

## Spatial and temporal variability of picocyanobacteria *Synechococcus* sp. in San Francisco Bay

**Abstract**—We collected samples monthly, from April to August 1998, to measure the abundance of autotrophic picoplankton in San Francisco Bay. Samples taken along a 160-km transect showed that picocyanobacteria (*Synechococcus* sp.) was a persistent component of the San Francisco Bay phytoplankton in all the estuarine habitats, from freshwater to seawater and during all months of the spring–summer transition. Abundance ranged from  $4.6 \times 10^6$  to  $5.2 \times 10^8$  cells  $L^{-1}$ , with peak abundance during the spring bloom (April and May) and during July with a persistent spatial pattern of smallest abundance near the coastal ocean and highest abundance in the landward domains of the estuary. The picocyanobacterial component (as estimated percentage of chlorophyll a concentration) was, on average, 15% of total phytoplankton biomass during the summer–autumn nonbloom periods and only 2% of chlorophyll biomass during the spring bloom. This result is consistent with the emerging concept of a gradient of increasing importance of picocyanobacteria along the gradient of decreasing nutrient concentrations from estuaries to the open ocean.

For two decades now biological oceanographers and limnologists have explicitly recognized the importance of micron-sized phytoplankton (picoplankton) as components of the autotrophic communities of pelagic systems. The picoplankton, predominantly coccoid cyanobacteria (*Synechococcus* sp., Johnson and Sieburth 1979; Waterbury et al. 1979), can be major contributors of phytoplankton biomass and production in the oceans (Joint 1986; Olson et al. 1990) and lakes (Stockner 1988). The size distribution of the phytoplankton, and in particular the partitioning between picoplankton and larger cells, is a fundamental aspect of pelagic systems that (a) reflects the source and cycling of nutrients, and (b) influences the pathways through which production is transferred to consumers. In general, we associate the picoplankton with low-nutrient conditions where primary production is sustained by regenerated nutrients (Chisholm 1992); picoplankton production is first transferred to consumers by protozoan grazing since most metazoans cannot effectively capture micron-sized algal cells (Tamigneaux et al. 1995; Vaquer et al. 1996). On the other hand, we associate the larger phytoplankton (especially fast-growing diatoms) with high-nutrient conditions where primary production is sustained by inputs of new nutrients; trophic transfer of large-cell production begins with metazoan grazing, and some fraction of this production is exported by sinking.

The distinction between picoplankton regenerating systems and large-cell new-production systems results, in part, from the competitive advantage of small cell size under con-

ditions of resource limitation (Raven 1986; Riegman et al. 1993). This competitive advantage disappears under high-nutrient conditions because the picoplankton population growth is tightly regulated by the fast-growing protozoan consumers (Ning and Vault 1992), whereas the larger cells have (at least temporary) refuge from predation by the slower-growing metazoan grazers (Malone 1992; Riegman et al. 1993). Therefore, inputs of new nutrients tend to promote net population growth and biomass accumulation of larger cells (Malone 1992). As a result of these differences in size-related growth and grazing rates, the picoplankton component of production is highest in the oligotrophic regions of the ocean (Joint 1986; Chisholm 1992). The picoplankton component also increases in regions (Joint 1986; Ning et al. 1996), and during seasons (Malone 1992; Li 1998) of high water temperature because the picoplankton have a stronger growth response to temperature variability than the larger eucaryotic cells (Andersson et al. 1994). So, the size-related aspects of pelagic primary production and trophic transfer seem to be determined largely by the nutrient-temperature regime (Malone 1992). This principle would suggest that estuaries, which have continual inputs of exogenous nutrients from their watersheds, might act as new-production systems that tend to favor production of large cells (Riegman et al. 1993). In fact, Iriarte and Purdie (1994) have proposed that phytoplankton size distribution changes along the eutrophication gradient from the land margin to the open ocean, with the picoplankton contribution >50% offshore, ~20% in the coastal ocean, and <10% in estuaries. The few studies of estuarine picoplankton ecology are generally consistent with this hypothesis, although there are exceptions such as the Thau Lagoon (France) where the picoplankton contribute nearly 40% of primary production (Vaquer et al. 1996). This special case might be explained by the unusual intensity of (size-selective) suspension feeding by oysters reared in this lagoon. Therefore, the balance between picoplankton and larger-cell production in estuaries might be determined by a combination of nutrient/temperature-driven differences in growth rate and the strength of grazing by benthic/epibenthic suspension feeders that typically select larger cells.

### *San Francisco Bay as a gradient of estuarine habitats*

Here, we present results of a study designed to measure the abundance of the picocyanobacteria (*Synechococcus*) in San Francisco Bay as an example of a nutrient-rich, temperate-zone estuary in which phytoplankton dynamics are influenced by the benthic suspension feeders. San Francisco Bay has been a site of sustained estuarine research for three de-

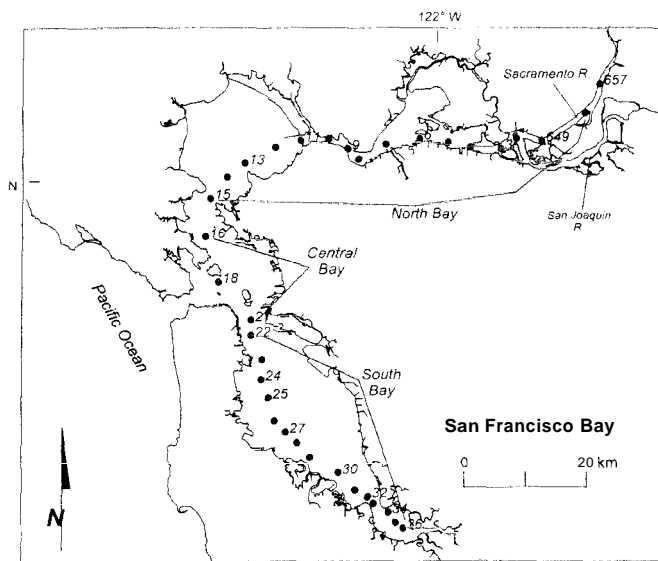


Fig. 1. Map of the San Francisco Bay estuarine system, showing locations of hydrographic sampling (CTD profiles, nutrients, chlorophyll) and sampling for cyanobacteria abundance (numbered circles).

acades, and one focus has been to identify the patterns and mechanisms of estuarine phytoplankton dynamics measured as spatial-temporal variability of chlorophyll biomass and primary production (Cloern 1996). Although studies have been conducted to partition biomass and production among algal size classes (Cole et al. 1986), there has been no study yet to measure the picocyanobacterial component of the phytoplankton in this estuary. San Francisco Bay is a useful site for general estuarine research because it comprises geographic subsystems that provide large gradients in the physical, chemical, and biological components of habitat that influence phytoplankton population dynamics, including those components thought to shape the composition of phytoplankton communities. The northern reach (North Bay, Fig. 1) is a partially stratified estuary of the Sacramento-San Joaquin Rivers, with longitudinal gradients of salinity, turbidity from suspended sediments, and dissolved inorganic nutrients. The North Bay is strongly influenced by seasonal fluctuations in river discharge, which varies from (monthly mean) flows of  $-2,000 \text{ m}^3 \text{ s}^{-1}$  during winter-spring to summer-autumn minima of  $-100-200 \text{ m}^3 \text{ s}^{-1}$ . By contrast, the South Bay is a semienclosed marine lagoon system that is influenced by riverine discharge only during the high-flow season, but persistently influenced by nutrient inputs from the densely populated local watershed (Hager and Schemel 1996). Between these distinct subsystems is the Central Bay (Fig. 1), a deep region where water masses from the North Bay, South Bay, and the coastal Pacific Ocean are mixed by tidal currents.

Past studies of bulk quantities (Chl a, primary production) have shown how phytoplankton dynamics in San Francisco Bay are influenced by the spatial gradients and seasonal variability of the bottom-up, top-down, and hydrodynamic processes that control the balance between phytoplankton production, consumption, and transport in estuaries. In

particular, nutrient (dissolved inorganic N, P, Si) concentrations are usually above levels that limit phytoplankton growth (Cloerli 1999); light limitation is a strong controlling force on phytoplankton growth rates, and spatial gradients of primary production closely parallel the river-ocean gradient of suspended sediments and light availability (Cloern 1996); top-down control is dominated by the consumption of phytoplankton cells by benthic suspension feeders, which balances primary production in the landward regions of the North Bay (Alpine and Cloern 1992) and exerts a strong seasonal control on phytoplankton dynamics in South Bay; key physical processes include tidally-driven vertical mixing and salinity stratification as these influence the growth-grazing balance (Lucas et al. 1998). The phytoplankton community, as a whole, responds to changing physical dynamics (river flow, tidal mixing, stratification) in the South Bay during spring, when a bloom occurs each year. On this foundation of past study, we ask here the first-order questions about picocyanobacterial ecology: What is their contribution to the total community biomass (and potential production), and how does this contribution vary (a) spatially along the large habitat gradients? and (b) seasonally in response to changes in the riverine and tidal forcings that are so prominent in estuaries'?

**Methods**—We conducted monthly sampling cruises from April through August 1998, to map the spatial distributions of habitat descriptors and picocyanobacteria abundance along a 160-km transect between the North Bay, Central Bay, and South San Francisco Bay. At each sampling location (Fig. 1), we measured vertical profiles of salinity and temperature (Sea-Bird Electronics SBE-9/11 CTD), chlorophyll fluorescence (Sea Tech fluorometer), and turbidity (D&A Instruments OBS sensor). Near-surface ( $-2 \text{ m}$ ) water samples were collected at some of these stations with a 5-liter Niskin bottle, and aliquots were analyzed for: Total Chl a (samples collected onto A/E glass fiber filters, extracted in 90% acetone, and concentration determined spectrophotometrically; Lorenzen 1967); suspended sediment concentration (measuring the dry weight of seston collected onto preweighed  $0.4 \mu\text{m}$  Nuclepore filters); and dissolved inorganic nitrogen and phosphorus (using filtrates passing  $0.4 \mu\text{m}$  Nuclepore filters, and analyzed with a Technicon Autoanalyzer II). The discrete measures of Chl a and suspended sediment concentration were used to calibrate the fluorometer and OBS sensor each cruise. Complete results of this sampling program are available over the Internet. Aliquots of some water samples were preserved in acidified Lugol's solution and later examined under light microscope to identify and count the eucaryotic phytoplankton.

Water samples for cyanobacteria enumeration were fixed in 1% paraformaldehyde and stored in polyethylene bottles. Sample bottles were held at room temperature for 10 min and then frozen immediately in liquid nitrogen and stored at  $-80^\circ\text{C}$ . Samples for microscopic determinations of autotrophic picocyanobacteria were filtered onto black polycarbonate membrane filters with a pore size of  $0.2 \mu\text{m}$ , and enumerated under an Olympus BH-2 epifluorescence microscope equipped with a 100 W mercury lamp and Olympus G filter set, or with a Nikon ECLIPSE E800 epifluorescence micro-

scope equipped with a 100 W mercury lamp and Nikon EF-4 FITC/TRITC (F-R) 25 mm dual filter cube. The G filter set was supplemented with an EO530 excitation filter and 0590 barrier filter (a long pass filter) to produce narrow-band green excitation around 530 nm. With this combination of excitation and emission filters, phycoerythrin-containing *Synechococcus* fluoresced bright orange-yellow, its emission wavelength around 590–630 nm (Hofstraat et al. 1991). Slides were counted using Plan Apo X40 objectives with the Olympus BH-2 and X60 or X100 oil-immersion objectives with the Nikon E-800 microscope with X15 oculars. For each sample, a minimum of 10 reticule fields with at least 400 cells were counted. For a few samples that had very low abundance, cell counts were accumulated over 20 reticule fields. For our procedures, counting error that included intercalibration between the two epifluorescence microscopes typically averaged 5% (C.V.). Dimensions (diameter of coccoid cells, diameter and length of rod-shaped cells) were recorded for all enumerated cells.

**Results and discussion**—This study was designed to follow changes during the spring–summer transition when river discharge recedes, water temperature increases, and chlorophyll biomass declines following the spring bloom. The top panels of Fig. 2 show the changing spatial distributions of near-surface salinity and temperature during the five sampling cruises. The first (April) sampling occurred after months of high river flow and diluted salinities throughout San Francisco Bay. Near-surface salinity ranged between about 10–17 psu in South Bay, 15 psu in Central Bay, and from 15–0 along the North Bay. As river flow receded, salinities progressively increased and reached August maxima of 20–25 in South Bay, 30 in Central Bay, and from 20–0 along the North Bay (Fig. 2). These changing salinity distributions reflect the changing balance between the riverine input of fresh water and the physical processes that drive horizontal advection and mixing along the estuary and exchanges with the coastal ocean. Shapes of the salinity profiles along the 160-km transect show that these balances were different for the South Bay, Central Bay, and North Bay. Together with the temperature profiles, these confirm the distinct character of the South Bay as a marine-brackish lagoon, the North Bay as a river-dominated estuary, and the Central Bay as an estuarine zone having a strong influence of mixing with the coastal ocean. Surface temperatures were fairly uniform in April (~13–14°C) and May (~15–16°C), but there were large horizontal temperature gradients in the summer months when water temperature increased rapidly in the landward domains of both the South Bay and North Bay. For example, during July we measured surface temperature of 13.7°C in the Central Bay and 23.6°C in the Sacramento River and upper estuary (Fig. 2).

The horizontal distributions of suspended particles, both sediments and phytoplankton (as chlorophyll biomass), were consistent with the notion of distinct subdomains within the San Francisco Bay system (Fig. 2). Spatial distributions of suspended particulate matter (SPM) along the North Bay–Central Bay showed a localized turbidity maximum that was seaward and intense in April, when near-surface SPM concentration was over 100 mg L<sup>-1</sup>. This turbidity maximum

became displaced landward as river flow receded during summer. SPM concentrations were consistently low in the Central Bay, reflecting the large distance from the riverine source of sediments and rapid exchange with the coastal ocean. In the lagoonal South Bay, SPM concentrations were highly variable, especially in April when high concentrations (>250 mg L<sup>-1</sup>) were measured at the landward extreme. Chlorophyll distributions showed an intense spring phytoplankton bloom in April 1998, with elevated concentrations of Chl a throughout San Francisco Bay. The highest Chl a concentrations occurred in the landward reach of the South Bay, with peaks >160 µg L<sup>-1</sup> and progressive dilution of chlorophyll toward the Central Bay. A second local maximum occurred in the landward reach of the North Bay, coincident with the turbidity maximum, where near-surface Chl a was 45 µg L<sup>-1</sup>. This same feature was observed in May (Fig. 2), but with reduced Chl a concentrations (13 µg L<sup>-1</sup>). The spring bloom was a period of high abundance of several species of coastal diatoms (*Skeletonema costatum*, *Chaetoceros debilis*, *C. subtilis*, *C. gracilis*), phytoflagellates (*Teulaxia arnphioxia*, *Rhodomonas salina*, *Pyrurnimonas orientalis*, *Plagioselmis prolonga*), chlorophytes (*Chlorella marina*, *Nannochloris atomus*), and the dinoflagellate *Heterocapsa rotundata*. We measured low Chl a concentrations throughout the estuary during the June, July, and August cruises, consistent with past observations of low phytoplankton biomass during summer.

Seasonal changes in dissolved inorganic nitrogen and phosphorus were also similar to those observed in other years, with highest concentrations of dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP) in the landward reaches of the South Bay, reflecting the large local inputs from the urban watershed (Hager and Schemel 1996). Nutrient concentrations were more homogeneous along the North Bay–Central Bay transect. In all three subregions, the DIP concentration was always above 0.75 µM, typically between 1–2 µM, and never at levels that would severely limit phytoplankton growth. DIN was also usually well above rate-limiting concentrations, except for measurements made in the seaward reach of the South Bay in April (Fig. 2). From previous observations, we infer that this localized depletion of DIN was ephemeral; by the May cruise, DIN concentrations in this region had already recovered to 10 µM. Therefore, while DIN depletion may have played a role in limiting the size of the spring bloom in South Bay, observations in 1998 were consistent with the idea that San Francisco Bay is a nutrient-rich estuary and that nutrient limitation plays only a minor role in regulating phytoplankton growth rate.

These results show that the spatial-temporal variability encountered during the study encompassed much of the habitat variability found in temperate-zone estuaries: salinity ranged from 0 to 30 psu; temperature ranged from 12.9 to 24.0°C; near-surface SPM concentrations ranged from 2 to >250 mg L<sup>-1</sup>; phytoplankton biomass ranged from nonbloom conditions of 1.3 µg L<sup>-1</sup> Chl a to a massive bloom with Chl a >160 µg L<sup>-1</sup>; and a short-term, localized event of DIN depletion occurred against a background of high DIN and DIP concentrations. Across this broad range of habitat conditions, we measured changes in cyanobacterial *Synechococcus*

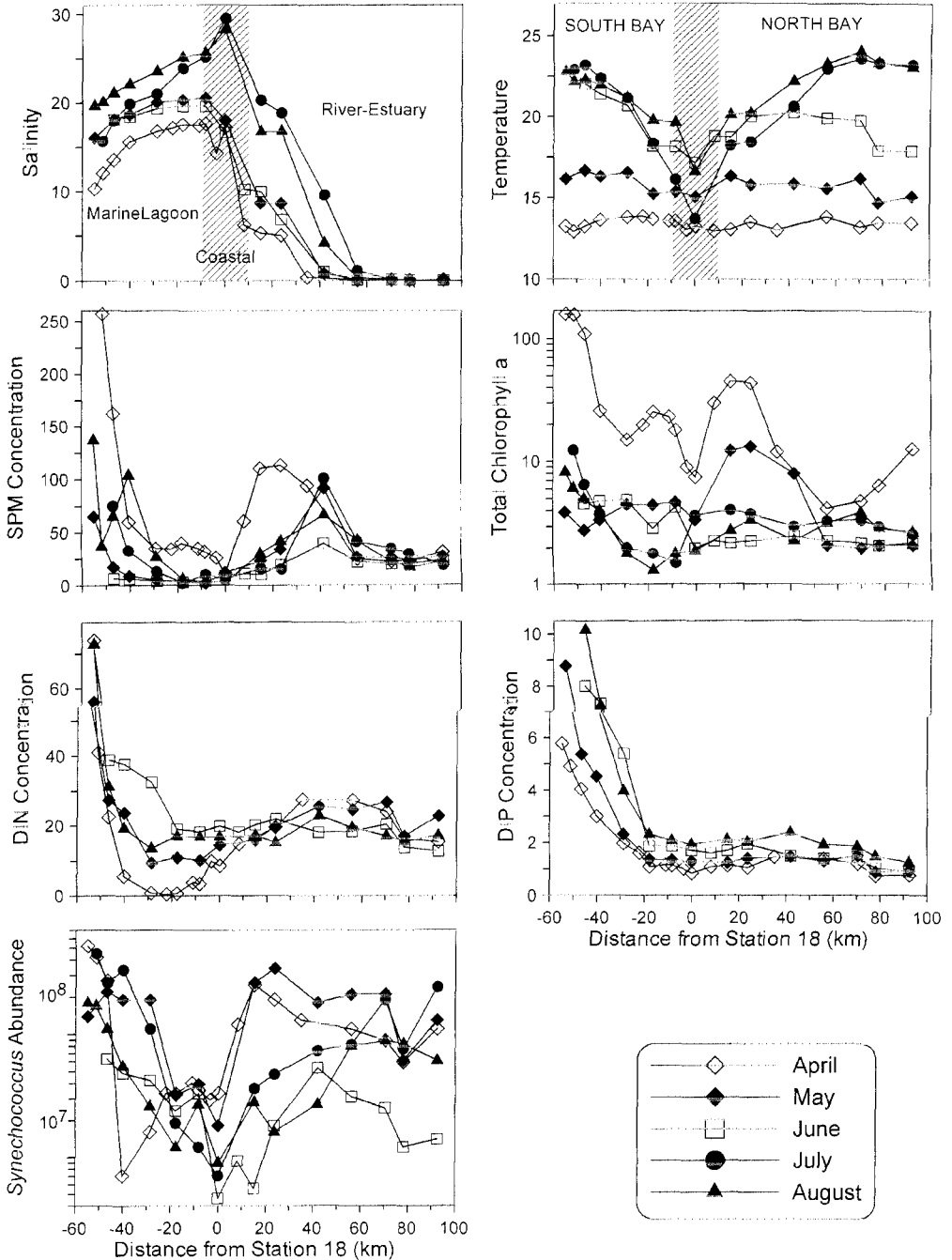


Fig. 2. Spatial distributions of habitat descriptors and *Synechococcus* abundance along the 160-km longitudinal transect in San Francisco Bay, comparing results from monthly sampling between April and August 1998. Distances are measured from Sta 18 in the Central Bay, with negative values in the South Bay and positive values in the North Bay. Distributions of salinity and temperature (upper panels) illustrate the marine/brackish character of the lagoonal South Bay, strong coastal influence in the Central Bay, and the river-estuary continuum of the North Bay. Panels below show, in sequence, the changing spatial distributions of SPM concentration ( $\text{mg L}^{-1}$ ), total Chl *a* concentration ( $\mu\text{g L}^{-1}$ ), dissolved inorganic nitrogen and phosphorus ( $\mu\text{M}$ ), and *Synechococcus* abundance ( $\text{cells L}^{-1}$ ).

Table 3. Estimated biomass of picocyanobacteria as chlorophyll concentration Pico-Chl *a* ( $\mu\text{g L}^{-1}$ ) and as percentage of total Chl *a* biomass (% total).

Month 1998	Bay*	Pico-Chl <i>a</i> ( $\mu\text{g L}^{-1}$ )		Pico-Chl <i>a</i> (% Total)	
		Range	Mean ( $\pm$ SD)	Range	Mean ( $\pm$ SD)
Apr	North Bay	0.46–1.95	1.04 $\pm$ 0.51	3.4–20.5	9.3 $\pm$ 6.1
	Central Bay	0.23–0.94	0.43 $\pm$ 0.34	1.5–3.5	2.7 $\pm$ 0.9
	South Bay	0.09–4.06	1.32 $\pm$ 1.60	0.4–2.5	1.6 $\pm$ 0.6
May	North Bay	0.25–0.58	0.41 $\pm$ 0.12	3.6–25.1	12.0 $\pm$ 8.5
	Central Bay	0.14–0.30	0.22 $\pm$ 0.11	4.1–6.5	5.3 $\pm$ 1.7
	South Bay	0.25–0.89	0.65 $\pm$ 0.25	5.6–31.9	18.4 $\pm$ 9.8
Jun	North Bay	0.07–0.41	0.18 $\pm$ 0.12	3.4–16.6	7.8 $\pm$ 4.6
	Central Bay	0.06–0.44	0.21 $\pm$ 0.20	3.1–10.3	6.3 $\pm$ 3.7
	South Bay	0.32–0.85	0.60 $\pm$ 0.22	11.1–18.4	13.6 $\pm$ 3.4
Jul	North Bay	0.28–0.97	0.47 $\pm$ 0.28	6.9–37.5	15.3 $\pm$ 11.0
	Central Bay	0.09–0.16	0.13 $\pm$ 0.05	2.5–10.8	6.7 $\pm$ 5.9
	South Bay	0.15–1.83	0.97 $\pm$ 0.68	8.2–35.3	19.4 $\pm$ 10.2
Aug	North Bay	0.12–0.68	0.43 $\pm$ 0.24	3.7–22.4	13.9 $\pm$ 7.0
	Central Bay	0.12–0.36	0.24 $\pm$ 0.17	6.3–20.2	13.3 $\pm$ 9.8
	South Bay	0.16–1.41	0.73 $\pm$ 0.55	10.7–21.8	15.1 $\pm$ 4.3

\* North Bay: Sta 15, 13, 11, 9, 6, 3, 649, 657; Central Bay: Sta 21, 20, 18, 16; South Bay: Sta 36, 34, 32, 30, 27, 25, 24, 22.

Francisco Bay system (Fig. 2). Rather, we observed high *Synechococcus* abundances in April (mean =  $1.3 \times 10^8$  cells  $\text{L}^{-1}$ ; Table 1) in association with the spring bloom, and in May (mean =  $1.6 \times 10^8$  cells  $\text{L}^{-1}$ ) when *Synechococcus* cells were mostly small (0.5–0.8  $\mu\text{m}$  diameter), but also in July (mean =  $1.4 \times 10^8$  cells  $\text{L}^{-1}$ ), when total chlorophyll biomass was low. Smallest abundances were observed in June (mean =  $2.7 \times 10^7$  cells  $\text{L}^{-1}$ ). High abundance in April suggests that the picocyanobacteria population responded to the changing physical dynamics of the estuary during spring, when the populations of diatoms and phytoflagellates also grew very rapidly; high abundance in May with smaller cell size reflected *Synechococcus* fast growth and less strong grazing by heterotrophic nanoplankton. High abundances in July are consistent with observations in other temperate-boreal estuaries (e.g., Malone 1992; Lewitus et al. 1998) where peak annual abundances are observed during some summer months. The low abundances in June and August suggest that the balance between cyanobacteria growth and grazing loss fluctuates at the monthly time scale. We know, from past studies (Ambler et al. 1985), that the population dynamics of protistan grazers, such as tintinnid ciliates, are characterized by high-amplitude fluctuations during spring–summer. We did not measure grazing loss rates of cyanobacteria in our study, but such measurements in other systems have shown tight regulation of cyanobacteria abundance by protistan grazing. For example, grazing rates by heterotrophic nanoplankton were high enough to balance the growth rates of picocyanobacteria in the English Channel (Ning and Vaulot 1992) and in North Inlet during summer (Lewitus et al. 1998).

In order to assess the potential ecological significance of cyanobacteria in San Francisco Bay, we transformed *Synechococcus* cell abundances into estimated chlorophyll biomass, and then compared these values to our measures of total chlorophyll concentration. Individual *Synechococcus*

cells displayed various shapes, such as spheres or rods, but most (>80%) were coccoid cells in the size range of 0.5–1.4  $\mu\text{m}$  diameter (the commonest was 0.8 to 1.2  $\mu\text{m}$  diameter). Biovolume was calculated using the formulas  $4/3 (\pi r^3)$  for coccoid and  $\pi r^2 h$  for rod-shaped cells. Cell volumes were transformed to carbon biomass, using the conversion factor 470 fg C  $\mu\text{m}^{-3}$  (Verity et al. 1992), corresponding to a carbon mass of 250 fg C for coccoid cells of diameter 1  $\mu\text{m}$ . For transforming cell carbon biomass to Chl *a*, we used the conversion factor 32 g C g Chl *a*<sup>-1</sup> (Takahashi et al. 1985). These kinds of conversions yield estimates that are highly uncertain because of the large variability in the size and carbon and chlorophyll contents of *Synechococcus* cells (e.g., Malone 1980). Estimated values of picocyanobacterial chlorophyll are summarized in Table 3.

The estimated picocyanobacterial component of Chl *a* biomass ranged from <1% to 38% in San Francisco Bay and, consistent with all similar assessments (e.g., Chisholm 1992; Iriarte and Purdie 1994), there was a strong inverse relation between the picocyanobacterial fraction (as percentage of total chlorophyll) and the total chlorophyll biomass (Fig. 3). This observation is also consistent with the notion that the picocyanobacterial component of biomass becomes significant during periods of low phytoplankton biomass, but this contribution is relatively small during bloom events when the biomass of larger eucaryotic cells grows explosively. We partitioned the full data set into bins corresponding to conditions of high phytoplankton biomass ("blooms") and low biomass, and then plotted picocyanobacterial biomass (as estimated Chl *a* concentration) against total Chl *a* concentration for each condition (Fig. 3, insets). Linear regressions were significant ( $P < 0.01$ ), and the best fits were obtained when we defined the high-chlorophyll condition as events when total Chl *a* > 7  $\mu\text{g L}^{-1}$ . The slopes of the two regression equations indicated that the mean picocyanobacterial contribution to total chlorophyll biomass was ~15% during

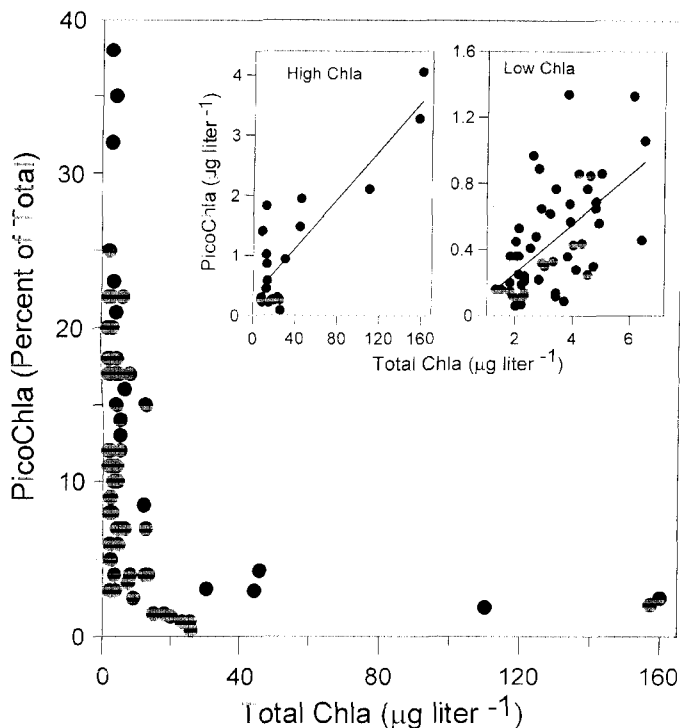


Fig. 3. Pico cyanobacteria biomass (as estimated percentage of Chl *a* concentration) vs. total phytoplankton biomass (as total Chl *a*), for the 76 samples collected in San Francisco Bay between April and August 1998. Upper insets show the correlations between picocyanobacteria biomass (as estimated Chl *a* concentration) and total Chl *a*. The data were partitioned into conditions of high Chl *a* ( $>7 \mu\text{g L}^{-1}$ ) and low Chl *a* ( $<7 \mu\text{g L}^{-1}$ ). Both regression lines were significant. High chlorophyll:  $y = 0.31 + 0.02x$  ( $r = 0.87$ ,  $n = 21$ ); Low chlorophyll:  $y = 0.04 + 0.15x$  ( $r = 0.59$ ,  $n = 55$ ).

nonbloom conditions but only 2% when Chl *a* exceeded  $7 \mu\text{g L}^{-1}$ . The overall mean picocyanobacterial Chl *a* concentration was  $0.61 \mu\text{g L}^{-1}$ , accounting for an estimated mean 11% of the total measured Chl *a* concentration.

We have not measured directly the contribution of the picocyanobacteria to total phytoplankton primary production in San Francisco Bay, but during a yearlong study of size-fractionated primary production at six sites, Cole et al. (1986) demonstrated that the  $<5 \mu\text{m}$  fraction contributed from 6% to 28% of total annual primary production. Moreover, Cole et al. showed that the chlorophyll-specific carbon assimilation rates of the  $<5 \mu\text{m}$ ,  $5\text{--}22 \mu\text{m}$ , and  $>22 \mu\text{m}$  components of the phytoplankton were not significantly different. This result implies that the contribution of each phytoplankton size class to total primary production scales directly with its contribution to total biomass. If this generality extends to the smallest (pico) size class, then the results presented here suggest that the picocyanobacteria might not contribute more than about 10% of the total primary production in San Francisco Bay. This figure might be an overestimate because our study of biomass was conducted during the warmest months when the picocyanobacterial contribution is expected to be greatest.

These conclusions are consistent with the hypothesis of Iriarte and Purdie (1994) that the picoplankton contribute

about 10% of primary production in nutrient-rich estuaries. Our results are also consistent with the hypothesis that, since picoplankton abundance is tightly regulated by fast-growing protistan grazers, the picoplankton component of biomass is relatively stable and oscillates around a steady mode as a "dynamic equilibrium" (Fogg 1991). We estimate that the picocyanobacteria never reached biomass greater than  $4.1 \mu\text{g L}^{-1}$  Chl *a*. On the other hand, total phytoplankton biomass reached  $160 \mu\text{g Chl L}^{-1}$  when the abundance of larger eucaryotic cells (diatoms, phytoflagellates) grew rapidly during the spring bloom. Therefore, San Francisco Bay does appear to function primarily as a new-production system in which nutrient concentrations are (almost always) above those that give selective advantage to small cells. There appear to be seasonal shifts in the relative importance of the new-production and regenerating systems, with small increases in the relative cyanobacterial component during the spring-summer transition. However, changes during this spring-summer transition are much smaller in San Francisco Bay than they are in other nutrient-rich estuaries such as Chesapeake Bay (Malone et al. 1991), the St. Lawrence estuary (Baie des Chaleurs, Tamigneaux et al. 1995), and the Baltic Sea (Uitto et al. 1997). Compared to these estuarine systems, San Francisco Bay is tidally energetic and subject to rapid turbulent mixing—a physical condition that precludes nutrient depletion of surface waters during summer (Fig. 2). Comparison among these ecosystems suggests that the relative importance of the picoplankton-selective regenerating state and the large-cell-selective new-production state (like many other aspects of pelagic dynamics) is strongly dependent upon physical dynamics, including processes that control the intensity of turbulent mixing and density stratification as these influence the relative importance of regenerated and exogenous sources of nutrients to estuarine phytoplankton.

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