

# **Sources, Mechanisms and Impacts of Changes in Nutrient Inputs to San Francisco Bay**

A Report for the San Francisco Bay Subtidal Goals Project (July 2008)

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## **Background on the Effects of Nutrient Inputs**

Nutrients are elements that organisms use for metabolism and growth. Macronutrients (carbon, oxygen, hydrogen, nitrogen and phosphorous, each typically constituting more than 1% of the dry weight of tissues; and sulfur, chlorine, potassium, sodium, calcium, magnesium, iron and copper, each typically constituting 0.2-1% of the dry weight of tissues) are the main components, while micronutrients (including aluminum, boron, bromine, chromium, cobalt, fluorine, gallium, iodine, manganese, molybdenum, selenium, strontium, tin, titanium, vanadium and zinc) are present in living tissues in smaller amounts (Pidwirny 2006). Silicon, which is a micronutrient for most organisms, is a macronutrient for diatoms. Nutrients occur in living organisms, in the wastes and dead organic matter derived from them, and as molecules in the environment. Chemically, they occur in both organic molecules (molecules with a carbon skeleton and oxygen and hydrogen atoms) and inorganic molecules. Inorganic nutrients are taken up by autotrophs (producer organisms, primarily algae and plants), and incorporated into living tissue, which may then be consumed by heterotrophs (animals). Nutrients are released from organisms as wastes or as dead tissue, broken down into detritus and transformed into one or more types of inorganic molecules by various bacteria or other decomposers. These inorganic molecules are available to be taken up again by autotrophs.

Concerns can arise when anthropogenic changes either deplete nutrient availability, restricting productivity, or increase nutrient supply, causing excessive growth of autotrophs. The latter has frequently been the case with nitrogen and phosphorous in aquatic ecosystems. Several human activities—including land clearing, the use of fertilizer, the discharge of human and animal wastes, and the burning of forests and fossil fuels—increased the flow of these nutrients into lakes, rivers and coastal waters (Cooper and Brush 1991). In many freshwater systems, loadings of nitrogen or phosphorous stimulated algal growth and increased the amount of organic matter settling to the bottom. Consequent increases in microbial decomposition sometimes depleted the oxygen in bottom waters, especially in stratified water bodies. This process

of eutrophication in freshwater ecosystems became a major focus of limnological research, management and regulation starting in the 1960s (Cloern 2001; Howarth and Marino 2006).

Increased loadings of these nutrients into coastal waters has similarly sparked algal blooms, decomposition and oxygen depletion in bottom waters and sediments (Howarth 1988; Nixon 1995). Other effects can include reduced water transparency; declines in perennial seaweeds and sea grasses and the promotion of fast-growing, ephemeral seaweeds; increases in blooms of toxic dinoflagellates; changes in the diversity and abundance of benthic invertebrates; a shift to anaerobic metabolism, stimulation of sulfate reduction and production of metal-sulfides and hydrogen sulfide in the sediments; seasonal shifts in the timing of phytoplankton growth; and possibly a shift to smaller demersal fish species (Cloern 2001). Changes in the relative concentrations of nitrogen, phosphorus and silicon (a nutrient important in the growth of diatoms) can also change phytoplankton community composition or toxicity. For example, an increase in the ratio of nitrogen to silicon can favor flagellates and dinoflagellates over diatoms, and favor armored over naked silicoflagellates (Paerl 1997; Cloern 2001; Howarth and Marino 2006). An increase in the ratio of nitrogen to phosphorous may contribute to higher levels of toxicity in prymnesiophytes and *Pseudo-nitzschia* diatoms (Paerl 1997), while a decrease in the ratio of nitrogen to phosphorous can support noxious blooms of the flagellate *Phaeocystis* (Cloern 2001).

### **Overview of Nutrient Input Effects in San Francisco Bay**

In San Francisco Bay, there have been occasional incidents of nuisance algal blooms, oxygen depletion, foul (hydrogen-sulfide) smells and/or fish kills (e.g. Horne and McCormick 1978; Nichols 1979; Luoma and Cloern 1982; Cloern and Oremland 1983; Josselyn and West 1985). Jassby (1992) noted past records of noxious accumulations of drift macroalgae in Alameda, decaying mats of the red drift alga *Polysiphonia* smothering benthic communities in the South Bay, dense accumulations of the green macroalgae *Ulva* and *Enteromorpha* in the Central Bay, and a pipe-clogging bloom of *Cladophora* in San Pablo Bay. Periodic *Ulva* and *Enteromorpha* blooms and decaying accumulations of washed-up *Polysiphonia* continue to occur on parts of the Bay shore (personal observations). Nutrient loadings from human activities may have caused or contributed to these incidents of rapid algal growth and high algal densities, though other environmental factors that affect nutrient availability or algal growth might also be responsible. Some incidents of oxygen depletion in the Bay may have resulted from the microbial decomposition of algal blooms stimulated by anthropogenic nutrient loadings, but the discharge of oxygen-demanding wastes (including both organic matter whose decomposition uses up oxygen, and reduced inorganic compounds that consume oxygen) may have caused or contributed to most incidents of hypoxia and ensuing nuisance odors and fish mortality.

Most of the time, light availability or benthic grazing appears to control algal growth in the Bay (Cloern 1979; Alpine and Cloern 1988; Cloern 1982; Nichols 1985; Jassby et al. 2002; Cloern et al. 2007). On most occasions when low nutrients do limit growth,

nitrogen appears to be the limiting factor (Cloern 1979; Jassby et al. 2003), as it commonly is in most temperate zone estuaries (Ryther and Dunstan 1971; Howarth 1988; Oviatt et al. 1995; Howarth and Marino 2006). During phytoplankton blooms in the South Bay, silicon is sometimes depleted to levels that limit diatom growth (Hager and Schemel 1996).

Since the construction of secondary treatment facilities for municipal wastewater in the 1970s and 1980s, hypoxic occurrences have become rare in San Francisco Bay, even though nutrient levels in the Bay have generally remained high (Nichols et al. 1996). Unlike many temperate-zone estuaries, management concerns in the Bay have focused on the issue of low primary productivity and its impact on food webs, rather than on the stimulation of excessive primary productivity (Cloern 2001). There has thus been relatively little research on nutrient loadings and their impacts.

Two recent lines of inquiry have begun to change or at least modify this view of the Bay. Records of increasing phytoplankton densities in South, Central and San Pablo bays since the late 1990s (Cloern et al. 2006) have led to consideration of conditions under which the Bay's "eutrophication resistance" could be reduced and the Bay might begin to respond to nutrient inputs (Cloern et al. 2007). Meanwhile, other researchers argued that ammonia, normally considered a nutrient, also has an inhibitory effect that limits productivity in the Bay by limiting the uptake of nitrate; and that changes in wastewater treatment processes have affected ammonia inputs and productivity in the Bay (Wilkerson et al. 2006; Dugdale et al. 2007).

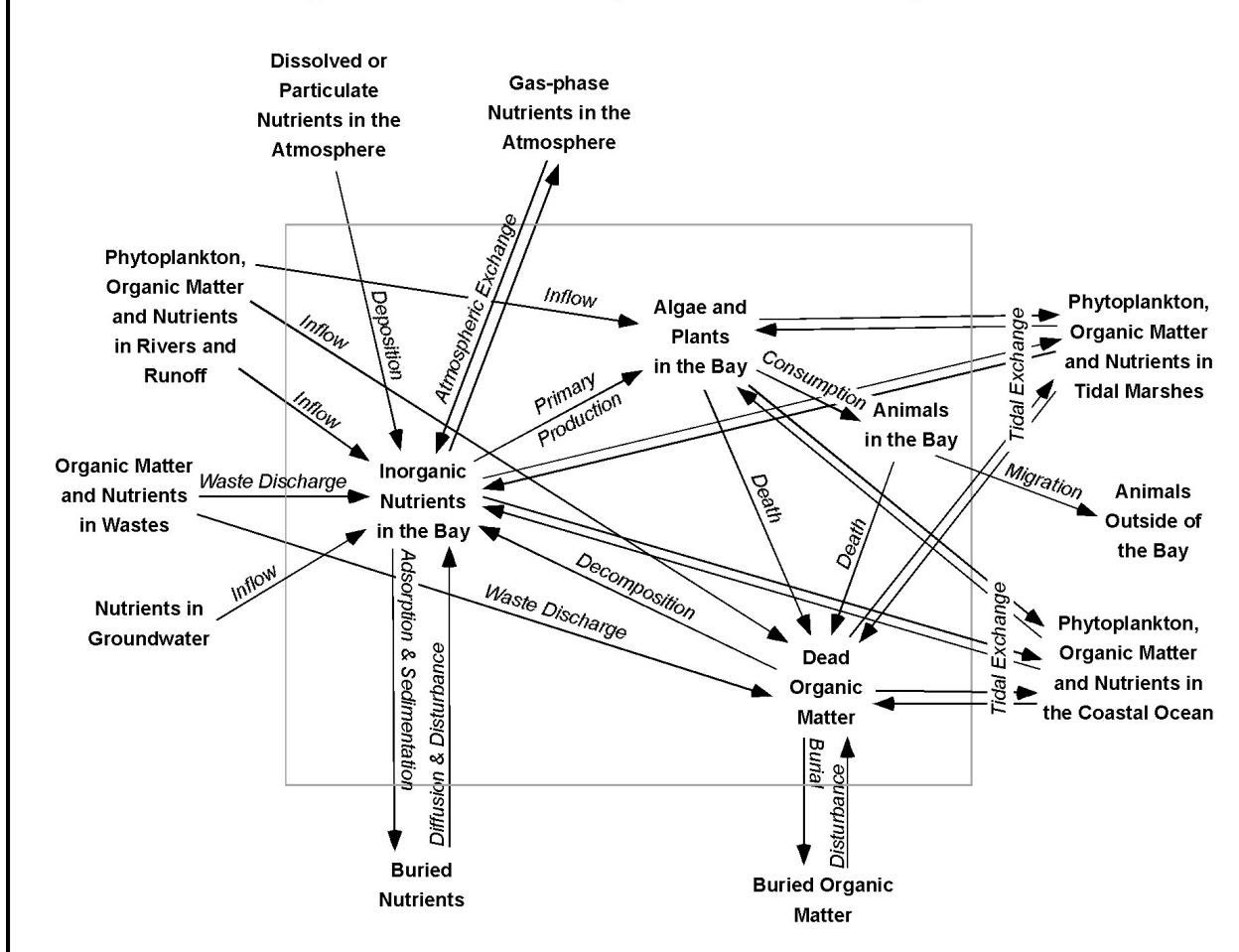
## **Nutrient Pathways**

Nutrients can move in and out of San Francisco Bay by a variety of pathways (Fig. 1). Nutrients can be carried into the Bay with freshwater in rivers or runoff, or in groundwater; enter the Bay directly in waste streams; be deposited from the atmosphere in dissolved or particulate form; be exchanged with the atmosphere in gaseous form; leave the Bay by burial in sediments, and return to the Bay by upward diffusion or by disturbance of the sediments; be carried between the Bay and the ocean or marshes in tidal currents; and enter or leave with migrating animals. These pathways are discussed below. Conomos et al. (1979) identified the main sources of nutrients in the Bay as Delta outflow, the ocean, sewage discharge and drainage from tidal marshes, and the main sinks as the ocean, the bottom and possibly the marshes.

### Rivers and Runoff

Nutrients can be carried into the Bay in flowing water as dissolved organic or inorganic nutrients, as inorganic nutrients adsorbed to sediment particles, as living organisms (primarily phytoplankton) and as dead organic matter. Changes in these inputs can come about through several mechanisms, including changes in the volume of flows into the Bay, changes in the concentration of suspended sediment and associated nutrients in the flows, changes in the production of phytoplankton in the Delta and other tributary waters, and changes in nutrient inputs to tributary waters in the form of treated sewage,

**Figure 1. Nutrient Pathways in San Francisco Bay**



applied fertilizers, other soil amendments, etc. For example, nearly 500,000 tons of nitrogen were applied to the land as fertilizer in California in 1975 (Peterson 1979) and the Bay watershed includes about 40% of California, suggesting that fertilizer could be the source of substantial nitrogen inputs to the Bay. Conomos et al. (1979) concluded, on the basis of Bay-wide concentration patterns, that Delta outflows and the ocean are the main sources of silica<sup>1</sup> and nitrate/nitrite for the northern reach of the Bay, and that loadings of all nutrients from the Delta are at least ten times higher in the winter than in the summer. Peterson (1979) estimated that outflow from the Delta provides 10,000 tons/yr each of dissolved inorganic nitrogen and particulate nitrogen and 100,000 tons of dissolved silica. Russell et al. (1982) estimated that inputs of total nitrogen from rivers and runoff had decreased from around 23,000 tons/yr in 1800 to 15,000 tons/yr in 1978, while inputs of total phosphorous decreased from around 4,000 to 3,000 tons/yr. Jassby and Cloern (2000) estimated the inflow to the Bay from the Delta of total organic nitrogen at 6,200 tons/yr. However, recent data show that nitrogen loading from the

<sup>1</sup> Silicon dioxide, the main form of inorganic silicon.

Sacramento River is now about three times what it was in the mid-1980s, due to population increases (David Dugdale pers. comm.).

Average water flows and peak flows are altered by freshwater storage and use, by increases in the portions of the watershed that are covered by hardened surfaces due to urban development, and by climate changes including changes in the timing, amount and type of precipitation, the amount of snow pack, the timing of snow melt and possibly the rate of evapotranspiration. Most observers believe that water storage and use has substantially decreased the flow of water into the Bay relative to pre-1850 conditions (e.g. Nichols et al. 1986). Peak flows have mostly been reduced by water storage, although hardened surfaces may have increased peak flows in some local watersheds. In some areas, summer flows have been increased by the storage and release or the delivery of water for agricultural or domestic irrigation. Climate changes in the Bay/Delta watershed over the past several decades have included increases in the frequency and intensity of extreme rainfall events and a shift toward earlier snow melt and earlier runoff peaks (Dettinger et al. 1995; Lund et al. 2007). Over the coming decades anthropogenic climate change is projected to continue these trends and to increase the interannual variability in precipitation, increase the number of large winter storms, and hasten and compress the period of snowmelt, with associated increases in peak winter runoff events (Lund et al. 2007). These changes may make it harder for dams to retain and store as large a fraction of the runoff as they do currently, due to constraints imposed by flood control operational requirements. Any increase in the evapotranspiration rate in the watershed, due to increased temperatures (projected to increase by 1-3° C by 2030 and by 2-10° C by 2100—Lund et al 2007) and higher plant growth rates in a hotter and more CO<sub>2</sub>-enriched environment, would tend to decrease the amount of inflow to the Bay. The net effect of all this, as mediated by human responses, on the timing and amount of inflows to the Bay is unclear.

In the last half of the 19th century, sediment loadings and suspended sediment concentrations in Bay tributaries were increased by land clearing and mining activities (Gilbert 1917; Krone 1979). Flood control levees constructed along these watercourses reduced overbank flooding and the deposition of sediment on floodplains, which further augmented the delivery of suspended sediments downstream. In the 20th century, especially after the early 1940s, extensive dam construction on these tributaries lead to the settling and retention of sediment in impoundments behind the dams, reducing the concentrations of suspended sediment downstream of the dams (Krone 1979). Water diversions, also increasing more rapidly since the early 1940s, divert sediments and associated nutrients, decreasing the total loadings to the Bay (Krone 1979).

Phytoplankton growth in the Delta decreases the amount of inorganic nutrients and increases the amount of phytoplankton in Delta outflows. Like the Bay, the Delta is nutrient-rich and light-limited (Jassby and Cloern 2000; Jassby et al. 2002), with phytoplankton productivity also limited by benthic grazing (Jassby et al. 2002; Lund et al. 2007) and possibly herbicides (Edmunds 1999; Jassby et al. 2003), though the evidence for herbicide limitation is weak (Alan Jassby pers. comm.). On the other hand, total suspended solids has declined and water transparency has been increasing, probably because of dams built upstream (Jassby et al. 2002). Nutrients are normally

present in substantial excess, because of wastewater effluent from Sacramento (Davis Dugdale, Alan Jassby pers. comm.) and agricultural drainage (Jassby et al. 2002, 2003). In a review of nutrient concentrations in 1968-1998, only 0.1% of dissolved inorganic nitrogen measurements, 0.15% of phosphate measurements, and none of the silica measurements in the Delta were at apparently limiting levels (with  $n > 8,000$ , 6,000 and 8,000, respectively—Jassby et al. 2002). Despite abundant nutrients and increasing light penetration, phytoplankton productivity in the Delta declined since the 1970s (Jassby et al. 2002; Cloern et al. 2006), but recently has more-or-less recovered (Alan Jassby pers. comm.). Changes in water diversions and storage, in precipitation and runoff patterns (resulting from anthropogenic climate change), in the topography of the Delta, in agricultural practices in tributary areas (including the types and application rates of fertilizers and herbicides<sup>2</sup>; irrigation and drainage methods; crop types; and the amount and location of land in production), and in other land use practices (the extent of urbanization) could affect phytoplankton growth in the Delta.

Jassby and Cloern (2000) concluded that river inflow is the main source of organic matter input (and associated organic nutrients) to the Delta, followed by autochthonous phytoplankton production and agricultural drainage from Delta islands; wastewater discharges, tidal marshes and other sources were of less importance. They found that because of water project exports from the Delta, the downstream export of organic matter to the Bay is nearly always less than the riverine inputs to the Delta, especially in dry years (export to Bay ranging from 20% of riverine inputs in the summer to 55% of riverine inputs in the winter, in critically dry years). The volume of water project exports thus has a large influence on the inflow of nutrients to the Bay. They considered the potential impact of other major actions on nutrient flows to the Bay. The construction of an isolated diversion facility (such as the Peripheral Canal) to shunt water from the Sacramento River to the water project pumps, and the use of flow barriers to restrict the flow of organic-matter-rich San Joaquin River water to the project pumps, would both tend to increase the annual flow of organic nutrients into the Bay, but the effect would be weakest in spring and summer when these resources are most likely to be used by biota. Increasing shallow water habitat by either flooding Delta islands or by inundating floodplain areas for longer or more frequent periods would increase total primary productivity (including both phytoplankton and benthic vegetation) and organic matter in the Delta. For floodplain inundation at least, this would probably not significantly increase export to the Bay (Jassby and Cloern 2000), but any phytoplankton biomass produced would likely be more bioavailable than riverine inputs of organic matter (Sobczak et al. 2002).

Agricultural drainage and runoff from lawns and golf courses can carry fertilizers and soil nutrients into the Bay and its tributary waters. Waste from domestic animals is carried in runoff from feedlots, and at times this can account for much of the agricultural loading of nitrogen into the San Joaquin River (Alan Jassby pers. comm.). Nutrient loadings from Central Valley farms increased with the increasingly widespread application of fertilizers after the late 1940s and with later increases in subsurface

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<sup>2</sup> Including a rapid shift from ammonia and nitrate fertilizers to urea fertilizers over the past decade (David Dugdale pers. comm.).

drainage, such that nitrate concentrations in the San Joaquin River increased fivefold between 1950 and 1980 (Nichols et al. 1996). Direct discharges of municipal wastewater into the Bay are discussed below, but wastewater discharges into tributary waters can contribute substantially to the nutrient loads in Bay inflows (Alan Jassby pers. comm.).

### Groundwater

Nitrogen inputs in groundwater can range from <10% to >30% of total nitrogen inputs into coastal waters, and in some cases may be comparable to riverine inputs (Paerl 1997). Globally, oceanic inputs from groundwater are comparable to inputs from biological nitrogen fixation, and about one-third to one-sixth of inputs from rivers and runoff. There is little information on the volume of groundwater inflows to San Francisco Bay or on the nutrient concentrations in those inflows (Jassby 1992). The enrichment of nitrogen in groundwater occurs mainly in agricultural areas, due to fertilizer applications and accumulation and storage of animal wastes.

### Waste Discharge

Wastewater disposal can discharge organic matter and organic and inorganic nutrients into the Bay. Following recurrent water quality problems in the Bay in the 1950s and 1960s, especially in parts of the South Bay, municipal treatment plants were upgraded in the 1970s and 1980s to provide at least secondary treatment (Russell et al. 1982). Secondary treatment is primarily designed to reduce suspended solids and biochemical oxygen demand (BOD) by 85-90%, but typically reduces nutrients by 50% or less; most non-particulate nutrients pass through the treatment system (Russell et al. 1982). Periodic problems with oxygen depletion in the far South Bay were resolved with further reductions in the oxygen demand of wastewater plant effluent, by adding advanced secondary treatment processes that discharge nitrate instead of ammonia (David Dugdale pers. comm.). Conomos et al. (1979) estimated that wastewater discharges to the Bay in 1975 carried 6,000 tons of organic nitrogen, 14,000 tons of inorganic nitrogen (mainly as ammonia) and 10,000 tons/yr of total phosphorous (similar estimates are provided by Russell et al. 1982; Peterson 1979 estimated nitrogen inputs to the northern reach of the Bay at 8,000 tons/yr). About 70% of these nutrients were discharged into the South Bay, with about 20-40% of the total going into the southern end of the South Bay below the Dumbarton Bridge. Conomos et al. (1979) concluded, on the basis of Bay-wide concentration patterns, that wastewater entering at the south end of the Bay was the main source of nitrogen and phosphate for the South Bay, and that wastewater was a significant source of silica and ammonia elsewhere in San Francisco Bay. Most of the current nutrient input to the North Bay is from wastewater (David Dugdale pers. comm.).

### Atmospheric Deposition and Exchange

Gunther et al. (1987) estimated that the deposition of airborne substances directly into the Bay could be responsible for minor but not insignificant loads of certain contaminants. The burning of forests and fossil fuels (especially the production of nitrogen oxides (NO<sub>x</sub>) in internal combustion engines), the industrial production and use of synthetic fertilizer, and animal wastes stored in open lagoons or applied as manures

(which can lose up to 70-80% of their ammonia through volatilization—Paerl 1997) all release nitrogen compounds to the atmosphere that can return to the earth in precipitation or dry deposition. In addition, atmospheric nitrogen is oxidized (fixed) by the heat of lightning strikes to form nitric acid, which washes out of the atmosphere dissolved in rain. Dissolved organic nitrogen can also form a substantial fraction of the nitrogen in atmospheric deposition (Paerl 1997). Paerl (1985) reported that rainfall events in nitrogen-limited waters off North Carolina were followed by increased phytoplankton growth. The largest increases occurred after acidic rainfall derived from continental regions, with less stimulation of growth after falls of rain with near-neutral pH derived from oceanic regions, which Paerl attributed to the elevated levels of nitrogen compounds in acid rain. Paerl (1997) estimated that overall about 0.3 to  $>1 \text{ g/m}^2\text{-yr}$  of nitrogen is deposited from the atmosphere into coastal waters, accounting for 20-40% of "new" nitrogen inputs. Rainfall in the San Francisco Bay area is mostly ocean-derived and not notably acidified (about  $10 \text{ }\mu\text{mol/L}$  of nitrate in northern California—Peterson et al. 1985). Russell et al. (1982) estimated that in 1978 atmospheric deposition was putting 980 tons/yr of total nitrogen into the Bay (about 6% of the inputs in rivers and runoff and 5% of the inputs in wastewater), along with 120 tons/yr of total phosphorous, which works out to about  $0.6 \text{ g/m}^2\text{-yr}$  of nitrogen and  $0.07 \text{ g/m}^2\text{-yr}$  of phosphorous.<sup>3</sup>

Nitrogen gas ( $\text{N}_2$ ) in the atmosphere is also fixed by certain bacteria and cyanobacteria (blue-green algae) to form nitrate ( $\text{NO}_3$ ) and ammonium ( $\text{NH}_4^+$ ). These are then taken up and utilized by plants and algae. Other groups of bacteria decompose dead plant and animal matter and animal wastes back to ammonia, nitrite ( $\text{NO}_2$ ) and nitrate. Denitrifying bacteria convert nitrate into nitrogen gas or nitrous oxide gas ( $\text{N}_2\text{O}$ ), which diffuse back into the atmosphere. While nitrogen-fixing bacteria are common in soil, and blooms of planktonic, nitrogen-fixing cyanobacteria are typical of nitrogen-deficient lakes (Flett et al. 1980), nitrogen-fixing is apparently less important in estuaries and coastal waters (Cooper 1937; Howarth 1988), though recent findings suggest it may be more important in the ocean generally than was previously thought (Arrigo 2005). Planktonic nitrogen-fixing cyanobacteria are uncommon or rare in most estuaries where salinities are above 10-12 ppt (Ryther and Dunstan 1971; Howarth 1988; Howarth and Marino 2006). Nitrogen-fixing by benthic cyanobacteria and cyanobacteria that are epiphytic on sea grasses may be significant in coastal waters where sufficient light penetrates to the bottom, but this excludes the major part of most temperate zone estuaries (including San Francisco Bay), except on intertidal mudflats (Howarth 1988; Howarth and Marino 2006). Denitrification rates in lakes and marine waters appear to be similar (Howarth 1988; Howarth and Marino 2006), with the released gases reaching the atmosphere through mixing and diffusion. Rates of nitrogen fixing and denitrification might be affected by changes in the abundance and composition of bacteria and cyanobacteria, or by changes in temperature or other environmental conditions that affect these organisms.

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<sup>3</sup> Assuming that Russell et al.'s loadings are spread over 371,000 acres estimated for the Bay at MHHW (Jassby 1992).



### Burial, disturbance and diffusion

Dead organic matter and nutrients in the water column or in surface sediments are available for microbial transformation or uptake by biota. Organic matter and nutrients buried in sediments below the zone of biological activity are unavailable for use by biota, but the depth at which this occurs is not clear. Various organisms may turn over or irrigate the sediment to depths of a few centimeters (snails, sea slugs, juvenile clams), to 10-30 cm (lugworms, deeper burrowing clams), or up to 50-75 cm (bat rays, various polychaetes, and ghost shrimp) (Rubin and McCulloch 1979; Peterson 1979; Haderlie and Abbott 1980; Haig and Abbott 1980; Cohen 2007). In some areas, sediment turnover resulting from tidal currents or wind waves (Krone 1979; Conomos et al. 1979; Nichols 1979) may be more significant than disturbance by animals. Over most of the Central and South bays physical turnover affects only the upper 2-5 cm of the sediment, but might reach depths of 40-100 cm at sites in the Central Bay with sandy sediments and fast tidal currents where sand waves form on the bottom (Rubin and McCulloch 1979; Hammond and Fuller 1979). Similar beds of sand waves occur in San Pablo Bay (Nichols 1979]. Various activities that disturb the bottom may increase the background rate of physical turnover, including dredging, sand or shell mining, and bottom trawling conducted for fisheries harvest, research or educational purposes (Cohen 2007). Nutrients may also pass out of the sediments by molecular diffusion through interstitial water, but this is minor relative to the fluxes due to turnover and irrigation (Hammond and Fuller 1979), and in practice extends only a few centimeters deep. The overall fluxes of nutrients out of bay sediments were estimated at about 6 g/m<sup>2</sup>-yr of nitrogen, 1 g/m<sup>2</sup>-yr of phosphorous and 60 g/m<sup>2</sup>-yr of silicon (Hammond et al. 1985). Peterson (1979) estimated fluxes from sediments in the northern reach to be about 10,000 tons/yr of nitrogen and 30,000 tons/yr of silicon.

Estimates of the portion of the organic matter supply that is lost by burial in an estuary range from about 1% to over 10% (Paerl 1997); Jassby et al. (2002) estimated that on average around 20% is lost in shallow water systems. Human activities that increase sediment inputs and sedimentation rates in the Bay can increase the rate of nutrient burial and loss from the Bay system. Alternately, activities that reduce sediment inputs and promote erosion in the Bay may expose these nutrients. Gilbert (1917), Smith (1965), Krone (1979, 1996), Atwater et al. (1979, Fig. 6), Capiella et al. (1999), Jaffe et al. (1998), Foxgrover et al. (2004) and Jaffe and Foxgrover (2006a,b) review and summarize changes in sedimentation rates in the Bay. Substantial increases in sediment production in the watershed resulted from hydraulic mining and agricultural activities in the late 1800s, with significant lags in the timing of sediment arrival in the Bay (Gilbert 1917, Krone 1979). The construction of dams and impoundments, and diversions of fresh water primarily for irrigation, subsequently reduced the delivery of sediments to the Bay (Krone 1979). In addition to overall changes in sediment inputs, dredging, sand and shell mining locally remove sediments and can expose buried nutrients, while the disposal of dredge sediments can bury nutrients locally.

The patterns of sedimentation and erosion in the Bay have been complex with some areas accumulating sediment even as nearby areas were losing it (e.g. Atwater et al. 1979; Capiella et al. 1999; Jaffe et al. 1998; Foxgrover et al. 2004). Capiella et al.

(1999) reported that Suisun Bay gained 61 million m<sup>3</sup> of sediment between 1867 and 1887, then lost 159 million m<sup>3</sup> by 1990. Earlier researchers, analyzing essentially the same hydrographic survey data, came to somewhat different conclusions: Smith (1965), reported a similar pattern of sediment gain followed by greater sediment loss but involving half or one-third as much sediment; while Krone (1979, 1996) also reported that there was a large gain of sediment in the late 1800s, but that it was followed by a modest overall gain through 1990 once sea level rise was taken into account. In San Pablo Bay, both Jaffe et al. (1998) and earlier researchers (Gilbert 1917; Smith 1965; Krone 1979, 1996) reported a very large accumulation of sediment in the last half of the 19th century (range of estimates of 252-294 million m<sup>3</sup>), followed by lesser but still substantial accumulation in the twentieth century, though the amounts reported differ, especially for the period after 1922. In Central Bay, while Gilbert (1917) reported a gain of 106 million m<sup>3</sup> in the late 1800s, Smith (1965) and Krone (1979) reported only a slight loss or a slight gain; for 1897-1990, Krone (1976, 1996) reported a gain of over 200 million m<sup>3</sup>, and Smith's (1965) calculations are reasonably consistent with this. There was less agreement on sediment changes in South Bay. Gilbert (1917) reported a net gain of over 40 million m<sup>3</sup> in the late 1800s, Smith (1965) reported a net loss of over 40 million m<sup>3</sup>, and Krone (1979) and Foxgrover et al. (2004) reported only small losses or gains. Authors (Smith 1965; Krone 1979; Foxgrover et al. 2004) agree that the South Bay lost sediment in the first half of the 20th century, but the range of loss estimates is from 25 to 90 million m<sup>3</sup>. Between the 1950s and around 1990, Krone (1996) reported a gain of 24 million m<sup>3</sup>, but Foxgrover et al. (2004) reported a loss of 71 million m<sup>3</sup>.

Activities that erode the margins of the Bay also release sediments and nutrients into the Bay. Atwater et al. (1979, Fig. 6) summarized tidal marsh shoreline changes, depicting a complex pattern of shoreline advance and retreat that is not easily interpreted. They suggest that sites of shoreline retreat may be due to local rise in relative sea level (resulting from a combination of eustatic and tectonic effects) and/or burrowing by the exotic isopod *Sphaeroma quoiana*.

### Tidal Exchange

Tidal marshes generally act as net exporters of organic matter and nutrients to the open waters of estuaries, though there are exceptions (Nixon 1980; Jassby 1992; Jassby et al. 1993). Much of the export from marshes may be in the form of detritus derived from marsh plants, while imports may occur from the trapping of sediment-associated nutrients and benthic filtering of open-water phytoplankton (Nixon 1980). It is estimated that diking and filling has reduced the Bay's tidal marsh to about one-fifth of its 1850 area (Goals Report 1999), and to about one-eighteenth of its former area for the Bay and Delta combined (Nichols et al. 1996). The Baylands Ecosystem Goals Project has recommended that tidal marsh in the Bay be increased from 40,000 acres in 1998 to 90,000-105,000 acres (Goals Report 1999). As most Bay tidal marshes will probably serve as net sources of organic matter and nutrients, the input from marshes is expected to increase substantially from current levels if these restoration plans are implemented. Marsh restoration that involves cutting through existing levees may also initially increase inputs of sediment and nutrients by eroding new channels.

The average amount of water entering and exiting the Bay on each tide cycle (the tidal prism) is about one-quarter of the Bay's volume at MLLW. Since most of this water just moves back and forth, the amount of water replaced with new water on each tide cycle is only about a quarter of the Bay's tidal prism, or about 6% of its low-tide volume (Russell et al. 1982). Still, this is about ten times the average amount of freshwater inflow during the same period, and with nearly two complete tide cycles a day adds up to a lot of water exchanged. When nutrient or organic matter concentrations or phytoplankton populations inside and outside of the Golden Gate differ significantly, the large volumes of water exchanged can have a substantial impact on Bay conditions. During spring-summer upwelling periods, northerly winds cause upwelling along the coast. Nutrients brought up with deep water stimulate blooms of large diatoms, which are carried into the Bay (Conomos et al. 1979; Cloern 1979). Conomos et al. (1979) concluded, on the basis of Bay-wide concentration patterns, that the ocean is a moderate source of phosphate and nitrogen for the Bay. Peterson (1975) notes the difficulty of determining even the direction of net exchange at the Golden Gate. Noting that silica concentrations are generally a good deal higher at the surface than at depth at the Golden Gate, and that due to gravitational circulation the net flux of water is oceanward in the upper part of the water column and landward at the bottom, he estimates that there is net export of silica from the Bay that is large but probably less than riverine inputs. Similarly, he estimates that ammonia is exported, that the direction of nitrate flux varies, and that there is probably a net loss of nitrogen from the Bay. A recent study of nutrient gradients at the Golden Gate concluded that there is always a net export of silica, and usually a net export of nitrate (David Dugdale pers. comm. citing Martin et al. 2007). By altering sea level and changing the Bay's tidal prism, or by changing coastal upwelling patterns (through changes in ocean heating and winds), climate change would change the flux of phytoplankton, nutrients and organic matter between the Bay and the coastal ocean.

### Migration

The active migration of animals can contribute to net fluxes of nutrients if the animals feed and grow in large numbers in one site and then spawn, die or deposit wastes in another. Well-known examples include Pacific species of salmon feeding and growing in the ocean then bringing nutrients back to their natal streams when they return to spawn and die; and fish-eating seabirds harvesting phosphorous from the sea and delivering it onto land sites as phosphate-rich guano deposits. For estuaries, the effect of such biotic transport is usually a net export of nutrients (Jassby 1992). Examples in the Bay would include Dungeness crab (*Cancer magister*), which enter the Bay as late-stage larvae or post-larval instars, feed and grow for about a year, and then remove nutrients from the Bay when they migrate out to the Gulf of the Farallones and coastal waters; and the approximately one million migratory shorebirds that winter on the Bay, building up fat stores by feeding on mudflat invertebrates when the tide is out, and removing nutrients from the Bay when they excrete wastes in marsh and upland resting areas when the tide is in, and migrate northward in the spring to their nesting areas. Striped bass (*Morone saxatilis*), which feed and grow in the Bay but spawn upstream, and northern anchovy (*Engraulis mordax*), which also feed and grow in the bay but may spawn primarily in coastal waters, may also result in net losses of nutrients (Jassby 1992).

Pacific herring (*Clupea harengus*), which enter the Bay in the winter to spawn, may represent either a gain or loss depending on whether the consumption and loss of herring eggs within the Bay outweighs the out-migration of the surviving young nine months later. If there's a net gain it would have to be less than the nutrients in the annual spawn of eggs, which is estimated to contain about 500 tons of nitrogen (Jassby 1992), assuming a C:N ratio of 4—Pilanti and Vanni 2007).

While migration overall probably results in a net export of nutrients from the Bay, there are few quantitative data. However, in developing a carbon model for the Bay Jassby (1992) judged that these were insignificant relative to other flows, and this is probably true for other nutrients as well. Thus even large anthropogenic impacts on these migrations would probably have little effect on overall nutrient flows.

### **The Bay's Response to Nutrient Inputs**

Compared to many other estuaries, nutrient concentrations in the San Francisco Bay system are relatively high, but its productivity is low (Cloern 2001; Cloern et al. 2006; Jassby 2008). Jassby et al. (2002) reported that relative to 14 other estuaries ranging in productivity from 11 to 560 g C/m<sup>2</sup>-yr (Underwood and Kromkamp 1999), San Francisco Bay came in at sixth lowest with productivity of 120 g C/m<sup>2</sup>-yr (Jassby et al. 2002), with the Delta ranking even lower with productivity of 70-75 g C/m<sup>2</sup>-yr. The Bay and Delta had similarly low rankings relative to a review of 25 river-dominated estuaries (Boynton et al. 1982; Jassby et al. 2002). Cloern (2001) reported that although San Francisco Bay has as much dissolved inorganic nitrogen and 10 times as much dissolved inorganic phosphorous as Chesapeake Bay, and higher annual loadings per square meter of both nitrogen and phosphorous, it has only one-fifth as much phytoplankton biomass and one-twentieth as much primary productivity<sup>4</sup>, and unlike Chesapeake Bay, its bottom waters are not commonly hypoxic in the summer. Since the mid-1990s, average productivity in South, Central and San Pablo bays has increased by nearly 80%, from 120 g C/m<sup>2</sup>-yr in 1993-96 to 215 g C/m<sup>2</sup>-yr in 2001-2004, while nitrogen and phosphate concentrations were declining as a result of reduced loadings from improved wastewater treatment (Cloern et al. 2006; Cloern et al. 2007). San Francisco Bay overall appears to have a much weaker response to changes in nutrient inputs than many other estuaries (Nichols et al. 1996; Cloern 2001). Conomos et al. (1979) stated that San Francisco Bay is naturally nutrient rich and that this may hide the effects of added nutrients, but non-nutrient factors limiting algal growth (turbidity, benthic grazing) provide a better explanation (Alan Jassby pers. comm.).

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<sup>4</sup> This is based on comparing an estimate for Chesapeake Bay productivity (>400 g C/m<sup>2</sup>-yr) to productivity in Suisun Bay in 1988 (20 g C/m<sup>2</sup>-yr) after invasion by *Corbula amurensis*; in 1980, before *Corbula*, productivity in Suisun Bay was 100 g C/m<sup>2</sup>-yr. Estimated productivity in Suisun Bay in 1977-1990 was 106 g C/m<sup>2</sup>-yr when benthic grazers were scarce (pre-*Corbula* invasion) and 39 g C/m<sup>2</sup>-yr when benthic grazers were abundant (mostly post-*Corbula* invasion) (Alpine and Cloern 1992). Cole and Cloern (1984) estimated net photic zone productivity at 93 to 150 g C/m<sup>2</sup>-yr at six shallow and deep sites in Suisun Bay, San Pablo Bay and South Bay in 1980-81; net water column productivity was lower, or even negative (losses from respiration exceeded gains from photosynthesis), for the deep sites (-130 to 70 g C/m<sup>2</sup>-yr) than for the shallow sites (56 to 131 g C/m<sup>2</sup>-yr) Cloern et al. (2006).

In the 19th and 20th centuries, municipal waste discharges into the Bay increased with population growth. By 1950 anaerobic conditions were common along the eastern and southern shores of the Bay and these continued to occur, along with fish kills and other water quality problems, until the construction of secondary and tertiary treatment facilities starting in the 1970s (Russell et al. 1982; Cloern and Oremland 1983; Nichols et al. 1996). Between the 1960s and the 1970s, fish kills became rarer in the Bay; BOD declined and oxygen levels improved in the South Bay, particularly at its southern end (Luoma and Cloern 1982; Nichols et al. 1996). It's unclear whether some of the earlier low oxygen episodes may have resulted from the decomposition of algal blooms stimulated by inorganic nutrient inputs, or if all were due to the discharge of incompletely decomposed organic matter. The latter was apparently the case in 1979 when partially-treated sewage was discharged from the San Jose-Santa Clara Waste Treatment Plant into Coyote Creek in the South Bay. During the three-week spill, dissolved oxygen was severely depressed in the creek and fish and pelagic invertebrates were absent. Phytoplankton biomass was also low. The plant effluent received only primary treatment during this time and contained twenty times its normal concentration of organic matter. The effects of the spill did not extend into the South Bay proper; "in effect, Coyote Creek operated as a sewage treatment plant." Once the real treatment plant resumed normal operations (including secondary and tertiary treatment of effluent), phytoplankton biomass increased and oxygen levels recovered (Cloern and Oremland 1983). The addition of advanced secondary treatment, which discharges nitrate instead of ammonia, has further reduced the oxygen demand from this treatment plant (David Dugdale pers. comm.).

In general, phytoplankton growth is thought to be limited in the Bay by high turbidity and low light availability<sup>5</sup> (Cloern 1979; Alpine and Cloern 1988; Jassby et al. 2002) mediated by the location and depth of phytoplankton stocks (the photic zone typically extends to about 10% of the water depth in the main channels and to 50-100% of the depth in the shallows—Cole and Cloern 1984), or limited by grazing by benthic organisms (primarily Asian and Atlantic species of clams) (Cloern 1982; Nichols 1985; Alpine and Cloern 1992). Most of the time, nutrient levels are more than high enough to support phytoplankton growth in all parts of the Bay. Dissolved phosphate always and silica nearly always exceeds growth-limiting concentrations (Cloern 1979; Conomos et al. 1979; Peterson 1979). Inorganic nitrogen, however, can sometimes be depleted to the point where it becomes limiting in the northern part of San Francisco Bay by late summer or fall (Peterson 1979; Cloern 1979; Peterson et al. 1985), and nitrogen sometimes becomes limiting during spring phytoplankton blooms in the South Bay (Jassby et al. 2003). Silica did drop to apparently limiting concentrations in the northern part of the Bay during a rare period of very low river flows and high air temperatures in July 1961 (Peterson 1979; Peterson et al. 1985). Thus, while light availability and grazing intensity may control the frequency, location and seasonality of bloom events, nutrient uptake rates during blooms that exceed nutrient regeneration rates may lead to nutrient depletion that controls the size of some bloom events (Cole and Cloern 1987).

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<sup>5</sup> While phytoplankton themselves contribute to light attenuation, the effect is generally small relative to that of other suspended particles (Cole and Cloern 1987).

Recently, Dugdale and colleagues have argued that high concentrations of ammonia in the Bay inhibit nitrate uptake, thus limiting productivity even when nitrate levels are high, and that blooms occur only when ammonia is first reduced to very low concentrations by dilution from large freshwater inflows and/or uptake by phytoplankton (Wilkerson et al. 2006; Dugdale et al. 2007). Dugdale et al. (2007) further suggest that the installation of secondary treatment systems in wastewater treatment plants in the late 1970s and early 1980s, which converted organic nitrogen to ammonia and increased ammonia loadings in wastewater discharges, increased ammonia concentrations in the Bay which suppressed nitrate uptake and contributed to a long-term decline in productivity. Conversely, advanced secondary treatment processes convert ammonia to nitrate, thereby reducing ammonia loadings, allowing nitrate uptake and increasing productivity.

Observations since the late 1990s of increases in phytoplankton biomass and changes in the timing of phytoplankton growth in South, Central and San Pablo bays suggest that the Bay may be starting to respond to its high nutrient concentrations (Cloern et al. 2006; Cloern et al. 2007). These observations include a progressive, significant increase in the baseline or minimum phytoplankton biomass, increases in the largest spring blooms, and blooms occurring during the previously bloom-less period of autumn and winter. Primary productivity increased by 75%. However, increased nutrients could not be the cause of these biomass and productivity increases, because during this time nitrogen and phosphorous concentrations were stable or weakly declining in the Bay, consistent with reductions in these nutrients in wastewater effluent (Cloern et al. 2006; Cloern et al. 2007). Rather, the increase in phytoplankton may have been caused by coastal oceanographic changes that increased the populations of some benthivore species that migrate into the Bay for parts of their life cycles, thereby triggering a top-down trophic cascade that reduced populations of filter-feeding bivalves and increased phytoplankton densities, as described in more detail below (Cloern et al. 2007).

Phytoplankton dynamics and productivity have been most extensively studied in Suisun Bay and South Bay.

### Suisun Bay

In Suisun Bay phytoplankton densities are low in winter and spring (and dominated by freshwater diatoms—Cole and Cloern 1984) when high river flows reduce the retention time in the embayment to days or weeks, which is comparable to or shorter than the time needed for phytoplankton populations to increase (doubling time of weeks to months (Alpine and Cloern (1992), or days to weeks (David Dugdale pers. comm.)); phytoplankton are thus washed downstream as fast or faster than they can reproduce, and the population cannot build up (Alpine and Cloern 1992). In addition, insolation and water temperature are low, reducing phytoplankton growth (Conomos et al. 1979). In most years before 1987, as flows subsided phytoplankton populations slowly increased over 2-3 months to large summer peaks dominated by large coastal/brackish diatoms (Cloern 1979; Alpine and Cloern 1992; Cole and Cloern 1984), achieving densities that were typically much higher than the annual phytoplankton peaks elsewhere in the Bay. The Suisun Bay peak coincided with the development of a zone of high turbidity in

Suisun Bay, thought to be controlled by gravitational circulation in the channel (Cloern 1979; Arthur and Ball 1980; Alpine and Cloern 1992).

In the summer of 1977, however, in the second year of a severe drought, there was no summer phytoplankton bloom. Two explanations were proposed. The first was that phytoplankton in the channel were trapped along with other particles in a null zone created by a gravitational circulation cell, which formed an observed zone of maximum turbidity within Suisun Bay and was often closely associated with the location of maximum netplankton (plankton >22 microns in size) and chlorophyll (Arthur and Ball 1980; Jassby et al. 1996). In most years this was located in Suisun Bay in the summer. The phytoplankton were then advected out over the broad adjoining shallows, where light penetration was sufficient for rapid phytoplankton growth. The high phytoplankton densities in Suisun Bay may also have been due in part to the trapping of exogenous phytoplankton by gravitational circulation, rather than *in situ* growth (Cole and Cloern 1984). In drought years with reduced freshwater inflows, the null zone moved upstream to the narrower and more uniformly deep waters of the Sacramento River, phytoplankton spent more time in deeper water where there was inadequate light for photosynthesis, so that growth was inhibited and the population never grew to a significant peak (Arthur and Ball 1980). The alternate explanation was that populations of filter-feeding organisms that preferred higher concentrations of salinity than were typically found in Suisun Bay, especially the Atlantic clam *Mya arenaria*, increased in Suisun Bay during the two-year drought, and by 1977 were abundant enough to consume phytoplankton as fast as they could reproduce (Nichols 1985). The relative contribution of these two mechanisms—null-zone relocation and benthic grazing—to Suisun Bay phytoplankton dynamics prior to 1987 was never disentangled, though Nichols (1985) opined that they were "certainly additive." In addition, summer measurements of currents in Suisun Bay in the 1990s often failed to show the presence of a gravitational circulation cell, and the simple picture of a particle and phytoplankton entrapment zone moving up and down the estuary in response to changes in flows, no longer seems to hold (Jassby et al. 1996).

Beginning in 1987, the filter-feeding Asian clam *Corbula amurensis* became abundant in Suisun Bay. Since then, phytoplankton densities have remained low through the summer in most years, with many observers concluding that benthic grazing is now the primary control on summer phytoplankton growth (Alpine and Cloern 1992; Jassby 2008). Annual primary productivity in Suisun Bay declined substantially (to 20 g C/m<sup>2</sup>-yr in 1988 compared to 100 g C/m<sup>2</sup>-yr in 1980—Alpine and Cloern 1992) along with phytoplankton biomass (Cloern et al. 2006; Dugdale et al. 2007). Dugdale et al. (2007), however, recently argued that the phytoplankton decline started in the decade before the first records of *C. amurensis* and was probably caused by increased ammonia in wastewater treatment plant discharges resulting from the adoption of secondary treatment processes. Ammonia discharged into the Sacramento and San Joaquin rivers from wastewater plant discharges increased over 1985-2005, and ammonia concentrations in the Delta and Suisun Bay rose in 1996-2005 (Jassby 2008). In Dugdale et al.'s (2007) view, the impact of *C. amurensis* was not that it ate up phytoplankton faster than the phytoplankton could reproduce, but rather that it

maintained the inhibition of nitrate uptake by keeping phytoplankton populations so small that they couldn't deplete ammonia, and by excreting wastes that added ammonia to the water.

After declining for two decades (Jassby et al. 2002; Dugdale et al. 2007; Jassby 2008), there was no upward or downward trend in the (low) phytoplankton densities in Suisun Bay in 1996-2005 (Jassby 2008). During this period, nutrient concentrations (dissolved inorganic nitrogen, soluble reactive phosphorous, and silica) were high enough to not limit growth (Jassby 2008). In the Delta, phytoplankton productivity and density increased over this period, and thus phytoplankton carried into Suisun Bay from the Delta must account for a larger component of Suisun Bay's phytoplankton than they did in prior decades (Jassby 2008). Two spring blooms were recorded between 2000 and 2003, a larger one in 2000 fueled primarily by nitrate uptake, and a smaller one in 2003 fueled by ammonia uptake (Wilkerson et al. 2006; Dugdale et al. 2007).

### San Pablo Bay

Cloern (1979) reported that phytoplankton peaked in San Pablo Bay in the spring, with large increases in the population of a coastal diatom, *Skeletonema costatum*. He interpreted these dynamics as resulting from *Skeletonema* proliferating in waters outside the Golden Gate as a result of nutrient enrichment due to upwelling, being advected into San Pablo Bay in the bottom layer of two-layered gravitational flow, trapped in the region of the null zone which is often located near San Pablo Bay in the spring, and then dispersed over the San Pablo Bay shallows, where enough light penetrated throughout the slight depth to promote rapid growth. Declines in the late summer or fall then resulted from reduced upwelling and decreased inputs of coastal diatoms, as well as movement of the null zone upstream and out of San Pablo Bay with declining Delta outflows (Cloern 1979). Dugdale and colleagues, however, have recently argued that spring blooms in San Pablo Bay and Central Bay result from *in situ* phytoplankton growth, sparked by nitrate uptake facilitated by low ammonia concentrations and adequate water transparency (Wilkerson et al. 2006; Dugdale et al. 2007).

The size of the baseline phytoplankton biomass from San Pablo Bay and the size of spring and fall blooms have increased significantly since the mid-to-late 1990s (Cloern 2006; Cloern et al. 2007). Cloern et al. (2007) argued that this was likely due to colder surface waters and greater upwelling along the central California coast (related to the start of an Eastern Pacific cold phase of the Pacific Decadal Oscillation), causing an increase within the Bay of some fish and crab species (Bay shrimp *Crangon* spp., Dungeness crab *Cancer magister* and English sole *Parophrys vetulus*) that prey on filter-feeding clams and mussels that live on the Bay bottom, a consequent reduction in the biomass of these filter feeders and their phytoplankton consumption rate, and thus an increase in phytoplankton density. This effect may have been augmented by advection into the Bay of coastal-produced phytoplankton, or resting stages or vegetative cells of coastal phytoplankton that could seed blooms within the Bay, whose coastal densities may have increased in response to upwelling changes (Cloern et al. 2007).



### Central Bay

Similar to San Pablo Bay, phytoplankton densities in Central Bay peak between May and June and consist mainly of coastal diatoms, including *Skeletonema costatum* and other species (Cloern 1979; Jassby et al. 1996). Cloern (1979) and Jassby et al. (1996) suggested that the Central Bay phytoplankton concentrations resulted from upwelling and offshore blooms outside of the Golden Gate, which were then carried into the Central Bay in tidal currents. Dugdale and colleagues, however, have recently argued that spring blooms in Central Bay are the result of phytoplankton growth within the Central Bay, based on nitrate uptake facilitated by low ammonia concentrations and suitable water transparency (Wilkerson et al. 2006; Dugdale et al. 2007). Water transparency has decreased in the Central Bay since the mid-to-late 1990s (Cloern et al. 2006), but as noted above for San Pablo Bay, the size of the baseline phytoplankton biomass and the spring blooms increased significantly, possibly resulting from coastal changes in upwelling and surface temperature causing a top-down trophic cascade that increased benthivorous predators, reduced filter-feeding bivalves and released phytoplankton blooms, possibly augmented by an influx of coastally-produced phytoplankton (Cloern et al. 2006; Cloern et al. 2007).

### South Bay

The South Bay is a brackish embayment with no large direct inflow of fresh water. Most of the nitrogen and phosphorous input is in wastewater discharges at a relatively constant rate throughout the year; large discharges at the southern end of the Bay produce a north-south gradient in nutrient concentrations (Conomos et al. 1979). The South Bay is generally less turbid than the river-dominated northern reach of the Bay and is usually well-mixed vertically (Conomos et al. 1979; Cole & Cloern 1984). However, under certain conditions when there are adequate freshwater inflows in the winter or spring, during periods of weak tidal and wind mixing, the South can stratify with lighter, low salinity water lying over denser, saltier water on the bottom. Phytoplankton are then retained in the upper layer where there is enough sunlight for rapid growth, and populations can build up rapidly (Conomos et al. 1979; Cloern 1979; Jassby et al. 1996). When the water is stratified, the phytoplankton populations in the upper layer are also kept apart from clams and other filter-feeding invertebrates on the bottom that could consume them (Cloern 1982; Cole & Cloern 1984; Jassby et al. 1996). Jassby et al. (1996) noted that phytoplankton blooms in the South Bay may require a low biomass of benthic filter feeders in the shallows to get started and to sustain for more than 1-2 weeks, and that the typically lower benthic biomass in the spring may explain why South Bay blooms have been more frequent and stronger in the spring than in the fall.

Studies in the early 1960s found that South Bay phytoplankton blooms were dominated by large diatoms typical of coastal waters (Storrs et al. 1963), but in the late 1970s-1980s blooms were dominated by microflagellates and small centric diatoms (Cloern 1979; Cole & Cloern 1984). It's unclear whether this is a sampling artifact or a real shift in phytoplankton composition (Cloern 1979). In the summer, large diatoms are common in the northern part of the South Bay, while microflagellates and small diatoms are

found in the south (Cloern 1982). Jassby et al. (1996) reported that South Bay spring blooms are dominated by diatoms and are sometimes followed by a red tide produced by a nontoxic ciliate, *Mesodinium rubrum*.

Similar to San Pablo and Central Bay, since the mid-to-late 1990s there were significant increases in the size of the baseline phytoplankton biomass in the South Bay, in the spring blooms in the northern part of the South Bay, and in fall blooms throughout the South Bay (Cloern et al. 2006; Cloern et al. 2007). As noted above for Central and San Pablo Bays, this may have resulted from coastal oceanographic changes triggering an increase in benthivorous predators and a consequent reduction in benthic filter-feeders,<sup>6</sup> allowing the phytoplankton to bloom, possibly augmented by an influx of larger numbers of coastal phytoplankton also related to the coastal oceanographic changes (Cloern et al. 2007).

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<sup>6</sup> Note, however, that the decline in the biomass of filter-feeding bivalves in the South Bay reported by Cloern et al. (2007, Fig. 3A at page 18563) began in 1999, and thus preceded the increase in benthivorous fish and crustaceans in the marine domains of the Bay (San Pablo Bay to South Bay) reported by Cloern et al. (2007, Fig. 3B), which began as a minor increase in 2000 and strengthened beginning in 2001. Furthermore, since these species of benthivores primarily feed on the newly settled or smaller bivalves, one might expect a lag of a year or more before seeing a significant impact on bivalve biomass.

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