

Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary

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Abstract

The recent invasion of San Francisco Bay by the suspension-feeding clam *Potamocorbula amurensis* has provided an opportunity to document the ecological consequences of a major biological disturbance. Previous work over the last two decades has shown that phytoplankton biomass in the upper estuary is low ($2\text{--}3\text{ mg Chl } a\text{ m}^{-3}$) during seasonal periods of high river flow and short residence time, and it is usually high (peak $> 30\text{ mg Chl } a\text{ m}^{-3}$) during the summer–autumn seasons of low river flow and long residence time. However since *P. amurensis* became widespread and abundant in 1987, the summer phytoplankton biomass maximum has disappeared, presumably because of increased grazing pressure by this newly introduced species. For the period 1977–1990, mean estimated primary production was only $39\text{ g C m}^{-2}\text{ yr}^{-1}$ during years when bivalve suspension feeders were abundant ($> 2,000\text{ m}^{-2}$), compared to $106\text{ g C m}^{-2}\text{ yr}^{-1}$ when bivalves were absent or present in low numbers. These observations support the hypothesis that seasonal and interannual fluctuations in estuarine phytoplankton biomass and primary production can be regulated jointly by direct physical effects (e.g. river-driven transport) and trophic interactions (episodes of enhanced grazing pressure by immigrant populations of benthic suspension feeders).

A fundamental challenge of aquatic ecology is to understand the complex interactions that control primary production. Contemporary theory is guided by two principles. The first states that primary production is regulated through both biotic mechanisms (trophic interactions including competition, predation) and abiotic mechanisms (nutrient fluxes, physical variability; Carpenter et al. 1987). The second states that temporal shifts can occur in the relative importance of biotic and abiotic mechanisms (Bartell et al. 1988), so that “top down” and “bottom up” forces work in concert but at time-varying rates. These principles have emerged largely from the study of small lakes through experimentation by manipulation of whole lakes (selective removal or addition of key predators—e.g. Shapiro and Wright 1984; Carpenter et al.

1987), by following the cascading effects of food-web disruption that result from either natural events (e.g. summer fish kills—Vanni et al. 1990) or accidental introductions of exotic species (see Kitchell et al. 1988), and analysis of long-term records to elucidate mechanisms of biotic and abiotic control of lake community structure or productivity (Mills and Forney 1988; Jassby et al. 1990).

We here address the question of whether these principles extend to other aquatic ecosystems such as estuaries. Ecosystem-level manipulation is usually not feasible in estuaries, and long-term data sets are relatively rare. However, estuaries are characterized by large natural fluctuations in the abundance of key species (often driven by abiotic forcings) and are susceptible to invasion by exotic species. Either of these events can produce population fluctuations at one trophic level that cascade to other trophic levels. We document such a sequence of events in the northern San Francisco Bay estuary. We describe changes in the distribution, biomass, and primary production of phytoplankton that have accompanied episodic fluctuations in the abundance of herbivore populations, including the recent invasion by the clam *Potamocorbula amurensis*. We interpret these

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changes as examples of temporal shifts toward top-down control that occur against a background of abiotic bottom-up control of phytoplankton productivity.

The estuary

Northern San Francisco Bay is a partially mixed estuary that receives seasonally variable inflows from the Sacramento and San Joaquin Rivers (Fig. 1). Fluctuations in the distribution of salinity, suspended particulate matter, dissolved and particulate nutrients, and biota are driven largely by fluctuations in river flow (see Cloern and Nichols 1985). For example, a turbidity maximum forms in the upper estuary (Suisun Bay) during the summer–autumn season of low flow. This turbidity maximum is the result of physical processes including the hydrodynamic trapping of suspended inorganic and organic particles by the combined motions of particle settling and estuarine gravitational circulation (Conomos and Peterson 1977). The localized accumulation of particulate organic matter is presumably an integral feature of the food web supporting early stages of valued fish species such as striped bass.

Seasonal phytoplankton dynamics are most often characterized by low biomass and primary productivity during the winter–spring seasons of high flow, followed by a slow (2–3 months) accumulation of biomass (dominated by diatoms) during summer in association with the formation of the turbidity maximum (Cloern et al. 1985). The estuary is nutrient-rich but turbid, so that algal productivity and population growth rates are limited primarily by light availability (Alpine and Cloern 1988). Hence the summer bloom develops under conditions of slow biological kinetics; from measures in 1980, mean phytoplankton population growth rate was 0.03 d^{-1} (doubling time >3 weeks; Cloern et al. 1985). This slow rate of population growth suggests that the summer biomass maximum results from the hydrodynamic trapping of phytoplankton by the same physical processes that concentrate inorganic particulates in the upper estuary during low river flow.

The annual cycle described above has been a recurrent phenomenon, except for the ex-

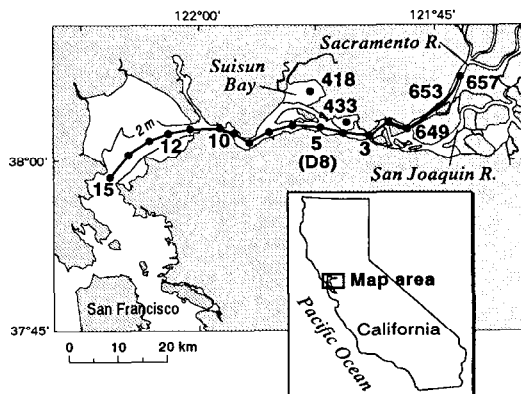


Fig. 1. Map of northern San Francisco Bay showing station locations. USGS station 5 is at about the same location as DWR station D8.

treme drought year 1977 when the summer maximum of phytoplankton biomass never developed. Nichols (1985) suggested that the absence of the summer diatom bloom in 1977 was a direct result of the upstream migration of marine suspension-feeding bivalves (primarily *Mya arenaria*) during the drought, with the result that the balance between phytoplankton production and consumption was disrupted. Our study was motivated by this hypothesis and by the occurrence of a similar event that began in 1986 with the invasion and rapid population growth of another clam species—*P. amurensis* (see Nichols et al. 1990 for a description of this invasion). Our objective was to repeat the preinvasion measurement program of 1980 (Cloern et al. 1985) in order to compare spatial distributions of phytoplankton biomass and productivity when benthic grazers were scarce (1980) and abundant (1988).

Materials and methods

Sampling was conducted along the deep channel and in the adjacent shallows of northern San Francisco Bay (Fig. 1) every 2–4 weeks from May through December 1988. During 1989 and 1990 monthly sampling was continued in the main channel, with the same measurements as in 1988 (excluding primary productivity). During the intensive sampling of 1988, measurements were made in both the channel and shallows because large lateral gradients of chloro-

phyll and turbidity (i.e. light availability) can exist across this estuary (Cloern et al. 1985). Vertical profiles of salinity, temperature, photosynthetically active radiation (PAR), and in vivo fluorescence (IVF) were made at all fixed stations along the channel. Salinity and temperature were measured with a Seabird CTD and IVF with a Sea Tech fluorometer. IVF values were calibrated with Chl *a* concentrations measured at 6–10 stations each date. At both the channel and shallow sites, light extinction coefficients (k_i) were calculated from depth distributions of irradiance measured with a LiCor 192S quantum sensor. Photic depths (Z_p) were assumed to be the depths of 1% surface irradiance [i.e. $Z_p = -\ln(0.01)/k_i$].

Phytoplankton biomass was measured as Chl *a* concentration determined at selected sites in the channel and shallows. Surface water samples were collected with a bucket, and samples from 1 m above the bottom were collected in the channel with a Niskin bottle. The phytoplankton in these samples were collected on Gelman A/E filters which were immediately frozen. Within 2 weeks, the filters were ground with a Teflon tissue grinder in 90% acetone and the Chl *a* concentration, corrected for pheopigments, was determined spectrophotometrically (Strickland and Parsons 1972).

Primary productivity measurements were concentrated in Suisun Bay and made monthly from May through October because ~75% of the annual production occurred during this period of 1980 (Cole and Cloern 1984). Channel sampling sites were chosen based on salinities of ~0, 5, and 10, plus the site of maximum chlorophyll concentration estimated from IVF. The sampling cruises were not synchronized with the tides, so spatial coverage was based on salinity distribution rather than on fixed geographic locations. Shallow sampling sites, where instantaneous salinities were not available, were fixed at stations 433 and 418 (Fig. 1).

Primary productivity was measured in surface water samples that were prescreened to remove macrozooplankton (59- μ m mesh) and then dispensed into 150-ml glass bottles. Chl *a* concentrations in screened and unscreened samples were similar, indicating

that the mesh did not remove phytoplankton biomass. Primary production was measured by the ^{14}C method in 24-h simulated in situ incubations in a deck incubator with procedures identical to those used in 1980 (Cole and Cloern 1984). Light was attenuated with nickel screens to seven light levels: 55, 30, 15, 8, 3, 1, and 0% (dark bottle) of ambient irradiance (I_0). After incubation, inorganic ^{14}C was removed from replicate 3-ml subsamples by the acid-bubbling technique. Aquasol was added and residual ^{14}C activity was measured with a liquid scintillation spectrometer. All uptake rates were corrected for dark uptake. Total inorganic C was quantified by gas chromatography. Daily incident solar radiation to the incubator was measured with a LiCor 190S quantum sensor and integrator.

Daily net primary productivity (P_n) was calculated by trapezoidal quadrature of C uptake rates over the photic depth. Simulated incubation depths were calculated as

$$z = -\ln(I_i/I_0)/k_i$$

where I_i/I_0 is the fraction of the surface irradiance received by bottle *i*. Total production over the growing season was calculated by integrating the average daily P_n at all sites over the period May through October. Annual production was then estimated by assuming that the growing season production accounted for 75% of total production. Maximum daily C assimilation rates ($P_{n,m}^{\#}$) were derived from photosynthesis-irradiance curves. Gauss-Newton curve-fitting was used to obtain the best fit of productivity measurements [as mg C (mg Chl *a*) $^{-1}$ d $^{-1}$] to the hyperbolic tangent function of irradiance (Platt and Jassby 1976).

Results and discussion

We hypothesize that the seasonal and interannual variability of phytoplankton biomass and production in northern San Francisco Bay is a consequence of both direct physical effects and trophic interactions. We explore this hypothesis in two ways. First we use a long-term record from Suisun Bay to demonstrate that interannual variability of phytoplankton biomass is associated with fluctuations in both river flow and abundance of benthic suspension feeders. Then

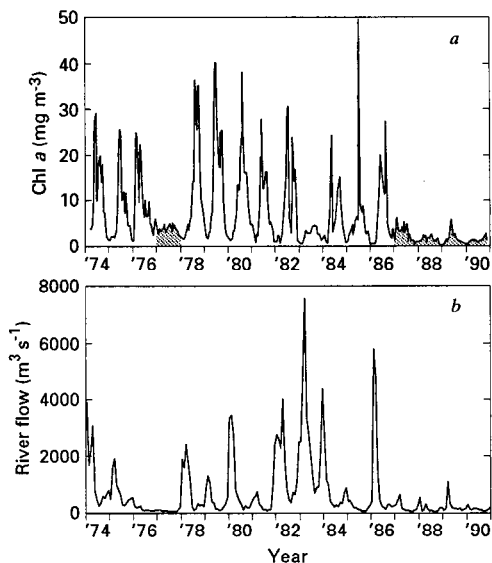


Fig. 2. [a.] Monthly or semimonthly measures of near-surface Chl *a* in Suisun Bay, 1974–1990. Combined data set from the California Department of Water Resources (DWR station D8, 1974–1987) and the U.S. Geological Survey (station 5, 1988–1990). Shaded areas represent periods when benthic grazers were abundant in the bay. [b.] Monthly mean river flow to northern San Francisco Bay from the Sacramento-San Joaquin Rivers (this is net delta outflow as calculated by the California DWR).

we compare observations from two years, 1980 (benthic grazers scarce) and 1988 (benthic grazers abundant), when the spatial distribution of phytoplankton biomass and productivity were measured monthly along the upper estuary.

Phytoplankton biomass, as Chl *a*, has been measured at least once monthly in the mid-Suisun Bay channel since 1974 (Fig. 2a), and benthic macrofauna have been sampled in the bay since 1977 (see Calif. Dep. Water Resour. 1990 for the most recent annual summary). During those years when benthic suspension feeders were absent or scarce, phytoplankton biomass increased each summer when river discharge (Fig. 2b) fell below $\sim 400 \text{ m}^3 \text{ s}^{-1}$. However, during winter–spring periods of high river discharge ($> 2,000 \text{ m}^3 \text{ s}^{-1}$), phytoplankton biomass usually declined in the upper estuary because the hydraulic retention time became short (days–weeks; Walters et al. 1985) relative to the population growth rate (doubling time of weeks–months; Cloern et al.

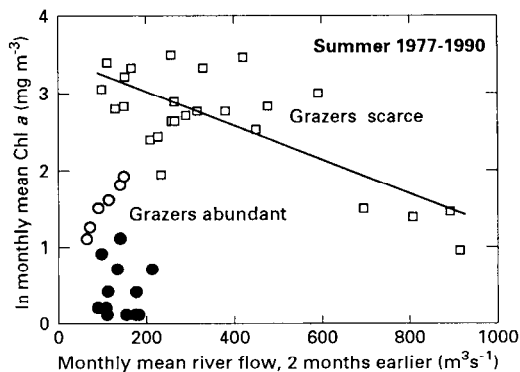


Fig. 3. Ln monthly mean Chl *a* concentration vs. monthly mean river flow 2 months earlier. Measurements are near-surface Chl *a* concentration at DWR station D8 or USGS station 5 for the 3 months of each year (1977–1990) centered around the annual phytoplankton maximum (see Fig. 2a). Years when benthic grazers were abundant (peak densities $> 2,000 \text{ m}^{-2}$) and no relationship exists between river flow and Chl *a* concentration—○. Measurements after the 1986 invasion by *Potamocorbula amurensis*—●. Years when benthic grazers were scarce, and regression analysis shows a statistically significant relationship between summer phytoplankton biomass and river flow for these years ($P = 0.001$)—□.

1985). This washout effect persisted even through summer 1983 (Fig. 2a), a year of sustained high river flow (minimum monthly mean discharge of $700 \text{ m}^3 \text{ s}^{-1}$ in August) and low phytoplankton biomass (maximum $4.5 \text{ mg Chl } a \text{ m}^{-3}$).

To explore this interannual variability of the seasonal phytoplankton biomass maximum, we calculated monthly mean Chl *a* concentrations in Suisun Bay for the 3 months of each year (1977–1990) centered around the timing of the summer chlorophyll maximum. We then partitioned these data into two records: measurements taken during those years when benthic bivalves were abundant ($> 2,000 \text{ m}^{-2}$) and those when mean bivalve population abundance was $< 2,000 \text{ m}^{-2}$.

For those years when benthic grazer populations were small, there was a significant negative correlation between summer phytoplankton biomass (ln Chl *a* concn) and the monthly mean river flow 2 months earlier (Fig. 3). A 2-month lag was used because this is the approximate time lag between the seasonal minimum in river flow and the subsequent maximum in phytoplankton

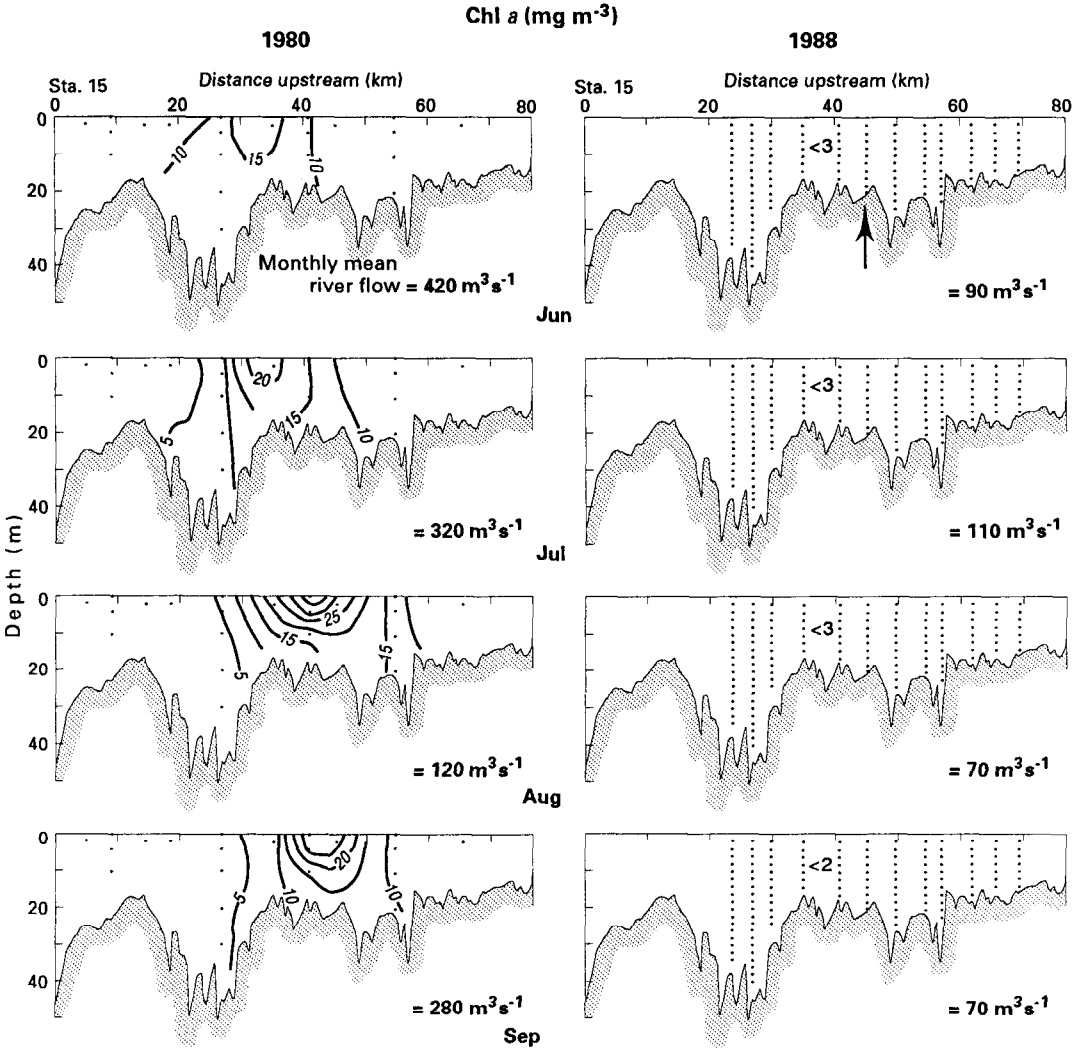


Fig. 4. Spatial distributions of Chl *a* along northern San Francisco Bay comparing summer 1980 and 1988. Location of the long-term monitoring site (USGS station 5; DWR station D8) is marked with an arrow at km 45 in the June 1988 panel. Monthly mean river flow is shown for each sampling date.

biomass. Observations during the years of small bivalve populations (i.e. 1978–1984 and 1986) are consistent with the hypothesis that seasonal and interannual phytoplankton dynamics are regulated largely by river-driven transport processes (abiotic control). However, there were marked departures from this relation in 1977 and 1987–1990 (Figs. 2 and 3), when phytoplankton biomass remained low even under hydrologic conditions that promote biomass accumulation in the upper estuary. These anomalous years may exemplify the

additional control of phytoplankton populations by trophic interactions, because the upper estuary was colonized by large populations of bivalve suspension feeders during 1977 (Nichols 1985) and 1987–1990 (Nichols et al. 1990; Hymanson 1991). Less severe declines in phytoplankton biomass occurred during summer–autumn 1985, when benthic grazers colonized the upper estuary but only very late in the year (Nichols et al. 1990).

Detailed measures of phytoplankton biomass distribution in the main channel and

Table 1. Comparison of monthly mean Chl *a* concentrations (mg m^{-3}) in the shoals of Suisun Bay (Sta. 418) during 1988 when benthic grazers were abundant and 1980 when they were scarce.

	1988	1980*
May	—	11.0
Jun	1.4	28.3
Jul	2.0	43.1
Aug	1.0	49.6
Sep	—	32.5
Oct	1.7	23.3
Nov	0.6	8.5
Dec	0.7	16.7

* Data from Cole and Cloern 1984.

in the adjacent shallows define the spatial extent of the reduced phytoplankton biomass observed in recent years. Figure 4 compares monthly contours of Chl *a* concentration along the main channel of northern San Francisco Bay during 1980 before the invasion by *P. amurensis* and during 1988 after *P. amurensis* had become widespread and abundant. Chlorophyll distributions during 1980 show the slow summer accumulation of biomass localized in Suisun Bay, where near-surface Chl *a* concentration peaked at 35 mg m^{-3} . However, throughout 1988, biomass remained below $3 \text{ mg Chl } a \text{ m}^{-3}$ along the entire upper estuary (Fig. 4). Chl *a* concentrations in the subtidal shoals of Suisun Bay showed similar differences between the two years (Table 1). These subtidal shoals were regions of maximum phytoplankton biomass ($50 \text{ mg Chl } a \text{ m}^{-3}$ during 1980) in the summer-autumn season of years when benthic grazer populations were small. However during 1988 (Table 1) and in subsequent years, phytoplankton biomass was consistently $\leq 2 \text{ mg Chl } a \text{ m}^{-3}$ at the shoal sites.

The persistent and widespread reduction of phytoplankton biomass in 1977 and 1987–1990 may have been a direct consequence of the enhanced abundance of, and phytoplankton consumption by, bivalve suspension feeders. During the drought year 1977, saline water intruded upstream and a marine benthic community dominated by *M. arenaria* invaded Suisun Bay and reached population densities sufficient to prevent the seasonal accumulation of phytoplankton biomass (Nichols 1985).

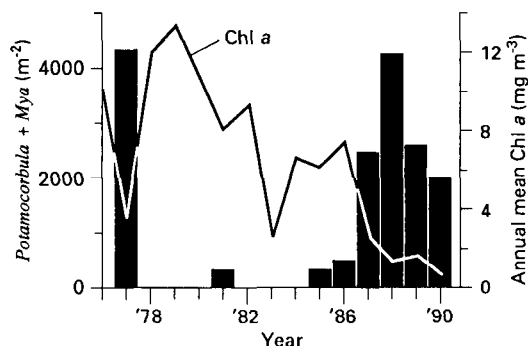


Fig. 5. Annual mean Chl *a* concentrations (solid line) and an index of benthic grazing potential (histograms show annual mean abundance of *Potamocorbula amurensis* plus *Mya arenaria*), 1977–1990. Annual chlorophyll concentrations were calculated from the data in Fig. 2a. Bivalve densities from California DWR (closest DWR station, D7).

During 1987–1990 the estuary was colonized rapidly by *P. amurensis* (Nichols et al. 1990). At annual mean densities $> 2,000$ individuals m^{-2} (Hymanson 1991), this species alone has the potential to remove algal biomass faster than phytoplankton population growth in northern San Francisco Bay (based on laboratory feeding measurements of *P. amurensis* by Cole et al. 1992). Figure 5 shows annual mean Chl *a* concentration for the period 1977–1990, with an index of benthic grazing pressure (total abundance of *P. amurensis* plus *M. arenaria*, the two most abundant macrofaunal species in Suisun Bay; F. H. Nichols pers. comm.). The annual mean Chl *a* concentration during the years of small benthic grazer populations was 8.4 mg m^{-3} ; during the years with abundant benthic grazers ($> 2,000 \text{ m}^{-2}$) the annual mean Chl *a* concentration was only 2.1 mg m^{-3} (means are significantly different, $P < 0.01$; Mann-Whitney-Wilcoxon test). Annual mean Chl *a* concentration has continually declined in northern San Francisco Bay since the invasion by *P. amurensis* in 1986 (Fig. 5).

We considered the alternative explanation that low phytoplankton biomass in recent years resulted from reductions in the rate of phytoplankton population growth. Phytoplankton biomass yield is set partly by the availability of inorganic nutrients N, P, or Si. Hence an alternative hypothesis is

Table 2. Primary production and related parameters for northern San Francisco Bay in 1988.

	Sta.	P_n (mg C m ² d ⁻¹)	Chl <i>a</i> (mg m ⁻³)	Z_p (m)	I_0 (Einst m ⁻² d ⁻¹)	P_n/B [mg C(mg Chl <i>a</i>) ⁻¹ d ⁻¹]
26 May	657	124	2.6	1.6	54.8	63
	653	158	3.5	1.3		77
	5	104	1.5	1.3		89
	7	182	1.6	1.8		140
23 Jun	657	137	1.4	1.7	59.5	105
	649	174	2.8	1.2		96
	4	141	1.5	1.6		123
	6	271	1.6	2.1		164
7 Jul	418	298	1.4	2.1		219
	433	131	1.8	1.0		140
	657	168	1.8	1.6	62.8	117
	649	206	2.9	1.6		85
21 Jul	4	242	2.8	1.9		107
	6	138	1.3	1.3		176
	657	104	1.5	2.2	48.4	68
	649	120	3.1	1.4		56
18 Aug	4	114	2.5	1.7		58
	6	101	1.7	1.4		82
	418	67	2.0	0.8		94
	433	65	1.8	0.9		93
15 Sep	657	48	1.2	1.2	53.6	77
	2	86	2.3	1.2		70
	4	84	2.0	1.6		54
6 Oct	7	91	0.7	1.9		140
	418	49	1.0	0.9		123
	433	46	1.0	1.0		105
	2	19	0.6	1.0	37.4	24
	5	19	0.8	1.1		60
	657	81	1.8	2.4	28.8	56
	4	55	1.5	1.5		41
	6	40	1.0	1.2		62
	418	24	1.7	0.4		93
	433	29	1.7	0.7		85

that the decreased river flow of recent years (Fig. 2b) has led to reduced riverine inputs of N, P, and Si such that the biomass yield of phytoplankton in San Francisco Bay has now become nutrient limited. However, even though the riverine supply of nutrients to the estuary was reduced during the 1987–1990 drought years, nutrient concentrations remained high. In fact, mean concentrations of dissolved inorganic N, P, and Si were higher during summer 1988 than they were in 1980 (Fig. 6). This observation is consistent with Peterson et al. (1985) who observed that dissolved N, P, and Si are distributed along the estuary as conservative constituents during periods of low phytoplankton productivity and nutrient uptake.

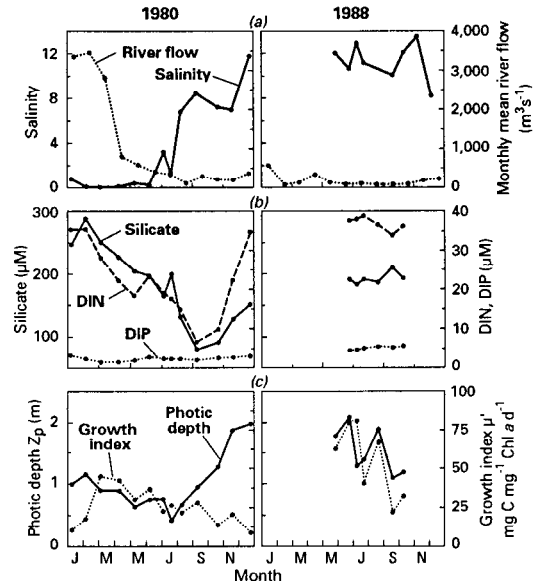


Fig. 6. Seasonal changes in selected physical-chemical measurements in Suisun Bay (USGS station 5), comparing 1980 and 1988. [a.] Monthly mean river flow and near-surface salinity. [b.] Near-surface concentrations of dissolved silicate, inorganic N ($\text{NO}_2^- + \text{NO}_3^- + \text{NH}_4^+$) (DIN), and reactive P (DIP). [c.] Photic depth Z_p and the index of phytoplankton population growth rate μ' . Nutrient data are from Ota et al. (1989) and S. W. Hager (unpubl. data).

To explore further the hypothesis that phytoplankton were resource limited during years of low biomass, we calculated an index of in situ population growth rate,

$$\mu' = P_n / (Z_p B)$$

where μ' is the mean photosynthetic C assimilation rate in the photic zone (μ' is primary productivity divided by Chl *a* biomass, assuming that Chl *a* is uniformly distributed over the shallow photic zone). During summer 1988, μ' ranged from 22 to 68 [mean = 51 mg C (mg Chl *a*)⁻¹ d⁻¹]. However in summer 1980, μ' ranged from 22 to 29 [mean = 25 mg C (mg Chl *a*)⁻¹ d⁻¹; Fig. 6]. These results suggest that the population turnover rate of phytoplankton may have been higher in 1988, a year of low biomass, than in 1980 when a summer biomass maximum developed. The twofold increase in μ' between 1980 and 1988 resulted, in part, from higher photosynthetic efficiencies (P_n/B) in 1988 (Table 2, Cole and Cloern 1984). We conclude, therefore, that

the persistently small biomass of phytoplankton in northern San Francisco Bay throughout 1988 was not a result of resource limitation or other mechanisms (e.g. accumulation of toxic contaminants during low flow) that led to reduced rates of population growth.

The small phytoplankton biomass and low productivity throughout 1988 led to substantial reductions in annual primary production in the upper estuary. Mean phytoplankton production over the growing season (May–October) of 1988 was only 14 g C m^{-2} , and we estimate total annual production to be 20 g C m^{-2} compared to measured annual primary production of 100 g C m^{-2} in Suisun Bay during 1980 (Cole and Cloern 1984).

Annual primary production has only been measured twice in this estuary (1980 and 1988), but we can construct estimates of daily primary productivity, and thus total annual phytoplankton primary production for other years, because of two circumstances. First, there is a linear relation between measured primary productivity and the composite parameter biomass (B) times an index of light availability (I_0/k_t) in San Francisco Bay (Cloern 1991). Second, biomass (B) and transparency have been measured at least monthly in northern San Francisco Bay by the California DWR for nearly two decades. Linear regression of our pooled productivity measurements from 1980 and 1988 (Fig. 7) yielded the equation

$$P'_n = 3.2(B I_0/k_t).$$

With this empirical equation we estimated daily productivity (P'_n) for 1977 to 1990 using the following data: B = measured Chl a concentration at USGS station 5 or DWR station D8; I_0 = long-term monthly mean incident solar radiation near Suisun Bay (Calif. Dep. Water Resour. 1978); and k_t = the estimated extinction coefficient (see Cloern 1991) from measured Secchi depth at DWR station D8. We then estimated annual primary production for the 14 yr of record using trapezoidal integration of the daily estimates of P'_n . Annual mean primary production during the years of small benthic grazer populations ($<2,000 \text{ m}^{-2}$) was $106 \pm 28 \text{ g C m}^{-2}$ (mean \pm SD) compared

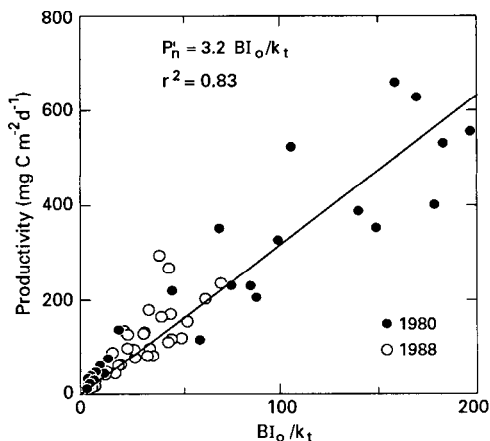


Fig. 7. Measured daily primary productivity vs. the composite parameter BI_0/k_t (1980 data from Cole and Cloern 1984). B is the phytoplankton biomass as Chl a concentration, I_0 is incident solar radiation ($\text{Einst m}^{-2} \text{ d}^{-1}$), and k_t is extinction coefficient (m^{-1}).

to an estimated annual mean production of only $39 \pm 25 \text{ g C m}^{-2}$ for the years when benthic grazers were abundant ($>2,000 \text{ m}^{-2}$).

The long-term observational program in northern San Francisco Bay demonstrates that food-web changes caused by immigration or invasion by herbivore species can have dramatic consequences for phytoplankton dynamics, which has also been demonstrated in lakes, primarily through the introduction of piscivorous or planktivorous fish (see Persson et al. 1988). Exotic species can alter trophic interactions, with effects that cascade through the food web and lead to disruptions in the magnitude and seasonal dynamics of phytoplankton primary production. The accidental introduction of the Zebra mussel (*Dreissena polymorpha*) into the Great Lakes, coincidentally also occurring in 1986, has apparently caused localized declines in phytoplankton biomass in Lake Erie. The normal summer diatom bloom did not occur in Lake Erie during 1990, and water clarity doubled presumably as a consequence of grazing by *D. polymorpha* (Roberts 1990).

Large-scale disturbances provide valuable opportunities ("experiments") to study ecosystem functions and can lead to the pursuit of new questions. For example, the invasion of San Francisco Bay by *P. amuren-*

sis has led to a redirection of our research programs, with emphasis on the questions: What sources of organic matter sustain the population growth of *P. amurensis*, and other heterotrophs, during years when phytoplankton primary production is very low? Has this invasion led to a permanent restructuring of the bay ecosystem or simply a temporary disturbance facilitated by the anomalous hydrologic condition of the 1987–1990 drought (see Nichols et al. 1990)?

Finally, it appears that principles concerning the regulation of primary production and biomass that have emerged from limnological research do extend to northern San Francisco Bay and perhaps estuaries in general. Long-term investigation suggests that both physical controls (river-driven transport) and trophic interactions (episodes of strong grazing pressure by invading species) regulate biomass and primary production in this estuary. We have also seen temporal shifts in the dominant control when food-web changes occur. Thus in this estuary, as in lakes, top-down and bottom-up forces work in concert to regulate phytoplankton dynamics at the seasonal and interannual time scales.

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