

Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes and Their Trophic Significance

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ABSTRACT

Several pelagic fish populations in the upper San Francisco Estuary have recently declined to historically low abundances, prompting an interest in the status of their food supply. Previous studies have indicated that the primary food supply for metazoans in the Delta is phytoplankton productivity, and the long-term decrease in phytoplankton over the last few decades may very well play a role in the long-term decline of pelagic fish abundance. Regional phytoplankton biomass trends during 1996–2005, however, are positive in the Delta and neutral in Suisun Bay, the two major sub-regions of the upper estuary. The trend in Delta primary productivity is also positive. Changes in phytoplankton biomass and production during the last decade are therefore unlikely to be the cause of these more recent metazoan declines. The main source of interannual phytoplankton variability in the Delta during 1996–2005, including the upward trend, appears to have been freshwater flow variability and its effect on particle residence time. This conclusion is supported by trend analyses; the concurrence of these time trends at widely-separated stations; empirical models at the annual and monthly time scales; particle residence time estimates; and experience from other estuaries.

A significant temperature increase was also noticed, at least partially independent of flow changes, but its net effect on the phytoplankton community is unknown because of differential effects on growth and loss processes. Phytoplankton biomass in Suisun Bay, in contrast to the Delta, did not increase during 1996–2005. Consistent with this observation, Suisun Bay phytoplankton exhibited relatively low responsiveness to flow variability. This behavior differs from earlier chlorophyll-flow relationships reported in the literature. The reason appears to be the invasion of Suisun Bay by a clam—*Corbula amurensis*—in 1986, which has since maintained the phytoplankton community mostly at low levels by vigorous filter-feeding. In the past, flows into Suisun Bay generally diluted the higher phytoplankton concentrations within the bay; now they bring in higher phytoplankton concentrations from upstream. The supply of phytoplankton carbon to Suisun Bay has always been dominated by allochthonous sources, at least for mean flow conditions. Now this dominance must be even more pronounced.

KEYWORDS

Corbicula fluminea, *Corbula amurensis*, estuary, flow, model, nutrients, phytoplankton, primary productivity, river, temperature, trend, variability

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INTRODUCTION

The major resident pelagic fish species of the upper San Francisco Estuary (Figure 1) have declined to record or near-record low abundances in recent years, including the native delta and longfin smelts (*Hypomesus transpacificus* and *Spirinchus thaleichthys*) as well as the introduced striped bass (*Morone saxatilis*) and threadfin shad (*Dorosoma petenense*) (Sommer et al. 2007). The decline of delta smelt in particular has resulted in a petition to change the federal listing of this endemic species from threatened to endangered, reflecting the belief that its extinction is imminent (Center for Biological Diversity et al. 2006).

These recent downturns have become known collectively as the *pelagic organism decline*, and their study has been organized under a conceptual model containing four major components (Sommer et al. 2007). One of these components—"bottom-up effects"—posits that food availability has affected fish abundance. Studies of other estuaries support the notion that low phytoplankton productivity can limit the productivity of metazoan populations, including fish (Nixon and Buckley 2002). Indeed, phytoplankton changes have been implicated as a causative factor in the longer-term declines of certain key zooplankton and fish species in the San Francisco Estuary (Bennett and Moyle 1996; Orsi and Mecum 1996; cf. Kimmerer 2002a).

Although allochthonous organic matter supports

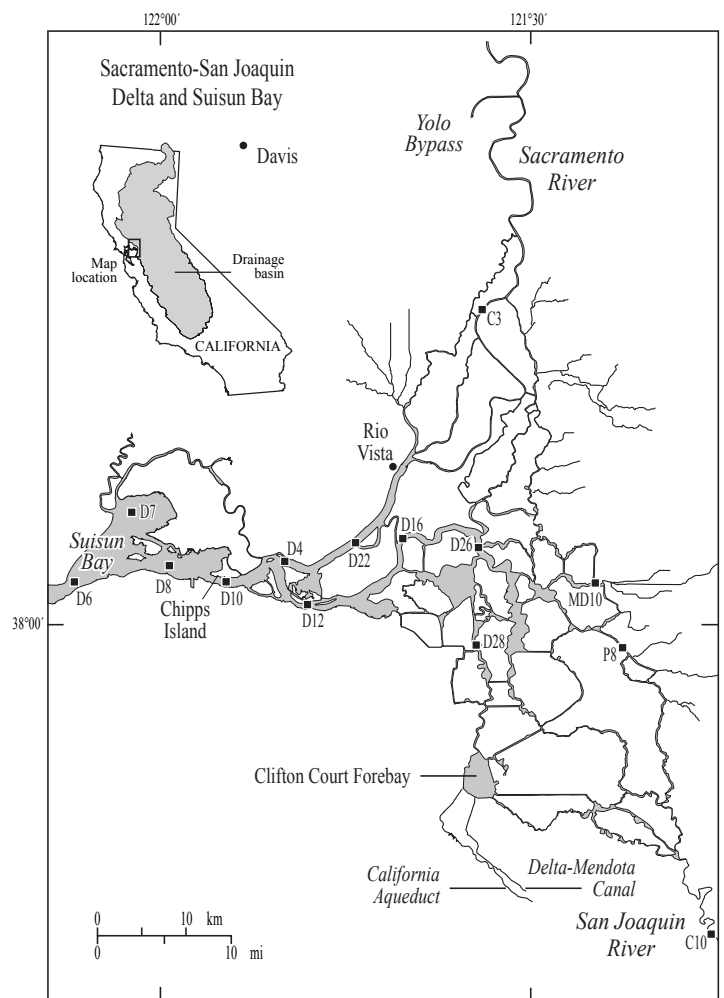


Figure 1. The upper San Francisco Estuary, consisting of Suisun Bay and the Sacramento-San Joaquin River Delta. Chipps Island marks the downstream boundary of the Delta. Filled squares, water quality stations.

most system (primarily microbial) respiration in the upper estuary, metazoan populations—especially in the Delta—are probably sustained by autochthonous phytoplankton production (Jassby and Cloern 2000; Mueller-Solger et al. 2002; Sobczak et al. 2002). Accordingly, trophic linkages are also consistent with a role for phytoplankton abundance in long-term metazoan changes. The more recent pelagic organism declines therefore raise important issues regarding phytoplankton variability.

What, for example, has been the temporal course of phytoplankton during the last decade? Does it extend or reverse the longer-term trend? The last analysis of

phytoplankton biomass and production in the upper estuary covered only the years 1975–1995, sacrificing temporal coverage to provide more comprehensive and balanced spatial coverage (Jassby et al. 2002). It is therefore time to ask what has happened to phytoplankton biomass and production in the intervening years. Beginning in 1996, data were no longer collected at a number of key stations needed for estimating overall system production. Monitoring has continued or since been restored at many stations, however, enabling us to examine phytoplankton and related data at a variety of sites, even if not on an average system-wide basis.

Can we find explanations of these more recent phytoplankton changes in flow rates, the physical environment, or macronutrient supply—as is the case at many, if not most, other estuaries? Phytoplankton variability in estuaries can most often be linked to the physical and chemical environment. Building on a legacy of limnological research, estuarine scientists have frequently invoked water residence time and macronutrient supply to explain variability at inter-annual and longer-term scales (Bricker et al. 1999). Although macronutrient supplies appear to be ample in the upper estuary (Jassby et al. 2002), many studies have demonstrated flow effects on variability of phytoplankton biomass (Table 1 of Kimmerer 2002b) and taxonomic composition (Lehman 1996).

In addition, as our understanding of the complexity of estuaries relative to inland waters has grown, physical-chemical processes that “filter” estuarine responses to nutrients and flow have become more apparent (Cloern 2001), most notably turbidity in the case of the San Francisco Estuary (Cloern 1999). The potential impact of higher water temperatures on estuaries has also become a relevant factor in the face of increasingly obvious climate change (Scavia et al. 2002).

Study Goals

The first goal of this paper, then, is to describe phytoplankton biomass trends in the upper estuary during the last decade, updating the longer-term trends. Comprehensive monitoring programs for water quality have existed in the upstream portion of the estu-

ary (Sacramento–San Joaquin Delta and Suisun Bay) since 1969, with monthly measurements of physical and chemical characteristics, as well as biological indices such as chlorophyll *a*.

The second goal is to examine the hypothesis that changes in certain major characteristics of the physical-chemical environment underlie phytoplankton trends. The emphasis here is on patterns and mechanisms that can be discerned from the discrete monthly water quality program. The major trends in physical and chemical water quality characteristics usually affecting growth rate—flow rate, temperature, suspended particulate matter, nitrogen, phosphorus, and silicon—will be described. In particular, the effect of flow on phytoplankton biomass will be examined in the context of an empirical model that attempts to separate contemporaneous flow conditions from other, perhaps unidentified, forces behind the long-term trend.

A final goal is to examine the implications of the phytoplankton and water quality trends for primary production. Mechanisms other than the physical-chemical environment can be addressed only indirectly in some cases and not at all in others using this monitoring record; a definitive resolution of their impact thus lies outside the scope of this study. Their possible involvement, however, will enter into the discussion.

System Description

The San Francisco Estuary is the largest estuary on the U.S. Pacific coast and at the core of the country's fourth largest metropolitan area. It drains almost half of California's runoff, providing drinking water to over 22 million people and irrigation water for one of the world's most productive agricultural centers. It supports 750 plant and animal species, including 80% of California's commercial salmon catch, and comprises the largest wetland habitat in the western U.S. (CALFED 2001).

The upper estuary (i.e. the Sacramento–San Joaquin River Delta and Suisun Bay) includes a network of linked channels, sloughs, shallow lakes, and estuarine embayments comprising about 2.7×10^8

square meters (m²) of open-water habitat in the Delta (Jassby and Cloern 2000) plus 1.0 × 10⁸ m² in Suisun Bay (Jassby et al. 1993). The legally defined boundary between the Delta and Suisun Bay is at Chipps Island, near the confluence of the Sacramento and San Joaquin Rivers (Figure 1). This is also the approximate boundary between the limnetic (salinity of 0–0.5) and oligohaline (salinity of 0.5–5) zones during median flow conditions.

Much of the Delta landmass is divided into tracts separated from open waters by levees. Some levees have been breached during large floods, creating a few shallow-lake habitats. Water depth ranges up to 15 m in the deepest channels.

Fresh water is delivered to the Delta by the two largest rivers in California, the Sacramento and San Joaquin Rivers, which flow into the north and south Delta, respectively (Figure 1). During water years 1969–2005 (a water year extends from October of the previous year through September), the Sacramento River flow contributed an average of 84% and the San Joaquin 12% of river inflow (IEP 2006). Inflows are highly seasonal, reflecting a climate of wet winters and dry summers (Figure 2). The recent decades have been a period

of extreme inter-annual variability of river inflow, ranging from an average of 230 cubic meters per second (m³ s⁻¹) during the dry El Niño–Southern Oscillation (ENSO) year 1977, to 2,700 m³ s⁻¹ during the wet ENSO year of 1983. There was an extended drought during 1987–1992.

Part of the Sacramento River discharge is diverted into the Yolo Bypass

floodplain during high flow events. These diversion events occur about once every three years, and they persist for weeks or months (Sommer et al. 2001). Water is exported by pumping to the State Water Project’s California Aqueduct and the Central Valley Project’s Delta–Mendota Canal. The exports amounted to an average of 24% of total river inflow during 1969–2005. Another 1% is diverted for local municipal use. An estimated 5% of the mean annual river inflow (net of precipitation) was depleted within the Delta, primarily as evapotranspiration. Siphons deliver water across levees to irrigated crops while irrigation drainage, seepage, and precipitation is pumped from farm fields back to the channels.

METHODS

Water Quality

Variables related to phytoplankton abundance and growth rate are currently measured in the upper estuary under the auspices of the Interagency Ecological Program (IEP) for the San Francisco Estuary, which has among its goals the determination of trends in ecological resources and the factors underlying these trends. The IEP Environmental Monitoring Program

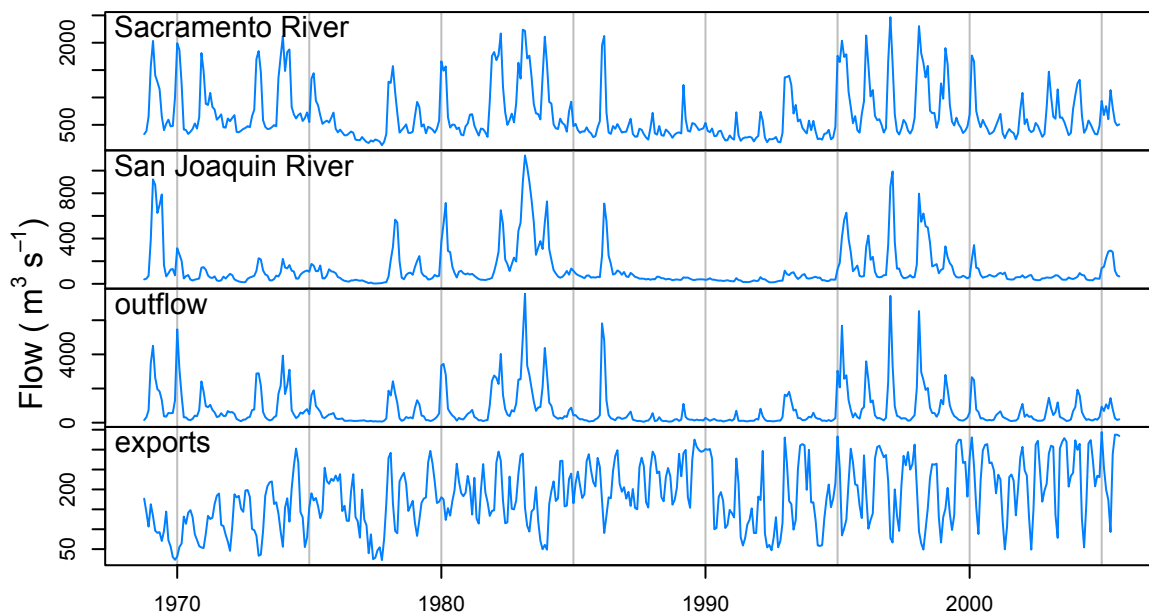


Figure 2. Historical flow variables for the Sacramento-San Joaquin Delta: freshwater inflows from the two main rivers, net Delta outflow past Chipps Island, and exports to state and federal water projects.

discrete sampling sites range from just downstream of Suisun Bay to the upstream boundaries of the Delta on the Sacramento, San Joaquin, and smaller rivers (IEP 2004).

Stations are sampled approximately monthly, usually from 1 meter (m) below the surface during high slack tide. Fourteen sites had a chlorophyll *a* (Chl-*a*) record without large gaps since at least 1975 (Figure 1: Stations with names ending in “A” were merged with nearby stations having the same root name—e.g., C3 and C3A—and only the root names are used here). These stations include one each at the upstream boundaries of the Delta on the main rivers (C3 and C10), the remainder representing conditions in the core of the Delta from the eastern extremity through Suisun Bay.

Environmental Monitoring Program data for 1975–2005 were obtained from the Bay Delta and Tributaries Project (2006). Water quality variables used here, in addition to Chl-*a*, include temperature, total suspended solids (denoted by SPM for “suspended particulate matter”), turbidity, nitrate plus nitrite, ammonium, total kjeldahl nitrogen, total phosphorus (TP), soluble reactive phosphorus (SRP) and dissolved silicate (DSi). Dissolved inorganic nitrogen (DIN) was estimated as the sum of nitrate plus nitrite and ammonium. Total nitrogen (TN) was estimated as the sum of total kjeldahl nitrogen and nitrate plus nitrate. Samples were analyzed using standard methods (IEP 2004). Earlier data for 1969–2005 (U.S. Bureau of Reclamation 1998) are shown in one Figure as a matter of historical interest, but analyses are confined to the IEP data set to ensure uniform sampling and analytical methods.

An index of gross primary production (GPP, in milligrams of carbon per square meter per day [$\text{mg C m}^{-2} \text{d}^{-1}$]) was calculated as described by Jassby et al. (2002) and as shown in Equation 1, using data for Chl-*a*, photosynthetically active radiation (PAR) at the surface, and the vertical attenuation coefficient for PAR,

Equation (1)

$$GPP = \Psi \frac{4.61BI_0}{k}$$

where B = chlorophyll concentration (micrograms per liter [$\mu\text{g L}^{-1}$])

I_0 = surface PAR (moles per square meter per day [$\text{mol m}^{-2} \text{d}^{-1}$])

k = vertical attenuation coefficient for PAR (per meter [m^{-1}])

Ψ = 0.73 ± 0.02 milligrams carbon per milligrams Chl-*a* per mole per square meter [$\text{mg C (mg Chl-}a\text{)}^{-1} (\text{mol m}^{-2})^{-1}$]

Ψ is the mean water column light utilization efficiency determined from field experiments throughout the upper estuary. Although the value of Ψ is a reliable estimate of the estuary-wide mean for these experiments, Ψ actually varies among stations and times (for more detail, see Jassby et al. 2002). In this study, however, GPP is treated simply as an index for the combined effects of B , I_0 and k . The historical data can tell us only how variability in these three factors has affected production. The contribution of any accompanying patterns in Ψ is unknown. The main point of including a mean Ψ is to give an idea of how much the variability in the other three factors could be affecting production. This point is made implicitly throughout the text by referring to GPP as an “index.”

Note that these production estimates are not corrected for respiration. Previous studies have estimated that net water column production is actually 20–30% lower than gross production in the San Francisco Estuary (Jassby et al. 1993; Jassby and Cloern 2000).

Annual GPP was determined for the period March–November only, as about half of the missing data occurred during the remaining months. Data gaps of three months or less during March–November were filled by linear interpolation. If a data gap exceeded three months, annual production was not estimated for that particular station and year.

Daily irradiance was obtained for Davis, California, the nearest location for which a long enough record is available (Univ. California Integrated Pest Management 2006). Daily mean irradiance (watts

per square meter [W m^{-2}]) was converted to PAR quantum irradiance ($\text{mol m}^{-2} \text{d}^{-1}$) using a factor of 0.18, assuming PAR is 45% of total irradiance and a conversion of 2.77×10^{18} quanta per second per watt ($\text{quanta s}^{-1} \text{W}^{-1}$) for PAR (Morel and Smith 1974). Although photometer measurements of vertical attenuation are available for the IEP program during 1975–1986, they probably overestimate the contribution of dissolved substances because of their spectral sensitivity. Vertical attenuation coefficients for PAR were therefore estimated from suspended particulate matter using a calibration based on quantum sensor data collected by an overlapping monitoring program (U.S. Geological Survey 2006).

Flow

The best estimate of historical mean daily flows at various points for the upper estuary is obtained with Dayflow, a software package developed in 1978 as an accounting tool for determining historical hydrology (IEP 2006). Some of these flow variables are based on observation, others on estimation and mass balance. Total Delta inflow (*QTOT*) is the sum of all observed river and floodplain flows to the Delta. The two major river components of *QTOT* are flows in the Sacramento River at Freeport near C3 (*QSAC*) and San Joaquin River at Vernalis near C10 (*QSJR*). Total Delta export (*QEXPORTS*) is the sum of all exports and diversions/transfers; its main components are Central Valley Project and State Water Project exports. The index of net Delta outflow past Chipps Island (*QOUT*) is the estimated outflow after correcting *QTOT* for exports and net within-Delta depletions.

Data Analysis

Data for each variable and station were binned by month using the mean to form a collection of monthly time series. To obtain a dataset that was approximately balanced with respect to sampling in space and time, analysis was confined to the 14 stations of Figure 1 and the period 1975–2005. Less than 3% of monthly Chl-*a* data were missing for these conditions.

The data were examined for groups of stations at which the Chl-*a* concentrations behaved similarly with

respect to time. The goal was to select representative stations for trend analysis and modeling, rather than repeating analyses for multiple stations that show the same variability pattern. An exploratory approach often used in meteorology and oceanography was followed, in which the variability for each station is viewed as the outcome of a number of underlying processes or modes of variability. Jassby (1999) describes the approach in the context of several ecological applications and provides appropriate references.

The starting point is a data matrix with columns representing monthly time series of Chl-*a* for 1996–2005. The principal components of the data matrix are then calculated, and a Monte Carlo technique known as *Rule N* is used to determine the number of significant components. This reduced set of important principal components is then rotated using the PROMAX method to find a new set of components (no longer principal) with so-called *simple structure*, in which individual stations are associated as much as possible with a single component. The end result is a small set of rotated components representing modes of variability. The temporal variability at any given station can be thought of as a combination of these modes, with the component coefficients representing the strength of each mode for that station. To the extent simple structure is achieved, the strength for a given station will be relatively large for only one mode.

The significance of 1975–2005 trends was determined by the nonparametric *Seasonal Kendall test* with serial correlation correction (Hirsch and Slack 1984). The overall trend slope is computed as the median of all slopes between data pairs within the same season (no cross-season slopes contribute to the overall slope estimate). This is sometimes known as the *Theil-Sen* slope.

Two criteria were used to ensure that data records for different variables and locations represented the same period so that trend results were comparable. First, tests were conducted for a particular water quality variable and station only if at least 50% of the total possible number of monthly values in the beginning and ending fifths of the record were present in the record. Second, more than 50% of the maximum pos-

sible number of comparisons had to be present for at least nine of the months.

The Seasonal Kendall test is sometimes applied to longer monthly series (greater than 10 years) after first removing influences of variables other than time, especially flow rates, to increase the power of the test. Here, long-term trends were estimated after adjusting for total river inflow using locally weighted regression with a span of 0.5 and a locally linear fit.

Trend significance for the shorter period of 1996–2005 was determined by the *Regional Kendall test* (Helsel and Frans 2006). Trends at a single station are much more difficult to detect over this shorter period using the Seasonal Kendall test. Just as the latter test looks for consistency in trend direction for all seasons of the year, the Regional Kendall test looks for evidence of a consistent trend direction throughout a region. The *Theil-Sen* slope in this case is the median of all slopes between data pairs for the same station. Individual stations can contribute some evidence toward a significant regional trend, even if the evidence is insufficient for that one station. In accordance with the recommendations for time series of 10 years or less, tests were not adjusted for river flow or serial correlation.

Models

As Equation (2) shows, the effect of flow on non-conservative water quality constituents is often described with an additive model that includes terms for flow and long-term trend, and periodic functions to describe that part of the annual cycle not accounted for by flow (e.g., Cohn et al. 1992):

Equation (2)

$$\log C_t = \beta_0 + \beta_1 \log Q_t + \beta_2 T + \beta_3 \sin(2\pi T) + \beta_4 \cos(2\pi T) + \eta_t$$

where C_t = Chl-*a* ($\mu\text{g L}^{-1}$) at time t
 Q_t = flow rate ($\text{m}^3 \text{s}^{-1}$)
 T = trend in decimal years (y)
 β_i = constants
 η_t = residuals

The sine and cosine terms constitute the simplest case

of a periodic function to describe seasonality and are usually sufficient (Helsel and Hirsch 1992). The maximum or minimum day for the annual cycle portion can be calculated from $(365/2\pi) \tan^{-1}(\beta_3/\beta_4)$.

A similar approach was used to examine flow effects on chlorophyll *a* during 1996–2005. Total inflow into the estuary (*QTOT*) was used as the flow variable in the absence of any single flow variable clearly more suitable. The results are essentially the same as for *QOUT* because inflow and outflow are so highly correlated. To reduce serial correlation in the residuals, the η_t values were modeled as a first-order auto-regressive process and the combined equations fit using generalized least squares (Pinheiro and Bates 2000).

The longer data set for 1975–2005 made possible the use of a more complex and informative model than Equation (2). Several modifications were made. First, a natural spline was used as a nonlinear transform for flow because previous work has shown that chlorophyll-flow relations in the estuary may not have been monotonic during at least the earlier years of the data record (Jassby and Powell 1994). Next, a natural spline was also used as a nonlinear transform for the time trend because of abrupt nonlinear declines in the record, especially in Suisun Bay chlorophyll *a* after a clam invasion in the mid-1980s (Alpine and Cloern 1992). The use of splines in general and natural splines in particular has advantages over other methods such as polynomials in representing nonlinear functions in a regression model (Harrell Jr. 2001). Finally, a term describing the interaction between flow and time was included to test for a change in the chlorophyll-flow relationship over time. The model can then be rewritten as Equation (3):

Equation (3)

$$\log C_t = \beta_0 + f(\log Q_t) + g(T) + f(\log Q_t) \times g(T) + \beta_1 \sin(2\pi T) + \beta_2 \cos(2\pi T) + \eta_t$$

where f and g are natural spline transforms.

The minimum of three knots was used for each spline term, requiring the estimation of only two parameters in each case (analogous to a quadratic term). The model was fit as described above. The significance of each explicit term in each of these equations was

tested with an analysis of variance that provided *F*-values and *P*-values for Wald tests (Pinheiro and Bates 2000). The implicit terms—the parameters and basis splines that constitute each explicit spline term in the equations—have no physical interpretation. It is only their combined effect that is of value here.

All calculations and tests, unless otherwise specified,

were carried out in the R software environment (R Development Core Team 2005). The U.S. Geological Survey's S-PLUS library was used for the Seasonal Kendall tests (Slack et al. 2003) and its program **Kendall.exe** for the Regional Kendall tests (Helsel et al. 2006). Modeling and analysis included extensive use of the **Hmisc** and **Design** (Harrell Jr. 2005) and **nlme** (Pinheiro et al. 2006) libraries for R.

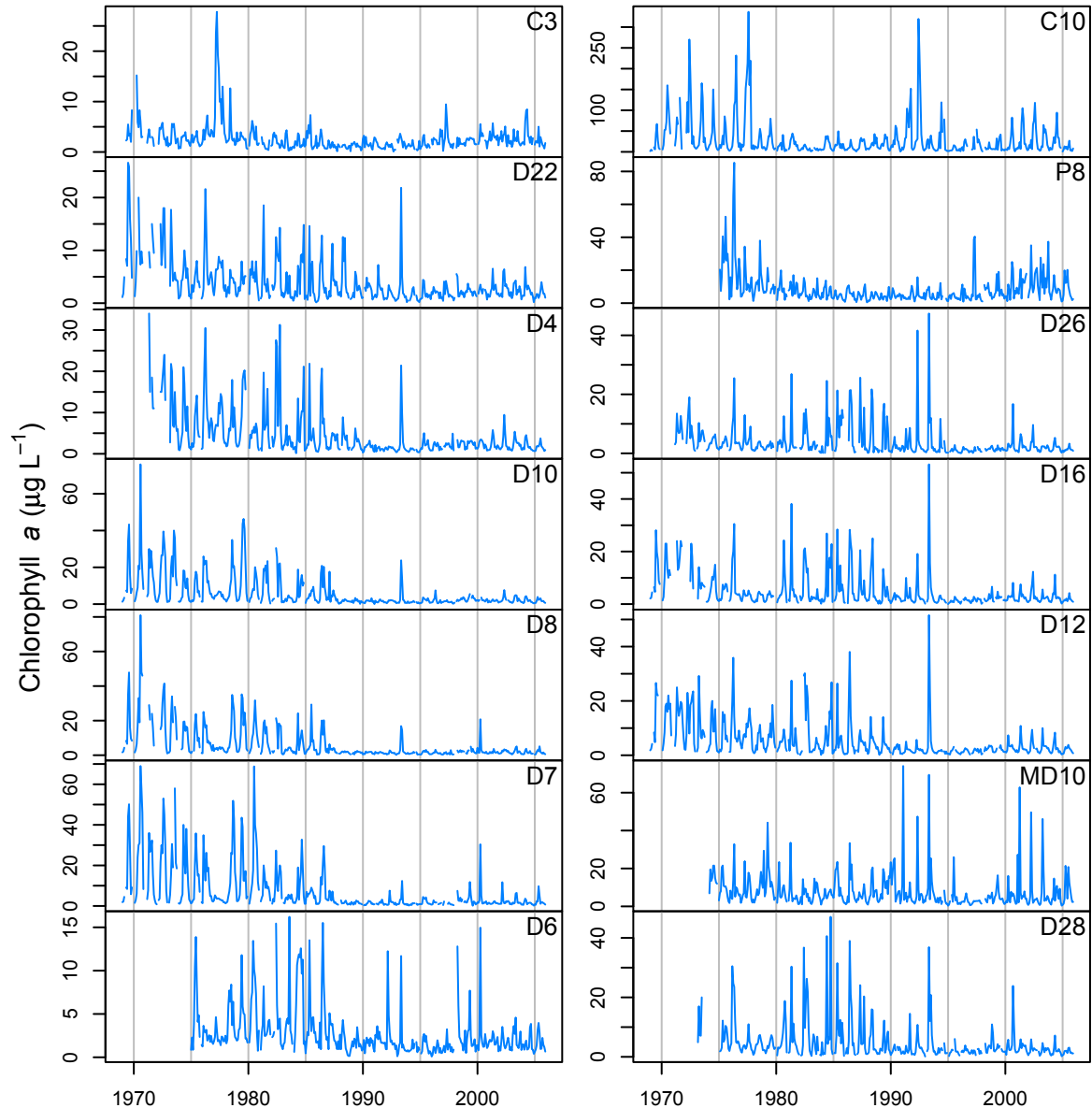


Figure 3. Long-term monthly time series of chlorophyll *a* at stations throughout the Delta and Suisun Bay. Note that *y*-axes differ from plot to plot. Plots in the left column are arranged in a sequence from the Sacramento River's upstream Delta boundary through Suisun Bay to San Pablo Bay. The first five plots in the right column are arranged in a sequence from the San Joaquin River's upstream Delta boundary to just before Suisun Bay.

RESULTS

Long-term Chlorophyll Variability, 1975–2005

The monthly chlorophyll time series for each station is plotted in Figure 3. Although it is difficult to discern much detail at this plotting scale, certain general features of the data can be seen easily. There is an impression of a long-term decline from 1970 at many stations (D22, D4, D10, D8, D7, D6, C10, P8, D12), followed by an obvious collapse of the phytoplankton community in Suisun Bay (D7, D8, D10) and vicinity (D6, D4, D12) after the clam *Corbula amurensis* invaded in 1986. A phytoplankton decline also occurred further upstream (D22, D16, D26, D28) but with a delay of several years.

The overall impression of a long-term decline in chlorophyll is confirmed by the inflow-adjusted trend

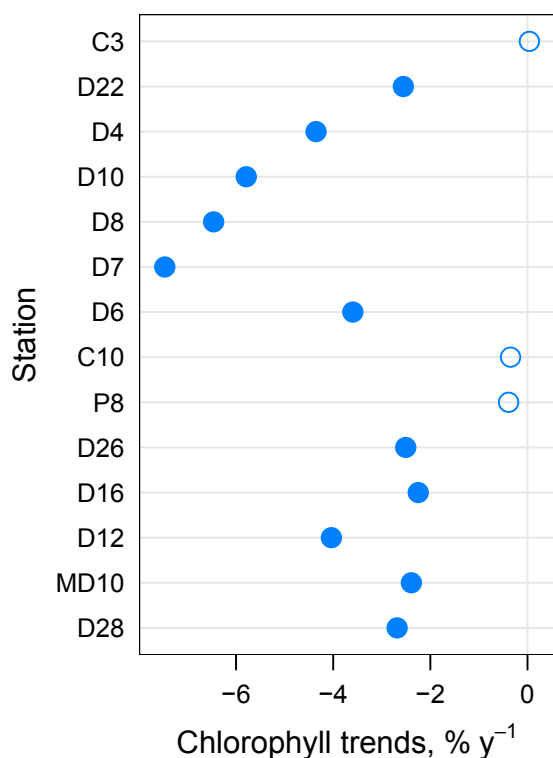


Figure 4. Long-term trends in Chl-*a* for 1975–2005. Trends are expressed as the Theil-Sen slope divided by the long-term median for the station. Trends are adjusted for river inflow, and *p*-values are corrected for seasonal serial correlation. Stations are arranged as in Figure 5 but with the left-column stations stacked on top of the right-column stations. *Solid circles*, *p* < 0.05 level according to the Seasonal Kendall test.

tests (Figure 4). The 1975–2005 trends are not statistically significant at most upstream stations (C3, C10, P8), but they are significant ($p < 0.05$) at all other stations. All significant trends are negative and their magnitude is large.

Recent Chlorophyll Variability, 1996–2005

A trend value depends, of course, on the window of time chosen for analysis. A higher-resolution graph of the chlorophyll series suggests that many Delta stations may have experienced chlorophyll *increases* during the last decade, 1996–2005 (Figure 5). Suisun Bay stations (D6, D7, and D8), on the other hand, do not exhibit a similar increase, except for the station closest to the Delta (D10).

The regionalization procedure using principal components analysis supports the notion that the Delta and Suisun Bay exhibited different kinds of behavior during 1996–2005 (Figure 6). Two significant modes of spatial variability in chlorophyll were identified, accounting for 53% of the total variance for the 14 stations. As described above, the temporal variability at any given station can be thought of as a combination of these two modes, with the component coefficients representing the strength of each mode for that station. The first mode (“delta” mode) is thus strongest for stations in the Delta, whereas the second mode (“suisun” mode) is strongest for stations in Suisun Bay. D10, which is transitional between the Delta and Suisun Bay, affiliates with the Delta rather than Suisun Bay.

A regional test for chlorophyll trend was carried out for all stations identified with the delta mode, i.e., all stations from D10 upstream. The annual pattern of the trend was revealed by conducting the regional test separately for each month (Figure 7). The Delta trend was statistically significant ($p < 0.05$) during March–September, ranging from 0.1 to almost 0.3 $\mu\text{g L}^{-1} \text{yr}^{-1}$ or 1–3 $\mu\text{g L}^{-1}$ for the decade. The period from March through June, which usually encompasses the spring bloom, will be the focus of interest in much of what follows. The regional trend during March–June was 0.22 $\mu\text{g L}^{-1} \text{yr}^{-1}$ (Table 1). Suisun Bay, on the other hand, had no significant regional trend in the past decade (Table 1; also see Table 4).

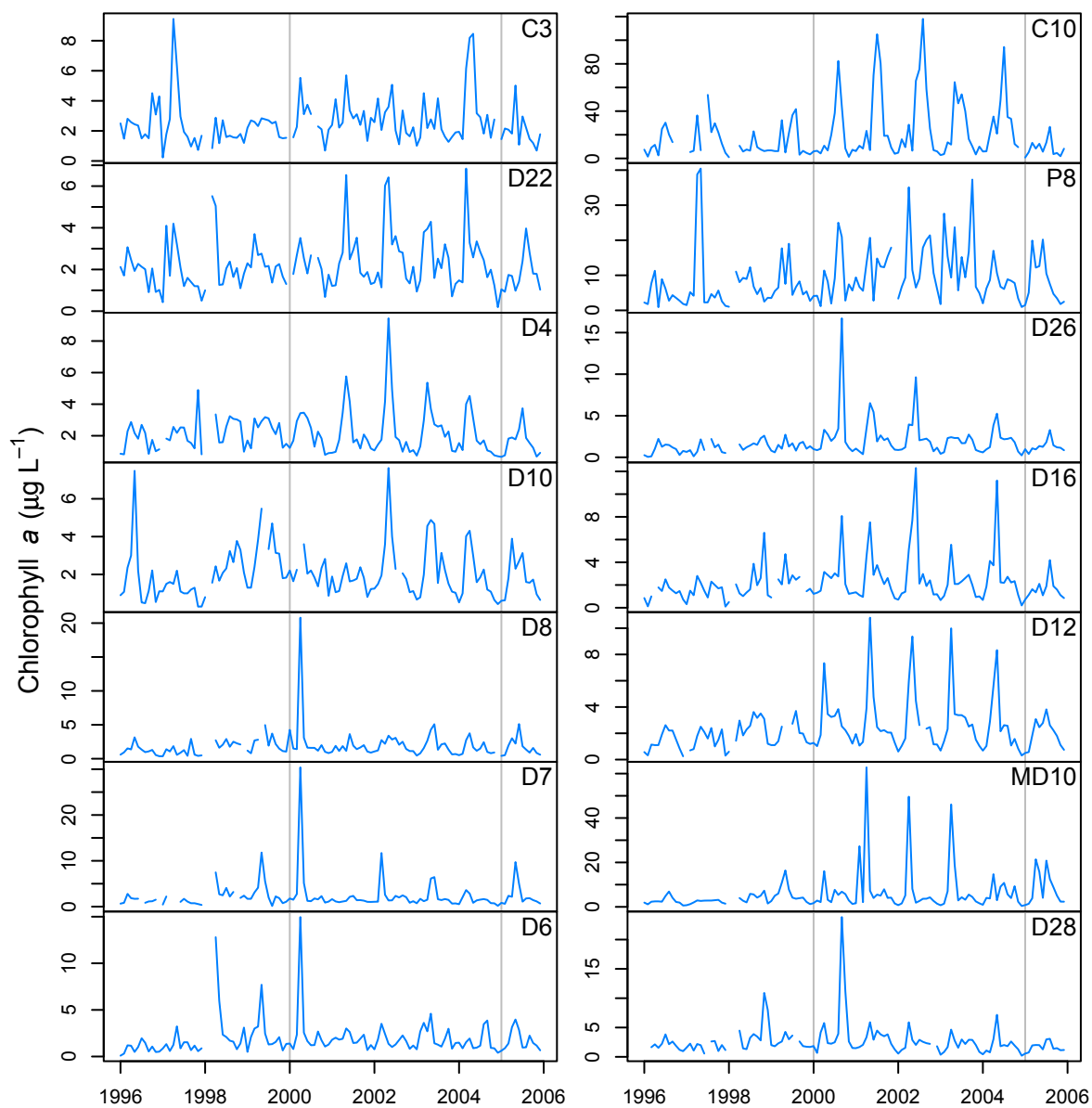


Figure 5. Monthly time series of Chl-*a* at stations throughout the Delta and Suisun Bay for 1996–2005. Plots arranged as in Figure 5.

Table 1. Regional trends for average March–June conditions during 1996–2005.

Variable	Delta		Suisun	
	Trend	<i>p</i> -value	Trend	<i>p</i> -value
chlorophyll <i>a</i> , µg L ⁻¹ y ⁻¹	0.22	< 0.001	0.12	0.30
temperature, °C y ⁻¹	0.21	< 0.001	0.025	0.84
SPM, mg L ⁻¹ y ⁻¹	-0.33	0.16	-0.89	0.22
ammonium, µmol L ⁻¹ y ⁻¹	0.18	0.032	0.18	0.042

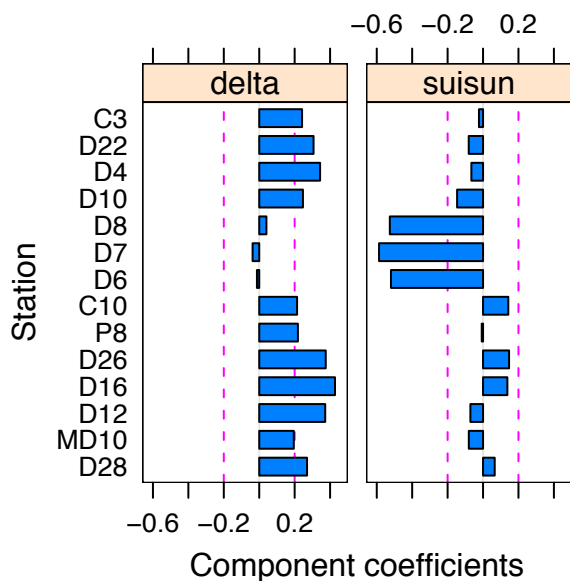


Figure 6. Two significant spatial modes of chlorophyll variability in the upper estuary during 1996–2005: the “delta” and “suisun” modes. *Dashed line*, reference level for comparison purposes.

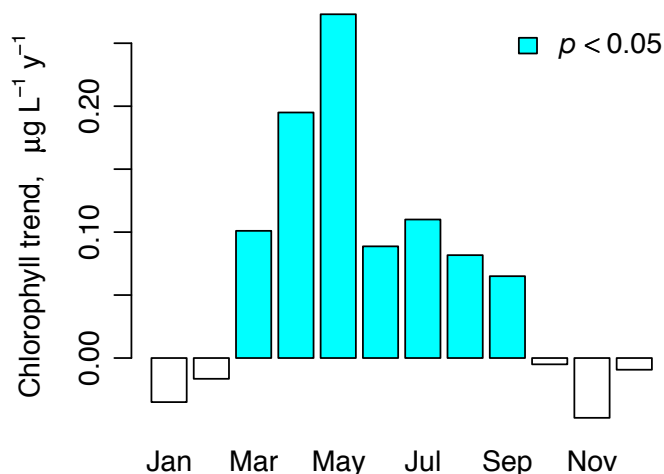


Figure 7. Chl-*a* trends in the “delta” subregion for 1996–2005. Trends are given by the Theil-Sen slope, and statistical significance is determined by the Regional Kendall test.

Flow Effects on Chlorophyll, 1996–2005

Inflows appear to have been generally lower during 2001–2005 compared to the previous five years (Figure 2). Indeed, trends in inflow during 1996–2005 are negative for every month and statistically significant for some of the late winter–early spring months

as well as for November (Figure 8). These observations suggest that inflow changes could have been the ultimate cause of chlorophyll increases. To test the sensitivity of chlorophyll levels to flow, annualized time series were prepared by averaging the March–June chlorophyll data for each station and then taking the median of the 11 delta-mode and, separately, the 3 suisun-mode stations. These were then compared with the annual time series of average February–June inflow data; February was included to account for any leading effect of flow due to particle residence times (see below).

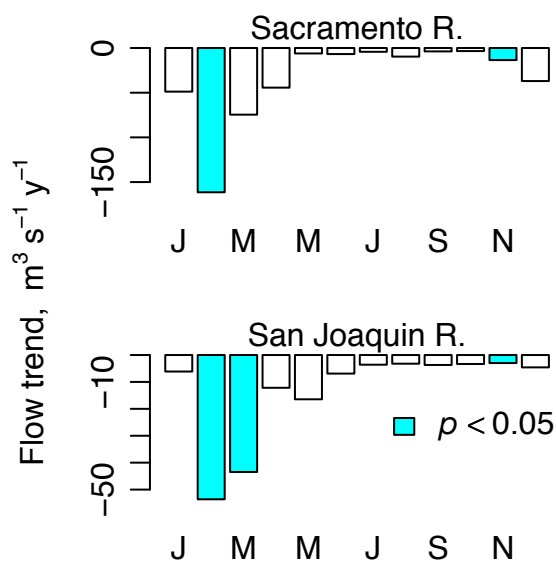


Figure 8. Trends in Delta inflow for 1996–2005. Trends are given by the Theil-Sen slope and statistical significance is determined by the Mann-Kendall test.

For the Delta, the resulting Kendall’s rank correlation between flow and chlorophyll during 1996–2005 was negative and statistically significant: $\tau = -0.60$ ($p = 0.017$). For Suisun Bay, in contrast, the correlation was positive and not significant: $\tau = +0.24$ ($p = 0.38$). A simple linear model of chlorophyll versus inflow (both log-transformed to improve normality) accounted for 49% of the overall variability in the Delta ($p = 0.029$; Figure 9).

For additional confirmation at the monthly scale, a “delta” time series was prepared by taking the median of the 11 delta-mode stations for each month; a similar series was prepared using the three suisun-mode

stations. Equation (2) was then fit to these two series for 1996–2005. Table 2 summarizes an analysis of variance, testing the overall significance of terms in the model. Inflow was a significant source of variability in the Delta but not in Suisun Bay during the last decade. Also, there was no significant trend apart from the effect of inflow. These results are also consistent with inflow variability underlying the recent regional trend observed in the Delta but not in Suisun Bay.

Table 2. Analysis of variance showing results of Wald tests for the terms of Equation (2). The model was fit to time series of median monthly chlorophyll *a* for delta- and suisun-mode stations, respectively, for 1996–2005.

Region	Terms	<i>d.f.</i>	<i>F</i>	<i>p</i>
delta	intercept	1	173	< 0.001
	flow	1	13.6	< 0.001
	trend	1	0.137	0.712
	sine	1	27.9	< 0.001
	cosine	1	30.3	< 0.001
suisun	intercept	1	26.7	< 0.001
	flow	1	0.602	0.439
	trend	1	0.269	0.605
	sine	1	20.3	< 0.001
	cosine	1	14.5	< 0.001

Flow Effects on Chlorophyll, 1975–2005

If inflow changes are indeed the mechanism ultimately behind recent Delta chlorophyll trends, then why is Suisun Bay chlorophyll relatively unresponsive to flow, unlike its behavior in earlier years of the monitoring program (Jassby and Powell 1994)? To address this issue, Equation (3), which allows for a changing chlorophyll–flow relationship, was fit to the same two series, i.e., delta-mode and suisun-mode stations, but for the period 1975–2006. Table 3 summarizes the analysis of variance for each application of the model. Flow and a long-term trend independent of flow were significant for both regions. But the interaction between flow and trend was significant only in Suisun Bay, indicating a change in the nature of

the chlorophyll response to flow between earlier and later years.

Table 3. Analysis of variance showing results of Wald tests for the terms of Equation (3). The model was fit to time series of median monthly chlorophyll *a* for delta- and suisun-mode stations, respectively, for 1975–2005.

Region	Terms	<i>d.f.</i>	<i>F</i>	<i>p</i>
delta	intercept	1	532	< 0.001
	flow	2	23.1	< 0.001
	trend	2	27.7	< 0.001
	flow × trend	4	0.813	0.517
	sine	1	28.3	< 0.001
	cosine	1	133	< 0.001
suisun	intercept	1	167	< 0.001
	flow	2	5.07	0.007
	trend	2	39.0	< 0.001
	flow × trend	4	3.39	0.010
	sine	1	9.36	0.002
	cosine	1	76.2	< 0.001

The flow responses based on Equation (3) are illustrated in Figure 10 for two different years (1980 and 2000), well before and after the clam invasion in 1986. This Figure emphasizes several key points arising from the analysis. First, the drop in mean response for the Delta between 1980 and 2000 was much smaller than for Suisun Bay. Second, chlorophyll responded strongly to flow, at least during the earlier period. Third, there was no significant change in the shape of the flow response for the Delta but a large one for Suisun Bay: in Suisun Bay, a possibly unimodal response that decreased with flows above about 500 m³ s⁻¹ changed to a monotonic response that increased slowly above these flow levels. Note also how all the responses appear to merge at the highest flows, when we would expect Suisun Bay simply to reflect upstream conditions.

Can these quantitative responses “distilled” by the model be observed qualitatively in the actual data? Figure 11 is based on individual chlorophyll observations in Suisun Bay during spring and summer of

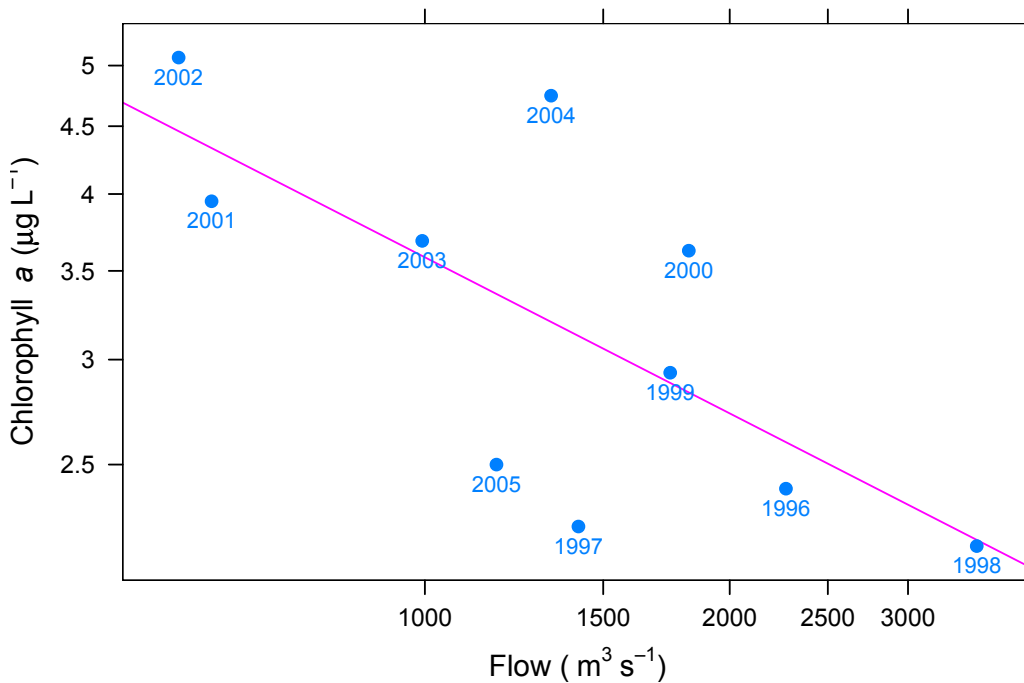


Figure 9. Relation between delta-mode chlorophyll and inflow during March–June 1996–2005. Solid line, linear regression fit.

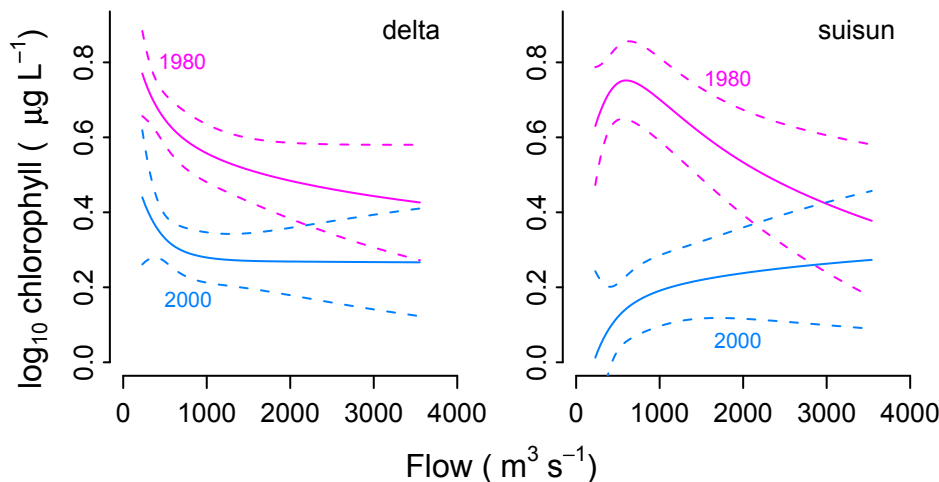


Figure 10. Chlorophyll responses to flow for the delta-mode and suisun-mode stations based on Equation (3) fit to 1975–2005 data. Two responses are shown for each station, one for 1980 and one for 2000. The sine and cosine terms in the model are set to their medians. Dashed lines, 0.95 confidence intervals for the mean response.

1975–2005. The data are separated into two bins based on occurrence before (1975–1986) and after (1987–2005) the *Corbula* invasion. Within each period, the data are then binned based on the cor-

responding quartile for net Delta outflow. The same features distilled by the model can be seen: drop in mean response between earlier and later periods, strong response to flow at least in the earlier period, and a change in the shape of the flow response between periods from unimodal to weakly monotonic.

Temperature Trends, 1996–2005

Water temperature increased during 1996–2005. The regional trend for average March–June temperature in the Delta was 0.2 degrees Celsius per year ($^{\circ}\text{C y}^{-1}$) ($p < 0.001$), expressed as the Theil-Sen slope (Table 1). This recent trend contrasts with more long-term changes in temperature that are not statistically significant (1975–2005: Figure 12).

The sensitivity of annualized temperature to flow was tested in the same way as for chlorophyll. For both the Delta and Suisun Bay, the resulting negative Kendall’s rank correlation between flow and temperature during 1996–2005 was not statistically significant: $\tau = -0.33$ ($p = 0.21$) and $\tau = -0.022$ ($p = 0.99$), respectively. A linear model of temperature versus flow accounted

for only 20% of the overall variability ($p = 0.20$). It is tempting to conduct a “back-of-the-envelope” calculation similar to that for residence time (see Discussion) to assess the impact of the temperature

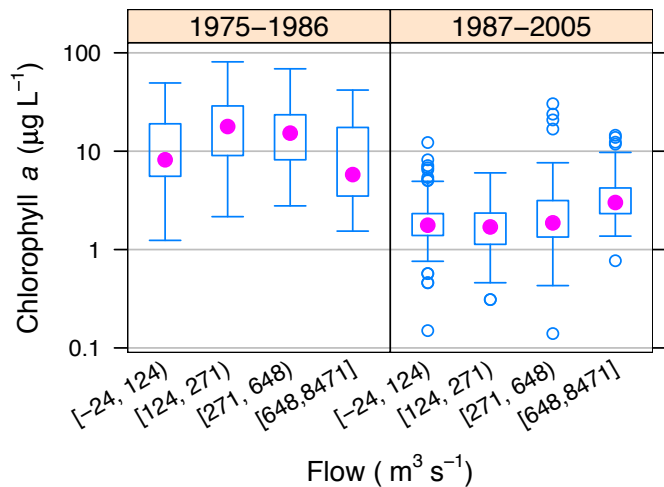


Figure 11. Distributions of chlorophyll responses to net Delta outflow (Figure 3) for stations in Suisun Bay during spring and summer. The data are first binned into earlier (1975–1986) and later (1987–2005) observations. Within each of these periods, the data are then binned according to the corresponding quartile of flow. Each quartile is described on the x -axis by its upper and lower boundary; negative flows indicate net landward flow into the Delta.

changes on chlorophyll. But temperature effects on the net increase rate are more complicated as they undoubtedly affect growth rate and losses—especially to primary consumers—differentially.

Suspended Matter Trends, 1996–2005

The status of suspended matter in the upper estuary is important because of evidence that phytoplankton production is light-limited (e.g., Jassby et al. 2002). Some indirect corroboration for light limitation comes from Equation (3). The sine and cosine terms enable us to calculate the peak day, on average, for that part of the annual cycle not accounted for by flow. That day was June 10 for the Delta and June 16 for Suisun Bay. These days are close to the summer solstice and indicate that the periodic term in both cases probably reflects the solar cycle, i.e., light availability is probably driving that part of the annual cycle not related to flow.

SPM decreased during 1996–2005 but changes were relatively small. The regional trends for average March–June SPM were negative but not statistically

significant (Table 1). In contrast to the 1996–2005 results, long-term declines remain statistically significant even when this more recent period is included (Figure 12; see also Table 4).

Macronutrient Distributions, 1996–2005

A recent review of the literature on nutrient limitation based on studies from both freshwater and marine systems (Reynolds 2006) was used to assess macronutrient distributions in the upper estuary during 1996–2005. The review concluded that reactive phosphorus concentrations required to saturate growth rates are generally under $0.13 \mu\text{mol L}^{-1}$. In addition, half-saturation constants for nitrogen uptake, although dependent on the exact form of DIN, are below $7 \mu\text{mol L}^{-1}$ for larger, low-affinity species and $0.7 \mu\text{mol L}^{-1}$ for oceanic picoplankton. Finally, half-saturation levels for silicon uptake are in the range $0.3\text{--}5 \mu\text{mol L}^{-1}$.

Figure 13 summarizes macronutrient distributions in the upper estuary during 1996–2005. In the cases of SRP and silica, concentrations appear to be high enough to saturate growth and/or uptake, although two of the SRP measurements were below their detection limits (one each at C3 and MD10). In the case of N, restriction of uptake might occasionally occur for low-affinity species, but these occasions would be rare: concentrations below $7 \mu\text{mol L}^{-1}$ occurred in only nine instances (1 at D28 and 8 at MD10).

Ammonium Trends, 1996–2005

Ammonium constituted about 20% of DIN during the period 2001–2005 at the 10 well-sampled stations. But ammonium has also been implicated in phytoplankton growth inhibition in Suisun Bay, and so its behavior in the last decade is of interest apart from its role as a DIN source (Dugdale et al. 2007). Ammonium concentrations during March–June of 1996–2005 were mostly above $4 \mu\text{mol L}^{-1}$, a threshold thought to indicate inhibition of phytoplankton growth rates (Figure 14).

Wastewater discharge is the dominant source by far of the river-borne ammonium load. The largest

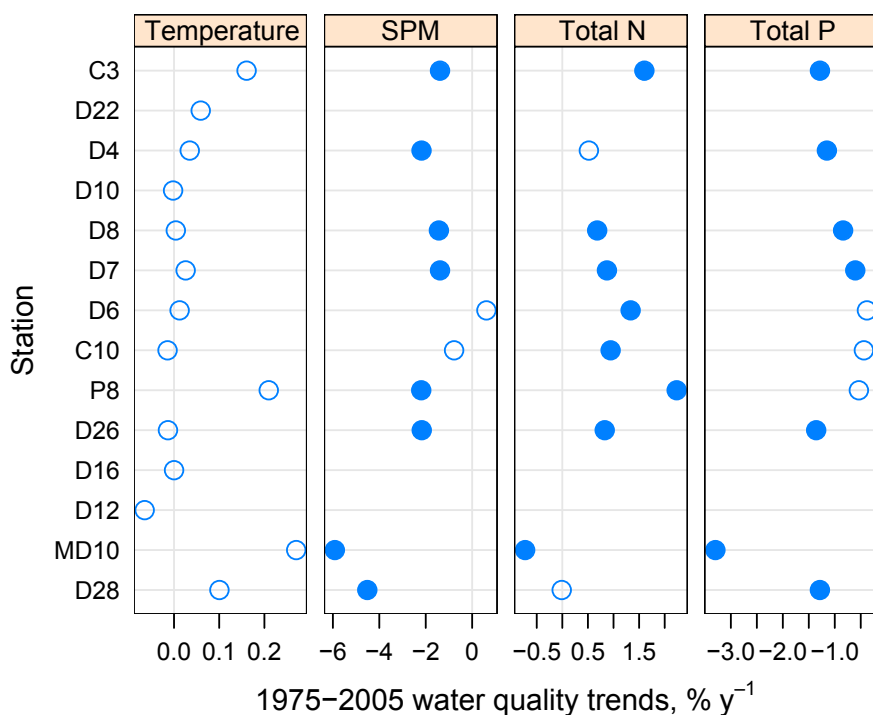


Figure 12. Long-term trends in water quality variables during 1975–2005. Trends are expressed as the Theil-Sen slope divided by the long-term median for the station. Trends are adjusted for river inflow and *p*-values are corrected for seasonal serial correlation. Trends are not plotted for stations with inadequate data during this period. *Solid circles*, *p* < 0.05 level according to the Seasonal Kendall test.

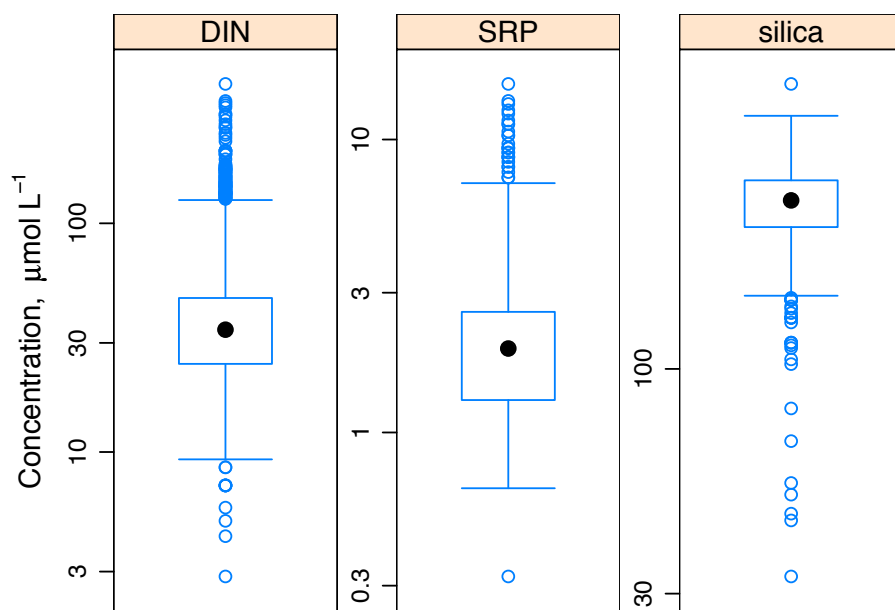


Figure 13. Macronutrient distributions during 1996–2005 for the stations of Figure 1 combined.

publicly-owned treatment works discharge of wastewater ammonium to the Delta is the Sacramento Regional Wastewater Treatment Plant. It discharged an average of 6.0×10^5 cubic meters per day ($m^3 d^{-1}$) (or 158 million gallons per day [MGD]) during 2001–2005 (County of Sacramento 2006).

The median annual wastewater ammonium discharge during 1985–2005 was 90% of the river ammonium load (range 78–108%) at Station C3 and its predecessor C3A, which are located 10–20 kilometers (km) downstream of the Sacramento discharge. The Spearman correlation between the two was 0.85 (degrees of freedom [d.f.] = 19, $p < 0.001$). Moreover, these wastewater sources appear to be on the rise. The average monthly load of ammonium-N was 391 ± 6 (standard error) metric tons per month ($t mo^{-1}$) during this period, an increase of 69% over 1986–1990 and 27% over 1996–2000 (Figure 15). This probably reflected population increases in the county, which also showed considerable, although somewhat smaller, growth.

Ammonium loading from the Stockton Regional Wastewater Control Facility grew at an even faster rate, but the magnitude of the load is much smaller (Jassby and Van Nieuwenhuysse 2005), averaging about $45 t mo^{-1}$ in recent years. Other treatment works also contribute a smaller amount than the Sacramento plant although they may be important locally. For example, the three treatment works discharging directly to Suisun Bay (Central Contra Costa Sanitation District, Fairfield Suisun Sewer District, and Delta Diablo Sanitation District) have a current

combined discharge of about $2.2 \times 10^5 \text{ m}^3 \text{ d}^{-1}$ (58 MGD; Central Contra Costa Sanitation District 2005).

Because of the trends in wastewater effluent ammonium, one would also expect an upward trend in dissolved ammonium as well. Regional trends for average March–June ammonium concentration during 1996–2005 were calculated separately for the delta-

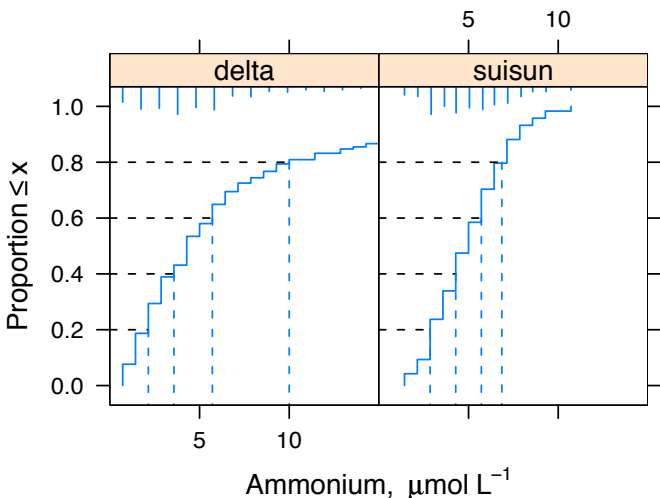


Figure 14. Empirical cumulative distribution of ammonium concentrations during March–June 1996–2005 at delta- and suisun-mode stations. A spike histogram of the data is included above each plot.

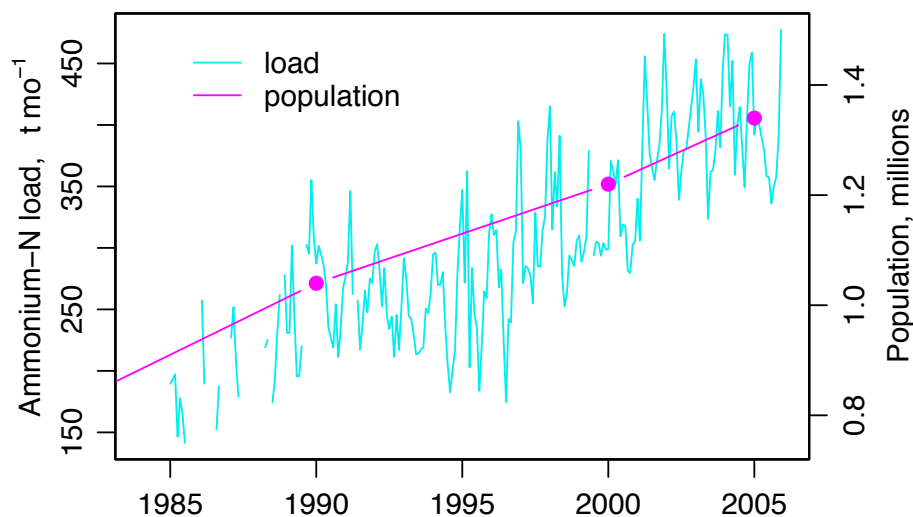


Figure 15. Monthly load of ammonium-N in wastewater from the County of Sacramento Regional Wastewater Treatment Plant. County population is also shown for comparison.

and suisun-mode stations. The median trends were indeed positive and significant (Table 1).

Primary Production, 1975–2005

What are the consequences of changes in chlorophyll for gross primary production? Estimates of GPP were confined to Delta stations because of evidence that Suisun Bay growth rates [and therefore Ψ in Equation (1)] are impaired due to water contaminants (Dugdale et al. 2007). Over the longer term, GPP declined by 42% from 1976–1980 to 1991–1995 (Table 4). This compares with a Delta-wide average of 43% for 1975–1995 using a more comprehensive set of stations (Jassby et al. 2002). Although the close agreement must be fortuitous, it does provide some confidence in the cruder approach forced on us here by the loss of stations after 1995. The GPP decline during 1976–1995 would have been even greater if a long-term decrease in SPM—and corresponding increase in water clarity—had not accompanied the long-term decrease in chlorophyll (Figure 12; see also Table 4). The two have compensated for each other, dampening long-term trends in primary production.

The decline in Delta GPP appears to have halted in 1991–1995. Median GPP in the Delta increased in the last five years over the previous five (Table 4).

The Regional Kendall test was applied to the annual data during 1996–2005, yielding a statistically significant regional trend of 3.7 milligrams carbon per square meter per day per year ($\text{mg C m}^{-2} \text{ d}^{-1} \text{ y}^{-1}$) ($p < 0.001$). Aside from the possible impairment by contaminants, one would expect GPP in Suisun Bay to have increased as well during this period because of lower SPM and resulting higher water clarity in that subregion.

Table 4. Five-year medians of March–November values for Suisun Bay (Stations D6, D7, and D8) and Delta (Stations C3, D4, C10, P8, D26, MD10, and D28).

Period	Delta Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	Suisun Chl- <i>a</i> ($\mu\text{g L}^{-1}$)	Delta SPM (mg L^{-1})	Suisun SPM (mg L^{-1})	Delta GPP Index ($\text{mg C m}^{-2} \text{d}^{-1}$)
1976–1980	7.0	5.1	24	32	430
1981–1985	5.4	5.4	18	30	390
1986–1990	4.3	1.9	15	30	340
1991–1995	2.7	1.5	12	27	250
1996–2000	2.8	1.6	13	33	250
2001–2005	3.4	1.6	11	24	330

DISCUSSION

Biomass and Production Trends

Even at the beginning of the historical record for the estuary, values of chlorophyll and estimated gross primary production were less than in most other temperate river-dominated estuaries (Day et al. 1989). A subsequent decline of about 60% in biomass and 40% in production between the late 1970s and the early 1990s then placed the Delta among the least productive tidal systems. The drop in Suisun Bay biomass was even more striking.

This decline must have had important trophic consequences. The relation between fisheries yield and primary production among estuaries is a noisy one, but a cross-section of estuarine data implies that the most likely response of overall fish production has been at least a similar decline (Nixon 1988). The implications for individual fish species are less certain, but food limitation clearly must be considered a possible major factor in the long-term decline of any fish species in the upper estuary during this period.

The chlorophyll data of Table 4 also have nutritional implications. Growth rate and egg production of at least some zooplankton species in the estuary respond strongly to values of less than about $10 \mu\text{g L}^{-1}$ (e.g., Mueller-Solger et al. 2002; Kimmerer et al. 2005). A dominant benthic bivalve in the upper estuary, *Corbicula fluminea*, also exhibits growth saturation at around $10 \mu\text{g L}^{-1}$ (Foe and Knight 1985). The long-term decline in median values from 7.0 to $2.7 \mu\text{g L}^{-1}$

in the Delta and from 5.1 to $1.5 \mu\text{g L}^{-1}$ in Suisun Bay therefore takes place in a critical range that could have had a dramatic impact on aggregate growth of primary consumers and, over the long term, the productivity of higher organisms dependent on them.

More recent declines of fish abundance, however, cannot be attributed simply to corresponding decreases in phytoplankton biomass and production. There appears to have been a general increase in phytoplankton biomass and production since the early 1990s. Trends in biomass have been close to neutral or positive over the last decade throughout the upper estuary. Median biomass and production in the Delta increased about 30% from the early 1990s to the early 2000s.

Although current phytoplankton biomass levels are still below the earliest-recorded ones, they do represent an ecologically significant change over the last decade or so. In contrast, many pelagic species of fish in the upper estuary declined markedly in recent years, including record lows for delta smelt and age-0 striped bass, and near-record lows for longfin smelt and threadfin shad during 2003–2005 (Sommer et al. 2007). The problem appears to be limited to fish dependent on the upper estuary because similar declines have not taken place downstream among species characteristic of San Francisco Bay. These changes have taken place despite moderate winter–spring flows considered favorable to the declining species. The opposing 1996–2005 trends in chlorophyll imply that recent changes in total phytoplankton biomass are probably not a cause of the recent declines at higher trophic levels. It is possible, though, that recent pelagic organism declines are a delayed legacy of the long-term drop in phytoplankton biomass as effects of diminished recruitment continue to play out.

Even though trends of total phytoplankton biomass and production are not consistent with recent fish declines, changes in species composition of the phytoplankton community could play a role independently of total biomass. Phytoplankton differ widely in their nutritional value to primary consumers, based in part on their highly unsaturated fatty acid content. Fatty acid content and nutritional value varies much

more between than within taxa. Diatoms and cryptophytes, for example, tend to be more nutritious than cyanobacteria for many zooplankton species (Brett and Mueller-Navarra 1997).

A decrease in percentage of diatom biovolume occurred during 1975–1989, caused by both a decrease in diatoms and an increase in green algae, cyanobacteria and flagellate species biovolume (Kimmerer 2005; Lehman 1996), i.e., probably in the direction of declining nutritional value per unit biomass. In principle, the total nutritional value of a community could decrease even as its biomass increases. Moreover, changes in size, shape, and motility of species comprising the phytoplankton community could also affect their availability as food particles for crustacean zooplankton and other consumers. An updated analysis of the phytoplankton community from this perspective would help resolve this area of uncertainty.

Other primary producers have mounted increasing competition for habitat in recent years. The first recorded toxic cyanobacteria blooms in the Delta occurred recently, for example (Lehman 2005). The organism in question, *Microcystis aeruginosa*, normally sampled by a surface horizontal tow with a 75- μ m net, is not efficiently collected by the routine phytoplankton sampling program and rarely occurs in the discrete monthly samples. It is therefore not directly behind the chlorophyll changes described here. In fact, one would expect a suppressive effect on other phytoplankton because of its ability to mass at the water surface.

Several aquatic macrophytes also compete with the phytoplankton community for habitat, chief among these being Brazilian waterweed (*Egeria densa*). It now occupies a significant and increasing area of the upper estuary (Grimaldo and Hymanson 1999; Underwood et al. 2006). There are no doubt at least local effects on phytoplankton habitat through direct competition, provision of refuge for zooplankton consumers, suppression of sediment resuspension and other phenomena known from studies of alternating stable states in shallow lakes (Scheffer 2001). Yet, as in the case with *Microcystis*, one would have expected an overall phytoplankton decrease, not increase,

if *Egeria* had been behind the recent phytoplankton changes.

The Effects of Macronutrient Supply

Macronutrient supply, on the basis of dissolved nutrient levels, does not seem to be important as a determinant of current phytoplankton variability. Moreover, in the case of phosphorus, SRP is a very conservative estimate of available phosphorus because intracellular storage can suffice for three or four cell doublings (Reynolds 2006).

Nutrients from wastewater effluent and fertilizer runoff are a global problem for estuaries, stimulating excessive phytoplankton production and often resulting in hypoxia or anoxia that directly or indirectly impairs estuarine fish and shellfish populations (Cloern 2001). In the Delta, elevated phytoplankton levels in the San Joaquin River already contribute to chronic hypoxia in the Stockton Deep Water Ship Channel and probably interfere with the habitat, spawning, and migration of both warm and cold freshwater fishes (Jassby and Van Nieuwenhuysse 2005). Even if nutrient levels no longer control phytoplankton variability directly, they permit the nuisance levels of biomass and production seen in parts of the Delta.

Furthermore, the forces that do currently limit biomass and production are not guaranteed to persist. There is always the potential for available nutrients to be fully utilized, resulting in degraded water quality elsewhere in the Delta. Although total P has decreased at all estuarine stations since 1975, in some cases dramatically, total N has increased (Figure 12). Management of nutrient loading therefore remains an important goal for this estuary, both to prevent spread of excessive phytoplankton production in the future and to address existing hypoxia in the San Joaquin River.

Ammonium is a special macronutrient case. Although a source of inorganic nitrogen, it supports lower phytoplankton growth rates than nitrate does. When present at high enough concentrations relative to nitrate, it may delay and even lower the probability of a spring bloom (Dugdale et al. 2007). The

main source of ammonium in the upper estuary is wastewater treatment effluent. This source has been increasing for many years, including during the last decade (Figure 15). In response, ammonium concentrations in both the Delta and Suisun Bay have increased (Table 1). Moreover, ammonium concentrations are frequently above $4 \mu\text{mol L}^{-1}$, a threshold thought to indicate inhibition of phytoplankton growth rates (Figure 14). Despite this environment of higher ammonium, there was an overall trend of increasing spring–summer chlorophyll in the Delta during the last decade (Figure 7). The physiological effect of ammonium is well-established, and it may very well play a role in the dynamics of specific phytoplankton events (Wilkerson et al. 2006). But it is one factor among many, and its ecological impact relative to other sources of variability underlying long-term phytoplankton patterns is not yet clear.

The Effects of Flow Variation

Among the physical and chemical factors, the most likely cause of phytoplankton biomass changes observed in the last decade is flow variability. In summary, (1) the overall trends of chlorophyll are positive, and total inflow negative; (2) the changes are happening concurrently at many widely-separated stations in the Delta; (3) the regression of March–June chlorophyll on inflow accounts for half the year-to-year variability; and (4) an empirical model of monthly chlorophyll demonstrates significant flow effects on top of the seasonal pattern, as well as the absence of any residual trend. The notion that changes in inflow underlie the recent phytoplankton trends is also consistent with many studies, including from this estuary, showing that freshwater inflow is a major factor in year-to-year variability of estuarine phytoplankton (see Chan and Hamilton 2001; Kimmerer 2002b; and citations in both).

Accompanying temperature increases could enhance or mitigate the flow effect, depending on the relative size of growth and grazing losses and their responsiveness to temperature change. Most of the year-to-year temperature variability does not appear to be connected with flow, at least insofar as this data-set can reveal, and so temperature impacts could repre-

sent an independent source of chlorophyll variability. The temperature data show no significant trend over the longer term of 1975–2005, but the more recent increase may not be simply a short-term phenomenon, given the current direction of climate change.

Further evidence for the importance of flow comes from a consideration of particle residence times. The most direct effects of flow are on residence time, which determines the time available for the phytoplankton net increase rate to be expressed as biomass changes. It is helpful to emphasize the potential magnitude of the effect. The focus is on the March–June period encompassing the spring bloom. Residence times for particles in the Delta during 1990–2004 were recently estimated by Sommer et al. (2006). They used as an index the time required for a fixed percentage of particles to be removed from the Delta. For 50% removal, the March–June 1996–2000 mean was 12 d for particles injected into the Sacramento River at Freeport, the upstream estuarine boundary where tides become negligible. The March–June 2001–2004 mean was 21 d. The mean residence time therefore increased by 9 d.

It is not clear where the inoculum originates for a phytoplankton population sampled at a given station, and so the relevance of the injection point is uncertain. But it is still interesting to examine the effect of increasing residence time by about one week, as if these inocula originated at the upstream boundaries. A conservative value (because of light limitation) for the exponential net increase rate during the spring bloom period is $r = 0.2 \text{ d}^{-1}$, which is equivalent to a doubling time of 3.5 d. A residence time increase of a week thus allows for two doublings or a four-fold increase in biomass. Although this crude calculation is subject to many uncertainties in both directions, the potential effects of flow on interannual chlorophyll variability are clearly quite high for conditions probably relevant in the Delta.

The relationship between chlorophyll and flow is by no means exact. One would expect substantial noise from tidal effects at downstream stations like D16 and especially D8, which undoubtedly partially obfuscates the chlorophyll–flow relationships (Jassby et al. 2005; Lucas et al. 2006).

Other more nuanced aspects of flow may be playing a role. San Joaquin River water, for example, can be diverted to the export pumps or allowed to flow to the western and central Delta. As the San Joaquin River generally carries much higher levels of phytoplankton than the Sacramento River, chlorophyll loading to the western Delta and Suisun Bay depends on the extent of this diversion, even if total inflow does not change (Jassby and Cloern 2000). Empirical models based on monthly data, such as the one presented here, are unlikely to resolve more complicated hypotheses involving flow because of limited data relative to the number of required predictor variables.

Other Factors Affecting Biomass and Production Trends

Additional mechanisms, not directly related to the physical and chemical environment, may also be involved in recent trends. A major candidate is certainly consumption by benthic bivalves. The importance of suspension-feeding bivalves has been demonstrated in many systems, including freshwater and oligohaline reaches of estuaries (Gerritsen and Holland 1994, Smith et al. 1998). Strong evidence already points to it underlying striking changes in Suisun Bay and the western Delta (Nichols 1985; Nichols et al. 1990; Alpine and Cloern 1992; Cole et al. 1992). Modeling and empirical studies also clearly point to benthic grazing as a dominant control on bloom formation in other parts of the estuary (Cloern 1982; Lucas et al. 1999; Jassby et al. 2002).

The opportunistic and widely-distributed bivalve *Corbicula fluminea* is probably the dominant benthic consumer in most freshwater reaches of the upper estuary (Hymanson et al. 1994). Its strong effects on phytoplankton biomass are known from studies of other systems (McMahon 2000), as well as in the upper San Francisco Estuary (Lucas et al 2002; Lopez et al. 2006). Although there are many possibilities in such a complex estuary as this one, primary consumption by benthic bivalves is a ready explanation at hand for a significant part of the interannual variability. Unfortunately, the lack of a comprehensive spatial record for the benthos upstream of Suisun Bay precludes any Delta-wide generalizations from the long-term data set.

Why is Suisun Bay chlorophyll now so unresponsive to flow variability compared with the Delta? When fit to Equation (3), the long-term data imply that the chlorophyll level for a given flow has shifted down in both regions but the very shape of the rating curve has changed in Suisun Bay. Flows above about $500 \text{ m}^3 \text{ s}^{-1}$ now slightly enhance Suisun Bay chlorophyll (albeit without statistical significance), while previously they suppressed it.

The most likely explanation is the *Corbula* invasion of the 1980s and subsequent increase in primary consumption of phytoplankton (Alpine and Cloern 1992; Cole et al. 1992). The impact of this consumption is to maintain phytoplankton at very low levels most of the time, despite the return of more normal flows after the 1987–1992 drought. Prior to the invasion, Suisun Bay chlorophyll was usually higher than the average in inflow from upstream; increased flow therefore resulted in net losses (Jassby and Powell 1994). Now Suisun Bay chlorophyll is usually lower, and increased flow results in net gains. This explanation is consistent with the merging of the two rating curves at high flows. A structural change in the ecosystem has thus led to a fundamental change in the shape of the chlorophyll rating curve (Figure 10 and Figure 11).

This change in flow response is related to an important consideration regarding the food supply to Suisun Bay. The loading of phytoplankton and phytoplankton-derived detritus accounts for much of the phytoplankton carbon supply to Suisun Bay. Jassby et al. (1993) estimated that the annual percentage attributable to river loading varied from 20% to 90% during 1975–1989. The percentage was 60% in 1980, a year in which inflow was close to the long-term mean. Similarly, Jassby and Cloern (2002) estimated mean river loading of total organic N during 1975–1995 as 17 t d^{-1} , compared to 3.9 t d^{-1} produced within Suisun Bay based on the previous study.

Both of these studies used data from before and after the clam invasion. Now the allochthonous supply must be even greater than before the invasion because Suisun Bay phytoplankton levels have decreased so much more than Delta levels since 1986.

Any conclusions about the food supply in Suisun Bay therefore cannot treat autochthonous production in isolation.

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