PHYTOPLANKTON BLOOM DYNAMICS IN COASTAL ECOSYSTEMS: A REVIEW WITH SOME GENERAL LESSONS FROM SUSTAINED INVESTIGATION OF SAN FRANCISCO BAY, CALIFORNIA

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Abstract. Phytoplankton blooms are prominent features of biological variability in shallow coastal ecosystems such as estuaries, lagoons, bays, and tidal rivers. Long-term observation and research in San Francisco Bay illustrates some patterns of phytoplankton spatial and temporal variability and the underlying mechanisms of this variability. Blooms are events of rapid production and accumulation of phytoplankton biomass that are usually responses to changing physical forcings originating in the coastal ocean (e.g., tides), the atmosphere (wind), or on the land surface (precipitation and river runoff). These physical forcings have different timescales of variability, so algal blooms can be short-term episodic events, recurrent seasonal phenomena, or rare events associated with exceptional climatic or hydrologic conditions. The biogeochemical role of phytoplankton primary production is to transform and incorporate reactive inorganic elements into organic forms, and these transformations are rapid and lead to measurable geochemical change during blooms. Examples include the depletion of inorganic nutrients (N, P, Si), supersaturation of oxygen and removal of carbon dioxide, shifts in the isotopic composition of reactive elements (C, N), production of climatically active trace gases (methyl bromide. dimethylsulfide), changes in the chemical form and toxicity of trace metals (As, Cd. Ni, Zn), changes in the biochemical composition and reactivity of the suspended particulate matter, and synthesis of organic matter required for the reproduction and growth of heterotrophs, including bacteria, zooplankton, and benthic consumer animals. Some classes of phytoplankton play special roles in the cycling of elements or synthesis of specific organic molecules, but we have only rudimentary understanding of the forces that select for and promote blooms of these species. Mounting evidence suggests that the natural cycles of bloom variability are being altered on a global scale by human activities including the input of toxic contaminants and nutrients, manipulation of river flows, and translocation of species. This hypothesis will be a key component of our effort to understand global change at the land-sea interface. Pursuit of this hypothesis will require creative approaches for distinguishing natural and anthropogenic sources of phytoplankton population variability, as well as recognition that the modes of human disturbance of coastal bloom cycles operate interactively and cannot be studied as isolated processes.

INTRODUCTION

Earth science of the 1980s and 1990s has been motivated partly by the challenge to understand global change, which in its broadest sense includes the myriad impacts of the human population on the Earth system. This problem persists as a difficult challenge because the component elements of global change, such as the climate system, hydrologic cycle, and biological populations, all have inherent large natural fluctuations. Superimposed onto these natural changes are those caused by human disturbance. This scientific challenge persists because human disturbance is often subtle, indirect, and sometimes confounded by natural changes that themselves are not well understood. This problem applies particularly to ecosystems at the continental margins, where natural change originates from processes in the coastal ocean, in the atmosphere, and on the land surface, and where human disturbance is highly focused. Seventy-five percent of the U.S. population will live within 75 km of a coast by the year 2010 [Williams et al., 1991]. As a result of this dense human settlement along the continental margins, coastal ecosystems are influenced by diverse human activities, including agricultural practices [Fleischer et al., 1987; *Nixon*, 1995]; the damming of rivers and manipulation of their flows [*Dynesius* and *Nilsson*, 1994]; inputs of wastes, including nutrients [*Justić* et *al.*, 1995] and toxic contaminants [*Windom*, 1992]; changing land use [Cooper, 1995; Hopkinson and *Vallino*, 1995] and habitat loss [Nichols et *al.*, 1986]; and disturbances of biological communities through harvest [*Rothschild* et al., 1994] or introductions of exotic species

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Table 1. Examples of Recent Ecological Change in Global Coastal Waters

Phenomenon	*Location(s)*	*Reference(s)*
Episodes of anoxia and associated mortalities of fish and shellfish	Baltic Sea	*Rosenberg et al.* [1990]
	Adriatic Sea	*Justić et al.* [1987]
	Black Sea	*Mee* [1992]
Harmful algal outbreaks	global coastal waters	*Smayda* [1989], *Hallegraeff* [1993]
Oyster population declines and disappearance of vascular plants	Chesapeake Bay	*Smith et al.* [1992], *Orth and Moore* [1983]
Changes in the community composition of phytoplankton	Bay of Aratu Salvador, Brazil	*Cowgill* [1987]
Doubling of the biomass and shifts in the communities of invertebrates	Dutch Wadden Sea	*Beukema* [1991]
Invasion by exotic invertebrates and restructuring of biological communities	north San Francisco Bay	*Alpine and Cloem* [1992], *Kimmerer et al.* [1994]
Interannual fluctuations in abundance and species of macroalgae	Peel-Harvey estuary, Australia	*Lavery et al.* [1991]
Mass mortalities of diverse marine biota	Scandinavian coastal waters	*Underdal et al.* [1989]
Seabird mortality	Monterey Bay	*Walz et al.* [1994]
Episodes of thick foam accumulation on beaches	southern North Sea	*Batje and Michaelis* [1986]
Persistent closures of commercial shellfish harvest	New Zealand coastal waters	*Mackenzie et al.* [1995]
Increased frequency of red tides and associated fish kills	Tolo Harbor, Hong Kong	*Hodgkiss and Yim* [1995]
	Seto Inland Sea, Japan	*Prakash* [1987]

[Carlton, 1985; *Carlton* and *Geller*, 1993]. Nearly a fifth of the total marine fish catch comes from these zones of intense human activity [*Pauly* and Christensen, 1995].

In recent decades we have observed remarkable changes in coastal waters of all the continents; examples are listed in Table 1. Many of these changes are related either directly or indirectly to changes in the species composition, abundance, or production rate of the phytoplankton, so this one biological community is central to the problem of environmental change at the land-sea interface. This theme is prominent in the recent initiatives to understand mechanisms of change in coastal ecosystems (Table 2). One fundamental feature of phytoplankton dynamics is the episodic rapid population increase as events that we traditionally refer to as "blooms," presumably in reference to *Schütt*'s [1892] description of the seasonal plankton cycles in Kiel Bight, (translation from Mills [1989, p. 125]):

> "and this play repeats itself year after year with the same regularity as every spring the trees turn green and in autumn lose their leaves: with just such absolute certainty as the cherries bloom before the sunflowers, so *Skeletonema* arrives at their yearly peak earlier than *Ceratium*."

My purpose here is to review some principles of phytoplankton bloom dynamics in their context as features of change in estuarine and nearshore coastal waters. This review is organized to address basic questions: What are phytoplankton blooms? What are their underlying mechanisms? How are they related to changes in ecosystem processes and the geochemistry of estuarine and coastal waters? The review is based around observations, models, and insights that have come from the U.S. Geological Survey (USGS) program of research focused on San Francisco Bay. I begin with a general description and conceptual model of phytoplankton bloom dynamics in shallow coastal ecosystems. Next is a

Table 2. Some Contemporary Research Initiatives to Describe and Explain Processes of Change in Coastal Ecosystems of North America and Europe

Program	*Sponsor(s)**	*Reference(s)*
LMER (Land Margin Ecosystem Research)	NSF	*Boynton et al.* [1992]
CoOP (Coastal Ocean Processes)	NSF. NOAA, ONK	*Bnnk et al.* [1992]
GLOBEC (Global Ocean Ecosystems Dynamics)	NSF. NOAA	*U.S GLOBEC* [1995]
NECOP (Nutrient Enhanced Coastal Ocean Productivity)	NOAA	*Wenzel and Scavia* [1993], *Atwood et al.* [1994]
ECOHAB (Ecology and Oceanography of Harmful Algal Blooms)	NSF, NOAA	*Anderson* [1995]
LOICZ (Land-Ocean Interactions in the Coastal Zone)	ICSU	*Holligan and de Boois* [1993]
EKOS (European River Ocean System) 2000	CEC	*Martin and Barth* [1989]

*Abbreviations are NSF. U S National Science Foundation; NOAA, U S National Oceanic and Atmospheric Administration; ONR, U S Office of Naval Research, ICSU, International Council for Scientific Unions; CEC, Commission of the European Communities

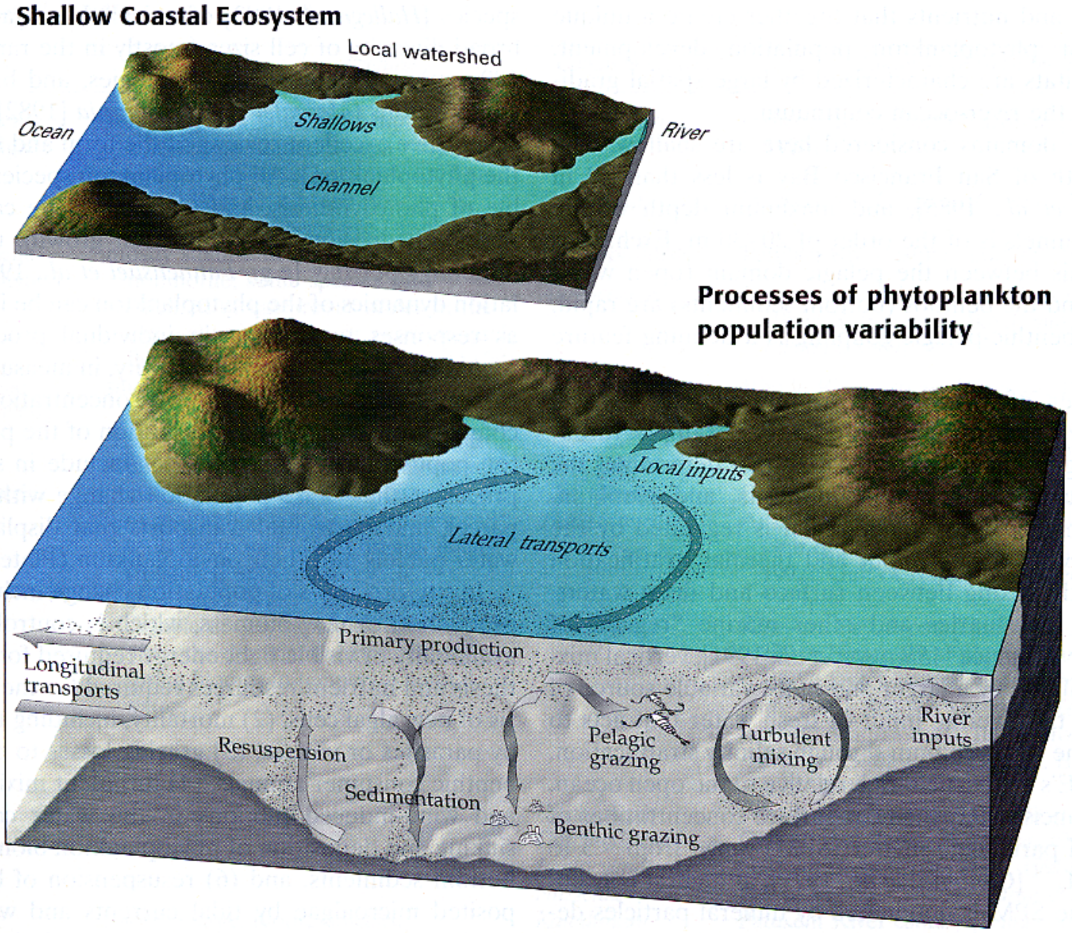

Plate 1. An idealized shallow coastal ecosystem (SCE) showing the key processes of phytoplankton population variability at the land-sea interface. Local processes include primary production (the source of new phytoplankton biomass), consumption by benthic and pelagic grazers, exchanges between the sediment surface and water column by sedimentation and resuspension, and turbulent mixing. Horizontal transport processes include exchanges with the coastal ocean, riverine inputs of phytoplankton, and longitudinal and lateral transports generated by density-, tide-, and wind-driven circulation and mixing. The color transition from green to blue represents the salinity gradient along the river-ocean continuum. Brightness represents the bathymetry, and white shadings indicate the lateral shallow domains common to coastal plain estuaries and lagoons.

detailed review of the approaches used in our analysis of the long term observations in south San Francisco Bay, with emphasis on the search for patterns and mechanisms of phytoplankton population variability. Then I describe the significance of blooms in the coastal zone, emphasizing the role of phytoplankton production as a mechanism of geochemical and ecological change. I conclude with some thoughts on the compelling questions and hypotheses that will guide research at the land-sea interface into the next century.

The USGS research program in San Francisco Bay began in 1968 and continues as one of the few long-term efforts of combined observation and research in the U.S. coastal zone. Other aspects of this program are described by *Conomos* [1979b], *Kockelman et al.* [1982], *Cloern and Nichols* [1985], *Nichols et al.* [1986], *Nichols and Pamatmat* [1988], *Peterson* [1989], *Cheng* [1990], *Luoma et al.* [1990], and *Peterson et al.* [1995].

THE GENERAL PROBLEM

Domains of Interest

San Francisco Bay has been the focus of sustained investigation because it has features common to many shallow coastal ecosystems (SCEs) that are influenced by natural and anthropogenic sources of variability. These SCEs include tidal rivers, estuaries, embayments, lagoons, and coastal river plumes, which are distinctly different ecosystems from the open ocean. The differences arise partly from the physical features illustrated in Plate 1, and they include the following.

1. SCEs are transition zones at the land-sea interface, so they are influenced both by inputs from the land surface and exchanges with the coastal ocean. Connections to the land surface are made through rivers that carry runoff from large-scale catchments or from smaller tributaries that carry runoff from the local watershed

(Plate 1). Riverine inputs are sources of fresh water, sediments, and nutrients that together create a unique habitat for phytoplankton population development. These habitats are characterized by large spatial gradients along the river-ocean continuum.

2. The domains considered here are shallow. The mean depth of San Francisco Bay is less than 10 m [Conomos et ul., 1985], and maximum depth of the central channels is of the order of 20–30 m. Exchanges of materials between the pelagic domain (open water column) and the benthos (bottom sediments) are rapid, so strong benthic-pelagic coupling is a defining feature of SCEs.

3. River-influenced SCEs are very different physical environments from the open ocean. For example, turbulent mixing is a key physical process that determines the vertical fluxes of heat, salt, nutrients, and plankton. Vertical mixing in the open ocean is regulated by the seasonal cycle of heat input and thermal stratification that retards mixing between surface and deep waters. However, in estuaries and other marine "regions of freshwater influence" [*Simpson* et *al.*, 1991], vertical mixing is regulated by a larger and more variable source of buoyancy, the riverine input of fresh water that acts to stabilize the water column through salinity stratification.

4. SCE's are particle-rich relative to the open ocean. In San Francisco Bay the near-surface concentrations of suspended particulate matter (SPM) range from <5 to >300 mg L^{-1} [Conomos et al., 1979]; at highest concentrations the SPM is dominated by mineral particles delivered by river flow or resuspended off the bottom by tidal and wind wave currents. Suspended particles absorb and scatter light, so SCEs are turbid habitats in which phytoplankton growth can be limited by the availability of sunlight to sustain photosynthesis [Wofsy, 1983; Cloem, 1987].

5. Many SCEs are nutrient-rich because of inputs from the land surface [*Malone et al.*, 1988; *Nixon*, 1995; *Justić* et *al.*, 1995] and geochemical and biological processes that act as "filters" to retain nutrients within estuaries [*Sharp* et *al.*, 1984]. In south San Francisco Bay, summer phosphate concentrations often exceed 10 μM compared with concentrations of <0.5 μM in the adjacent Pacific Ocean [Van Geen and Luoma, 1993]. Similar enrichment exists for other nutrients such as nitrogen (N) and silica (Si). Therefore the potential for phytoplankton production can be much higher in SCEs than in most regions of the ocean, and the phytoplankton population fluctuations in SCEs are highly amplified.

General Overview and Conceptual Model of Phytoplankton Blooms in SCEs

Shallow coastal ecosystems maintain plankton populations distinct from those beyond the freshwater and oceanic interfaces. Much of the biogeochemical variability within these SCEs originates with fluctuations in the phytoplankton population, and Riley [1967] provided the conceptual framework for understanding these fluctuations. 'The phytoplankton (Table **3)** include 5000 marine species [*Hallegraeff*, 1993] of unicellular algae having a broad diversity of cell sizes (mostly in the range of 1 to 100 μm), morphologies, physiologies, and biochemical compositions (Margalef [1978], Soumia [1982], and Fogg [1991] give excellent reviews of the form and function of the phytoplankton). All phytoplankton species are capable of photosynthesis, and many have the capacity for rapid cell division and population growth, up to four douhlings per day [e.g., *Fahnenstiel* et al., 1995]. Population dynamics of the phytoplankton can be interpreted as responses to changes in individual processes that regulate the biomass (total quantity, in measures such as carbon, nitrogen, or chlorophyll concentration), species composition, and spatial distribution of the phytoplankton population. These processes include in situ (local) processes that cause population change within a water parcel, and horizontal transports that displace or mix water parcels and their phytoplankton (Plate 1).

In situ processes of population change include (1) the production of new biomass, which is controlled by the availability of visible light energy required for photosynthesis and nutrient resources required for the biosynthesis of new algal cells, (2) mortality, including that caused by parasites or viruses, (3) grazing losses to pelagic and benthic consumer animals, (4) turbulent mixing by tide- and wind-induced motions in the water column, *(5)* sinking and deposition of phytoplankton biomass on the bottom sediments, and (6) resuspension of bottom-deposited microalgae by tidal currents and wind waves. Horizontal transports follow water circulations that are driven by tidal currents, wind stresses on the water surface. and horizontal gradients of water density [Fischer *et* al., 1979]. These transports displace phytoplankton biomass longitudinally along the river-ocean continuum and laterally between shallow and deep domains, which are very different habitats for phytoplankton growth [Cloem and Cheng, 1981; *Malone* et al., 1986]. Although techniques exist to measure or estimate each process shown in Plate 1, comprehensive process-specific measurement programs are expensive, logistically challenging, and rarely done. Rather, phytoplankton dynamics in SCEs are often followed by measuring changes in biomass (usually as the concentration of chlorophyll a, the photosynthetic pigment contained in all phytoplankton cells), species composition, and photosynthesis as an index of population growth rate. These measurements are often done in conjunction with basic hydrographic measurements (salinity, temperature, tides) that can be used to infer patterns of water circulation and transports, and surveys of the pelagic and benthic herbivores that can used to estimate potential rates of grazing loss.

Phytoplankton populations often exist in a static .'quasi-equilibrium" [Evans and *Parslow*, 1985] in which the rate of biomass production (the primary productivity) is balanced by the phytoplankton losses and transports. Under this condition the net population growth

Table 3. Characteristics of the Primary Classes of Algae That Form Phytoplankton Blooms in Tidal Rivers, Estuaries, and Shallow Coastal Waters

Class	*Distinguishing Features*	*Common Genera*	*Examples of Occurrence*
Chlorophyceae (green algae)	forms include unicells or multicelled colonies or filaments; cell walls contain cellulose; zero, two or four equal flagella; storage product is starch; most species are freshwater	*Nannochloris*	Calico Creek, North Carolina [*Mallin*, 1994]
		Dunaliella	lagoons of NE Spain [*Comin*, 1982]
Chrysophyceae (chrysophytes)	mostly small unicells, motile or nonmotile; some species with silicified or calcareous scales in the cell wall; either one or two (unequal) flagella; storage products are lipid (fat)	*Pseudopedinella*	Pamlico River estuary [*Mallin*, 1994]
		Aureococcus	Long Island embayments [*Cosper et al.*, 1989]; Narragansett Bay [*Smayda and Villareal*, 1989]
Cryptophyceae (cryptophytes)	small, flattened, motile cells; cell coverings of minute proteinaceous plates; two equal flagella; ubiquitous but rarely dominate bloom biomass	*Cryptomonas*	Rhode River estuary [*Gallegos*, 1992]
		Chroomonas	Neuse River estuary [*Mallin*, 1994]; San Francisco Bay [*Cloern et al.*, 1985]
Diatomophyceae (diatoms)	nonmotile cells shaped like discs, needles, or multicelled colonies or chains; cell walls composed of two organic shells (frustules) impregnated with amorphous silica; some species are capable of very rapid cell division; often the dominant components of spring blooms in temperate coastal waters	*Chaetoceros*	Bedford Basin, Canada [*Kepkay et al.*, 1993]
		Thalassiosira	Auke Bay, Alaska [*Ziemann et al.*, 1991]; Gulf of St. Lawrence [*Levasseur et al.*, 1992]; Gulf of Naples, Italy [*Zingone et al.*, 1995]
		Skeletonema	Kinu-ura Bay, Japan [*Hama and Handa*, 1994]; Fraser River plume [*Harrison et al.*, 1991]; Dutch coastal waters [*Brussaard et al.*, 1995]; Scottish sea lochs [*Tett et al.*, 1986]; Madras coast, India [*Sivaswamy and Prasad*, 1990]; Patos Lagoon, Brazil [*Abreu et al.*, 1995]
		Rhizosolenia	French coastal waters [*Sournia et al.*, 1987]
		Coscinodiscus	Otsuchi Bay, Japan [*Nakaoka*, 1992]
		Leptocylindricus	German Bight [*Colijn et al.*, 1990]
		Nitzschia	Bay of Fundy, Canada [*Martin et al.*, 1990]
Dinophyceae (dinoflagellates)	(mostly) large, motile unicells; multilayered cell covering, formed into distinct plates in the "armored" species; two unequal flagella (one transverse, one longitudinal); some species capable of rapid swimming and vertical migration; responsible for visible colored (red, green) blooms; many species are mixotrophic (capable of both photosynthetic and heterotrophic nutrition)	*Katodinium*	Patuxent River estuary [*Sellner et al.*, 1991]
		Gymnodinium	Tomales Bay [*Cole*, 1989]; Ria de Viso, Spain [*Fraga et al.*, 1992]
		Alexandrium	Gulf of Maine [*Franks and Anderson*, 1992]; Chinhae Bay, Korea [*Han et al.*, 1992]
		Peridinium	Baltic Sea [*Heiskanen and Kononen*, 1994]
		Dinophysis	French Atlantic coast [*Delmas et al.*, 1992]
		Prorocentrum	Chesapeake Bay [*Tyler and Seliger*, 1978]
Cyanophyccac (blue-green algae, or cyanobacteria)	very small, procaryotic (bacteria-like) cells with no defined internal structures (e.g., no nucleus or chloroplasts); unicells or multicelled colonies or filaments; no flagella; gas vacuoles allow buoyancy regulation and dense accumulations at the water surface; some species fix N_2	*Microcystis*	Neuse River estuary [*Rudek et al.*, 1991]
		Nodularia	Baltic Sea [*Wasmund*, 1994]; Peel-Harvey estuary, Australia [*Lukatelich and McComb*, 1986]
		Aphanizomenon	Baltic Sea [*Grantli et al.*, 1990]
		Synechococcus	Changjiang (Yangtse River) plume, China [*Ning et al.*, 1988]
Prasinophyceae	small, motile cells; one, two, or four flagella that are covered with minute scales or hairs; most species have cell coverings with organic scales	*Pyramimonas*	Tampa Bay [*Gardiner and Dawes*, 1987]
		Micromonas	Fraser River plume [*Harrison et al.*, 1991]; Sundays River estuary, South Africa [*Hilmer and Bate*, 1991]
Prymnesiophyceae	most species are small, motile cells, but some form colonies of nonmotile cells; cell coverings include one or more layers of organic scales or calcite plates (coccoliths); one or two flagella, with some species also having a short appendage (haptonema) for attachment to surfaces; complex life cycles of alternating cell forms and diverse modes of nutrition	*Phaeocystis*	Dutch coastal waters [*Cadée*, 1990]; Narragansett Bay [*Verity et al.*, 1988]
		Emiliania	Black Sea [*Sur et al.*, 1994]
		Chrysochromulina	Scandinavian coastal waters [*Maestrini and Grantli*, 1991]
		Prymnesium	Norwegian fjords [*Kaartvedt et al.*, 1991]

Table 3. (continued)

Class	*Distinguishing Features*	*Common Genera*	*Examples of Occurrence*
Phototrophic ciliates	chlorophyll-containing protozoans capable of rapid photosynthesis and population growth; swimming structures (cilia) allow rapid vertical migrations; form intense visible (nontoxic) red tides; a unique nonalgal component of the marine phytoplankton	*Mesodinium*	San Francisco Bay [*Cloern et al.*, 1994]; Patos Lagoon. Brazil [*Abreu et al.*, 1994]; Sechelt Inlet. Canada [*Haigh et al.*. 1992]; Southampton Water, U.K. [*Iriarte and Purdie*, 1994]; Strait of Georgia [*Harrison et al.*, 1983]

Based on the algal taxonomy of *Chrétiennot-Dinet et al.* [1993] and descriptions of *Morris* [1967] and *Soumia* [1982]. Algae are classified on the basis of their photosynthetic pigments. storage products (food reserves), cell walls (external coverings). and number and type of flagella (propulsive organs).

rate is near zero and the biomass remains constant. Phytoplankton blooms are transient departures from quasi-equilibrium when the primary productivity temporarily exceeds the losses and transports and the population grows rapidly and reaches exceptionally high biomass [Paerl, 1988; Legendre, 1990]. Phytoplankton blooms usually are not single discrete events but rather are a series of fluctuations in which the biomass and the species composition (Table 3) of the phytoplankton population change rapidly.

We can very generally classify blooms into three types: (1) recurrent seasonal events that usually persist over periods of weeks, (2) aperiodic events that often persist for periods of days [e.g., Takahashi et *al.*, 1977], and (3) exceptional events that are typically dominated by few species (sometimes noxious or toxic forms) and persist for months [e.g., *Nixon*, 1989]. Seasonal blooms can occur in spring [*Malone* et al., 1988; Ziemann et al., 1991; Lignell et al., 1993], summer [Sinclair, 1978; Cole, 1989; Vant and Budd, 1993]; autumn [*Zingone* et al., 1995], and winter [Hitchcock and Smayda, 1977; *MacKenzie and* Gillespie, 1986; *Sellner* et al., 1991]. These events are often dominated by different groups of species each season as the phytoplankton community adapts to changes in resources and the physical environment [*Margalef*, 1978; Srnetacek and Pollehne, 1986]. A common annual cycle begins with large winter–spring diatom blooms followed by summer blooms of small flagellates, dinoflagellates, and diatoms and then autumn blooms dominated by dinoflagellates [Smetacek, 1986; Tett et al., 1986; *Mallin* et al., 1991] .

The underlying mechanisms of phytoplankton blooms are diverse and can be organized with a simple population budget that describes biomass fluctuations at a fixed geographic reference,

$$\Delta B/\Delta t = \pm(\mu - r)B - G_p - G_b \pm E \pm X \qquad (1)$$

where ΔB is the change in phytoplankton biomass over time increment Δt and terms on the right-hand side represent the individual process illustrated in Plate 1: μ is the growth rate, a function of light and nutrient availability; r is loss rate to respiration (note that $(\mu - r)$ is the net growth rate and $(\mu - r)B$ is the net rate of biomass production); G_p is the loss rate to pelagic (zooplankton) grazing; G_b is the loss rate to benthic grazing; E represents exchanges of biomass between the bottom sediments and overlying water column; and X represents all horizontal transports by advective and turbulent diffusive processes. Blooms are periods in which $\Delta B/\Delta t$ is large and positive, so [from Legendre, 1990]

$$(\mu - r)B >> (G_p + G_b + E + X) \qquad (2)$$

Equation (2) can be satisfied under environmental conditions in which the net growth rate $(\mu - r)$ is large. When nutrients are abundant, the net growth rate is directly proportional to light availability. For example, in San Francisco Bay, $(\mu - r)$ is correlated with the mean daily irradiance **I** to which phytoplankton cells are exposed as they are moved within the water column by turbulent mixing [Alpine *and* Cloern, 1988]. The mean irradiance in a uniform mixed layer of thickness H is

$$I \approx I_0/(kH) \qquad (3)$$

where I_0 is the daily quantity of photosynthetically active radiation penetrating just below the water surface and k is the light attenuation coefficient that defines the exponential decay of light with depth.

Equation (3) shows that the depth-averaged quantity of light available to sustain phytoplankton photosynthesis and growth is directly proportional to surface irradiance I_0 and inversely proportional to turbidity k and the depth scale H. Blooms can be triggered by changes in each of these three quantities. The spring bloom in Swedish coastal waters begins when the daily surface irradiance I_0 reaches a threshold value of about 30 E m^{-2} d^{-1} [*Båmstedt*, 1985]. In Dutch coastal waters the spring bloom begins first in offshore regions where k is small and **I** reaches the threshold value earlier than in the more turbid (high k) inshore regions [*Gieskes* and *Kraay*, 1975]. Short-term, aperiodic fluctuations of phytoplankton biomass can be caused by wind events that resuspend fine bottom sediments and increase *k* to the point where mean *I* and the net growth rate become very small [*Tett* and *Grenz*, 1994].

Blooms often develop when the effective mixing depth of the water column (depth scale H) is reduced by vertical stratification. If the water density is uniform over depth H, then wind and tidal stirring can move phytoplankton cells rapidly between the surface photic zone (where sufficient light exists to sustain photosynthesis and a positive net growth rate) and the deeper aphotic zone (where light is absent and the net growth rate is negative). Surface heating and freshwater inputs are sources of buoyancy that can establish vertical density gradients in the water column. Strong vertical stratification can effectively isolate phytoplankton in a shallow (small H) surface layer in which the mean irradiance I is much higher than the irradiance averaged over the full water column height. As a result, the net growth rate of phytoplankton in the surface layer increases after the establishment of vertical stratification. Seasonal blooms can be triggered by seasonal fluctuations in river flow and the intensity of salinity stratification [*Pennock*, 1985]. At shorter timescales the intensity of vertical stratification fluctuates with changes in the strength of tidal stirring. Regular weekly fluctuations of vertical stratification often coincide with the fortnightly neap-spring tidal cycle, with alternations between well-mixed (spring tide) and stratified (neap tide) conditions. In many tidal SCEs the neap tide periods of enhanced stratification are periods of phytoplankton biomass growth, and the proximal agent of these weekly blooms is the increased growth rate of phytoplankton confined in a shallow surface layer [*Winter et al.*, 1975; *Sinclair*, 1978; *Haas et al.*, 1981; *Cloern*, 1984; *de Madariaga et al.*, 1989; *Roden*, 1994; *Ragueneau et al.*, 1996].

The second critical resource for phytoplankton growth is the pool of nutrients required for the biosynthesis of new cells. The potential magnitude of phytoplankton blooms is set by the supply rate of the least abundant nutrient elements. In addition, the growth efficiency of phytoplankton in low-light habitats increases with nutrient availability [*Cloern et al.*, 1995]. Therefore phytoplankton blooms can be responses to seasonal fluctuations in the riverine inputs of nutrient elements such as N [*Malone et al.*, 1988] and P [*McComb and Humphries*, 1992]. Episodic blooms can follow pulsed inputs of nutrients from runoff produced in the local watershed during storms [*Gallegos et al.*, 1992; *Hama and Handa*, 1994], direct inputs of atmospheric nitrogen from rainfall [*Paerl et al.*, 1990], or the input of nutrients from the coastal ocean during upwelling events [*Lara-Lara et al.*, 1980].

The necessary condition for bloom initiation (equation (2)) is that the primary productivity must be large relative to all mechanisms of phytoplankton loss, including consumption (grazing) by pelagic and benthic animals. Therefore blooms can develop through mechanisms that lead to reduced grazing loss. The spring blooms in temperate and high-latitude coastal waters begin when the zooplankton biomass and grazing rate are near their annual minima [*Båmstedt*, 1985]. Diatom blooms can follow rapid declines in zooplankton abundance caused by episodes of intense predation on copepods (small pelagic crustaceans that feed on phytoplankton), so the timing and magnitude of blooms can be regulated by top down processes originating at higher trophic levels [*Deason and Smayda*, 1982].

In many SCEs the total biomass (and therefore potential grazing rate) of the benthic consumer animals is much higher than the biomass of the copepods and other zooplankton [*Cloern*, 1982; *Knox*, 1986; *Colijn et al.*, 1988]. Suspension-feeding benthic invertebrates, such as polychaete worms and bivalve mollusks (clams, mussels), actively remove phytoplankton biomass from just above the sediment-water interface: other benthic animals consume phytoplankton biomass deposited on the sediment surface. Therefore the rate of benthic grazing can be limited by the vertical flux of phytoplankton biomass from the water column to the sediment-water interface [*Morzismith et al.*, 1990]. In south San Francisco Bay, blooms are controlled by the seasonal and weekly fluctuations in salinity stratification because strong stratification retards the turbulent diffusive flux of phytoplankton from the productive surface layer to the bottom zone of active consumption by benthic animals. Stratification acts to decouple phytoplankton from the bottom grazers [*Cloern*, 1991b]. Therefore stratification promotes blooms by (1) establishing conditions of rapid phytoplankton growth in the surface layer and (2) slowing the delivery of phytoplankton biomass to the benthic consumers [*Koseff et al.*, 1993]. In some SCEs the rate of benthic grazing continually overwhelms phytoplankton primary production. This is the current situation in upper reaches of northern San Francisco Bay, where summer blooms disappeared after an exotic clam (*Potamocorbula amurensis*) became so abundant that its grazing rate balances phytoplankton productivity [*Alpine and Cloern*, 1992] (see Figure 3b below). Similar dramatic declines in phytoplankton biomass have been observed in other coastal systems after aquaculture activities increased the abundance of filter-feeding mollusks through cultivation [*Motoda et al.*, 1987].

The last term in (2) represents the horizontal transports, which can also be mechanisms of bloom regulation. Plankton populations can be maintained in a coastal basin only when the net rate of biomass production, $(\mu \quad r)B$, exceeds the net rate of transport losses, X [*Malone*, 1977; *Kikuchi et al.*, 1992]. In SCEs coupled to large river systems, the hydraulic residence time can be short relative to the phytoplankton population growth rate during periods of high discharge. Blooms can develop only when the river discharge falls to a level at which the residence time within the SCE is longer than the phytoplankton population doubling time [*Cloern et al.*, 1983; *Relexans et al.*, 1988]. Horizontal transports can be sources of phytoplankton when coastal [*Malone*, 1977] or riverine [*de Madariaga et al.*, 1992] blooms are advected into coastal basins. Exceptional blooms can follow exceptional climate patterns that cause slow horizontal transports and long hydraulic residence time within coastal basins [*Vieira and Chant*, 1993].

Other mechanisms of water circulation and mixing influence plankton dynamics. The spring bloom in Chesapeake Bay develops when densily-driven circulations cause a landward transport and accumulation of phytoplankton biomass in the upper estuary [*Malone et al.*, 1988]. In south San Francisco Bay, localized blooms that develop over the lateral shallows are dissipated quickly by strong wind or river flow events that generate pulses of enhanced circulation and rapid horizontal transports [*Huzzey et al.*, 1990]. Red tide blooms can be triggered by intrusions of coastal water that alter the vertical circulation pattern and carry dormant algal cells (cysts) from the sediments to the water column, where they seed the rapid population growth of dinoflagellates [*Figueiras and Pazos*, 1991]. Sharp discontinuities between different water masses (fronts) can be sites of phytoplankton accumulation. Tidal fronts at the interface between shallow mixed waters and deeper stratified waters promote the growth and physical accumulation of phytoplankton and can be zones of intense dinoflagellate blooms [*Simpson and Hunter*, 1974]. Buoyancy fronts between a low-salinity (low density) and a high-salinity water mass can also be regions of active phytoplankton growth and accumulation [*Franks*, 1992].

The conceptual model outlined above places great emphasis on the changing physical and chemical environment as a mechanism of phytoplankton population change. However, it is important to remember also that the plankton species living in SCEs have evolved in these habitats and acquired behavioral, biochemical, and life-history adaptations to the physical and chemical variability characteristic of coastal waters. For example, the photosynthetic ciliate *Mesodinium rubrum*, which forms visible red tides in San Francisco Bay [*Cloern et al.*, 1994] and other temperate estuaries, has a behavioral mechanism that acts to retain this species within tidal SCEs: active swimming toward the surface on incoming flood tides, and then downward migration to retard seaward transports by the ebb tides [*Crawford and Purdie*, 1992]. Some dinoflagellates [*Horstmann*, 1980] and other swimming species [*Watanabe et al.*, 1995] have vertical migrations cued to the diurnal (daylight) cycle that allow for exploitation of sunlight at the surface during the day and nutrient resources in the bottom waters at night. Other species produce resting cells that sink to the sediments when growth resources become limited; these then seed blooms when environmental conditions become favorable for population growth [*de Madariaga et al.*, 1989; *Figueiras and Pazos*, 1991]. Recent evidence suggests that overwintering dormant stages of some phytoplankton species begin their development into active cells when the daylength reaches about 13 hours in spring, so blooms of these species are life cycle responses cued to the annual photoperiod cycle [*Eilertsen et al.*, 1995]. Therefore phytoplankton are not absolutely passive organisms subjected to the constraints imposed by their physical-chemical environment. They have diverse abilities of adaptation.

THE SAN FRANCISCO BAY EXAMPLE

A Representative Shallow Coastal Ecosystem

The sustained investigation of San Francisco Bay provides a case study to illustrate the patterns and mechanisms of phytoplankton blooms in one shallow coastal ecosystem. San Francisco Bay is a useful site for comparative estuarine science because it comprises two connected, but distinct, subsystems (Figure 1). The north bay is the estuary of the Sacramento and San Joaquin Rivers, which carry runoff from a large (150,000 km^2) watershed between the Sierra Nevada mountains and the Pacific Ocean. The north bay has features characteristic of partially mixed estuaries, including large horizontal gradients of salinity, suspended sediments, nutrients, and biological communities. In contrast, the south bay is a semienclosed basin with salinity that is near-oceanic during the low-flow seasons and is diluted by freshwater inputs during the high-flow winter–spring. The San Francisco Bay system has complex bottom topography with broad shallow embayments that are incised by a deeper channel, channel constrictions between the embayments, and connection to the Pacific Ocean through a deep (100 m), narrow entrance at the Golden Gate (Figure 1). The estuary is nutrient-rich, with nutrient sources dominated by agricultural inputs carried by river flow and sewage inputs from the local population of 8 million.

Much of the phytoplankton population variability within San Francisco Bay originates with fluctuations in physical forcings at the oceanic, atmospheric, and watershed interfaces. A primary forcing at the estuary-watershed interface is the input of fresh water, which has strong seasonal and interannual variability. Figure 2a shows fluctuations of the freshwater inflow to north San Francisco Bay during four of the years in which phytoplankton population variability has been measured. These records show that annual fluctuations in river flow are dominated by a wet season (from winter storms and spring snowmelt) and a dry summer–autumn season when precipitation stops. These records also show pronounced year-to-year fluctuation of river flow to San Francisco Bay: 1983 was the wettest year of this century, 1986 was dominated by an extreme flood event (the highest recorded flow of this century), and the 1989 and 1993 hydrographs show seasonal patterns of river flow during representative dry and wet years, respectively. Freshwater inputs from the smaller local streams are more immediately responsive to winter storms, and local streamflows to the south bay stop entirely during summer–autumn (Figure 2b). These seasonal and interannual fluctuations in river flow are driven by large-scale atmospheric circulations that control the strength and position of the Pacific high-pressure system, which de-

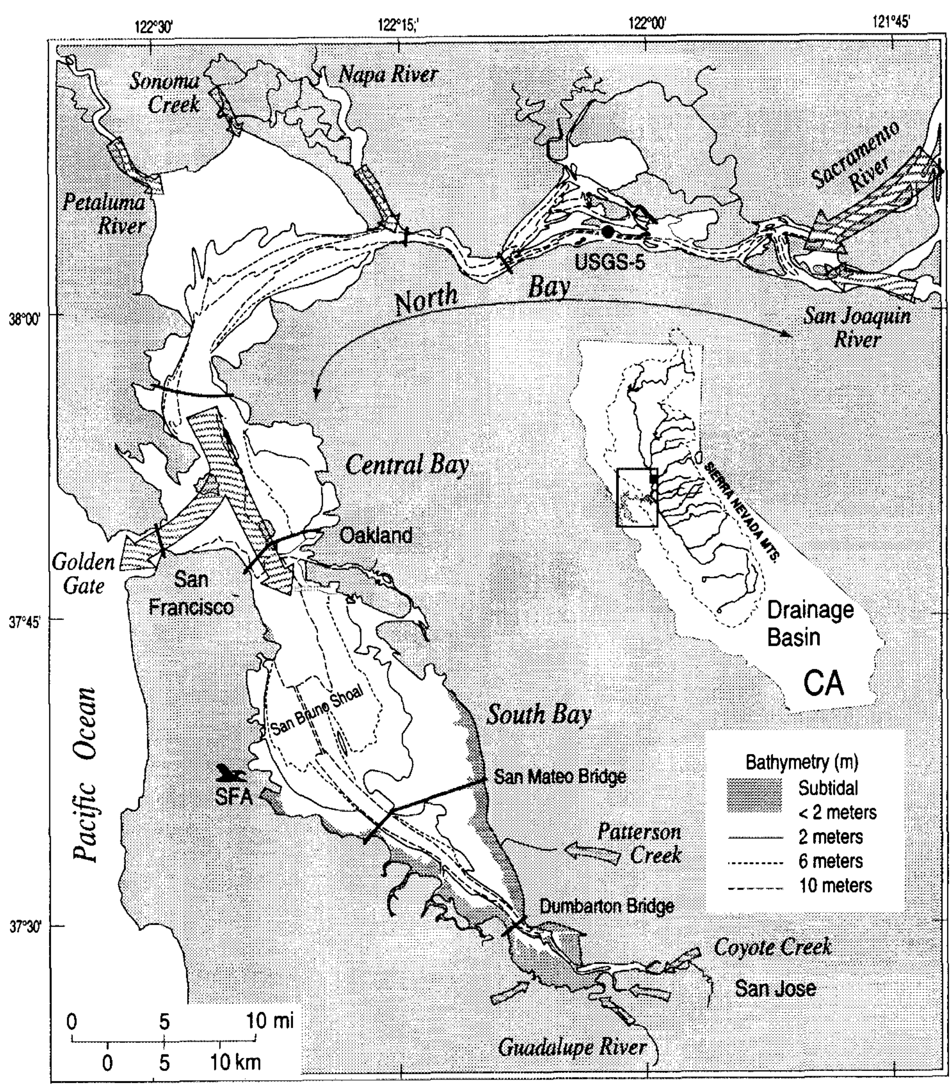

Figure 1. Map of San Francisco Bay, a shallow coastal ecosystem influenced by tides at the oceanic boundary (the Golden Gate) and freshwater inflows at the watershed boundaries. Arrows show sources and flows of fresh water during periods of high runoff. SFA is San Francisco International Airport. The inset shows the drainage basin and major tributaries of the Sacramento–San Joaquin River system.

flects moisture-bearing storms to the north of California [*Peterson et al.*, 1995].

Physical forcings at the estuary-atmosphere interface include wind stress at the water surface that stirs the upper water column, resuspends bottom sediments, and drives horizontal circulations. In the San Francisco Bay region, winds have maximum speeds in summer (Figure 2c) associated with the westerly sea breeze [*Conomos et al.*, 1985]. Episodic fluctuations in wind stress are associated with storms, particularly winter storms that typically come from the southwest. Irradiance has regular seasonal periodicity and daily fluctuations associated with storms and intrusions of coastal fog during summer (Figure 2d).

A primary physical forcing at the estuary-ocean interface is the tide, which propagates into San Francisco Bay through the Golden Gate. In this region of the northeast Pacific, the tides have a strong semidiurnal component with two unequal flood and ebb cycles every 24.84 hours. A second important component of the tide is the fortnightly neap-spring cycle (Figure 2e) of two unequal spring and neap tides each lunar month (27.5 days). In the south bay the tidal amplitude (difference between water elevation at high and low tide) is about 2 m, the tidal excursion (horizontal displacement of a water parcel during a tidal cycle) ranges between 7 km at neap tide and 13 km at spring tide, and maximum tidal current speed U is about 0.75 m s^{-1} [*Conomos*, 1979a; *Walters et al.*, 1985]. Therefore San Francisco Bay is a mesotidal SCE with tidal influence smaller than that in macrotidal systems such as the English Channel and Bay of Fundy (tidal amplitude > 10 m), but larger than in the microtidal Gulf of Mexico, Baltic Sea, and Mediterranean Sea (tidal amplitude < 0.5 m).

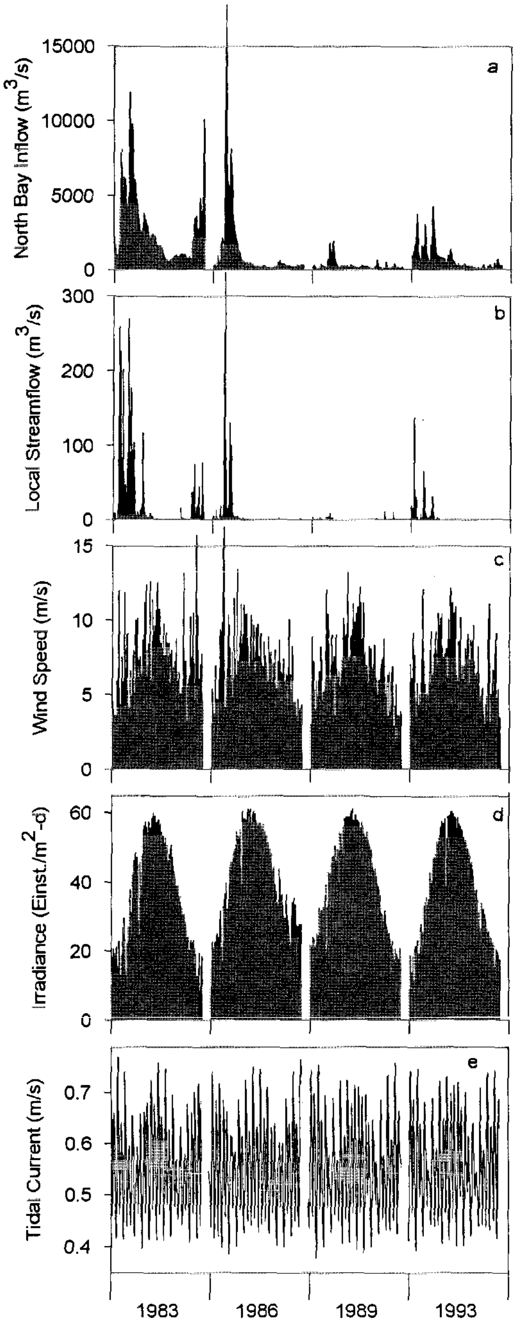

Figure 2. Daily fluctuations of five physical forcings that influence population dynamics of phytoplankton in San Francisco Bay. Series are for four contrasting hydrologic years (1983, 1986, 1989. and 1993), showing (a) net freshwater inflow from the Sacramento and San Joaquin Rivers (a calculated quantity, the Delta Outflow index, from the California Department of Water Resources), (b) daily discharge of a local stream (Patterson Creek) that discharges into south San Francisco Bay (from U.S. Geological Survey (USGS), California District), (c) mean daily wind speed at the San Francisco airport (from the National Climatic Data Center? National Oceanic and Atmospheric Administration), (d) daily irradiance, measured as quantum flux of photosynthetically active radiation, and (e) maximum daily tidal current speed in the channel of south San Francisco Bay, calculated with harmonic constants from long-term current measurements *[Cheng and Gartner*, 1985].

The Issue of Scale

Each of the physical forcings illustrated in Figure 2 contributes to phytoplankton population variability by influencing the rates of vertical mixing, horizontal transport, production, or grazing. Each forcing has characteristic timescales of variability, such as the 12.42-hour and ≈14-day tidal periods; the diel (24 hours) light cycle; 2- to 5-day storm events of enhanced streamflow and wind stress; seasonal cycles of irradiance and temperature; and the pronounced interannual variability of river flow. Therefore phytoplankton populations in SCEs are exposed to physical forcings that have timescales of variability ranging from hours to years: "a hierarchy of forcing functions which drive the various biological response mechanisms at different time and length scales" [Mackas et *al.*, 1985, p. 653]. Each of these timescales can be identified in the population fluctuations of the phytoplankton.

Biomass fluctuations at the short timescales can be measured with moored fluorometers that detect and record chlorophyll fluorescence at a fixed location. A sample record in Figure 3a shows a 2-week series of hourly measurements in south San Francisco Bay. The first week of the record shows periodic fluctuations in chlorophyll fluorescence over the semidiurnal tidal period, with chlorophyll peaks at the two low slack tides each day. This high-frequency variability is caused by tidal advection as chlorophyll spatial gradients oscillate over the sensor with the tide *[Cloern et al.,* 1989]. Spectral analyses of such chlorophyll series confirm a high variance at the tidal frequencies [Litaker et al., 1993]. Short-term fluctuations can result from other processes such as diel cycles of chlorophyll synthesis and zooplankton grazing [Litaker et *al.*, 1993] and wind-wave resuspension of algal cells off the bottom [*Demers* et al., 1987; de *Jonge and* van Beusekom, 1995]. The second half of the record in Figure 3a shows a 6-day period of exponential chlorophyll increase. Here the semidiurnal tidal variability is overwhelmed by the rapid growth of phytoplankton biomass along the entire channel; this period of the record illustrates daily-scale variability during a bloom event. Day-to-day fluctuations in phytoplankton biomass or physiological condition are commonly associated with hydrologic-meteorologic events, such as rainfall pulses, wind events, or periods of abrupt warming [*Côté* and *Platt,* 1983], and with fluctuations in tidal mixing over the neap-spring period [*Sinclair* et *al.*, 1981; *Cloern*, 1991b].

Longer-term fluctuations of phytoplankton biomass are illustrated in Figure 3b, a series of monthly chlorophyll a measurements in north San Francisco Bay from 1974 to 1995. Three scales of variability are evident in this record: a seasonal cycle with peak biomass during the low-flow summers, interannual variability with a damped summer bloom during years of extremely high river flow and short residence time (e.g., 1983), and an apparent permanent change in the nature of the record, with the virtual disappearance of summer blooms after

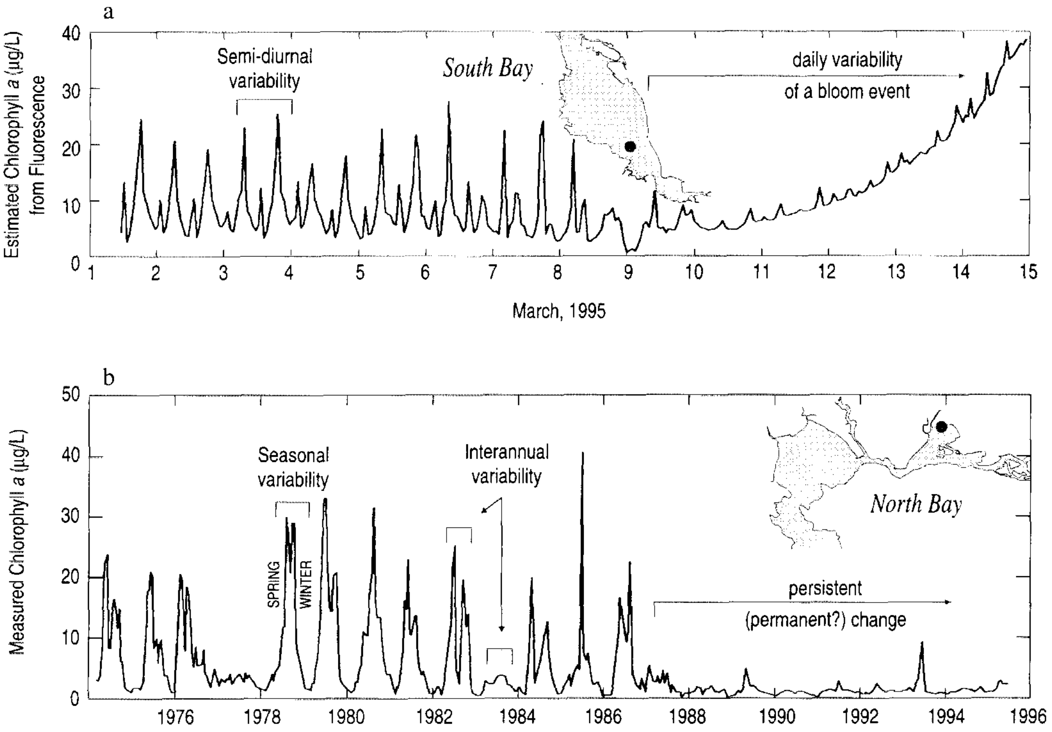

Figure 3. Some timescales of phytoplankton biomass variability in San Francisco Bay. (a) A 14-day record of hourly measurements with an in situ fluorometer placed 2 m above the bottom near station 28 in south San Francisco Bay (Figure 5); the fluorometer was calibrated with discrete chlorophyll *a* measurements made at the beginning and end of the record (fluorometer data from D. A. Cacchione, personal communication, 1995). (b) A 21-year record of monthly (or semimonthly) measurements of surface chlorophyll *a* concentration near station 5 in north San Francisco Bay (Figure 1); this record includes data from the California Department of Water Resources (1974–1986) and USGS (1986–1995).

the North Bay was colonized in large numbers by the clam *Potamocorbula amurensis* in 1987. *Jassby and Powell* [1994] examined a period of this chlorophyll record and concluded that most of the interannual variability is driven by two hydrodynamic processes, one associated with fluctuations in river flow (a natural source of variability), and one associated with managed diversions of fresh water from the upper estuary (an anthropogenic source of variability).

Spatial variability (patchiness) is also observed across a spectrum of scales [*Mackas et al.*, 1985]. Phytoplankton patchiness can be measured with continuous profiles of chlorophyll fluorescence along horizontal transects [*Wilson and Okubo*, 1980; *Childers et al.*, 1994; A. D. Jassby et al., Towards the design of sampling networks for characterizing water quality changes in estuaries, submitted to *Estuarine, Coastal, and Shelf Science*, 1996]. Horizontal variability in south San Francisco Bay is illustrated in Figure 4, which shows the spatial structure of chlorophyll fluorescence along a longitudinal channel transect (Figure 4a) and along a transverse transect between the channel and adjacent shallows (Figure 4b). The longitudinal profiles show measurements spaced every 25 m, and variability is evident even at this small spatial scale. This small-scale variability is superimposed onto larger-scale patterns (mesoscale variability) that often show trends of decreasing chlorophyll fluorescence in the seaward direction (February 28, 1995; Figure 4a) and increasing chlorophyll across the shallows (March 21, 1985; Figure 4b). Both small-scale and mesoscale patchiness are influenced by hydrodynamic processes because the plankton are transported by their fluid environment [*Mackas et al.*, 1985]. Therefore the spatial variability patterns, both of chlorophyll biomass and of individual species [e.g., *Kononen et al.*, 1992; *Zingone et al.*, 1995], are shaped by the turbulent advective transports of phytoplankton within a spatially variable growth environment. These features of spatial structure are not stable or persistent. The mesoscale trends change from season to season [*Glibert et al.*, 1995] and day to day [*Wilson and Okubo*, 1980], while the small-scale variability changes over the tidal period [*Dustan and Pinckney*, 1989].

Figures 3 and 4 show that phytoplankton biomass in shallow coastal ecosystems varies at timescales from hours to decades and at spatial scales from tens of meters to tens of kilometers. *Levin* [1992] suggests that the central problem in ecology is the problem of pattern and scale, where pattern is the description of spatial or temporal variability and the mechanisms of pattern formation are scale-dependent. Therefore studies of population fluctuations such as phytoplankton blooms require

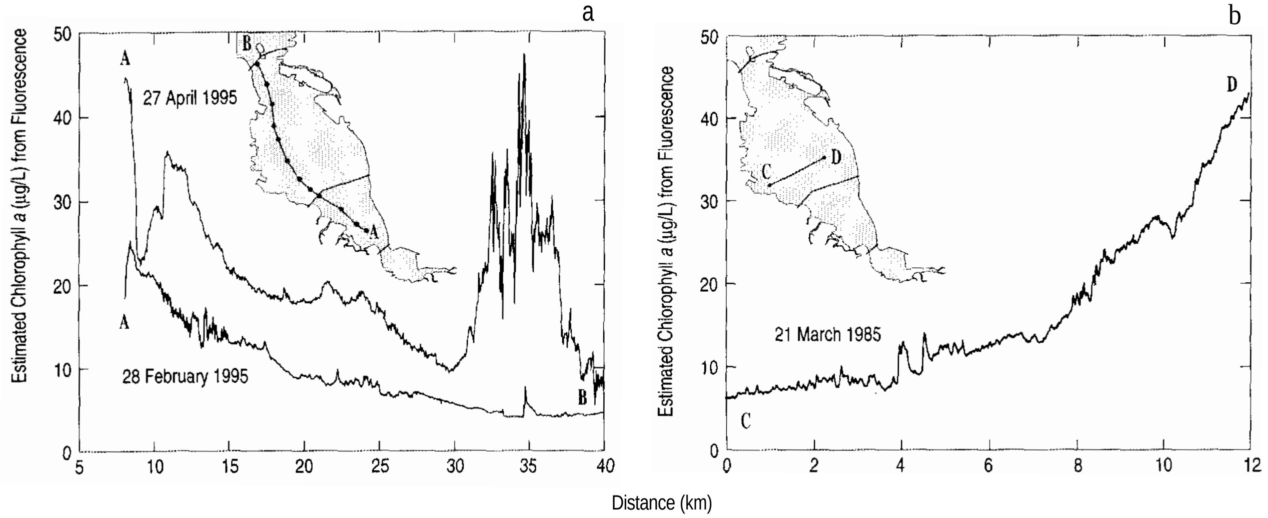

Figure 4. Horizontal variability of phytoplankton biomass from continuous measures of chlorophyll fluorescence along (a) longitudinal transects and (b) a lateral transect of south San Francisco Bay. Near-surface water was pumped to a shipboard fluorometer that was calibrated with 6–10 discrete measurements of chlorophyll a concentration taken along each transect. Inset maps show locations of the transects.

explicit choices about the scales at which population variability can be observed and explained. The long-term observational program in San Francisco Bay was designed to characterize mesoscale spatial variability along the longitudinal axis, at timescales of weeks to years. Even though (large) population variance exists at other scales, the data set described below is not appropriate for analysis of the small-scale fluctuations illustrated in Figures 3 and 4.

The South San Francisco Bay Data Set

Patterns of Variability. South San Francisco Bay has been the site of focused research on phytoplankton

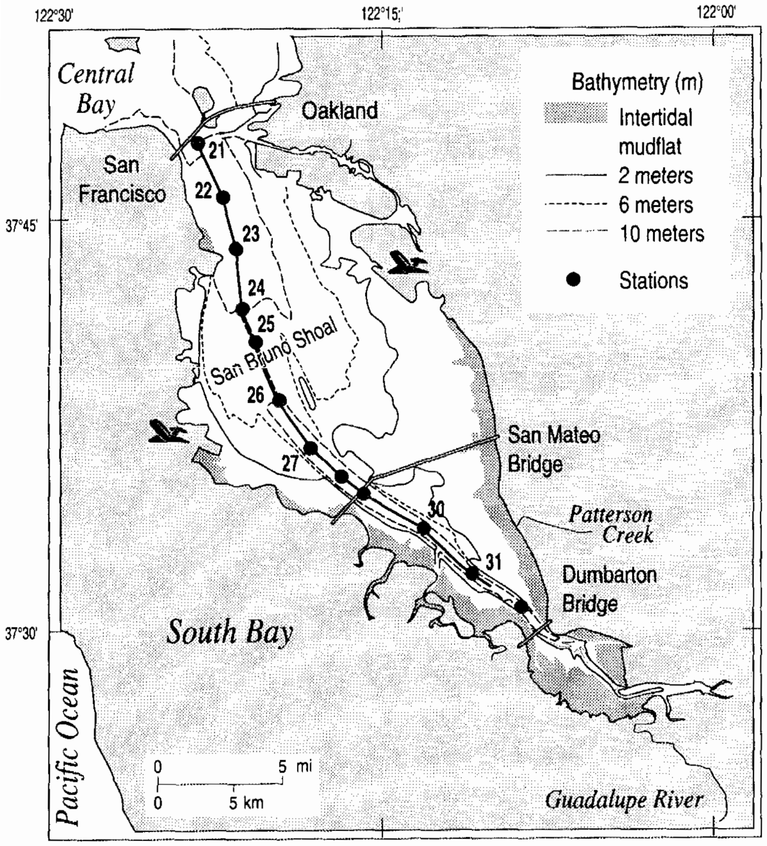

Figure 5. Map of south San Francisco Bay showing locations of fixed sampling stations along the longitudinal channel.

Table 4. Phytoplankton Species Commonly Observed During Spring Blooms in South San Francisco Bay

Class	*Species*
	Diatoms
Diatomophyceae	*Chaetoceros debile*
	Chaetoceros decipiens
	Chaetoceros didymus
	Chaetoceros gracilis
	Chaetoceros socialis
	Chaetoceros vistulae
	Chaetoceros wighami
	Coscinodiscus curvatulus (*Actinocyclus curvatulus*)
	Coscinodiscus lineatus (*Thalassiosira leptopus*)
	Coscinodiscus radiatus
	Cyclotella meneghiniana
	Cyclotella sp.
	Cyclotella striata
	Ditylum brightwelii
	Eucampia zoodiacus
	Leptocylindrus minimus
	Nitzschia seriata (Pseudo-nitzschia seriata)
	Paralia sulcata
	Rhizosolenia setigera
	Skeletonema costatum
	Thalassiosira decipiens (*Thalassiosira angulata*)
	Thalassiosira rotula
	Nondiatoms
Chlorophyceae	*Chlorella marina*
	Chlorella salina
	Monoraphidium convolutum
	Nannochloris atomus
Chrysophyceae	*Chromulina* sp.
	Kephyrion sp.
	Ochromonas sp.
Cryptophyceae	*Chroomonas acuta* (*Teleaulax acuta*)
	Chroomonas amphioxeia (*Teleaulax amphioxeia*)
	Chroomonas salina (Rhodomonas salina)
Dinophyceae	*Gonyaulax tamarensis* (*Alexandrium ostenfeldii)*
	Heterocapsa triquetra
	Katodinium rotundatum
	Prorocentrum minimum
	Protoperidinium claudicans
Prasinophyceae	*Pyramimonas* micron (or *P. orientalis*)
	Tetraselmis gracilis
Photosynthetic ciliates	*Mesodinium rubrum*

From samples taken during 1992–1995 and microscopic enumerations/identifications of R G Dufford (personal communications, 1992–1995). Names in parentheses are revisions based on the taxonomy of *Tomas* [1993, 1996]

bloom dynamics because it has a recurrent, somewhat predictable period of rapid biomass increase during the spring months. This lagoon-like basin has an irregular bottom topography with sharp bathymetric transitions between the 10- to 25-m-deep axial channel and the lateral shallows (Figure 5). and a large transverse shoal (San Bruno) that slows horizontal exchanges between the seaward and landward estuary. Local streams carry runoff to the lower (landward) estuary. The open connection to the central bay allows fresh water from the Sacramento and San Joaquin Rivers to intrude into the south bay during periods of high river flow (Figure 1) and allows tidal exchange between the South Bay and coastal ocean. The basin's residual (tidally averaged) circulation is slow, with mean seaward flow along the eastern shallows and landward flow along the channel [*Cheng and Gartner*, 1985] and a hydraulic residence time of several months [*Walters et al.*, 1985]. This weak mean circulation can be disrupted by strong wind events or freshwater inputs that alter the strength and direction of the residual flows [*Huzzey et al.*, 1990]. Water density is often vertically uniform, indicating rapid vertical mixing of the water column. The channel can become salinity stratified after periods of runoff that deliver low-density fresh water as a source of buoyancy, but stratification occurs only during neap tides when the tidal stirring is weak [*Cloern*, 1984]. Phytoplankton primary production is the largest source of organic carbon to south San Francisco Bay [*Jassby et al.*, 1993], and much of the total annual primary production occurs during the spring [*Cole et al.*, 1986].

The south San Francisco Bay spring bloom has been followed every year since 1978, and the patterns of variability within this series can be used to illustrate some general lessons of phytoplankton bloom dynamics in SCEs. The core measurement program in south San Francisco Bay includes vertical profiles of salinity, temperature, chlorophyll (by calibrated fluorometry), and turbidity at sampling stations (Figure 5) spaced about every 3–4 km along the channel (detailed methods are given in annual data reports [e.g., *Edmunds et al.*, 1995]). Water samples are also taken for microscopic examination to determine the abundance of phytoplankton species present during the spring blooms (Table 4). The sampling frequency in 1978–1979 was once monthly; after 1979 the sampling frequency was increased to once or twice weekly during the period of the spring blooms.

Bloom dynamics are characterized here with the chlorophyll measurements made along the channel transect (Figure 5). Near-surface chlorophyll is used as a measure of biomass in the photic zone (i.e., the quantity that contributes to primary production), and vertical variability is not considered here. Lateral variability is also not considered, although there is coherence between the seasonal dynamics of phytoplankton biomass in the channel and adjacent shallows [*Cloern and Cheng*, 1981; *Cloern et al.*, 1985; *Vidergar et* al., 1993]. Plate 2 depicts the chlorophyll fluctuations in south San Francisco Bay with color, and several prominent patterns of variability stand out. First, the solid background shows that biomass is usually less than 5 μg L^{-1} chlorophyll *a*. Second, a period of rapid biomass growth (a bloom) occurs during the spring of every year. Third, bloom intensity is often greatest in the landward estuary. consistent with the trends in the high-resolution chlorophyll transects.

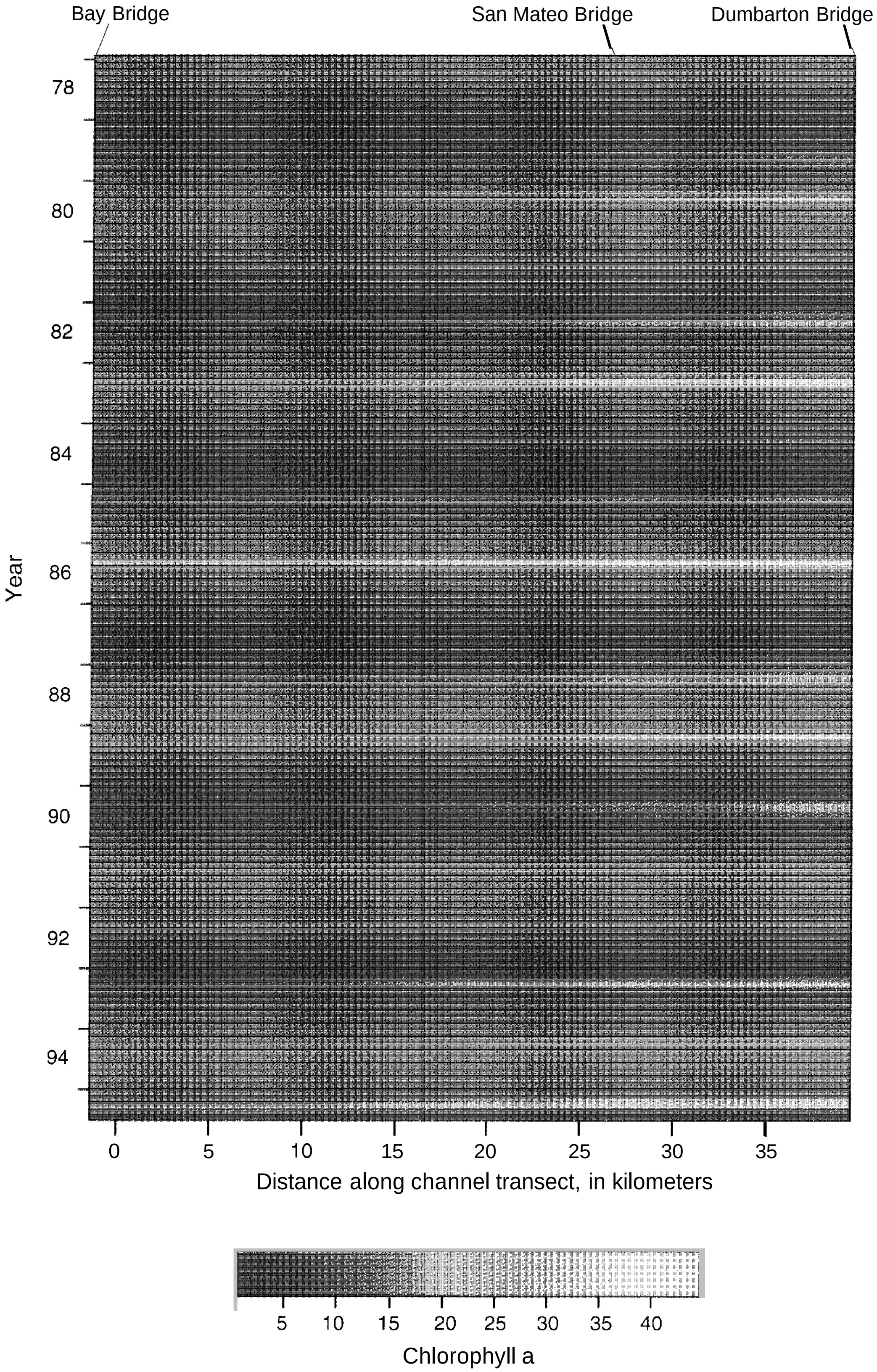

Plate 2. Color representation of spatial-temporal variabiliiy of phytoplankton biomass (chlorophyll a concentration) in south San Francisco Bay. Blooms are shown as departures from the low background biomass (green), with bloom intensiiy proportional to color brightness. The vertical axis represents time from January 1978 to July 1995, and the horizontal axis represents spatial variability along the channel transect from the seaward estuary (station 21) to the landward estuary (siation 32). Color contours were produced from a matrix of interpolated values based on 4449 measurements of surface chlorophyll a concentration on 417 dates.

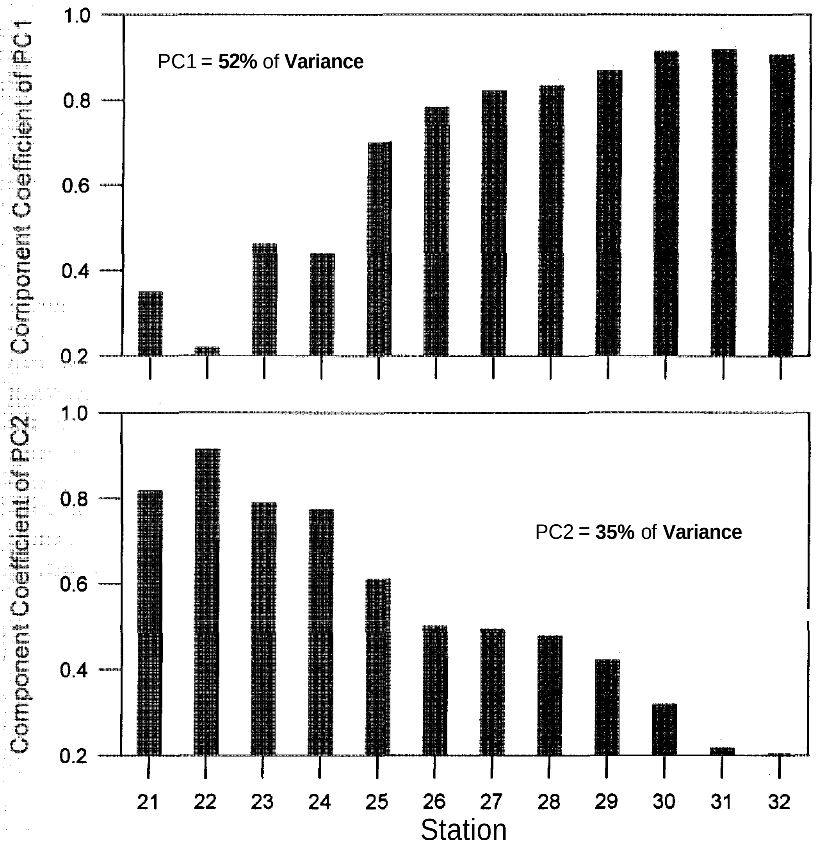

Figure 6. Coefficients (loadings) of the first two principal components, which account for 87% of the chlorophyll variance along the south San Francisco Bay transect, for the period January 1978 to July 1995. Principal component analysis was done on the correlation matrix, and results are varimax-rotated solutions [*Jassby and* Powell, 1990]. This analysis suggests two independent spatial modes of phytoplankton biomass variability: one (PC1) in the landward estuarine basin south of station 25, and a second (PC2) in the seaward estuary north of station 25.

Finally, the nature of the spring bloom changes from year to year. For example, the 1986 spring bloom was a monthlong event of very high chlorophyll concentration (maximum >70 μg L^{-1}) along the entire transect. The 1991 spring bloom was a short-lived event confined to the landward estuary, where maximum chlorophyll concentration was only 12 μg L^{-1}. The patterns revealed in this image illustrate two lessons that apply generally to shallow coastal ecosystems: (1) phytoplankton blooms are spatially heterogeneous, and (2) the timing and magnitude of the seasonal blooms change from year to year.

The patterns of population variability in time and space can be formalized with multivariate techniques such as principal components analysis (PCA). If we consider measurements at sampling stations as variables, and sampling dates as individual cases, then PCA can reveal patterns of spatial coherence in the temporal fluctuations of biomass along a transect. This PCA of the south San Francisco Bay data set identifies two principal components that together account for 87% of the total chlorophyll variance. The first principal component (PC1), which accounts for 52% of the chlorophyll variance, has small coefficients (or loadings) at the seaward stations and progressively larger coefficients at the landward stations (Figure 6). The second component (PC2), accounting for an additional *35%* of the variance, has largest coefficients at the seaward stations. This PCA shows that most of the phytoplankton biomass variability in south San Francisco Bay can be explained with only two spatial modes (patterns): the first is expressed strongly in that region of the estuary landward of station 25, and the second is expressed strongly in the region of the estuary seaward of station 25 (Figure 6). This separation of the two spatial modes at station 25 corresponds to the location of the San Bruno Shoal (Figure *5),* a topographic control of horizontal mixing. The tidally averaged circulation of south San Francisco Bay is characterized by a slowly rotating gyre that acts to retain fluid within the central basin of the estuary, below the San Bruno Shoal [Cheng and Casulli, 1982]. The PCA result is consistent with this mean circulation that maintains two spatial domains separated by a topographic control of mixing [Powell et al., 1986]. This lesson applies to other coastal ecosystems where the mesoscale spatial variability of plankton reflects the water circulation patten [*Jouffre* et al., 1991] and where distinct spatial domains can have different temporal patterns of bloom evolution [*Therriault* and Levasseur, 1986; *Kahru* and *Nômmann*, 1990; *Glibert* et al., 1995].

A second result of PCA is the series of scalar amplitudes (or scores) that express the relative importance of each principal component over time [Jassby and Powell, 1990]. Figure 7 shows the time series of amplitudes for PC1. This series is a representation of pattern in the temporal variability of phytoplankton biomass in the landward basin. This temporal pattern is dominated by episodic spikes that occur in the spring of each year, with

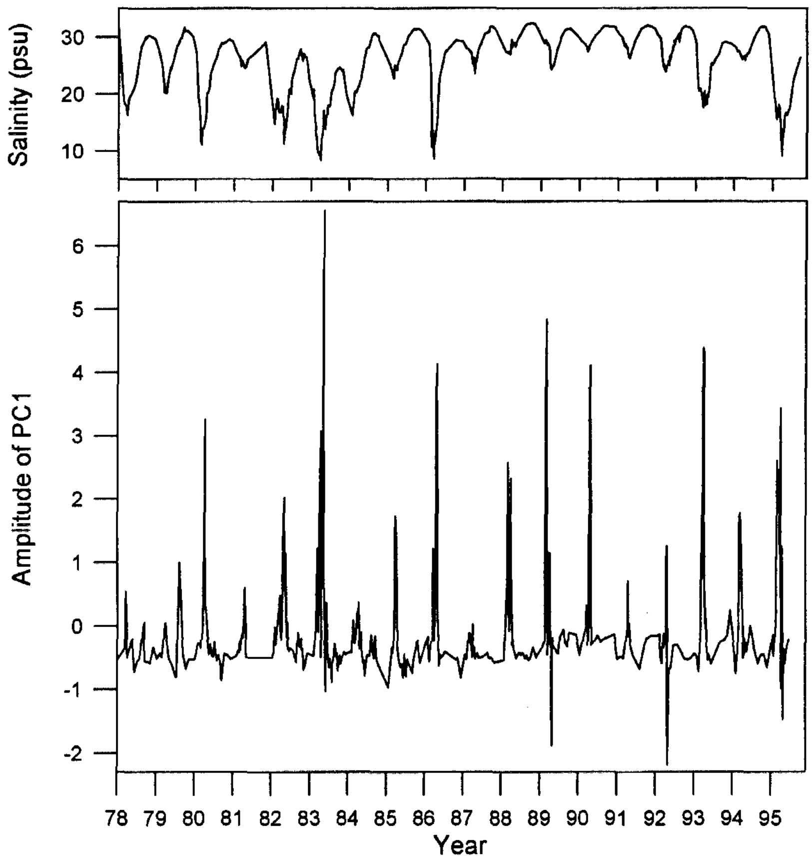

Figure 7. (bottom) Time series of amplitudes (scores) for the first principal component of chlorophyll variability in south San Francisco Bay. Large amplitudes correspond to events of high phytoplankton biomass (blooms) in the landward estuary. (top) Parallel series of near-surface salinity in the landward estuary (mean of measurements at stations 26–32), illustrating that blooms occur during the wet season of high river flow and annual salinity minima.

prominent year-to-year fluctuation in the timing, duration, and magnitude of these spikes.

Mechanisms of variability. The series of principal component amplitudes in Figure 7 is consistent with the notion of phytoplankton blooms as departures from population quasi-equilibrium. Blooms are population outbursts that can appear and dissipate within a period of weeks. What determines the timing of these outbursts, their duration, and their magnitude, and why do these features change from year to year? The two series in Figure 7 show that blooms occur in south San Francisco Bay during the wet season, when surface salinity is diluted by fresh water. This seasonal coherence between bloom development and low salinity results, in part, from the stabilization of the water column by the salinity stratification induced by freshwater inflows [*Cloern*, 1991a, b]. The absence of blooms in summer–autumn is also a response to the seasonal cycles of the benthic suspension-feeding animals, whose biomass and grazing rate are highest in summer. Therefore the seasonal distribution of blooms in this particular estuary appears to be a response to seasonal fluctuations in hydrology (river flow and its influence on density stratification) and trophic interactions (grazing losses to benthic consumers).

At shorter timescales, too, the timing of blooms is regulated by physical processes that influence the balance between phytoplankton production and losses. Simulation experiments with numerical models show that this balance is sensitive to the rate of vertical mixing in the water column [*Cloern*, 1991b]. Vertical mixing is brought about by tidal stresses applied at the bottom and wind stresses on the water surface [*Simpson et al.*, 1991], and in mesotidal SCEs the tidal stresses often dominate. Weak tidal stirring promotes blooms by (1) slowing the turbulent diffusive loss of phytoplankton biomass from the photic zone [*Koseff et al.*, 1993], (2) deepening the photic zone (growth habitat) as tidal resuspension of bottom sediments weakens [*Schoellhamer*, 1996], and (3) reducing the vertical flux of phytoplankton to benthic consumer animals [*Cloern*, 1991b]. Blooms develop during periods of weak tidal energy, and they dissipate during periods of strong tidal energy. This lesson is illustrated in Figure 8, which shows the evolution of the 1985 spring bloom and the simultaneous changes in the daily tidal current amplitude U. Rapid biomass (chlorophyll) growth occurred during the neap tide in late March; this bloom dissipated soon after the subsequent spring tide in early April.

The association between weekly-scale chlorophyll variability and the tidal regime is a prominent feature of phytoplankton population dynamics in south San Francisco Bay. This association is illustrated in Figure 9, which shows a linear relationship between the rate of biomass change and the antecedent tidal current speeds for all the large spring blooms observed between 1978 and 1995. The rate of biomass change, R, was calculated as

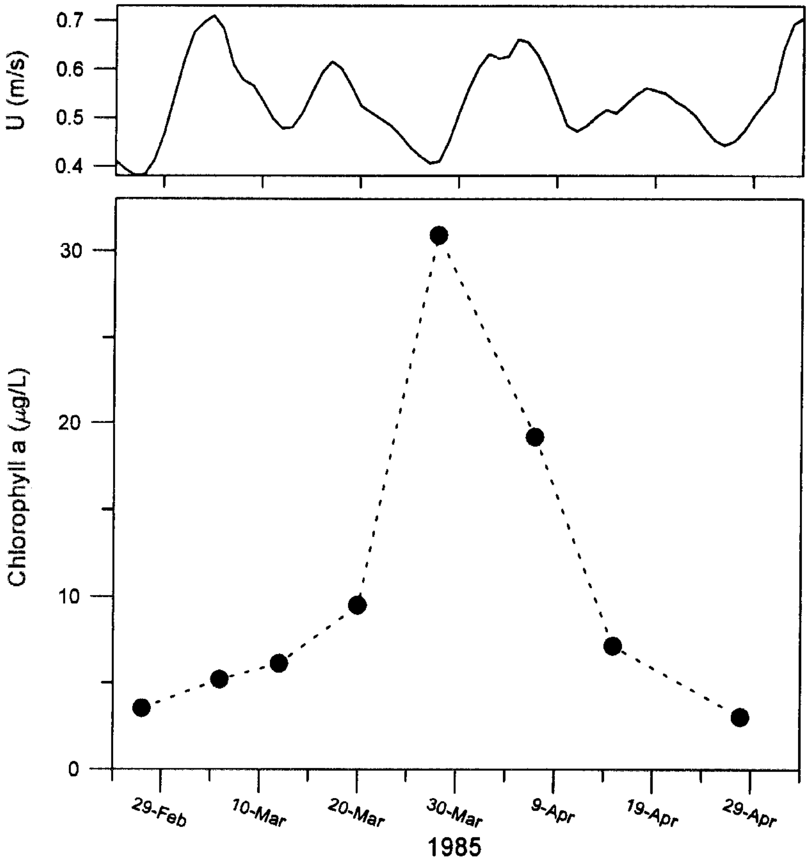

Figure 8. The 1985 spring bloom in south San Francisco Bay: (bottom) weekly fluctuations of phytoplankton biomass in the landward estuary (mean chlorophyll *a* concentration at stations 26–32) and (top) daily fluctuations in the tidal current amplitude *U*. Current amplitudes were computed from tidal harmonic constants derived from long-term current measurements in the central south bay channel [*Cheng and Gartner*, 1985] (predicted *U* from J. W. Gartner (personal communication, 1995)). Biomass increased rapidly after March 20, when *U* was less than 0.5 m s^{-1}.

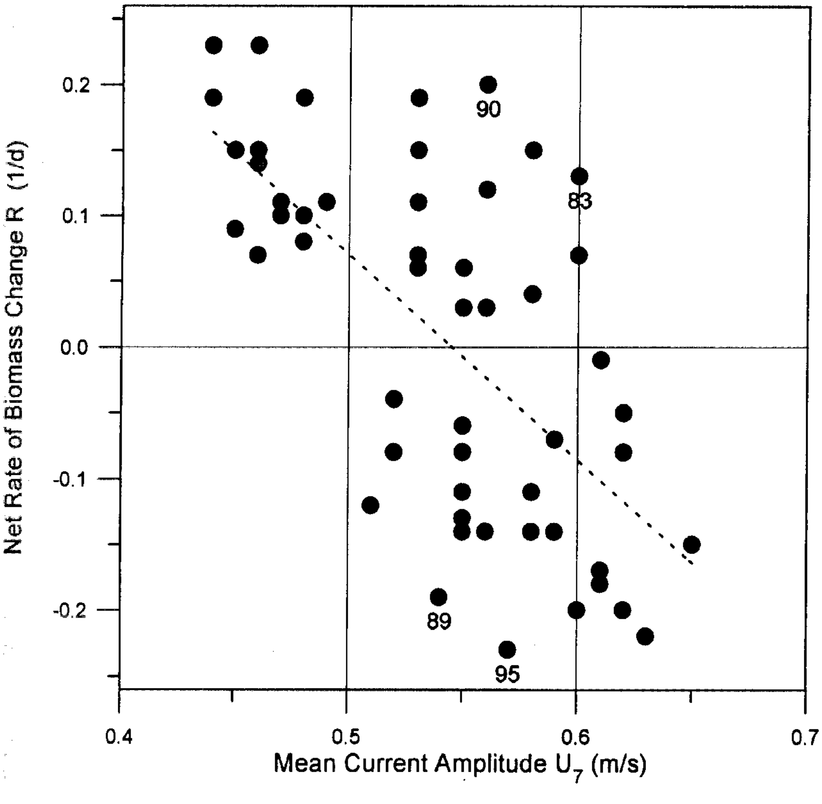

Figure 9. Tidal forcing and phytoplankton blooms in south San Francisco Bay. The net rate of biomass change, *R*, was calculated from the week-to-week changes in mean chlorophyll *a* concentration in the landward estuary (stations 26–32). The tidal regime is represented by the 7-day mean current amplitude, U_7. Points represent all the weekly-scale events of 1978–1995 in which the mean chlorophyll *a* concentration fell below or increased above 10 μg L^{-1} (updated and revised from Figure 4 of *Cloern* [1991b]). The dashed line is the least squares regression of *R* against U_7 ($r = 0.66$). Deviations around this regression in 1983, 1989, 1990, and 1995 are examined in Figures 10–13 to illustrate other mechanisms of bloom variability.

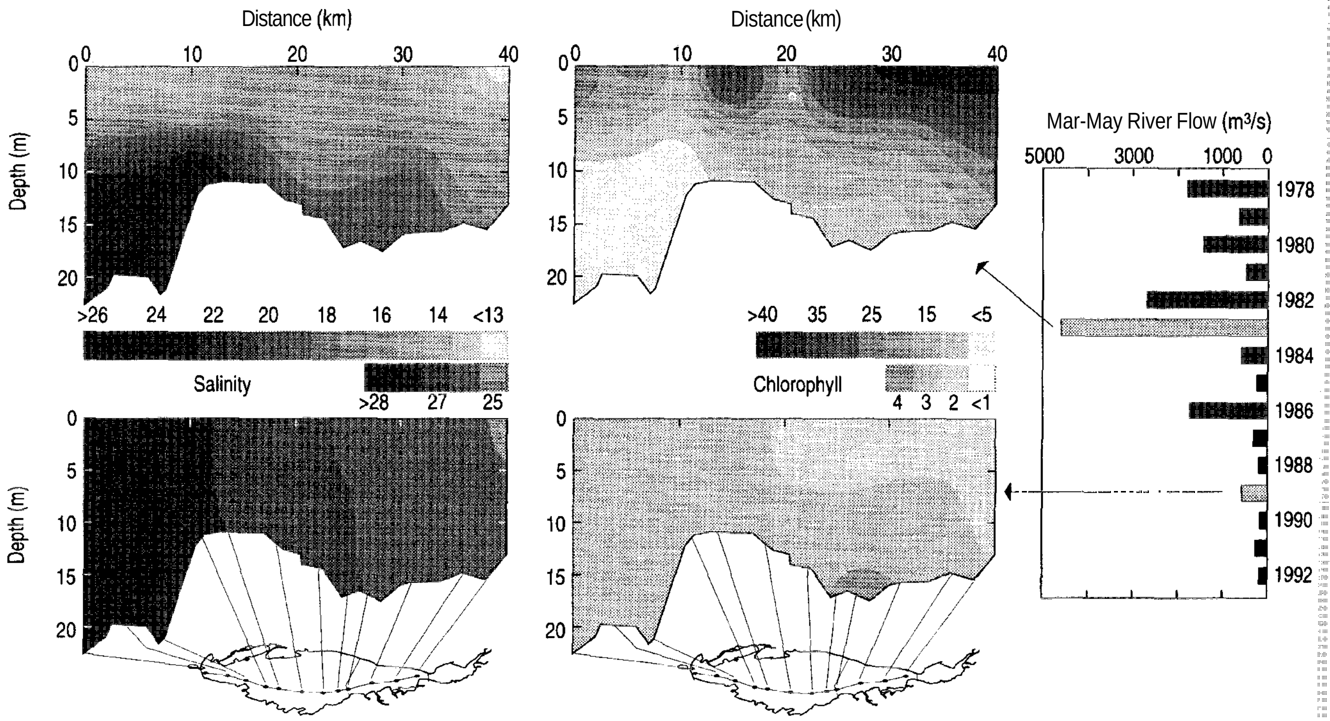

Figure 10. Sectional (vertical-longitudinal) contour plots of the (left) salinity and (right) chlorophyll a distributions along the south San Francisco Bay channel, going from the seaward (station 21) to landward (station 32) estuary. Top panels show strong vertical gradients in May 1983 following a period of exceptionally high river discharge. Bottom panels show vertical homogeneity in May 1989 that is representative of the estuarine condition after periods of lower river flow. The mean freshwater inflow to north San Francisco Bay (Delta Outflow Index, from the California Department of Water Resources) for the months March–May is shown at far right. The spring of 1983 was the wettest in this century.

$$R = \ln [B_{t+\Delta t}/B_t]/\Delta t \qquad (4)$$

where $B_{t+\Delta t}$ is biomass (mean chlorophyll a in the landward estuary) at time $t + \Delta t$; B_t is biomass at previous time t; and $R(1/d)$ is the specific rate of biomass change over time increment Δt. The rate R represents the net result of all the processes of biomass change. This net rate is inversely related to the tidal current amplitude averaged over the previous week, U_7 (Figure 9). The distribution of points in Figure 9 shows that the biomass change R was always positive (i.e., a bloom developed) when U_7 was less than 0.5 m s^{-1}: phytoplankton biomass increased during extremely weak neap tides. Conversely, R was always negative when U_7 exceeded 0.6 m s^{-1}: blooms dissipated during the highly energetic spring tides. For tidal regimes between these extremes, R was either positive or negative: blooms can either grow or dissipate at intermediate tidal energies.

The linear relation between R and U_7 suggests that the timing of bloom inception is set by the astronomical tides. However, deviations around this linear relation are large, especially at the intermediate tidal regimes (Figure 9), so other processes must come into play. The individual deviations around the linear relation between R and U_7 can reveal some of these other mechanisms of population variability. As an example, the rate of biomass growth during May 1983 was much larger than that predicted from the tidal regime alone (see Figure 9). This positive deviation ($+R$) from the linear model can be explained by the unusual hydrography of 1983: exceptionally high river flow and strong salinity stratification that persisted into May (Figure 10). The intense stratification observed in May of 1983 (but not other years) stimulated rapid biomass increases in the surface layer. The combined effects of large buoyancy input plus weak tidal stirring created an unusually stable water column and unusually large blooms during 1983 (Figure 7). Therefore the year-to-year fluctuations in spring bloom magnitude are determined partly by annual fluctuations in precipitation and river flow, with exceptionally large blooms (1982, 1983, 1986, 1995) during years of exceptionally high river flow [*Cloern* and *Jassby*, 1995].

Climate can modulate the development of blooms in other ways. The positive growth rate deviation ($+R$) in 1990 occurred during a period of unusually calm winds in late March and early April (Figure 11), when the bloom magnitude was amplified by the small inputs of mixing energy at the surface [*Koseff et* al., 1993]. On the other hand, the negative growth-rate deviation ($-R$) in 1989 followed an event of strong westerly winds that persisted for several days. Westerly winds of 10 m s^{-1} generate a seaward flow along the channel at speeds up to 10 km d^{-1} [Walters, 1982; *Cheng* and Casulli, 1982].

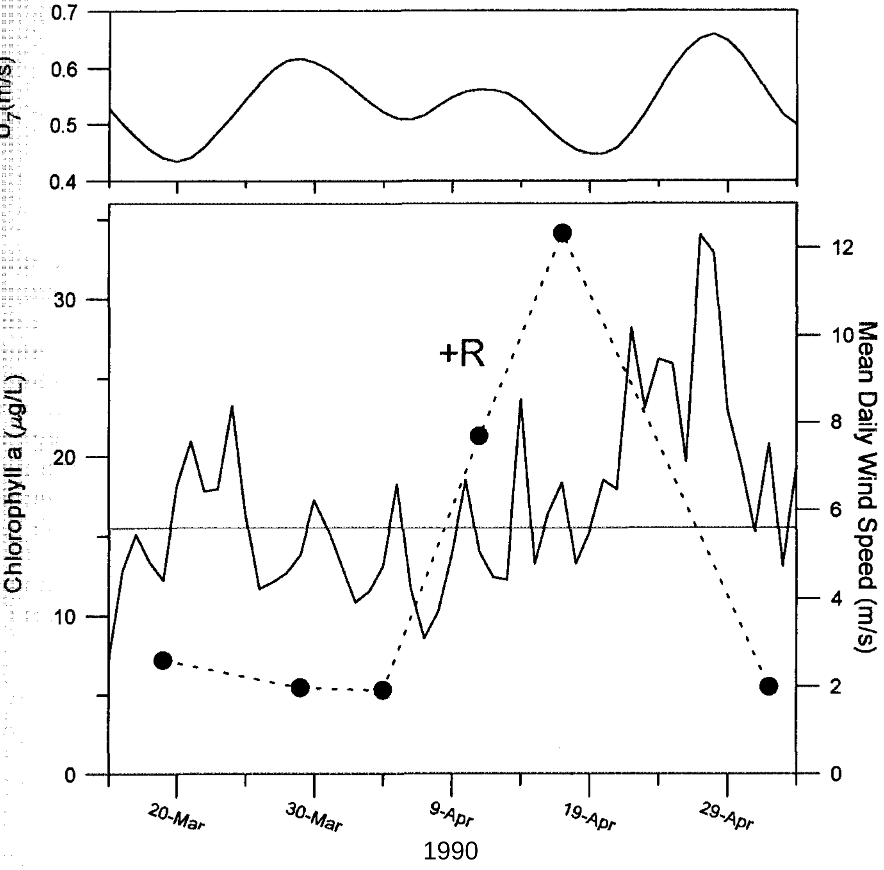

Figure 11. The 1990 spring bloom in south San Francisco Bay. (bottom) Weekly changes in chlorophyll a concentration in the landward estuary (dashed line) and daily fluctuations in mean wind speed (solid line). The horizontal line shows the long-term mean wind speed for March–April (5.6 m s^{-1}). (top) The 7-day running mean tidal current amplitude U_7. A period of unusually rapid biomass increase $(+R)$ occurred in early April, following 2 weeks of unusually calm winds.

Therefore the negative deviation in early March 1989 (Figure 12) was probably the result of wind-driven pulsed flows that carried phytoplankton biomass away from the landward estuary, coupled with the negative effects of rapid vertical mixing by the surface wind stress.

The negative growth rate deviation (−R) in 1995 illustrates another mechanism of bloom regulation. The 1995 spring bloom began in late February, and high biomass persisted for over a month. This period of sustained high biomass led to a steady depletion of dissolved inorganic nitrogen (Figure 13) as the phytoplankton assimilated nutrients faster than they were replaced by inputs and regeneration. By late March the initial high stock of dissolved inorganic nitrogen was exhausted, and the potential rate of further biomass production became limited by the availability of N. As a result, the phytoplankton biomass declined rapidly in early April. This example illustrates that phytoplankton biomass production can be episodically nutrient limited, even in SCEs that receive large inputs of nutrients.

A Synthetic Picture of Bloom Mechanisms

This detailed analysis of chlorophyll variability in south San Francisco Bay leads to a general picture of how the timing and magnitude of the spring bloom change from year to year. The proximal agents of blooms are changes in the physical state of the estuary as determined by inputs of energy at the interfaces with the coastal ocean, rivers, and the atmosphere (Figure 14). Tides originate in the ocean, propagate into the estuary, and influence turbidity and light availability for photosynthesis (through tidal resuspension of bottom sediments), the intensity of turbulent mixing, and the patterns of horizontal circulation. The strength of the tidal forcing fluctuates, and episodes of minimal tidal energy occur within each neap-spring and lunar monthly period. The monthly minimum tides create a physical condition that promotes bloom development through several different mechanisms, and these periods of weak tides provide windows of opportunity for the phytoplankton population to grow. The timing of potential bloom development is set by the astronomical tides and is therefore predictable in estuaries such as south San Francisco Bay.

The degree to which phytoplankton populations can respond to the tidal windows is determined by hydrology, weather, nutrient availability, and the activity of consumer organisms. River flow delivers fresh water that establishes density-driven circulations, and it is a source of buoyancy to stratify the water column and inhibit vertical mixing. If freshwater buoyancy inputs are large enough to offset the effects of tidal and wind stirring, then the water column remains stratified for a sufficiently long period that phytoplankton biomass can grow and reach high levels. Other sources of buoyancy, such as rapid heating of the surface layer during periods of calm, stable weather, can have the same effect. Winds

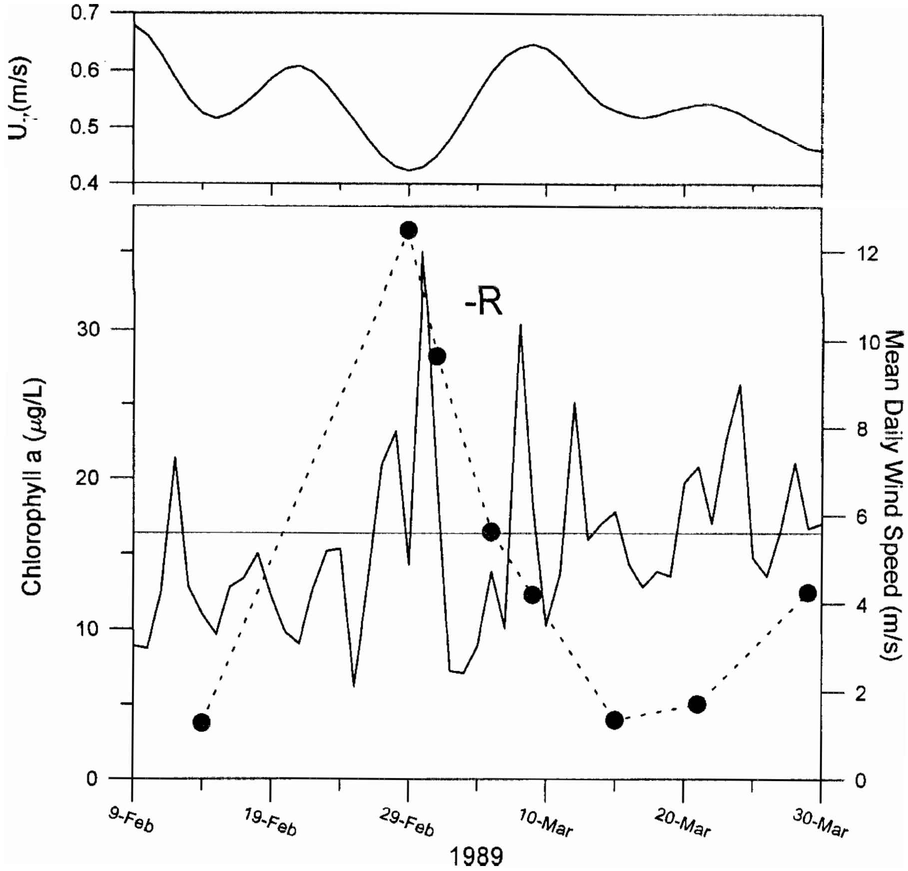

Figure 12. The 1989 spring bloom in south San Francisco Bay. (bottom) Weekly changes in chlorophyll a concentration in the landward estuary (dashed line) and daily fluctuations in mean wind speed (solid line). The horizontal line shows the long-term mean wind speed for March–April (5.6 m s^{-1}). (top) The 7-day running mean tidal current amplitude U,. The rapid biomass decline (– R) in early March followed a storm when daily wind speeds exceeded 12 m s^{-1}.

further influence the development of blooms by altering the circulation patterns and transport of phytoplankton, turbidity and the light climate (through wind-wave resuspension of bottom sediments), and the breakdown of stratification and enhancement of vertical mixing (Figure 14).

The magnitude of the spring bloom in south San Francisco Bay is set by the initial stocks of nutrients required for biomass production, the water circulation pattern as it determines phytoplankton residence time within the estuarine basin, the potential losses to pelagic and benthic grazers, and the particular combination of climatic-hydrologic conditions during the tidal windows

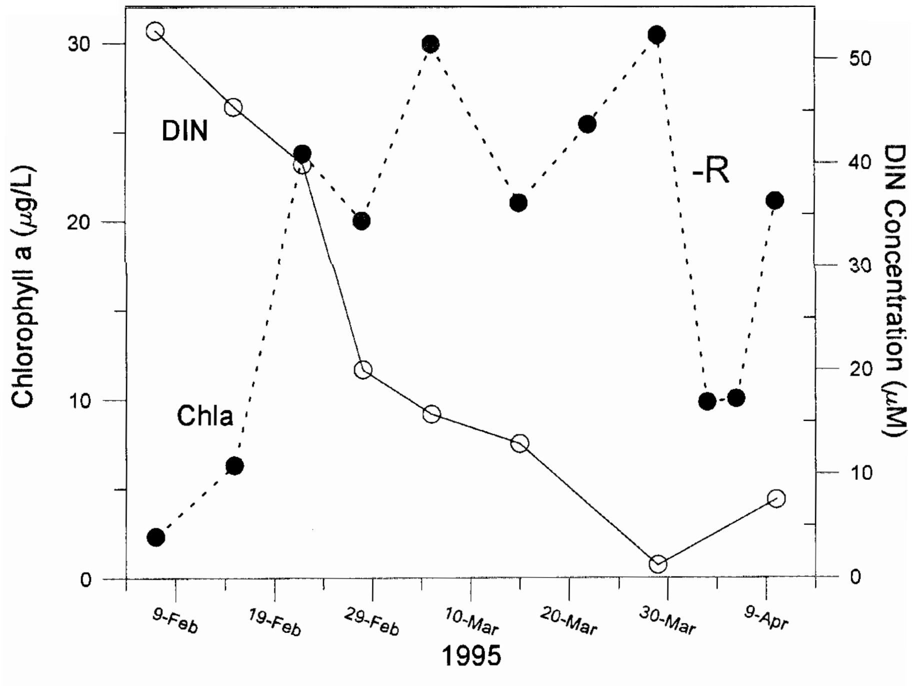

Figure 13. The 1995 spring bloom in south San Francisco Bay. The dashed line shows the weekly fluctuations in mean chlorophyll a concentration in the landward estuary (stations 26–32); the solid line shows parallel changes in the concentration of dissolved inorganic nitrogen (DIN = nitrate + nitrite + ammonium). The event of unusually rapid biomass decline (– R) in early April occurred after the large initial stock of inorganic nitrogen became depleted. Nutrient data from S. W. Hager (personal communication, 1995).

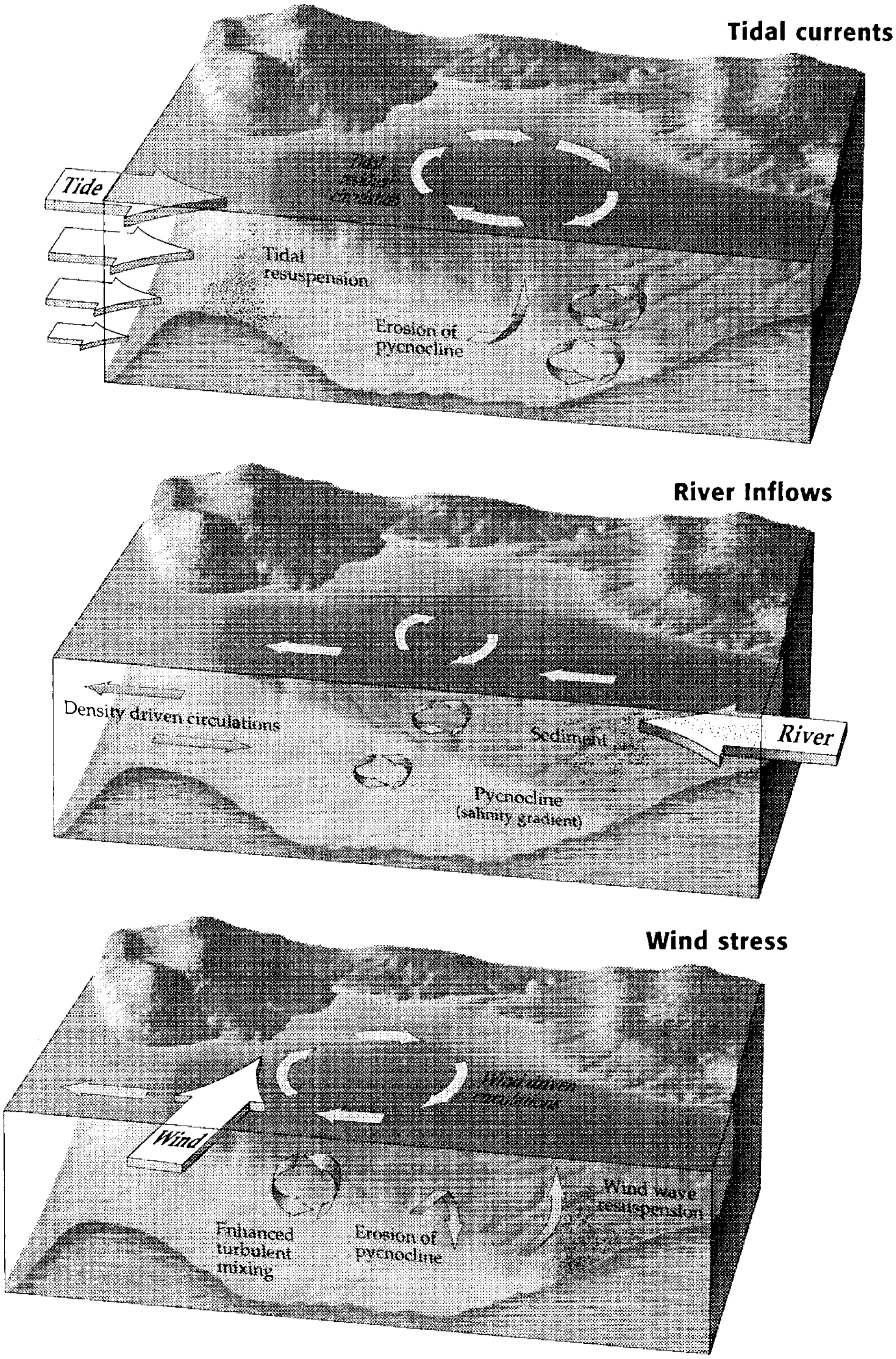

Figure 14. Cartoon diagrams of three physical forcings that operate at the interface between SCEs and the coastal ocean (tides), watershed (river inflow), and atmosphere (wind). Each physical forcing influences the growth rate of the resident phytoplankton population through, for example, its influence on the distribution of suspended sediments and turbidity. Each forcing also influences the rate of vertical mixing, with riverine inputs of fresh water as a source of buoyancy to stratify the water column and the tide and wind as sources of kinetic energy to mix the water column. Each forcing is also a mechanism of water circulation that transports phytoplankton horizontally. Much of the variability of phytoplankton biomass during blooms can be understood as responses to fluctuations in these interfacial forcings.

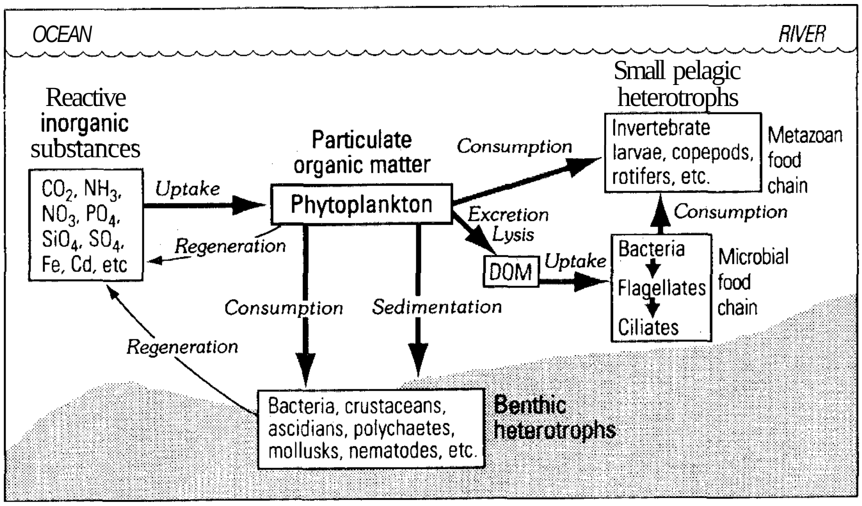

Figure 15. Schematic illustrating the central role of phytoplankton as agents of biogeochemical change in shallow coastal ecosystems. Phytoplankton assimilate reactive inorganic substances and incorporate these into particulate (POM) and dissolved organic matter (DOM) which support the production of pelagic and benthic heterotrophs. Arrows indicate some of the material fluxes between these different compartments.

of potential population growth. Blooms are biological responses to physical variability [*Paerl*, 1988], where the timescales of bloom variability are set by the timescales of the prominent physical forcings [*Legendre and Demers*, 1984]: semidiurnal, daily, and weekly tidal fluctuations; seasonal, episodic, and interannual fluctuations in river flow; and seasonal and event-scale fluctuations in wind stress.

LINKAGES OF PHYTOPLANKTON TO THE BIOGEOCHEMICAL SYSTEM

The preceding section presented the patterns and mechanisms of phytoplankton bloom variability in San Francisco Bay to illustrate the strong linkages between the climate system, hydrologic cycle, and biological populations in the coastal zone. Here we explore the geochemical and ecological implications of these phytoplankton population fluctuations. Geochemists and ecologists use mass balances to describe the dynamical nature of the systems they study. Figure 15 is an example showing some of the linkages between the phytoplankton and other components of estuarine-coastal ecosystems. This diagram shows exchanges between five pools of matter: reactive inorganic substances (RIS; see Table 5) that are transformed by biogeochemical processes; particulate organic matter (POM), which includes phytoplankton, detritus, and organic matter sorbed onto suspended sediments; dissolved organic matter (DOM) including metabolites produced by phytoplankton and released into the water; and populations of the pelagic and benthic consumer organisms (heterotrophs) that use phytoplankton-derived organic matter for their nutrition.

Phytoplankton are linked to the pool of reactive inorganic substances through their uptake and assimilation of CO, and the other raw materials required for photosynthesis and the biosynthesis of new phytoplankton biomass. Heterotrophs are linked to the phytoplankton either through their direct consumption of live algal biomass or their consumption/assimilation of algal-derived detritus or DOM. Phytoplankton consumption occurs in the water column, by pelagic heterotrophs, and in the sediments, by benthic heterotrophs (Figure 15). The heterotrophs are not perfectly efficient at transforming food into new biomass, so their feeding and metabolic activities return a portion of the ingested organic matter back to the RIS or DOM pools (the process of regeneration or remineralization).

Although the pools of reactive materials and their

Table 5. Frequently Used Acronyms and Abbreviations

Abbreviation	*Definition*
DIC	dissolved inorganic carbon (all species of CO_2), m*M*
DIN	dissolved inorganic nitrogen (total of NO„, NO_2^-, NH_4^+), μ*M*
DOC	dissolved organic carbon
DOM	dissolved organic matter
DRP	dissolved reactive phosphorus, μ*M*
DSi	dissolved silicate, μM
$\delta^{13}C$	measure of the ratio $^{13}C : ^{12}C$ relative to a standard, ‰
$\delta^{13}C$ POM	measure of the ratio $^{13}C : ^{12}C$ in the particulate organic matter, ‰
$\delta^{15}N$	measure of the ratio $^{15}N : ^{14}N$ relative to a standard, ‰
PCA	principal component analysis
PC1, PC2	first and second principal components
PC	particulate carbon, yg L^{-1}
PC:PN	ratio of particulate carbon to particulate nitrogen, mol mol^{-1}
PN	particulate nitrogen, yg L^{-1}
POM	particulate organic matter
PP	particulate phosphorus
PUFA	polyunsaturated fatty acids
RIS	reactive inorganic substances
SCE	shallow coastal ecosystem
SPM	suspended particulate matter, mg L^{-1}
u	tidal current speed amplitude, m s^{-1}

linkages are more complex than is suggested in Figure 15, this diagram illustrates how phytoplankton primary production acts to transform inorganic substances into organic matter. This newly produced organic matter exists in forms that are readily available to consumer organisms. Thus phytoplankton primary production is a key process in both the cycling of reactive elements and in trophic dynamics (the transfers of matter and chemical energy between organisms). These transformation processes operate continuously, but they are not easily observed when the rates of RIS uptake and regeneration, or the rates of phytoplankton production and consumption, are balanced. These balances are disrupted during phytoplankton blooms, when the rate of primary production temporarily exceeds the rate of consumption. Blooms are biological events that cause large geochemical changes (transformations of RIS into POM or DOM), followed by accelerated consumption and metabolism of organic matter by the heterotrophs. Therefore all the roles played by phytoplankton in element cycling and trophic dynamics are amplified during blooms. This central role of the phytoplankton can be illustrated with some geochemical and biological responses to the spring blooms observed in south San Francisco Bay.

Phytoplankton biomass in south San Francisco Bay is low except during the spring blooms, when chlorophyll concentrations exceed 10 $\mu g\ L^{-1}$ and reach peaks in the range of 50–70 $\mu g\ L^{-1}$ (Figure 16a). Phytoplankton primary productivity is typically <0.5 g C $m^{-2}\ d^{-1}$, except during the spring blooms when the rate of production can exceed 1 g C $m^{-2}\ d^{-1}$ and reach peaks of the order of 2–3 g C $m^{-2}\ d^{-1}$ (Figure 16b). Primary productivity is a measure of the rate at which new organic matter is produced and made available to the heterotrophs, and rates of other biological processes (in composite, the system metabolism) accelerate as a response to these new inputs of food. This response is seen, for example, in the production rate of pelagic bacteria, which peaks during March–April (Figure 16c). Pelagic respiration (measured as oxygen consumption), an index of total microbial metabolism in the oxygenated water column, also peaks in spring (Figure 16d). These accelerated rates of biological activity are general responses to phytoplankton blooms: pelagic respiration is correlated with phytoplankton biomass and primary productivity [*L. M. Jensen et al.*, 1990; *Iriarte et al.*, 1991], and bacterial and primary productivity are tightly coupled in coastal ecosystems where phytoplankton are the dominant source of labile organic matter [*Lancelot and Billen*, 1984; *Billen and Fontigny*, 1987; *Cole et al.*, 1988; *Lignell et al.*, 1993].

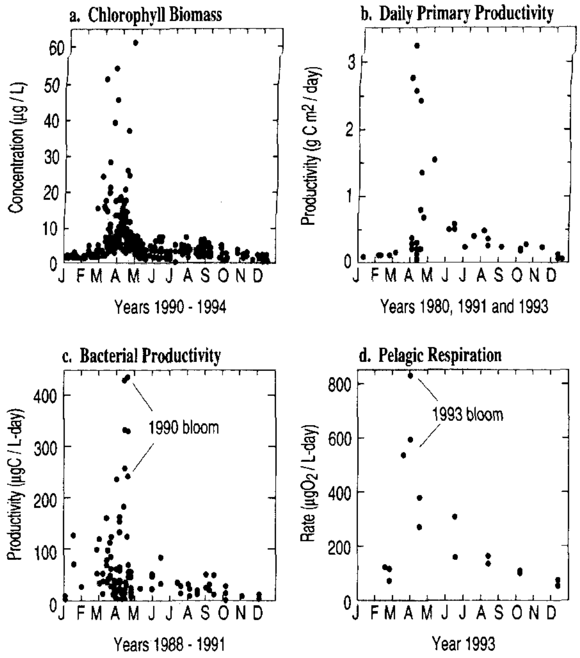

Figure 16. Seasonal distributions of phytoplankton biomass (as chlorophyll *a*) and three indices of system metabolism in south San Francisco Bay: (a) near-surface chlorophyll *a* concentrations (measurements between USGS stations 29 and 33 for the years 1990–1994; data from *Wienke et al.* [1991, 1992, 1993], *Caffrey et al.* [1994], and *Edmunds et al.* [1995]), (b) primary productivity (between USGS stations 27 and 32 for the years 1980, 1991, and 1993; data from *Cole and Cloern* [1984, 1987] and B. E. Cole (personal communication, 1993)), (c) pelagic bacterial productivity (between USGS stations 21 and 36 for the years 1988–1991; data from *Hollibaugh and Wong* [1996]), and (d) pelagic respiration measured as oxygen consumption during 24-hour incubations of sample water in dark bottles (USGS stations 27 and 32 during 1993; data from *Rudek and Cloern* [1996]).

One consequence of the shallow water depth of SCEs is a close linkage between the pelagic and benthic domains. Food delivery to the benthos is enhanced during blooms, either by the active particle capture of suspension-feeding macrofauna (e.g., bivalve mollusks, polychaete worms, and crustaceans) or through the deposition of phytoplankton-derived POM onto the sediment surface. Blooms can terminate as mass sedimentation events triggered by resource depletion [*Bienfang et al.*, 1982; *Smetacek*, 1985; *Waite et al.*, 1992] or by the formation of dense algal aggregates [*Riebesell* 1991a, b; *Jackson and Lochmann*, 1992], leading to pulsed inputs of POM to the sediments [*Riebesell*, 1989; *Lignell et al.*, 1993]. Benthic microbial and animal communities respond quickly to these events of enhanced food supply, leading to rapid acceleration of oxygen consumption and CO_2 and NH_4^+ release from the sediments [*Kelly and Nixon*, 1984; *Hansen and Blackburn*, 1992; *Conley and Johnstone*, 1995]. This direct coupling between benthic metabolism and phytoplankton dynamics gives rise to a general correlation between phytoplankton productivity and the rate of oxygen consumption in coastal marine sediments [*Nixon*, 1981; *Dollar et al.*, 1991].

Much of the POM delivered to sediments is consumed through anaerobic pathways of metabolism, including those coupled to the bacterial respiration of

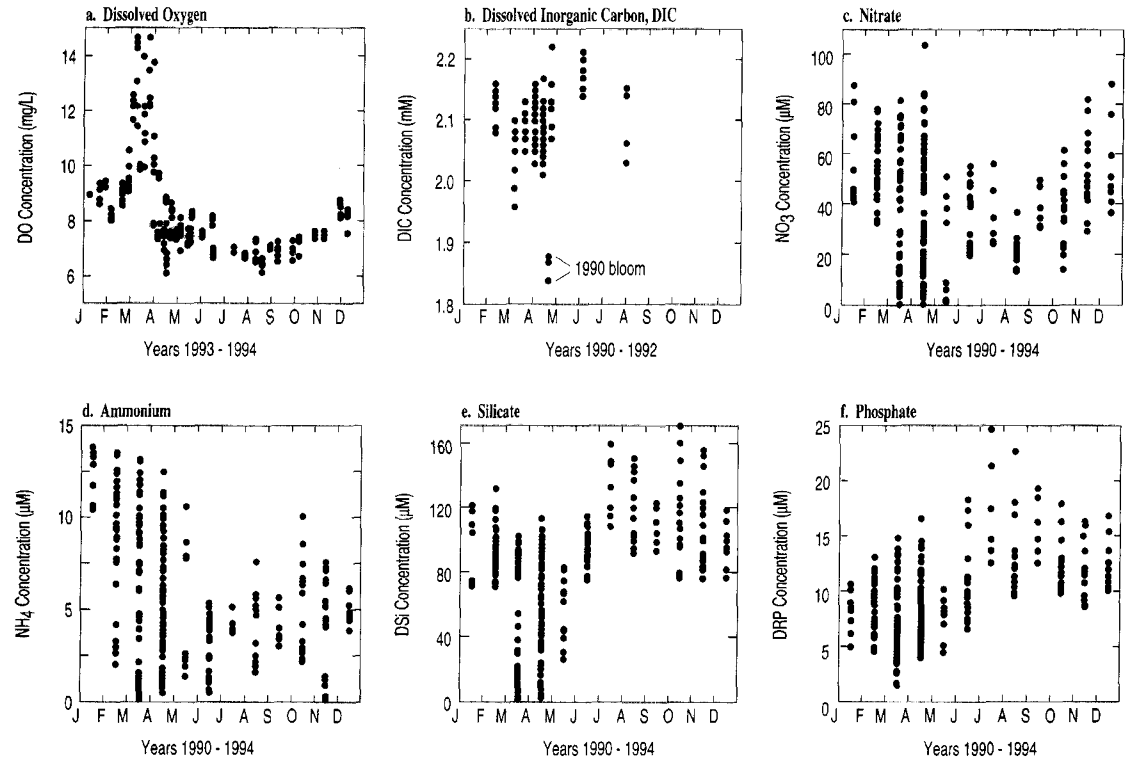

Figure 17. Seasonal distributions of some reactive inorganic substances in south San Francisco Bay: near-surface concentrations of (a) dissolved oxygen (between USGS stations 29 and 33 for the years 1993 and 1994; data from *Caffrey et al.* [1994] and *Edmunds et al.* [1995]), (b) dissolved inorganic carbon (between USGS stations 29 and 33 for the years 1990–1992; data from M. Huebner (personal communication, 1992)), and (c) NO_3^-, (d) NH_4^+, (e) DSi, and (f) DRP (between USGS stations 27 and 33 for the years 1990–1994; data from *Hager* [1993, 1994, also S. W. Hager, personal communication, 1995]).

sulfate (the process of sulfate reduction, producing S^{--} from SO_4^{--}) or nitrate (denitrification, which produces gaseous N_2O and N_2 from NO_3^-). Total benthic metabolism (combined anaerobic plus aerobic processes) can be measured as biogenic heat production in the sediments, and this index also accelerates in response to inputs of POM from phytoplankton blooms [*Graf*, 1992]. The geochemical implications of this benthic-pelagic coupling are that rates and pathways of element cycling in shallow coastal environments are strongly influenced by seasonal phytoplankton blooms. The rate of sulfate reduction in coastal sediments increases with phytoplankton primary productivity [*Indrebø et al.*, 1979]. Sedimentation of diatom-derived POM leads to rapid increases in the flux of NH_4^+ from sediments to the overlying water and a shift from net release to net consumption of NO_3^- in the sediments, because nitrification (microbial oxidation of NH_4^+ to NO_3^-) is inhibited while denitrification is stimulated by oxygen reductions that follow inputs of labile organic substrates [*M. H. Jensen et al.*, 1990]. Similar linkages between N cycling and blooms have been established in south San Francisco Bay, where the production of NH_4^+ in sediment porewaters increases more than tenfold during spring [*Caffrey*, 1995].

Dissolved Substances

Even before *Redfield*'s [1958] seminal paper, oceanographers recognized the importance of biological processes in changing the chemical composition of seawater. A key biological process of geochemical change is phytoplankton primary production (Figure 15), and the impact of this process is evident during blooms, when primary productivity exceeds the rates of remineralization processes. In south San Francisco Bay the concentration of dissolved oxygen is usually below 8 mg L^{-1} and it is undersaturated with respect to atmospheric oxygen (Figure 17a). Exceptions occur in the spring, when the rate of photosynthetic oxygen production by phytoplankton exceeds losses from respiration and atmospheric exchange. During the spring blooms, dissolved oxygen becomes supersaturated in the water and reaches concentrations 50–60% higher than those at equilibrium with atmospheric O_2. The CO_2 content of seawater is large relative to the photosynthetic demand of phytoplankton, but sustained bloom events can lead to measurable decreases of dissolved inorganic carbon (DIC) [*Nakatsuka et al.*, 1992]. In south San Francisco Bay the DIC concentration is usually in the range 2–2.2 m*M*, except during blooms, when photosynthetic uptake depresses DIC to about 1.85 m*M* (Figure 17b). This removal of CO_2 leads to pH increases in the water, and seasonal fluctuations of pH are common responses to seasonal fluctuations in phytoplankton productivity [*Hinga*, 1992].

These large fluctuations in the inorganic carbon and oxygen content of the water are indications that the net ecosystem metabolism (balance between total photosynthesis by all primary producers and total community respiration) changes during phytoplankton blooms. Depletion of DIC and supersaturation of O_2 indicate that community photosynthesis exceeds community respiration (the ecosystem is net autotrophic). Conversely, undersaturation of O_2 and excess CO_2 indicate that respiration exceeds photosynthesis (the ecosystem is net heterotrophic). The net metabolism is used as an integrative descriptor of coastal ecosystems as tranformers of reactive materials as they are carried from the land surface to the coastal ocean [Smith et al., 1991]. Although most assessments of system metabolism have been made as annual averages [Smith and *Hollibaugh*, 1993], phytoplankton blooms can lead to large, episodic shifts from net system heterotrophy to net autotrophy [*Relexans* et *al.*, 1988]. These episodic shifts in trophic state must be considered in the calculation of annual budgets of reactive elements such as C and O_2.

Phytoplankton blooms also give rise to large changes in the concentrations of dissolved inorganic nutrients. South San Francisco Bay receives continual inputs of nitrogen, phosphorus, and silica from treated sewage [*Hager* and *Schemel*, 1996], so the concentrations of dissolved inorganic nitrogen (DIN), dissolved reactive phosphorus (DRP), and dissolved silicate (DSi) are very high. In the landward estuary, nutrient concentrations during winter months usually fall in the following ranges: $NO_3^- = 40–80\ \mu M$, $NH_4^+ = 10–15\ \mu M$, DSi = $70–130\ \mu M$, and DRP = $5–10\ \mu M$. These concentrations are much higher than those typically seen in the open ocean, but they are representative of nutrient concentrations observed in estuaries and bays influenced by agricultural. riverine, and municipal inputs. The variability of inorganic nutrient concentrations in south San Francisco Bay is highest in spring (Figures 17c to 17f), and this nutrient variability is a result of the fluctuating uptake and assimilation of reactive inorganic substances around the timing of the spring blooms. As phytoplankton biomass increases, the winter stock of DIN can be almost completely depleted. Phytoplankton blooms also change the isotopic composition of the DIN because algal uptake of the light nitrogen isotope (^{14}N) is faster than ^{15}N uptake. As nitrate assimilation accelerates during a bloom. the residual pool of nitrate becomes enriched in ^{15}N by this biological fractionation, especially in estuaries where phytoplankton uptake is the dominant NO_3^- sink [*Horrigan* et al., 1990]. Seasonal depletions of DSi reflect the spring bloom dominance by silica-requiring diatoms (Figure 17e), and although DRP is not completely depleted, minimum concentrations ($\approx 1\ \mu M$) occur during peaks of phytoplankton biomass. Nutrient concentrations (DIN, DRP, DSi) progressively increase during summer months, when phytoplankton productivity decreases and nutrient uptake rates become smaller than the nutrient sources (Figures 17c to 17f). These seasonal-scale connections between phytoplankton photosynthesis and the distributions of O_2, CO_2, and nutrients are well-characterized features of estuarine variability that include oxygen supersaturation [*Gržetić* et al., 1991; Ragueneau et *al.*, 1994] and depletions of DIN, DRP, and DSi during blooms [Peterson et *al.*, 1985; Froelich et al., 1985; Robert et al., 1987; Meybeck et *al.*, 1988; Jordan et *al.*, 1991a, b; *Conley* and *Malone*, 1992; Wetsteyn and *Kromkamp*, 1994; Pennock *and Sharp*, 1994].

Recent improvements in analytical precision have given us new tools to explore phytoplankton-mediated transformations of trace substances such as dissolved metals. The traditional conceptual model of metal dynamics in estuaries placed emphasis on geochemical processes such as exchange reactions on particle surfaces or complexation reactions. However, phytoplankton uptake and biochemical transformations can also play important roles in the cycling of some trace elements [Froelich et al., 1985; Sanders and Riedel, 1993], perhaps through pathways analogous to those of nutrient cycling. In south San Francisco Bay the concentrations of dissolved cadmium, zinc, and nickel decreased from 0.8 to 0.4 n*M*, 20 to 3 n*M*, and 40 to 30 n*M*, respectively, during the 1994 spring bloom (A. Van Geen and S. N. Luoma, manuscript in preparation, 1996). Similar depletions of dissolved zinc [Reynolds and Hamilton-Taylor, 1992], aluminum [*Moran* and Moore, 1988], and cadmium [Gonzalez et *al.*, 1991] have been observed during blooms, when phytoplankton remove these metals from solution and transform them into particulate forms. High concentrations of reduced iron Fe(II) occur in surface waters during blooms, when algal metabolites (hydroxycarboxylic acids) facilitate the photoreduction of the low-solubility form Fe(III) [Kuma et *al.*, 1992]. The biological availability of some metals, such as copper, fluctuates in response to the extracellular production of organic ligands (complexing agents) by phytoplankton [Zhou and *Wangersky*, 1989; *Shine* and Wallace, 1995]. Phytoplankton can reduce and methylate arsenic, increasing its toxicity to animals [Sanders and Riedel, 1993]; rates of these biotransformations are proportional to primary productivity [Sanders, 1983]. Because of these observations, the contemporary conceptual model of metal cycling includes algal uptake and biotransformation among the key processes that influence the chemical form, toxicity, and incorporation of some trace metals into estuarine food webs, with the recognition that these aspects of metal geochemistry can change rapidly during blooms.

Parallel revisions are occurring in the conceptual models of estuarine organic geochemistry. The largest pool of organic matter is the dissolved pool, and distributions of dissolved organic carbon (DOC) within estu-

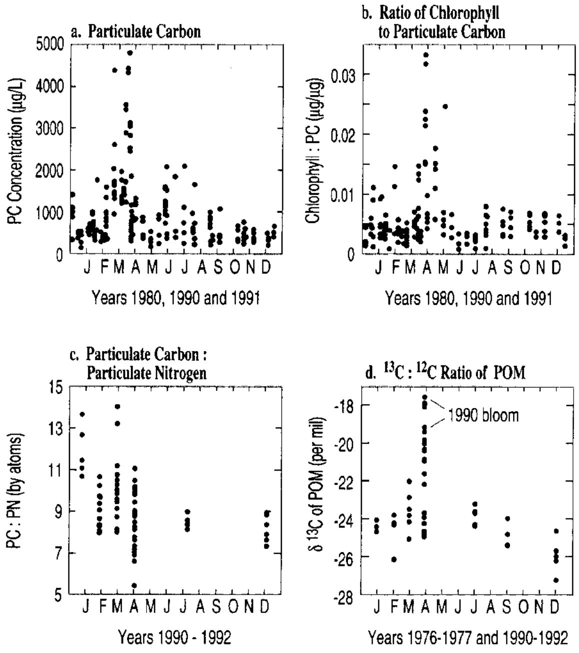

Figure 18. Seasonal distributions of four characteristics of the suspended particulate matter in near-surface waters of south San Francisco Bay: (a) concentration of particulate carbon and (b) ratio of chlorophyll *a* to particulate carbon (between USGS stations 21 and 32 for the years 1980 and 1990–1991; data from *Wienke and Cloern* [1987] and *Cloern et al.* [1993]), (c) ratio of particulate carbon to particulate nitrogen (between USGS stations 21 and 34 for the years 1990–1992; data from *Cloern et al.* [1993]), and (d) $^{13}C:^{12}C$ ratio, expressed as $\delta^{13}C$ (between USGS stations 27 and 32 for the years 1976–1977 [*Spiker and Schemel*, 1979] and 1990–1992 [*Cloern et al.*, 1993]).

aries often follow conservative patterns of mixing between high-DOC fresh water and low-DOC seawater. These distributions are consistent with the traditional view that estuarine DOC is refractory (resistant to rapid microbial degradation) and originates primarily from riverine inputs of terrestrial material. However, recent observations indicate that the estuarine DOC pool is reactive and altered by internal sinks and sources, including the synthesis and release of algal metabolites [*Peterson et al.*, 1994]. The mechanisms of DOC release by phytoplankton are not well understood, but algal cells excrete low-molecular-weight compounds such as amino acids [*Poulet et al.*, 1985; *Fuhrman*, 1990], and when blooms are terminated by nutrient limitation [*Van Boekel et al.*, 1992] or viral infection [*Suttle et al.*, 1990; *Bratbak et al.*, 1993], algal cells can rupture and release their dissolved contents into the water. Changes in the DOC pool during blooms include rapid increases in the extracellular release of organic carbon [*Baines and Pace*, 1991]; the bulk DOC concentration [e.g., *Norrman et al.*, 1995]; the low-molecular-weight components [*Kepkay et al.*, 1993], including volatile hydrocarbons [*Milne et al.*, 1995]; the turnover rate of labile compounds [*Kirchman et al.*, 1991]; aliphatic hydrocarbons associated with rapid algal cell division (e.g., heneicosahexaene [*Osterroht et al.*, 1983]); and aldehydes produced from algal fatty acids [*Jalliffier-Merlon et al.*, 1991].

Coastal phytoplankton blooms also play important roles in the production and release of chemically active trace gases to the atmosphere. An example is dimethylsulfide [*Stefels et al.*, 1995], which is oxidized to sulfate in the atmosphere and then contributes to the acidity of rainfall [*Turner et al.*, 1988] and climate modulation [*Charlson et al.*, 1987]. Coastal phytoplankton production is also a globally significant source of ozone-depleting halocarbons, such as methyl bromide [*Lobert et al.*, 1995].

Particulate Organic Matter

As phytoplankton transform inorganic materials into particulate organic matter during blooms (Figure 15), they change the abundance and chemical composition of the particles suspended in water. These changes are sometimes obscured because the total concentration of suspended particulate matter (SPM) can be high in shallow coastal waters [*Ward and Twilley*, 1986]. The SPM of estuaries is often dominated by mineral particles, and the small organic fraction is composed of complex molecules that are difficult to characterize chemically [*Fichez et al.*, 1993]. The suspended POM of estuaries originates from many sources, including riverine inputs derived from freshwater or terrestrial plants, sewage, detritus from surrounding marshes, marine plankton, or primary production by vascular plants and algae. During blooms the phytoplankton production of POM can dominate the other sources, and the SPM becomes more biogenic in character (the labile, or utilizable, components become important relative to the refractory components). These changes in the SPM are reflected in the quantity of specific classes of organic compounds such as lipids [*Kattner and Brockmann*, 1990], proteins [*Billen and Fontigny*, 1987], and carbohydrates [*Fichez et al.*, 1993]. One geochemical consequence of the algal assimilation of reactive elements, such as C, N, P, Si, is a large shift in elemental composition (or "repackaging") [*Lebo and Sharp*, 1992] from dissolved inorganic forms to particulate organic forms [*Ward and Twilley*, 1986; *Zwolsman*, 1994]. In south San Francisco Bay, concentrations of particulate carbon (PC) vary over nearly 2 orders of magnitude, with maximum concentrations of biogenic PC during spring when phytoplankton biomass is high (Figure 18a). A common feature of blooms is a rapid increase in the concentrations of particulate carbon and nitrogen [*Nakatsuka et al.*, 1992], particulate phosphorus [*Sakamoto and Tanaka*, 1989], and biogenic silica [*Ragueneau et al.*, 1994].

Geochemists use a variety of measurements to infer the origin, reactivity, and biochemical composition of the complex mixture of organic substances in coastal waters. These measurements can be sensitive indicators of the changing phytoplankton component of the POM during blooms. One simple indicator of the biogenic fraction of SPM is the ratio of particulate carbon to SPM. This ratio is commonly <0.05 [*Zwolsman*, 1994], but it can reach values as high as 0.35 during periods of high primary productivity [Cauwet, 1991]. A simple indicator of the phytoplankton fraction of POM is the ratio of chlorophyll *a* to PC [*Jordan* et *al*., 1991a; *Cifuentes et al*., 1988]. In south San Francisco Bay this index ranges from 0.001 to 0.03 (Figure 18b). Although the ratio of phytoplankton chlorophyll to carbon varies with growth conditions [Cloem et al., 1995], the maximum chlorophyll:PC ratio of 0.03 observed in spring is close to the ratio expected in a suspension of pure algal biomass. The minimum chlorophyll:PC ratio of 0.001 indicates that most of the POM was then associated with components other than living phytoplankton biomass. *Canuel et al*. [1995] used analyses of lipid biomarkers to confirm that phytoplankton biomass constitutes most of the particulate carbon in San Francisco Bay during blooms but less than 20% of the particulate carbon during nonbloom conditions.

A related index is based on the "standard" elemental composition of healthy phytoplankton, C:N:P -- 106:16:1 [*Redfield*, 1958]. If phytoplankton composition follows this Redfield ratio, then pure algal suspensions should have molar ratios of particulate carbon to particulate nitrogen (PC:PN) of 6.6 and ratios of PC to particulate phosphorus (PC:PP) of about 106. Departures from these ratios indicate that the POM might be composed of organic matter other than phytoplankton. In south San Francisco Bay the PC:PN ratio is typically greater than 8–9 except during spring, when it can fall to values below 7 (Figure 18c). In many other estuaries the PC:PN ratio lies in the range 6–8 during algal blooms but is >10 when the POM is dominated by nonphytoplankton components [*Ward and Twilley*, 1986; *Jordan et al*., 1991a]. Similar fluctuations in the PC:PP ratio occur in coastal waters, with highest ratios (230) during nonbloom periods and lowest ratios (96) during blooms [*Sakamoto and Tanaka*, 1989].

Different sources of estuarine organic matter (anthropogenic, terrestrial, and marine) have different compositions of stable isotopes of elements such as C and N. These differences have been the basis for using isotope ratios of the POM to infer the relative importance of these different sources. The approach is based on the assumption that isotopic composition of estuarine POM is controlled by mixing between end-member sources. However, we now recognize that biogeochemical processes, including primary production, alter the isotopic composition of POM. In south San Francisco Bay the ratio of ^{13}C to ^{12}C in the POM (expressed as $\delta^{13}C$, the deviation of the measured $^{13}C:^{12}C$ ratio from that in a carbonate standard [Fy and Wainright, 19911) usually falls in the range -27 to -23‰ (Figure 18d). However, this ratio changes during spring blooms, when phytoplankton constitute the bulk of the POM and the $\delta^{13}C$ POM increases to -18 to -17‰ (indicating enrichment in ^{13}C). Comparable (or larger) shifts in the carbon isotopic composition of the POM have been observed in other estuaries [*Fogel* et al., 1992]. Fast growing coastal diatoms become particularly enriched in ^{13}C (with $\delta^{13}C$ up to -13‰ [*Fry* and Wainright, 1991]), and during diatom blooms the $\delta^{13}C$ POM can increase from -21 to -16‰ in less than 1 week [Nakatsuka et al., 1992]. Although there is uncertainty about the biochemical mechanisms behind the variable discrimination of C isotopes by photosynthesis [Fy and Wainright, 1991; *Fogel* et *al*., 1992], it is clear now that phytoplankton primary production can alter the isotopic composition of particulate carbon. Similarly, phytoplankton primary production alters the N isotopic composition of POM, with rapid shifts of $\delta^{15}N$ from $+9$ to $+1$‰ during blooms as algae preferentially assimilate $^{14}NO_3^-$ and produce POM that is enriched in ^{14}N [Nakatsuka et *al*., 1992]. Interpretation of the variability of C and N isotopes in estuaries requires consideration of these biogeochemical transformations that become pronounced during blooms [Pennock et al., 1996].

Another emerging technique for characterizing POM is based on analyses for biomarkers, organic molecules that can be traced to specific groups of organisms [Mayzaud et *al*., 1989]. The lipid components of POM, particularly sterols and fatty acids, can give clues about the relative importance of algal, bacterial, or vascular plant sources of POM because each group of organisms synthesizes a characteristic set of lipid molecules [Scribe et al., 1991]. For example, 14- and 16-carbon fatty acids are the most common fatty acids synthesized by algae, and these molecules are used as indicators of phytoplankton activity [*Hama*, 19911. In south San Francisco Bay the lipid composition of the POM changes during the spring bloom, with large increases in the relative abundance of 14:0, 16:0, and 16:1ω7c fatty acids [Canuel et al., 1995]. These same changes have been followed closely during the exponential growth phase of other coastal diatom blooms [*Kattner* and Brockmann, 1990]. The specific molecular composition of lipids can give information about the community composition of the phytoplankton because different classes of algae synthesize different signature molecules [Fraser et al., 1989; Mayzaud et *al*., 19891. In south San Francisco Bay the abundance of 24-methylenecholesterol increases markedly during the spring bloom [Canuel et al., 1995; Canuel and Cloem, 1996], and this sterol is a major component of marine diatoms of the genus Thalassiosira (common members of the spring bloom community in this estuary; see Table 4).

Responses of the Heterotroph Populations

The complex suite of geochemical changes caused by algal blooms is an important mechanism of habitat change for consumer organisms. Some of these changes are beneficial because most of the DOM and POM produced during blooms can be used as a food resource

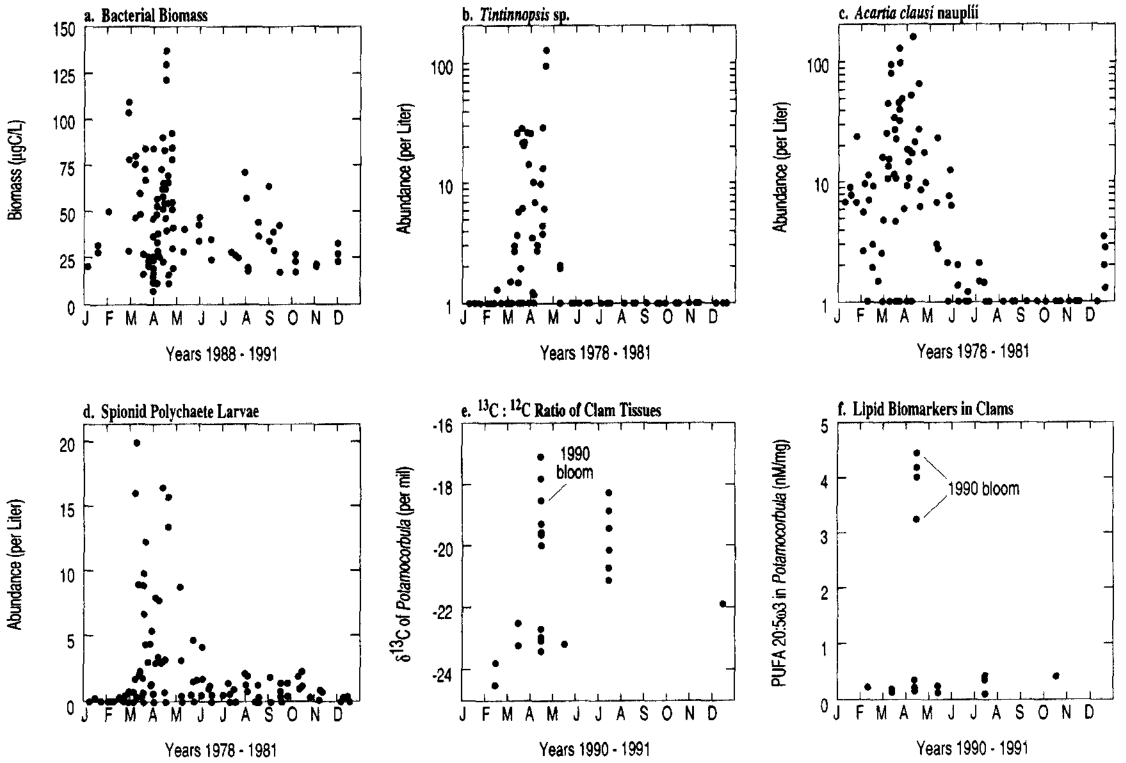

Figure 19. Seasonal changes in the abundance or biochemical composition of heterotrophs in south San Francisco Bay: (a) pelagic bacterial biomass (between USGS stations 21 and 32 for the years 1988–1991; data from *Hollibaugh and Wong* [1996]); abundances of (b) the tintinnid ciliate protozoan *Tintinnopsis* sp., (c) nauplii of the copepod *Acartia clausi*, and (d) larvae of spionid polychaete worms (from near-surface pump samples at USGS stations 30 and 32 for the years 1978–1981; data from *Hutchinson* [1981, 1982]); and (e) ratio of $^{13}C : ^{12}C$, expressed as $\delta^{13}C$, and (f) concentration of the biomarker fatty acid 20:5ω3 in tissues of the clam *Potamocorbula amurensis* (between USGS stations 28 and 33 for the years 1990–1991; data from *Cloern et al.* [1993]).

by bacteria, protozoans, and invertebrates. There are two different pathways through which phytoplankton-derived organic matter can be assimilated and converted into new biomass (production) of heterotrophs (Figure 15). The microbial food chain is based on the assimilation of DOM by bacterioplankton; it directly supports the production of protozoan communities [e.g., *Van Boekel et al.*, 1992]. The metazoan (multicellular animal) food chain is based on the consumption of phytoplankton and organisms of the microbial food chain. Both pathways are important, and investigations of the past decade have shown that much (up to 60%) of the phytoplankton primary production passes through the bacterial trophic level [*Fuhrman*, 1990] or is consumed directly by protozoans [*McManus and Ederington-Cantrell*, 1992].

The linkage is now well established between the production of algal metabolites and the rapid utilization of these as substrates to support bacterial production in coastal waters [*Larsson and Hagström*, 1982; *Lancelot and Billen*, 1984]. As the rate of bacterial production increases in response to the enhanced primary productivity of blooms, we would then expect corresponding increases in the abundance or biomass of the bacterioplankton. This population response is well documented in mesocosm (large enclosure) experiments [*Painting et al.*, 1989; *Riemann et al.*, 1990; *Norrman et al.*, 1995] and in some coastal waters [*Billen and Fontigny*, 1987; *Van Boekel et al.*, 1992] and sediments [*Yap*, 1991]. However, strong correlations between bacterial abundance and phytoplankton primary productivity are not always observed in nature because bacterioplankton populations are influenced by losses to microzooplankton (protozoan) grazers or bacterial viruses [*Bratbak et al.*, 1990]. Bacterial losses to the microzooplankton can equal the rate of bacterial production [*Coffin and Sharp*, 1987]. This means that the rate of energy flow through the microbial food chain can increase in proportion to primary productivity, even when the total biomass of bacteria changes little. This may explain why the biomass of bacterioplankton in south San Francisco Bay is most variable during spring months (Figure 19a), because rapid increases in bacterial biomass are often followed by increased abundance of bacterial consumers [*Van Boekel et al.*, 1992]. The degree of coupling between bacterial and primary productivity is temperature-dependent [*Coffin and Sharp*, 1987; *Pomeroy et al.*, 1991], and it can be damped by the input of terrestrial sources of DOM that can also support bacterial production [*Ducklow and Kirchman*, 1983; Kirchman et *al*., 1989].

Other populations of the pelagic food web respond to the production of high-quality organic matter during blooms, because the heterotrophs are often food-limited [*Durbin et al*., 1983]. In south San Francisco Bay, some species of tintinnid ciliates (protozoans that build protective shells) are present only in spring (Figure 19b). Sudden large population outbreaks of these protozoans are common in coastal waters, and these events are closely linked to seasonal changes in phytoplankton primary productivity. Tintinnid ciliates produce cysts when food availability is low; the cysts sink to the sediments and remain dormant until food availability increases. The development of cysts into active cells is triggered by dissolved organic substances produced by the phytoplankton [Kamiyama, 1994], and this adaptive response allows the tintinnids to exploit conditions of high food availability during blooms.

Some species of copepods also have dormant stages that are produced and hatch in response to changing food availability. This explains why nauplii (larval stages) of the copepod *Acartia* clausi are most abundant in south San Francisco Bay during spring (Figure 19c). Nauplii develop from resting eggs in the sediments (a function of temperature [Sullivan and *McManus*, 19861) and from the eggs produced by the existing adult stock. For estuarine-coastal copepods such as *Calanus pacificus*, Acartia *tonsa*, and *Acart*ia hudsonica the rate of egg production is highly influenced by the abundance and composition of the phytoplankton [Durbin et al., 1983; *Runge*, 1985; *Beckman* and Peterson, 1986; Sullivan and *McManus*, 1986]. These copepods have a common response of negligible egg production at chlorophyll a concentrations of 1–2 $\mu g\ L^{-1}$ [*Durbin* et al., 1983] and maximal egg production rates when chlorophyll a concentration exceeds about 10 $\mu g\ L^{-1}$. These zooplankton species store only small food reserves, so the population growth rate of copepods is sensitive to fluctuations in phytoplankton biomass in the range of 1–10 $\mu g\ L^{-1}$ chlorophyll a. This coupling between zooplankton production and phytoplankton blooms may propagate to higher levels of the food web because strong coherence has been observed between larval fish abundance and spring plankton blooms in some coastal waters [Townsend, 1984].

Benthic and pelagic heterotrophs share the same food resource in shallow coastal waters, so population responses of the benthic animals are also coupled to phytoplankton dynamics. Biologists have long recognized a close timing between the onset of reproduction of benthic invertebrates and phytoplankton blooms [Starr et *al*., 1990]. In south San Francisco Bay the pelagic larval stages of some polychaete worms are most abundant during the spring (Figure 19d), and reproduction of other species such as mussels, urchins [Staw et al., 1990], barnacles [Starr et al., 1991], and oysters [Ruiz et al., 1992] is coupled to the timing of phytoplankton blooms. This synchrony provides the obvious advantage of ensuring an abundant food supply for larvae as they develop in variable environments. The mechanism of this synchrony is the induction of spawning by metabolites produced and released into the water by the phytoplankton [Staw et al., 1990].

A second response of benthic invertebrates is their seasonal growth cycle. The cosmopolitan estuarine clam *Macoma* balthica has monthly fluctuations of growth rate in San Francisco Bay that are coherent with monthly fluctuations in phytoplankton biomass: the growth period coincides with the seasonal phytoplankton blooms, and the growth rate changes from year to year in response to the magnitude of the annual phytoplankton bloom [Thompson and Nichols, 1988]. Comparable studies with other species in other estuaries, such as the mussel Mytilus edulis [Smaal and van Stralen, 1990], the clam Yoldia notabilis [Nakaoka, 1992], and the oyster Ostrea edulis [Ruiz et al., 1992], show that the growth rate of benthic suspension feeders is often near zero (or negative) except during episodes of rapid growth supported by the enhanced food availability during phytoplankton blooms. Interannual fluctuations in the population growth of benthic invertebrates are caused by year-to-year fluctuations in the abundance of the phytoplankton food resource during the growing season [*Beukema* and *Cadée*, 1991; Powell et al., 1995].

The biochemical composition of the benthic invertebrates changes as animals grow and accumulate storage products, such as lipids and carbohydrates, during periods of high phytoplankton biomass [Wenne and *Styczynska-Jurewicz*, 1985; Ruiz et al., 1992]. These changes in the biochemical composition of consumer organisms can be linked directly to fluctuations in phytoplankton biomass with the same biomarker analyses used to characterize POM. The approach is based on observations that the biochemical composition of animals, including the $^{13}C:^{12}C$ ratio of their tissues, reflects the composition of their food resources [*DeNiro* and Epstein, 1978]. In south San Francisco Bay the carbon isotopic composition of the clam Potamocorbula amurensis has a seasonal cycle very similar to the seasonal fluctuations in $\delta^{13}C$ POM. Carbon in the tissues of P. amurensis has an isotopic signature indicative of nondiatom food sources ($\delta^{13}C$ of -25 to -22‰) during winter and early spring (Figure 19e). However, the $\delta^{13}C$ of *P. amurensis* increases rapidly during spring and reaches an annual maximum of -17‰ in April, similar to the $\delta^{13}C$ of the POM when phytoplankton biomass constitutes most of the POM. This coherence between the seasonal fluctuations of ^{13}C enrichment in both the food source and *P.* amurensis shows that the growth of this filter feeder is supported by the assimilation of phytoplankton produced during the spring bloom. *Fry* and Wainright [1991] also interpreted seasonal enrichments of zooplankton ^{13}C as evidence that ^{13}C-rich diatom carbon is transferred to the zooplankton trophic level.

Molecular biomarkers provide confirmatory evidence that algal biomass is directly incorporated into the production of organisms at higher trophic levels. Fatty acids are useful biomarkers because some polyunsaturated fatty acids (PUFA) are essential dietary factors for animals that can only be synthesized by algae. An example is the 20-carbon fatty acid $20{:}5\omega 3$, one of the major PUFAs produced by diatoms [*Fraser et al.*, 1989]. In south San Francisco Bay the concentration of this fatty acid in the tissues of the clam *Potamocorbula amurensis* increased by a factor of 10–30 within weeks after the spring diatom bloom in 1990 (Figure 19f). Mesocosm experiments have also been used to demonstrate the enhanced transfer of dietary fatty acids from phytoplankton to zooplankton and then to larval fish during phytoplankton blooms [*Fraser et al.*, 1989].

The Importance of Algal Species Composition

We conclude this section with a reminder that not all phytoplankton species are equal. The rapid production of dimethylsulfide in coastal waters is associated with blooms of only some phytoplankton species (*Emiliania huxleyi* [*Wolje et al.*, 1994]; *Gyrodinium aureolum* [*Turner et al.*, 1988]; *Phaeocystis* sp. [*Stefels et al.*, 1995]). The flux of this climatically active trace gas to the atmosphere is therefore a function of the phytoplankton community composition as well as biomass and productivity. Only some species of cyanobacteria fix atmospheric nitrogen [*Carpenter et al.*, 1992], only the diatoms and silicoflagellates influence the cycling of silica [*Tréguer et al.*, 1995], and the methylated forms of arsenic produced during blooms are species-dependent [*Froelich et al.*, 1985]. Nondiatoms appear to fractionate inorganic carbon [*Fry and Wainright*, 1991] and nitrogen [*Montoya and McCarthy*, 1995] isotopes less than diatoms. The fate of phytoplankton (e.g., grazing versus sedimentation) depends on the size and sinking rate of the cells produced during blooms [*Fahnenstiel et al.*, 1995]. Therefore the rates and pathways through which blooms act as agents of geochemical change are highly dependent on the species composition of the bloom communities.

This same comment applies to the linkage between algal blooms and other trophic levels, because phytoplankton communities include a diverse array of cell sizes, morphologies, and biochemical compositions. Within this diversity of forms is a broad range of suitability as food resources for consumer organisms. Copepods can select among food items, and estuarine-coastal species appear to have a preference for dinoflagellates and microzooplankton over diatoms [*Kleppel et al.*, 1991]. The production of viable eggs by the copepod *Temora stylifera* is 4–6 times faster on a diet of *Prorocentrum minimum* (a dinoflagellate) compared with the diatom *Thalassiosira rotula* [*Ianora and Poulet*, 1993]. This may be partly a response to the higher nutritional quality of the dinoflagellate species, although the diatom *T. rotula* produces a powerful inhibitor of cell division that can block the development of copepod eggs [*Poulet et al.*, 1994]. Other species, such as the prymnesiophyte *Phaeocystis pouchetii*, can suppress feeding [*Bautista et al.*, 1992] and egg production [*VanRijswijk et al.*, 1989] of copepods. Among the dinoflagellates, some species are poor food resources for copepods [*Huntley et al.*, 1986], and others (e.g., *Dinophysis acuminata*) synthesize toxins that repel copepod grazers [*Carlsson et al.*, 1995]. Therefore species composition of the phytoplankton community ultimately affects zooplankton production by changing the feeding and reproduction rate of copepods [*Poulet et al.*, 1994]. This appears to be true for the benthic fauna as well [*Beukema and Cadée*, 1991].

Although phytoplankton primary production is a prominent source of organic matter to support production at higher trophic levels, exceptional blooms dominated by one or several species can cause major ecological disturbance, sometimes leading to large economic losses. Blooms of the red tide flagellate *Olisthodiscus luteus* disrupt plankton food webs by inhibiting the growth of microzooplankton [*Verity and Stoecker*, 1982]. Dense, persistent blooms of species such as the chrysophyte *Aureococcus anorexefferens* [*Cosper et al.*, 1987; *Tracey*, 1988] or the red tide dinoflagellate *Ptychodiscus brevis* [*Summerson and Peterson*, 1990] can cause reproductive failure and mortality of shellfish such as mussels and bay scallops. Toxin-producing species can cause mortality at higher levels of the food web: the prymnesiophyte *Chrysochromulina polylepsis* produces a toxin that can cause mass mortalities of fish [*Estep and MacIntyre*, 1989], the newly discovered "phantom" dinoflagellate *Pfiesteria piscicida* causes fish kills in the Pamlico and Neuse estuaries [*Burkholdeu et al.*, 1992], and diatoms of the genus *Pseudonitzschia* produce domoic acid, which is toxic to vertebrates and has caused mortalities of pelicans and cormorants [*Walz et al.*, 1994]. Because of these strong species-specific attributes of the phytoplankton, the linkages between algal bloom dynamics and the biogeochemical system are best established through programs that include measures of phytoplankton community composition to identify the occurrence of species that play particular roles in the cycling of elements and production of heterotrophs.

SOME LESSONS AND QUESTIONS TO GUIDE FUTURE RESEARCH

My primary objective in this review was to present phytoplankton ecology as an example of multidisciplinary science. The problem of coastal bloom dynamics requires consideration of the linkages between the geologic, hydrodynamic, climatic, hydrologic, geochemical, and biological components of the Earth system. Results from sustained investigation of San Francisco Bay illustrate some general lessons about these linkages. They also help to identify the large gaps in our understanding of these linkages, and I conclude with three questions that will persist as central elements of coastal ecosystem research into the next century.

Some Lessons

1. Phytoplankton blooms are key agents of geochemical variability in coastal ecosystems. A biogeochemical function of phytoplankton primary production is the transformation of reactive inorganic substances into organic matter. During blooms these transformations are rapid and give rise to measurable changes in oxygen concentration; CO, and pH; dissolved nutrients such as nitrate. phosphate, and silicate; speciation and form of reactive trace metals such as cadmium, zinc, and arsenic; production of climatically active trace gases such as dimethylsulfide; and isotopic fractionation of elements such as C and N.

2. The rapid production of fresh organic matter during blooms triggers a complex suite of responses at other trophic levels. These responses include stimulation of bacterial productivity, growth of microzooplankton, and reproduction and growth of consumer animals (zooplankton, mollusks, worms, and crustaceans).

3. Phytoplankton blooms can be understood in the context of a simple population budget that expresses rate of population change as the sum of local (in situ) processes plus transport processes. Both sets of processes respond to fluctuations in physical forcings that originate in the ocean, atmosphere, and watershed. As an example, vertical mixing is a key determinant of phytoplankton population growth rate; mixing is influenced by tidal (oceanic) current stresses at the bottom, wind (atmospheric) stresses on the water surface, and riverine (watershed) inputs of fresh water.

4. Phytoplankton biomass varies at all spatial and temporal scales at which we make measurements, and blooms do not necessarily develop uniformly within an estuarine basin. Temporal and spatial variability are coupled; small-scale patchiness is ephemeral, but the mesoscale patterns of variability can persist for days or weeks. Mesoscale patchiness is shaped by the basin-scale water circulation and mixing, and it can be altered rapidly by events that disrupt the mean circulation. The timescales of phytoplankton biomass variability are determined by the timescales of the physical sources of biomass change, such as the semidiurnal and neap-spring tidal fluctuations, seasonal and interannual fluctuations of river flow, and episodic and seasonal fluctuations of the wind forcing.

5. In south San Francisco Bay the timing of blooms is set partly by the tides, which fluctuate and establish windows of opportunity for phytoplankton population growth as periods of low tidal energy and slow vertical mixing. The magnitude of the spring blooms is set, at least in part, each year by the particular hydrologic and weather conditions operating during these tidal windows. Therefore the timing of blooms (from an astronomical forcing) is predictable, but the magnitude of blooms is determined by aperiodic forcings and is therefore unpredictable. This observation could be the basis for a framework of estuarine comparison, organized around the hypothesis that strongly tidal SCEs have strongly periodic variability, whereas weakly tidal SCEs are characterized by aperiodic fluctuations around the seasonal cycles.

6. Although SCEs have recurrent annual cycles of phytoplankton blooms, the timing, magnitude, and species composition of these blooms all change from year to year. Large departures from the mean annual pattern are caused by exceptional climatic or hydrologic conditions, such as events of extreme precipitation and river discharge or anomalous regional wind forcings.

7. Colonization of SCEs by exotic species can lead to major (sometimes permanent) disturbance at the ecosystem level. The invasion of northern San Francisco Bay by the clam *Potamocorbula amurensis* has caused a fivefold reduction in annual primary production, near complete disappearance of the summer diatom bloom, and diverse changes in the pelagic heterotroph community. Coastal ecosystems are particularly susceptible to this mode of global change, and our conceptual models of coastal ecosystems must include recognition that the ecosystems we are currently studying can be profoundly altered in the future by the introduction of exotic species that disrupt trophic interactions.

8. Shallow coastal waters are nutrient-rich, turbid, characterized by large variability at short timescales and small spatial scales, and highly influenced by the rapid exchanges of materials with the bottom sediments. Therefore the traditional conceptual models of pelagic oceanography do not work as a framework for understanding phytoplankton bloom dynamics in the shallow coastal zone.

Question 1: What Determines Species Composition of Blooms?

The lessons noted above come from a search for patterns, mechanisms, and ecosystem-level responses to phytoplankton blooms as revealed through measurements made at one set of scales. Emphasis is placed on chlorophyll variability as an index of the phytoplankton population response to physical variability. These kinds of lessons can be used as a first step in the process of understanding coastal blooms as features of the Earth system that are subject to change as we alter the climate system and hydrologic cycle, as we alter the water chemistry through inputs of contaminants and nutrients, and as we continue to translocate species. However, this first step is based on a narrow perspective that does not consider the rich details of phytoplankton population variability at the species level. *Smetacek and Pollehne* [1986, p. 404] call these details a "source of irritation to modern empirical ecologists." Hopefully it is clear at this point why the details are important. The recent discovery of *Poulet et al.* [1994] that some diatom species produce a potent chemical inhibitor of egg development is a compelling example of why we need to understand the processes that determine species composition of phytoplankton blooms. If we want to fully understand population fluctuations of copepods, sea urchins, or fish, then we need to understand the forces that select for those algal species that play critical roles in the production of food and in the synthesis of molecules that interfere with population recruitment at these higher trophic levels. Similarly, geochemists need to understand population variability of those phytoplankton species that are active in the production of trace gases, the isotopic fractionation of C and N, the biochemical transformations of trace metals, and the cycling of nutrients. Smetacek and *Pollehne* [1986] suggest that our inability to understand or predict bloom dynamics at the species level is the result of a conceptual framework that overemphasizes the "physicochemical paradigm." Smetacek [1986] suggests the need for an "ecosystem paradigm" based on a natural history orientation to understand life history cycles, with recognition that phytoplankton species distributions reflect not only adaptations to the immediate environment during the growth (bloom) phase of population cycles, but also life cycle strategies, such as production of resting stages, that ensure persistence of the population through the nongrowth phases. Work toward an ecosystem paradigm should be based on *Margalef*'s [1978] reminder (cited by *Legendre* et *al.* [1984, p. 6291) that "Organisms are not only carriers of molecules, but they are subject to natural selection."

Question 2: How Do Toxic Contaminants Alter Blooms and Their Biogeochemical Functions?

The urgency of this question comes from the certainty that coastal ecosystems in the developed world are contaminated with toxic substances such as heavy metals, chlorinated hydrocarbons, and petrochemicals and the likelihood that SCEs in the developing world will become progressively more contaminated in the future [*Windom*, 1992; *Nixon*, 1995]. It is now well established that phytoplankton blooms can change the concentration and geochemical form of some trace metals [*Slauenwhite* and Wangersky, 1991]. However, there is much less certainty about the impacts of toxic contaminants on phytoplankton community composition, primary production, and population growth. The limited experimental work suggests that chronic low level inputs of toxic elements can alter the evolution of phytoplankton communities by eliminating sensitive species (e.g., dinoflagellates [Brand et al., 19861) and selecting for more tolerant forms [*Sanders and* Cibik. 1988: Kuwabara et *al*., 1989].

A second aspect of this question comes from the likelihood that interactions between toxic substances and phytoplankton blooms produce effects that propagate to upper trophic levels. One mode could be through phytoplankton uptake of trace metals (or organic contaminants such as PCBs and DDT [Mailhot, 1987] and subsequent transfer of these toxic substances to animals that ingest and assimilate phytoplankton. It appears that the transfer efficiency of metals from phytoplankton to consumers depends on the degree to which algae can assimilate and sequester the different elements inside their cell membranes [*Reinfelder* and *Fisher*, 19911. Therefore ecosystem-level effects of toxic contaminants may be set, in part, by the efficiency with which phytoplankton can act as agents of bioaccumulation and trophic transfer. Ecosystems scientists are beginning to recognize that toxic contaminants are human forces of change just as potent as global warming, habitat destruction, and introductions of exotic species. As we pursue this hypothesis, one focus should be directed to understanding the role of blooms as events that move toxic substances into the food resource of animals and to those substances for which phytoplankton are especially efficient at assimilation and trophic transfer.

Question 3: How Is Nutrient Enrichment Changing Coastal Ecosystems?

This question is motivated by concern about the harmful effects of nutrient enrichment caused by the application of fertilizers in river basins, the discharge of urban wastes, and the combustion of fossil fuels [*Justić* et al., 1995]. A simplistic answer to this question is that nutrient enrichment stimulates primary production (the process of eutrophication [*Nixon*, 1995]), leading to accumulations of phytoplankton biomass, episodes of noxious blooms, depletions of dissolved oxygen as the blooms decay, and mortality of fish or shellfish. Although this sequence of acute responses to nutrient enrichment has been observed [*Justić*, 1987; Rosenberg and Loo, 1988], responses to chronic nutrient enrichment in most coastal ecosystems are probably more subtle, are more difficult to detect or measure, and follow a sequence of stages leading toward these acute symptoms. There is considerable evidence that increased nutrient concentrations in coastal waters have led to biological change in recent decades; compelling examples come from long-term observations in the Baltic [Rosenberg et al., 1990; *Granéli* et *al*., 1990], German Bight [*Radach et al*., 1990], Chesapeake Bay [*Harding*, 1994; *Cooper*, 19953, and southern North Sea [*Cadée*, 1986; *Cadée and Hegeman*, 1991]. However, there is als considerable uncertainty about how nutrient enrichmen leads to ecosystem change in the coastal zone. As w work to answer this question, our broad goal should b a global conceptual model of how coastal eutrophicatio works. This conceptual model should recognize the fo lowing:

1. Eutrophication is an ecological process, so should be studied from an ecosystem perspective th considers all the interacting physical, chemical, troph and life history processes of phytoplankton populati fluctuation [*Hecky* and Kilham, 1988]. Creative applic tions of this perspective will also be required to resol the relative importance of natural processes such climate anomalies [e.g., *Vieira* and Chant, 1993] a anthropogenic nutrient enrichment as mechanisms th trigger exceptional blooms of harmful algal species.
2. Ecosystem responses to chronic nutrient enric ment might occur as a sequence of successional stag

and the early responses might be subtle community shifts in the phytoplankton, benthic invertebrates [*Elmgren*, 1989], attached algae [*McComb and Lukatelich*, 1995], or rooted plants [*Orth and Moore*, 1983].

3. Changing nutrient ratios is an important element of coastal eutrophication that appears to selectively promote blooms of nondiatom species [*Conley et al.*, 1993] as human activities increase the availability of N and P relative to Si [*Justić et al.*, 1995].

4. A conceptual framework is needed to explain the great range of sensitivity to nutrient enrichment among different coastal water bodies. It is not clear at this point why some SCEs, such as San Francisco Bay, do not exhibit obvious symptoms of nutrient enrichment. The strong couplings between primary production and benthic consumption may be a partial explanation [*Cloern*, 1982; *Herman and Scholten*, 1990; *Hily*, 1991]. Coastal ecosystems with a short retention time [*Balls et al.*, 1995] or strong tidal mixing [*Tréguer and Quéguiner*, 1989; *Monbet*, 1992] appear to be more resilient to the acute effects of nutrient enrichment than weakly tidal systems with slow circulation. Therefore this global conceptual model should incorporate both the trophic interactions and the physical processes that influence the pathways through which nutrient enrichment can alter phytoplankton populations.

These three research questions are closely interconnected, so they should be pursued together as components of integrated programs to identify the patterns of ecosystem change in the coastal zone, the underlying mechanisms of those changes, and the interactions between these different mechanisms of change.

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