

Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, USA)

Estuary
Salinity stratification
Phytoplankton
Primary productivity
San Francisco Bay
Estuaire
Stratification de salinité
Phytoplancton
Productivité primaire
Baie de San Francisco

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ABSTRACT

South San Francisco Bay (USA) has periodic variations in salinity stratification that coincide with neap-spring tidal variations during the winter "wet" season, but it remains well-mixed during summer and fall. The degree of salinity stratification, and timing of stratification events, can be predicted from a simple empirical function of river discharge and tidal current speed. During periods of prolonged salinity stratification, phytoplankton biomass and primary productivity are high, phytoplankton patchiness increases, turbidity and nutrient (N) concentrations decline in the surface layer, and residual currents accelerate.

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RÉSUMÉ

Variations dans le temps et signification écologique de la stratification de salinité dans un estuaire (sud de la baie de San Francisco, États-Unis)

Pendant la saison pluvieuse de l'hiver, la partie meridionale de la baie de San Francisco (États-Unis) est sujette à des variations periodiques de stratification de salinité coïncidant avec le cycle des marées; en revanche, pendant l'été et l'automne, les eaux restent bien mélangées. La mise en évidence de la stratification hivernale et le déroulement des processus qui la caractérisent, peuvent être prédits par une fonction simple et empirique entre la crue et la vitesse du courant de marée. Pendant les périodes prolongées de stratification de salinité, la biomasse phytoplanctonique et la productivité primaire sont élevées, la turbidité et la concentration de l'azote inorganique dissous sont peu élevés dans la couche superficielle, et les courants d'eau résiduels par suite de la circulation gravitationnelle deviennent accélérés.

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INTRODUCTION

A paradigm of aquatic ecology is that phytoplankton respond in a predictable manner to changes in water column stability (*i.e.*, vertical density stratification). Where nutrients are not limiting, phytoplankton biomass increases in the surface layer during periods of stratification (Riley, 1942; Sverdrup, 1953; Pingree *et al.*, 1976; Haas *et al.*, 1981); however, in nutrient-poor waters phytoplankton biomass increases only after periods of instability when nutrients are mixed from bottom waters to the photic zone (Pingree *et al.*, 1977;

Takahashi *et al.*, 1977). Frontal zones between stratified and mixing water masses commonly support high phytoplankton biomass and primary productivity (Pingree *et al.*, 1978; Simpson *et al.*, 1979; Bowman *et al.*, 1981).

Stability of coastal waters is controlled by the balance between buoyancy flux (from surface heating or freshwater inflow) and the dissipation of kinetic energy by wind and tidal mixing. Horizontal variations in stratification correlate with the parameter h/u^3 , an index of tidal mixing rate (h = depth; u = mean tidal current speed; Simpson, Hunter, 1974; Bowman, Esaias, 1981),

and this correlation has been useful in predicting horizontal variations of phytoplankton biomass in coastal waters and estuaries (Pingree *et al.*, 1978; Simpson *et al.*, 1979; Bowman *et al.*, 1981). However, this predictive capability has not yet been applied to temporal variations, even though tidal current speed (and thus h/u^3) varies predictably over the semi-annual and neap-spring tidal cycles. Here, I present results of a study of temporal variations in salinity (density) stratification in a eutrophic estuary (South San Francisco Bay, California, USA), and responses of the phytoplankton community to stratification. A simple bulk parameter Q/u_m^3 (Q = river discharge; u_m = maximum tidal current speed) explains most of the temporal variability in stratification and therefore can be useful in predicting temporal dynamics of phytoplankton.

METHODS

South San Francisco Bay (SSFB) is a shallow coastal embayment that usually receives only small inputs of freshwater from local tributaries and a large influx of freshwater derived from the Sacramento River (Fig. 1) during peak discharge in winter (Conomos, 1979). Sampling was done throughout 1982, with highest frequency during the spring period of prolonged neap tides. This period corresponded to the timing of maximum stratification and phytoplankton blooms in previous years (Cloern, 1979; 1982). Results presented here are means of measurements made at four stations (Fig. 1) in the central channel; station depths range from 10 to 16 m. Vertical profiles of salinity were obtained at each station with a submersible pump and inductive salinometer (Schemel, Dedini, 1979); the salinometer was calibrated each cruise with bottle samples that were analyzed in the laboratory (Lewis, 1980). A simple stratification index $\Delta S/h$ (ppt/m) was calculated as the difference between near-bottom and

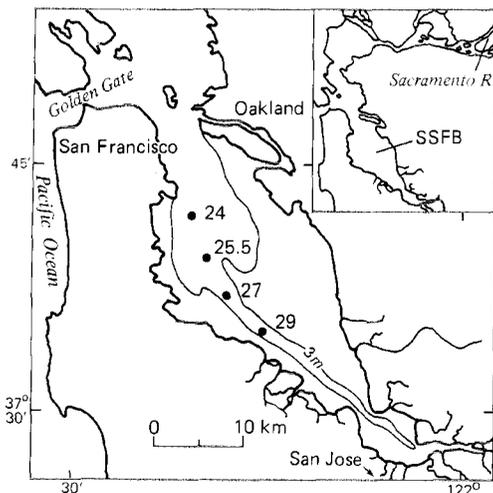


Figure 1
Map of South San Francisco Bay (SSFB), California, showing locations of sampling stations (filled circles).

surface salinity (ΔS) divided by depth of the bottom sample (h). Chlorophyll *a* was determined spectrophotometrically (Lorenzen, 1967) from samples collected at 2 m; correction was made for phaeopigments. Primary productivity was measured at station 27 using simulated *in situ*, 24-h incubations with carbon-14 (Cloern, 1982; Cole, Cloern, 1984). Nutrient samples were collected from 2 m at station 27, filtered through a Gelman AE glass fiber filter then a Nuclepore filter having 0.4 μm pore size, and frozen. Dissolved inorganic nitrogen ($\text{DIN} = \text{NO}_3^- + \text{NO}_2^- + \text{NH}_4^+$) concentration was determined in the laboratory with a Technicon AutoAnalyzer (Peterson, 1979).

RESULTS AND DISCUSSION

Salinity stratification was pronounced during the winter-spring "wet" season when discharge of the Sacramento River was high ($> 1,000 \text{ m}^3/\text{sec.}$), and it was absent during the summer-fall "dry" season (Fig. 2). During the wet season, the degree of

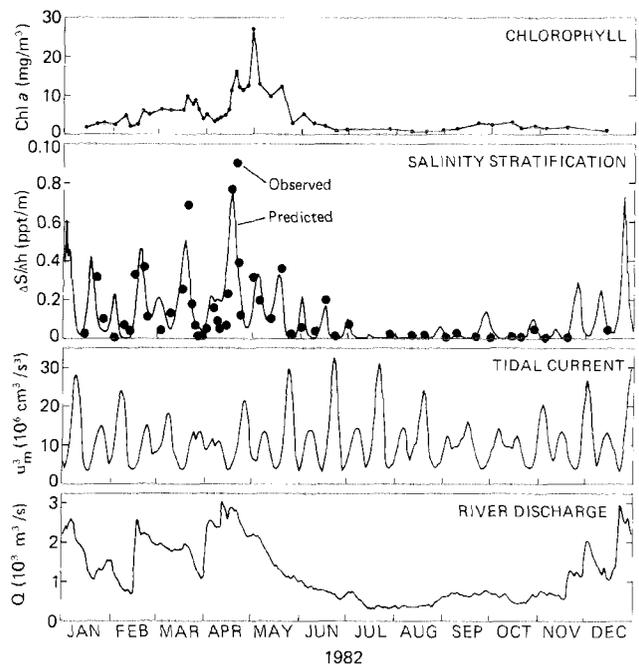


Figure 2

Temporal changes in a) near-surface chlorophyll *a* concentration in SSFB; b) observed and predicted salinity stratification $\Delta S/h$; c) daily values of maximum tidal current speed u_m^3 at Golden Gate (NOAA, 1981); and d) daily discharge Q (computed freshwater discharge to San Francisco Bay, from US Bureau of Reclamation, Sacramento, California).

stratification varied periodically in concert with the neap-spring cycle: $\Delta S/h$ exceeded 0.3 during minor neap tides, $\Delta S/h$ fell below 0.05 after major spring tides, and $\Delta S/h$ reached an annual maximum value of 0.9 on April 19 after about three weeks of slow tidal currents (Fig. 2). Similar covariations in salinity stratification and tidal current speed have been described qualitatively for other estuaries (Haas, 1977; Sinclair *et al.*, 1981). Temporal dynamics of stability suggested that stratifi-

cation events occur when weak tides coincide with high rates of freshwater inflow, such that kinetic energy of turbulent motion is insufficient to overcome the stabilizing effects of buoyancy input from freshwater. Furthermore, the obvious correlations in Figure 2 suggested that the degree of salinity stratification could be predicted from a simple empirical function of river discharge Q (a measure of buoyancy flux) and the cube of maximum daily tidal current speed u_m (an index of the dissipation rate of kinetic energy from tides; Pingree *et al.*, 1978). Linear regression of $\Delta S/h$ against the simple parameter Q/u_m^3 showed that 75% of the variation in $\Delta S/h$ observed during 1982 was associated with variations in Q/u_m^3 ($\Delta S/h = -0.07 + 1150 [Q/u_m^3]$; $n = 50$; $r^2 = 0.75$; the best fit was obtained when Q was the four-day running mean of discharge and u_m was the three-day running mean of predicted maximum tidal current speed at Golden Gate prior to each sampling date). The predictive capability of this simple model is somewhat surprising because the parameter Q/u_m^3 does not take into account the effects of local freshwater inflow, spatial variations in water depth or tidal current speed, enhanced stability from surface heating, or the effects of wind mixing, all of which influence vertical density structure. However, predicted values of $\Delta S/h$ from the regression equation match closely the timing and magnitude of stratification events observed over both short and long time scales (Fig. 2). This is consistent with Fischer's (1972) hypothesis that the degree of salinity stratification in estuaries depends primarily upon the estuarine Richardson number, which is proportional to Q/u_m^3 .

The phytoplankton community responds to stratification in SSFB, and the ability to predict the timing and persistence of water column stability may facilitate studies of plankton ecology (as well as hydrodynamics, sediment dynamics, and geochemistry). For example, phytoplankton biomass was low (1-3 mg/m³ chlorophyll *a*) throughout the dry season when the water column was vertically mixed (Fig. 2). However, phytoplankton biomass was greater during the wet season and it increased in the surface layer, sometimes very rapidly, either during or shortly after periods of maximum stratification (Fig. 2). The major seasonal phytoplankton bloom corresponded to the five-week period from April 13 to about May 20, during the longest continuous period of predicted stratification of the year (Fig. 2). The mechanism(s) of biomass increase are not known for certain, but spring blooms probably result from 1) increased cell division rates as vertical mixing slows and light availability increases to algal cells in the shallow (≈ 5 m) surface layer (Sverdrup, 1953; Pingree *et al.*, 1976; Haas *et al.*, 1981); and 2) decreased grazing pressure from benthic suspension feeders while phytoplankton are retained in the surface layer (Cloern, 1982).

The general response of increasing biomass during periods of stratification is modulated by other factors, such as weather. For example, the first half of April was cold and stormy (mean air temperature and daily insolation at San Jose were 16°C and 270 g cal/cm²; Bay Area Air Pollution Control District), whereas the

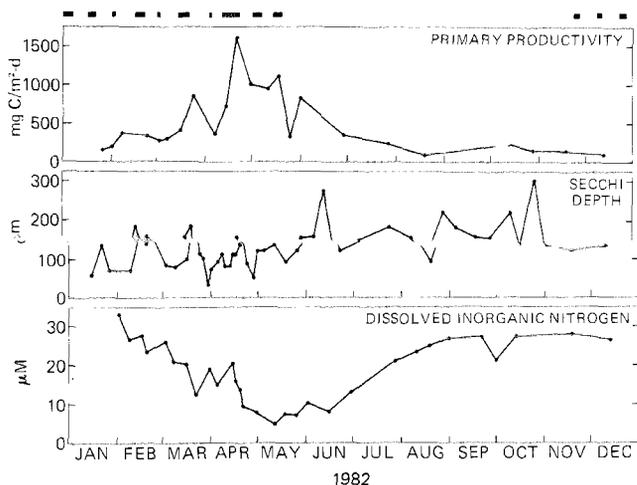


Figure 3

Temporal changes in a) net daily primary productivity; b) Secchi depth (cm); and c) near-surface concentration of dissolved inorganic nitrogen at station 27. Solid bars at top represent stratification events, defined as periods when $\Delta S/h > 0.2$.

second half of April was warm and sunny (24°C; 470 g cal/cm²). This probably explains the lag between the timing of maximum stratification (April 19) and maximum chlorophyll (April 30; Fig. 2).

Phytoplankton primary productivity was highest during the spring blooms and lowest during the periods of vertical homogeneity. Depth-integrated productivity in the photic zone usually exceeded 1 g C/m²-d from mid-April to mid-May (a daily maximum of 1.6 g C/m²-d was measured on April 26), but was consistently less than 0.3 g C/m²-d during summer and fall (Fig. 3). Annual primary productivity at station 27 was estimated to be 140 g C/m², of which half was produced during the March-May period of maximum stratification and biomass. High rates of primary production resulted from increased phytoplankton biomass and decreased turbidity (*see below*) associated with neap tides, rather than from physiological responses to reduced vertical mixing (*e.g.* increased maximum assimilation rate P_m^B ; Demers, Legendre, 1982). P_m^B varied seasonally, ranging from a minimum of 37 mg C/mg chl *a*-d during January to a maximum of 180 mg C/mg chl *a*-d during August, and there was no correlation between integral productivity and P_m^B .

Species composition and spatial heterogeneity of phytoplankton were also different during periods of stratification than during periods of rapid mixing. The spring blooms resulted primarily from increased abundances of planktonic diatoms (*Thalassiosira* spp., *Skeletonema costatum*, *Cyclotella caspia*, *Leptocylindricus danicus*), whereas diatoms were less abundant during summer-fall when the phytoplankton community was dominated by microflagellates (*Chroomonas* spp., *Gyrodinium aureolum*, *Pyramimonas* spp.). Near-surface profiles of *in-vivo* fluorescence showed a high degree of horizontal patchiness during periods of stratification, and a more homogeneous distribution of chlorophyll when tidal currents were rapid. This is consistent with the changing relative importance of physical and biological processes as turbulent mixing slows (Denman,

Platt, 1976). Spatial heterogeneity was pronounced on April 21 when patches of red water were visible throughout SSFB. These localized red tides were composed of surface accumulations ($\text{chl } a > 100 \text{ mg/m}^3$) of the pigmented ciliate *Mesodinium rubrum* and *Peridinium* sp.

Temporal dynamics of density stratification have implications for other properties of the estuary. For example, SSFB is turbid but becomes more transparent during periods of stratification. During the wet season, transparency was highly correlated with salinity stratification: Secchi depth at station 27 was usually greater than 150 cm during stratification events and less than 75 cm during periods of mixing (Fig. 3). Apparently, suspended particles sink out of the surface layer when the water column is stable, and they are resuspended during mixing events. Moreover, residual (tidally-averaged) currents are generally slow ($\approx 1\text{--}3 \text{ cm/sec.}$) in SSFB except during periods of stratification when the seaward-flowing surface current and landward-flowing bottom current accelerate (up to 15 cm/sec. ; R.A. Walters, personal communication). These currents and vertical mixing bring oceanic water (and perhaps seed populations of neritic diatoms) into SSFB, remove brackish water from the surface, and may facilitate the removal of contaminants by direct water replacement (for example, tissue burdens of Cu and Ag in the clam *Macoma balthica* are inversely related to seasonal discharge of the Sacramento River; Luoma, Cain, 1979). Stratification may also indirectly influence secondary production by herbivores: zooplankton biomass is highest during spring (Hutchinson, 1982), and growth and productivity of some benthic invertebrates is most rapid in spring (Nichols, Thompson, 1982) when phytoplankton biomass and primary productivity are highest. Finally, temporal dynamics of phytoplankton influence the distribution of nutrients in SSFB. For example, the concentration of dissolved inorganic nitrogen at station 27 was consistently greater than $25 \mu\text{M}$ during the summer-fall season of low phytoplankton biomass, but DIN fell to an annual minimum of $5 \mu\text{M}$ during the April-May

bloom (Fig. 3). The inverse correlation between DIN and primary productivity (Fig. 3) suggests that phytoplankton uptake is a major sink for inorganic nitrogen, and that seasonal variations in uptake rate are related to seasonal variations in water column stability.

CONCLUSIONS

Density stratification of South San Francisco Bay varies over fortnightly and seasonal time scales in response to temporal variations in tidal current speed and freshwater inflow. Temporal dynamics of stratification are predictable, which is fortuitous because many important features of the estuary vary with changes in water column stability. Phytoplankton dynamics (biomass, community composition, primary productivity, patchiness), zooplankton biomass, concentrations of dissolved inorganic nutrients and suspended particulates, and residual currents are all influenced by salinity stratification. Additional research is required to determine whether the distribution of oxygen and rates of nutrient regeneration vary with the degree of stratification (D'Elia *et al.*, 1981; Phoel *et al.*, 1981), or whether microbial processes of decomposition (such as sulfate reduction) accelerate following periods of high phytoplankton productivity (Indrebø *et al.*, 1979). However, the capability to predict the timing of stratification events will facilitate the design of experiments to answer these and other questions relevant to temporal dynamics of estuaries.

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