorophyll data at 11 stations regularly sampled through his time period of interest. Flow explained 49% of the variability in Delta chlorophyll, with chlorophyll decreasing with increasing flow (i.e., slower appears to be greener). Why might Jassby's Delta analysis only reflect the upper (green) curves in Fig. 4, and not the broader range of behavior suggested by the map in Fig. 6? One reason might be related to the limited number of Delta stations for which the requisite long-term data were available. Moreover, these are deep, dispersive channel stations where we would expect measured chlorophyll *a* to reflect an integration of conditions across nearby habitats. It is possible that the regional environment influencing station measurements was comprised of more growth-dominated than loss-dominated acreage, with less frequent loss-dominated habitats contributing to the scatter in Jassby's relationship.

#### *Applicability and caveats*

The models and approaches presented could be modified to include other phytoplankton loss processes not explicitly accounted for herein (e.g., senescence, death by parasitism or disease, or cell sedimentation). Because the depth-averaged rates of loss to sedimentation and benthic grazing in well-mixed water columns take the same mathematical form, (Lucas et al. 1999, Lucas and Cloern 2002, Deleersnijder et al. 2006, de Brauwere and Deleersnijder 2010), those two loss processes have equivalent effects on

phytoplankton biomass and productivity in the context of changing water depth or transport time. Therefore, if sedimentation to the bed were considered significant, the sinking speed ( $W_s$ ) might simply be added to *BG* and the sum substituted for "*BG*" in our models, equations, or plots. In such a case, sedimentation loss would not change the curves in Figs. 3 and 4—it might just change which curve applies. Sedimentation would thus amplify the effect of benthic grazing on the relationship between phytoplankton and water depth (and transport time, as well). Such a simple additive approach to combining  $W_s$  and *BG* may be appropriate in situations where bivalve density is low enough to not interfere significantly with sinking cells reaching the bed, or where resuspension of sedimented cells off the bottom is either negligible or already accounted for in  $W_s$  (de Brauwere and Deleersnijder 2010). This formulation would represent an "upper bound" estimate of the combined loss terms. On the other hand, if bivalves were densely distributed (potentially intercepting a large proportion of cells and preventing them from reaching the bed) or if resuspension were significant, then the simple addition of  $W_s$  and *BG* could substantially overestimate their actual combined effect; in such a case, neglect of  $W_s$  and use of *BG* (by itself) may be most appropriate, thus representing a "lower bound" estimate of the combined losses. A practical way to use the models and types of plots presented, while accounting for the potential added effects of sedimentation, might be to implement both upper and lower bounds, providing an estimate of the range of the combined influence of benthic grazing and sedimentation on phytoplankton biomass and productivity. Phytoplankton sinking speeds can vary with species, cell size, physiological status, and ability to form colonies and aggregates.  $W_s$  has been reported to range from zero to  $Order(10)$  m/d (Huisman and Sommeijer 2002, Ptacnik et al. 2003), which overlaps with the range of published *BG*. So, sedimentation loss can be less than, greater than, or about the same as benthic grazing loss. Since our models and results do not explicitly include sedimentation, they may be considered conservative representations of the effect of loss processes that vary inversely with depth. Likewise, the observation based estimates of phyto-

plankton effective growth rate in Fig. 6 may also be considered a conservative representation of the potential frequency of loss-dominated habitats at our case study site.

The approaches and lessons presented apply not only to tidal systems like our case study site, but also to rivers and lakes. It is important, however, to note some assumptions fundamental to this work. Both models implemented employ the assumption of vertical homogeneity, so they may not apply to environments that experience strong and persistent vertical density stratification. In addition, the phytoplankton-transport time model (for testing Hypothesis 2) employs the assumptions of plug flow (e.g., uniformity of all properties across the flow-cross section, no longitudinal mixing), that the system is in steady-state, and that geometry, velocity, and growth-loss parameters are longitudinally uniform and constant (Lucas et al. 2009b). Rivers are natural systems that do not entirely satisfy all these assumptions (Reynolds 2000); nonetheless, they may still in some cases best represent the aquatic system type to which application of this model may be simplest, best aligned with model assumptions, and most quantitatively successful. For complex (e.g., bidirectional) flows, care should be taken in estimating the transport time (Monsen et al. 2002, Lucas et al. 2009b, Lucas 2010). Even where some of the model's assumptions are violated, the growth-loss balance within a habitat ( $\mu_{\text{eff}}$ ) serves as an informative, qualitative indicator of whether phytoplankton biomass and production will increase or decrease with changing transport time.

Because phytoplankton growth rate in our models was strictly light limited, our calculated cases with high biomass and *NPP* might be tempered if nutrient limitation were accounted for. Our analyses presume that the phytoplankton under consideration are non-motile (e.g., diatoms). Our models and findings would likely break down in the case of cyanobacteria that can regulate their buoyancy and rise quickly to the water surface when vertical mixing weakens (Moreno-Ostos et al. 2009, Paerl and Paul 2012), thus escaping consumption by benthic grazers. Our models also assume the bivalve grazers under consideration are benthic infauna, inhabiting sediments at the bottom of the water column. Some prominent non-native freshwater

bivalves (e.g., *Dreissena polymorpha*) are known to successfully colonize hard substrate on the side walls of waterways. The grazing loss term for side-dwellers may be most appropriately distributed over the depth, rendering results from our phytoplankton-depth model with bottom grazers inapplicable. Conclusions regarding control of the phytoplankton-transport time relationship by the growth-loss balance ( $\mu_{\text{eff}}$ ) should apply, but bivalve grazing loss would likely need to be determined differently.

Tidal shallowing and deepening of a water column can substantially affect phytoplankton dynamics, relative to the case of a constant *H* (Lucas and Cloern 2002). In particular, where benthic grazing is strong and the ratio of tidal range to mean depth is adequately large (e.g., in shallow water), enhanced benthic grazing loss during low tides could significantly reduce algal biomass in the long-term, compared to the constant *H* case. The models used herein (which keep *H* constant in time) may therefore overestimate algal biomass for shallow tidal habitats with strong benthic grazing, likely providing a conservative estimate of the impact of bivalve grazing for such cases.

Our calculations employ a limited and largely fixed set of parameters that in reality vary seasonally, interannually, episodically, and spatially within and between aquatic systems. Changes in any of these parameters could cause changes in the details of Figs. 3–6, so those particular results should not be used predictively or expected to apply uniformly across space or time. That said, data from other estuary and river systems have revealed both growth-dominated ( $\mu_{\text{eff}} > 0$ ) and loss-dominated ( $\mu_{\text{eff}} < 0$ ) functionalities, with strong depth-dependent loss processes such as bivalve grazing and/or sedimentation underlying the loss-dominated cases (Lucas et al. 2009b). Therefore, we expect the broad range of possible phytoplankton-transport time relationships (shown in Fig. 4) to apply to other (types of) systems.

## IMPLICATIONS AND CONCLUSIONS

Our analyses highlight how biotic ecosystem stressors, such as the globally common and increasing challenge of non-native invasive bivalves, can interact substantially with physical

habitat attributes. Our results are important globally because: (1) large numbers of aquatic ecosystems around the world have been, are becoming, or will be invaded by non-native bivalves (Strayer 1999, Karatayev et al. 2007) and, in contrast to other forms of pollution, invasions by non-native species, including bivalves, are viewed as extremely long-lasting or irreversible (Strayer et al. 1999, Mills et al. 2003, Lodge et al. 2006); (2) resource managers in all parts of the world are concerned with phytoplankton biomass and productivity, whether the problem is “too much”, “too little”, or an issue of community composition (Anderson 2009, Ramdani et al. 2009, Stich and Brinker 2010, Carstensen et al. 2011, Paerl and Paul 2012). The approaches and lessons presented are adequately generic to apply to low- and high-productivity systems alike, and to a broad range of aquatic ecosystem types including lakes, rivers, and estuaries (within model assumptions).

Our findings have important implications for restoration and management of our case study site. Numerous factors (e.g., historic loss of shallow aquatic habitat, hydrologic manipulation and channelization leading to decreased transport times, intense turbulent mixing, high turbidity, non-native grazers) may contribute to the Delta’s generally low primary productivity. In that ecosystem, abiotic factors may represent the most easily turned management “knobs”, e.g., creation of new habitats of a specified depth and/or manipulation of transport times by adjusting water diversion structures or habitat-scale geometry. Our results suggest that such abiotic controls on the system should not be manipulated without explicitly considering interactions with the other major biotic factors. If specific habitat depths and flow rates are targeted based only on interactions with the process of light-limited algal growth and neglect interactions with benthic grazers, the low-productivity problem could be exacerbated rather than alleviated. Moreover, if we examine Figs. 3E, F and 4 with the management goal of heightened Delta productivity in mind, we see how the non-native *C. fluminea* has constrained management options (Strayer et al. 2005): whereas in the absence of bivalves shallow, slow habitats would represent a reasonable restoration target, no obvious productivity-enhancing options appear if bivalve

grazing has the potential to be strong. In fact, those shallow, slow habitats could represent worse options than deep, fast habitats if bivalve grazing is rapid.

Our tools and findings are not only relevant to low-productivity systems like the Delta; they can also inform management of eutrophic environments. In high productivity systems with weak benthic grazing, the intuitive remedy of enhanced flushing could indeed help control excessive algal blooms, as could a deeper water column (unless stratification developed). With strong bivalve grazing, more sluggish horizontal transport and a shallower water column could enhance the ability of bivalves to graze down algal biomass. For systems without a significant bivalve population but susceptible to their invasion, our results provide an idea of how relationships between water depth, transport rate, and phytoplankton productivity could shift if an invasion occurs.

Although prediction of non-native species responses to ecosystem management is difficult, it is known that ecosystem disturbances such as habitat restoration can facilitate the spread or introduction of non-natives (Strayer et al. 2005). In addition, the widespread bivalve species considered herein (*C. fluminea*) is known to accumulate in the vicinity of high food concentrations (Vaughn and Hakenkamp 2001). Therefore, in invaded low-productivity systems like the Delta, it is possible that actions to increase phytoplankton biomass could lead to an increase in biomass of the non-native bivalve. Habitats specifically designed to be phytoplankton producers could be particularly susceptible to bivalve colonization, either within or just outside the habitats’ boundaries.

Given the interactions, complexities and uncertainties posed by non-native bivalves, how can ecosystem management proceed? Manipulation of controllable factors such as habitat geometry or flow rate should be conducted within the context and constraints of factors less easily controlled (e.g., non-native species). Mathematical models like those presented here can illuminate the relationships between the different stressor classes and reveal whether ranges for controllable factors exist that could allow management goals to be met with minimal uncertainty. Moreover, physical habitats may be

designed to minimize hospitality to non-natives. In the Delta, for example, floodplains may represent a promising restoration option toward increased productive habitat in part because seasonal drying precludes clam colonization (Sommer et al. 2004, ICF International 2012b).

In conclusion, we have used mathematical models and field observations to demonstrate how the relationships between ecosystem stressors and valued ecological functions can be changed by a non-native species. The specific interactions explored are those between two abiotic factors—water depth and hydrodynamic transport rate—and phytoplankton biomass and production. We show that intuitive rules-of-thumb regarding how to manipulate habitat depth or hydrodynamics for controlling primary productivity may not work if bivalve grazing is rapid. In fact, strong benthic grazing can reverse the phytoplankton-depth (or –transport time) relationship. Where bivalve grazing is potentially significant, shallower and hydrodynamically slower habitats are not necessarily characterized by higher phytoplankton biomass or productivity, so habitat depth and transport time should not be used as indicators of phytoplankton biomass and production. Because the competing processes of light-limited algal growth and depth-averaged benthic grazing loss are both amplified in shallow and slow systems, those environments are associated with a particularly wide range of potential outcomes and thus greater uncertainty regarding ultimate algal biomass and productivity. Management of abiotic factors, which are sometimes the most easily manipulated, should therefore be conducted with explicit consideration of interactions with other major (including biotic) stressors. Even simple mathematical models like those implemented here can reveal critical stressor relationships and provide guidance to resource managers as they create and implement plans to optimize valued populations and functions in continuously evolving ecosystems.

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## SUPPLEMENTAL MATERIAL

### APPENDIX

#### Model for Testing Hypothesis 1

Exploration of the general relationship between phytoplankton and water depth was carried out with a simple time-dependent model of growth, loss, and accumulation of phytoplankton biomass (as chlorophyll *a*) in a generic water column. The model was coded in Fortran. Solutions for water depths (*H*) of 0.05 m to 10 m were calculated numerically over 7 days using a 0.5 h time step ( $\Delta t$ ), and water columns were discretized vertically into cells of height 0.05 m. For an individual water column, depth was assumed to be constant in time; therefore, tidal oscillations in water depth were not accounted for. During each time step, vertically variable photosynthesis ( $p$ , mg C·(mg chl *a*)<sup>-1</sup>·h<sup>-1</sup>), gross growth ( $\mu_{\text{gross}}$ , 1/d), and net growth ( $\mu_{\text{net}}$ , 1/d, gross growth minus respiration) were computed at cell centers as a function of spatially and temporally varying irradiance. Growth rates were integrated numerically to obtain day-averaged and depth-averaged values. The time variation in growth rate was driven by the diurnal light cycle and a light attenuation coefficient ( $k_v$ , 1/m) that changed over time due to phytoplankton self-shading (Bannister 1974). Daily irradiance at the water surface ( $I_0$ , mol quanta·m<sup>-2</sup>·d<sup>-1</sup>) and daylength ( $D$ , h) were transformed into a diurnal light cycle centered around noon (Cloern et al. 1995) and then used to calculate exponentially decaying irradiance down through the water column (Lucas et al. 1998). Most parameters used in these generic calculations were based on measurements from the central Delta for June conditions (Edmunds et al. 1999, Lucas et al. 2002, Lopez et al. 2006; J. Edmunds, *personal communication*). To illustrate

seasonal variability of the  $\mu_{\text{net}}\text{-}H$  relationship, surface irradiance and daylength were varied; however, all other parameters (e.g.,  $p_{\text{max}}$  and  $a$ ) were kept constant since values were not available for all seasons.

Employing the assumption of vertical homogeneity, we combined growth and local loss processes into one index “ $\mu_{\text{eff}}$ ” (1/d) to represent the total “effective” growth rate of phytoplankton in a given water column (Lucas et al. 1999). The depth-averaged, day-averaged net growth rate ( $\langle \overline{\mu_{\text{net}}} \rangle$ ) was combined with zooplankton grazing rate ( $ZP$ , 1/d), water depth, and benthic grazing rate ( $BG$ , m<sup>3</sup>·m<sup>-2</sup>·d<sup>-1</sup>) as follows:

$$\mu_{\text{eff}} = \underbrace{\langle \overline{\mu_{\text{net}}} \rangle}_1 - \underbrace{ZP}_2 - \underbrace{\frac{BG}{H}}_3 \quad (\text{A1})$$

(Angle brackets represent a day-average, and an overbar represents a depth-average.)  $ZP$  is presumed uniform in the vertical dimension. Therefore, any variation of  $\mu_{\text{eff}}$  with water depth in our calculations is due to terms 1 and 3 in Eq. A1; a change in  $ZP$  merely shifts  $\mu_{\text{eff}}$  independent of  $H$ . Phytoplankton biomass  $B$  (mg chl *a*/m<sup>3</sup>) was advanced through time according to:

$$B(t + \Delta t) = B(t)\exp(\mu_{\text{eff}}\Delta t/24.0) \quad (\text{A2})$$

where  $t$  is time in hours. Depth-averaged, day-averaged phytoplankton net primary productivity ( $NPP$ , mg C·m<sup>-2</sup>·d<sup>-1</sup>) was calculated as:

$$NPP = \langle B \cdot \overline{\mu_{\text{net}}} \cdot H \cdot [C:\text{chl}] \rangle \quad (\text{A3})$$

The numerical approach employed here for calculating phytoplankton growth rate is more computationally intensive than other estimation approaches (see below), but was implemented for these particular calculations because of its higher accuracy, especially for very small  $H$ ,



given our goal of performing these calculations over a range of water depths. Further details regarding calculations and parameters are contained in Table 1.

### Model for Testing Hypothesis 2

To explore the general relationship between phytoplankton and transport time, we extended the following simple model describing the streamwise distribution of phytoplankton biomass within an idealized aquatic habitat under steady-state, (unidirectional) plug-flow conditions (Lucas et al. 2009b):

$$B(x) = B_{\text{in}} \exp\left(\frac{\mu_{\text{eff}} x}{u}\right) \quad (\text{A4})$$

The one-dimensional habitat under consideration has length  $L$  (m), and the variable  $x$  describes distance along the streamwise habitat axis, with  $x = 0$  at the upstream boundary (or inlet) and  $x = L$  at the downstream boundary (or outlet). Water and phytoplankton are advected through the habitat with velocity  $u$  (m/d).  $B_{\text{in}}$  is the biomass concentration entering the habitat through the inlet.

Integration of Eq. A4 over the habitat length and estimation of transport time through the habitat as  $\tau_{\text{tran}} = L/u$  (a “transit time”) results in the following expression for steady-state biomass averaged over the entire habitat length (in mg chl  $a/m^3$ ):

$$B_{\text{hab}} = \frac{B_{\text{in}}}{\mu_{\text{eff}} \tau_{\text{tran}}} [\exp(\mu_{\text{eff}} \tau_{\text{tran}}) - 1] \quad (\text{A5})$$

We selected a relatively shallow  $H$  (3 m) and, from the calculations described in the previous section for June conditions, obtained the corresponding  $\langle \mu_{\text{net}} \rangle$  for day 1 of that simulation (0.8 1/d). We combined that  $H$  and  $\langle \mu_{\text{net}} \rangle$  with  $ZP$  and a reasonable range of  $BG$  (see Table 1) to calculate  $\mu_{\text{eff}}$  (Eq. A1) for each  $BG$ . Effective growth rate is imposed uniformly throughout the habitat (it is not calculated dynamically, so in this model time dependent processes such as self-shading are not explicitly incorporated).  $B_{\text{in}}$  was set equal to  $B_0$  (see Table 1). For each  $BG$  (and associated  $\mu_{\text{eff}}$ ), Eq. A5 was used to compute  $B_{\text{hab}}$  for transport times ranging from 0-7 d and results were checked against a numerical integration of Eq. A4. Because the analytical expression above experiences singularities at  $\mu_{\text{eff}} = 0$  (a case of

interest herein) and  $\tau_{\text{tran}} = 0$ , the numerical results are presented. (We include Eq. A5, nonetheless, because of its potential usefulness.)

$NPP(x)$ , net primary productivity at location  $x$  within the habitat, was estimated as  $B(x)[C:chl]/\langle \mu_{\text{net}} \rangle H$  (in mg C·m<sup>-2</sup>·d<sup>-1</sup>). Making use of Eq. A4 and once again integrating over habitat length  $L$ , we obtained the following analytical expression for steady-state habitat-averaged net primary productivity (in mg C·m<sup>-2</sup>·d<sup>-1</sup>):

$$NPP_{\text{hab}} = \frac{B_{\text{in}}[C:chl]\langle \mu_{\text{net}} \rangle H}{\mu_{\text{eff}} \tau_{\text{tran}}} [\exp(\mu_{\text{eff}} \tau_{\text{tran}}) - 1] \quad (\text{A6})$$

As with  $B_{\text{hab}}$ , results from Eq. A6 were checked against a numerical solution for transport times ranging from 0-7 d and, due to the singularities at  $\mu_{\text{eff}} = 0$  and  $\tau_{\text{tran}} = 0$ , the numerical results are presented. Calculations were performed in Matlab.

### Effective Growth Rate Estimates for a Real Aquatic System

A map of effective growth rate across the Delta was produced, using measurements of benthic biomass (F. Parchaso and J. K. Thompson, *personal communication*), solar irradiance, and water quality over three time periods (August 2001, April–June 2002, May 2003). Eq. A1 was used to estimate  $\mu_{\text{eff}}$ . Water depths are based on instantaneous depth soundings aboard sampling vessels.

To estimate clam grazing rate, benthic samples were collected to estimate *C. fluminea* biomass (g ash-free dry weight/m<sup>2</sup>) using a 0.05-m<sup>2</sup> van Veen grab. Clams retained on a 0.5-mm sieve were preserved in 10% formalin, followed by 70% ethyl alcohol. Dry weight of each individual clam was either measured directly (Crisp 1971) or estimated using length-weight relationships developed for each location and sampling period. *C. fluminea* pumping rate (ml·[mg dry tissue wt]<sup>-1</sup>·h<sup>-1</sup>) was estimated using published dry weight-pumping rate data and adjusting for water temperature (Foe and Knight 1986). The effect of algal depletion in near-bed concentration boundary layers was conservatively accounted for following O’Riordan et al. (1995) to arrive at a modified pumping rate or “grazing rate” (m<sup>3</sup>·m<sup>-2</sup>·d<sup>-1</sup>).

In these calculations for real sites across the Delta, net phytoplankton growth rate was estimated using an empirical formulation for primary productivity shown to work well in nutrient rich systems, including the Delta (Cole and Cloern 1987, Jassby et al. 2002, Brush et al. 2002). This “BZI” (for “biomass-photic depth-irradiance”) approach is simple and computationally efficient, and can circumvent the need to assign case-specific photosynthesis-irradiance parameters ( $p_{\max}$ ,  $a$ ) which can vary by an order of magnitude across seasons and habitats within an ecosystem (Edmunds et al. 1999). Since the basic BZI relationship does not hold for water columns shallower than the photic depth, a correction factor ( $\%P_t$ ) was implemented (Brush and Brawley 2009). Combining the corrected BZI formulation with an empirical relationship for respiration (Cloern et al. 1995; Table 1), the following expression was derived for water column net phytoplankton growth rate:

$$\langle \overline{\mu_{\text{net}}} \rangle = \frac{0.85(\%P_t)(4.61 \cdot \psi \cdot I_0)}{100[C:chl]H \cdot k_t} - 0.015 \quad (\text{A7})$$

(Although strict depth- and time-averaging is not used to obtain this net growth rate estimate, we use the overbar and angle brackets to convey that this is a daily, water column value generally comparable to the numerical estimate described above.)  $\psi$  is the empirical constant found by fitting the BZI to primary productivity measurements across seasons and habitats in the Delta (Jassby et al. 2002;  $\psi = 0.728$ ,  $R^2 = 0.952$ ). As for

other parameters implemented in these calculations,  $\psi$  may vary between and spatially or temporally within systems (Brush et al. 2002). An increase (decrease) in  $\psi$  would increase (decrease) estimated primary productivity and the likelihood that an environment is growth-dominated. Direct measurements of light attenuation coefficient (i.e., from measured irradiance profiles) were not available for all sampling stations and dates; therefore, a variety of methods was implemented to obtain  $k_t$  for these calculations. Eq. A7 was not implemented in the generic water column (hypothesis testing) computations described above because, for the parameter combinations explored here, its behavior deviates significantly from the more accurate numerical approach for  $H$  less than about 0.5 m. Moreover, the generic calculations allowed for the selection of a single  $p_{\max}$ - $a$  pair. Habitats with  $-0.1 < \mu_{\text{eff}} < 0.1$  (in 1/d) were classified as approximately balanced between growth and loss; habitats with estimated  $\mu_{\text{eff}} \geq 0.1$  were classified as growth-dominated; and habitats with estimated  $\mu_{\text{eff}} \leq -0.1$  were classified as loss-dominated. See Table 2 for further details on calculations and parameters.

## SUPPLEMENT

Fortran and Matlab files for conducting model calculations described in the main text (*Ecological Archives* C003-014-S1).