

PHYTOPLANKTON SPATIAL DISTRIBUTION IN SOUTH SAN FRANCISCO BAY: MESOSCALE AND SMALL-SCALE VARIABILITY

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Abstract: Horizontal transects of surface salinity and in-situ fluorescence indicate the existence of three distinct spatial regimes in South San Francisco Bay. A mid-Bay region of low phytoplankton biomass with little small-scale variance is bounded to the north and south by water masses having higher in-situ fluorescence and enhanced small-scale variability. Autocorrelation analyses demonstrate that the length scale of phytoplankton patchiness is longest in the mid-Bay region. The persistent discontinuities of in-situ fluorescence and salinity are associated with topographic features - a large shoal to the north and a constriction to the south. The three spatial regimes are consistent with measured zooplankton distributions, existing current meter data, estimated longitudinal transports, and numerical simulations of residual circulations that show one (and perhaps two) large-scale gyre(s) bounded by the northern shoal and southern constriction. Topographic features are the most important physical factors controlling mesoscale (~ 10 km) variability of phytoplankton in South San Francisco Bay. We speculate that vertical current shear and salinity stratification (and their effects upon turbulence and diffusion) control small-scale patchiness, but quantitative estimates are needed to determine the influence of large-scale (and local) phytoplankton growth and loss processes.

Introduction

San Francisco Bay has been the site of considerable basic research into estuarine processes and properties during the past decade (Conomos 1979; Cloern and Nichols 1985). One reason for the scientific interest is that the Bay comprises two different estuary types in a single body of water. The North Bay is a river-dominated estuary while the South Bay is a lagoon-type estuary with no large riverine inflow. Phytoplankton population dynamics and productivity have been studied in the South Bay nearly continuously since 1978 (Cloern et al. 1985). These investigations have focused on the temporal dynamics of mean

properties (e.g., chlorophyll-a concentration or primary productivity) averaged over large geographic sub-regions. Although these studies have described variability of average properties on a crude spatial scale, the problems of (1) characterizing and (2) defining mechanisms of spatial variability have not been addressed previously. These problems motivated the study of the South Bay described here.

South San Francisco Bay is a shallow embayment with a seaward connection through a deep basin (Central Bay) inside the Golden Gate (Fig. 1). This basin is a mixing zone for waters originating from the nearshore coastal ocean, the North Bay (San Pablo and Suisun Bays, Fig. 1), and the South Bay. The southern portion of the Bay receives inputs of treated sewage effluent and freshwater runoff through small local tributaries during the winter-spring wet season (Conomos 1979). Bathymetry of the South Bay is characterized by broad lateral shoals (e.g., note the position of the 2-m isobath in Fig. 1) incised by a channel about 10-20 m deep; a transverse shoal (San Bruno shoal, Fig. 1) reduces water depth in the channel to about 7-8 m. Phytoplankton dynamics are characterized by an annual cycle with an intense spring bloom, beginning in March or April and lasting for about one month, followed by persistently low biomass the remainder of the year. During the bloom, biomass can approach 40-50 $\mu\text{g l}^{-1}$ chlorophyll-a and daily primary productivity can exceed 2 $\text{g C m}^{-2} \text{d}^{-1}$, in contrast to biomass and productivity of 2-5 $\mu\text{g l}^{-1}$ chlorophyll a and $< 0.5 \text{g C m}^{-2} \text{d}^{-1}$ during other times of the year (Cloern *et al.* 1985). Salinity stratification plays a critical role in triggering the spring bloom (Cloern 1984); the onset coincides with a neap tide when stratification is strong. Although the spring bloom is a baywide event, it is not clear whether it begins in the channel following stratification of the deep water column there, or in the shoals. Chlorophyll concentrations in these lateral shoals, however, are always greater than or equal to those in the channel.

Physical processes in San Francisco Bay have also been investigated in recent years (Conomos 1979; Walters *et al.* 1985). The dominant flows are, of course, tidal with primarily semi-diurnal periods (Cheng and Gartner 1985). Whereas the tidal flows dominate the instantaneous current speed, low frequency variations in currents are important to the long-term distribution of solutes and suspended constituents (Cheng and Casulli 1982; Walters 1982; Walters and Gartner 1985; Walters *et al.* 1985). These latter include tidally-driven and density-driven residual currents, and wind-driven flows. For example, South Bay current records indicate eastward, tidally-driven residual currents along the northern edge of the San Bruno shoal, with northward flows along the eastern boundary of the main channel (Walters *et al.* 1985). The overall picture suggests: a clockwise gyre in the entrance to South Bay north of the San Bruno shoal and a counterclockwise rotating flow in and adjacent to the main channel south of the San Bruno shoal. Model studies (Walters and Cheng 1980; Cheng and Casulli 1982) also suggest a larger scale counterclockwise gyre in the central portion of the South Bay (between the San Bruno shoal and the San Mateo Bridge), but direct current meter evidence is not available to confirm this assertion. Residence times for the South Bay (estimated by either the replacement

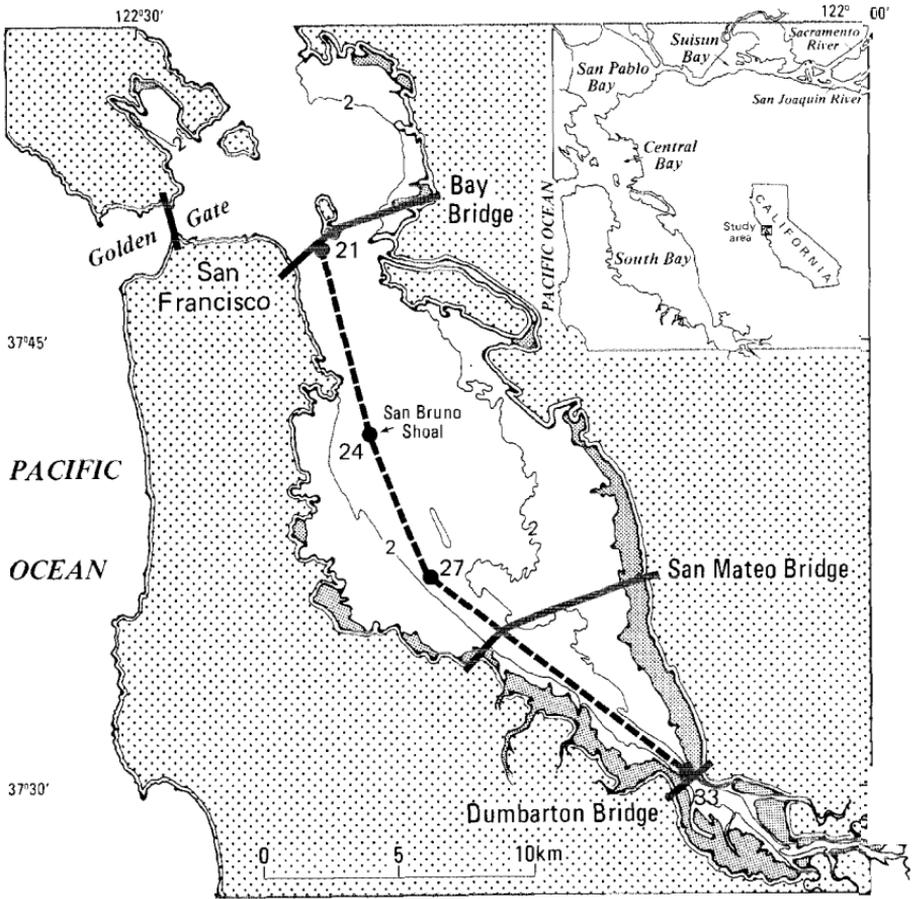


Figure 1. South San Francisco Bay, California, showing the sampling transect between the Bay Bridge and Dumbarton Bridge. The 2-m isobath and position of the transverse San Bruno shoal are also shown.

time for the freshwater fraction or the hydraulic flushing time) are on the order of months. This long residence time may be related to the suggested gyre circulation that could retain fluid in the central basin. During brief episodes in spring, freshwater inflow from the North Bay alters density stratification sufficiently to drive a gravitational circulation. This enhances mixing between the South Bay and the Central Bay, reducing South Bay residence times to less than a month (Walters *et al.* 1985). Local mixing in the South Bay is most intense around the San Bruno shoal.

From the above sketches of past studies we conclude that horizontal variability is an important aspect of the estuarine environment of South San Francisco Bay. For example, lateral shoal areas differ from the main channel: phytoplankton biomass, turbidity, and net primary productivity are higher over the shoals, while nutrient concentrations and tidal current speed are lower there (Cloern

and Nichols 1985). Moreover, physical and biological processes in the central basin of the South Bay may differ from those north of the San Bruno shoal or south of the San Mateo Bridge, because of the enhanced residence time and relatively high local mixing there. We are thus led to ask two questions about San Francisco Bay. First, what are the characteristic spatial scales over which physical and biological processes vary? Second, are the scales of physical variability related to the scales of biological variability, and, if so, how? Here we limit ourselves to the study of the South Bay and consider only variability along the main axis of the estuary—approximately north-south along the main channel. We are particularly interested in defining and characterizing features of spatial variability that persist over the annual cycle. This precludes study of spatial changes that may occur over shorter time scales, such as day-to-day, as studied by Wilson *et al.* (1979) and Wilson and Okubo (1980) in Long Island Sound. Accordingly, we defer study of the rapid spatial changes that occur during the short period of the spring bloom.

Recent reviews (Denman and Powell 1984; Mackas *et al.* 1985) examined the coupling between biological and physical processes in a number of aquatic environments, although estuaries were not emphasized. The two works explored the idea that variability occurring at a given spatial scale in, for example, physical processes, might be expected to lead to variability in biological processes at the same scale. This rationale motivated the present study. Many investigators have looked at the general question of the scales of spatial variability in estuaries (Platt *et al.* 1970; Platt 1972; Lekan and Wilson 1978; Lewis and Platt 1982), and several have considered how physical processes acting at a particular spatial scale affect estuarine phytoplankton. For example, Bowman and Esaias (1978), Bowman *et al.* (1981), and Tyler and Seliger (1978, 1981) explored the impacts of fronts and gravitational circulation on the distribution and life-histories of phytoplankton. The present study is the first to explore the progression of spatial variability in an estuary over an annual cycle, though a similar study has been done in a large lake (Abbott *et al.* 1982).

Sampling Methods

From 27 March 1984 to 16 April 1985, 19 transects were made along the main channel in South San Francisco Bay between the Dumbarton Bridge and the Bay Bridge (Fig. 1). The sampling dates were chosen to include anticipated periods of high and low phytoplankton biomass, high and low density stratification [from an empirical model of Cloern (1984)], and high and low tidal currents (*i.e.*, neap-spring variation), thus ensuring a broad spectrum of physical and biological conditions. Water was pumped continuously from a subsurface port at 2-m depth to a fluorometer (Turner Designs Model 10) and an induction salinometer (Schemel and Dedini 1979) while the ship was underway. Fluorescence, salinity, and water depth were measured every second and mean values recorded every five seconds on a digital-data-acquisition system. The five-second sampling frequency corresponds to a distance of approximately 18 m, based on the average speed of the vessel.

Four to eight water samples were collected during each transect. From these we measured salinity [using the method of Lewis (1980) to calibrate the salinometer], and chlorophyll-a [using the spectrophotometric technique of Lorenzen (1967) to calibrate the fluorometer]. The regression between fluorescence and chlorophyll had an overall r^2 of 0.84. We used separate regressions from each cruise to calculate chlorophyll-a from *in-vivo* fluorescence at each sample point.

Results

Spatial variability occurs on all scales in aquatic systems. The first part of our presentation focuses on the large scale, where quantities vary only over distances approximating the size of the estuary; the second concentrates on much smaller patterns.

Large-Scale Variability

Figure 2 presents a plot of the fluorescence and salinity taken during one of the transects— 27 March 1984. Figures 3A-D show chlorophyll data from four representative transects in 1984 (including 27 March). The two traces of Fig. 3A, B (March and April) represent chlorophyll distributions during the modest spring bloom of 1984, and the two of Fig. 3C, D (May and October) are generally representative of traces in the remainder of the year. Qualitative examination of Fig. 2 shows two breaks— positions along the transect where the character of the record changes significantly— at about 17 and 28 km. Below 17 km, the small-scale variability in fluorescence was high; beyond 17 km the record became smoother. Below 28 km the salinity trace was very smooth, but

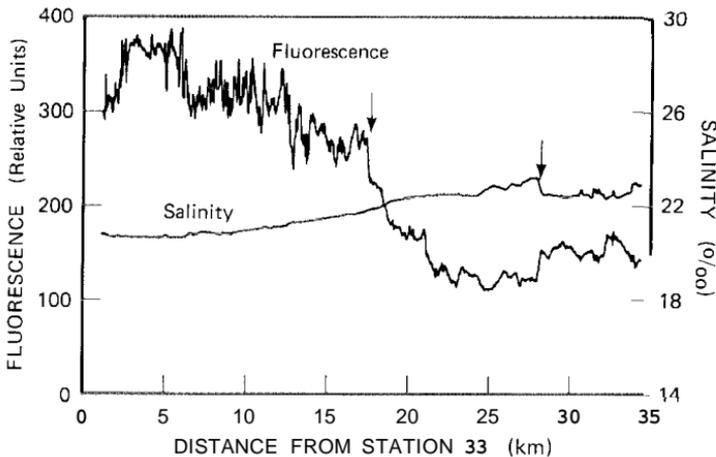


Figure 2. Continuous records of *in-vivo* fluorescence (relative units) and salinity along the transect from Dumbarton Bridge (station 33; Fig. 1) to Bay Bridge, on 27 March 1984. Arrows denote breaks in the qualitative nature of the fluorescence trace (~ 17 km) and the discontinuity in the salinity trace (~ 28 km).

beyond the prominent discontinuity at 28 km small-scale salinity features were more evident. Fluorescence exhibited a parallel discontinuity at 28 km, and salinity and fluorescence appeared to be inversely correlated beyond that discontinuity. In all records we were able to choose two similar break points: one in the south near 15 km on the basis of qualitative changes in the nature of the fluorescence record; and one in the north near 27 km from discontinuities in the salinity trace. Moreover, the segment of the fluorescence record between these breaks contained the fluorescence minimum of South Bay, except during spring bloom periods.

Chlorophyll data derived from the fluorescence records of all 19 transects exhibited the general characteristics of the fluorescence trace of Fig. 2. Four representative samples are shown in Figs. 3A-D.

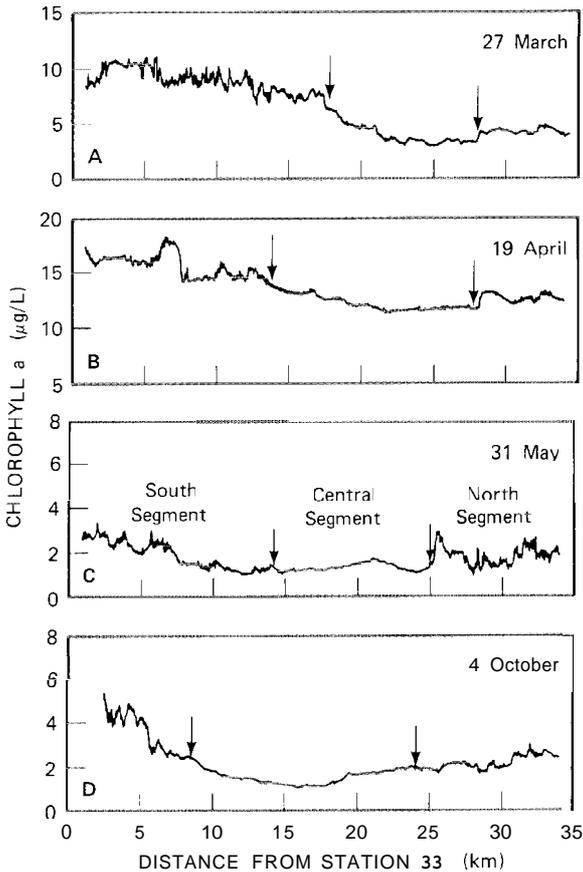


Figure 3. Chlorophyll-*a* traces along the South Bay channel transect that are representative of bloom (A, B) and non-bloom (C, D) periods in 1984. Arrows show the locations of break points identified from qualitative changes in the corresponding fluorescence/salinity traces.

The southern segment of the traces (approximately south of the San Mateo Bridge, at 15 km) was characterized by high variability in chlorophyll, that is the southern portions of the records were more "spiky" and patchy than the portions to the north (Fig. 3). The central segment of the traces was characterized by low variability in both chlorophyll and salinity. The northern segment (north of the San Bruno shoal at 28 km) was characterized by higher variability in salinity and chlorophyll than found in the central segment; the average levels of salinity and chlorophyll were also higher than those measured in the central segment.

Although the transects were made randomly with respect to the semi-diurnal tidal cycle, and the tidal excursion along the channel axis is about 10 km (Walters *et al.* 1985), these breaks appeared consistently near 15 km and 27 km. These boundaries correspond to topographic features in the bathymetry and morphology of the South Bay (Fig. 1): the boundary at 15 km corresponds to the narrowing seen where the San Mateo Bridge (with its closely spaced pilings, and shallow depth) crosses the bay, and the break at 27 km corresponds to the northern limit of the San Bruno shoal.

An important exception to the general picture sketched above can occur during the spring bloom period. A transect was made on 21 March 1985 (Fig. 4), at the initiation of the 1985 spring bloom. Peak values of chlorophyll ($40 \mu\text{g l}^{-1}$) occurred one week after that --- on 29 March 1985. A chlorophyll maximum occurred in the central segment on this transect, not the typical minimum.

Small-Scale Variability

The difference in variability at small scales has been one of the signatures of the three larger regimes we have identified in South San Francisco Bay. For example, we noted that the southern segment had a higher level of chlorophyll variation than the central segment. We will now describe this small-scale variability focusing

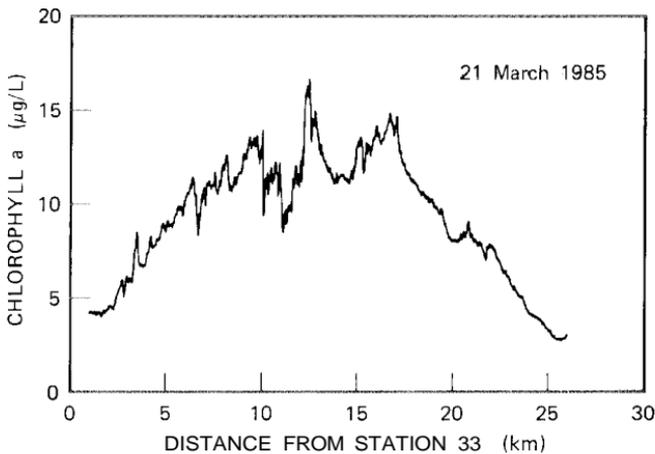


Figure 4 Chlorophyll-a traces along the South Bay Channel (same as Fig. 3, but for spring bloom conditions during 1985).

on the southern and central segments. The northern segment of South Bay was characterized by highly variable salinity, presumably resulting from the tidal advection of water into South Bay from the mixing basin north of the Bay Bridge. We believe much of the spatial variability here results from the incomplete mixing of coastal oceanic water and estuarine waters derived from both the North Bay and South Bay. Because spatial variability in this northern segment may be dominated by circulation and mixing of oceanic and estuarine waters—processes that are complex and not well understood in South San Francisco Bay—we focus our analysis of small-scale variability on the two southern segments which are more representative of resident South Bay water. Moreover, our analysis is restricted to spatial variability of fluorescence, although we recognize the critical need for parallel studies of small-scale salinity variation.

Analysis of small-scale fluctuations focuses on residuals about trends identified as large-scale variability. Figure 5A shows the variability in the fluorescence trace from one representative transect segment (in this case, the southern seg-

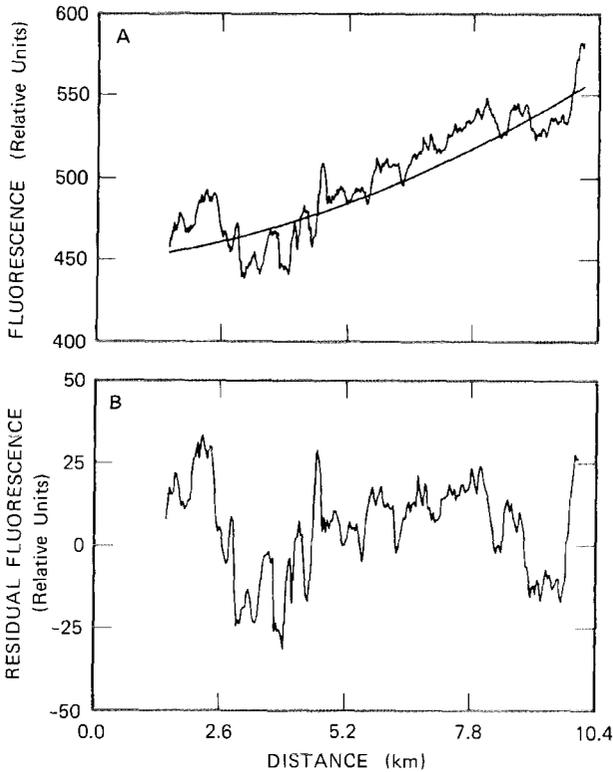


Figure 5. (A) Fluorescence vs. distance for the southern segment of South Bay on 29 March 1985 (ship direction was north to south). Also shown is the quadratic function fitted to the fluorescence. (B) Residuals obtained from the data of (A) by subtracting the fitted quadratic equation from the raw fluorescence data.

ment on 29 March 1985). Also shown is a least squares quadratic fitted through the points. For all but three sampling dates, similar quadratic curves fit the large-scale variation in both the southern and central segments (the coefficient of determination r^2 , averaged over the entire set of transects was ~ 0.73). Residuals in fluorescence were calculated about these least square lines to examine the statistical characteristics of the small-scale fluctuations. The fitting of the quadratic was a simple way of filtering--a high pass filter in this case (Kendall 1976). Figure 5B shows the residuals for the record of Fig. 5A with the large-scale trend removed.

The standard error of the residuals in the southern segment for all 19 transects was consistently larger than the standard error in the central segment. The standard error (SE) = [(variance of the residuals in fluorescence)/(mean fluorescence) 2] $^{1/2}$. The ratio of standard errors, $SE_{\text{south}}/SE_{\text{central}}$ averaged over all 19 transects, was 2.2 ± 0.3 (Fig. 6). This demonstrates quantitatively that the small-scale variability of chlorophyll in the southern segment was higher than that in the central segment, as we saw earlier (Fig. 3). This robust result was violated during the 1985 spring bloom (Fig. 6), again pointing out how anomalous that period is.

The autocorrelation function (ACF) gives further quantitative information about the "patchy" structure of the small-scale variations. The autocorrelation function, the lagged correlation of the spatial record with itself, is a function of lag distance (Kendall 1976; Chatfield 1984). As an example, Fig. 7 shows the autocorrelation function of the residuals from the southern segment on 29 March 1985 (Fig. 5B). The initial exponential decay as a function of lag distance is apparent. For small lag distances, ℓ , all autocorrelation functions (from all transects in both the southern and the central segments) could be fitted by the form

$$\text{ACF}(\ell) = e^{-\ell/\lambda} \quad (1)$$

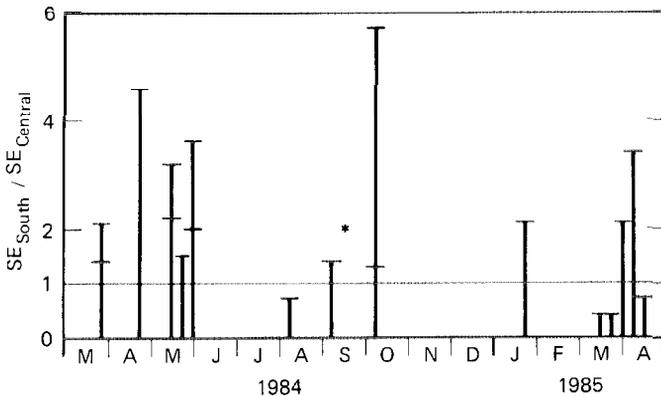


Figure 6. Ratio of the standard error of residuals (e.g., Fig. 5B) for the southern segment to that calculated for the central segment of South San Francisco Bay. Replicate transects were made on four dates.

The average r^2 for all exponential fits was 0.97. Here λ is the distance where the ACF falls to e^{-1} of its value at zero lag ($\bar{\lambda}$ is called the "e-folding length"). We interpret λ as the patch length in an environment in which there is variability at many overlapping (even continuously overlapping) scales. This definition of patch "size" has appeal because it encompasses our intuitive picture of discrete patches. Note that for a tow through a large patch, high phytoplankton biomass would be positively correlated with lagged, but still high, phytoplankton abundances for large distances (i.e., many lags) and therefore lead to large value of λ . The converse would be true for small patches.

The average patch size (λ) in the central segment was 30 lags ($= 0.54$ km), larger than the average patch size in the southern segment, 21 lags ($= 0.38$ km; Fig. 8). Moreover, λ was more than twice as variable in the southern segment than in the central segment: the coefficient of variation for λ in the southern segment was 50%, while in the central segment it was 24%. The impact that spring bloom conditions have upon patch size is unclear. For example, the smallest patches found for all 19 transects were obtained during the early stages of the spring bloom in both 1984 and 1985 in the southern segment - approximately 7 lags ($= 0.13$ km) on 27 March 1984 and 9 lags (approximately 0.17 km) on 14 and 21 March 1985. However, in the central segment during the 1985 spring bloom (Fig. 4), the patch size remained between 27 and 30 lags ($= 0.49$ to 0.54 km), statistically indistinguishable from the annual average of 30 lags (Fig. 8B).

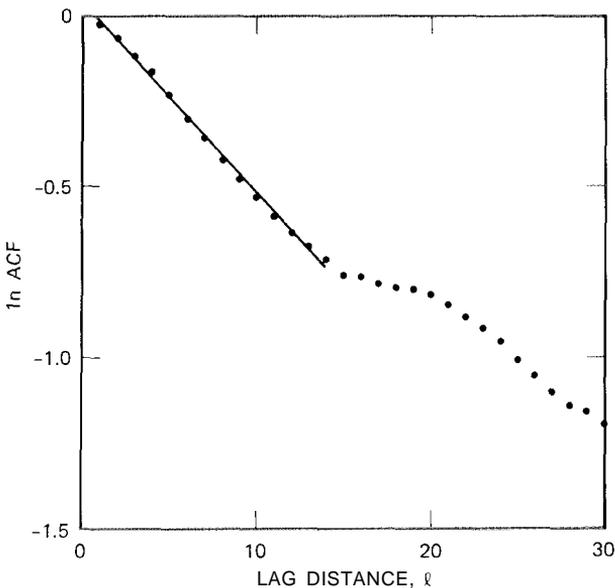


Figure 7. Autocorrelation function (ACF) of the residuals vs. lag distance, for fluorescence data collected in the southern segment on 29 March 1985 (Fig. 5B).

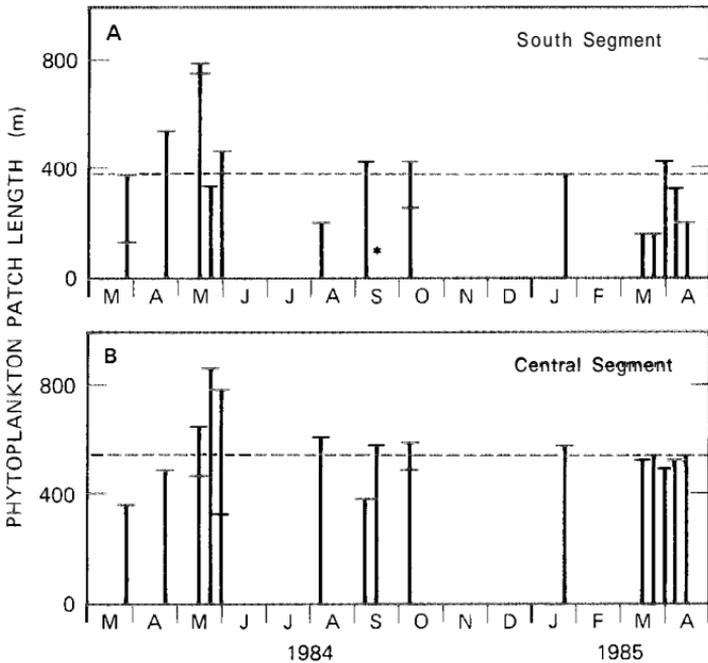


Figure 8. Estimated phytoplankton patch length (λ) in the southern (A) and central (B) segment of South San Francisco Bay during 1984-85. The dashed line shows the mean value of λ in each segment when all transects are averaged.

Discussion

Our analysis of chlorophyll and salinity variability has partially answered the questions posed earlier. First, we have identified two important spatial scales of horizontal variability in the South Bay channel: (1) mesoscale (~ 10 km) variability which suggests that the South Bay is partitioned into three distinct spatial regimes, and (2) small-scale (~ 0.3 - 0.5 km) variability that differs among these spatial regimes. Second, the role of physical processes in determining the mesoscale variability of both chlorophyll and salinity seems plausible, if not proven. In particular, the inferred boundaries between spatial regimes coincide with major topographic features (a shoal to the north and channel constriction to the south) that can induce variability in physical processes. Examples of such processes might be: (1) enhanced vertical mixing caused by the San Bruno shoal; (2) the influence of basin morphometry on residual circulations in the South Bay, including the inferred gyre(s) in the central segment; and (3) the prolonged residence time in the central segment, presumably the result of the interaction between vertical and horizontal transports there. The persistently smooth distributions of salinity and chlorophyll in the central segment could be a direct consequence of the enhanced vertical mixing generated by the San Bruno shoal.

Our picture of three large-scale regimes is supported by additional information. Ambler *et al.* (1985) examined zooplankton distributions in San Francisco

Bay and found a distinct boundary at the San Bruno shoal between a northern zooplankton community that included neritic species (e.g., *Paracalanus parvus*) and a community to the south dominated by estuarine *Acartia* species. They also showed a persistent temperature discontinuity at the San Bruno shoal with cooler temperatures to the north. These discontinuities support our conception of a northern regime with a close coupling to the coastal ocean and a southern regime with its own particular estuarine character, largely derived from the vertical mixing and residual circulations found therein.

That boundaries between large-scale regimes are associated with topographic features is a familiar result from other bodies of water. For example, a model of residual circulation in the North Sea showed several large closed eddies substantially controlled by topography (Nihoul and Rondonay 1975). Nihoul (1975) further demonstrated the importance of such circulations for biological and sedimentary processes with data from a gyre off the Belgian coast that corresponded closely to an eddy in the Nihoul-Rondonay model.

Topographic features may also be important to the small-scale structure observed in the South Bay, but biological processes can be of equal or greater importance. The spatial distribution of phytoplankton is controlled by the simultaneous action of two processes: those that distribute phytoplankton in any body of water, like advection or turbulent diffusion; and those that contribute to in situ gains or losses, like growth, death, sinking, or grazing (Kierstead and Slobodkin 1953; Denman and Platt 1976; Denman et al. 1977; Okubo 1980; Bennett and Denman 1985). The San Bruno shoal causes increased current speeds, leading to increased horizontal (and vertical) shear, turbulence, and diffusion (horizontal and vertical) of substances in the water column. This should increase the size of patches, and could account for the large patch dimensions in the central segment. On the other hand, the large patch sizes in mid-bay could also be explained by biological processes that result in low net growth rates. Small patches which are growing slowly will be rapidly diffused away, so diffusion will only permit large patches which are growing slowly (Okubo 1978). This, if the low chlorophyll levels in the central segment reflect low net growth rate, then the large patch dimensions there could result from low net growth rate. One might speculate, then, that patch sizes should be smallest at the time of the spring bloom when net growth rates increase. This may be true in the southern segment; but, perversely, the patch dimensions in the central segment were remarkably constant during the entire 1985 spring bloom. We note, however, that the spring bloom occurs when vertical stratification is most intense and freshwater infusions can induce an estuarine circulation in the central basin (Walters et al. 1985). Both effects can enhance horizontal transport and mixing, thus increasing the patch size even when growth rate increases.

This paper presents the initial descriptive stages in what we hope will become a detailed analysis of spatial variability in San Francisco Bay. Our preliminary results have defined some robust features of spatial heterogeneity in the South Bay and they have identified specific questions that now should be the focus of future work. The qualitative coupling of topographic features to such

physical processes as mixing, residual circulations, and increased residence time seems straightforward, but the detailed mechanisms allowing such processes to generate the three mesoscale regimes in phytoplankton variability remain to be elucidated. Similarly, mechanisms that permit the persistent chlorophyll minimum in the central region of South Bay cannot be explained from fluorescence records alone. Understanding of this feature will require direct measurement of those biological and physical processes that jointly control phytoplankton biomass. The observation of near-constant phytoplankton patch size in mid-South bay is surprising. Although net rates of phytoplankton growth vary markedly over the annual cycle (Cloern *et al.* 1985), our one measure of spatial heterogeneity (patch size) seems remarkably constant. A related question is why patch sizes are small in the southern segment, both during bloom and non-bloom conditions. Moreover, the relationship of horizontal variability along the axis of the South Bay channel to that transverse to the channel is unexplored. The high degree of small-scale variability in the southern segment could result from the nearness of the narrow channel to the lateral shoals there (Fig. 1). Finally, anomalies associated with the spring bloom (decreased patch size in the southern segment; a chlorophyll maximum in the central basin: the breakdown of the three mesoscale regimes) suggest that the general "rules" governing spatial heterogeneity during most of the year may be changed during the spring bloom. Because the spring bloom coincides with periods of enhanced density stratification, the interactions between vertical and horizontal structure (Okubo 1971; Evans 1978; Kullenberg 1978; Wilson and Okubo 1980) should also be included in more detailed and quantitative studies of spatial variability.

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References Cited

- Abbott, M. R., T. M. Powell, and P. J. Richerson. 1982. The relationship of environmental variability to the spatial patterns of phytoplankton biomass in Lake Tahoe. *J. Plank. Res.* 4:927-941.
- Ambler, J. W., J. E. Cloern, and A. Hutchinson. 1985. Seasonal cycles of zooplankton from San Francisco Bay. *Hydrobiologia* 129:177-198.
- Bennett, A. F., and K. L. Denman. 1985. Phytoplankton patchiness, inferences from particle statistics. *J. Mar. Res.* 43:307-335.
- Bowman, M. B., and W. E. Esaias (eds.) 1978. *Oceanic fronts in coastal processes*. Springer-Verlag, Berlin 114 pp.
- Bowman, M. B., W. E. Esaias, and M. B. Schnitzer. 1981. Tidal stirring and the distribution of phytoplankton in Long Island and Block Island Sounds. *J. Mar. Res.* 39:587-603.
- Chatfield, C. 1984. *The analysis of time series: an introduction* (Third ed.). Chapman and Hall, London. 286 pp.
- Cheng, R. T., and V. Casulli. 1982. On Lagrangian residual currents with application in South San Francisco Bay. *Water Resources Res.* 18:1652-1662.

- Cheng, R. T., and J. W. Gartner. 1985. Harmonic analysis of tides and tidal currents in South San Francisco Bay, California. *Estuar. Coastal Shelf Sci.* 21:57-74.
- Cloern, J. E. 1984. Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, U.S.A.). *Oceanol. Acta* 7:137-141.
- Cloern, J. E., and F. H. Nichols (eds.) 1985. Temporal variability in an estuary: San Francisco Bay. *Developments in Hydrobiology* No. 30. Dr. W. Junk Publisher, The Hague, Neth. 237 pp.
- Cloern, J. E., B. E. Cole, R. L. J. Wong, and A. E. Alpine. 1985. Temporal dynamics of estuarine phytoplankton, a case study of San Francisco Bay. *Hydrobiologia* 129:153-176.
- Conomos, T. J. (ed.) 1979. San Francisco Bay, the urbanized estuary. Pacific Division, Amer. Assoc. Adv. Sci., San Francisco. 493 pp.
- Denman, K. L., and T. Platt. 1976. The variance spectrum of phytoplankton in a turbulent ocean. *J. Mar. Res.* 34:593-601.
- Denman, K. L., A. Okubo, and T. Platt. 1977. The chlorophyll fluctuation spectrum in the sea. *Limnol. Oceanogr.* 22:1033-1038.
- Denman, K. L., and T. M. Powell. 1984. Effects of physical processes on planktonic ecosystems in the coastal ocean. *Oceanogr. Mar. Bio. Ann. Rev.* 22:125-168.
- Evans, G. T. 1978. Biological effects of vertical-horizontal interaction. pp. 157-179. In: Steele, J. H., (ed.), *Spatial pattern in plankton communities*. Plenum, New York. 470 pp.
- Kendall, M. G. 1976. *Time series* (2nd ed.) Griffin, London. 197 pp.
- Kierstead, H., and L. B. Slobodkin. 1953. The size of water masses containing plankton blooms. *J. Mar. Res.* 12:141-147.
- Kullenberg, G. E. B. 1978. Vertical processes and vertical-horizontal coupling, pp. 43-71. In: Steele, J. H., (ed.), *Spatial pattern in plankton communities*. Plenum, New York. 470 pp.
- Lekan, J. F., and R. E. Wilson. 1978. Spatial variability of phytoplankton biomass in the surface water off Long Island. *Estuar. Coastal Mar. Sci.* 6:239-250.
- Lewis, E. L. 1980. The practical salinity scale 1978 and its antecedents. *I.E.E.E. J. Ocean Eng.* OE-5:3-8.
- Lewis, M. R., and T. Platt. 1982. Scales of variability in estuarine ecosystems, pp. 3-20. In: Kennedy, V. S. (ed.), *Estuarine Comparisons*. Academic Press, New York.
- Lorenzen, C. J. 1967. Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnol. Oceanogr.* 12:343-346.
- Mackas, D., K. L. Denman, and M. R. Abbott. 1986. Patchiness: biology in the physical vernacular. *Bull. Mar. Sci.* (in press).
- Nihoul, J. C. 1975. Effect of the tidal stress on residual circulation and mud deposition in the Southern Bight of the North Sea. *Pure Appl. Geophys.* 113:577-581.
- Nihoul, J. C., and F. C. Ronday. 1975. The influence of the "tidal stress" on the residual circulation. application to the Southern Bight of the North Sea. *Tellus*, 27:484-490.
- Okubo, A. 1971. Horizontal and vertical mixing in the sea. pp. 89-168. In: Hood, D. W., (ed.), *Impingement of man on the Oceans*. Wiley-Interscience, New York.
- Okubo, A. 1978. Horizontal dispersion and critical scales for phytoplankton patches, pp. 21-42. In: Steele, J. H., (ed.), *Spatial pattern in plankton communities*. Plenum, New York.
- Okubo, A. 1980. Diffusion and ecological problems: mathematical models, vol. 10 *Biomathematics*. Springer-Verlag, Berlin. 254 pp.
- Platt, T. 1972. Local phytoplankton abundance and turbulence. *Deep-Sea Res.* 19:183-187.
- Platt, T., L. M. Dickie, and R. W. Trites. 1970. Spatial heterogeneity of phytoplankton in a near-shore environment. *J. Fish. Res. Bd. Canada*. 27:1453-1473.
- Schemel, L. E., and L. A. Dedini. 1979. A continuous water-sampling and multiparameter system for estuaries. U.S. Geol. Survey *Open-File Rep.* 79-272.

- Tyler, M. A., and H. H. Seliger. 1978. Annual subsurface transport of a red tide dinoflagellate to the bloom area: water circulation patterns and organism distributions in the Chesapeake Bay. *Limnol. Oceanogr.* 23:227-246.
- Tyler, M. A., and H. H. Seliger. 1981. Selection for a red tide organism: physiological responses to the physical environment. *Limnol. Oceanogr.* 26:310-324.
- Walters, R. A. 1982. Low-frequency variations in sea level and currents in South San Francisco Bay. *J. Phys. Oceanogr.* 12:658-668.
- Walters, R. A. and R. T. Cheng. 1980. Calculations of estuarine residual currents using the finite element method pp 60-69. In D. H. Norris (ed.) *Proceedings Third Int. Conf. Finite Elements in Flow Problems*. University of Calgary, Calgary, Alberta, Canada.
- Walters, R. A., and J. W. Gartner. 1985. Subtidal sea level and current variations in the northern reach of San Francisco Bay. *Estuar. Coastal Shelf Sci.* 21:17-32.
- Walters, R. A., R. T. Cheng, and T. J. Conomos. 1985. Time scales of circulation and mixing processes of San Francisco Bay waters. *Hydrobiologia* 129:13-36.
- Wilson, R. E., and A. Okubo. 1980. Effects of vertical-horizontal coupling on the horizontal distribution of chlorophyll *a*. *J. Plank. Res.* 2:33-47.
- Wilson, R. E., A. Okubo, and W. E. Esaias. 1979. A note on time-dependent spectra for chlorophyll variance. *J. Mar. Res.* 37:485-491.