

# Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem

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## Abstract

Although nutrient supply often underlies long-term changes in aquatic primary production, other regulatory processes can be important. The Sacramento–San Joaquin River Delta, a complex of tidal waterways forming the landward portion of the San Francisco Estuary, has ample nutrient supplies, enabling us to examine alternate regulatory mechanisms over a 21-yr period. Delta-wide primary productivity was reconstructed from historical water quality data for 1975–1995. Annual primary production averaged  $70 \text{ g C m}^{-2}$ , but it varied by over a factor of five among years. At least four processes contributed to this variability: (1) invasion of the clam *Potamocorbula amurensis* led to a persistent decrease in phytoplankton biomass (chlorophyll *a*) after 1986; (2) a long-term decline in total suspended solids—probably at least partly because of upstream dam construction—increased water transparency and phytoplankton growth rate; (3) river inflow, reflecting climate variability, affected biomass through fluctuations in flushing and growth rates through fluctuations in total suspended solids; and (4) an additional pathway manifesting as a long-term decline in winter phytoplankton biomass has been identified, but its genesis is uncertain. Overall, the Delta lost 43% in annual primary production during the period. Given the evidence for food limitation of primary consumers, these findings provide a partial explanation for widespread Delta species declines over the past few decades. Turbid nutrient-rich systems such as the Delta may be inherently more variable than other tidal systems because certain compensatory processes are absent. Comparisons among systems, however, can be tenuous because conclusions about the magnitude and mechanisms of variability are dependent on length of data record.

Phytoplankton primary productivity in lakes, estuaries, and the ocean plays an essential role in element cycling, water quality, and food supply to heterotrophs (Cloern 1996). Although we implicitly recognize primary productivity as a time-varying process, much of our effort to measure and understand this variability has focused on time scales of 1 yr or less. How much does annual primary production vary from year to year or over periods of decades, and what are the underlying mechanisms of variability at these longer time scales? These time scales are of particular interest from a practical viewpoint: they span the period over which we must separate anthropogenic influences from natural variability in order to understand the effects of our current use of water resources. Long-term studies of annual primary production in individual systems can also help us to understand

differences among ecosystems in their annual production. Sustained investment of resources to measure primary productivity over multiple decades is rare, however (Underwood and Kromkamp 1999). Moreover, the long-term records rarely include sufficient spatial sampling to allow assessments of variability at the scale of ecosystems. Our understanding of long-term variability of annual primary production is limited by the global scarcity of appropriate data sets.

We know that changes in nutrient supply can be the dominant mechanism of variability in many ecosystems and that this mechanism operates at all scales longer than a year. Indeed, delineating the role of nitrogen and phosphorus in long-term (decadal) change was one of the earliest, significant practical achievements in limnology (Edmondson 1991). Phosphorus and nitrogen supply is also known to drive year-to-year variability in primary production of many freshwater (Lake Tahoe, Jassby et al. 1992), estuarine (Neuse River Estuary, Paerl et al. 1998), and coastal ocean (northern Adriatic Sea, Harding et al. 1999) systems. In fact, most long-term studies have emphasized change in nutrient input as the mechanism of change in annual primary production.

How do changes in other regulatory processes of phytoplankton growth rate and biomass influence annual primary production? Borum's (1996) analysis of annual phytoplankton production from many different coastal areas indicated that only about 36% of the variability could be attributed to nutrient (N) loading. Cloern (2001) described four important attributes of estuarine systems that distinguish them from most lakes and modulate their response to nutrient enrich-

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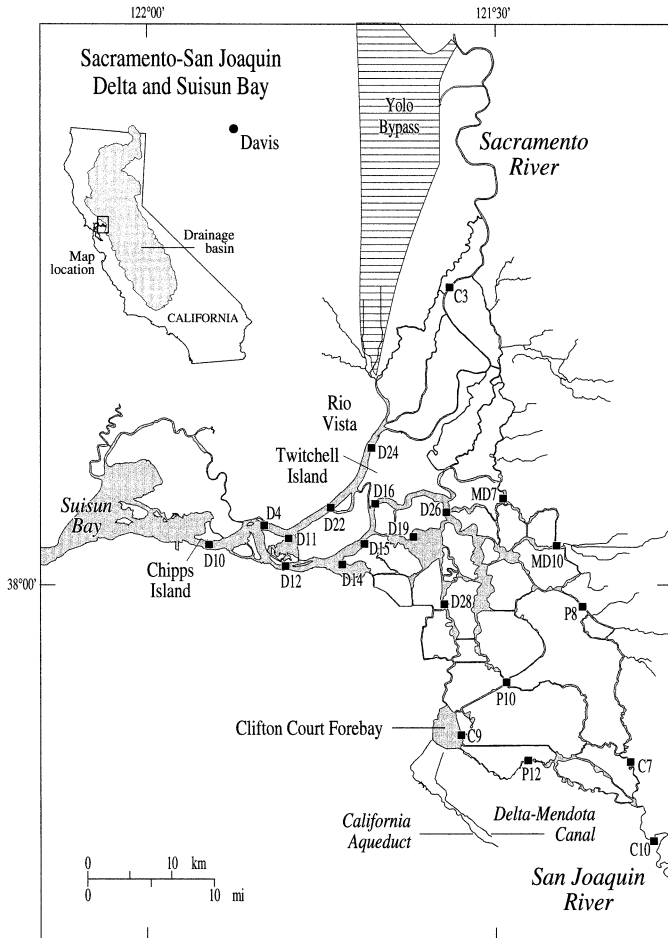


Fig. 1. The Sacramento–San Joaquin River Delta and Suisun Bay. Chipps Island marks the downstream boundary of the Delta, and Suisun Bay is the most upstream of the embayments comprising San Francisco Bay. Water quality stations are indicated by filled boxes.

ment: the presence of tides, strong horizontal transport and subsequent short residence times, a more important suspended mineral particle contribution to optical properties, and strong top-down control by benthic suspension feeders. Apart from astronomical tides, which are more or less reproducible from year to year, these attributes are therefore also candidates for driving interannual variability. The large signal from nutrient variability draws attention away from other relevant processes. Nonetheless, the total variability driven by these other processes may in fact be greater than that due to nutrients in many systems.

In this study, we combine a long-term record of water quality monitoring from a nutrient-rich tidal ecosystem, the Sacramento–San Joaquin River Delta (the Delta), with measurements of water column light utilization efficiency to reconstruct historical primary productivity and investigate its interannual variability and longer term behavior. The Delta (Fig. 1) is a mosaic of waterways linking the great rivers of northern California to the downstream embayments comprising San Francisco Bay; together, the Delta and Bay form the San Francisco Estuary. The Delta data set—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 consistency over time, and its multiplicity of measured variables. Because nutrient limitation is not operative, these series provide an unusual opportunity to search for effects of transport processes, optical properties, and grazing pressures on long-term variability of system-wide annual primary production.

For the Delta, the understanding of these mechanisms is also of great practical import. Many fish species traditionally using the Delta as a migration route, nursery, or permanent home have dramatically declined, are at risk of extinction, or have already become extinct (Bennett and Moyle 1996). The abundances of many resident zooplankton species, including rotifers, cladocerans, native copepods, and mysids, have also declined dramatically (Kimmerer and Orsi 1996; Orsi and Mecum 1996; Mecum and Orsi 2001). Because some of these organisms are primary consumers, feeding at the base of the food web, the declines have raised questions about the primary food supply (i.e., the sources of organic matter and energy that support the food web). A recent study of organic matter sources concluded that phytoplankton from both autochthonous primary productivity and river inputs is the dominant primary food resource in spring and summer, which are critical seasons for postlarval development of fish (Jassby and Cloern 2000). These results underline the significance of phytoplankton productivity to the Delta's food web and also provide motivation for the more general questions we ask here: What is the nature of variability in annual phytoplankton primary production? What are the regulatory mechanisms? How generalizable are these mechanisms to other estuarine systems?

## System description

Once a vast tule (*Scirpus* spp.) marsh fed by the Sacramento, San Joaquin, and smaller rivers and streams draining 40% of California (Atwater et al. 1979), the Delta has been transformed by levee building over the last 130 yr into a highly dissected region of channels and leveed islands used for agriculture (Fig. 1). The Delta's waterways have an area of about  $2.3 \times 10^8$  m<sup>2</sup>, with depths ranging from <1 m in the shallowest lake habitat to >15 m in the deepest channels. Water flowing out of the Delta discharges past Chipps Island into Suisun Bay, the most landward of the subembayments constituting San Francisco Bay. About 90% of the Bay's inflow first passes through the Delta. Water is also exported from the Delta for agricultural, industrial, and domestic use, primarily through large pumping facilities in the southern Delta feeding the State Water Project (California Aqueduct) and federal Central Valley Project (Delta–Mendota Canal). Water is also diverted for irrigation in the Delta by thousands of siphons; much of this water is lost to evapotranspiration, although some returns through hundreds of agricultural drainage points. The Sacramento River has flood bypasses and basins for water diverted during winter storms. The Yolo Bypass routes this water around the Sacramento metropolitan area to enter the river just upstream of Rio Vista. The

recent work by Jassby and Cloern (2000) contains further details on Delta hydrology and the ecological changes observed over the past few decades. A previous estimate has been made of mean primary productivity during 1975–1989 for the upper portion of the Delta only (Jassby and Powell 1994), but data available at the time were insufficient to analyze long-term variability. Lehman (2000) recently summarized long-term changes in phytoplankton community composition for the Delta, emphasizing the effects of climatic variability. Kratzer and Shelton (1998) describe nutrient sources and trends in San Joaquin River nutrient levels since the early 1950s. Fertilizer runoff, subsurface agricultural drainage, wastewater treatment plant discharges, and runoff from dairies have contributed to increasing concentrations over the last 50 yr.

## Materials and methods

**Water quality**—The data set used for this study consists of various water quality measurements, including chlorophyll *a* (Chl *a*) as a measure of phytoplankton biomass, for the period 1968–1998 at 21 stations distributed throughout the Delta (Fig. 1). Samples were collected and analyzed by the U.S. Bureau of Reclamation (USBR) and the California Department of Water Resources (CDWR) using standard methods (CDWR 1993). The samples were taken approximately on a monthly basis, usually from 1 m below the surface during high slack tide. We created regularly spaced time series by binning all data by month, using the median when there was more than one monthly value.

Daily flow estimates were taken from the DAYFLOW database management system (CDWR 1986), which provides estimates of inflow to the Delta, diversion within the Delta primarily for irrigation, export from the Delta to canals, outflow from the Delta downstream into the Bay, and flows past miscellaneous stations within the Delta. Jassby and Cloern (2000) tabulate these various flows in more detail.

**Morphometry**—Morphometric data were based on a 25-m grid using the CDWR bathymetry database (CDWR 1998), with the addition of data from National Oceanographic and Atmospheric Administration (NOAA) surveys in 1990–1992 (Monsen 2001). These data cover all open water habitat up to mean tidal level (MTL) but exclude tidal marsh habitat and Clifton Court Forebay, which feeds the export pumps (Fig. 1). In order to estimate mean Delta-wide productivity, biomass, and other water quality characteristics, we divided the Delta into approximately homogeneous subregions. The purpose of regionalization is to provide more accurate stratified sampling estimates of Delta-wide means. The stations within each subregion are treated as replicate samples of the subregion mean. Hypsometric data were estimated for each subregion, including area and volume at MTL. The hypsometric data and subregion means were then combined to produce subregion estimates, which were summed to produce Delta-wide estimates. We used a total of eight subregions (Jassby and Cloern 2000).

**Phytoplankton productivity**—Model: Water column primary productivity can be predicted from theoretical consid-

erations, using idealizations for the vertical distribution of photosynthetically active radiation (PAR) and phytoplankton Chl *a* (Falkowski 1981; Platt 1986). Under the assumptions that vertical attenuation of PAR does not change with depth, water column depth exceeds photic zone depth, Chl *a* is vertically homogeneous, and primary productivity is proportional to light absorbed by photosynthetic pigments, the relationship shown in Eq. 1 can be derived.

$$P_g = \psi B I_0 z_p = 4.61 \psi \frac{B I_0}{k} \quad (1)$$

$P_g$  (mg C m<sup>-2</sup> d<sup>-1</sup>) is gross primary productivity in the water column,  $\psi$  (mg C [mg Chl *a*]<sup>-1</sup> [E m<sup>-2</sup>]<sup>-1</sup>) is an efficiency factor,  $B$  (mg m<sup>-3</sup>) is Chl *a* concentration,  $I_0$  (E m<sup>-2</sup> d<sup>-1</sup>) is surface PAR,  $z_p$  (m) is photic zone depth (i.e., the depth to which 1% of surface PAR penetrates), and  $k$  (m<sup>-1</sup>) is the vertical attenuation coefficient for PAR. Equation 1 has been verified in many estuarine systems when  $\psi$  is calibrated for local conditions (Heip et al. 1995; Kromkamp et al. 1995).

**Model calibration:** We calibrated the equation with direct measurements of primary productivity using water samples collected in 1997. Samples were collected biweekly from May through November at nine sites in the north, central, and south Delta, yielding a total of 51 cases to characterize spatial and seasonal variability of phytoplankton productivity.

Irradiance was measured at 5–15 depths with a LI-COR 192S quantum sensor sensitive to PAR (400–700 nm), from which the light attenuation coefficient  $k$  was estimated. Daily surface irradiance was measured with a LI-COR 190 quantum sensor.

Bulk water samples were collected just below the water surface of the well-mixed water column for primary productivity and other water quality variables (Chl *a*, specific conductivity, temperature, total suspended solids, macronutrients, and phytoplankton community composition). Primary productivity was measured with short-term incubations of NaH<sup>14</sup>CO<sub>3</sub>-spiked water samples in a photosynthetron (Lewis and Smith 1983), a temperature-controlled incubator that provides a range of irradiance from darkness to full sunlight. A 20- $\mu$ Ci spike of NaH<sup>14</sup>CO<sub>3</sub> was added to a 50-ml water sample. Then, 2-ml aliquots of the radioactively labeled sample were dispensed into 17 liquid scintillation vials. The 2-ml aliquots were incubated for 30 min, then acidified with 0.4 ml of 0.5 N HCl and agitated in a hood for 1 h to purge the unincorporated NaH<sup>14</sup>CO<sub>3</sub> from the sample. Also, abiotic uptake of NaH<sup>14</sup>CO<sub>3</sub> was determined by acidifying triplicate NaH<sup>14</sup>CO<sub>3</sub>-spiked samples immediately after the spike was added. The measure of abiotic <sup>14</sup>C uptake was subtracted from the activity of each incubated sample. Optiphase HiSafe3 liquid scintillation cocktail was added prior to determining the radioactivity of each sample in a Pharmacia-Wallac 1209 liquid scintillation spectrometer. Total dissolved inorganic carbon (DIC) concentration in the bulk water was measured by chromatographic analysis of the CO<sub>2</sub> generated by acidification (100 ml of 6 N HCl) of a 4-ml sample in a sealed serum bottle. The concentration of CO<sub>2</sub> vapor was measured with a Perkin-Elmer Sigma 2000



gas chromatograph. Edmunds et al. (1999) describe the methods for the other water quality variables.

Photosynthetic carbon assimilation rate  $p$  (mg C [mg Chl  $a$ ]<sup>-1</sup> h<sup>-1</sup>) was calculated by normalizing the volumetric rate of carbon uptake by Chl  $a$  concentration. Results from each incubation assay were used to generate a photosynthesis–irradiance function, fitting measured carbon assimilation at 17 irradiance levels by nonlinear least squares to Eq. 2.

$$p = p_{\max}[1 - \exp(-\alpha I/p_{\max})] \quad (2)$$

$p_{\max}$  and  $\alpha$  are fitted parameters. We then used the series solution of Platt et al. (1991) to evaluate daily depth-integrated primary productivity (mg C m<sup>-2</sup> d<sup>-1</sup>) from Eq. 2, Chl  $a$ , light attenuation  $k$ , and daily surface irradiance. Finally, the full set of 51 daily depth-integrated measurements was fit to Eq. 1 by linear least squares to determine a characteristic value of photosynthetic efficiency  $\psi$  for the Sacramento–San Joaquin Delta system.

**Historical reconstruction:** We used solar radiation data collected by the California Irrigation Management Information System, obtained from the University of California State-wide Integrated Pest Management project (UCSIPM 1999). The station closest to the Delta with a daily record spanning the period of interest (1968–1995) is Davis (Fig. 1). Monthly means at stations in the Delta correspond closely to those at Davis for overlapping time periods. The CDWR water quality data set used in this study includes approximately 10,600 measurements of total suspended solids (TSS) and 4,200 photometric measurements of attenuation coefficient  $k$ . When values of  $k$  were missing, we used a station-specific linear regression of  $k$  on TSS to fill in the data set. Phytoplankton is usually only a small component of suspended particulate matter in the Delta and northern San Francisco Bay (Cloern 1987), and we found that partitioning TSS into algal and nonalgal contributions did not improve the estimation.

A monthly time series for  $P_g$  at each station was reconstructed using Eq. 1. Estimates within each subregion were averaged, weighted by the subregion area, summed, and divided by Delta area to provide a Delta-wide estimate of  $P_g$ . We also estimated a monthly time series for phytoplankton respiration at each station as the sum of a daily basal biomass-dependent rate and a photosynthesis-dependent rate.

$$R = 0.015\omega BH + 0.15P_g \quad (3)$$

$R$  is respiration rate (mg C m<sup>-2</sup> d<sup>-1</sup>),  $\omega$  is the characteristic C:Chl  $a$  ratio of 35 (Cloern et al. 1995),  $B$  is phytoplankton biomass (mg Chl  $a$  m<sup>-3</sup>), and  $H$  is water column depth (m). As in the case of  $P_g$ ,  $R$  was averaged for each of the eight subregions, weighted by subregion area, summed, and divided by Delta area to yield a Delta-wide estimate. Net phytoplankton productivity  $P_n$  (mg C m<sup>-2</sup> d<sup>-1</sup>) was then estimated by  $P_n = P_g - R$ .

**Data-analytical methods—Trend detection:** Trends were estimated with robust nonparametric methods that are efficient in the presence of nonnormal residuals and outliers (Helsel and Hirsch 1992). In particular, monotonic trends were estimated by the Theil slope, which is the median slope

of the lines joining all possible pairs of points in the series. The test of significance for a nonzero slope is the same as for Kendall's rank correlation coefficient  $\tau$ . An estimate of intercept is also available.

The Theil slope was also used to estimate monotonic trends in residuals after accounting for exogenous variables using locally weighted regression (Cleveland and Devlin 1988). A span of one and a locally linear fit were used with this technique.

Step trends were estimated by the Hodges–Lehmann estimator, which is the median of all possible pairwise differences between the earlier and later data (Helsel and Hirsch 1992). The large-sample approximation to the rank sum test was used to test significance of the estimate.

**Principal component analysis decomposition of time series:** The use of principal component analysis (PCA) for analyzing interannual variability in time series is described in detail by Jassby (1999). This unique application of PCA reveals the number of independent underlying modes of variability, the time of year in which they are most important (represented by the component coefficients), and their relative strength from one year to the next (represented by the amplitude time series). These features often provide strong constraints on and clues for the identity of the underlying mechanisms. When analyzing a monthly time series, such as the  $P_g$  series, an  $n$  by  $p$  data matrix is first formed, in which each of the  $p$  (=12) columns represents a specific month for the  $n$  years of record. Each row should break at a month of the year where component coefficients are low for all modes; a given row of 12 months therefore does not necessarily represent a calendar year. Principal components (PCs) were estimated by singular value decomposition of the correlation matrix of the data matrix. The number of significant principal components must be chosen because, if at least two significant PCs are found, the subset of significant PCs should be rotated (Richman 1986). We used a Monte Carlo technique known as *Rule N* (Overland and Preisendorfer 1982). We rotated significant PCs using the varimax algorithm (Richman 1986), calculating the new component coefficients and amplitude time series.

**Phytoplankton mass balance:** We calculated an annual mass balance for phytoplankton C in the Delta to assess relative sizes of different inputs and outputs. In addition to  $P_n$ , we estimated transport into the Delta from river loading of Chl  $a$  and transport of Chl  $a$  out of the Delta either downstream into Suisun Bay (outflow), into the export canals (export), or into within-Delta diversions (diversion). Monthly transport rates were determined from the product of median Chl  $a$  measurements and monthly DAYFLOW flow estimates at key locations; the detailed calculations are described by Jassby and Cloern (2000). Chl  $a$  transport was converted to phytoplankton C transport using a C:Chl  $a$  ratio of 35. We considered only the upstream Delta (i.e., the Delta upstream of Rio Vista and the Twitchell Island stations, D24 and D16). Similar calculations cannot be performed for the entire Delta because tidal dispersion is important at the downstream boundary and a hydrodynamic model is required for accurate transport estimates. We also

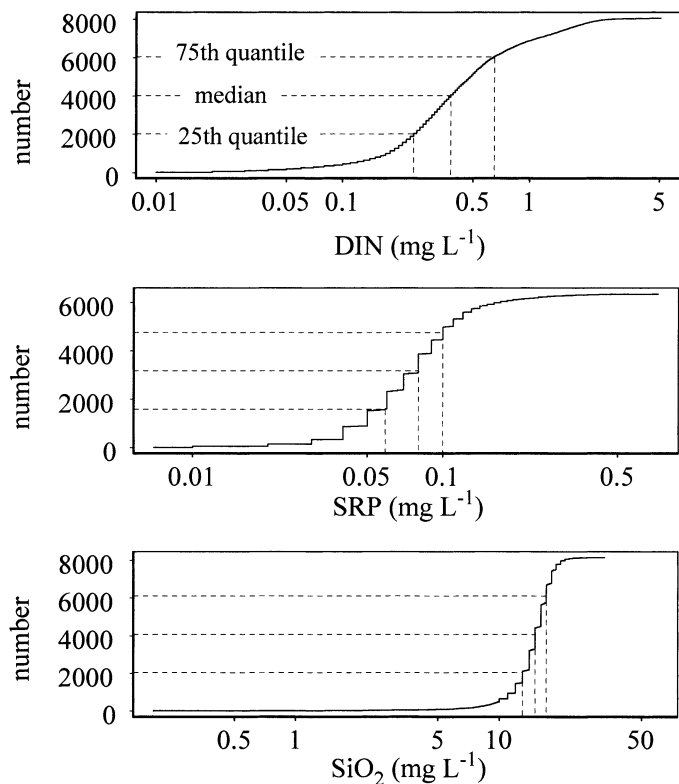


Fig. 2. Empirical cumulative distribution functions for dissolved inorganic N (DIN), soluble reactive P (SRP), and silica ( $\text{SiO}_2$ ) based on measurements in the Delta during 1968–1998.

considered only the months March–October and years 1975–1993 to minimize the need for interpolating missing data. To obtain a complete balance for these months and years, interpolations were necessary for only 3 months.

## Results

**Nutrients**—Over 8,000 measurements each of dissolved inorganic N ( $\text{DIN} = \text{NH}_4 + \text{NO}_2 + \text{NO}_3$ ) and  $\text{SiO}_2$  and over

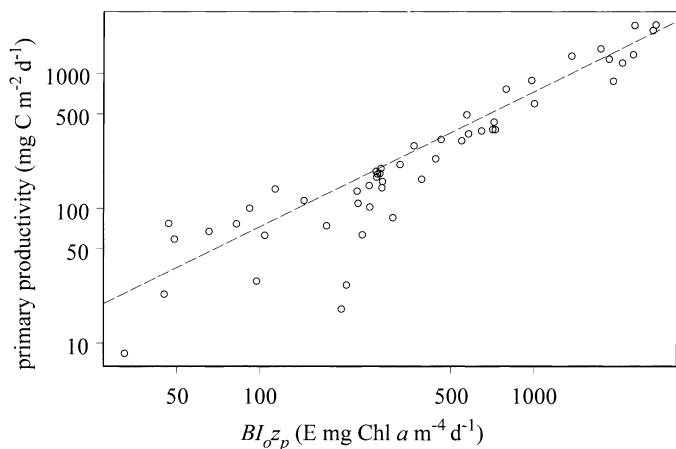


Fig. 3. Measured primary productivity versus measured predictor variables as specified by Eq. 1. The dashed line represents the values predicted by Eq. 1 with  $\psi = 0.728$ .

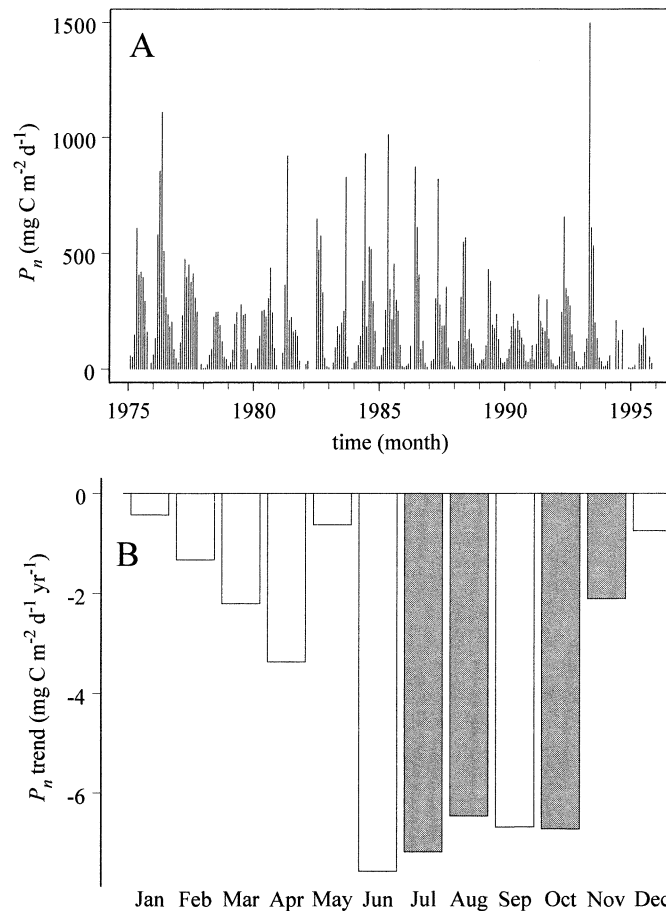


Fig. 4. Net primary productivity in the Delta. (A) Time series of monthly medians; (B) annual trend for each month based on the Theil slope. Shaded bars are significantly greater than zero ( $p < 0.05$ ) according to Kendall's tau test.

6,000 measurements of soluble reactive P (SRP) have been made since 1968 in the Delta. Their empirical cumulative distribution functions are illustrated in Fig. 2. In comparison, typical half-saturation constants for nutrient-limited phytoplankton growth are  $0.01 \text{ mg L}^{-1}$  DIN,  $0.003 \text{ mg L}^{-1}$  SRP, and  $0.05 \text{ mg L}^{-1}$   $\text{SiO}_2$  (Chapra 1997). The numbers of measurements in the Delta less than these values are only nine for DIN, nine for SRP, and none for  $\text{SiO}_2$ . Nutrient limitation is therefore extremely rare in the Delta.

**Delta phytoplankton productivity**—The correspondence between water column primary productivity and the predictor variables as specified by Eq. 1 is shown in Fig. 3. The estimated value of  $\psi$  was  $0.728 \pm 0.023 \text{ mg C (mg Chl } a)^{-1} (\text{E m}^{-2})^{-1}$  ( $R^2 = 0.952$ ,  $P < 0.001$ ,  $n = 51$ ). Overall, the model predicts productivity well, especially at the higher values that contribute most to annual production. We also examined a linear model that included an intercept, but the intercept was insignificant ( $-40 \pm 30 \text{ SE}$ ).

Delta-wide  $P_n$  could be estimated for most months between 1975 and 1995 (Fig. 4A). If data were missing for any station for any month, then a Delta-wide estimate was not made for that month. Before and after this period, many

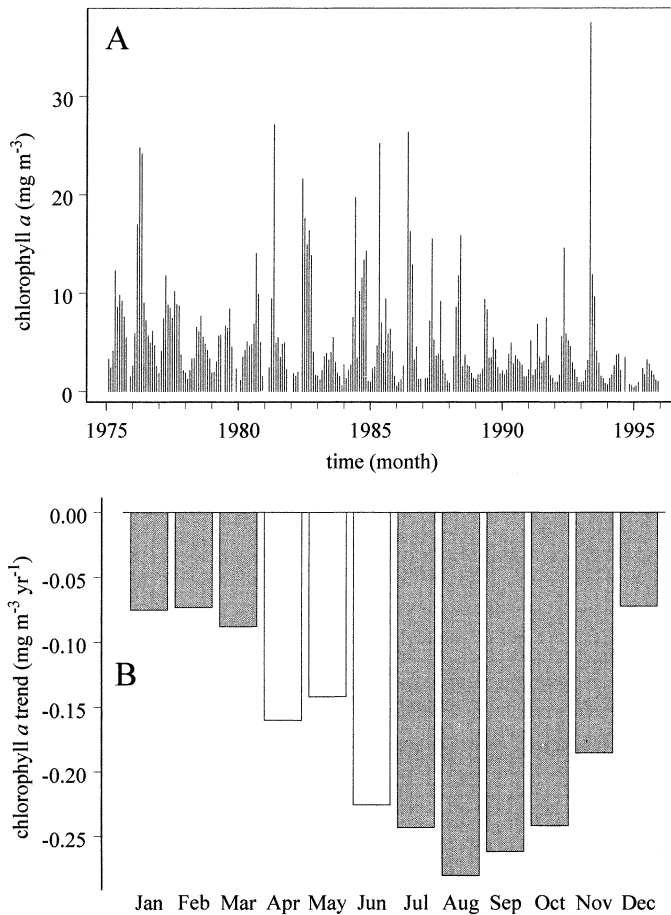


Fig. 5. Chl *a* in the Delta. (A) Time series of monthly medians; (B) annual trend for each month based on the Theil slope. Shaded bars are significantly greater than zero ( $\rho < 0.05$ ) according to Kendall's tau test.

key stations necessary for a Delta-wide estimate were not sampled. Overall, the median monthly and mean  $P_n$  was 132 and 201 mg C m<sup>-2</sup> d<sup>-1</sup>, respectively. For the 9 yr in which no monthly data were missing, seasonal productivity was highest in spring, substantially lower in summer, and lowest in winter and autumn.

The long-term trend (1975–1995) in  $P_n$  is negative for all months (Fig. 4B). The downward trends are most pronounced during summer and autumn, and all statistically significant trends are found during these two seasons. The long-term linear trend in annual primary production amounts to a yearly loss of  $1.9 \pm 0.9$  g C m<sup>-2</sup> yr<sup>-1</sup>, or 43% over the period of record.

**Chlorophyll *a***—Equation 1 implies that long-term variability in the  $P_n$  series is driven by the dynamics of Chl *a* and suspended mineral particles, the latter through its effect on light attenuation. To understand  $P_n$  variability, then, we must understand these two variables. Delta Chl *a* resembles  $P_n$  (Fig. 5A), although there are sometimes major differences, as in 1983. The long-term trend for Chl *a* is even more pronounced than for productivity (Fig. 5B). All except spring months show a statistically significant downward

movement. The long-term linear trend in annual mean Chl *a* amounts to an annual loss of  $0.20 \pm 0.07$  mg m<sup>-3</sup> yr<sup>-1</sup> ( $R^2 = 0.328$ ,  $P = 0.007$ ,  $n = 21$ ).

To further understand interannual and decadal variability in the Chl *a* time series, we applied the PCA decomposition technique. Preliminary analysis showed the May component coefficient to be low for all modes; each row of the PCA data matrix therefore extends from June through May of the following year. According to Rule N, only the first two eigenvalues for  $P_n$  are significantly higher than expected.

The first rotated principal component (Mode 1) accounts for 30.4% of the variance (Fig. 6). It is characterized by high component coefficients during summer and autumn (June–November). A long-term pattern is present in that the amplitude time series is consistently lower after 1986. We tested for a step change in the amplitude time series beginning in 1987 because the Asian corbulid clam *Potamocorbula amurensis*, a primary consumer of phytoplankton, invaded the estuary in 1986. The Hodges–Lehmann estimator of the difference, 2.05, was significant (95% confidence interval of 1.16 and 4.91). Having identified a potential mechanism through the PCA decomposition, we can ask whether its signal is also observable in the original Delta Chl *a* data. Indeed, mean June–November Chl *a* exhibits the same step trend downward beginning in 1987 (the Hodges–Lehmann estimate of the step decrease is 3.20 mg m<sup>-3</sup>, with 95% confidence limits of 1.48 and 6.18). We also examined residual values after removing the step trend from the June–November Chl *a* data but could find no other long-term trends and no relationship with any hydrological parameters.

The second rotated component (Mode 2) accounts for a smaller but comparable variance of 25.2%. It is characterized by high component coefficients during winter and early spring (January–April). The corresponding amplitude time series for Mode 2 shows the occasional large absolute value, such as during 1976–1977 and 1986. Because these large values often occurred during unusually dry (1976–1977) or wet (1986) winters (Fig. 7), we tested for the (Spearman rank) correlation between mean January–April river flow into the Delta and the amplitude time series for Mode 2. The correlation of  $-0.507$  is significant ( $P = 0.027$ ,  $n = 20$ ). As before, we can ask whether the signal of this potential mechanism is observable in the original time series. Mean January–April Chl *a* is in fact negatively correlated with mean January–April river flow into the Delta (the Spearman rank correlation is  $-0.570$ ,  $P = 0.011$ ,  $n = 21$ ).

The amplitude time series for Mode 2 shows an additional feature, namely, a long-term decreasing trend. The trend is not due to a trend in river inflow and, in fact, becomes stronger when we remove the effects of inflow. It is also observable in the original time series: when we remove the effects of January–April river inflow on mean Chl *a* during the same period using locally weighted regression, the Theil slope of the resulting residuals is negative according to the Kendall tau test ( $\tau = -0.600$ ,  $P < 0.001$ ,  $n = 21$ ; Fig. 8).

We repeated all analyses on the  $P_n$  series. The PCA decomposition of net primary productivity (not shown) is very similar to that of Chl *a*. Most important, it displays the two modes, one operating in June–November and the other in January–April. Mean June–November  $P_n$  exhibits a step

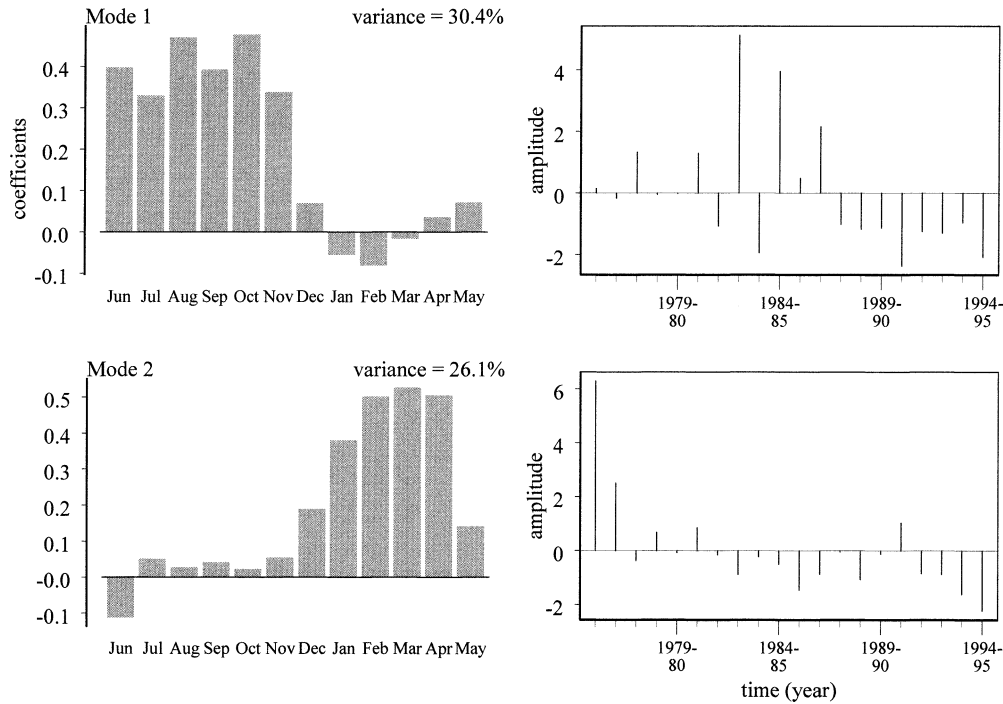


Fig. 6. Component coefficients and amplitudes for the first two principal components of Chl *a*.

trend downward after 1986 (the Hodges–Lehmann estimate of the step decrease is  $99.1 \text{ mg C m}^{-2} \text{ d}^{-1}$ , with 95% confidence limits of 43.0–178). This step in  $P_n$  represents a 36% decrease compared to the 1975–1986 median, whereas that in Chl *a* represents a larger 47% decrease. We also examined residual values after removing the step trend but could find no other long-term trends and no relationship with any hydrological parameters. Mean January–April  $P_n$  is negatively correlated with mean January–April river flow into the Delta (the Spearman rank correlation is  $-0.700$ ,  $P = 0.002$ ,  $n = 21$ ), a stronger relationship than that shown by Chl *a*. When we remove the effects of January–April river inflow on mean  $P_n$  during the same period using locally weighted regression, the Theil slope of the resulting residuals is negative accord-

ing to the Kendall tau test ( $\tau = -0.429$ ,  $P = 0.007$ ,  $n = 21$ ).

**Phytoplankton mass balance**—The phytoplankton C mass balance, based on  $P_n$  and Chl *a* transport, provides information on the magnitudes of inputs and outputs independent of the statistical analyses. The average mass balance for the upstream Delta is summarized in Fig. 9. The retained portion consists of incorporation into the food web plus burial (changes in phytoplankton C of the upstream Delta are insignificant compared to inputs and outputs). On average, 68% of the phytoplankton supply ( $P_n$  plus river inputs) is retained within and 32% is flushed from the upper Delta.

**Total suspended solids**—A long-term downward trend in TSS is obvious from the monthly time series (Fig. 10A). Individual months exhibit a downward trend over the years, and eight of these trends are statistically significant (Fig. 10B).

The PCA decomposition of the TSS series resulted in only one significant mode that has similar component coefficients for almost all months. It is therefore analytically equivalent and more intuitive to examine the annual mean rather than this mode. In order to reveal possible hydrological effects on annual mean TSS, we used the water year (October–September) mean rather than calendar year mean. The long-term linear trend amounts to an annual loss of  $0.717 \text{ mg L}^{-1}$ , or 50% over the period of record.

We noted that deviations from the long-term trend tended to be low during certain extreme dry years (1976–1977) and high during certain extreme wet years (1983). The effect of the long-term trend in water year mean TSS was removed

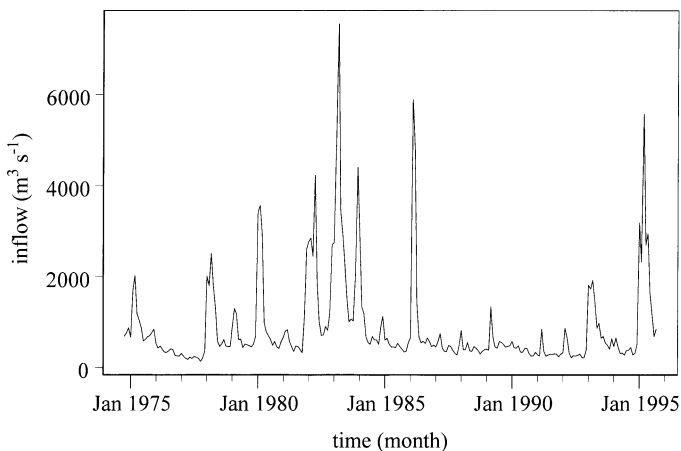


Fig. 7. Monthly mean river flow into the Delta.



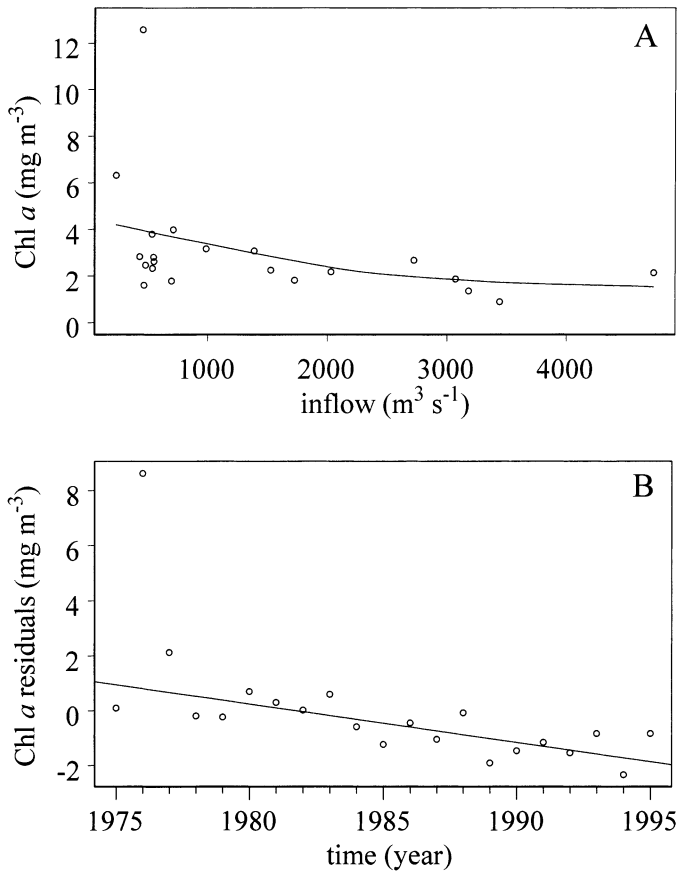


Fig. 8. Chl *a* trend during winter and early spring. (A) Scatter plot of January–April Chl *a* vs. river flow into the Delta during the same period, including the locally weighted regression line; (B) time series of residuals from locally weighted regression, including the Theil slope estimate of the trend.

using locally weighted regression, enabling us to examine the correlation between trend residuals and water year mean flows into the Delta (Fig. 11). The overall Spearman rank correlation of 0.606 was indeed statistically significant ( $P = 0.008$ ,  $n = 20$ ), although the relationship is weak at times.

## Discussion

**Water column light utilization efficiency**—The model specified by Eq. 1 assumes implicitly that the depth-integrated photosynthesis light curve is linear. Platt et al. (1988) have shown that the error accompanying this assumption depends on  $P_m/k$ , where  $P_m$  is the maximum photosynthesis attainable (not normalized to biomass). In systems where light attenuation is due mostly to nonalgal material,  $P_m$  and  $k$  are uncoupled and the ratio is low. The model should therefore be especially appropriate for relatively turbid waters like the Delta. If the error were important, a linear regression of primary productivity on  $BI_{0,z_p}$  would have a positive intercept on the ordinate (Platt et al. 1988); in contrast, the intercept for the Delta is insignificant.

The value of  $\psi$  ( $0.73 \pm 0.02$ ) is relatively high but not unexpected for nutrient-rich systems (Falkowski and Raven

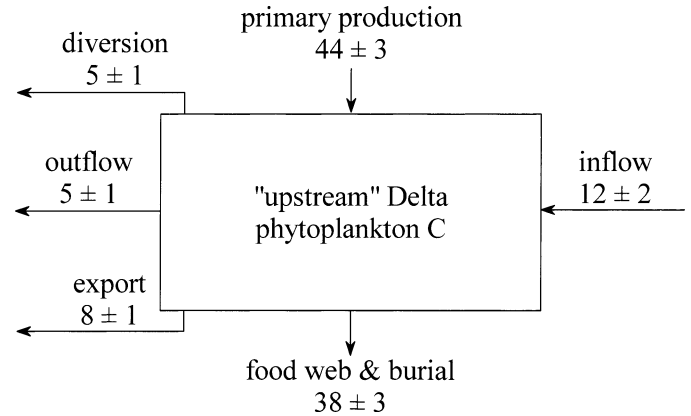


Fig. 9. Phytoplankton C budget ( $\text{tons d}^{-1} \pm \text{SE}$  among years) for the upstream Delta, averaged for March–October during 1975–1993. Primary (net) production is estimated as described in this publication. Inflow, outflow, diversion, and export are estimated as described by Jassby and Cloern (2000). Food web and burial is the residual amount required to balance the other flows.

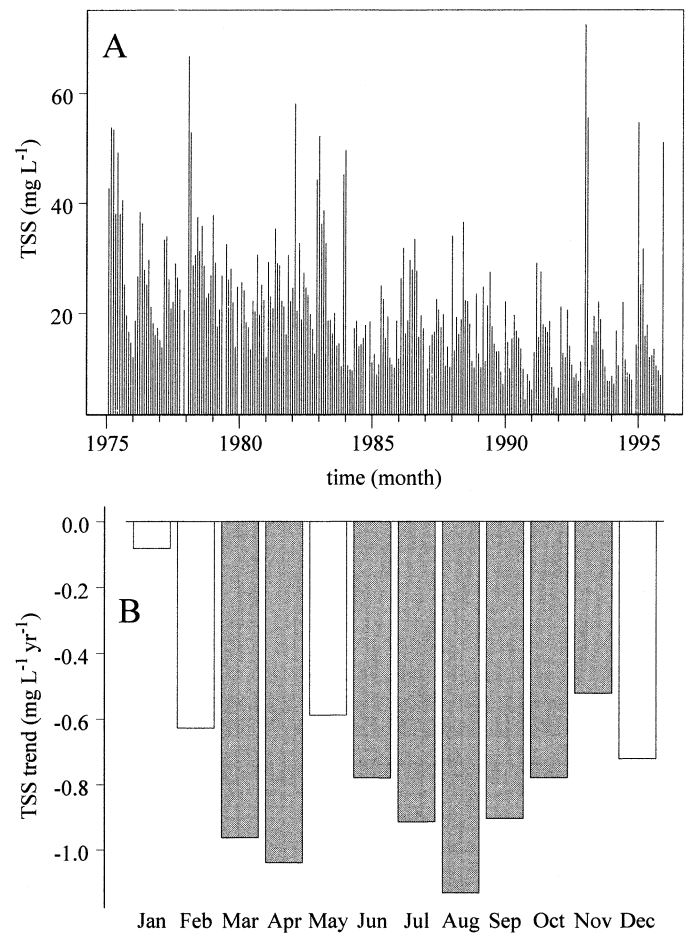


Fig. 10. TSS in the Delta. (A) Time series of monthly medians; (B) annual trend for each month based on the Theil slope. Shaded bars are significantly greater than zero ( $p < 0.05$ ) according to Kendall's tau test.



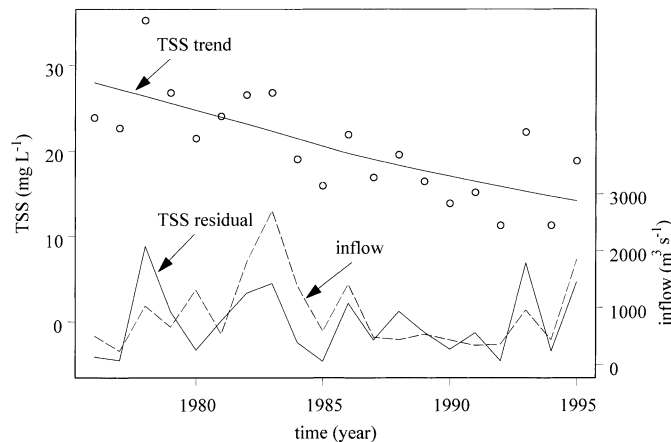


Fig. 11. Mean TSS for the water year with the locally weighted regression trend line and the time series of TSS residuals from trend line. Mean inflow for the water year is also plotted for comparison with the TSS residuals.

1997). Heip et al. (1995) listed 24 estuarine estimates of  $\psi$ . Comparison among these values and with the Delta is tenuous because of different methods and possible model misspecifications (in particular, nonzero intercepts in plots of primary productivity vs.  $BI_{0z_p}$ ). Nonetheless, it is worthwhile to note that all but three estimates are 0.72 or less, offering further evidence that the efficiency measured here is at the high end but within the range of values observed elsewhere.

Although Eq. 1 appears to be an appropriate model for the Delta, the historical reconstruction also rests on the assumption that  $\psi$  is approximately constant. The low uncertainty in the estimate of  $\psi$  based on 1997 data, despite the wide range of habitats and seasons, supports the use of a single Delta-wide value. But how appropriate is the assumption of constancy in a Delta-wide  $\psi$  over the decadal time scale considered here?  $\psi$  is directly proportional to the initial slope of the biomass-normalized photosynthesis light curve for phytoplankton (Platt 1986). We know that this initial slope—and therefore  $\psi$ —is not constant globally and can sometimes vary with nutrient concentrations, irradiance and other factors (Cullen 1990). In principle then,  $\psi$  is an additional source of long-term variability in  $P_n$  that we cannot estimate quantitatively. This variability may be small, however: the only comparable estimate of  $\psi$  in this system was made in 1980 for northern San Francisco Bay, which receives water directly from the Delta and resembles it in terms of high turbidity and nutrient concentrations (Cole and Cloern 1987). The mean value of  $0.67 \pm 0.12$  mg C (mg Chl  $a$ )<sup>-1</sup> (E m<sup>-2</sup>)<sup>-1</sup> obtained for four sites during 1980 is essentially equivalent to the value of  $0.73 \pm 0.02$  obtained for the Delta during 1997.

Further considerations suggest that variability in  $\psi$  could not negate the long-term trends implied by the biomass and turbidity data. First, we found no relationship in our 1997 data set between  $\psi$  and any water quality variable (temperature, mean water column irradiance, macronutrients), except for conductivity and less so for its correlates (alkalinity, DIC, pH). Although incorporation of conductivity as an additional variable into the model can improve the fit, it has

little effect on long-term trends in estimated productivity (Jassby and Cloern 2000). Second, although nutrient concentrations have increased over the past decades, they were already far above levels saturating phytoplankton growth in 1975. Third, the turbidity decrease and accompanying increase in mean water column irradiance conceivably could have been accompanied by an efficiency decrease (i.e., implying a higher value of  $\psi$  in the past). But a much higher value is unlikely because current levels are in the upper range for estuaries. Furthermore, a higher value in the past would imply an even greater trend of declining primary productivity than estimated here. Fourth, although year-to-year variability in phytoplankton community composition has been high (Lehman 2000), we found no effect of community composition on  $\psi$  in the 1997 data set. Moreover, Cole et al. (1986) detected no differences in  $\psi$  among different phytoplankton size fractions (and presumably different groups of species) in the 1980 study.

Finally, regardless of the size and nature of  $\psi$  variability, the analysis of mechanisms underlying biomass and turbidity change—and, through them, at least some of the primary productivity change—is independent and stands on its own.

*Magnitude of annual primary production*—Net annual phytoplankton production can be estimated in several ways from the monthly time series. The most reliable way, but confined to the fewest years, is simply to use the 9 yr in which no monthly estimates are missing. The value is  $75 \pm 11$  g C m<sup>-2</sup>. A second way is to interpolate missing months for the period 1975–1995, which yields  $70 \pm 6$  g C m<sup>-2</sup>. Clearly, the exact method is unimportant. Heip et al. (1995) have illustrated how net productivity calculations sometimes depend strongly on assumptions about respiratory losses. The above estimates assume that our short-term incubations measured gross primary productivity. If they in fact measured photic zone net primary productivity, as suggested by Williams and Lefèvre (1996), the respiration correction should be smaller. We re-estimated net annual production after modifying Eq. 3 to include only the basal respiration rate, yielding  $90 \pm 13$  g C m<sup>-2</sup>. Most of the analyses undertaken here depend on relative rather than absolute values, in which case the uncertainty due to respiration estimates is less important than implied by this potential systematic error.

Single or even a few estimates of annual primary production from estuaries may not be very characteristic of the long-term average. One should therefore question attempts to draw generalizations from multiple estuarine data sets when many of the examples represent single annual estimates, perhaps not even based on comprehensive spatial and seasonal coverage. That said, it is useful to inquire where the Delta falls on the spectrum of estuarine primary production, insofar as existing data can reveal. A recent compilation lists annual primary production, either single estimates or a range, from 31 subregions of 14 estuaries (Underwood and Kromkamp 1999). In order to compare with the Delta-wide estimate, we summarized each subregion range by its median and each system by the median of its subregions. Note that not all subregions were measured for all systems. Values for the 15 systems, including the Delta, ranged from 11 to 560, with an overall median of 200 g C m<sup>-2</sup>. The Delta ranks

fourth from the bottom, between the Bristol Channel (49 g C m<sup>-2</sup>, Joint and Pomroy 1981) and the Ems-Dollard (90 g C m<sup>-2</sup>, Colijn 1983). It is therefore quite low in primary production. Note that San Francisco Bay ranks sixth lowest (120 g C m<sup>-2</sup>, Cole and Cloern 1984, 1987; Cloern 1996), just above the Ems-Dollard. In a similar compilation of annual primary production for 25 river-dominated estuaries (Boynton et al. 1982), all but two values are higher than that for the Delta.

Why is Delta annual production low compared with other systems, given that nutrients are plentiful and the water column light utilization efficiency is high? We summarized the mean Chl *a* values for these systems (Underwood and Kromkamp 1999) in the same manner as annual production, obtaining results for 12 systems, including the Delta. The range was 2.6 to 20 mg m<sup>-3</sup>. The Delta again ranked fourth from the bottom (5.2 ± 0.7 mg Chl *a* m<sup>-3</sup>), approximately tied with the Oosterschelde (Wetsteyn and Kromkamp 1994). Low biomass therefore probably plays a role in low production. Reasons for low biomass are considered below.

Relatively high TSS is an additional reason underlying relatively low annual production. High TSS results in high light attenuation: the median of all Delta photic zone depth estimates is only 1.31 m. The attenuation is due overwhelmingly to nonphytoplankton matter (Cloern 1987). Heip et al. (1995) postulate that systems with annual production <160 g C m<sup>-2</sup> are light-limited, and the Delta is certainly consistent with this hypothesis. Cloern (1987) showed that primary productivity in the downstream estuary, San Francisco Bay, is also limited by light availability.

*Variability in Delta primary production*—Our annual primary production estimates are unusual in that they account for much spatial and seasonal variability and do so over many years, leading to one of the more reliable records of year-to-year change. This variability is large (Fig. 4). For the 9 yr of complete data, annual primary production ranges from 39 to 131 g C m<sup>-2</sup>, and for the 1975–1995 period, the range is 24–131 g C m<sup>-2</sup>, a factor of more than five. Even from one year to the next (e.g., 1993–1994), primary production can change by a factor of almost three. Nutrients in the Delta are usually far in excess of needs and unlikely to be a driving force. What, then, are the processes underlying such high interannual variability? As pointed out above, this is equivalent to asking what drives variability in Chl *a* and suspended mineral colloids.

*Chlorophyll a*: The PCA decomposition of the Delta-wide Chl *a* time series is highly revealing. The main mode of variability operates primarily during June–November, and the most striking feature of its amplitude time series is the consistent suppression after 1986 (Fig. 6). In 1987, an exotic clam *Potamocorbula amurensis* spread throughout Suisun Bay, probably after being discharged with ship ballast water into the Bay (Nichols et al. 1990). Filter feeding by clams in Suisun Bay increased phytoplankton losses to primary consumption, suppressed phytoplankton concentrations, and diverted a higher proportion of primary productivity away from the pelagic to the benthic food web (Alpine and Cloern 1992). Growth rates of clams, and probably ingestion rates,

are highest in the summer months (Thompson and Nichols 1996) when the coefficients for this mode are also highest (Fig. 6). Kimmerer and Orsi (1996) hypothesized that tidal mixing between Suisun Bay—where *P. amurensis* has persisted and continues to suppress phytoplankton—and the western Delta results in increased dispersive transport of phytoplankton out of the Delta, lowering Chl *a* concentrations. The western Delta stations do, in fact, exhibit a larger suppression after 1986 than the upstream stations (not shown). The first mode therefore likely represents the grazing effect of *P. amurensis*.

The second and smaller variability mode, operating primarily during January–April, also reveals its underlying mechanism through the corresponding amplitude time series (Fig. 6), which is negatively associated with mean winter river inflow to the Delta. This negative relationship most likely represents a residence time effect: the higher the flow, the shorter the time available for phytoplankton populations to build up in the Delta under winter conditions of lower surface irradiance. Net transport effects should be relatively easier to detect in winter than in summer because colder water temperatures (median 11°C) suppress both zooplankton and macrobenthic grazing. Moreover, river inflow has the highest interannual variance in winter, with hydraulic residence times ranging from 2.8 (1983) to 56 d (1977). The opportunity therefore exists for large differences in the proliferation of phytoplankton biomass. For example, if the growth rate were 0.1 d<sup>-1</sup> and 50% were removed by within-Delta consumption, a patch of phytoplankton could increase in concentration by only 15% in 2.8 d but by over 1,600% in 56 d.

The genesis of the long-term decline during winter is unknown at this time. Nonetheless, we can eliminate many possibilities. First, the large nutrient pool (Fig. 2), the increase in water transparency due to decreasing TSS (Fig. 10), and the lack of evidence for Delta-wide pesticide inhibition (Edmunds et al. 1999) all suggest that growth rate has, if anything, increased and cannot account for the trend. Second, although distributions of submerged and floating aquatic vegetation, especially Brazilian waterweed (*Egeria densa*) and water hyacinth (*Eichhornia crassipes*), increased in the Delta during 1975–1995, the plants die back in winter, and in any case, the maximum coverage for both species is probably less than 10% of the Delta's area (Jassby and Cloern 2000). Third, although river inflow is an important factor in year-to-year variability of winter Chl *a*, neither inflow nor other hydrological variables show a long-term trend during 1975–1995. In fact, inflow obfuscates the trend, which becomes more obvious when the effects of inflow are removed (Fig. 8).

By elimination, then, primary consumers are implicated. Among the mesozooplankton, however, rotifers and cladocerans declined during the 1975–1995 period (Mecum and Orsi 2001). Native copepods have also declined but have been replaced by exotic copepods, with no clear trend in total copepod biomass. Careful inspection of Figs. 5 and 8 also reveals that the winter decline predates the appearance of *P. amurensis*. Possibly some other macrobenthic filter feeders are behind this variability. *Corbicula fluminea*, a freshwater clam that invaded the Delta in the 1930s, is prob-

ably the dominant filter feeder, based on its abundance at the two Delta stations (D19, D28) that have been monitored regularly for the benthos. *C. fluminea*, however, is a classic invasive species that can rapidly reestablish populations after disturbance, leading to extreme density fluctuations (McMahon 2000); these two stations alone are therefore insufficient to describe interannual variability in the Delta. We believe that the answer must await an analysis in progress of phytoplankton variability at individual stations where the record can be extended from the mid-1960s to recent years. We do know, however, that phytoplankton consumption by *C. fluminea* can exceed the rate of primary productivity in shallow Delta habitats (Lucas et al. in press).

**Mass balance implications:** The time series analysis suggests primary consumers play a major role in the interannual variability of phytoplankton biomass. How consistent is this conclusion with results of the mass balance? Although the mass balance is an average for all seasons and years—the uncertainty in the residuals would be too large for an informative comparison of mass balances based on subsets of seasons or years—it reveals the overall magnitudes of the contributing processes. It therefore indicates whether these processes are large enough to play, at least in principle, a pivotal role in interannual variability (Fig. 9). The residual term in the mass balance consists of phytoplankton biomass that is consumed in the Delta, which occurs either through incorporation into the food web or through permanent burial. Although burial has been estimated in south San Francisco Bay (Hammond et al. 1985), it has never been measured in the Delta. Nixon (1981) showed that, in shallow systems such as the Delta, an average of 24% of the organic matter supply ended up being metabolized in the sediments. Heip et al. (1995) summarized data from 16 stations in 10 estuaries, which showed that burial averaged 90% of benthic organic matter metabolism. Together, these two generalizations suggest that, on average, about 20% of the organic matter supply becomes buried. Although the exact value for the Delta is unknown, the implication is that most of the mass balance residual is consumption within the microbial and metazoan food web, not burial of recalcitrant material.

The upstream Delta is quite efficient at utilizing its organic matter inputs. Approximately 68% of the phytoplankton supply—whether from river inflow or photosynthesis—is consumed within the upstream Delta. Primary consumption is therefore playing a major role in setting the balance point between phytoplankton inputs and outputs. The net transport loss (outflow + export + diversion – inflow) is 6 tons C d<sup>-1</sup>, compared to within-Delta consumption of 38 tons C d<sup>-1</sup>. Net flushing of phytoplankton from the Delta therefore has a smaller but still notable effect on the mass balance. These magnitudes alone do not necessarily imply that either loss process underlies variability in phytoplankton biomass; either process could, in principle, be fairly constant from year to year. The fact that they are both large terms, however, demonstrates their possible role in generating variability.

Note that our qualitative conclusions regarding the mass balance are robust to assumptions regarding the interpretation of <sup>14</sup>C uptake and C:Chl *a* ratios. If we alternately in-

terpreted our uptake measurements as net rather than gross productivity (*see Magnitude of annual primary production*), then net primary productivity in the upstream Delta would amount to 53 tons d<sup>-1</sup> and the food web plus burial estimate would rise to 47 tons d<sup>-1</sup>, with net transport loss unchanged at 6 tons d<sup>-1</sup>. Similarly, if we used a C:Chl *a* ratio of 50 instead of 35, the food web plus burial estimate would decrease to 36 tons d<sup>-1</sup> and net transport loss would rise to 8 tons d<sup>-1</sup>.

**Total suspended solids:** Two processes of interannual variability were identified for the Delta-wide TSS series: one involving a long-term decreasing trend and the other year-to-year fluctuations about the trend. Possible reasons for the long-term trend have been discussed by Ball (1987). A major cause appears to be upstream sediment trapping by dams constructed in the watershed over the past few decades, with gradually decreasing amounts of sediment available downstream for resuspension and transport. Reduction of suspended sediment loading from agriculture may also play a role. The change in transparency accompanying this TSS decrease is large. For example, the trend line decreases from 28 mg L<sup>-1</sup> TSS in water year 1976 to 14 mg L<sup>-1</sup> in 1975 (Fig. 11). Using the conversion between attenuation coefficient *k* and TSS based on all Delta data, this drop in TSS is equivalent to a 25% increase in photic zone depth and, therefore, phytoplankton growth rate ( $P_n/B$ ; Eq. 1). Without this substantial growth rate increase, the decline in productivity observed over the last few decades would have been even more severe.

The second process—year-to-year fluctuations—appears to be controlled by river inflow: the higher the inflow, the more positive the fluctuation from the long-term trend. Arthur et al. (1996) attributed this phenomenon to increased scouring of upstream areas during high flows. In any case, suspended sediment concentration typically increases with discharge because of sheet erosion and bed remobilization. These deviations from the long-term behavior can be significant, sometimes reaching almost 9 mg L<sup>-1</sup> (1978).

**Primary production:** These mechanisms underlying variability in annual primary production of the Delta can be summarized in a cause–effect diagram (Fig. 12). Note that many factors influence the magnitude of annual production, but this diagram focuses just on those driving interannual variability that have been recognized for the Delta. Three sets of “ultimate” causes are identified on this diagram: invasion of macrobenthic suspension feeders; climate, in the form of precipitation on the watershed; and dam construction or other activities affecting TSS trends, such as decreased agricultural loading and increased export into water projects. Many different anthropogenic influences are behind or modify these three ultimate causes, including discharge of ballast water, production of greenhouse gases, hydrograph management, reservoir construction, and agricultural practices.

It is interesting to note that the analysis has uncovered a role for each attribute of estuarine systems, aside from tides, that distinguishes them from most lakes and modulates their response to nutrient enrichment (*see the introduction and Cloern 2001*): low residence times, high inorganic turbidity,



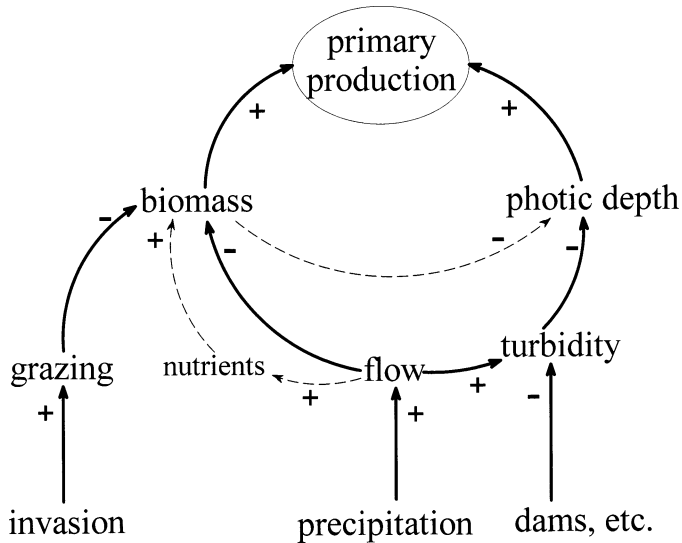


Fig. 12. Cause-effect diagram summarizing main variability mechanisms identified for Delta-wide annual primary production. Dashed lines indicate pathways missing in the Delta but present in less turbid, nutrient-limited ecosystems.

and high biomass of benthic suspension feeders (Fig. 12). In some cases, these attributes combine with each other (low residence time and high inorganic turbidity due to high river inflow in winter) and in some cases they offset each other (long-term increase in benthic suspension feeders and decrease in inorganic turbidity in summer and autumn). Furthermore, the long-term variations can take the form of a step (suspension feeding) as well as a monotonic change (turbidity). The dynamics are therefore neither additive nor linear and must be dissected carefully.

**Ecosystem implications of declining primary production**—The overall decline in primary productivity and the strong interannual variability are likely affecting organisms at the primary consumer level. A recent organic carbon budget demonstrated that phytoplankton productivity in the Delta is an important source of organic matter for consumers in all seasons except winter of above-normal rainfall years and a dominant source in spring and summer of below-normal rainfall years (Jassby and Cloern 2000). Bioassay experiments further demonstrate that cladoceran growth in Delta water is closely related to Chl *a* concentrations up to  $\sim 10 \text{ mg m}^{-3}$ , much more closely than to the general pool of particulate organic carbon (Müller-Solger et al. in press). Because of superior phytoplankton food quality, primary productivity is therefore even more important to the food web than suggested by its role in the organic carbon budget alone. Moreover, Chl *a* concentrations in the Delta were mostly below  $10 \text{ mg m}^{-3}$  in each year during 1975–1995 (55–93% of measurements, depending on the year), suggesting food limitation may have been chronic in the Delta and exacerbated by the long-term January–April and June–November phytoplankton declines.

These results are consistent with observations made on primary consumers in the Delta. Food limitation probably has contributed to declining abundance of rotifers and cla-

docerans (Kimmerer and Orsi 1996). Estuarine copepods (*Eurytemora affinis* and *Pseudodiaptomus forbesi*) also exhibit evidence of food limitation (Kimmerer and Peñalva 2000). Moreover, Orsi and Mecum (1996) concluded that food limitation is the primary mechanism of decline in the native mysid *Neomysis mercedis*. Laboratory and field experiments of Foe and Knight (1985) showed that growth of the clam *Corbicula fluminea* is also limited in some regions of the Delta because of suboptimal phytoplankton biomass. Whether or not these effects propagate to higher trophic levels remains to be seen (Bennett and Moyle 1996), but the lower consumer levels of this tidal river system appear to be highly sensitive to the kind of year-to-year and decadal variability in primary production and biomass documented here.

**Comparative system variability**—Prolonged nutrient enrichment, as well as river discharge-controlled nutrient loading, appears to be the most common mechanism invoked to explain long-term and interannual variability in estuarine primary production (Underwood and Kromkamp 1999). In the case of the Delta, high turbidity and an ample macronutrient supply removes this most prominent source of variability. Heip et al. (1995, p. 21) suggest that “interannual variation is to a large extent dependent on climatological factors such as irradiance and rainfall” in temperate, nutrient-rich, turbid estuaries. Indeed, precipitation is a major source of variability in the Delta. Precipitation operates through its proximate effects on river flow and its subsequent effects on both biomass and suspended solids. Other sources are important as well, however, as illustrated by the cause-effect diagram in Fig. 12. The invasion of *P. amurensis* has had a notable effect on annual primary production in the Delta through grazing on phytoplankton. Moreover, anthropogenic changes such as dam construction are likely playing a role in the long-term decrease of turbidity in the Delta.

Certain estuaries offer parallels to the Delta. In the Hudson River estuary, the zebra mussel (*Dreissena polymorpha*) became established at high biomass in 1992, remaining high during 1993 and 1994 (Caraco et al. 1997). During these 2 yr, grazing pressure on phytoplankton was over 10-fold greater than it had been prior to the zebra mussel invasion and led to an 85% decline in phytoplankton biomass. This estuary also exhibited enhanced primary productivity during dry summer periods in 1995 and 1997, accompanied by higher water residence times and the deepening of the photic zone (Howarth et al. 2000), similar to the causal pathway for climate identified in the Delta. These authors noted that regional climate change models predict lowered summer freshwater discharge in the northeastern U.S. and, therefore, enhanced summer primary productivity in the Hudson River estuary. In contrast, regional climate models project appreciable increases in precipitation for California over the next century: 20–30% in spring and fall with somewhat larger increases in winter (Wolock and McCabe 1999). According to the results summarized by Fig. 12, these changes acting alone should result in further winter decreases in biomass and primary productivity.

Narragansett Bay presents different kinds of parallels, in that long-term changes are similar but the causes are different. Borkman and Smayda (1998) describe a trend of in-

creasing clarity in that estuary, but the main cause was decreased loading of sewage. Li and Smayda (1998) also document a long-term decrease in phytoplankton biomass, but zooplankton grazing, wind, and temperature were the driving forces for change.

Figure 12 shows two cause–effect linkages that are absent in the Delta but apparently common where phytoplankton particles play the major role in regulating transparency and in nutrient-limited systems. In systems where phytoplankton contributes significantly to light attenuation, Eq. 1 implies that changes in biomass are balanced to some extent by compensating changes in photic zone depth, with the result that productivity does not vary as much as biomass. In the Delta, on the other hand, phytoplankton constitute only a few percentage of TSS, and there is essentially no adjustment of photic depth for changes in biomass. Similarly, in nutrient-limited systems, the decreased nutrient loading that accompanies lower flows will compensate to some extent for the lower flushing rate and decrease in nonalgal suspended matter. Heip et al. (1995) suggest that this kind of homeostatic mechanism dampened primary productivity response to a major engineering works in the Oosterschelde. The construction of dams and a barrier led to decreased input of fresh water and lower nutrients but increased water transparency; primary productivity did not change significantly (Wetsteyn and Kromkamp 1994). In the Delta, however, no such balancing can take place. The Delta thus lacks two compensation mechanisms, one because of its turbidity and one because of its nutrient sufficiency, that would otherwise dampen  $P_n$  variability from year to year and indeed at all time scales. We suggest that turbid nutrient-rich systems may be inherently more prone to variability. Most of the ranges observed for other estuaries or their subregions are much smaller than observed in the Delta, the central region of the Ems-Dollard being a notable exception (Underwood and Kromkamp 1999). The Marsdiep, one of the few comparable systems in terms of record length (1964–1992), exhibits less than a threefold range (Cadée and Hegeman 1993). We cannot conclude, however, that the Delta has unusual variability in annual primary production without comparable records from many other systems.

In any case, the size of the variability is noteworthy and should make us cautious about assigning “characteristic” values of primary production to a system based on the results of 1 yr. How many years are in fact necessary to assess interannual variability? It may be most accurate to say that no record length is sufficient. Many ecological variables appear to behave like “pink noise,” the variance increasing with the length of the series and never reaching a plateau (Halley 1996). Different variability mechanisms have different frequencies of occurrence, and more mechanisms play a role as the series length increases. For example, climate fluctuations often dominate variability in records only a few years long. As the series length increases to the decade scale, the chance of a severe climate event or a biological invasion adding to the variability is greater. As it increases to the century scale, dams or even volcanoes (Columbia River Estuary, Small et al. 1990) may have an effect. We can observe this phenomenon in Delta primary production. Figure 13 shows the coefficient of variation (C.V.) in  $P_n$  as a function

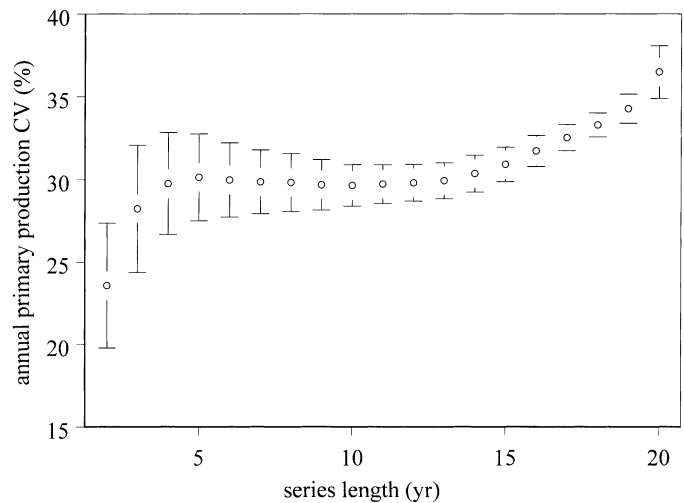


Fig. 13. Coefficient of variation (C.V.) in Delta-wide annual primary production as a function of series length. Each box plot shows the bootstrap mean and standard error of the coefficient of variation for all subseries with the corresponding length. Bootstrap statistics are based on 1,000 bootstrap replicates. Subseries are composed of consecutive years.

of series length. For example, the first value is the coefficient of variation for all series consisting of two consecutive years. The mean and standard error shown for each series length is the bootstrap estimate (Efron and Tibshirani 1993). The mean coefficient of variation stabilizes quickly at about 30% as the series length approaches 5 yr, a long enough interval to characterize routine year-to-year fluctuations in climate and river inflow (Fig. 12). Note that once the series length exceeds 10 yr, however, it becomes more likely to straddle systemic changes because of lower frequency events, in particular a prolonged drought from 1987–1992 and the accompanying invasion of *P. amurensis* (Fig. 12; Cloern 1996). The variance increases accordingly. Conclusions about the magnitude and mechanisms of interannual variability are therefore highly dependent on series length. When we compare variability of different systems, the time scales must be similar; furthermore, the possible presence of rare events with respect to the time scale must be taken into account.

The nature and genesis of year-to-year variability is of great importance in estuarine ecology, especially for systemic properties such as primary productivity that have strong implications for water quality, fisheries productivity, and contaminant transport and bioaccumulation. We often have to decide whether a time series is exhibiting shorter-term annual variability or a longer-term “trend.” There is also a need to separate anthropogenic influences from natural variability, enabling a more rational management of water resources. We are in the “natural history” stage of ecosystem variability, in the sense that we still need to document properly the sources of interannual variability at times scales of 1 to 100 yr (Jassby 1998). If we are to make continued progress in this area, we need to ensure a certain consistency in choosing the spatial scale and time period under study, or at least understand the consequences of the scales in our data sets. Our analyses also need to include the quantitative im-

portance of variability mechanisms, not just their identification. Only then will the body of knowledge grow in a way that permits confident and useful generalizations.

## References

- ALPINE, A. E., AND J. E. CLOERN. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnol. Oceanogr.* **37**: 946–955.
- ARTHUR, J. F., M. D. BALL, AND S. Y. BAUGHMAN. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay–Delta Estuary, California, p. 445–495. *In* J. T. Hollibaugh [ed.], *San Francisco Bay: The ecosystem*. Pacific Division, AAAS.
- ATWATER, B. F., S. G. CONARD, J. N. DOWDEN, C. W. HEDEL, R. L. MACDONALD, AND W. SAVAGE. 1979. History, landforms and vegetation of the estuary's tidal marshes, p. 347–385. *In* T. J. Conomos [ed.], *San Francisco Bay: The urbanized estuary*. Pacific Division, AAAS.
- BALL, M. D. 1987. Phytoplankton dynamics and planktonic chlorophyll trends in the San Francisco Bay–Delta Estuary. Exhibit 103. U.S. Bureau of Reclamation, Sacramento.
- BENNETT, W. A., AND P. B. MOYLE. 1996. Where have all the fishes gone? Interactive factors producing fish declines in the Sacramento–San Joaquin Estuary, p. 519–542. *In* J. T. Hollibaugh [ed.], *San Francisco Bay: The ecosystem*. Pacific Division, AAAS.
- BORKMAN, D. G., AND T. J. SMAYDA. 1998. Long-term trends in water clarity revealed by Secchi-disk measurements in lower Narragansett Bay. *ICES J. Mar. Sci.* **55**: 668–679.
- BORUM, J. 1996. Shallow waters and land–sea boundaries, p. 179–203. *In* B. B. Jørgensen and K. Richardson [eds.], *Eutrophication in marine systems*. American Geophysical Union.
- BOYNTON, W. R., W. M. KEMP, AND C. W. KEEFE. 1982. A comparative analysis of nutrients and other factors influencing estuarine phytoplankton production, p. 69–90. *In* V. S. Kennedy [ed.], *Estuarine comparisons*. Academic.
- CADÉE, G. C., AND J. HEGEMAN. 1993. Persisting high levels of primary production at declining phosphate concentrations in the Dutch coastal area. *Neth. J. Sea Res.* **31**: 147–152.
- CARACO, N. F., J. J. COLE, P. A. RAYMOND, D. L. STRAYER, M. L. PACE, S. E. G. FINDLAY, AND D. T. FISCHER. 1997. Zebra mussel invasion in a large, turbid river: Phytoplankton response to increased grazing. *Ecology* **78**: 588–602.
- [CDWR] CALIFORNIA DEPARTMENT OF WATER RESOURCES. 1986. DAYFLOW program documentation and data summary user's guide. California Department of Water Resources, Sacramento.
- . 1993. Water quality conditions in the Sacramento–San Joaquin Delta during 1991. California Department of Water Resources, Sacramento.
- . 1998. Delta modeling. Delta Modeling Section, California Department of Water Resources. <http://www.delmod.water.ca.gov/docs/index.html>, accessed 25 February 1999.
- CHAPRA, S. C. 1997. *Surface water-quality modeling*. McGraw-Hill.
- CLEVELAND, W. S., AND S. J. DEVLIN. 1988. Locally weighted regression: An approach to regression analysis by local fitting. *J. Am. Stat. Assoc.* **83**: 596–610.
- CLOERN, J. E. 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont. Shelf Res.* **7**: 1367–1381.
- . 1996. Phytoplankton bloom dynamics in coastal ecosystems—a review with some general lessons from sustained investigation of San Francisco Bay (California, USA). *Rev. Geophys.* **34**: 127–168.
- . 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* **210**: 223–253.
- , C. GRENZ, AND L. VIDERGAR-LUCAS. 1995. An empirical model of the phytoplankton chlorophyll:carbon ratio—the conversion factor between productivity and growth rate. *Limnol. Oceanogr.* **40**: 1313–1321.
- COLE, B. E., AND J. E. CLOERN. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. *Mar. Ecol. Prog. Ser.* **17**: 15–24.
- , AND ———. 1987. An empirical model for estimating phytoplankton productivity in estuaries. *Mar. Ecol. Prog. Ser.* **36**: 299–305.
- , ———, AND A. E. ALPINE. 1986. Biomass and productivity of three phytoplankton size classes in San Francisco Bay. *Estuaries* **9**: 117–126.
- COLIN, F. 1983. Primary production in the Ems-Dollard Estuary. Ph.D. thesis, Univ. of Groningen.
- CULLEN, J. J. 1990. On models of growth and photosynthesis in phytoplankton. *Deep-Sea Res.* **37**: 667–684.
- EDMONDSON, W. T. 1991. *The uses of ecology: Lake Washington and beyond*. Univ. of Washington Press.
- EDMUNDS, J. L., K. M. KUIVILA, B. E. COLE, AND J. E. CLOERN. 1999. Do herbicides impair phytoplankton primary production in the Sacramento–San Joaquin River Delta? p. 81–88. *In* D. W. Morganwalp and H. T. Buxton [eds.], *Contamination of hydrologic systems and related ecosystems*. U.S. Geological Survey Water Resources Investigation Report 99-4018B. U.S. Geological Survey, Washington.
- EFRON, B., AND R. J. TIBSHIRANI. 1993. *An introduction to the bootstrap*. Chapman & Hall.
- FALKOWSKI, P., AND J. RAVEN. 1997. *Aquatic photosynthesis*. Blackwell Science.
- FALKOWSKI, P. G. 1981. Light–shade adaptation and assimilation numbers. *J. Plankton Res.* **3**: 203–216.
- FOE, C., AND A. KNIGHT. 1985. The effect of phytoplankton and suspended sediment on the growth of *Corbicula fluminea* (Bivalvia). *Hydrobiologia* **127**: 105–115.
- HALLEY, J. M. 1996. Ecology, evolution and 1/f-noise. *TREE* **11**: 33–37.
- HAMMOND, D. E., AND OTHERS. 1985. Benthic fluxes in San Francisco Bay. *Hydrobiologia* **129**: 69–90.
- HARDING, L. W., JR., D. DEGOBBIS, AND R. PRECALI. 1999. Production and fate of phytoplankton: Annual cycles and interannual variability, p. 131–172. *In* T. C. Malone [ed.], *Ecosystems at the land–sea margin: Drainage basin to coastal sea*. American Geophysical Union.
- HEIP, C. H. R., N. K. GOOSEN, P. M. J. HERMAN, J. KROMKAMP, J. J. MIDDELBURG, AND K. SOETAERT. 1995. Production and consumption of biological particles in temperate tidal estuaries. *Oceanogr. Mar. Biol. Annu. Rev.* **33**: 1–149.
- HELSEL, D. R., AND R. M. HIRSCH. 1992. *Statistical methods in water resources*. Elsevier.
- HOWARTH, R. W., D. P. SWANEY, T. J. BUTLER, AND R. MARINO. 2000. Climatic control on eutrophication of the Hudson River estuary. *Ecosystems* **3**: 210–215.
- JASSBY, A. D. 1998. Interannual variability at three inland water habitats: Implications for sentinel ecosystems. *Ecol. Appl.* **8**: 277–287.
- . 1999. Uncovering mechanisms of interannual variability from short ecological time series, p. 285–306. *In* K. M. Scow, G. E. Fogg, D. E. Hinton, and M. L. Johnson [eds.], *Integrated assessment of ecosystem health*. CRC Press.
- , AND J. E. CLOERN. 2000. Organic matter sources and rehabilitation of the Sacramento–San Joaquin Delta (California, USA). *Aquat. Conserv. Mar. Freshw. Ecosyst.* **10**: 323–352.
- , AND T. M. POWELL. 1994. Hydrodynamic influences on



- interannual chlorophyll variability in an estuary: Upper San Francisco Bay–Delta (California, U.S.A.). *Estuar. Coast Shelf Sci.* **39**: 595–618.
- , C. R. GOLDMAN, AND T. M. POWELL. 1992. Trend, seasonality, cycle and irregular fluctuations in primary productivity at Lake Tahoe, California–Nevada, U.S.A. *Hydrobiologia* **246**: 195–203.
- JOINT, I. R., AND A. J. POMROY. 1981. Primary production in a turbid estuary. *Estuar. Coast Shelf Sci.* **13**: 303–316.
- KIMMERER, W. J., AND J. J. ORSI. 1996. Changes in the zooplankton of the San Francisco Bay Estuary since the introduction of the clam *Potamocorbula amurensis*, p. 403–424. *In* J. T. Hollibaugh [ed.], San Francisco Bay: The ecosystem. Pacific Division, AAAS.
- , AND C. PEÑALVA. 2000. *Potamocorbula* revisited: Results of experimental and field work on the effects of clams on estuarine food webs. IEP Newsl. (California Department of Water Resources, Sacramento) **13**(4): 45–54.
- KRATZER, C. R., AND J. L. SHELTON. 1998. Water quality assessment of the San Joaquin–Tulare basins, California: Analysis of available data on nutrients and suspended sediment in surface water, 1972–1990. U.S. Geological Survey professional paper 1587. U.S. Geological Survey, Washington.
- KROMKAMP, J., J. PEENE, P. VAN RIJSWIJK, A. SANDEE, AND N. GOOSEN. 1995. Nutrients, light and primary production by phytoplankton and microphytobenthos in the eutrophic, turbid Westerschelde estuary (The Netherlands). *Hydrobiologia* **311**: 9–19.
- LEHMAN, P. W. 2000. The influence of climate on phytoplankton community biomass in San Francisco Bay Estuary. *Limnol. Oceanogr.* **45**: 580–590.
- LEWIS, M. R., AND J. C. SMITH. 1983. A small volume, short-incubation-time method for measurement of photosynthesis as a function of incident irradiance. *Mar. Ecol. Prog. Ser.* **13**: 99–102.
- LI, Y., AND T. J. SMAYDA. 1998. Temporal variability of chlorophyll in Narragansett Bay, 1973–1990. *ICES J. Mar. Sci.* **55**: 661–667.
- LUCAS, L. V., J. E. CLOERN, J. K. THOMPSON, AND N. E. MONSEN. *In press*. Functional variability of shallow tidal habitats in the Sacramento–San Joaquin Delta: Restoration implications. *Ecol. Appl.*
- MCMAHON, R. F. 2000. Invasive characteristics of the freshwater bivalve *Corbicula fluminea*, p. 315–343. *In* R. Claudi and J. H. Leach [eds.], Nonindigenous freshwater organisms: Vectors, biology, and impacts. Lewis.
- MECUM, W. L., AND J. J. ORSI. 2001. Zooplankton and mysid shrimp. IEP Newsl. (California Department of Water Resources, Sacramento) **14**(2): 12–15.
- MONSEN, N. 2001. A study of sub-tidal transport in Suisun Bay and the Sacramento–San Joaquin Delta, California. Ph.D. thesis, Stanford Univ.
- MÜLLER-SOLGER, A., A. D. JASSBY, AND D. MÜLLER-NAVARRA. *In press*. Nutritional value of particulate organic matter for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento–San Joaquin Delta, USA). *Limnol. Oceanogr.*
- NICHOLS, F. H., J. K. THOMPSON, AND L. E. SCHEMEL. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. *Mar. Ecol. Prog. Ser.* **66**: 95–101.
- NIXON, S. W. 1981. Remineralization and nutrient cycling in coastal marine ecosystems, p. 261–290. *In* B. J. Neilson and L. E. Cronin [eds.], Estuaries and nutrients. Humana.
- ORSI, J. J., AND W. L. MECUM. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento–San Joaquin Estuary, p. 375–401. *In* J. T. Hollibaugh [ed.], San Francisco Bay: The ecosystem. Pacific Division, AAAS.
- OVERLAND, J. E., AND R. W. PREISENDORFER. 1982. A significance test for principal components applied to a cyclone climatology. *Mon. Weather Rev.* **110**: 1–4.
- PAERL, H. W., J. L. PINCKNEY, J. M. FEAR, AND B. L. PEIERLS. 1998. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. *Mar. Ecol. Prog. Ser.* **166**: 17–25.
- PLATT, T. 1986. Primary production of the ocean water column as a function of surface light intensity: Algorithms for remote sensing. *Deep-Sea Res.* **33**: 149–163.
- , S. SATHYENDRANATH, C. M. CAVERHILL, AND M. R. LEWIS. 1988. Ocean primary production and available light: Further algorithms for remote sensing. *Deep-Sea Res.* **35**: 855–879.
- , D. F. BIRD, AND S. SATHYENDRANATH. 1991. Critical depth and marine primary production. *Proc. R. Soc. Lond. Ser. B* **246**: 205–217.
- RICHMAN, M. B. 1986. Rotation of principal components. *J. Climatol.* **6**: 293–335.
- SMALL, L. F., C. D. MCINTIRE, K. B. MACDONALD, J. R. LARALARA, B. E. FREY, M. C. AMSPOKER, AND T. WINFIELD. 1990. Primary production, plant and detrital biomass and particle transport in the Columbia River estuary. *Prog. Oceanogr.* **25**: 175–210.
- THOMPSON, J. K., AND F. H. NICHOLS. 1996. Control of a phytoplankton bloom in San Francisco Bay, California by the filter-feeding bivalve *Potamocorbula amurensis* [abstract]. *Proc. Pac. Div. AAAS* **13**: 98.
- [UCSIPM] UNIVERSITY OF CALIFORNIA STATEWIDE INTEGRATED PEST MANAGEMENT. 1999. California weather databases. UCSIPM. <http://www.ipm.ucdavis.edu/WEATHER/weather1.html>, accessed 12 February 1999.
- UNDERWOOD, G. J. C., AND J. KROMKAMP. 1999. Primary production by phytoplankton and microphytobenthos in estuaries, p. 93–152. *In* D. B. Nedwell and D. G. Raffaelli [eds.], Advances in ecological research; estuaries. Academic.
- WETSTEYN, L.P.M.J., AND J. C. KROMKAMP. 1994. Turbidity, nutrients and phytoplankton primary production in the Oosterschelde (The Netherlands) before, during and after a large-scale coastal engineering project (1980–1990). *Hydrobiologia* **282/292**: 61–78.
- WILLIAMS, P. J. L., AND D. LEFÈVRE. 1996. Algal <sup>14</sup>C and total carbon metabolism. *J. Plankton Res.* **18**: 1941–1959.
- WOLOCK, D. M., AND G. J. MCCABE. 1999. Estimates of runoff using water-balance and atmospheric general circulation models. *J. Am. Water Res. Assoc.* **35**: 1341–1350.

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