Phytoplankton Blooms and Nitrogen Productivity in San Francisco Bay

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ABSTRACT: San Francisco Bay has been considered an HNLC or HNLG (high nutrient low chlorophyll or low growth) region with nonlimiting concentrations of inorganic nutrients yet low standing stocks of phytoplankton. Most of the studies leading to this conclusion come from the South Bay and little is known about nutrient processes and phytoplankton productivity in the northern and central parts of the estuary. Data collected over 3 yr (1999–2003) in Suisun, San Pablo, and Central Bays describe the availability of dissolved inorganic nitrogen (DIN), silicate, and phosphate and the seasonal variability in phytoplankton abundance. Rate measurements of fractionated nitrogen productivity provide the relative contributions of different forms of DIN (ammonium and nitrate) and different sized phytoplankton to the development of seasonal phytoplankton blooms. Regional differences in bloom dynamics are observed with Suisun Bay, the least saline, highest nutrient, most turbid region having less phytoplankton biomass and productivity than San Pablo and Central Bays, except in the abnormally wet spring of 2000. Spring blooms in San Francisco Bay are driven primarily by high rates of nitrate uptake by larger phytoplankton cells following a period of increased ammonium uptake that depletes the ambient ammonium. The smaller occasional fall blooms are apparently fueled mostly by ammonium uptake by small sized phytoplankton. The data suggest that the HNLC condition in the northern and central parts of San Francisco Bay is due primarily to light availability modulated by the interaction between ammonium and nitrate, and the relative amounts of the two forms of the DIN pool available to the phytoplankton.

Introduction

The San Francisco Bay (SFB) is of tectonic origin and can be separated into the northern estuary and the South Bay, which has been studied intensively (e.g., Conomos 1979; Nichols and Thompson 1985; Cloern 1996; Hollibaugh 1996; Kimmerer 2004). The northern estuary that has been less studied is dominated by the discharge at the Delta of the San Joaquin and Sacramento Rivers. Water passes through the embayments of the Suisun, San Pablo, and Central Bays with exit to the ocean through the Golden Gate (Peterson et al. 1996). Nutrient conditions in SFB have been considered nonlimiting with relatively high levels of nitrate (NO_3), silicate ($Si(OH)_4$), and phosphate (PO_4; Schemel and Hager 1986; Hager and Schemel 1996), resulting from primarily riverine and agricultural sources. Ammonium (NH_4) is also high in this urbanized estuary because of anthropogenic inputs (Hager and Schemel 1992). This upper region of SFB was ranked next to the lowest for phytoplankton production in a series of 24 river-dominated estuaries by Boynton et al. (1982).

Prior studies attribute a low standing stock of phytoplankton and low rates of primary productivity (Cole and Cloern 1984; Cloern 1996) to turbidity

(Cloern 1987, 1991) resulting in light limitation (Alpine and Cloern 1988). Also implicated is benthic grazing (Nichols and Thompson 1985; Kimmerer and Orsi 1996; Lehman 2000) especially by invasive species such as the asian clam, *Potamocorbula amurensis* (Alpine and Cloern 1992), now known as *Corbula amurensis* (Coan 2002). Seasonal phytoplankton blooms have been observed following periods of high freshwater flow, when stratification reduces both the effects of benthic grazing and light limitation (Cloern 1982, 1984, 1991; Cloern et al. 1983; Lucas et al. 1998). Reported primary productivity values for the estuary (e.g., Cloern 2001) are mostly derived from the commonly used primary productivity model of Cole and Cloern (1984, 1987) recently updated for use in the Delta (Jassby et al. 2002) that empirically derives carbon fixation from values of chlorophyll, incident light, and transparency. Following the use of $Si(OH)_4$ depletion to estimate primary productivity in the northern estuary (Peterson et al. 1975, 1985), Kimmerer (2005) more recently used this approach to provide an integrated picture of primary production by diatoms. Direct measurements of primary productivity, nutrient assimilation, or phytoplankton growth rates in the northern estuary are rare compared to the South Bay (e.g., Cloern 1996, 2001; Jassby et al. 1996; Lucas et al. 1998). There are no published measurements of nitrogen productivity using the stable isotope ^{15}N, except for a year-long

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401

study (1998–1999) in Central Bay by Hogue (2000) and Hogue et al. (2005). Our study was carried out since there is little known about the variability of phytoplankton production and nutrient use in Suisun, San Pablo and Central Bays.

The aim of this study was to evaluate whether phytoplankton biomass and productivity were low in the northern estuary and to assess any environmental causes by measuring the seasonal variability of nutrients, size fractionated chlorophyll, and nitrogen assimilation. Data collected over 3 yr in Suisun, San Pablo, and Central Bays describe the relative contributions of different forms of dissolved inorganic nitrogen (DIN = NH_4 and NO_3) to the development of seasonal phytoplankton blooms and provides nitrogen productivity rate data for the region.

Materials and Methods

Time Series Sampling

Surface water was sampled monthly from November 1999 to August 2003 aboard the R/V *Questuary* in San Francisco Bay at three locations described in Hogue et al. (2001) and on the United States Geological Survey (USGS) Water quality web site (http://sfbay.wr.usgs.gov/access/wqdata). These locations were in Suisun Bay (USGS sampling station 6, 38°3.9′N, 122°2.1′W), San Pablo Bay (USGS Station 13, 38°1.7′N, 121°22.2′W), and Central Bay (37°53.83′N, 122°25.5′W) and were sampled using 10-l Niskin bottles mounted on an SBE-33 carousel. During March and April sampling frequency was increased to weekly. Hydrographic data (temperature and salinity) were recorded from a Seabird SBE-19 CTD. A standard oceanographic Secchi disk was used to determine relative light penetration. Samples were taken for analyses of nutrients (NO_3, $Si(OH)_4$, PO_4, and NH_4), extracted chlorophyll *a* (chl *a*), and ^{15}N labeled NO_3 or NH_4 uptake. These analyses, including incubations for rate measurements, were carried out at the Romberg Tiburon Center near the Central Bay station location.

Nutrient, Chl A, and ^{15}N Uptake Analyses

NO_3, $Si(OH)_4$, and PO_4 were analyzed using a Bran and Luebbe AutoAnalyzer II, NO_3 and PO_4 according to Whitledge et al. (1981), and $Si(OH)_4$ using Bran and Luebbe Method G-177-96 (Bran Luebbe AutoAnalyzer Applications 1999). If samples for NO_3, $Si(OH)_4$, and PO_4 analysis were frozen before analysis then they were thawed 24 h prior to analysis to avoid polymerization effects on $Si(OH)_4$ measurements and poor reproducibility (MacDonald et al. 1986). NH_4 was analyzed according to Solorzano (1969) after the samples were prefiltered

through precombusted GF/F filters to remove sediment. Samples to be analyzed for NH_4 were never frozen. Chl *a* was determined by in vitro fluorometry (Arar and Collins 1992) using a Turner Designs Model 10 fluorometer, calibrated with commercially available chl *a* (Sigma Chemical Company or Turner Designs) on samples filtered onto either 25 mm Whatman GF/F filters (nominal pore size, 0.7 μm) or Nucleopore filters with either 5 or 10 μm pore size to collect the larger cells. ^{15}N uptake incubations were carried out in 280 ml polycarbonate bottles, for 24 h on incubation tables cooled with filtered SFB water and under window screening to expose them to 50% of ambient light. Because of steaming time from the sampling locations to the Romberg Tiburon Center where the incubations were carried out, most incubations were started towards the end of the light photoperiod. We selected a 24 h incubation period to encompass a natural light-dark photoperiod knowing that some regeneration of nutrients would result in an underestimation of uptake rates. On the assumption that any regeneration of organic nitrogen to NH_4 would occur at about the same rates as NH_4 uptake, the calculated underestimate of NH_4 uptake due to this regeneration would be 10–20%. ^{15}N inoculations were of trace additions (approximately 10% of ambient NO_3 or NH_4 concentrations) of either $K^{15}NO_3$ or $^{15}NH_4Cl$ (99 atom % ^{15}N). Incubations were ended by filtration onto precombusted (450°C for 4 h) 25 mm GF/F filters or Poretics silver filters with 5 μm pore size, and frozen until analysis for ^{15}N enrichment with a Europa Tracermass or PDZ 20/20 mass spectrometer system (Wilkerson and Dugdale 1992). Both transport rates (ρ) and biomass specific uptake (V; normalized to particulate nitrogen of the sample obtained by mass spectrometry) were calculated according to Dugdale and Wilkerson (1986). These data of ρNO_3 and ρNH_4 uptake are referred to as nitrogen productivity when they are summed, recognizing that there may be other small sources of nitrogen not measured here. Urea can be the predominant source of nitrogen fueling phytoplankton production in estuaries (Lomas et al. 2002; Glibert et al. 2005). Although urea was not measured in this study, there are a few spring and summer data available (Cochlan and Herndon unpublished data; Hogue unpublished data). Values measured in spring 2006 in San Pablo and Central Bays averaged 0.7 ± 0.2 μM (approximately 16% of the corresponding mean NH_4 concentrations) (Hogue unpublished data). Surface urea concentrations measured by Cochlan and Herndon (unpublished data) in SFB over the period of May to the end of August 2005 ranged from 0.3 to 3.8 μM (mean = 1.0 μM) on the eastern side of the Tiburon Peninsula

(adjacent to Paradise Cay), whereas on the western side of the Peninsula (Richardson's Bay) they were 0.2 to 2.5 μM (mean also = 1.0 μM). These ambient urea concentrations represent on average 41% and 31% of the corresponding NH_4 concentrations for the eastern and western embayments, respectively, and only occasionally were urea levels equal or greater than NH_4 (Cochan and Herndon unpublished data). These values indicate that urea is unlikely to be a predominant source of nitrogen compared to NO_3 that can reach 35 μM (Hogue et al. 2005).

Results

TIME SERIES DATA FOR SUISUN BAY

Seasonal changes in temperature (Table 1) occurred with warmer summer temperatures (mean of 20°C for June–August) and cooling down to mean temperature of 10.96°C during the winter (December–February). Salinity values also varied seasonally (Fig. 1, Table 1) with fresher water (2 psu or below) typically in March and April. Maximum salinity values in Suisun were 13.40 psu, with values above 10 psu rare, occurring usually in December, except for August to October 2002. Inorganic nutrient concentrations were high throughout the year in Suisun Bay with $NO_3 > 30$ μM, $Si(OH)_4 > 200$ μM, and $PO_4 > 2$ μM (Fig. 1). The most variable nutrient was NH_4, ranging from 1.3 to almost 16 μM and showing seasonal maxima in December–January (accompanying the higher salinity water) and dips in April/May (2000, 2003, accompanying chlorophyll peaks) and September (2000 and 2001).

Chlorophyll concentrations in Suisun Bay (Fig. 1) were constant and low during the monthly sampling (1–2 μg l^{-1}) except for two peaks (blooms of 30 μg l^{-1} in April 2000 and 8.5 μg l^{-1} in April 2003). The chlorophyll during these peaks was dominated by cells >5 μm in diameter measured as fractionated chlorophyll data (Table 1).

NO_3 and NH_4 uptake rates (Fig. 1) by phytoplankton in Suisun Bay were low most of the year, both as the absolute rates (ρ) and the biomass specific rates (V that gives a more physiological estimate of the phytoplankters capacity; Table 2). There was an obvious peak in NO_3 uptake (ρ = 0.3 μmol l^{-1} h^{-1}; Fig. 1), accompanying the spring bloom condition on April 11, 2000. This maximum in ρNO_3 uptake rate was higher than any measured ρNH_4 uptake rate. The fractionated NO_3 uptake data show uptake in spring was dominated by cells >5 μm in size (Table 2). Interestingly the small increase in chlorophyll in May 2003 was not accompanied by higher NO_3 uptake in Suisun Bay, but instead showed a slight increase in NH_4 uptake.
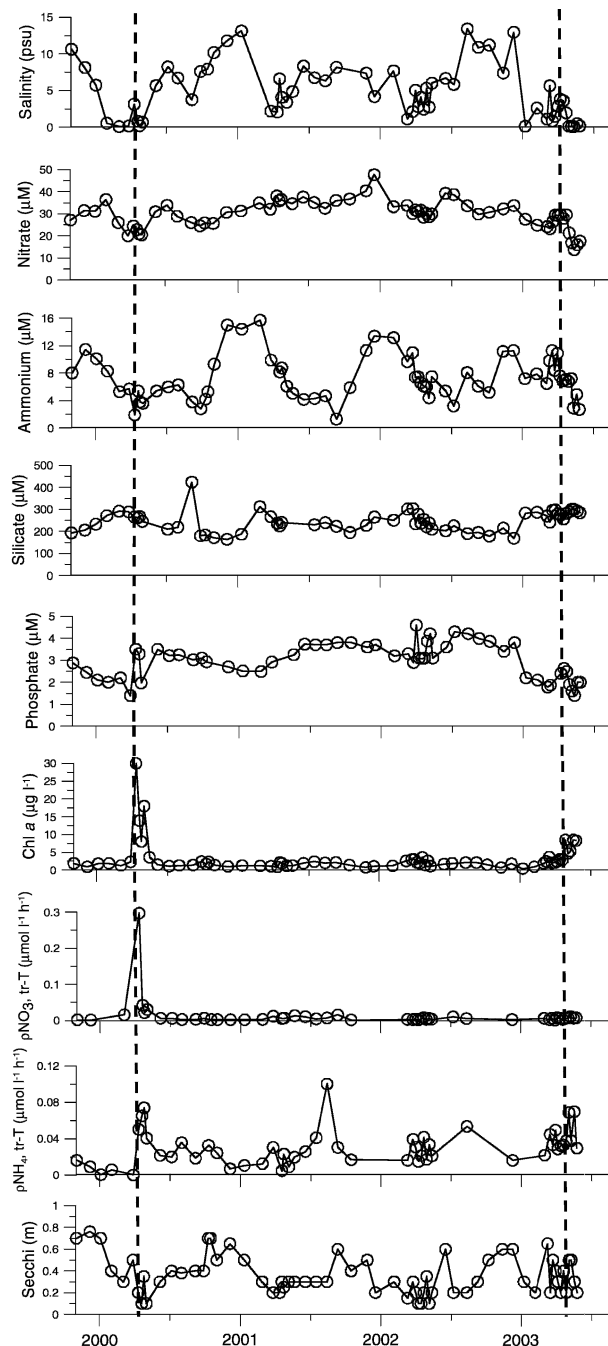

Fig. 1. Time series surface data from Suisun Bay from November 1999 to August 2003. Salinity (psu), NO_3 (μM), NH_4 (μM), $Si(OH)_4$ (μM), PO_4 (μM), chlorophyll a (μg l^{-1}), $\rho^{15}NO_3$ (μmol l^{-1} h^{-1}), $\rho^{15}NH_4$ (μmol l^{-1} h^{-1}), and Secchi depth (m). Dotted vertical lines show spring blooms described in text.

NH_4 uptake rates were more variable than NO_3 ranging from 0.0002 to 0.0247 μmol l^{-1} h^{-1} (Fig. 1), with peaks in April 2000 (ρ = 0.07 μmol l^{-1} h^{-1}), August 2001 (ρ = 0.1 μmol l^{-1} h^{-1}), and April and

TABLE 1. Mean surface hydrographic and chlorophyll data (±SD) and number of samples for Suisun, San Pablo, and Central Bays calculated as seasonal means for winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) from November 1999 to August 2003.

Bay	Season	Temperature (°C)	Salinity (psu)	NO$_3$ (μM)	Si(OH)$_4$ (μM)	PO$_4$ (μM)	NH$_4$ (μM)	Chl a (μg l^{-1})	>5 μm Chl (μg l^{-1})	% Chl > 5 μm	Secchi (m)
Suisun	Winter	10.96 (2.25) 11	7.04 (4.77) 11	32.5 (5.8) 12	235.0 (50.1) 12	2.6 (0.6) 12	11.3 (3.0) 12	1.2 (0.5) 12	0.8 (0.3) 12	66.7	0.5 (0.2) 12
	Spring	15.35 (1.95) 35	2.46 (1.94) 35	27.5 (6.02) 31	264.6 (26.5) 30	2.7 (0.8) 24	6.8 (2.4) 33	4.6 (5.8) 35	2.9 (3.5) 34	63.0	0.3 (0.1) 33
	Summer	20.21 (1.19) 9	7.54 (2.39) 9	34.4 (3.5) 9	216.7 (17.1) 7	3.6 (0.4) 9	5.3 (1.4) 9	1.8 (0.4) 9	1.3 (0.5) 9	72.2	0.3 (0.1) 9
	Fall	17.66 (6.04) 9	8.26 (3.39) 9	30.7 (5.5) 10	219.2 (74.5) 10	3.5 (0.4) 9	6.0 (3.3) 11	1.6 (0.6) 11	0.6 (0.3) 9	37.5	0.5 (0.1) 11
San Pablo	Winter	10.96 (0.85) 11	20.77 (5.63) 11	26.8 (5.9) 12	127.1 (45.9) 12	3.8 (4.2) 12	8.0 (2.6) 12	2.3 (0.9) 12	1.1 (0.6) 12	47.8	0.9 (0.2) 12
	Spring	14.76 (1.40) 34	17.08 (5.19) 34	18.1 (4.2) 30	128.0 (41.2) 31	3.4 (4.9) 25	3.5 (1.9) 34	6.5 (3.6) 36	5.2 (4.0) 36	80.0	0.7 (0.4) 33
	Summer	19.06 (1.00) 9	23.32 (1.50) 9	23.9 (5.9) 9	106.2 (17.5) 9	3.6 (0.7) 9	4.1 (2.2) 9	3.0 (1.6) 9	1.7 (0.7) 9	56.7	0.7 (0.4) 9
	Fall	17.13 (1.89) 13	24.28 (5.17) 13	19.0 (3.8) 14	96.3 (6.57) 14	3.1 (0.3) 14	5.4 (2.2) 14	3.2 (1.2) 14	1.2 (0.7) 14	37.5	1.2 (0.5) 14
Central	Winter	11.48 (0.74) 12	27.29 (3.48) 12	21.7 (4.44) 11	75.9 (29.3) 12	2.4 (0.4) 11	6.7 (2.2) 12	2.1 (0.7) 12	1.0 (0.4) 12	47.6	1.1 (0.3) 11
	Spring	13.68 (0.91) 36	25.04 (3.80) 36	15.6 (3.7) 31	80.6 (26.9) 31	2.1 (0.7) 25	3.2 (1.7) 34	5.8 (2.8) 35	4.2 (3.8) 28	72.4	1.1 (0.4) 36
	Summer	17.14 (1.16) 10	28.33 (1.57) 10	20.7 (3.6) 9	73.0 (19.7) 9	2.9 (0.6) 9	4.9 (1.7) 9	3.4 (1.5) 9	0.9 (0.4) 8	26.5	1.1 (0.4) 10
	Fall	16.01 (1.34) 13	30.40 (1.09) 13	14.0 (3.6) 13	57.4 (10.9) 13	2.5 (0.4) 13	6.1 (1.3) 14	4.0 (1.8) 14	1.5 (0.8) 11	37.5	1.6 (0.3) 14

TABLE 2. Mean surface nitrogen uptake and primary productivity values (±SD) and number of samples for Suisun, San Pablo, and Central Bays calculated as seasonal means for winter (December, January, February), spring (March, April, May), summer (June, July, August), and fall (September, October, November) from November 1999 to August 2003.

| Bay	Season	VNO$_3$ in all cells (×10^{-3} h^{-1})	pNO$_3$ in all cells (×10^{-3} μmol l^{-1} h^{-1})	pNO$_3$ in cells >5 μm (×10^{-3} μmol l^{-1} h^{-1})	VNH$_4$ in all cells (×10^{-3} h^{-1})	pNH$_4$ in all cells (×10^{-3} μmol l^{-1} h^{-1})	pNH$_4$ in cells >5 μm (×10^{-3} μmol l^{-1} h^{-1})	Calculated pC (μg l^{-1} d^{-1})	f ratio
Suisun	Winter	0.27 (0.83) 8	2.04 (1.59) 8	0.61 (0.51) 8	3.04 (1.75) 8	11.13 (8.17) 8	4.65 (5.19) 8	25.02	0.15
	Spring	2.53 (7.60) 32	17.69 (1.82) 32	10.52 (31.2) 31	3.74 (2.59) 33	32.23 (18.9) 33	27.79 (28.7) 31	94.9	0.35
	Summer	0.69 (1.50) 9	7.06 (4.9) 9	3.65 (5.0) 9	6.09 (6.6) 9	37.3 (35.9) 9	16.35 (16.78) 9	84.3	0.16
	Fall	0.030 (2.2) 10	4.68 (5.24) 70	2.2 (3.17) 7	2.98 (5.24) 7	24.55 (0.61) 7	17.79 (5.9) 5	55.6	0.16
San Pablo	Winter	0.6 (0.3) 7	2.33 (1.37) 7	0.5 (0.42) 7	6.11 (4.21) 7	20.45 (13.4) 7	10.81 (8.90) 7	43.3	0.10
	Spring	6.76 (11.89) 33	49.4 (70.69) 33	43.05 (63.0) 32	8.84 (5.35) 35	75.63 (35.94) 35	61.1 (86.7) 32	233.4	0.40
	Summer	3.2 (6.49) 9	8.24 (8.89) 9	5.7 (6.69) 9	7.52 (6.95) 9	30.50 (31.96) 9	20.67 (23.44) 9	73.6	0.21
	Fall	1.85 (3.57) 13	13.10 (25.4) 13	9.61 (15.6) 13	15.23 (15.1) 9	52.01 (43.19) 9	37.58 (37.31) 9	123.8	0.20
Central	Winter	0.79 (0.43) 7	2.88 (1.42) 7	1.55 (1.71) 7	5.98 (2.25) 7	19.37 (7.78) 7	16.48 (15.77) 7	42.3	0.13
	Spring	6.44 (7.49) 30	59.33 (82.5) 30	57.91 (87.82) 29	8.56 (5.01) 32	67.76 (140.22) 32	47.11 (33.26) 29	241.6	0.47
	Summer	3.0 (1.97) 89	11.53 (7.45) 8	8.24 (8.22) 9	10.1 (7.05) 9	38.46 (38.75) 9	32.0 (33.32) 9	95.0	0.23
	Fall	1.56 (1.36) 12	10.63 (12.07) 12	8.23 (10.47) 13	12.11 (8.78) 9	70.1 (173.4) 9	44.0 (38.93) 9	153.5	0.13
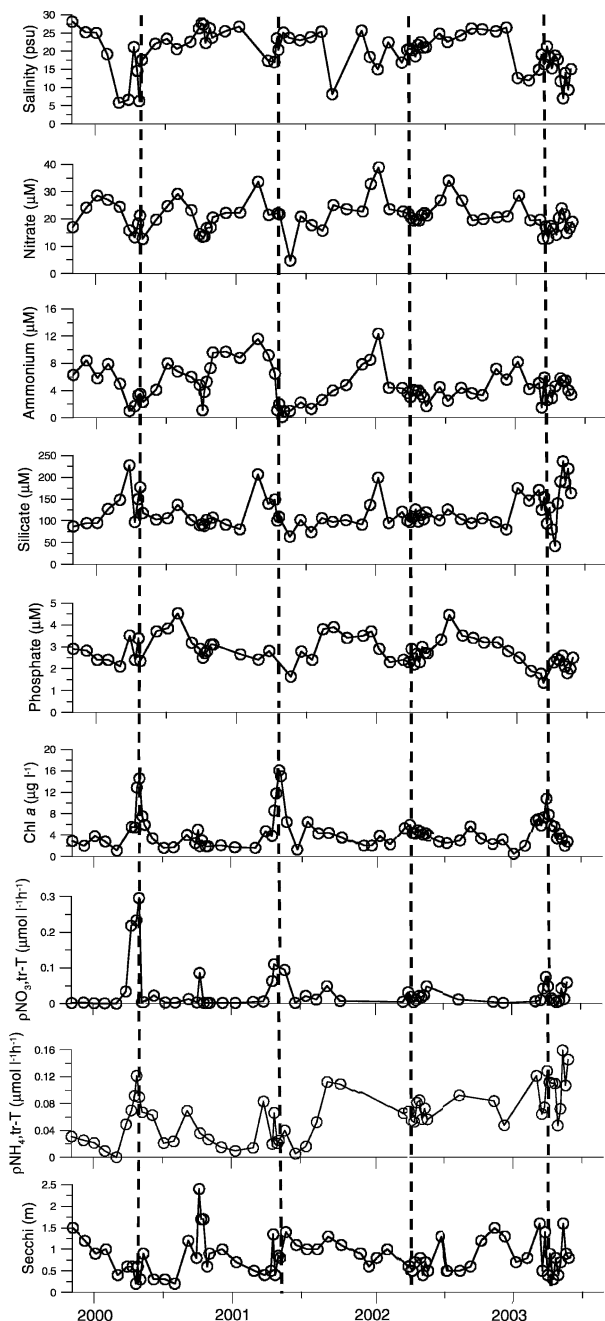
Fig. 2. Time series surface data from San Pablo Bay from November 1999 to August 2003. Salinity (psu), NO$_3$ (μM), NH$_4$ (μM), Si(OH)$_4$ (μM), PO$_4$ (μM), chlorophyll a (μg l^{-1}), ρ^{15}NO$_3$ (μmol l^{-1} h^{-1}), ρ^{15}NH$_4$ (μmol l^{-1} h^{-1}), and Secchi depth (m). Dotted vertical lines show spring blooms described in text.

September 2002 and May 2003, accompanied by slightly higher chlorophyll values.

Light availability was low most of the year with maximal light penetration (Secchi depths of 0.6 to 0.8 m) occurring from November to December and

with the lowest values of 0.1 to 0.2 during April–May of each year (Fig. 1).

TIME SERIES DATA FOR SAN PABLO BAY

A similar range of mean seasonal temperatures to that in Suisun Bay was measured in San Pablo Bay with higher values in summer (mean of 19.06°C) and lower values in winter (mean of 10.96°C, Table 1). Salinity values (Fig. 2) were different than Suisun Bay with higher minimum values (>6 psu) and maxima reaching almost 28 psu. Lower values (i.e., <10 psu) occurred in March 2000, May and September 2001, and May 2003.

Nutrient concentrations showed greater variability than in Suisun Bay, with NO$_3$ (4.8–38.9 μM), Si(OH)$_4$ (41.8–236.6 μM), and PO$_4$ (1.36–4.53 μM; Fig. 2) showing peaks in January, February, and March of all years and small peaks in August 2000, September 2001, and July 2002. NH$_4$ concentrations were less than in Suisun Bay, but like Suisun, maximal concentrations (12 μM) occurred during the winter (December, January, February) months. The maximal value in January 2003 only reached 8 μM compared to 12 μM in Suisun Bay. Chlorophyll concentrations tended to be higher than in Suisun, and showed spring increases from the annual mean concentration of 3.5 μg l^{-1} (not shown). The spring peaks occurred later than in Suisun, reaching 15 μg l^{-1} in May 2000, 16 μg l^{-1} in May 2001, 6 μg l^{-1} in late March 2002, and 11 μg l^{-1} in April 2003, at the same time as the lowest NH$_4$ concentrations were measured. The spring concentrations of chlorophyll were dominated by the larger phytoplankton cells (Table 1).

Nitrogen transport rates tended to be higher in San Pablo Bay than Suisun Bay. Increases in NO$_3$ uptake were observed every spring (Fig. 2) and also small increases in fall 2000 and 2001, at the same time as the increases in chlorophyll concentrations. The April 2002 bloom had lower chlorophyll and lower NO$_3$ uptake rates than the other years in San Pablo Bay. The fractionated uptake rates show the NO$_3$ uptake during spring times to be dominated by larger cells (Table 2). During the times with increased chlorophyll, NH$_4$ uptake (Fig. 2) did not reach the highest values measured for NO$_3$ uptake (maximum ρNO$_3$ = 0.3 μmol l^{-1} h^{-1} versus maximum ρNH$_4$ = 0.16 μmol l^{-1} h^{-1}). Both sources of DIN are used but in the spring NO$_3$ uptake exceeds NH$_4$ (i.e., ρNO$_3$ > ρNH$_4$) and is the major source used for growth.

Light penetration and availability was greater in San Pablo (Fig. 2) than Suisun with average Secchi depth of 0.9 m, with minima of 0.2 m in April and clearer waters in November (maximum of 2.4 m).
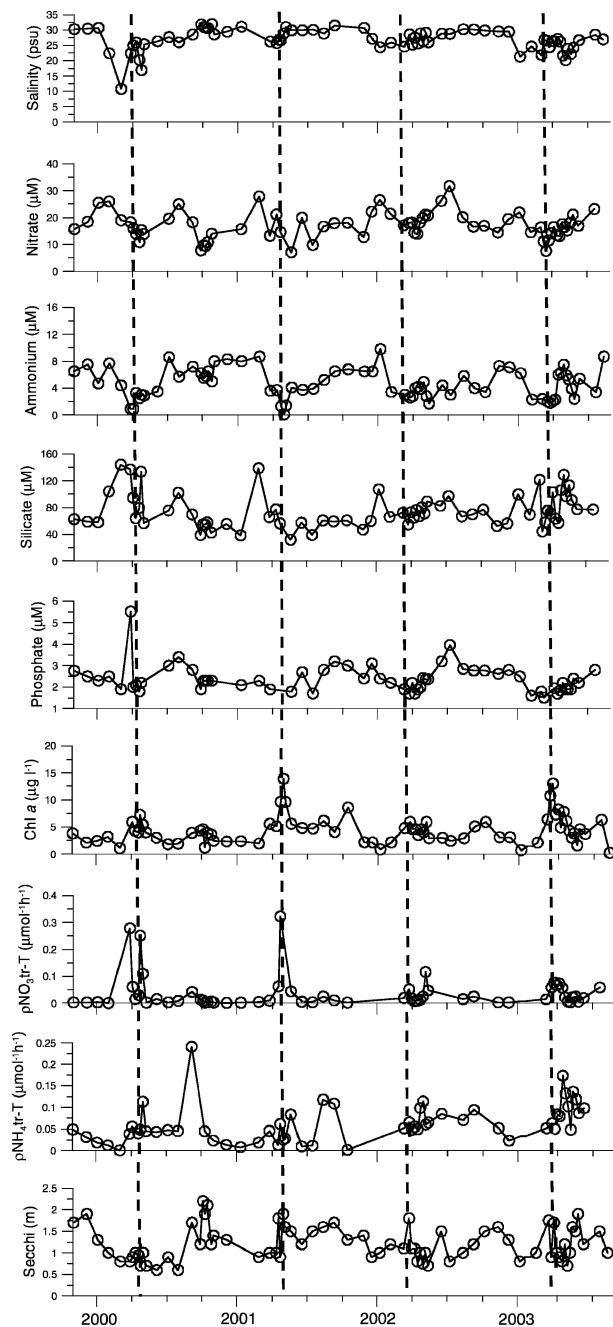
Fig. 3. Time series surface data from Central Bay from November 1999 to August 2003. Salinity (psu), NO_3 (μM), NH_4 (μM), $Si(OH)_4$ (μM), PO_4 (μM), chlorophyll a ($\mu g\ l^{-1}$), $\rho^{15}NO_3$ ($\mu mol\ l^{-1}\ h^{-1}$), $\rho^{15}NH_4$ ($\mu mol\ l^{-1}\ h^{-1}$), and Secchi depth (m). Dotted vertical lines show spring blooms described in text.

TIME SERIES DATA IN CENTRAL BAY

Surface temperatures in Central Bay showed the same seasonal trends as the other bays but with lower mean summer temperatures (17.14°C versus 19.06°C in San Pablo and 20.21°C in Suisun Bays;

Table 1). Salinities were much more oceanic, saltier, and less variable (Fig. 3) than the other bays with most values >25 psu (compared to 6 psu in San Pablo and 2 psu in Suisun), except in March 2001 when there was a large freshwater input (10.8 psu). Maximal values of 32 psu were measured, typically in September.

Nutrients tended to be lower in Central Bay (maximum NO_3 = 31.7 μM, NH_4 = 9.8 μM, $Si(OH)_4$ = 144 μM, and PO_4 = 5.5 μM; Fig. 3) than Suisun and San Pablo Bays. NH_4 was almost depleted in March 2000, similar to San Pablo Bay, and also in March–April 2001, 2002, and 2003. Seasonal maxima in nutrients were shifted slightly earlier than San Pablo with peaks in January and February each year and also in July 2000, June 2002, and June 2003. As in San Pablo Bay, nutrient decreases followed the peaks and were matched by increases in chlorophyll later.
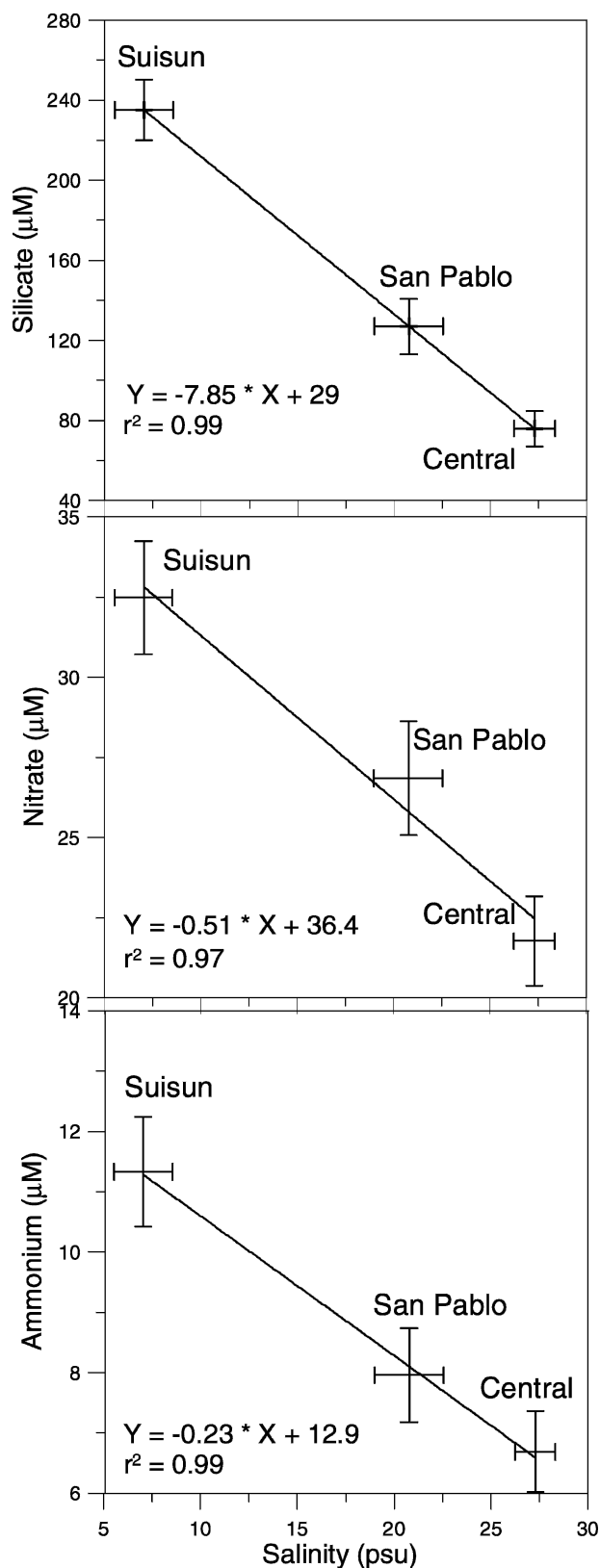
Seasonal spring increases in chlorophyll (Fig. 3) matched those of San Pablo with maxima (above the average 3.5–4 $\mu g\ l^{-1}$) in April–May 2000 and 2001 of 7 and 14 $\mu g\ l^{-1}$ and April 2002 and March 2003 of 6 and 13 $\mu g\ l^{-1}$. There were also small increases in October 2000, 2001, and 2002. The fractionated chlorophyll data showed that biomass was dominated by the larger cells in spring (Table 1).

NO_3 uptake (ρNO_3) in Central Bay (Fig. 3) peaked each spring accompanying the chlorophyll blooms, reaching 0.25 $\mu mol\ l^{-1}\ h^{-1}$ in April 2000, 0.32 $\mu mol\ l^{-1}\ h^{-1}$ in April 2001, 0.1 $\mu mol\ l^{-1}\ h^{-1}$ in May 2002, and 0.09 $\mu mol\ l^{-1}\ h^{-1}$ in March 2003. Specific uptake rates (VNO_3) showed the same seasonal trend (Table 2). Larger phytoplankton contributed significantly at times when there was higher mean ρNO_3 uptake. Unlike in Suisun and San Pablo Bays, ρNH_4 uptake did not show the same springtime variability as ρNO_3 uptake. NH_4 uptake (Fig. 3) never reached the maximal values of ρNO_3 uptake (maximum ρNH_4 = 0.24 $\mu mol\ l^{-1}\ h^{-1}$) and showed peaks in September 2000, 2001, and 2002 as well as in spring.

The trend for deeper Secchi depths going seaward continued and the annual mean Secchi depth in Central Bay was 1.2 m (not shown) with a maximum of 2.2 m. Shallowest values (0.6 m) were measured in April (Fig. 3), as was observed in San Pablo and Suisun Bays although the very shallow Secchi depth of 0.1 m measured in Suisun was not observed in Central Bay.

MEAN SEASONAL DATA FOR THE THREE BAYS

To be able to compare the three bays more easily, the 3 yr surface data were condensed to mean seasonal values (Tables 1 and 2), using data from three monthly cruises for each season of the 3 yr

Suisun

Y = -7.85 * X + 29
r² = 0.99

San Pablo

Central

Silicate (µM)

Suisun

San Pablo

Y = -0.51 * X + 36.4
r² = 0.97

Central

Nitrate (µM)

Suisun

San Pablo

Central

Y = -0.23 * X + 12.9
r² = 0.99

Ammonium (µM)

Salinity (psu)

except in spring when the sampling frequency was increased to weekly and means are based upon more cruises. Typically, winter (December–February), summer (June–August), and fall (September–November) means are based on 10 ± 1 samples and spring (March–May) means on 30 ± 5 samples. The winter values provide a way to assess the effect of freshwater and ocean inputs of nutrients to the three bays, since biological activity is minimal. Mixing diagrams (of winter mean nutrient concentrations versus salinity, Fig. 4), with straight lines linking the three bays indicate that the sources of all three high nutrient concentrations (NO_3, $Si(OH)_4$, and NH_4) are fresher waters, from the head of the estuary, diluted to lower values in the lower two bays (San Pablo and Central Bays) by the low nutrient, high salinity ocean water. PO_4 (not shown) exhibited no such clear pattern with maximum values in San Pablo Bay suggesting a strong local source of that nutrient.

When mean nutrient values for all four seasons are plotted together against salinity, the seasonal progressions from winter to fall of $Si(OH)_4$, NO_3, and NH_4 in the three bays can be observed (Fig. 5). For each nutrient, the location of each bay between the freshwater and oceanic end points is clearly indicated without overlap. The seasonal cycle for $Si(OH)_4$ commences with an increase from winter to spring, most noticeably in Suisun Bay due to increased freshwater input followed by a decrease to summer and fall as salinity increases (runoff and freshwater input decreases). NO_3 decreases from winter to spring due to uptake of NO_3 by the phytoplankton (Fig. 6, Table 2) as salinity decreases; then increases in summer and decreases again in fall (Fig. 5). $Si(OH)_4$ does not track the NO_3 decreases from winter to spring as $Si(OH)_4$ is also taken up biologically but the amount is overwhelmed by the very high concentrations of $Si(OH)_4$ in the freshwater input. As runoff decreases into summer, $Si(OH)_4$ concentrations decrease (as the high $Si(OH)_4$ supply in the freshwater input ceases) but mean NO_3 concentration does not since the spring biological uptake of NO_3 has stopped and NO_3 remains in the water. The fall decreases in both $Si(OH)_4$ and NO_3 are correlated with salinity increases and are mostly due to dilution by low nutrient, salty oceanic water. NH_4 concentration declines rapidly from winter to spring (Fig. 5), partly due to dilution by fresh water and

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Fig. 4.   Mean nutrient concentration ($\pm$SE) for Suisun, San Pablo, and Central Bays versus mean salinity for all three years for the winter months (December, January, February), $Si(OH)_4$, NO_3, and NH_4.
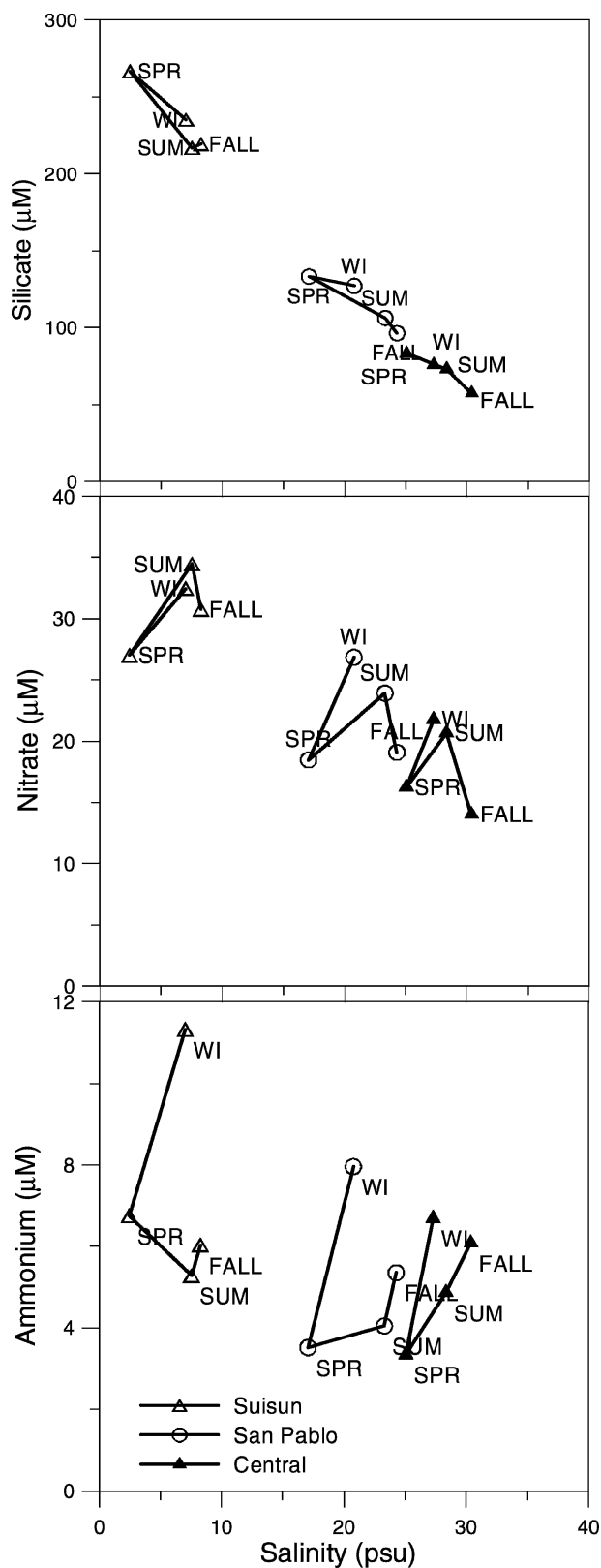
also due to phytoplankton uptake, remaining relatively low or increasing slightly in summer and into fall. The spring minimum in NH_4 decreases in the seaward direction to below about 4 µM in Central and San Pablo Bays when NO_3 uptake (Fig. 6) then increases contributing to the spring bloom (Figs. 2 and 3). This does not happen in Suisun Bay where mean spring NH_4 values remain high (7 µM).

The mean values of VNO_3 for all three bays and all seasons plotted against NH_4 concentration (Fig. 6), show the values of VNO_3 to rise steeply as NH_4 concentrations are reduced to about 4 µM during spring bloom conditions. Sharp rises in mean VNO_3 from winter to spring occurred in parallel in both San Pablo and Central Bays. A much smaller increase is observed for Suisun Bay, where the mean spring value is driven by the one higher value from spring 2000. NO_3 uptake (as VNO_3) then decreases in all three bays from spring to summer and fall values. In contrast to VNO_3, all three bays show a much smaller increase in mean VNH_4 from winter to spring, a period of decreasing mean NH_4 concentration. Both San Pablo and Central Bays show large increases in VNH_4 from summer to fall when only small increases in mean NH_4 concentrations occur. Suisun Bay shows only one relatively small increase from spring to summer and has lower values of VNH_4 than the other two bays.

The ^{15}N uptake values can be used to calculate the f-ratio (an indicator of NO_3 to total DIN use), the ratio of $^{15}NO_3$ uptake (ρNO_3) to total DIN uptake (i.e., $\rho NO_3 + \rho NH_4$). The f-ratio is used here only to evaluate the relative use of NO_3 and NH_4, not to separate new and regenerated production as NO_3 and NH_4 have both new and regenerative sources in SFB. The plot of f-ratio versus NH_4 (Fig. 6), shows low values of about 0.2 in all bays and all seasons, except in spring when f-ratio values (based upon mean uptake values) increase to about 0.5, indicative of greater use of NO_3. These mean f-ratios representing percent NO_3 uptake (<0.5) in Table 2 and Figs. 6 and 7 do not reflect the true contribution of NO_3 uptake that occurs during these seasons since they average all conditions. For example, the nonaveraged data from San Pablo Bay (Fig. 2) yields a maximum f-ratio of 0.7 at the peak of the spring 2000 bloom (compared to the mean f-ratio for the spring of 0.35; Table 2). Mean chl *a* concentrations

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Fig. 5. Mean nutrient concentration for Suisun, San Pablo, and Central Bays versus mean salinity for all three years for winter (WI), spring (SPR), summer (SUM), and fall (FALL) months, a) $Si(OH)_4$, b) NH_4, and c) NO_3.
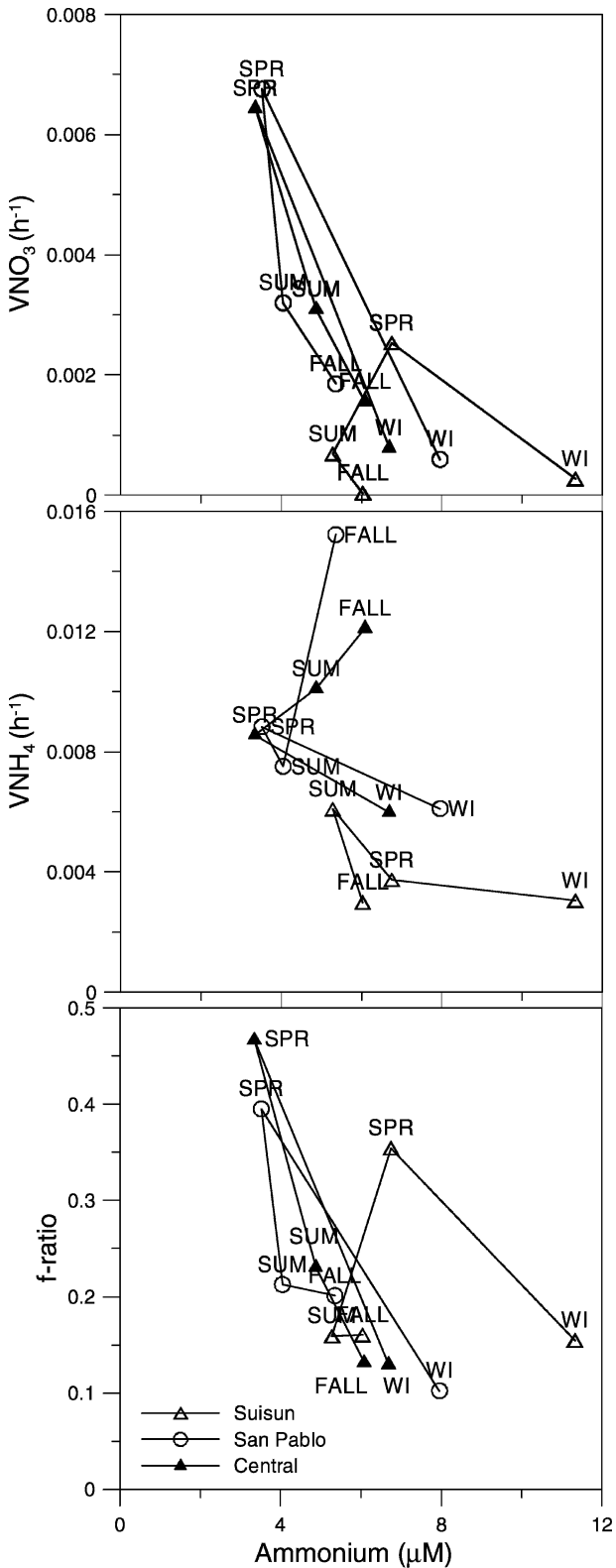
(for the entire community) plotted against NH_4 concentration (Fig. 7) show parallel increases in all three bays from winter to spring values as NH_4 decreases. Suisun Bay has lower mean chlorophyll concentrations than San Pablo and Central Bays. All three bays show steep declines in chlorophyll from spring to summer. When plotted versus f-ratio, there is a linear relationship, with higher mean chlorophyll at higher mean f-ratios (i.e., NO_3 use) in the spring. Suisun Bay has lower nitrogen uptake and chlorophyll values than San Pablo and Central Bays at all seasons in the 3 yr mean data set (Figs. 6 and 7, Tables 1 and 2).
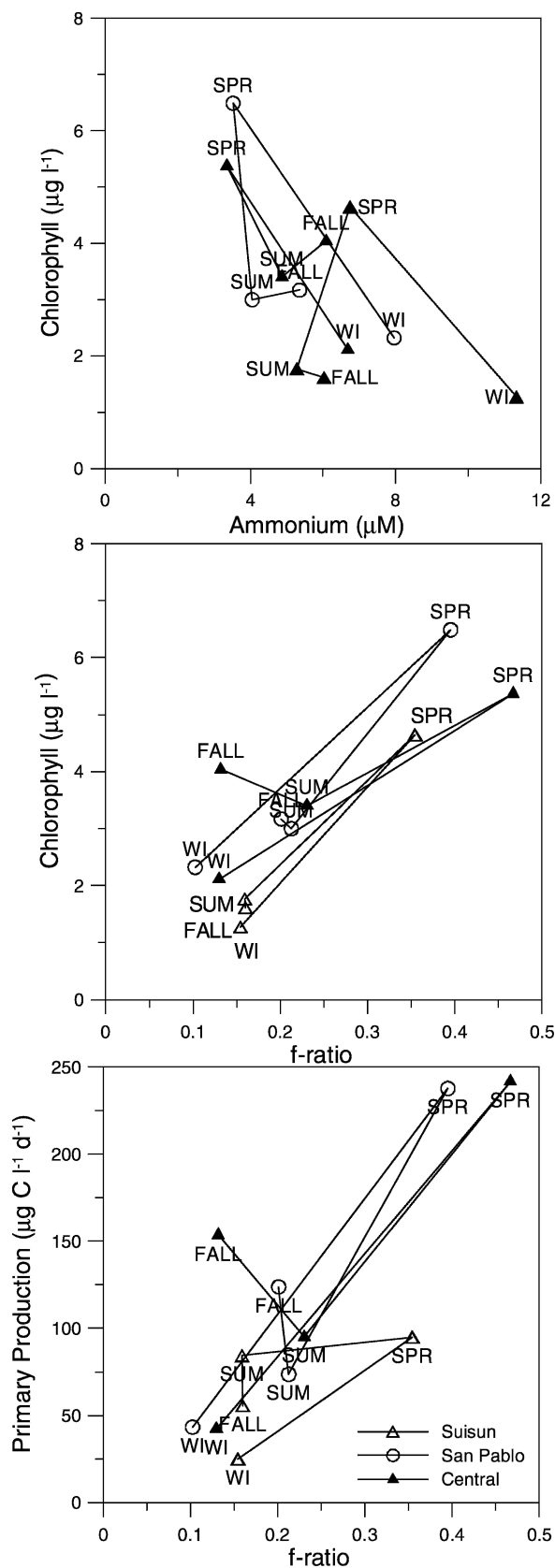
The mean data for nitrogen uptake can be used to estimate primary productivity as carbon uptake (Dugdale and Wilkerson 1992) by summing the mean ρNO_3 and ρNH_4 and multiplying by the Redfield ratio for carbon:nitrogen, 6.6 on a molar basis, multiplied by 12 to convert to mass units, and multiplied by 24 to give units of $\mu g\ C\ l^{-1}\ d^{-1}$ (Table 2). When carbon uptake values are plotted against mean f-ratios (Fig. 7), the seasonal cycles track the chlorophyll data and San Pablo and Central Bays can be seen to follow similar patterns with strong spring blooms at higher mean f-ratios (i.e., primary productivity based both on NO_3 and NH_4) and smaller, fall blooms at low f-ratios (based more on NH_4). Suisun Bay shows a small mean spring bloom, reduced primary production in summer, and no fall bloom. Suisun Bay differs from San Pablo and Central Bays in the lack of a fall bloom and a reduced spring bloom, and lower productivity that may be due to salinity stress or low irradiance conditions (Secchi values are shallower in Suisun compared to San Pablo and Central Bays; Figs. 1, 2, and 3, Table 1).

FRACTIONATED BIOMASS AND PRODUCTIVITY DATA

Biomass samples (as chl *a*) and nitrogen uptake-productivity measurements were obtained for the entire (total) phytoplankton community and also for the cells that were >5 μm in diameter, by using filters of 5 and 10 μm pore size to fractionate the samples. These data show that chl *a* concentration and NO_3 uptake are dominated by the larger cell sized population in all bays (Figs. 8 and 9) as the data all fall very close to the 1:1 line of fractionated versus total values. The chlorophyll data show good linear correlations (r^2 = 0.83 and 0.85) for regres-

sions of >5 μm and >10 μm cells versus chl a. The similarity in slopes between the chlorophyll in cells >5 μm versus total chlorophyll (y $=$ 0.84x $-$ 0.64) and chlorophyll in >10 μm cells versus total chlorophyll (0.81x $-$ 1.16) regressions indicates that most of the larger cells are actually greater than 10 μm. The contribution by the larger cells is greatest at higher values of chlorophyll with an average of 90% of the total chlorophyll represented in the >5 μm cells at ambient chlorophyll concentrations of >10 μg l^{-1} (i.e., mean percentage of 90% for the 12 circled data points in Fig. 8).

NO$_3$ uptake (Fig. 9) shows an even tighter relationship between the larger cells and the total phytoplankton community with linear correlation, r^2 of 0.93 and slope of 0.84 suggesting that 84% of the time, uptake values measured were dominated by uptake in the larger cell size fraction. The dominance of the larger cells was greatest at the higher uptake rates, with larger cells contributing 87% of the total NO$_3$ uptake at values >0.2 μmol l^{-1} h^{-1} (i.e., mean of 7 data points circled in Fig. 9). This was not evident for the NH$_4$ uptake data that showed wide scatter in the data with the fractionated data not so close to the 1:1 line and a linear regression, r^2 of 0.64. The slope of 0.53 indicates that 53% of the values have uptake by cells >5 μm, i.e., both large and small cells are contributing to the uptake compared to the dominance by the larger cells in NO$_3$ uptake.

Discussion

All three bays in northern and central SFB exhibit high nutrients throughout the year with relatively low mean seasonal chlorophyll concentrations ranging from 1.2 to 6.5 μg l^{-1}. The specific NO$_3$ and NH$_4$ and uptake rates (and VNO$_3$ and VNH$_4$ $<$ 0.01 h^{-1}) for most of the year are in the range of oligotrophic ocean values (Dugdale and Wilkerson 1992b). These conditions are essentially high nutrient low chlorophyll (HNLC; Cloern 2001) or high nutrient low growth (HNLG; Sharp 2001) known previously from open ocean studies (Minas et al. 1986). Primary nutrients are typically in excess of requirements and are exported from the estuary. Increase in biomass, i.e., phytoplankton blooms, occurs only with sudden bursts in growth rate, outpacing temporarily the losses, primarily grazing. These bursts result from an increase in NO$_3$ uptake

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Fig. 7.   Suisun, San Pablo, and Central Bays for all three years for winter (WI), spring (SPR), summer (SUM), and fall (FALL) months, mean chlorophyll concentration versus mean NH$_4$ concentration and mean f ratio, mean calculated primary productivity versus mean f ratio.
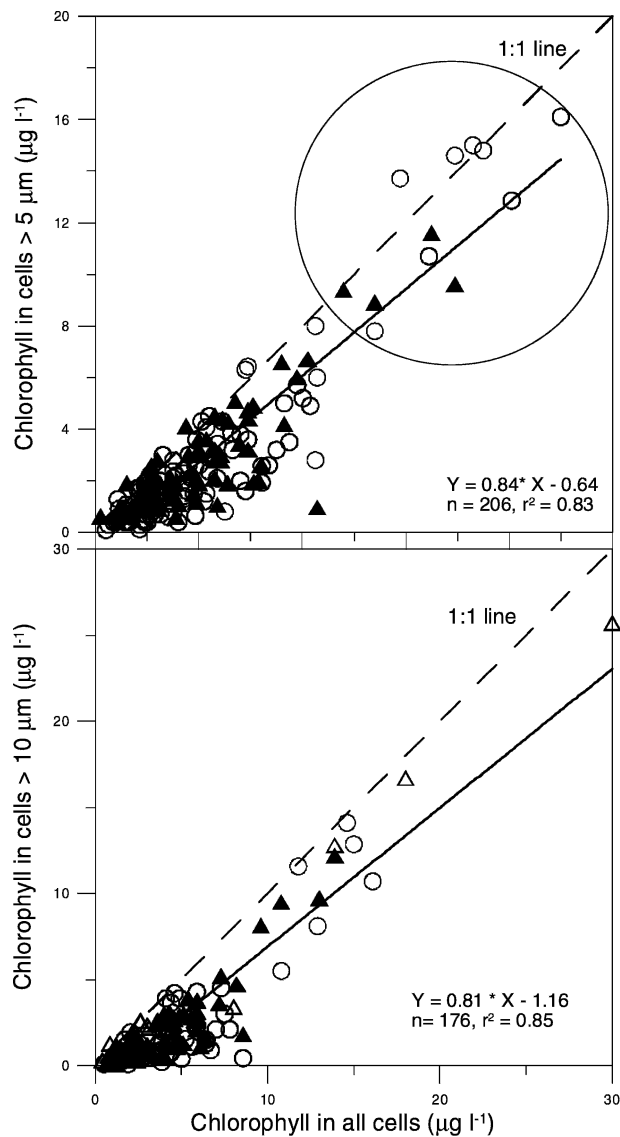
Fig. 8. Chlorophyll in cells >5 μm diameter and chlorophyll in cells >10 μm diameter versus total chlorophyll collected on a GF/F filter for all surface data collected between October 1999 and August 2003 from Suisun (circles), San Pablo (crosses), and Central (triangles) Bays. Linear regression and 1:1 relationship are indicated. Points within the circle are all values with total chlorophyll >10 μg l^{-1}.

Fig. 9. NO_3 uptake by cells >5 μm diameter versus NO_3 uptake in all cells and NH_4 uptake by cells >5 μm diameter versus NH_4 uptake in all cells for all surface data collected between October 1999 and August 2003 from Suisun (circles), San Pablo (crosses), and Central (triangles) Bays. Linear regression and 1:1 relationship are indicated. Points within the circle are all values with ρNO_3 >0.2 μmol l^{-1} h^{-1}.

processes and are supported by access to the large NO_3 pool, but only occur when vertical salinity stratification improves the light conditions (e.g., in spring) and in the presence of low, noninhibitory concentrations of NH_4 (Figs. 1–3). Phytoplankton growth during most of the year is supported by NH_4 at relatively low growth rates (e.g., 0.013 h^{-1} in Central Bay in summer). These rates are likely held low by insufficient irradiance. When Central Bay water is enclosed and then exposed to ambient
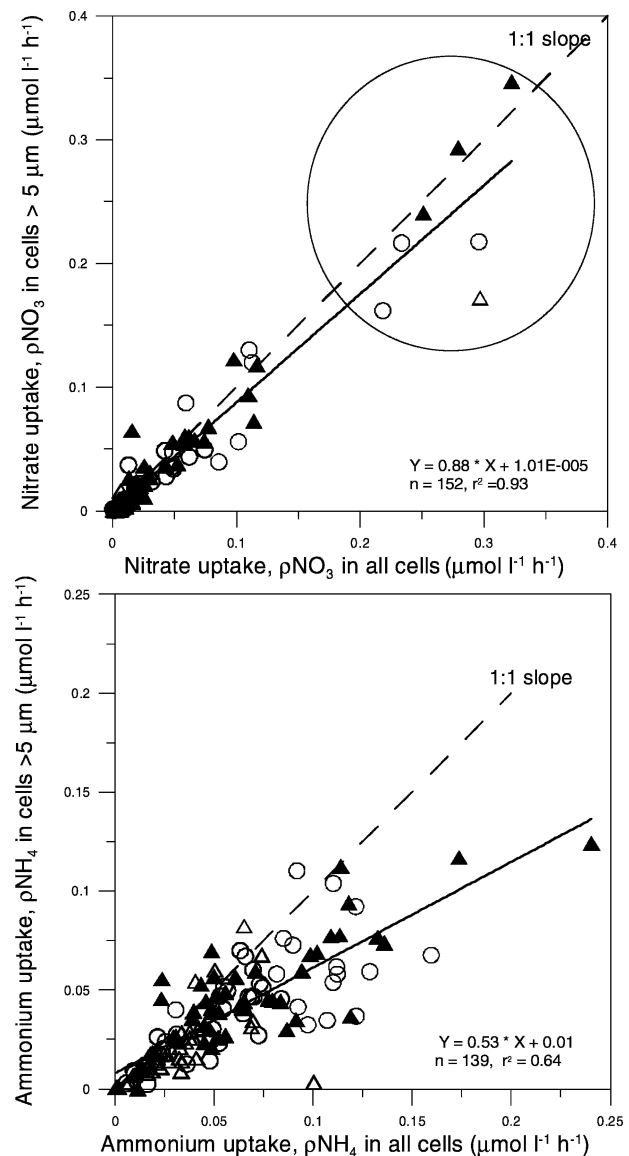
light, the VNH_4 rises rapidly to 0.03–0.05 h^{-1} indicating a primary light limitation (Dugdale unpublished data; Parker personal communication). Light limited low NH_4 based growth rate combined with relatively high NH_4 inputs to SFB results in high ambient NH_4 concentrations that would inhibit NO_3 uptake by the phytoplankton (e.g., Dortch 1990). Improved light conditions that result in higher VNH_4 should produce an increase in biomass, but only to the extent of the available

NH_4 pool, about 5 μM. If improved light conditions continue long enough at elevated NH_4 uptake rates, reducing ambient NH_4 concentrations below inhibiting levels, NO_3 uptake can begin with a biomass increase that is set by the much higher pool of NO_3, 20–30 μM.

From our ^{15}N measurements of nitrogen productivity, annual primary productivity in northern SFB can be separated into three seasons on the basis of nutrient processes: a spring bloom period dependent primarily on NO_3 uptake but initiated by NH_4 uptake, a quasi-steady state condition in summer with low productivity based primarily on NH_4, and a fall bloom period with chlorophyll increases lower than in spring and using primarily NH_4 as indicated by the low f-ratio, 0.13 to 0.2. Productivity performance in these seasons is also dependent on the position of the three northern bays in the salinity-nutrient gradient with higher nutrients and low salinity to the north and lower nutrients and high salinity to the south. The more southern San Pablo and Central Bays behave in relatively similar ways with strong spring phytoplankton blooms, weaker fall blooms, and lower mean nutrients and higher salinity. Suisun Bay separates out from these two on the basis of lower salinity, higher nutrients, and lower mean productivity (Tables 1 and 2). The lower productivity value is partly due to lack of spring blooms in Suisun Bay in 3 of the 4 yr studies here. This lack of spring blooms was likely a consequence of higher ambient NH_4 concentrations in Suisun inhibiting NO_3 uptake and by lower light availability.

Summer productivity in northern SFB, which tends to be much lower than the NO_3 fueled spring productivity (Cloern 1996), is based primarily on NH_4 as indicated by the low value of the f-ratio, 0.2 (Table 2). Mean phytoplankton growth rates for the summer calculated from the sum of specific NH_4 and NO_3 uptake rates are similar in San Pablo and Central Bays (0.011 and 0.013 h^{-1}, respectively) and lowest in Suisun Bay (0.007 h^{-1}; data from Table 2). Little change in NH_4 concentration occurs during summer, allowing a quasi-steady state condition to be assumed and the possible NH_4 inputs can be calculated from the NH_4 uptake data. Using Central Bay as an example, with mean summer of $\rho NH_4 = 0.038$ μmol l^{-1} h^{-1} and mean $NH_4 = 4.9$ μM, the turnover time is 5.4 d (using a 24 h day for uptake), i.e., roughly 20% of the NH_4 in the dissolved pool is consumed and replaced daily from inputs. The gradient between bays is small in summer precluding significant net input from upstream, indicating that the NH_4 demand (i.e., phytoplankton uptake) is met by regeneration locally at the sediment interface (Caffrey 1995; Grenz et al.

2000), by grazing, or by sewage inputs from secondary treatment plants. The combination of inputs, losses, and the light field maintains the high NH_4 concentration that blocks access by the phytoplankton to the larger NO_3 pool. Sorting out the relative effects of these processes will require additional field work and modeling. The major element in the DIN regulation of productivity is the high NH_4 input and this is likely to be a major contributor to the cause of low seasonally integrated productivity in all three bays.

In other turbid estuaries with high NO_3 and high NH_4 conditions, low levels of NO_3 uptake have been reported. The mean specific nitrogen uptake rates for northern and central SFB (Table 2) are remarkably similar to those reported for a series of European turbid estuaries (Middelburg and Nieuwenhuize 2000a, their Table 2). The range of mean VNH_4 in SFB was 0.003–0.01 h^{-1} (winter–summer) compared to 0.004–0.012 h^{-1} reported for the Loire, and VNO_3 ranged from 0.0002 to 0.003 h^{-1} in SFB (winter–summer) compared to 0.0003–0.00275 h^{-1} in the Loire. The low NO_3 uptake rates in the European turbid estuaries result in export to the sea of most of the NO_3 entering or being produced in the estuaries; the same condition occurs in SFB for most of the year when phytoplankton blooms are absent.

The effect of climate, primarily through effects of precipitation on dilution of nutrient concentrations, on this seasonal variability is important. Mean spring salinities for the three bays were low in 2000, about half the values in the succeeding two years (2001 and 2002). The year 2000, based upon precipitation, was categorized by the California Department of Water Resources (http://cdec. water.ca.gov/cgi-progs/iodir/wsihist) as above normal and NH_4 concentrations in Suisun and San Pablo Bays were about half that of the following 2 yr, which were classified as dry. The effect of the above normal precipitation in 2000 on NH_4 concentration was to dilute it to below inhibitory levels and likely this contributed to the bloom that was observed in Suisun Bay that year, whereas in the dry years with less freshwater dilution and higher NH_4 concentrations, chlorophyll blooms were not observed. The wetter spring of 2000 resulted (through dilution) in lower NH_4 levels and higher phytoplankton NO_3 uptake and a chlorophyll peak in Suisun Bay. The other years were dry, NH_4 levels were high, NO_3 uptake was low, and no phytoplankton blooms were observed.

An alternative hypothesis to the role of NH_4 as the cause of low summer chlorophyll concentrations in Suisun Bay is grazing by the clam *C. amurensis*, as proposed by Cloern and Alpine (1991). To establish the role of the clam, grazing rates were compared to

phytoplankton growth rates estimated from nitrogen assimilation data. In a balanced system, grazing rates require matching phytoplankton growth rates. Published pumping rates for the bivalve population imply a daily turnover of the entire water column (Cole et al. 1992; Werner and Hollibaugh 1993), i.e., a turnover rate of $1/24 = 0.04$ h^{-1}. The mean summer surface growth rates in Suisun Bay of 0.007 h^{-1} (i.e., sum of VNO$_3$ and VNH$_4$) are an order of magnitude less than the calculated turnover rate for the water column used here as a proxy for clam grazing. The value of the phytoplankton growth rate would be even lower if calculated on a depth integrated basis. This suggests that the clam and phytoplankton populations are not in equilibrium and the role of clam grazing may not be the universal cause of the lower phytoplankton production and growth rates. The similarity of the mean specific NH$_4$ uptake rates in summer in the three bays, even though significant populations of *C. amurensis* have not been observed in Central Bay (Thompson personal communication), also argues against a simple bivalve grazing-phytoplankton growth system during summer. The clam population is also at a minimum in Suisun and San Pablo Bays during the spring bloom period and is unlikely to be a major factor in the difference between spring productivities in Suisun versus San Pablo and Central Bays.

The elevated chlorophyll levels making up the blooms in the northern and central parts of SFB are made up predominantly by larger cells, as illustrated by the high percentage of chlorophyll in cells >5 μm in diameter making up the population (Fig. 8, Table 1). This matches studies of eutrophic areas that are capable of supporting blooms that develop with the addition of large size classes (e.g., Malone 1980; Raimbault et al. 1988; Chisholm 1992) and thrive under conditions of high nutrients (e.g., Tamigneaux et al. 1995). It was previously described for SFB by Cloern and Dufford (2005) who observed that cells <8 μm contributed only 40% of community biomass and by Hogue et al. (2001) who showed dominance by large cells during the spring bloom period. NO$_3$ uptake in SFB also showed significant contribution by the larger cell sized phytoplankton (linear regression of all surface data indicating that 84% of uptake was due to cells >5 μm; Fig. 9). A similar analysis made for phytoplankton in the upwelling area of Monterey Bay that has high NO$_3$ concentrations and uptake rates showed similar relationships (Wilkerson et al. 2000), with 87% of the total phytoplankton NO$_3$ uptake dominated by larger cells and with larger cells contributing 60% to the total chlorophyll. Interestingly in the Thames estuary where NO$_3$ is extremely high (650 μM), very small cells, i.e., bacteria, were responsible for most of the NO$_3$ uptake (Middelburg and Nieuwenhuize 2000b).

When nitrogen productivity in northern SFB is sufficient for biomass to be built up and exceed grazing and other loss factors, then the phytoplankton contributing most to the process are larger cells. This is the case for the spring blooms in all three bays studied here. In SFB these larger phytoplankton are likely to be diatoms especially *Skeletonema costatum*, *Chaetoceros* species, *Thalassiosira* species, and *Coscinodiscus* (Cloern and Dufford 2005). Diatoms thrive in the high NO$_3$ environments, have inherently high growth rates, and are well suited to be the dominant functional group as reviewed by Cloern and Dufford (2005). Consequently, alleviating any HNLC-HNLG condition in SFB leading to higher NO$_3$ utilization should lead to a healthy food chain based upon larger cells (Fig. 8), likely diatoms, rather than driving the system towards more typical results of added nutrients or eutrophication as classically described in east coast estuaries, i.e., anoxia and harmful algal blooms (e.g., Sharp 2001; Hallegraeff 1993). The fall bloom in SFB, apparently supported more by NH$_4$ uptake (e.g., Figs. 2 and 3), is not dominated by larger cells, but by smaller cells (Fig. 9), most likely flagellates. These typically do not include toxic dinoflagellates in SFB (Cloern and Dufford 2005), although some harmful algal members have been observed episodically. For example blooms of *Heterosigma akashiwo* were observed in Richardson Bay (Herndon et al. 2003) and an anomalous unprecedented red tide in Central Bay of *Akashiwo sanguinea* (= *Gymnodinium splendens*) was observed in September 2004, that reduced NO$_3$ and NH$_4$ to some of the lowest concentrations measured (Cloern et al. 2005a,b).

This extensive time series data shows the HNLC-HNLG condition of northern SFB overlaid with regular seasonal increases in phytoplankton and their nitrogen assimilation rates. The primary production environment of SFB should be viewed as primarily light limited in which suboptimal light conditions hold phytoplankton growth rates low. Bursts of productivity (blooms) occur with periods of favorable light conditions, especially those that last for sufficient length of time to reduce NH$_4$ concentrations to levels allowing access to the larger NO$_3$ pool. The frequency and strength of these events, secondarily controlled by NH$_4$ and NO$_3$ interactions, are likely to have a strong influence on the integrated annual phytoplankton production. The effect of water management changes, i.e., changing DIN loading, can now be modeled using these nitrogen productivity data as a framework to understand the importance of different nutrient concentrations in the development of phytoplankton blooms in the northern SFB.

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