Time scales and mechanisms of estuarine variability, a synthesis from studies of San Francisco Bay

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Abstract

This review of the preceding papers suggests that temporal variability in San Francisco Bay can be characterized by four time scales (hours, days-weeks. months, years) and associated with at least four mechanisms (variations in freshwater inflow, tides, wind, and exchange with coastal waters). The best understood component of temporal variability is the annual cycle, which is most obviously influenced by seasonal variations in freshwater inflow. The winter season of high river discharge is characterized by: large-scale redistribution of the salinity field (e.g. the upper estuary becomes a riverine system); enhanced density stratification and gravitational circulation with shortened residence times in the bay; decreased tissue concentrations of some contaminants (e.g. copper) in resident bivalves; increased estuarine-inputs of river-borne materials such as dissolved inorganic nutrients (N. P, Si), suspended sediments, and humic materials; radical redistributions of pelagic organisms such as copepods and fish; low phytoplankton biomass and primary productivity in the upper estuary; and elimination of freshwater-intolerant species of macroalgae and benthic infauna from the upper estuary. Other mechanisms modulate this river-driven annual cycle: (I) wind speed is highly seasonal (strongest in summer) and causes seasonal variations in atmosphere-water column exchange of dissolved gases, resuspension, and the texture of surficial sediments; (2) seasonal variations in the coastal ocean (e.g. the spring-summer upwelling season) influence species composition of plankton and nutrient concentrations that are advected into the bay; and (3) the annual temperature cycle influences a few selected features (e.g. production and hatching of copepod resting eggs). Much of the interannual variability in San Francisco Bay is also correlated with freshwater inflow: wet years with persistently high river discharge are characterized by persistent winter-type conditions.

Mechanisms of short-term variability are not as well understood, although some responses to storm events (pulses in residual currents from wind forcing, erosion of surficial sediments by wind waves, redistribution of fish populations) and the neap-spring tidal cycle (enhanced salinity stratification, gravitational circulation, and phytoplankton biomass during neap tides) have been quantified. In addition to these somewhat predictable features of variability are (1) largely unexplained episodic events (e.g. anomalous blooms of drift macroalgae), and (2) long-term trends directly attributable to human activities (e.g. introduction of exotic species that become permanent members of the biota).

Introduction

Estuaries are strongly influenced by temporally variable events occurring at their riverine and oceanic boundaries as well as those impinging on the water surface. For example, the river system is affected by variations in precipitation and the coastal ocean by variations in wind patterns. Estuarine responses to this temporal variability are complex and often difficult to understand simply from field

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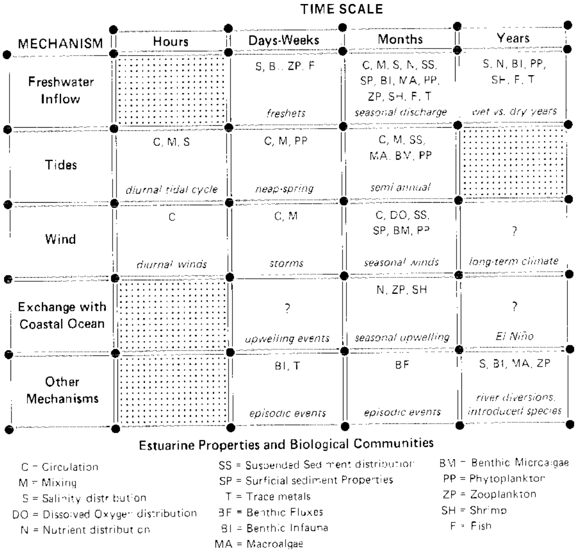
observations. especially in a large estuary like San Francisco Bay with geographically and morphologically distinct sub-basins. Nevertheless, a number of observations and insights have allowed identification of some of the important time scales and associated mechanisms of temporal variability in San Francisco Bay, many of which may apply to other estuaries.

Fig. 1 represents a summary of the important concepts presented in this volume. It identifies four time scales and five mechanisms of temporal variability, organized as a matrix with entries showing those processes or properties that have been studied in San Francisco Bay. It is apparent from the number of entries in this matrix that our best understanding is of the mechanisms of seasonal (monthly) variability, that is. events and processes associated with an annual cycle. This emphasis reflects both the relative infancy of comprehensive, long-term research in San Francisco Bay and the fact that initial stages of field-oriented research are logically focused on the annual cycle. Less is known about interannual variability, although we have had an opportunity over the past decade to make observations during hydrologically extreme years. the 1976–77 drought and the exceptionally wet years of 1982–83. Even less is known about short-term variability, although we have identified some responses to storm events and the semi-diurnal and neap-spring tidal cycles.



TIME SCALE

MECHANISM	Hours	Days-Weeks	Months	Years
Freshwater Inflow	▨	S, B., ZP, F *freshets*	C, M, S, N, SS, SP, BI, MA, PP, ZP, SH, F, T *seasonal discharge*	S, N, BI, PP, SH, F, T *wet vs. dry years*
Tides	C, M, S *diurnal tidal cycle*	C, M, PP *neap-spring*	C, M, SS, MA, BM, PP *semi annual*	▨
Wind	C *diurnal winds*	C, M *storms*	C, DO, SS, SP, BM, PP *seasonal winds*	? *long-term climate*
Exchange with Coastal Ocean	▨	? *upwelling events*	N, ZP, SH *seasonal upwelling*	? *El Niño*
Other Mechanisms	▨	BI, T *episodic events*	BF *episodic events*	S, BI, MA, ZP *river diversions, introduced species*

Estuarine Properties and Biological Communities

C = Circulation
M = Mixing
S = Salinity distribution
DO = Dissolved Oxygen distribution
N = Nutrient distribution
SS = Suspended Sediment distribution
SP = Surficial sediment Properties
T = Trace metals
BF = Benthic Fluxes
BI = Benthic Infauna
MA = Macroalgae
BM = Benthic Microalgae
PP = Phytoplankton
ZP = Zooplankton
SH = Shrimp
F = Fish

Fig. I. Matrix showing time scales and mechanisms of estuarine variability. Entries in each box represent properties or biological communities that have been studied in San Francisco Bay.

Our objective here is to summarize results from preceding papers that illustrate the nature of temporal variability in San Francisco Bay. We use Fig. 1 as a frame of reference for this discussion, and begin with a generalized description of the annual cycle.

The annual cycle

Freshwater inflow

Annual cycles in estuaries are partly driven by cyclic variations in energy sources such as freshwater inflow, tides, winds, and insolation (Fig. 2). For San Francisco Bay, the seasonal variation of freshwater inflow (synonymous in this volume with 'river discharge' and 'Delta discharge') is the most obvious and extensive mechanism of temporal variability: virtually every process or property studied in the bay has a seasonal component of variability related to the seasonal variation of river inflow (Fig. 1).

The great importance of river flow to variability in San Francisco Bay is a consequence of two features that may be partly specific to this estuary. First, the region has a Mediterranean climate in which the year is partitioned into two hydrologic seasons, wet and dry. This partitioning contributes to a natural experimental research design in which measurements can be made when freshwater inflow is 'on' or 'off. Second, the range of variation in freshwater inflow is much greater than that of other mechanisms shown in Fig. I. Inflow from the Sacramento-San Joaquin Rivers can vary by about a factor of 100 (100 10,000 $m^3 s^{-1}$; Fig. 2A), in contrast to tidal currents whose daily maximum speed varies by a factor of 3 (about 1–3 $m s^{-1}$), daily wind speed that varies by a factor of 10 (0.5–5 $m s^{-1}$; Fig. 2C), water temperature that varies by a factor of 2 (10–20 °C), and daily insolation that varies by about a factor of 10 (6 60 Einsteins $m^{-2} d^{-1}$; Fig. 2E). System-wide responses to the annual hydrologic cycle are evident from comparisons of estuarine properties during the dry and wet seasons.

The dry season. From about May through October precipitation ceases in central California, run-

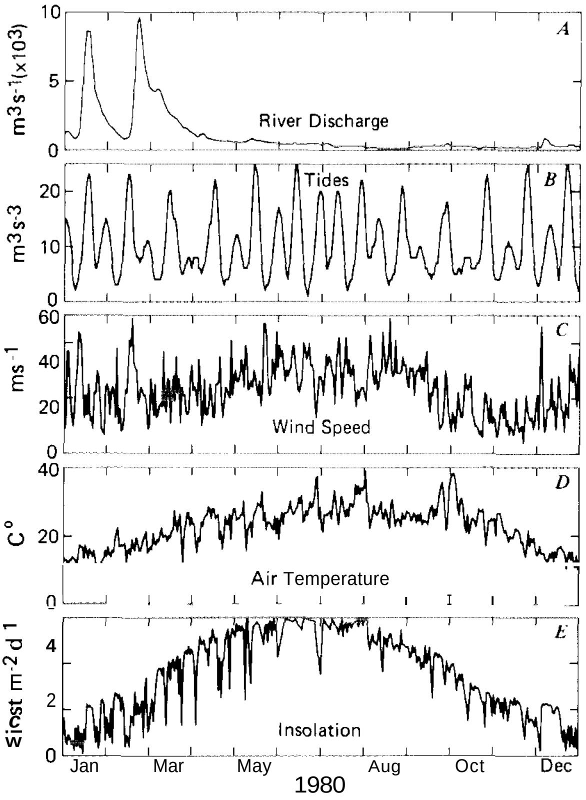


Fig. 2. Typical seasonal patterns in the forcing mechanisms that induce variability in San Francisco Bay.

off from small tributaries is negligible (Conomos et al., Fig. 9B) and discharge of the Sacramento-San Joaquin Rivers is typically less than 500 m^3 s^{-1} (Cloern *et* al., Fig. 8B). During this stable dry season saltwater penetrates upstream to the confluence of the rivers, and Northern San Francisco Bay is partially mixed with a well-defined turbidity maximum in Suisun Bay (Conomos *et al.*, Fig. 13). Vertical salinity gradients are small, and the horizontal density gradient drives a slow gravitational circulation with mean current speeds of about 10 cm s^{-1} (Walters *et al.*, Figs. 7A-7C). South San Francisco Bay is nearly isohaline with salinity ranging between 25-30‰, and mean circulation there results primarily from wind stress and tidally-driven residual flows having current speeds of a few centimeters per second, such that residence time is on the order of months (Walters et *al.*, Table 2). The dry season is characterized by low input of river-derived sediments. Suspended sediment concentrations range from 20 to >100 mg l^{-1} in the northern reach and are typically <30 mg l^{-1} in South Bay (Conomos et *al.*, Fig. 13). Riverine inputs of nutrients (N, P, Si) are also low, and concentrations can be affected by nutrient sinks (e.g. phytoplankton uptake). Thus horizontal nutrient distributions in the northern reach are typical of nonconservative constituents, and localized depletions of nutrients can occur (see Peterson *et al.*, Figs. 6–9).

Sustained periods of low discharge allow the upstream migration of marine-estuarine species of macroalgae and benthic infauna, and summer is the season of maximum biomass and diversity of macroalgae (Josselyn & West, Figs. 4, 5). Phytoplankton communities include neritic and estuarine species (e.g. *Skeletonema costatum* and *Thalassiosira decipiens*). Biomass is high (≅30–40 mg m^{-3} chlorophyll a) in Suisun Bay because gravitational circulation enhances the residence time of planktonic diatoms there (Cloern et *al.*). However phytoplankton biomass is seasonally minimal (<5 mg m^{-3} chlorophyll a) in South Bay, presumably because of rapid consumption by benthic infauna when the water column is vertically mixed. The zooplankton community includes sequential populations of different copepod species along the horizontal salinity gradient of the North Bay: Sinocalanus doerrii occurs near the estuary head, *Eurytemora affinis* occurs in Suisun Bay, Acartia spp. dominate in San Pablo Bay, and neritic species (e.g. *Paracalanus parvus*) are found near the estuary mouth. In South Bay, the macrozooplankton community is dominated only by Acarria *californiensis*, presumably because of the homogeneous salinity distribution there.

The *wet* season. The onset of precipitation in winter causes a large increase in river inflow (and inputs of watershed materials) that is sustained for months, and discrete peaks in the hydrograph associated with storms (Fig. **2A).** The physical character of the bay changes in response to high winter river flow as follows: the salinity field is rapidly altered, first in the North Bay and subsequently in South Bay following sustained high discharge. Salinity of the upper estuary (Suisun Bay) falls from 5–10‰ during summer-autumn to zero (Conomos et *al.*, Fig. 12) while surface salinity in South Bay can fall below 15‰ during wet winters (Armor & Herrgesell, Fig. 3). High freshwater flows result in enhanced salinity stratification during winter-spring in North Bay, and a salt wedge during extreme floods (Walters et al.). Gravitational circulation is also enhanced, most obviously in the upper estuary where winter peaks in discharge generate rapid currents (up to 50 cm s^{-1}). As a result the advective residence time is reduced from months to days (Walters et *al.*, Table 2).

Winter high flows also affect circulation in South Bay. The first winter peaks in river discharge depress salinity of Central Bay below that of South Bay, creating a horizontal density gradient that drives surface flows into South Bay and seaward flows at depth. Conversely, when river discharge recedes in spring and salinity increases in Central Bay, the horizontal density gradient and gravitational circulation reverse: surface currents then flow seaward and saltwater intrudes at depth (Walters et al.). Hence mean circulation in South Bay is highly dynamic during the wet season, and density-driven currents (which are absent in summer) enhance mixing rates between South Bay and Central Bay, perhaps by a factor of 3–10 (Walters et *al.*). This accelerated mixing in winter may partly explain the seasonal variations in trace metal contamination of benthic infauna: minimum concentrations of copper and silver in South Bay clams were consistently observed during winter (Luoma et *al.*, Figs. 2, 6) when mixing rates are rapid.

The wet season is further characterized by increased inputs of river-borne constituents such as nutrients, suspended sediments, and humic materials. Dissolved inorganic N, P, and Si have conservative distributions in the upper estuary and minimum winter concentrations are 15 μM, 1–2 μM, and about 50 μM respectively (Peterson et al., Fig. 5). Suspended sediment concentrations increase to the range of 60 to >200 mg l^{-1} in the upper estuary and 40 to about 100 mg l^{-1} in South Bay (Conomos *et al.*, Fig. 12), thus reducing light penetration. A seasonal deposition of river-derived fine-grain sediments onto mudflats also occurs in San Pablo Bay (Nichols & Thompson, Fig. 2B) and in South Bay (Thomson-Becker & Luoma, Fig. 3). accompanied by an increase in organic carbon in the sediments (Thomson-Becker & Luoma, Fig. 7).

Winter-spring increases in river discharge also influence biological communities. For example, pelagic species such as the copepods *Eurytemora affinis* and *Sinocalanus doerrii* are advected (as far as 40 km) downstream in the North Bay following winter floods (Ambler et *al.*, Fig. 4). Ovigerous females of the bay shrimp Crangon *franciscorum*, a species that prefers salinities between 0.5 and 20‰, are most abundant near the mouth of the bay during winter, then migrate into North Bay during summer as freshwater inflow declines and salt intrudes upstream (Hatfield, Fig. 2). Some species of pelagic fish (e.g. northern anchovy) are completely displaced from the upper estuary, whereas some marine demersal species (e.g. English sole) move into the bay from offshore following large peaks in freshwater inflow (Armor & Herrgesell, Figs. 5, 6). Freshwater intolerant benthic organisms are eliminated from the upper estuary as salinity is reduced during winter. For example, the amphipod *Ampelisca abdita* may initially respond to lowered salinity by migrating to deeper water or moving downstream: eventually the abundance of Ampelisca declines baywide during winter, perhaps due to lowered salinity as well as to natural mortality that follows annual reproduction (Nichols & Thompson, Fig. 6). There is also a marked reduction in the number of macroalgal species during winter, mostly due to the intolerance of marine species to low salinity (Josselyn & West). Phytoplankton biomass and primary productivity are persistently low in the upper estuary during winter when residence time is short and growth rate is severely light-limited by high turbidity (Cloern et al., Figs. 6, 7). On the other hand, phytoplankton biomass in the South Bay is seasonally maximal (≅25 mg m^{-3} chlorophyll a) during spring (Cloern *et al.*, Fig. 5) when the water column is stratified.

Other *mechanisms*

Superimposed on the river-driven seasonality are other sources of variability contributing to an annual cycle. Local winds, for example, are consistently strong in summer but calm in autumn (Fig. 2C; see also Conomos *et* al., Fig. 6). Wind shear is a dominant control on gas exchange between the water column and atmosphere, so the residence time of dissolved gases (e.g. oxygen) in the water column ranges from about 2 days during windy summer periods to about 15 days during calm winter periods (Hartman & Hammond, Fig. 1). There also appears to be an annual cycle in the rate of bottom-sediment resuspension that results from simultaneous maxima in wind and tidal current speeds during summer (Nichols & Thompson, Fig. 3). This seasonal enhancement of suspended-sediment load, evidenced by mid-summer maxima in turbidity over the broad shoals, reduces light availability and phytoplankton growth rates (e.g. Cloern *et al.*, Figs. 6B, E).

Seasonality of resuspension also influences the partitioning of microalgae (especially diatoms) between the water column and benthos: chlorophyll a concentrations in Suisun Bay are high in the water column and low in the surficial sediments during summer, but they decrease in the water column (from 40 to 10 mg m ^{3}) and simultaneously increase in the sediments (from about 100 to >200 mg m ^{2}) during autumn. This suggests that wind-driven resuspension sustains high biomass in the water column during summer. whereas reduced turbulence during autumn enhances the vertical flux of diatoms to the benthos (Nichols & Thompson; Cloern *et* al.). Other sediment properties vary with seasonal wind mixing as well: grain size of surficial sediments increases during summer (Thomson-Becker & Luoma, Figs. 3, 4; Nichols & Thompson, Fig. 2), and the organic content of surficial sediments can vary seasonally with organic-rich sediments (up to about 2% organic carbon by weight) occurring during the calm periods (autumn, winter) and organic-poor sediments (down to 0.5% organic carbon) occurring during summer (Thomson-Becker & Luoma, Fig. 7).

Seasonal variability of the tides is another mechanism of the annual cycle due to the semi-annual component of tidal variability such that weakest tides occur in April and October while strongest tides occur in January and June (Fig. 2B). The resultant seasonal differences in current speed have implications for vertical mixing and the nature of residual circulation: density stratification and gravitational circulation are enhanced during periods of weak tidal mixing (spring and autumn) but tidally-driven residual flow becomes an important mechanism of circulation during winter and summer when tidal currents are strongest (Walters *et* al.). Low-frequency tidal variations also have an interesting interaction with the photoperiod that governs daily light exposure of intertidal mudflats. During spring, lowest tidal elevation occurs at daylight whereas during autumn it occurs at night. Hence, the intertidal zone receives the greatest exposure to sunlight in spring-summer (Nichols & Thompson. Fig. 3), and this partly explains why the annual maximum of macroalgal biomass occurs at mid-year (Josselyn & West, Fig. 6).

Another potential, but largely unexplored source of intra-annual variability in San Francisco Bay is the seasonal variation in nearshore oceanic circulation. During summer northwest winds drive the southerly-flowing California Current and induce coastal upwelling. During winter the winds originate from the south. causing the northerly-flowing Davidson Current to move near shore, and upwelling ceases (Conomos *et al.*). Hence, coastal waters that mix into San Francisco Bay have a different source and composition during the upwelling and non-upwelling seasons. The coastal ocean can be a source of nitrate during the summer upwelling season (Peterson *et* al.) when NO_3 concentrations at the estuary mouth approach 25 μM (this contrasts with NO_3 concentrations less than 5 μM during winter). Zooplankton community composition is also influenced by seasonal changes in coastal circulation: the neritic copepod Paracalanus *parvus* (a warm-water species) can be abundant in Central San Francisco Bay, but only during the autumn and winter when coastal waters originate from the south; copepods with northern zoogeographic affinities are present in the bay during summer when coastal currents flow south (Ambler *et al.*). Shrimp life cycles also involve migrations between the bay and coastal waters (e.g. larvae are advected seaward in the surface layer and juveniles are advected into the bay with bottom currents). particularly during spring when females and larvae are centered in coastal waters outside the Golden Gate just prior to the timing of peak recruitment to the bay (Hatfield).

Compared to mechanisms described above, the annual temperature cycle is not a major source of temporal variability for geochemical or biological processes in San Francisco Bay. This contrasts with results from other temperate estuaries, and is a consequence of the small annual temperature range here (about 10 to 20 °C). Among the few seasonally varying processes observed to be temperature-related are: (1) the seasonal succession of two copepod (Acartia) species that presumably results from the temperature-dependent production and hatching of resting eggs (Ambler *et al.*); (2) the small effect of seasonal temperature variations on atmospheric gas exchange (Hartman & Hammond, Fig.

4); and (3) the effect of seasonal temperature variations on macroalgal growth rate (Josselyn & West). Otherwise, temperature variation has been excluded as an important driving force in this estuary. Seasonal variations in rates of benthic exchange in South Bay were attributed to other mechanisms; for example, the increased rate of silica regenerationduring early summer was attributed to the input of fresh biogenic silica following the spring phytoplankton bloom (Hammond *et al.*). And growth in a number of benthic invertebrates, limited in most cases to a short period in spring, is probably keyed to food availability rather than to temperature (Nichols & I hompson).

Interannual variations

Responses ro annual variations in river discharge

Results from the few long-term studies show that the chemistryand biology of San Francisco Bay can vary markedly among years, and that most interannual (like seasonal) variability is attributable to variations in precipitation and freshwater inflow (Fig. 1). Our best understanding, from a long-term perspective, is of the annual patterns in nutrient distributions of the North Bay. A partitioning of the past two decades into 'wet', 'dry', and 'very dry' years, illustrates that each water-year type is characterized by distinct nutrient distributions (Peterson *et al.*, Figs. 6–9). During wet years (when combined discharge of the Sacramento-San Joaquin Rivers persistently exceeds about 500 $m^3 s^{-1}$), distributions of nitrate, phosphate, and silicate are often near-linear with respect to salinity (conservarive behavior) because biological processes of removal are small relative to the large riverine source of N, P, and Si. During dry years (discharge $<200 m^3 s^{-1}$), nutrient distributions are nonconservative in summer because of a shift in the balance between the source and sink terms. For example, ammonia depletion can occur during summer of dry years but not wet years. During very dry years (summer discharge $\cong 100 m^3 s^{-1}$), nutrient concentrations increase and distributions become conservative again, reflecting low phytoplankton biomass. Hence, nutrient distributions are directly coupled, in a nonlinear fashion, to the magnitude of annual freshwater inflow.

Much of the interannual variability of phytoplankton biomass is also coupled to annual variations in freshwater inflow. During hydrologically extreme years (the 1976–77 drought and the very wet year of 1982), the 'typical' summer phytoplankton bloom was absent from Northern San Francisco Bay (Cloern *et al.*, Fig. 8A). This observation supports the hypothesis that river-induced gravitational circulation is necessary for the summer biomass accumulation there: during wet years phytoplankton are rapidly advected downstream, whereas during very dry years planktonic diatoms are concentrated upstream in the deeper river where light becomes limiting (Cloern *et al.*). Phytoplankton dynamics in South Bay are influenced in a very different manner by interannual variations in freshwater inflow: blooms occur there only during periods of salinity stratification, and the intensity of stratification is directly related to the rate of freshwater inflow. Hence, years of high freshwater inflow are characterized by intense spring blooms of long duration (months), and years of low discharge by ephemeral blooms. Long-termand baywide studies of other pelagic communities have not been done in San Francisco Bay, but results from a three-year study do show that abundance of many fish populations (including marine species) and the shrimp *Crangon franciscorum* appear to increase during wet years (Armor & Herrgesell; Hatfield).

The distribution of benthic organisms also varies with annual river discharge, largely in response to salinity distribution, but perhaps to circulation as well. The amphipod *Ampelisca abdita* was eliminated from a South Bay mudflat during years of unusually prolonged high freshwater inflow (1974 and 1982), while the bivalve *Macoma balthica* increased in abundance during those pears. A competitive interaction between these two species, resulting in poor recruitment of *Macoma* during normal and dry years when *Ampelisca* is abundant, may be partially responsible (Nichols & Thompson. Fig. 9). The persistently low freshwater inflow and increased salinity in the upper estuary during the 1976–77 drought permitted the temporary colonization of Suisun Bay sediments by freshwater-intolerant species (e.g. *Mya arenaria)* usually restricted to the lower estuary (Nichols & Thompson, Fig. 8). Conversely, brown (Phaeophyta) and red (Rhodophyta) macroalgae were eliminated from San Pablo Bay during the wet years of 1982 and

1983 because of the persistently low salinity there.

Conceptual models suggest that circulation and mixing processes in San Francisco Bay should also vary among years in response to annual variations in freshwater inflow (Walters et *al.*). Although this is, as yet, an untested hypothesis, we do know that the duration and intensity of stratification events in South Bay are greatly enhanced during wet years, and that density-driven currents and horizontal mixing accelerate (residence time decreases) when the South Bay is stratified (Walters et *al.*). Interannual variations in circulation and mixing may play an important role in determining the exposure of estuarine biota to contaminants. For example, body burdens of silver in South Bay populations of bivalves are low (50 ppm) during wet years and higher (about 200 ppm) during dry years when water residence time is long (Luoma et ul.. Fig. 9). Bioaccumulation of trace metals by benthic infauna is further influenced by physico-chemical properties of sediments, which also vary among years. For example, the eight-year record of measurements on a South Bay mudflat shows large differences among years in winter concentrations of extractable organic material (i.e. humic materials) and iron in surficial sediments (Thomson-Becker & Luoma, Fig. 11).

Other *mechanisms*

Other sources of interannual variability for San Francisco Bay are not well defined (Fig. 1). This is the'case, in part because most long-term, baywide research programs have begun only in the past decade, and in part because this decade was characterized by extreme annual variations in river discharge (severe drought and major floods) that may have masked other sources of annual variability. We know, from seasonal studies, that the coastal ocean can influence nutrient distributions and biological communities in San Francisco Bay. It is likely, then. that large-scale climate forcing of the ocean (e.g. El Niño events) is another important mechanism of long-term temporal variability in the bay, but this coupling has not been explored.

In addition to the (mostly) predictable responses to river discharge described above, San Francisco Bay also experiences year-to-year variability in the form of aperiodic and largely unexplained events, such as: (1) a massive bloom of the drift macroalga *Cladophora* sericea in the North Bay during 1979 (Josselyn & West); (2) the previously unreported observation of a red tide (*Prorocentrum* sp.) localized in the San Pablo Bay channel during 1983 (H. Proctor. pers. comm.); and (3) unusually high abundances of the ctenophore Pleurobrachia *bachei* in South Bay during spring 1985 (S. Hatfield, pers. comm.). Although the mechanisms of these annual anomolies are unknown, episodic events are an important feature of interannual variability that can have ramifications for other estuarine processes. As one example, the intertidal benthic community of a South Bay mudflat was greatly altered during 1975 following an unusual bloom of the drift macroalga *Polysiphonia* denudata, that was deposited as a mat on the sediment surface. Decomposition of the algal mat (1) produced anoxia at the sediment surface and eliminated or severely depleted infaunal populations for months (Nichols & Thompson), and (2) altered sediment trace metal geochemistry: highly elevated concentrations of copper were observed in the tissues of *Macoma* balthica, presumably because the anoxia mobilized sediment-bound copper into a form with high bioavailability (Luoma et *al.*).

Long-term trends

In addition to the interannual variability associated with climate forcing. which we perceive as cyclical in nature, San Francisco Bay (like other estuaries) has experienced long-term changes that are more permanent. Many of these are directly attributable to human activities. For example, a major source of long-term biological change has been the introduction of exotic plants and animals: most of the benthic infauna in the bay comprises species that have been sporadically introduced over the past 130 years (Nichols & Thompson); introduced macroalgal species are prominant in the bay (Josselyn & West); some fish species (including the striped bass. *Morone saxatilis*) are introduced; finally, the recent introduction of the copepod *Sinocalanus* doerrii has resulted in the displacement of native copepod species in the upper estuary and demonstrates that this mechanism of change is ongoing (Ambler et al.). Some physical and chemical attributes of the bay have changed over the long term as well. Freshwater inflow has been gradually reduced as water was impounded upstream of the estuary, primarily for irrigation (Conomos *et al.*), and the rivers and bay have been used for the disposal of human, industrial and agricultural wastes (e.g. Luoma *et al.*). These changes, presumably with long-term consequences, are now the focus of intensified study.

Higher frequency variation

Most research in San Francisco Bay has addressed questions about large-scale spatial variability and long-term (>weeks) temporal variability with an under-representation of short-term processes. However, the significance of seasonal or annual variations cannot be assessed without comparing these to the variability on short time scales (e.g. the tidal cycle) or the variability caused by single events (e.g. storms). One component of short-term variability that has been examined is that occurring as a result of the neap-spring tidal cycle. Studies of circulation and mixing show that: (I) mean tidal current speed in San Francisco Bay can vary from about 20–50 cm s^{-1} over the fortnightly neap-spring cycle (Walters *et al.*, Fig. 11): (2) the tidal excursion increases from about 7 km on neap tides to about 13 km on spring tides in the South Bay channel; (3) vertical mixing rates vary by a factor of two to three over the neap-spring cycle; (4) density-driven residual flows accelerate (from about 1–2 to 15 cm s^{-1} in South Bay) during neap tides when vertical mixing is reduced; and (5) extreme weekly variations in vertical salinity stratification can occur in South Bay (Walters *et al.*, Fig. 14). Phytoplankton biomass increases rapidly in the surface layer of South Bay during stratification events, thus neap-spring effects on water column stability are an important cause of daily to weekly variability of phytoplankton biomass there (Cloern *et al.*).

Some physical processes respond to storm events that typically persist for a period of several days. For example, decreases in atmospheric pressure cause rises in sea level on the order of 20–30 cm (Walters *et al.*, Fig. 3A), and radical shifts in wind speed and direction during storms exert a large influence on residual circulation: current pulses in the South Bay (where mean speed approximately doubled) were highly correlated with wind stress (Walters *et al.*, Fig. 11). Little is known about the responses of biological communities or geochemical processes to storm events, except observations of short-term disturbances of the benthic habitat (e.g. an event in which surficial sediment of a mudflat was eroded 8 cm between monthly sampling); such disturbances are one of the important mechanisms of temporal change in benthic community structure (Nichols & Thompson).

Gaps in our understanding

This volume is not intended as a final or definitive discussion of temporal variability in the San Francisco Bay estuary. While many aspects of the estuarine ecosystem have been covered in the papers of this volume, large gaps remain in our understanding of how the bay functions and the contribution of natural variability to those functions. An important purpose of this volume, in addition to providing a summary from which workers in other estuaries can draw parallels or contrasts, is to identify areas where further research should now be addressed. Obvious problems related to the topic of temporal variability include: (I) the characterization of circulation and mixing processes during wet and dry years, particularly with respect to estimating residence times or flushing rates: (2) the pattern of sediment resuspension and transport during the semi-diurnal tidal cycle and during discrete winter storms; (3) the influence of freshets on geochemical characteristics and biotic distributions; (4) all aspects of coupling between the bay and coastal ocean; and (5) the significance of short-term variability. The summary of studies to date (Fig. I) further shows that there are important estuarine properties which, for San Francisco Bay, remain almost completely unstudied. These include sediment dynamics and transport, primary production of benthic microalgae, virtually all aspects of microbial ecology and biogeochemistry, the nature and role of microzooplankton, sources and fates of toxic contaminants (particularly organic compounds). nutrient budgets, and riverine inputs of organic material. Finally. although much of the research in San Francisco Bay has been descriptive in nature, it has been most useful in formulating hypotheses. We anticipate that the next decade will see more emphasis on process-oriented research designed to test these hypotheses.

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