

Annual variations in river flow and primary production in the South San Francisco Bay Estuary (USA)

James E. Cloern

U.S. Geological Survey, MS-496, 345 Middlefield Road, Menlo Park, CA 94025, USA

Offprint from
Estuaries and Coasts: Spatial and Temporal Intercomparisons
ECSA19 Symposium

Edited by
Michael Elliott &
Jean-Paul Ducrest

Published by
Olsen & Olsen, 1991

ISBN 87-85215-17-1

Abstract

Phytoplankton biomass and productivity in South San Francisco Bay are low except for periods of rapid increase that can occur in spring. The spring bloom is typically associated with density stratification of the water column that is induced by river flow. In the past decade of climatic and hydrologic extremes, the magnitude of the annual spring bloom (mean biomass and estimated primary production) was strongly correlated with the magnitude of river flow during the wet season. This investigation demonstrates one mechanism, of many, through which climatic and hydrologic variability can lead to variability of biological processes in estuaries.

Keywords: estuaries, phytoplankton, primary production, annual variability. San Francisco Bay.

Introduction

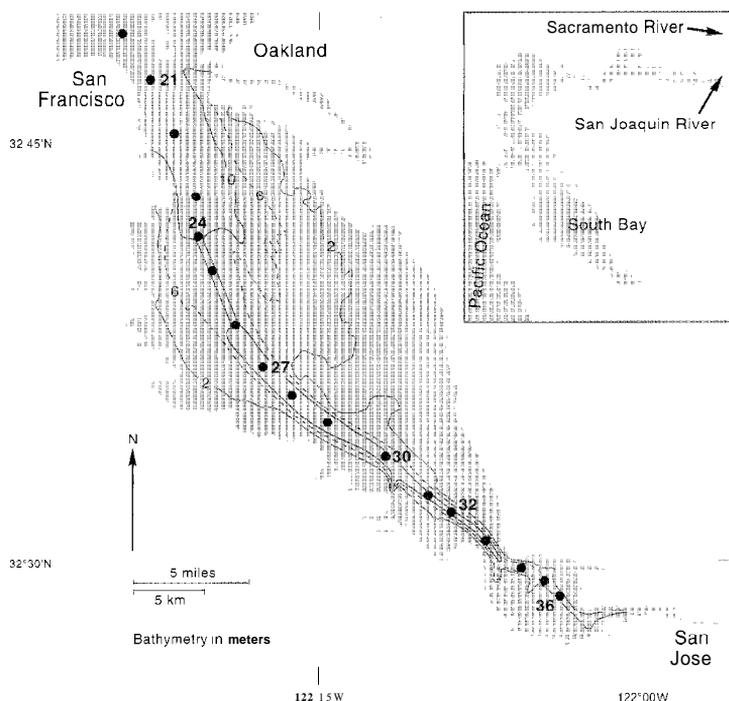
The growing interest in climate variability is motivated by the prospect that human activities will alter global temperatures. The ability to anticipate specific climatological responses to global warming is limited, and we have an even more rudimentary knowledge of how complex ecological systems, including those of the coastal zone, might respond to altered climate regimes. One effective approach to pursue this topic is through long-term observational programs that can be used to exploit natural experiments of climate variability. This approach is particularly instructive during climate extremes such as those in western North America during the past decade. Selected data from a study of San Francisco Bay during that period illustrate one response of estuarine ecosystems to climate variability at two important time scales. Both seasonal and interannual variations in precipitation and runoff in the tributary river basins have a large influence on the physical structure and phytoplankton dynamics of this estuary.

San Francisco Bay is the estuary of California's two largest rivers, the Sacramento and San Joaquin, which have a combined drainage area of 160 000 km². River discharge to the estuary is highly seasonal and 65% of the total annual runoff occurs from January to April. As a consequence, the river-driven circulation patterns and longitudinal distributions of salt, nutrients, suspended sediments and biota of San Francisco Bay all vary markedly from the summer-fall dry season to the winter-spring wet season (Cloern & Nichols 1985). In addition, large interannual variations in precipitation and river runoff are associated with interannual variations in atmospheric circulation (Cayan & Peterson 1989), which have been remarkable in the past decade. The continuous study of phytoplankton dynamics in the southern part of San Francisco Bay during this period provides an example of how one biological community can respond to climatic-hydrologic variability at these longer time scales.

Methods

Sampling was at fixed locations (Figure 1) along the longitudinal axis of South San Francisco Bay to define hydrographic properties (salinity, temperature, turbidity) and phytoplankton biomass along the deep channel. Sampling frequency was monthly or fortnightly during periods of low phytoplankton biomass, and was accelerated (to twice weekly) during the

Figure 1. Position of sampling locations along the channel of South San Francisco Bay (California, USA). Inset shows the location of major tributaries, the Sacramento and San Joaquin Rivers.



spring phytoplankton blooms. Results presented here are from 217 such sampling cruises conducted from 1980 to 1987.

Vertical profiles of salinity and temperature were obtained by pumping water to an induction-type salinometer and thermistor (Schemel & Dedini 1979), from the surface to near-bottom. Water density (as σ_t) was calculated from Knudsen's (1901) equations, and the vertical density gradient ($\Delta\sigma_t/h$) was calculated as the difference between bottom and surface σ_t divided by water depth h . Phytoplankton biomass was mapped as chlorophyll-*a* concentration estimated from *in-vivo* fluorescence, which was measured with a Turner Designs Model 10 fluorometer. The fluorometer was calibrated each cruise with five to ten discrete chlorophyll-*a* measurements. Samples were collected onto Gelman A/E filters and chlorophyll-*a* concentration was determined spectrophotometrically (Strickland & Parsons 1972) from acetone extracts, using the phaeopigment correction of Lorenzen (1967). The mean deviation between discrete measures of chlorophyll-*a* and estimated chlorophyll-*a* from *in-vivo* fluorescence was less than 10%.

The light attenuation coefficient k_t (m^{-1}) was determined either from vertical profiles of irradiance (using a LiCor 192S quantum sensor) or from Secchi depth (Sd, m) using the relation $k_t = 0.40 + 1.09/Sd$ ($r^2 = 0.89$) determined from 278 simultaneous measurements of k_t and Sd made during 1980. Photic depth (Z_p) was calculated as the depth of 1% surface irradiance [$= -\ln(0.01)/k_t$].

Primary productivity was measured at station 27 (mid-Bay, Figure 1) on 41 dates between 1980 and 1982. ^{14}C uptake was measured with samples held for 24 h in a deck incubator receiving natural illumination. Nickel screens were used to simulate irradiance at eight depths, from the near-surface to Z_p (Cole & Cloern 1984). Integral daily productivity in the photic zone was then calculated by trapezoidal integration. These measurements were used to develop an empirical model for estimating daily productivity on other dates, as follows:

The rate of photosynthesis p is a hyperbolic function of irradiance (I), such as (Peterson *et al.* 1987):

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

where B is biomass ($mg\ chl-a \cdot m^{-3}$), p_{\max} is maximum photosynthetic rate ($mg\ C \cdot mg^{-1}\ chl-a \cdot d^{-1}$), and α defines photosynthetic efficiency. Then, the depth distribution of photosynthesis in a well-mixed photic zone is:

$$p(z) = B p_{\max} [1 - \exp(-\alpha I_0 \exp\{-k_t z\})] , \quad (2)$$

where z is depth, k_t defines light attenuation with depth, and I_0 is surface irradiance ($Einsteins \cdot m^{-2} \cdot d^{-1}$). Using the series approximation [$\exp(x) = 1 + x + \dots$], equation (2) can be rewritten as:

$$p(z) = B p_{\max} [\alpha I_0 \exp(-k_t z)] . \quad (3)$$

This approximation can then be integrated from the water surface to depth Z_p , yielding an expression for integral daily production in the photic zone:

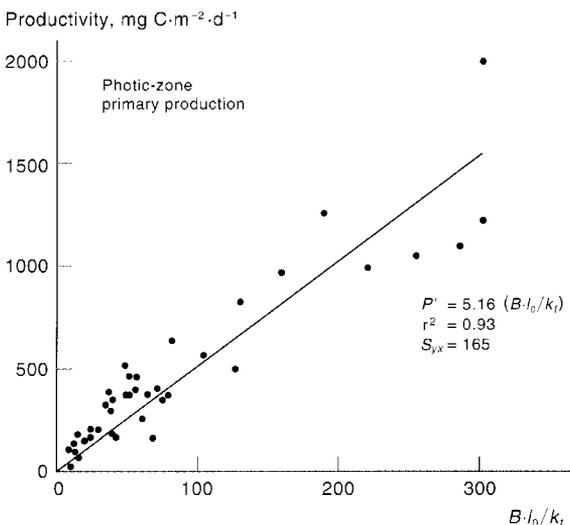
$$\int_0^{Z_p} p(z) dz = P' = 0.99 \alpha p_{\max} [B \cdot I_0 / k_t] . \quad (4)$$

Equation (4) implies that integral productivity in the photic zone is a linear function of biomass [B] times an index of light availability [I_0/k_t]. The 41 measurements of daily productivity in South San Francisco Bay were fit to equation (4) by linear regression (Figure 2), giving:

$$P' (mg\ C \cdot m^{-2} \cdot d^{-1}) = 5.16 [B \cdot I_0 / k_t] . \quad (5)$$

Equation (5) was used to estimate daily productivity for the period 1980-1987, using: B = mean chlorophyll-*a* concentration between stations 24 and 30 (interpolated between sampling dates); k_t = mean attenuation coefficient along that transect; and I_0 = daily irradiance measured at San Jose (Bay Area Air Pollution Control District). Note that equation (5) estimates daily primary productivity in the *photic zone*, which can differ substantially from productivity over the water column depth (Cloern 1987).

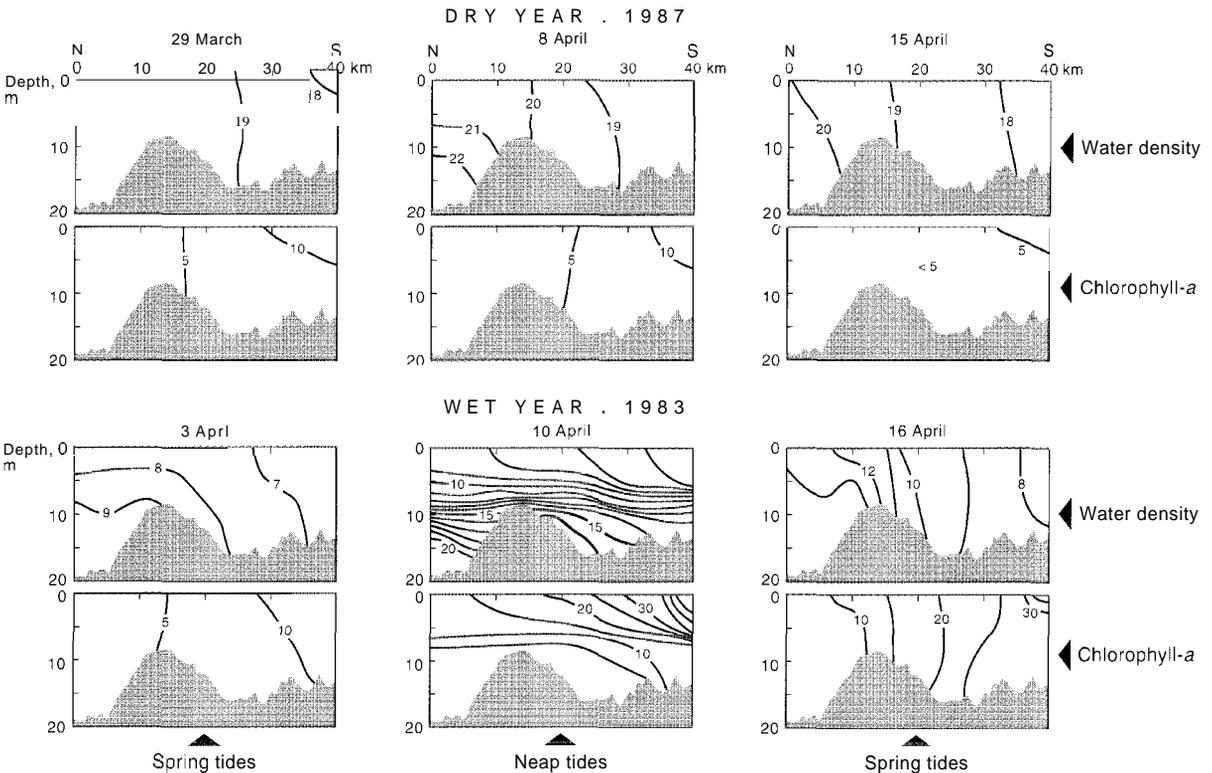
Figure 2.
Photic-zone primary productivity versus the index [$B \cdot I_0 / k_t$].



Results and discussion

During this eight-year period, freshwater inflow to San Francisco Bay varied over two orders of magnitude, spanning the full range of hydrologic conditions observed this century. For the period of record 1921–present, the highest January–April river flow into San Francisco Bay occurred in 1983; 1986 and 1982 were the years of 7th and 10th highest inflows, respectively. However, inflow was among the seven lowest values during 1981, 1985, and 1987.

During the dry seasons and during dry years, South San Francisco Bay was marine in character (salinity ≈ 30 ‰) and vertically mixed. However following major runoff from winter storms or spring snowmelt, sufficient buoyancy was introduced from freshwater inflow to allow for density stratification. The degree of vertical stratification is modulated by tidal stirring (Haas 1977, Sinclair *et al.* 1981, Cloern 1984), which varies over fortnightly (neap–spring) and lunar monthly frequencies. As an example, Figure 3 shows the vertical density gradients during spring–neap–spring tide sequences of an extreme spring dry year (1987) compared to an extreme wet year (1983). Throughout 1987 the density gradients were small, indicating that the water column was well-mixed (top panels, Figure 3). However following large freshwater inputs during 1983, the water column became highly stratified during neap tides (Figure 3) when the production of tidal kinetic energy was insufficient to overcome buoyancy forces.



All periods of strong stratification ($\Delta\sigma_t/h > 0.5$) observed in South San Francisco Bay over the past decade have coincided with rapid increases in phytoplankton biomass. During the April 1983 stratification event, phytoplankton biomass in the surface layer increased about fourfold in one week (lower panels, Figure 3). Similar responses occurred during the other years of high river flow and strong density stratification. In contrast, phytoplankton biomass was persistently low and homogeneously distributed during 1987 (Figure 3) and the other dry years when density stratification was weak.

The connection between density structure and phytoplankton population dynamics may result from two mechanisms. First, the formation of a density discontinuity slows the rate of mixing and effectively partitions the water column into two layers that intermix slowly. Algal cells in the upper layer receive sufficient light energy to sustain rapid photosynthesis and cell division (nutrient concentrations typically exceed levels that limit phytoplankton growth: dissolved N > 15 μM , P > 5 μM , Si > 50 μM , Conomos 1979). This contrasts with periods of mixing

Figure 3. Vertical distributions of water density (σ_t) and chlorophyll-a concentration ($\text{mg} \cdot \text{m}^{-3}$) along the channel of South San Francisco Bay, comparing April 1987 with April 1983.

when mean light exposure in the entire water column is insufficient to sustain rapid population growth (Alpine & Cloern 1988). Second, the loss rate of phytoplankton biomass to benthic grazers may also be related to vertical mixing intensity. Molluscs, polychaetes, and other sessile suspension feeders are sufficiently abundant to consume all phytoplankton production in South San Francisco Bay (Cloern 1982). However the actual rate of phytoplankton removal by this community is influenced by the diffusive transport of phytoplankton cells to the narrow zone above the bottom sediments where ingestion occurs. This vertical flux of algal biomass is presumably small under stratified conditions, when tidal stirring is weak and when algal biomass is produced in the upper layer faster than it is lost due to sinking.

If density structure of the water column responds to freshwater inflows, and if phytoplankton dynamics follow closely the degree of density stratification, then temporal variations in the abundance of phytoplankton are expected to have seasonal and interannual components reflecting these components of variability in river flow. Both components are evident in the time series of river flow and phytoplankton biomass for the period 1980-1987 (Figure 4 A,B). The seasonal charac-

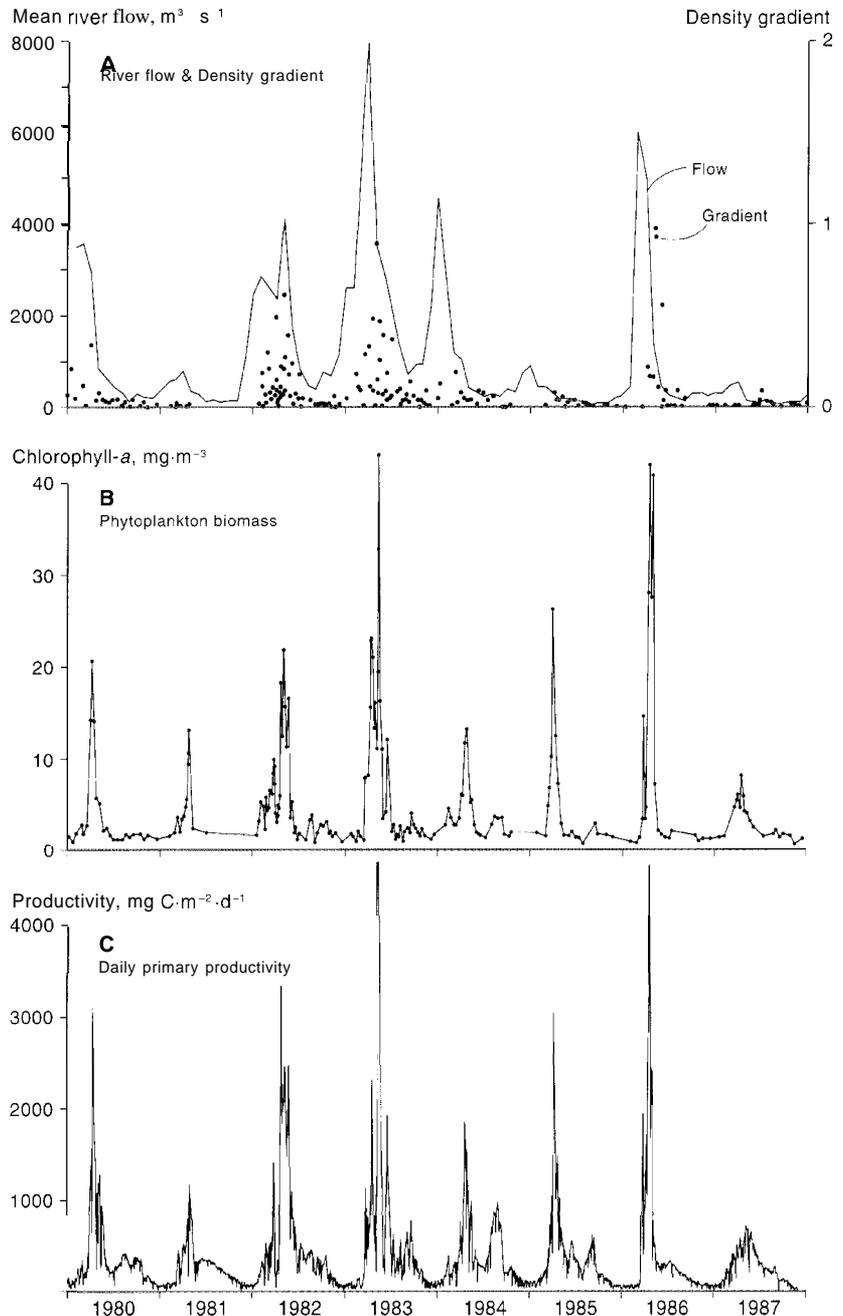


Figure 4.

A: Mean monthly inflow to San Francisco Bay from the Sacramento-San Joaquin River drainages, 1980-1987 (California Dept. Water Resources); also shown is the mean density gradient ($\Delta\sigma_t/h$) at stations 24, 27, and 30 (Figure 1).

B: Mean near-surface chlorophyll-a concentration between stations 24-30.

C: Estimated daily primary productivity, from equation (5)

ter of the hydrograph is evident, with peak flows generally occurring January through April. Phytoplankton biomass had similar seasonality, but with increases occurring during March-May; biomass was persistently low the remainder of the year when river inflow was also low. During years of high river discharge (1982, 1983, 1986), the South Bay had episodes of strong stratification (Figure 4A). In these years the spring phytoplankton bloom persisted over a period of months and was characterized by very high biomass near the times of strongest stratification (Figure 4B). However, the dry years (particularly 1981, 1987) were characterized by weak stratification and short (<1 month) bloom events with smaller biomass increases (Figure 4B). Thus the magnitude of the spring bloom was highly correlated with river flow (Figure 5A). This correlation ($r = 0.87$) was significant at $p < 0.01$ (the more conservative Spearman rank correlation, which may be more appropriate for this small number of observations, indicates a significance level of $p < 0.05$).

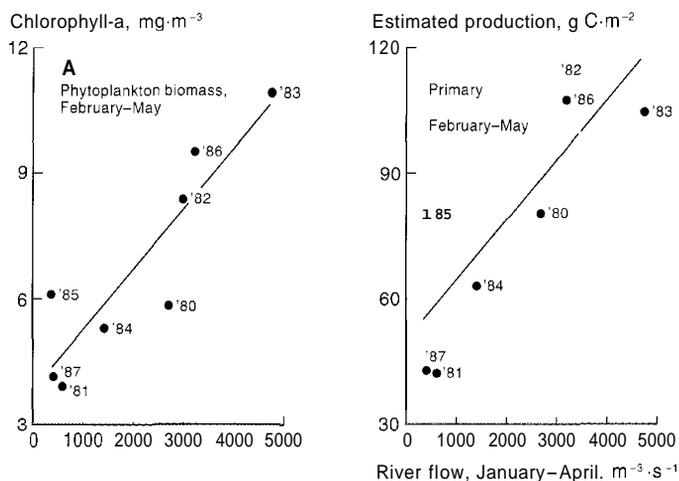


Figure 5. A: Mean phytoplankton biomass during spring months (February-May) of 1980-1987, versus mean river flow (January-April). B: Estimated total phytoplankton production (February-May) versus spring river flow.

The correlation between phytoplankton biomass and river flow suggests the possibility that variations in annual primary production are the result of hydrologic variability. The time series of estimated daily productivity (Figure 4C), derived from equation (5), was used to explore this possibility. Estimated daily productivities were summed over the months February-May for each year. These estimates of total spring primary production ranged from about 40 to 110 g C·m⁻², and also were correlated with river flow (Figure 5B). This correlation ($r = 0.81$) was significant at $p < 0.025$ (or $p < 0.05$ using the rank correlation). Note the anomaly of 1985 when primary production was relatively high in the absence of high river flow. This indicates that secondary mechanisms, such as local weather conditions (e.g. wind speed, cloud cover), contribute to the variability of biomass and production at the seasonal time scale. However, the correlation coefficient between spring production and river flow indicates that about 65% of the variability of annual primary production is correlated with river discharge.

Therefore a fundamental biological process, the photosynthetic production of biomass, is regulated largely by variations in climate (winter precipitation and river discharge), mediated by the hydrologic influence on vertical mixing intensity. Other biological processes and communities respond to these seasonal and annual variations in primary production. For example, the abundance and productivity of pelagic bacteria increase about tenfold in South San Francisco Bay during the spring bloom (J.T. Hollibaugh, pers. comm.). In other coastal systems microbial activity in the sediments (Graf *et al.* 1983, Hargrave 1973, Indrebø *et al.* 1979), and associated rates of nutrient regeneration (Kelly & Nixon 1984), also respond to inputs of phytoplankton biomass following blooms. Zooplankton biomass (copepods and ciliates) is generally highest in South San Francisco Bay during spring when primary productivity peaks (Cloern & Nichols 1985). Seasonal and annual variability in the growth rate of benthic herbivores (e.g., the clam *Macoma balthica*) also parallel that of phytoplankton production (Thompson & Nichols 1988).

These results suggest that much of the ecological and biogeochemical variability in this estuary is driven, ultimately, by variations in precipitation and river flow. Few long-term records of primary production exist for estuaries, so it is difficult to speculate on the generality of this conclusion. However, it is known

that other mechanisms exist for hydrologic control of estuarine production. For example, annual delivery of nutrients from the Susquehanna River to upper Chesapeake Bay appears to determine, in part, annual phytoplankton production in that estuary (Malone *et al.* 1988). Sustained investigation, across a spectrum of estuary types, is therefore required to develop general insights into the mechanisms through which climatic-hydrologic variability determines biological variability in estuarine ecosystems.

Acknowledgements

The data set presented here is a result of the diligent and sustained efforts of my colleagues Andrea Alpine, Brian Cole and Sally Wienke, and the crew of the RV *Polaris*, Byron Richards and Scott Conard. Sheila Greene and Randy Brown (California Dept. Water Resources) kindly provided river flow data. I thank Fred Nichols, Dave Peterson, Tom Powell and two anonymous referees for their thoughtful reviews of this paper.

References

- Alpine, A.E. & J.E. Cloern, 1988. Phytoplankton growth rates in a light-limited environment. San Francisco Bay. – *Mar. Ecol. Prog. Ser.* 44:167-173.
- Cayan, D.R. & D.H. Peterson, 1989. The influence of north Pacific atmospheric circulation on streamflow in the west. – In D.H. Peterson (ed.): *Aspects of Climate Variability in the Pacific and the Western Americas*, pp. 375-398. Am. Geophys. Un., Geophysical Monograph 55, Washington, D.C.
- Cloern, J.E., 1982. Does the benthos control phytoplankton biomass in South San Francisco Bay (USA)? – *Mar. Ecol. Prog. Ser.* 9: 191-202.
- Cloern, J.E., 1984. Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, USA). – *Oceanol. Acta* 7: 137-141.
- Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. – *Cont. Shelf Res.* 7: 1367-1381.
- Cloern, J.E. & F.H. Nichols, 1985. *Temporal dynamics of an estuary: San Francisco Bay*. – Kluwer Academic Publishers, Dordrecht, Netherlands. 237 pp.
- Cole, B.E. & J.E. Cloern, 1984. The significance of biomass and light availability to phytoplankton productivity in San Francisco Bay, USA. – *Mar. Ecol. Prog. Ser.* 17: 15-24.
- Conomos, T.J. (ed.), 1979. *San Francisco Bay: The urbanized estuary*. – Pacific Div., Am. Ass. adv. Sci., San Francisco, California. 493 pp.
- Graf, G., R. Schulz, R. Peinert & L.-A. Meyer-Reil, 1983. Benthic response to sedimentation events during autumn to spring at a shallow-water station in the western Kiel Bight. I. Analysis of processes on a community level. – *Mar. Biol.* 77: 235-246.
- Haas, L.W., 1977. The effect of the spring-neap tidal cycle on the vertical salinity structure of the James, York and Rappahannock Rivers, Virginia, U.S.A. – *Estuar. coast. mar. Sci.* 5: 485-496.
- Hargrave, R.T., 1973. Coupling carbon flow through some pelagic and benthic communities. – *J. Fish. Res. Bd Can.* 30: 1317-1326.
- Indrebo, G., B. Pengerud & I. Dundas, 1979. Microbial activities in a permanently stratified estuary. I. Primary production and sulfate reduction. – *Mar. Biol.* 51: 295-304.
- Kelly, J.R. & S.W. Nixon, 1984. Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community. – *Mar. Ecol. Prog. Ser.* 17: 157-169.
- Knudsen, M., 1901. Hydrographical tables. – G.E.C. Gad, Copenhagen. 63 pp.
- Lorenzen, C.J., 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. – *Limnol. Oceanogr.* 12: 343-346.
- Malone, T.C., L.H. Crocker, S.E. Pike & B.W. Wendler, 1988. Influences of river flow on the dynamics of phytoplankton production in a partially stratified estuary. – *Mar. Ecol. Prog. Ser.* 48: 235-249.
- Peterson, D.H., M.J. Perry, K.E. Bencala & M.C. Talbot, 1987. Phytoplankton productivity in relation to light intensity: a simple equation. – *Estuar. coast. Shelf Sci.* 24: 813-832.
- Schemel, L.E. & L.A. Dedini, 1979. A continuous water-sampling and multiparameter system for estuaries. – U.S. Geol. Surrey Open-File Rep. 79- 273.
- Sinclair, M., D.V. Siribu Rao & R. Couture, 1981. Phytoplankton temporal distributions in estuaries. – *Oceanol. Acta* 4: 239-246.
- Strickland, J.D.H. & T.R. Parsons, 1972. *A practical handbook of seawater analysis*. Bull. Fish. Res. Bd Can. 167. 310 pp.
- Thompson, J.K. & F.H. Nichols, 1988. Food availability controls the seasonal cycle of growth in the bivalve *Macoma balthica*. – *J. exp. mar. Biol. Ecol.* 116: 43-61.

Résumé

La biomasse et la productivité phytoplanctoniques restent basses dans la baie de San Francisco sauf pendant des périodes de croissance rapide se produisant au printemps. La floraison printanière est typiquement associée à la stratification de la colonne d'eau dépendant elle-même du débit des apports continentaux. Au cours de la dernière décennie, connue pour ses extrêmes climatiques et hydrologiques, l'importance de la floraison printanière de l'année (biomasse moyenne et production primaire estimée) est fortement corrélée au débit des rivières au cours de la saison humide. Le présent article démontre un mécanisme, parmi d'autres, sur lequel peuvent jouer la variabilité climatique et hydrologique conduisant à la variabilité des processus biologiques en estuaires.