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Phytoplankton Regulation in a Eutrophic Tidal River (San Joaquin River, California)

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ABSTRACT

As in many U.S. estuaries, the tidal San Joaquin River exhibits elevated organic matter production that interferes with beneficial uses of the river, including fish spawning and migration. High phytoplankton biomass in the tidal river is consequently a focus of management strategies. An unusually long and comprehensive monitoring dataset enabled identification of the determinants of phytoplankton biomass.
Phytoplankton carrying capacity may be set by nitrogen or phosphorus during extreme drought years but, in most years, growth rate is light-limited. The size of the annual phytoplankton bloom depends primarily on river discharge during late spring and early summer, which determines the cumulative light exposure in transit downstream. The biomass-discharge relationship has shifted over the years, for reasons as yet unknown. Water diversions from the tidal San Joaquin River also affect residence time during passage downstream and may have resulted in more than a doubling of peak concentration in some years. Dam construction and accompanying changes in storage-and-release patterns from upstream reservoirs have caused a long-term decrease in the frequency of large blooms since the early 1980s, but projected climate change favors a future increase. Only large decreases in nonpoint nutrient sources will limit phytoplankton biomass reliably. Growth rate and concentration could increase if nonpoint source management decreases mineral suspensoid load but does not decrease nutrient load sufficiently. Small changes in water storage and release patterns due to dam operation have a major influence on peak phytoplankton biomass, and offer a near-term approach for management of nuisance algal blooms.

KEYWORDS

blooms, climate, dams, estuary, light, nutrients, phytoplankton, rivers, streamflow, turbidity

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INTRODUCTION

Most estuaries in the U.S. exhibit moderate to high eutrophic conditions and elevated macronutrient concentrations (Bricker et al. 1999). Increased organic matter production and depleted dissolved oxygen are common symptoms, resulting in habitat loss, fish kills, and sometimes offensive odors. The tidal San Joaquin River, one of two major rivers draining into the San Francisco Estuary, is representative of this general pattern. Phytoplankton chlorophyll *a* concentrations sometimes exceed 400 µg L^{-1} in summer and, downstream, the river frequently exhibits low dissolved oxygen conditions, annually violating regional water quality objectives. This chronic hypoxia interferes with several beneficial uses of the river, including spawning and migration of warm (striped bass, sturgeon, and shad) and cold (Chinook salmon and steelhead) freshwater fishes, as well as warm and cold freshwater species habitat (CVRWQCB 1998, 2003). Phytoplankton biomass transported from upstream of low dissolved oxygen locations is considered to be a major source of oxygen-demanding materials and has been the focus of management activities.

Most estuaries exhibiting eutrophic conditions are also moderately to highly influenced by anthropogenic nutrient inputs (e.g., wastewater treatment plant effluent and agricultural drainage), which have therefore been identified as the most important management targets on a national basis. It is natural to assume that such a course is also warranted for the San Joaquin River because of intense agriculture and animal husbandry throughout its watershed, resulting in nutrient inputs within and upstream of the estuary. However, many uncertainties surround the regulation of phytoplankton biomass in tidal rivers, and regional differences in nutrient sources and estuarine functioning are significant. Cloern (2001) has emphasized the spectrum of estuarine responses to increased nutrient loading—from resistant to highly sensitive. He showed that a variety of attributes can act as a filter to modify effects of excessive nutrients, including strength of tidal mixing, magnitude of horizontal transport, water clarity, and abundance of benthic suspension-feeders. The early conceptual model linking nutrient loading inexorably to biomass accumulation, derived largely from experience with lakes, is now understood to be inadequate for understanding estuarine systems, including their tidal river reaches.

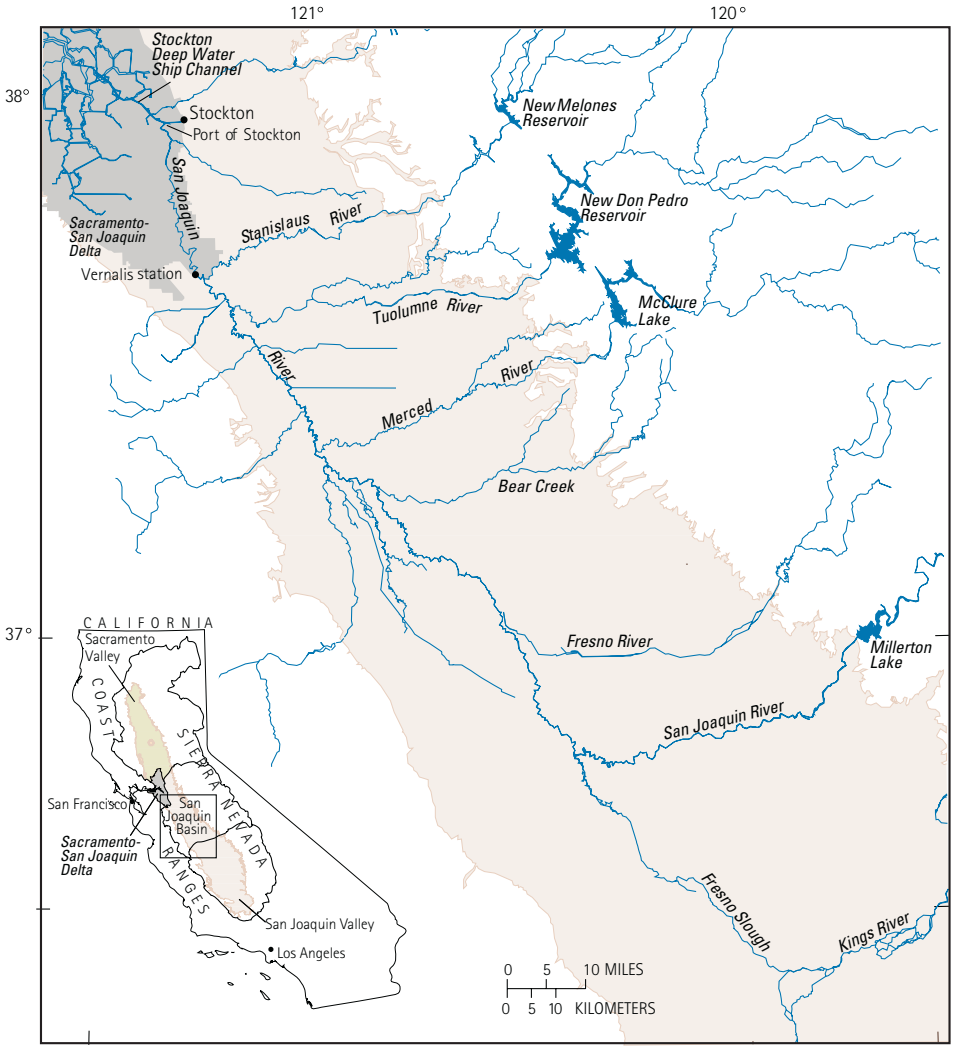

Figure 1. Map of the San Joaquin Basin and River, including a portion of the Delta (modified from Figure 1 of Kratzer et al. 2004, with permission).

What, then, controls phytoplankton biomass in the tidal San Joaquin River upstream of major diversions and low dissolved oxygen conditions; how will reduction in nutrient loading affect existing phytoplankton levels; and what other opportunities exist to manage phytoplankton in this river reach? Strategies for phytoplankton regulation in this subregion of the estuary must also consider the negative consequences of *low* phytoplankton biomass. The tidal river is one of the few productive habitats for an estuarine food web that otherwise appears to be relatively unproductive and food-limited (Sobczak et al. 2002), and the small centric diatoms that dominate the reach are a highly nutritious base for the food web supporting higher organisms. The goal, then, should not be to aim for arbitrarily low levels, but rather to explore ways in which phytoplankton biomass can be regulated more finely, if possible.

The large collection of retrospective data for the upper estuary is a useful resource for understanding phytoplankton regulation in the San Joaquin River. Several government agencies have maintained monitoring programs for decades, mostly for determining compliance with water quality objectives. This dataset—the result of a sustained commitment to environmental monitoring by the California departments of Water Resources and Fish and Game and the U.S. Bureau of Reclamation—is exceptional in its spatial coverage, its duration, and its multiplicity of measured variables. It has proven useful for analyses of long-term trends and interannual variability in primary productivity, phytoplankton biomass, and phytoplankton community composition in various subregions of the Delta (Lehman 2000, Jassby et al. 2002). Particularly important for the San Francisco Estuary is a dataset that encompasses drought and flood years. Interannual variability in freshwater flow to this estuary is high, and the biota show one of the strongest and broadest responses to flow among large estuaries (Kimmerer 2002). Conclusions from a single year or a small subset of climatic conditions are likely to be misleading. Here, the Delta dataset is used to evaluate the regulating factors for phytoplankton biomass in a turbid, nutrient-enriched tidal river and, more specifically, to improve understanding of the lower San Joaquin River system.

Study area

The tidal San Joaquin River is located in the upper part of the estuary known as the Delta, a mosaic of waterways linking the Sacramento and San Joaquin rivers of northern California to the downstream embayments comprising San Francisco Bay; together, the Delta and Bay form the San Francisco Estuary. The San Joaquin River extends from the westernmost Delta upstream past the city of Fresno, draining a watershed area of about 19,000 km^2 (Kratzer et al. 2004; Figure 1). Its river valley is a major center of agricultural production. Despite the loss of most of its wetlands, it also remains a critical habitat for fish and wildlife, including many federally-listed threatened and endangered plants and animals (CVRWQCB 2003). Hydrology of the river and its major tributaries—the Merced, Tuolumne, and Stanislaus rivers—upstream of the Delta is highly managed through dams, diversions, and artificial conveyances. The river reaches the southern boundary of the Delta near the town of Vernalis, where estuarine tides begin to affect its flow (Figure 2). The long-term (1956-2002) mean flow at Vernalis is about 130 $m^3\ s^{-1}$, with annual means ranging from 13 $m^3\ s^{-1}$ in 1961 to 650 $m^3\ s^{-1}$ in 1983 (IEP 2003). Further downstream, a portion of the water is diverted down Old River to large pumping facilities feeding the State Water Project and federal Central Valley Project, where it is exported for agricultural, industrial, and domestic use. Annually, temporary barriers have been placed at the head of Old River to increase flows down the mainstem, with the intention of alleviating low dissolved oxygen conditions downstream and facilitating Chinook salmon migration (see Methods). Water is also diverted for irrigation in the Delta by more than 2000 siphons; much of this water is lost to evapotranspiration, although some returns through many agricultural return flows. The river averages about 3 m in depth and 50 m in width between the Vernalis station and the Stockton Deep Water Ship Channel (Ship Channel), a portion of the river between San Francisco Bay and the city that has been dredged to allow the passage of ocean-going vessels to the Port of Stockton. Just upstream of the Ship Channel, the Regional Wastewater Control Facility (RWCF) discharges its effluent into the river. The river enters the Ship Channel at the eastern point of Rough and Ready Island. River width increases to about 75 m

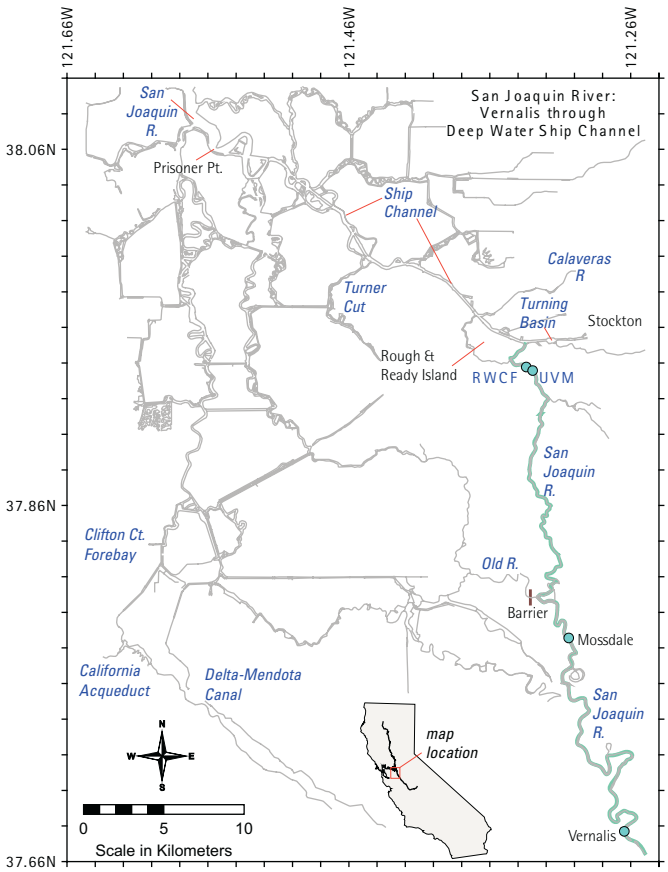

Figure 2. The San Joaquin River from Vernalis through the Stockton Deep Water Ship Channel. The locations of the Vernalis and Mossdale long-term monitoring stations are indicated, as well as the Regional Wastewater Control Facility effluent (RWCF) and tidal velocity station (UVM). *Green line*, tidal portion of the river upstream of the Ship Channel.

in the Ship Channel, and the Channel is dredged to a depth of about 11 m between the Port of Stockton and the Bay. The tidal range is about 1.5 m in this region. Low dissolved oxygen conditions occur in the Ship Channel approximately from the Turning Basin at the Port of Stockton downstream to Turner Cut.

METHODS

Data sources

A variety of data sources was used in this study. Of particular note is the discrete water quality monitoring program originally started by the U.S. Bureau of Reclamation in the late 1960s. It is now carried out jointly with the California Department of Water Resources, assisted by the California Department of Fish and Game and the U.S. Geological Survey, under the auspices of the Interagency Ecological Program's Environmental Monitoring Program (EMP). Data are collected from throughout the Delta on an approximate monthly basis. The number of monitoring stations has ranged from a high of 26 to the current 11 stations. The program's primary purpose is to provide information for compliance with flow-related water quality standards specified in water rights permits that allow export by the state and federal water projects. This data set, unusual in its spatial and temporal coverage, as well as the variety of variables considered, is the main evidence used in this analysis of water quality in the San Joaquin River upstream of the Ship Channel. The two stations relevant to this study are the Vernalis and Mossdale stations (Figure 2) on the tidal river upstream of the Ship Channel. Samples are collected from about 1 m below the surface only, which necessitates the assumption that this shallow river reach is well-mixed vertically. Water quality variables utilized here include chlorophyll *a*, phytoplankton taxa, total suspended solids and turbidity, vertical light attenuation, total nitrogen and phosphorus, silica, and temperature. A description of the sampling and analytical methods is available (IEP 2004). Triboli et al. (2004) examine in detail the methodology for chlorophyll, the most important measurement considered in this study. The longest record for chlorophyll *a* is at Vernalis, where it has been measured regularly since 1969. The time series for Mossdale began in 1975 and was stopped in 1995. Within each time series, the data gaps are few.

Phytoplankton and optical parameters

The long-term dataset indexes phytoplankton biomass in terms of chlorophyll *a*. Chlorophyll *a* must be converted to organic carbon in order to estimate nutrient content of phytoplankton cells. Cloern et al. (1995) developed an empirical expression for the chlorophyll *a* to carbon ratio (Chl:C) in terms of temperature, mean water column irradiance, and nutrient concentration:

$$\text{Chl:C} = 0.003 + 0.0154\left(\frac{N}{k_n + N}\right)\exp(0.050T)\exp(-0.059 I_{av}) \quad (1)$$

where T (°C) is water column temperature, I_{av} (mol m^{-2} d^{-1}) is daily photosynthetically active radiation (PAR) averaged over the mixed layer, N (mg L^{-1}) represents the concentration of the growth-limiting nutrient, and k_n (mg L^{-1}) the half-saturation constant that defines sensitivity of growth to changes in nutrient concentration. The equation was based on 12 published studies involving 219 different growth conditions for unialgal cultures, mostly of coastal and estuarine diatoms. As discussed below, nutrient limitation rarely occurs in the Delta and especially the San Joaquin River upstream of the Ship Channel. The assumption that $N/(k_n + N) = 1$ is therefore made in this study. Assuming an exponential decline of PAR with depth and a well-mixed water column, average PAR can be described by

$$I_{av} = \frac{I_0}{K_d H}\left[1 - \exp\left(-K_d H\right)\right] \tag{2}$$

where I_0 (mol m^{-2} d^{-1}) is PAR just below the water surface, K_d (m^{-1}) is the vertical attenuation coefficient for downwelling PAR, and H (m) is average water depth. I_0 values were based on daily irradiance for Davis, California, the nearest location for which a complete irradiance record is available (CDWR 2004a). A factor of 0.18 was used to convert daily mean irradiance (W m^{-2}) to PAR quantum irradiance (mol quanta m^{-2} d^{-1}), assuming PAR is 45% of total irradiance and a conversion of 2.77 x 10^{18} quanta s^{-1} W^{-1} for PAR (Morel and Smith 1974). Because K_d measurements are available for only a portion of the record (1975-1979 at Vernalis and 1975-1986 at Mossdale), K_d was estimated using combined data from Mossdale and Vernalis ($R^2 = 0.65$, $n = 296$, $P < 0.001$):

$$\ln K_d = -\left(0.49 \pm 0.08\right) + \left(0.51 \pm 0.02\right) \ln M \tag{3}$$

where M (mg L^{-1}) refers to particulate matter as estimated by total suspended solids, and coefficient values ± standard errors are shown explicitly. Thus, K_d is approximately proportional to $M^{0.5}$.

Instantaneous values of average water column PAR also must be estimated in order to assess light limitation. Daylength Γ (h) was determined from latitude (Forsythe et al. 1995), and mean *daily* irradiance was converted to mean *daylight* irradiance based on daylength. Maximum irradiance I_{max} (µmol m^{-2} s^{-1}) was estimated based on the ratio of maximum to mean daylight, using a simple sinusoidal light curve to describe diurnal surface irradiance (Platt et al. 1990). Average water column values were then obtained from Equation 2.

The general procedure of Reynolds and Maberly (2002) was used to estimate the phytoplankton carrying capacity from macronutrient availability. Total nitrogen (N_{tot}) and total phosphorus (P_{tot}) were used to calculate carrying capacities for nitrogen and phosphorus, in order to determine maximum values and to avoid the uncertainty in estimating the bioavailable fraction of nutrients. Carrying capacities are therefore overestimates. The theoretical stoichiometric yield of phytoplankton cell carbon is C:N = 5.7 and C:P = 41 (Stumm and Morgan 1981). The carrying capacity in chlorophyll *a* units for nitrogen is then simply N_{tot}(C:N)(Chl:C), and for phosphorus, P_{tot}(C:P)(Chl:C). This approach differs from Reynolds and Maberly's, however, in that the Chl:C ratio was not considered to be constant. Rather, Equation 1 was used. Because the C:Si ratio for diatoms is highly variable among taxa, a carrying capacity for silicon was not estimated.

The derived equation of Reynolds (Reynolds and Maberly 2002) was used to estimate the supportive capacity of light, B_{max} (µg chlorophyll *a* L^{-1}):

$$B_{max} = \frac{1}{\kappa}\left[\frac{0.75 P_r \Gamma}{24 H} \ln\left(\frac{1.4 I_{max}}{I_k}\right) - K\right] \tag{4}$$

where P_r is the dimensionless ratio of maximum photosynthetic rate to basal respiration rate at the same temperature, I_k (µmol m^{-2} s^{-1}) is PAR at the onset of light saturation. κ [m^2 (mg chlorophyll *a*)$^{-1}$] is the vertical light attenuation due to chlorophyll *a*, and K (m^{-1}) is the non-phytoplankton-associated vertical light attenuation. By definition, they are related to the vertical attenuation coefficient K_d as follows:

$$K_d = \kappa B + K \tag{5}$$

The parameter values suggested by Reynolds and Maberly (2002) were also used: $\kappa = 0.01$, $P_r = 15$, and $I_k = 20$. Γ and I_{max} were determined as above. K was estimated from Equation 5. There is much uncertainty in the parameter values chosen by Reynolds and Maberly (2002), and therefore corresponding uncertainty in the estimates of B_{max}. Although there are other ways to arrive at maximum biomass estimates, they all suffer from similar uncertainties.

Growth rate estimates are required to understand the demands on nutrient resources in transit to the Ship Channel. Daily gross primary production P (mg C m^{-2} d^{-1}) is described well in the Delta by

$$P = 4.61 \frac{\Psi B I_0}{K_d} \tag{6}$$

where Ψ [mg C (mg chlorophyll a)$^{-1}$ (mol m^{-2})$^{-1}$] is the water column light utilization efficiency and B (µg L^{-1}) is chlorophyll a concentration. This relationship is based on theoretical considerations for low light conditions and has been shown experimentally to apply to Delta primary productivity (Cole and Cloern 1987). It follows that growth rate r (d^{-1}) can be expressed in terms of P by

$$r = (1-\rho_0)\frac{P}{B}\frac{(\text{Chl:C})}{H} - \rho_1 = 4.61(1-\rho_0)\Psi(\text{Chl:C})\frac{I_0}{K_d H} - \rho_1 \tag{7}$$

where respiratory losses are divided into a photosynthesis-dependent fractional loss ρ_0 and a basal metabolic loss ρ_1 (d^{-1}). The term (Chl:C)/H simply converts volumetric chlorophyll a concentrations B into areal carbon concentrations. The right-hand side has been written to emphasize the physical interpretation: Ψ(Chl:C) is the efficiency with which light is manifested as growth rate, and $I_0/K_d H$ is the mean light in the water column assuming, as in the San Joaquin River, that essentially all light is absorbed before the bottom. The efficiency Ψ is taken to be 0.73 (Jassby et al. 2002). Values for the respiration parameters are based on the study of Cloern et al. (1995), who summarized empirically the results of many experiments in the literature in which both photosynthesis and growth rates were measured: $\rho_0 = 0.15$ and $\rho_1 = 0.015$. The estimation of Chl:C is also based on the latter study, as described above.

Hydrological estimates

Values of net discharge into the Ship Channel are also necessary to estimate phytoplankton demands on river nutrients. The U.S. Geological Survey has operated an Ultrasonic Velocity Meter (UVM) station in the San Joaquin River just upstream of the Ship Channel since August 1995 (http://sfbay.wr.usgs.gov/access/delta/tidalflow; Figure 2). A 15-minute interval UVM tidal flow record is computed and converted to discharge using water-surface elevation, channel geometry survey data, and Acoustic Doppler Current Profiler measurements.

The best estimate of historical mean daily flows in the Delta is obtained with Dayflow, a computer program developed in 1978 as an accounting tool for determining historical Delta boundary hydrology (IEP 2003). Input data include monitored and estimated values of the principal stream inflows, precipitation, exports from the Delta, and diversions and drainage within the Delta. Output data include discharge rates at important locations throughout the Delta, based on input data and mass balance calculations. Dayflow output itself does not contain estimates of discharge into the Ship Channel, but the question naturally arises as to whether a surrogate net flow series can be constructed by determining a relationship between net discharge measurements and Dayflow variables. The largest effects on tidally-averaged net flow should be the upstream flow in the San Joaquin River and the split in flow taking place at the head of Old River. The latter is driven by exports from the Delta into the federal Central Valley Project and State Water Project. Estimates of San Joaquin River discharge at Vernalis and of exports are available from Dayflow output (http://iep.water.ca.gov/dayflow).

Net flow is also affected by the presence of a temporary rock barrier—the Head of Old River barrier—constructed annually at the confluence of the Old and San Joaquin rivers to protect migrating Chinook salmon from the federal and state pumping plants (http://sdelta.water.ca.gov/web_pg/tempmesr.html). The

barrier has been in place most years since 1963 for some portion of the period September 15-November 30. It was also installed in 1992, 1994, 1996, 1997, 2000, 2001, 2002, and 2003 for some portion of the period April 15-May 30. A monthly variable B_{hor} was defined equal to the actual proportion of the entire month during which the barrier was in place. Because installation and removal take more than one day, the barrier was assumed to be in place from the installation completion date until the removal completion date.

Net flow was estimated by

$$Q_{net} = c_0 + c_1 Q_{vern} + c_2 Q_{exp}(1 - B_{hor}) \tag{8}$$

where Q_{net} ($m^3\ s^{-1}$) is monthly mean net flow into the Ship Channel, Q_{vern} ($m^3\ s^{-1}$) is monthly mean flow at Vernalis, and Q_{exp} ($m^3\ s^{-1}$) is monthly mean water export from the Delta. The effect of the barrier is complicated by the addition of culverts in recent years that allow some flow through the barrier, and by temporary rock barriers installed further downstream on Old River to increase water levels in south Delta sloughs, primarily for agriculture diversions. Neither complication is reflected in B_{hor}.

Unimpaired discharge or full natural flow represents the natural water production of a river basin, unaltered by upstream diversions, storage, or by export or import of water to or from other watersheds. We estimated monthly unimpaired runoff at Vernalis from the sum of estimates for the Stanislaus, Tuolumne, Merced, and San Joaquin rivers. These flows are based on calculations done by project operators on the respective rivers, the U.S. Army Corps of Engineers, and/or California Cooperative Snow Surveys. The San Joaquin Valley Water Year Hydrologic Classification identifies each water year (extending from October 1 of the previous calendar year through September 30) as one of five types, depending on unimpaired discharge: critical, dry, below normal, above normal, and wet. Exact definitions and data for unimpaired discharges and water year type are available at the California Data Exchange Center (CDWR 2004b).

Data analyses

Unless otherwise stated, replicate samples for all variables have been averaged and data within the same month aggregated by their median, in order to avoid bias when comparing seasons with different amounts of raw data. When necessary, small gaps in monthly time series were imputed using a time series modeling procedure known as TRAMO (Time series Regression with ARIMA noise, Missing observations, and Outliers; Gómez and Maravall 2002), which retains the autocorrelation structure in the series. When assessing trends by month in time series, a robust measure—sometimes known as the Theil trend—is used. This is simply the median slope of the lines joining all pairs of points in the series. The Kendall-tau test can be used to determine the significance of the trend (Helsel and Hirsch 1992).

Principal component analysis (PCA) of monthly time series was used to investigate interannual variability (Jassby 1999). PCA in this context of time series analysis reveals the number of independent underlying mechanisms, sometimes called modes of variability, that together combine to produce the overall interannual variability. Consider, for example, a hypothetical case in which the year-to-year variability of river phytoplankton is due to both discharge variability during May-August and grazing variability in July-October. As long as the two mechanisms are not highly correlated among years, PCA will identify that there are two mechanisms; the importance of each mechanism seasonally; and their strength from one year to the next. These features often provide strong constraints on the underlying mechanisms while also providing clues for their identity. The time series is first reshaped into a years × months data matrix. Principal components (PCs) were estimated by singular value decomposition of the covariance matrix of the data matrix. The number of significant PCs was determined using used a Monte Carlo procedure known as Rule N (Overland and Preisendorfer 1982).

Restricted cubic splines were used as transforms for predictors in regression relationships (Harrell 2001). A cubic spline is a piecewise polynomial of order three that is smooth (specifically, it has continuous first and second derivatives) at the knots (i.e., points joining the

different polynomial pieces). A restricted cubic spline or natural spline is further constrained by being linear beyond the outer knots. The use of splines in general and restricted cubic splines in particular has many advantages over other methods in representing nonlinear functions in a regression model when the exact form of the nonlinearity is unknown. To minimize the number of parameter estimates, a restricted cubic spline with only three knots was used, requiring only two parameters. The knot positions—at the 0.1, 0.5, and 0.9 quantiles—were chosen based on general recommendations from simulation studies, and were not tailored in any way for the current data set. The spline functions can therefore be described in general by

$$f(x) = b_1 x + b_2[(x-k_1)_+^3 - (x-k_2)_+^3 (k_3-k_1)/(k_3-k_2) + (x-k_3)_+^3 (k_2-k_1)/(k_3-k_2)] \quad (9)$$

where b_1 and b_2 are constant coefficients, the k_i are the 0.1, 0.5, and 0.9 quantiles of x, and

$$y_+ = \begin{cases} 0 & y \le 0 \\ y & y > 0 \end{cases} \quad (10)$$

Multivariate regression model results are illustrated as partial residual plots, which attempt to show the relationship between a given independent variable and the response variable, while accounting for the other independent variables in the model. Specifically, a partial residual plot here refers to a plot of $r_i + b_k x_{ik}$ versus x_{ik}, where r_i is the ordinary residual for the i-th observation, x_{ik} is the i-th observation of the k-th predictor, and b_k is the regression coefficient for the k-th predictor.

RESULTS

Historical time series

Interannual variability in chlorophyll *a* is strong (Figure 3A and B). Phytoplankton at both Vernalis and Mossdale can reach very high concentrations. Monthly medians reached 337 µg/L in August 1977 during the extreme dry El Niño-Southern Oscillation event (ENSO) of 1976-1977. The record individual measurement of 499 µg/L was taken on 18 June 1992 during the last year of a six-year drought. At the other extreme, concentrations remained below 10 µg/L the entire year

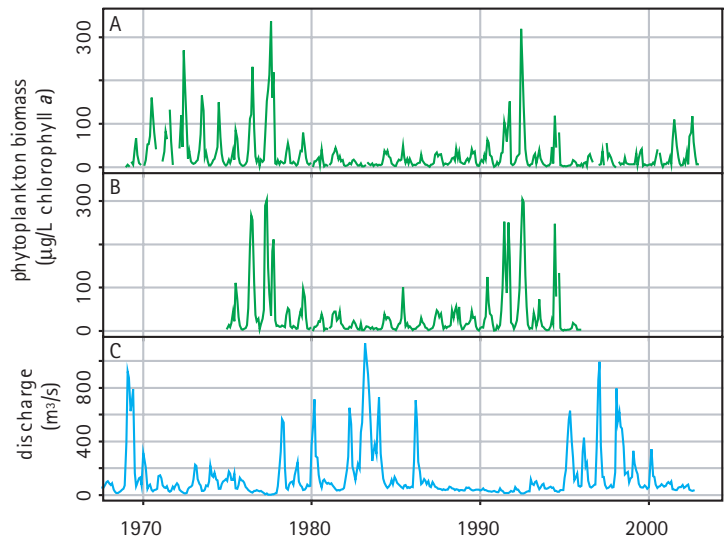

Figure 3. Monthly time series of (A) chlorophyll *a* at Vernalis; (B) chlorophyll *a* at Mossdale; and (C) San Joaquin River discharge at Vernalis.

during the extreme wet event of 1983. A principal component analysis of the Vernalis time series demonstrated that there was only one significant mode of interannual variability, accounting for 72% of the overall variability (Figure 4A). This mode was centered in June-August, the period when phytoplankton almost always reaches its annual maximum (Figure 4B), although there is one case each of the annual chlorophyll maximum occurring in May (1983), September (2000), and October (1991). Interannual variability is thus determined by the size of the annual chlorophyll *a* peak, and the time series of maximum annual chlorophyll *a* concentrations contains almost as much information as the time series of monthly values. Regulation of the annual chlorophyll *a* peaks is therefore the relevant focus for understanding interannual variability.

The seasonal pattern also reflects precipitation and runoff, with lowest values of chlorophyll *a* typically in December-January during the wet season, and highest values typically in July-August during the dry season (Figure 3C). The maximum biomass at Mossdale was typically higher than at Vernalis by a mean of 32 ± 8% (standard error). Only 4 of 21 years showed a downstream decrease: 2 of these were the extreme dry

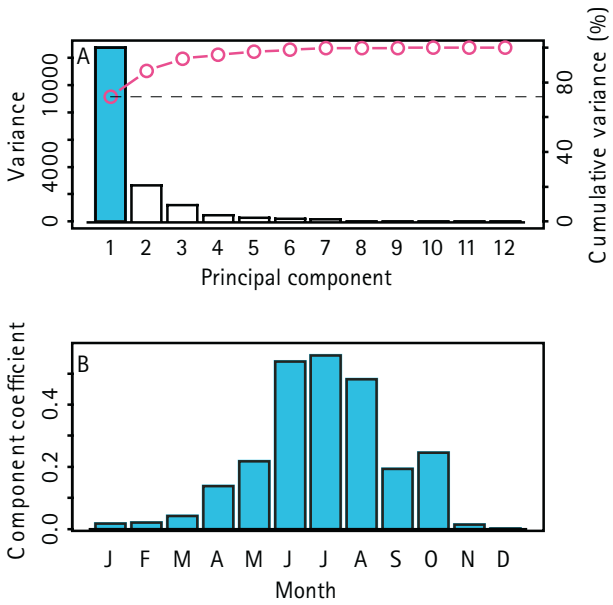

Figure 4. Principal component analysis of the chlorophyll *a* monthly time series. (A) Variance (bars) and cumulative variance (circles) corresponding to each principal component. *Shading,* statistically significant according to Rule N ($P < 0.05$). (B) Coefficients for the first principal component.

years 1977 and 1992, and all 4 showed a decrease of less than 5%. The phytoplankton is thus usually in its (longitudinal) increasing phase in this reach. The summer biomass peaks at the Vernalis and Mossdale stations were almost always dominated by small centric diatoms characteristic of turbid, well-mixed rivers, most commonly of the genera *Cyclotella* and *Thalassiosira* (20 of 27 years, 1975-2001). Leland et al. (2001) found similar dominants in their four-year study of algal species composition in the San Joaquin River upstream of Vernalis, implying a continuity of the main populations along the mainstem.

Resource constraints on carrying capacity and growth rates

To determine if resource availability controlled phytoplankton biomass, the carrying capacity for each macronutrient and for incident light was estimated for the time when annual peak chlorophyll *a* occurred. Data for Mossdale were used, because biomass usually increases between Vernalis and Mossdale and approaches carrying capacity more closely at the latter station. Carrying capacities are surprisingly similar for macronutrients and light (Figure 5). On average, observed peak chlorophyll *a* values reach only a small percentage of the carrying capacity, from 10% (light) to 13% (phosphorus). They are also less than 50% of the carrying capacity in almost all years for each resource. In the extreme dry years such as 1976-77 and 1991-92, however, they can be more than 50% of carrying capacity: The maximum percentages are 59% for light (1977), and 69% for nitrogen (1977) and 66% for phosphorus (1991). The latter two percentages show that at least two-thirds of the total nitrogen or phosphorus was actually available for phytoplankton growth in these years.

Phosphorus carrying capacity was lower than nitrogen carrying capacity in 15 of 20 years, and the relative sensitivity to phosphorus limitation appears to be increasing. There is no overall upward or downward trend over the whole record for either total nitrogen or phosphorus (not shown). Indeed, although the trends for total nitrogen by month are mostly upward, and for total phosphorus mostly downward, only in one

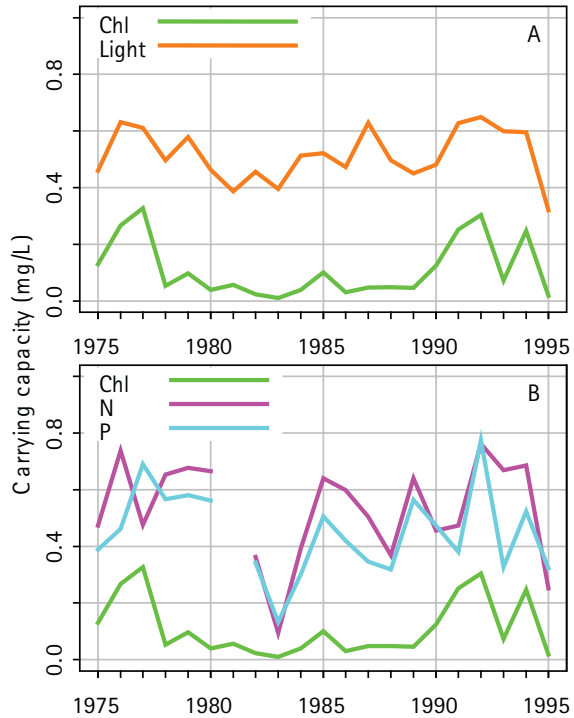

Figure 5. Estimated carrying capacities of available resources at Mossdale for phytoplankton, compared with actual chlorophyll *a* values. (A) Light carrying capacity. (B) Nitrogen and phosphorus carrying capacities.

month each were the trends significant ($P < 0.05$): +0.050 mg L^{-1} yr^{-1} nitrogen in June, and -0.019 mg L^{-1} yr^{-1} phosphorus in September. In contrast, the total nitrogen to phosphorus ratio exhibits a clear rise over time, at least since the 1976-77 ENSO (Figure 6A), and the monthly trends are significant for most of March-October, covering the main growth period for phytoplankton (Figure 6B). Values early in the record are close to the Redfield ratio of 16, typical of phytoplankton. In the last decade, however, this ratio has been exceeded almost every month.

Resource constraints on growth rate, as opposed to carrying capacity, were also investigated. Nutrient limitation of phytoplankton growth typically becomes significant only when dissolved nutrient concentrations fall below about 0.07 mg L^{-1} nitrogen and 0.03 mg L^{-1} phosphorus; these values are at least five

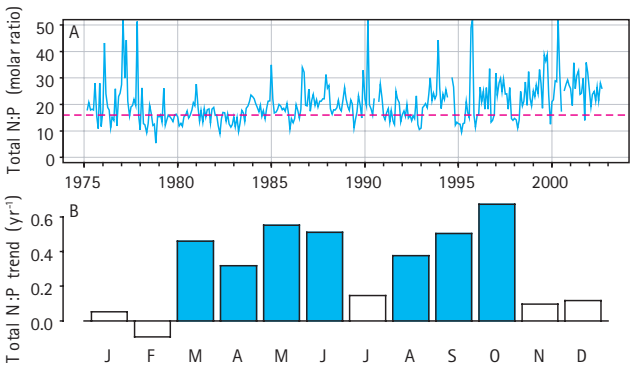

Figure 6. (A) Molar ratio of total nitrogen to phosphorus at Vernalis. *Dashed line*, ratio = 16, characteristic of phytoplankton. (B) Long-term (Theil) trends by month for the molar ratio of total nitrogen to phosphorus at Vernalis, 1975-2002. *Shading*, significantly different from zero ($P < 0.05$), according to the Kendall-tau test.

times typical half-saturation constants for uptake (Fisher et al. 1995). Nutrient concentrations were examined for those months in which the peak annual biomass occurred. At Vernalis, the minimum nutrient concentrations at those times were 0.30 mg L^{-1} dissolved inorganic nitrogen and 0.040 mg L^{-1} soluble reactive phosphorus, i.e., above the threshold for nutrient limitation of growth rate. Median values were 1.67 and 0.090 mg L^{-1}, respectively. At Mossdale, the medians were similar—1.42 and 0.085 mg L^{-1}, respectively—but soluble reactive phosphorus decreased to 0.010 mg L^{-1} in the dry years of 1976, 1977, and 1991, and dissolved inorganic nitrogen was as low as 0.110 mg L^{-1} in both 1991 and 1992. It is therefore possible that nutrient limitation occurs at Mossdale in extreme dry years. But this must be more the exception than the rule because nutrient levels are usually much higher than the thresholds for limitation even at Mossdale. Moreover, soluble reactive phosphorus may underestimate available phosphorus because of uncertainty about intracellular storage and other dissolved fractions (Bradford and Peters 1987).

Although carrying capacities for silicon cannot be estimated with any certainty, the dissolved concentrations are informative. The median value for silicon at Mossdale during 1975-1995 was 15 mg L^{-1} and the absolute minimum (1977) was 1.2 mg L^{-1} silica. In lakes, silicon limitation does not occur until silica concentrations drop well below 1 mg L^{-1} (Lund 1964). In marine diatoms, Azam and Chisolm (1976) found half-saturation constants of 0.15 mg L^{-1} silica or less for silicic acid uptake. Kilham and Kilham (1975) argued on the basis of distributional data that *Aulacoseira granulata* grows best where silicon is not limiting, and this species is often abundant in the San Joaquin River. Silicon limitation of growth rate is thus unlikely. Even if diatom biomass at Mossdale did become limited by silicon availability in extreme droughts, non-diatoms would then simply have the advantage and in principle would play the dominant role at those times. Nitrogen and phosphorus are therefore the focus in what follows.

Light conditions in the water column were examined at the time of peak biomass each year. Average water column irradiance at the time of maximum daily irradiance ranged from 53 to 195 µmol m^{-2} s^{-1} over the years, with a median of 91. In comparison, characteristic values for the irradiance level promoting maximum primary productivity are usually in the range 200-800 µmol m^{-2} s^{-1}, even taking into account photoadaptation (Padisák 2004). Phytoplankton growth rate in the San Joaquin River is therefore probably light-limited at the time of the annual phytoplankton peak. Growth rates at Mossdale during times of peak phytoplankton biomass were estimated using Equation 7. Growth rates are mostly in the range 0.3-0.6 d^{-1} (Figure 7). As pointed out above, nutrient limitation may have been present at Mossdale in 1976-77 and

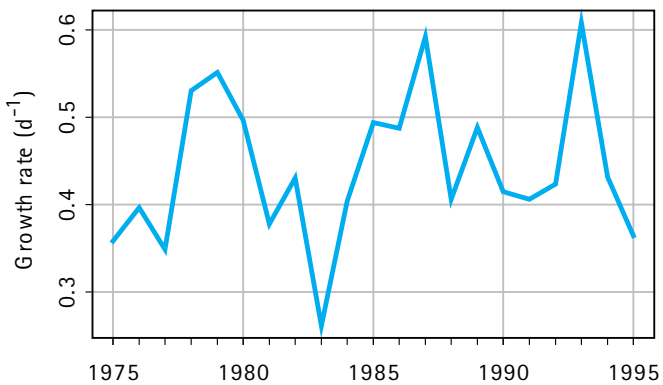

Figure 7. Estimated phytoplankton community growth rates at Mossdale during the time of annual peak biomass, based on equations 1 and 7.

1991-92, in which case $N/(k_n + N) < 1$ in Equation 1 and growth rates would have been lower.

Note that light attenuation is usually due mostly to mineral suspensoids, as opposed to phytoplankton. Phytoplankton contributes little, on average, to total suspended matter at Mossdale, even at peak annual biomass. For example, assuming a Chl:C ratio given by Equation 1 and a carbon to dry weight ratio of 0.3 for diatoms (based on data from Lund 1964), the median contribution during the annual peak was 12% (1975-1995). Contributions during extreme dry years can be much higher, though, as high as 45% in 1977. Using a typical value of 0.01 m^2 (mg chlorophyll *a*)$^{-1}$ for PAR attenuation, the chlorophyll *a* contribution to observed K_d at Mossdale was a median of only 14% but reached as high as 82% in 1977 (1975-1985). The very dry years thus favor high chlorophyll *a* concentration even more than high total suspended solids.

Phytoplankton biomass and river discharge

San Joaquin River discharge appears to be a dominant controlling factor for chlorophyll *a* concentrations at Vernalis and Mossdale. This can be appreciated by comparing monthly chlorophyll *a* concentrations with discharge rates (Figure 3). Peak annual values of chlorophyll *a* appear to be determined by discharge rates during early summer. For example, the two peaks over 300 µg/L in 1977 and 1992 correspond to the two lowest discharge values. In the early years of the 1987-1992 drought, summer discharge remained relatively high and peak chlorophyll *a* values correspondingly low. As summer discharge declined throughout the drought, summer chlorophyll *a* increased. In fact, the disappearance of high chlorophyll *a* values after 1977 until the early 1990s can be understood based on early summer discharge rates alone. Figure 8 illustrates the relationship between annual maximum chlorophyll *a* at Vernalis and discharge during the same month. Peak chlorophyll *a* increases dramatically as concurrent discharge decreases. There is some indication of a rapid rise below about 50 m^3 s^{-1}, and a (weak) suggestion of saturation at the highest chlorophyll *a* level in 1977.

The frequency of large blooms appears to have declined since the late 1970s (Figure 3A). The dependence of bloom size on discharge (Figure 8) naturally leads to the question: Has early-summer discharge changed in some systematic way since the 1970s? Flow in the tidal San Joaquin River is highly managed, responding to

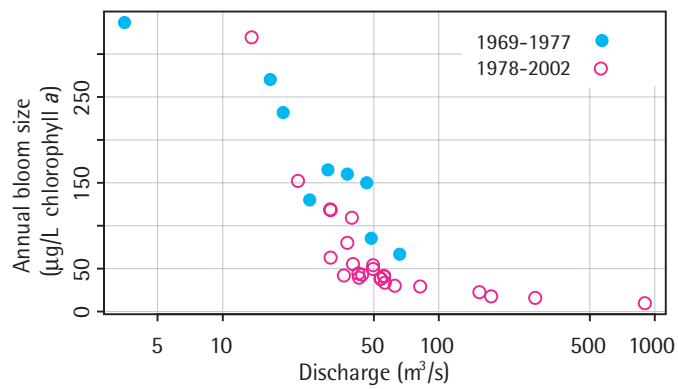

Figure 8. Annual peaks of median monthly chlorophyll *a* at Vernalis versus mean river discharge during the same month in which the peak occurred, 1969-2002. *Filled circles*, observations before 1978.

storage-and-release patterns from upstream reservoirs on the mainstem and three tributaries: the Merced, Tuolumne, and Stanislaus rivers. Construction of Friant Dam on the mainstem was completed in 1942. The seasonal flow pattern at Vernalis has since changed markedly, typically with lower flows during March-July and higher during September-December (Figure 9A). Combined with high agricultural nutrient sources, lower flows during March-July made possible the large phytoplankton blooms observable in the historical record

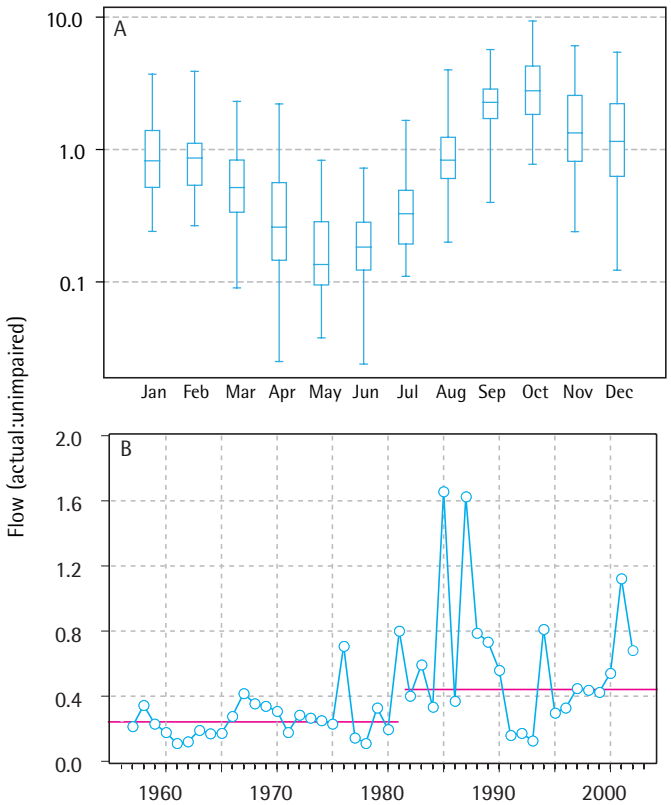

Figure 9. Ratio of actual to unimpaired flow at Vernalis. (A) Monthly boxplots of the ratio for 1956-2003 (whiskers extend to full range of data). (B) Time series of the ratio for July. *Horizontal lines*, median values for 1956-1981 and 1982-2003, respectively.

(Figure 3A). The last of the large reservoirs, the New Melones on the Stanislaus, was constructed in 1979 (Figure 1), although full dam operations did not begin until 1982 because of public opposition. One of the dam's functions is to decrease Delta salinity intrusions during summer by providing auxiliary flow to the San Joaquin River. The Stanislaus has contributed a median of about 35% of the San Joaquin discharge in July since dam construction, compared to 21% before. About 7.1% of the total annual Stanislaus discharge now occurs in July, compared to only 2.7% before the dam was built. The result of changed storage-and-release patterns from the New Melones and other reservoirs since the early 1980s has been almost a doubling of median July flow at Vernalis, and in some years July flow has exceeded the unimpaired level (Figure 9B). During 1982-2002, July flow exceeded the 50 $m^3 s^{-1}$ threshold 11 times, whereas during the prior 21 years, it exceeded the threshold only 6 times (Figure 10). Even during dry and critically dry years, flow now approaches the threshold. This alone is sufficient to explain the long-term change in bloom magnitude.

There is much variability in the relationship between bloom size and flow at intermediate discharge values. Much of this variability appears to be due to a change in the relationship over the years, with earlier chlorophyll *a* observations tending to be higher for a given discharge level. The different behavior in early com-

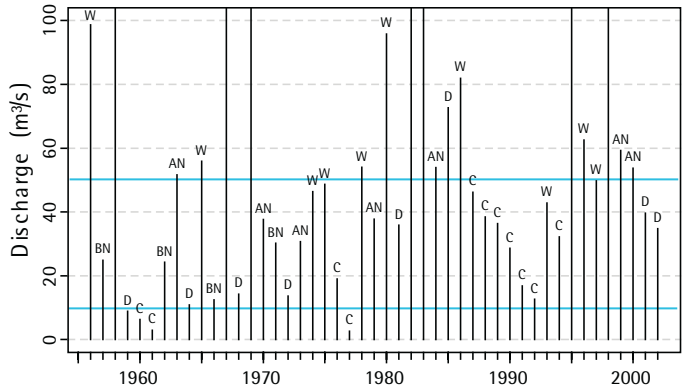

Figure 10. San Joaquin River discharge near Vernalis during July, including the water year type for each year. *C*, critical (critically dry). *D*, dry. *BN*, below normal. *AN*, above normal. *W*, wet. *Horizontal solid lines*, range in which bloom size is sensitive to discharge (10-50 $m^3 s^{-1}$).

pared to later years was explored by modeling chlorophyll *a* as a function of discharge and time. Based on Figure 8, a power relationship between chlorophyll *a* and discharge was assumed, with the addition of a time trend. In order to allow the data themselves to determine the form of the trend, the trend was modeled as a restricted cubic spline transform of time. Only three knots were used for the spline, requiring only two additional coefficients to be estimated:

$$\ln(B) = a_1 + a_2 \ln(Q_{vern}) + f(Y) + \varepsilon_t \qquad (11)$$

where B is chlorophyll a, Q_{vern} is discharge at Vernalis, Y is the year, f is the spline-estimated transform of year, a_1 and a_2 are constant coefficients; and ε_t is an independent normal process. The spline function is given by Equation 9.

Parameters of Equation 11 were determined using ordinary least-squares regression. The residuals are free of serial correlation and approximately normal. All variables are important according to the partial *F* tests, including the nonlinearity in the trend (Table 1), and the adjusted R^2 = 0.83.

Table 1. Partial *F* tests for the Vernalis chlorophyll *a* model of Equation 11.

Factor	*d.f.*	*Partial Sum Sq.*	*Mean Sq.*	*F-statistic*	*Probability*
Discharge	1	15	15	110	<0.001
Trend	2	2.4	1.2	9.0	<0.001
Trend nonlinearity	1	1.5	1.5	12	0.002
Regression	3	22	7.2	55	<0.001
Error	30	3.9	0.13		

The results indicate an approximate power relation between chlorophyll *a* and river discharge ($B \propto Q^{-0.76}$), with the effect of a given discharge value less in later versus early years (Figure 11). Although there is some hint of an upturn in recent years, the standard errors indicate that it lacks statistical significance. The trend is constrained to be smooth because the data allow only one interior knot, but the partial residuals for the trend suggest that an abrupt drop may have occurred around the 1976-77 ENSO.

Discharge affects phytoplankton biomass not only through transit time but also through growth rate, because of changes in light attenuation due to discharge impacts on suspended matter. The relationship between suspended matter and discharge depends on the season. Suspended matter decreases with flow for any given month from late winter to early fall, but not during the remaining months (Figure 12). April and December show strongly opposite relationships with discharge. Although the correlation with discharge is significant for March-July and December, most of the variability appears to be due to other factors. The variability explained by discharge in July, for example, is only R^2 = 0.29. The dependence of suspended matter on discharge is also much weaker than the inverse dependence of transit time on discharge: The exponent of the power relationship in July is only -0.23.

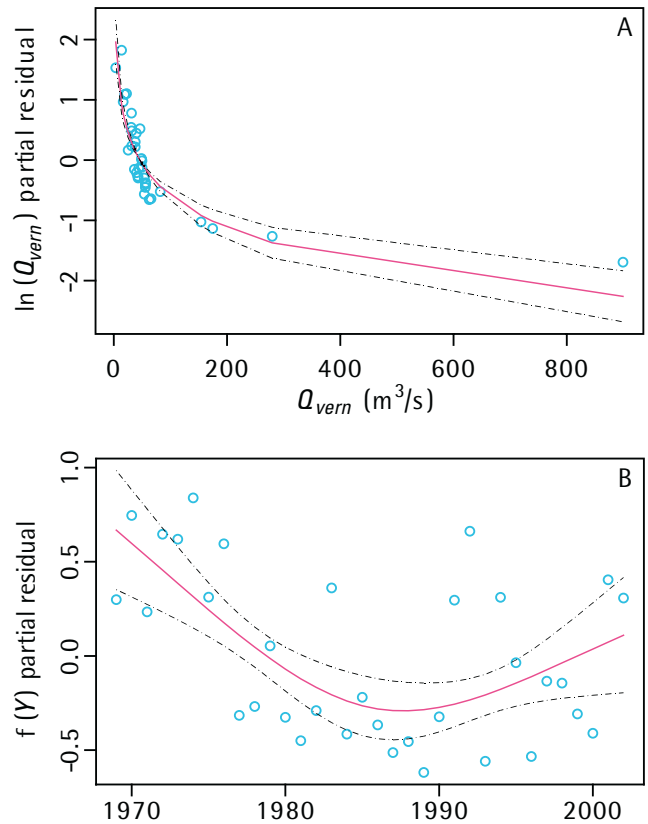

Figure 11. Partial residual plots for the Vernalis peak chlorophyll *a* model (Equation 11). (A) Partial residuals for discharge. (B) Partial residuals for the time trend. *Solid lines*, partial fit. *Dashed lines*, standard errors. *Circles*, partial residuals.

Net river discharge and export effects

Mossdale is 26 km from the entrance to the Ship Channel, so there is further opportunity for phytoplankton growth between Mossdale and the Ship Channel. Water exports via Old River, however, decrease river discharge and increase travel time from Mossdale to the Ship Channel. It is interesting to consider the impact of flows down Old River on travel time and subsequent phytoplankton growth between Mossdale and the Ship Channel.

Net discharge Q_{net} into the Ship Channel was estimated using Equation 8. This model describes the overall data well, and is also well-behaved statistically (Figure 13, Table 2). The adjusted R^2 = 0.93, and the residuals are not serially correlated. The model describes the low-flow data less well than the entire dataset. The model was refit using only data for

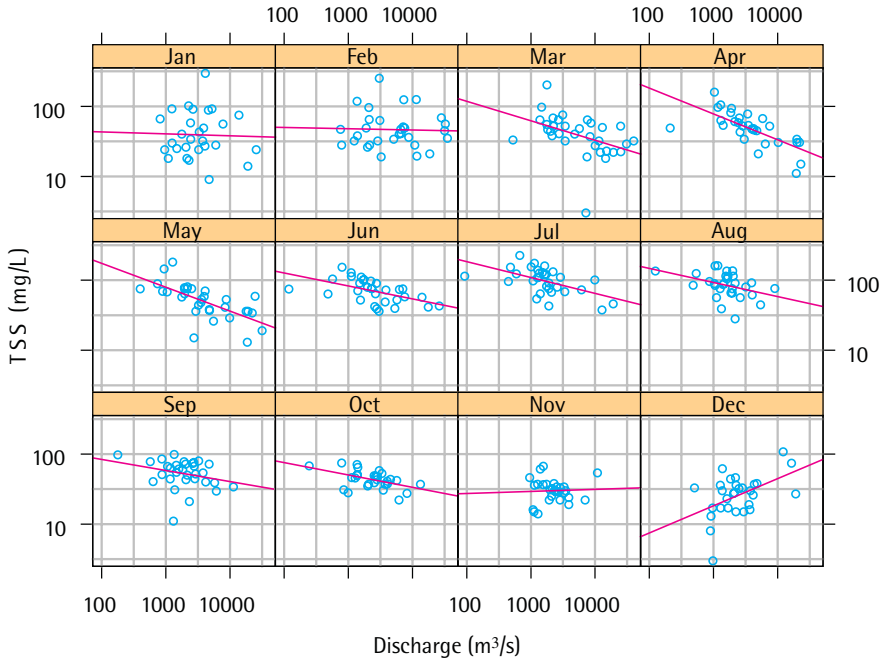

Figure 12. Total suspended solids versus discharge by month at Vernalis, 1969-2002. *Straight lines*, power relation between suspended matter and discharge.

Q_{net} <85 m³ s⁻¹. The overall fit was, of course, poorer, but the fit for low-flow data also did not improve. The lack of fit for low values probably represents physical processes missing from the model and cannot be corrected solely through statistical means. The overestimation of low flows by the model could possibly be remedied by the inclusion of a term representing culverts through the Head of Old River barrier. Diversion of water for irrigation downstream of the Old River branch may also play a role. In any case, the model was considered adequate for the application at hand. As net discharge should be less than or equal to discharge at Vernalis, the smaller of Q_{net} and Q_{vern} was used to represent net discharge.

Travel times between Mossdale and the Ship Channel were estimated from net discharge using a relationship developed by Jones & Stokes (2002) for this reach of the river. Travel time estimates assume zero tidal dispersion but, in reality, transit times will be somewhat shorter or longer in the tidal river. At the time of peak phytoplankton biomass, travel times averaged 2.1 ± 0.4 days during 1975-1995, ranging from 0.099 in 1983 to 8.4 days in 1977. If the barrier at the head of Old River had been in place and completely effective during this time, travel times would have averaged 1.4 ± 0.4 days.

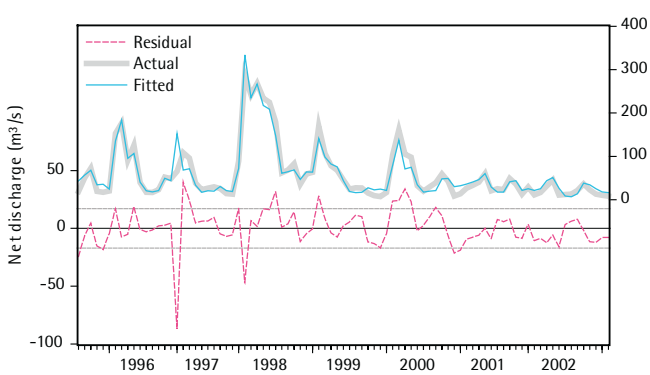

Figure 13. Fitted values and actual observations of net discharge into the Ship Channel. Fitted values are based on the model described by Equation 8. *Horizontal dashed lines*, standard error of residuals.

Table 2. Coefficient values for the model of Equation 8 describing average monthly net discharge into the Ship Channel (n = 71).

Variable	*Coefficient*	*Std. Error*	*t-Statistic*	*Prob.*
Intercept	20	5	4.2	<0.001
Q_{vern}	0.40	0.01	30	<0.001
$Q_{exp}(1-B_{hor})$	-0.081	0.019	-4.3	<0.001

Some idea of the potential effects on phytoplankton biomass can be obtained by combining transit times with the growth rates estimated for Mossdale, although the latter could change on the way downstream and nutrient or light resources could become limiting before phytoplankton reached the Ship Channel. Note also that water within a few kilometers upstream of the Ship Channel is subject to mixing with Ship Channel water because of tidal dispersion, so that concentrations in this region do not reflect the true net increase in biomass of a population starting out at Mossdale. In any case, calculations imply that water movement down Old River could have increased peak biomass during 1975-1995 at the Ship Channel by a

mean of 38 ± 10%. In three of the driest years—1977, 1991, and 1992—exports were negligible. In other years, however, diversions down Old River could have caused a notable increase in phytoplankton biomass downstream. In 1989, for example, potential downstream concentrations at the time of the peak would have been only 73 µg L^{-1}, instead of 177 µg L^{-1} (potential concentrations assume no dilution of the biomass with Ship Channel water).

DISCUSSION

Nutrient management and phytoplankton

The concentrations of dissolved inorganic nitrogen, soluble reactive phosphorus, and dissolved silica indicate that macronutrient limitation is unlikely at Vernalis or Mossdale, except perhaps during extreme drought years (such as 1976-77 and 1991-92). Apart from these extreme years, though, nutrient concentrations do not appear to restrict either phytoplankton growth rate or biomass. There is much uncertainty in the estimates made here. For example, chlorophyll *a* concentrations can exhibit more than a two-fold diel variation in the Delta (Schraga et al. 2003). In addition, total elemental concentrations overestimate carrying capacity. Yet Figure 5 illustrates a sufficiently large difference between estimated biomass and carrying capacities that macronutrient limitation is probably rare, despite the uncertainty. Whether the situation changes in transit to the Ship Channel, i.e., whether phytoplankton achieve carrying capacity in more than just extreme dry years, remains in question because of probable changes in growth rate, losses to primary consumers, and downstream losses or gains in total elemental concentrations. There are insufficient long-term data between Mossdale and the Ship Channel to address the question. Moreover, water just a few kilometers upstream of the Ship Channel is subject to dilution because of tidal dispersion. For measurements made in the vicinity of the Channel, the effects of phytoplankton growth in transit downstream could therefore easily be swamped by dilution with much lower phytoplankton biomass from the Channel.

Which of nitrogen or phosphorus would require the smaller percentage reduction to achieve nutrient limitation, i.e., which nutrient is more liable to be limiting in the San Joaquin River? The N:P molar ratio for phytoplankton averages 16, but Downing and McCauley (1992) found that nitrogen rather than phosphorus limitation (albeit in lakes) was more frequent until total N:P exceeded 31. The ratio at Vernalis is typically below this threshold (median 18) and sometimes even below 16. Dissolved inorganic N:P values are substantially higher (median 27), but it is difficult to interpret this ratio in the San Joaquin River: The true availability of phosphorus, for example, can be underestimated because of internal cellular storage. The ratios are therefore in a band where interpretation is uncertain and we cannot conclude definitely that the river is more prone to either nitrogen or phosphorus limitation. It is not uncommon for estuarine phytoplankton communities to be prone to colimitation by nitrogen and phosphorus (Conley 2000), and the same tendency may characterize this tidal reach of the San Joaquin River. In any case, the long-term trend for both total N:P (Figure 6) and inorganic N:P values since 1980 has been in the direction of higher ratios and more susceptibility to phosphorus limitation.

Kratzer and Shelton (1998), in their study of 1972-1990 water quality, noted a long-term increase in nitrate concentration in the San Joaquin River, which they attributed to native soil nitrogen from expanding subsurface agricultural drainage. Other changes possibly affecting the nitrogen and phosphorus balance over time included an increase in aeration of municipal wastewater ponds and land application of domestic wastewater. More recently, Kratzer et al. (2004) observed that all but a few $\delta^{15}N$ and $\delta^{18}O$ values of nitrate measured in the San Joaquin River fell within the range of animal waste and sewage. They concluded that animal waste or sewage now represented a significant source of nitrate in the San Joaquin River at the time of their sampling. During the summer and early autumn when their study took place, higher temperatures and longer travel times from sources favor conversion of dissolved organic nitrogen and ammonium to nitrate. Consistent with these observations, Kratzer and Shelton (1998) reported that about 53% of total nitrogen sources in the drainage basin for the San Joaquin River near Vernalis were of ani-

mal origin. The nitrate increase could therefore be due, at least in part, to an increase in animal waste and sewage sources.

How much reduction in nitrogen or phosphorus is required to limit phytoplankton bloom size to acceptable levels? It is difficult to provide a general answer to this question, because nutrient and suspended sediment loading is year-dependent, and peak biomass depends on water year type and seasonal patterns of storage and release from upstream impoundments. Downstream of Old River, it also depends on water exports. The monitoring data, however, can provide an answer from a historical perspective. Consider, for discussion purposes, the OECD (1982) boundary between mesotrophy and eutrophy of 25 µg L^{-1} maximum annual chlorophyll *a* as an acceptable level. Reductions of this amount probably would not affect the algal food supply to planktonic food webs, which may be saturated at a level of about 10 µg L^{-1} chlorophyll *a* in the Delta (Müller-Solger et al. 2002). Recall also that as much as two-thirds of total nitrogen or phosphorus can be available for growth, based on the high chlorophyll *a* concentrations attained in dry years. Depending on the year, the 25 µg L^{-1} goal would have required reductions at Mossdale of 61 to 95% for nitrogen or 72 to 95% for phosphorus, under the assumption that two-thirds of the nitrogen and phosphorus were available for growth. These are very challenging goals to achieve. Moreover, under the same assumptions, an average nutrient reduction of more than 50% would be required to have any effect on the annual bloom size. Therefore, although it is possible that even moderate nutrient control would have some beneficial effect in the driest years, levels of nutrient reduction attainable in the short term will probably leave peak phytoplankton biomass unchanged in many years.

Light-attenuating materials

Historical year-to-year changes in mineral suspensoid concentrations in the San Joaquin River, unlike macronutrient changes, probably had important effects on phytoplankton growth and biomass. Average light levels experienced by phytoplankton are relatively low and neither photosynthesis nor growth rate are proceeding at maximum attainable levels. Total suspended solids concentrations in July have ranged from 38 mg L^{-1} in 1998 to 226 mg L^{-1} in 1976. Even considering that $K_d \propto M^{0.5}$, this represents about a 2.4-fold change in growth rate, according to Equation 7. Although this includes year-to-year variability in the phytoplankton as well as the mineral suspensoid portion, the latter must still be considerable given that the phytoplankton accounts for a minority of suspended matter during the annual peak. The implication is that watershed or river management actions must reflect an understanding of the consequences for mineral suspensoids in the river. For example, dam removal may decrease transparency and reduce growth rate by eliminating the trapping of suspended matter that occurs in reservoirs. Conversely, erosion control measures for fine-grained soils in the Coast Range on the west side of the Valley or for agricultural lands on the east side may increase transparency. Growth rate and even biomass could increase if nonpoint source pollution management decreases mineral suspensoid load but does not decrease nutrient load sufficiently. The effects can be very large: Reservoirs in Germany and Austria decreased suspended matter and improved water clarity in the Danube River during the 1970s, resulting in a ten-fold increase in phytoplankton with no change in nutrient supply (Kiss 1994). Transparency responses therefore should be an explicit component of models intended for assessing different strategies to manage loads to the Ship Channel.

Effects of river discharge on biomass

River discharge during June-August has the strongest identifiable effect on peak phytoplankton biomass at Vernalis. Although phytoplankton may reach the carrying capacity set by macronutrients during extreme drought years, phytoplankton is usually well below this level. Growth rate is light-limited due to high levels of mineral suspensoids, compounded by high nutrient levels that have permitted phytoplankton to reach values near the top of the range found in rivers. Maximum phytoplankton biomass in most years therefore depends primarily on river discharge, which determines the cumulative light exposure in passage to Vernalis. Based on historical evidence, maintaining river discharge above 50 m^3 s^{-1} during late spring and early summer could eliminate nuisance algal blooms

at Vernalis. Downstream of Mossdale, however, export flows down Old River can further reduce mainstem river discharge, and further increase the cumulative light exposure in passage to the Ship Channel. These export flows may result in more than a doubling of peak biomass at the entrance to the Ship Channel in specific years.

Because of impoundment patterns of water storage and release, the seasonal hydrograph has shifted to lower discharge in late spring and early summer relative to pre-impoundment conditions (Knowles 2002; Figure 9A), allowing development of the massive blooms observable since routine monitoring began in the 1960s. During the early years of the 1986-1992 drought, peak biomass remained relatively low, despite the overall dry conditions. This change from earlier drought years such as 1976-77 appears to be due simply to the fact that discharge remained elevated and residence times accordingly low during early summer. The change in median July discharge during critical and dry years since the early 1980s falls mostly within 10-50 $m^3\ s^{-1}$, the most sensitive portion of the biomass-discharge relationship (Figure 8 and Figure 10). This increase can be attributed to the changed pattern of storage-and-release from major upstream reservoirs, including the newest one created by the New Melones Dam on the Stanislaus River.

Climate change may mean future long-term shifts in bloom size as well. Knowles and Cayan (2002) used projected temperature anomalies from a global climate model to drive a model of watershed hydrology for the San Francisco Estuary. They estimated that, by 2090, spring runoff could be reduced by 20% compared to historical annual runoff, with associated increases in winter flood peaks. According to Figure 8, large increases in bloom size would be expected for flow decreases within the range of 10-50 $m^3\ s^{-1}$.

Discharge controls cumulative light exposure, not only through residence time, but also through mean light availability in the water column. Light availability in the water column depends on optical depth, a dimensionless term equal to K_dH in the case of an optically homogeneous water column (Equation 2). Discharge affects optical depth through both K_d and H. In particular, higher discharge causes both a decrease in K_d and an increase in H. The effect on K_d appears to be a negligible one compared to the effect on residence time. As pointed out in the Results, total suspended solids M is approximately proportional to $Q^{-0.2}$ during June-August (Figure 12). Because K_d is approximately proportional to $M^{0.5}$ (Equation 3), a doubling of discharge thus leads to an increase of only about 7% in growth rate, according to Equation 7. Consider a biomass of 100 µg L^{-1} chlorophyll *a*, a growth rate of 0.4 d^{-1}, and a transit time of 2 days to some second location downstream. The net affect of doubling discharge is to decrease biomass at the downstream location from 196 to 143 µg L^{-1}. Without any effect on growth rate, final biomass would have been 140 µg L^{-1}, a negligible difference, and so effects of discharge on water transparency can probably be ignored.

The same cannot be said of water depth, however, because the relationship between discharge and mean water depth over this reach of the river is unknown. The necessary data are available only for Vernalis and do not apply for the reach as a whole. As a result, it has been necessary to conduct the analyses under the assumption of a constant depth, a source of bias and uncertainty in many of the quantitative results presented in this analysis. The increase in H with discharge offsets to some extent the decrease in K_d, but even the sign of the net effect of discharge on optical depth is not known for sure.

Long-term shift in biomass-discharge relationship

Although most of the interannual variability in biomass is directly attributable to differences in early summer discharge, a long-term shift in the relationship between biomass and discharge can also be observed (Figure 11B). The shift accounts for relatively little of the overall year-to-year variability but is statistically significant (Table 1), as well as ecologically significant for intermediate discharges of 30-50 $m^3\ s^{-1}$ (Figure 8). What is the mechanism behind this shift? It is possible that operation of the New Melones Dam has an effect on bloom size apart from the impact of concurrent discharge. This is especially true if lagged discharge effects are also important, because winter and spring discharge was generally much higher prior to 1980. Abundances of planktonic grazers with generation

times longer than planktonic algae are likely to be dependent on these earlier discharges. Pace et al. (1992), for example, found that advective transport regulates zooplankton biomass in the Hudson River and in other tidal rivers, estuaries, and lakes where the appropriate data could be found. Gosselain et al. (1998), however, maintain that planktonic grazing pressure on phytoplankton is unlikely to be important during low river residence times, such as in spring. In any case, no convincing statistical evidence for lagged effects could be found, and zooplankton data are not routinely collected in this reach.

A climate regime shift in the eastern Pacific and contiguous Americas occurred around 1976 (Trenburth and Hurrell 1994), coincident with major step-like changes in chlorophyll, salmon, crabs, and many other environmental variables (Ebbesmeyer et al. 1991). The main effect of climate change on the San Joaquin River, however, is a change in the discharge hydrograph, which should already be accounted for by the discharge term in Equation 11. As we have seen, the disappearance of large blooms in dry years after 1976-77 appears to have nothing to do with a climate regime shift, but rather with changes in water management. Nonetheless, this part of the estuary is relatively poorly studied in terms of metazoa, and it is possible that the 1976-77 ENSO event itself had unobserved impacts on primary consumers, especially benthic macroinvertebrates. River depths of several meters in this reach are compatible with intense benthic-pelagic coupling and major impacts of benthic suspension feeders on planktonic communities. Given the continuity of the Vernalis with the upstream phytoplankton, based on taxonomic composition and chlorophyll *a* concentrations, the impact could have been on the upstream community. Elsewhere in the estuary, persistent (multi-year) low flows have allowed upstream colonization by marine benthic macroinvertebrates, such as *Mya arenaria* during the 1976-77 drought (Nichols 1985). The drought beginning in 1986 allowed invasion of Suisun Bay by an Asian corbulid clam, resulting in persistently lower phytoplankton and primary production in Suisun Bay and the western Delta (Alpine and Cloern 1992, Jassby et al. 2002). Relevant long-term data, however, are not available for this reach of the San Joaquin River, and the few recent surveys suggest that freshwater clams such as *Corbicula fluminea* are currently not abundant enough to control phytoplankton biomass here (J. Thompson, USGS, pers. comm.).

Concluding remarks

The observations and analyses in this study lead to a specific conception of bloom control in this critical reach of the tidal San Joaquin River, summarized by the cause-and-effect diagram of Figure 14. It is a minimal conception in the sense that there were insufficient data to include primary consumer effects in our study, and these may play a big role. Nor were changes in phytoplankton species community composition considered, which may determine, among other things, the magnitude of light-limited growth rates. Climate, water management, and watershed material inputs are the ultimate causes in the conception illustrated here. The amount of water available in spring and early summer depends on winter precipitation, but the temporal pattern depends on dam operations,

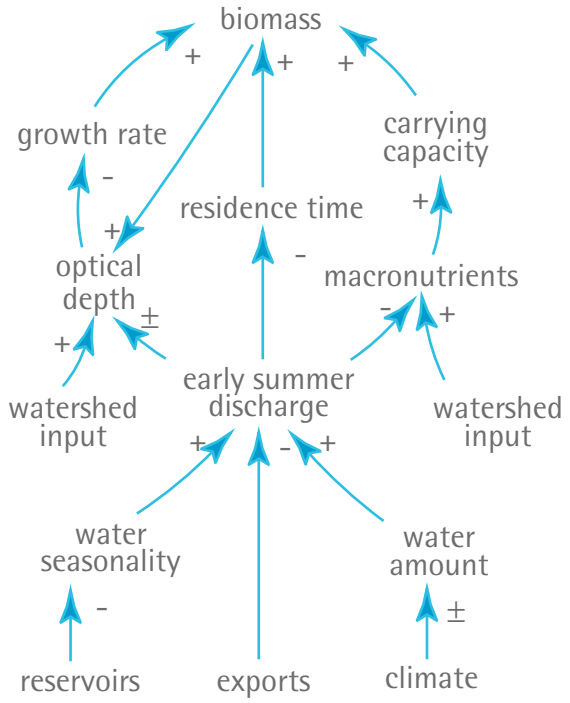

Figure 14. Cause-and-effect diagram summarizing the linkages described in this study for regulation of peak annual phytoplankton biomass.

which are operated in a manner that suppresses historical seasonality and enhances early summer flows relative to spring flows. Combined, these two factors determine the actual magnitude of early summer discharge. Discharge then affects another hydrological property, average residence time in any given reach of the river; average residence time downstream is further affected by water exports down Old River. Discharge also affects two water quality properties, optical depth and the concentrations of macronutrients. Both are also affected by variable watershed inputs, and optical depth in addition can be affected by feedback from phytoplankton biomass in dry years when biomass is very high. Optical depth in turn affects growth rate, which is usually light- but not nutrient-limited. Macronutrients determine the carrying capacity or maximum possible phytoplankton biomass, which may be attained during extremely dry years. For most years, however, bloom size is set by residence time and specific growth rate. Reductions of macronutrient inputs from the watershed would increase the percentage of years in which blooms are limited by carrying capacity, but order-of-magnitude reductions are required and these would probably not be obtainable in the near-term for social as well as logistical reasons. Moreover, strategies for macronutrient reduction from the watershed must consider accompanying impacts on optical depth via reduced suspended matter inputs from the watershed, which could result in higher growth rates and larger blooms during years when carrying capacity is not reached. In contrast, the sensitivity of bloom size at Vernalis to early summer discharge, and the effect of water exports on phytoplankton biomass as it moves downstream, offer effective, near-term management tools. In both cases, modification of the seasonal pattern rather than changes in the overall annual amount may be sufficient to control large blooms.

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