CHANGES IN CHLOROPHYLL *a* CONCENTRATION AND PHYTOPLANKTON COMMUNITY COMPOSITION WITH WATER-YEAR TYPE IN THE UPPER SAN FRANCISCO BAY ESTUARY

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Spatial and temporal changes in chlorophyll *a* concentration and phytoplankton community composition were a function of interannual changes in water-year type for the upper San Francisco Bay estuary. Changes in chlorophyll *a* concentration and phytoplankton community composition were determined from monthly or semi-monthly samples taken at 16 to 25 stations within the upper San Francisco Bay estuary between 1970 and 1993. Water year types were categorized as wet, normal, dry or critical based on inflows to the upper estuary. Among water-year types, average chlorophyll *a* concentration in the upper estuary increased by 11% in normal years, 8% in wet years and 4% in dry years but decreased by 17% in critical years. Within water-year types, chlorophyll *a* concentration often differed between upstream and downstream regions, with high chlorophyll *a* concentration upstream during critical years and downstream during wet years. Phytoplankton community composition also varied with water-year type between upstream and downstream regions. Upstream, diatoms, greens and cryptophytes were abundant during normal and critical years while flagellates were abundant during critical and wet years. Downstream, diatoms and greens were abundant during normal and wet years while bluegreens and flagellates were abundant during critical years. The coincident change in phytoplankton size structure and cellular carbon content with community composition suggests the influence of water-year type on community composition may be an important factor influencing the estuarine food web because of its influence on zooplankton food quality and quantity.

Research has demonstrated the influence of streamflow or variables related to streamflow on chlorophyll *a* concentration and phytoplankton community composition. Streamflow affects the accumulation of chlorophyll *a* and size distribution of species due to processes associated with tides and gravitational circulation in the turbidity maximum (Arthur & Ball 1979; Cloern *et al.* 1985), accumulation of biomass through effects on residence time within rivers (Lehman 1992) and transport of phytoplankton carbon downstream (Jassby & Powell 1994). High streamflows carry nutrients needed for phytoplankton growth (Conomos 1979; Peterson *et al.* 1985) and suspended sediments, which affect the light available within the water column for photosynthesis (Peterson & Festa 1984; Peterson *et al.* 1989). Recent studies suggest streamflow may control the removal of phytoplankton biomass by influencing the density of benthic grazers (Nichols 1985). Long-term studies also suggest streamflow is associated with interannual changes in environmental factors that affect phytoplankton biomass and community succession (Lehman & Smith 1991; Lehman 1992).

Streamflows in the upper estuary and their influence on estuarine ecology are primarily controlled by climate, despite water management practices. Cayan & Peterson (1989) demonstrated the association between climate and streamflow along the west coast of North America, including streamflow in the Sacramento River. Peterson *et al.* (1989) developed this relationship into a conceptual model of how climate, through effects on streamflow, can influence phytoplankton production and productivity in San Francisco Bay. Climate was subsequently correlated with long-term changes in streamflow and other environmental factors that control chlorophyll *a* concentration (Lehman 1992). The long- term influence of climate on phytoplankton ecology in the upper estuary was further suggested by an association between the 1976 climate shift in the eastern Pacific (Quinn & Neal 1985) and phytoplankton community composition and environmental variables (Lehman & Smith 1991). Water management practices can influence streamflows in the upper estuary (Jassby & Powell 1994), but management is largely based on water-year type. Despite an awareness of the influence of streamflow on phytoplankton ecology, the influence of water-year type on chlorophyll *a* concentration and phytoplankton community composition and its potential influence on the estuarine food web has not been studied.

The purpose of this study is to determine if chlorophyll *a* concentration and phytoplankton community composition vary spatially and temporally with water-year type and how this might affect food availability at the base of the food web. These findings are discussed in relation to long-term climate change and provide insight into the role of natural processes on shaping estuarine ecology.

METHODS

Description of Study Area. The upper San Francisco Bay estuary is bounded by the lower reach of the Sacramento River on the north, the lower reach of the San Joaquin River on the south, and San Pablo Bay on the west (Fig. 1). Together, the Sacramento and San Joaquin Rivers and their tributaries drain approximately 153,000 km^2, or 40% of California. The region upstream of the confluence of the Sacramento and San Joaquin Rivers is a convex-shaped delta containing a network of interconnected channels and islands. The region downstream of the confluence consists of deep channels and two shallow bays. Yearly average outflows from the Sacramento and San Joaquin Rivers range from about 120 to 1740 m^{3}s^{-1}.

Chlorophyll a Concentration and Phytoplankton Community Composition. Chlorophyll *a* concentration and phytoplankton community composition were determined from water samples collected monthly or semi-monthly at 1m depth between October 1970 and September 1993 by the California Department of Water Resources and the U.S. Bureau of Reclamation. Chlorophyll *a* concentrations were measured at 25 stations (Fig. 1) between 1970 and 1993 using the spectrophotometric methods of Strickland and Parsons (1968). Water samples for phytoplankton analysis were collected using a Van Dorn bottle at 15 stations between 1975 and 1993 and at San Pablo Bay between 1980 and 1993. Samples were preserved with Lugol's solution and prepared for analysis using the Utermohl method (1958). Phytoplankton cells and colonies (*e.g.*, filaments) were enumerated and identified to genus, or to species for common forms. Phytoplankton genera and species were also grouped into eight groups based on taxonomy and morphology (Table 1).

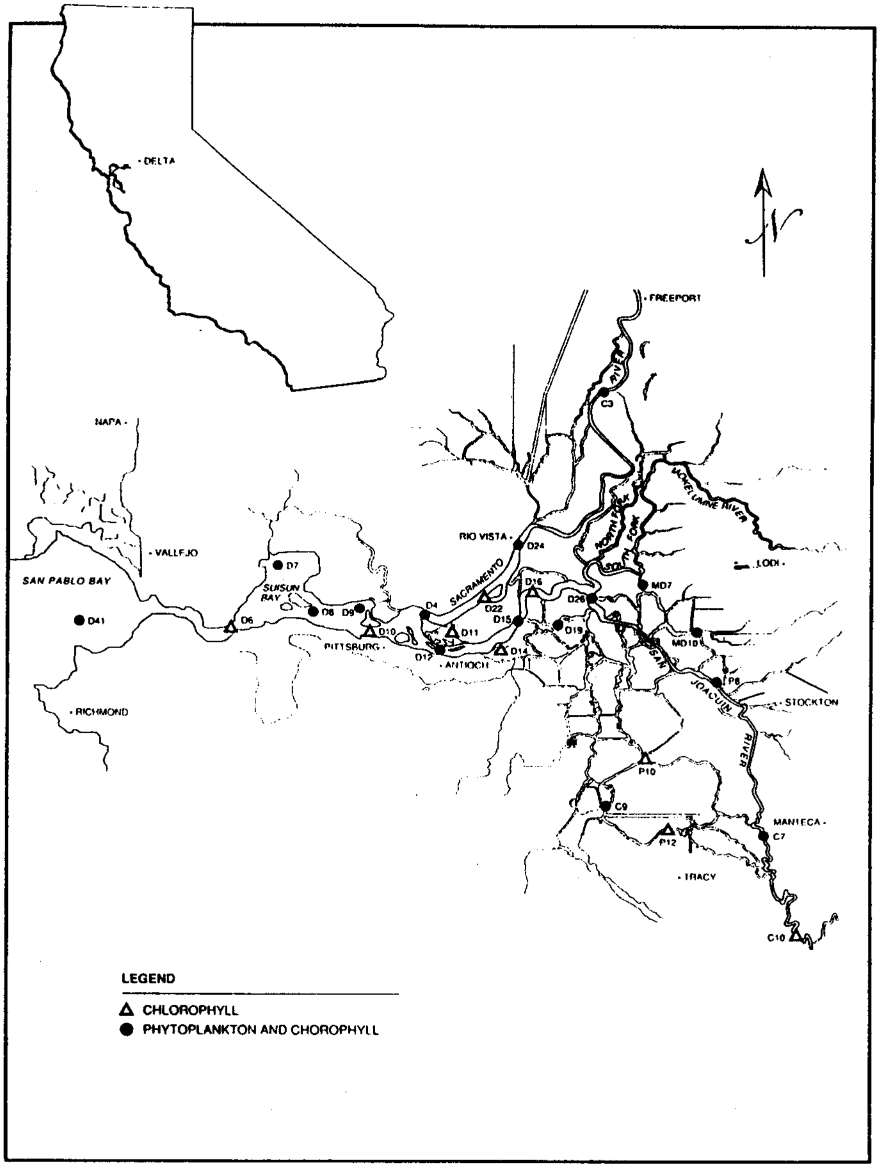

FIGURE 1. Sampling stations for chlorophyll *a* concentration and phytoplankton community composition in the upper San Francisco Bay estuary.

Changes in methodology and personnel occurred during the 19-year phytoplankton study period. Magnification was 280X between 1975 and 1981, 350X in 1982 and 1983 and 750X between 1984 and 1993. Personnel changed in 1977, 1982, 1988, 1989 and 1990 (G. Weber, pers. commun.). These methodology differences did not affect the long term trends in the results, since similar percent

TABLE 1. Eight groups used to summarize phytoplankton species composition. Representative genera and species within each group are listed.

Group	Representative Species
1 Diatom	*Synedra actinastroides, Melosira granulata, Actinella* spp., *Neidium* spp., *Skeletonema potamos, Thalassiosira eccentrica, Ceratoneis arcus, Cyclotella glomerata, Coscinodiscus* spp.
2 Green	*Micractinium* spp., *Actinastrum hantzschii, Westella botryoides, Sphaerocystis schroeteri, Chlorella* spp., *Carteria Klebsii, Pediastrum simplex, Chlamydomonas* spp.
3 Chrysophyte	*Chromulina* spp., *Chrysochromulina parva, Chrysococcus* spp., *Synura uvella, Mallomonas* spp.
4 Cryptophyte	*Rhodomonas* spp., *Rhodomonas lacustris, Chroomonas* spp., *Cryptomonas erosa, Cryptomonas* spp.
5 Bluegreen	*Anabaena circinalis, Agemenellum elegans, Anacystis limnecticus, Agmenellum* spp., *Anacystis* spp., *Aphanizomenon* spp., *Ocillatoria* spp.
6 Dinoflagellate	*Glenodinium* spp., *Gymnodinium* spp., *Glenodinium quadridens, Hemidium* spp., *Gyrodinium* spp.
7 Green Flagellate	*Euglena deses, Lepocinclis* spp., *Phacus* spp., *Euglena* spp., *Trachelmonas* spp.
8 Misc Flagellate'	unidentified flagellates

diatom composition was measured for 1979 to 1981 by independent investigators (Wong & Cloern 1981; 1982).

Phytoplankton densities were converted to relative densities because individual cells within colonies were not counted separately. Relative density was calculated as the phytoplankton cell count for each species divided by the maximum count for that species at each station. Analyzing the data in this fashion created a value that was more quantitative than presence or absence. Phytoplankton densities were used in conjunction with cell dimensions to produce estimates of phytoplankton cell carbon concentrations using equations developed by Strathmann (1967). Approximately 90% of the phytoplankton had cell dimensions that could be used to calculate cell carbon.

Data Analysis. Water year type was used as an index of streamflow. A water-year describes precipitation for a period beginning October 1 and ending September 30 of the following year and is an appropriate classification for the upper estuary where precipitation normally falls between October and June. Water years are classified in the Sacramento River Basin as wet, above normal, below normal, dry and critical water-year types based on the Sacramento River Basin index. The index is developed from stream inflow data and is available for years since 1906 (State of California 1993). For this study, water years were divided into wet, normal, dry and critical water-year types. Above and below normal water-year types were combined into one category, since there were only 3 years in these two water-year types during the 23 water years of this study. The normal water-year type was maintained because as a commonly occurring water-year type before 1970, it might provide insight into conditions in the past.

Chlorophyll *a* concentrations and phytoplankton densities among water-year types were compared using monthly percent deviations from the long-term mean. Percent deviations from the mean normalized the data and provided a common base from which to compare the relative magnitude of change among water-year types. Positive deviations describe values higher than the long-term mean, while negative deviations describe values lower than the long-term mean. Monthly percent deviations from the mean for chlorophyll *a* concentration and phytoplankton density were calculated for each station as the monthly mean minus the long term mean divided by the long term mean times 100.

Standard deviation units were used to compare time series of phytoplankton groups. Standard deviation units were calculated for each species as the monthly mean relative density minus the long-term mean relative density divided by the standard deviation of the long-term mean relative density.

Percent deviations among water years were compared using the non-parametric, multiple comparison Kruskal-Wallis test. A non-parametric statistical method was chosen because percentages were not normally distributed and sample sizes were unequal (Zar 1984). It is recognized that because of the large number of comparisons, some comparisons may be significant by chance. This problem is reduced by the conservative nature of non-parametric methods and the large sample size.

Sampling stations within the upper estuary were grouped into regions for analysis based on combined and individual hierarchical cluster analysis of monthly data for 14 physical and chemical variables and chlorophyll *a* concentration (Table 2). An independent analysis for phytoplankton community composition produced a similar grouping (Lehman & Smith 1991).

RESULTS

Water-Year Type

The 24-year period 1970 to 1993 was characterized by decreasing inflow in the Sacramento River Basin. Only wet and normal years occurred between 1970 and

TABLE 2. Regions of the upper Estuary and their associated sampling stations.

	Region	Sampling Stations
Upstream		
1	Northern	C3
2	Western	D11, D12, D 14, D15
3	Lower Sacramento River	D4, D22, D24
4	Southern	C7, C9, C10, P8, P10, P12
5	Eastern	MD10, MD7
6	San Joaquin River	D16, D19, D26
Downstream		
7	Suisun Bay	D6, D7, D8, D9, D10
8	San Pablo Bay	D41

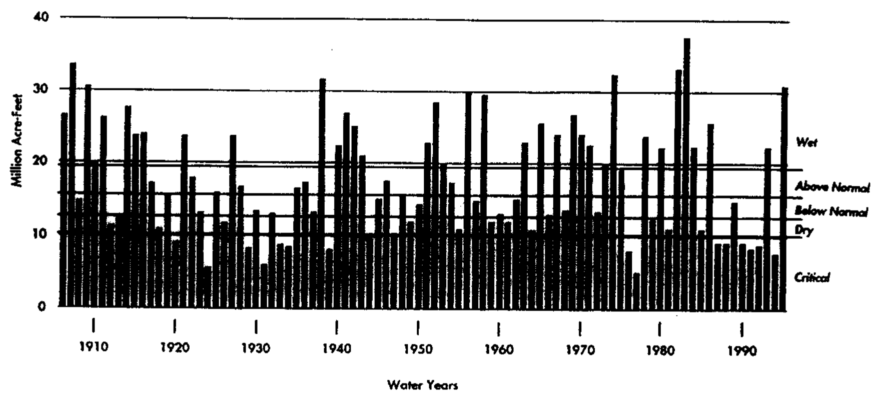

FIGURE 2. Sacramento River Basin index for water years between 1906 and 1993.

1975 (Fig. 2). These years were followed by two critical years and then a 9-year period 1978 to 1986 that alternated between wet and dry years. The driest period was between 1987 and 1993, when 5 out of 7 years were critical.

Water-year types between 1970 and 1993 differed from previous 24-year periods. Nearly half of the years between 1970 and 1993 were critical and dry. In contrast, a quarter of the years between 1946 and 1969 were dry, with no critical years. The dry period 1922 to 1945 was probably the period most similar to 1970 through 1993 because it also had an extended drought. Between 1922 and 1945, however, there were twice as many wet and normal years than dry and critical years. Prior to 1922, the pattern of water years was similar to other periods before 1970, with the total number of dry and critical years comprising less than half of the total number of wet and normal years.

Chlorophyll *a* Concentration

Long-term Trend. Chlorophyll *a* concentrations in the upper estuary were highly variable among water years but, on the average, decreased after 1976. Over time, average monthly chlorophyll *a* concentrations in the upper estuary ranged from 1 to 47 *ug*/l (Fig. 3) (CV = 84%) and encompassed a wide range of monthly values among stations (0.0 - 336 *ug*/l). Among regions, chlorophyll *a* concentrations were significantly higher in the southern region where average values reached 160 *ug*/l. In contrast, concentrations in the northern region rarely exceeded 5 *ug*/l. Despite high regional variability, average chlorophyll *a* concentrations decreased after 1977 by at least a factor of 2. Chlorophyll *a* concentrations decreased further in 1987 through 1990, before returning to 1977-1986 values.

Water year Type Variation. Among water-year types, higher chlorophyll *a* concentrations occurred in normal years. Average chlorophyll *a* concentrations were 11% higher than the mean in normal years and 17% lower than the mean in critical years (Fig. 4). Normal years also had higher chlorophyll *a* concentrations than dry and wet years which only increased by 4% and 8% above the mean.

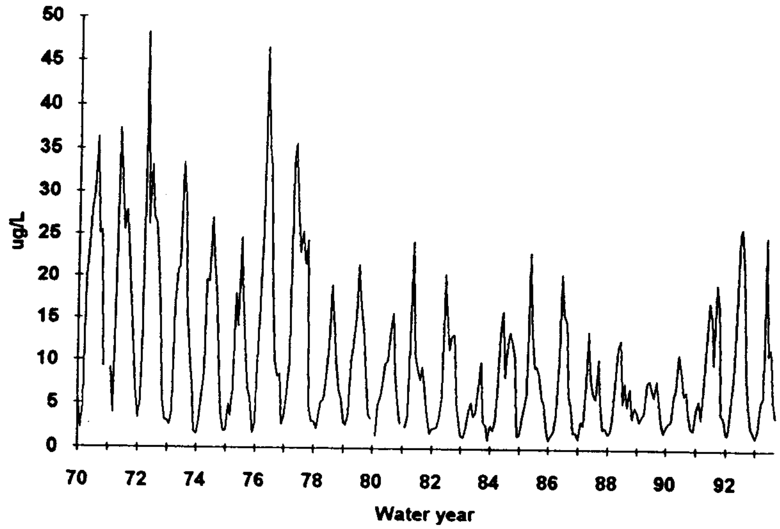

FIGURE 3. Average monthly chlorophyll *a* concentrations in the upper San Francisco Bay estuary for water years 1971 through 1993.

respectively. Among years, only concentrations during wet and dry years were not significantly different.

Chlorophyll *a* concentrations within water-year types were variable among stations. During normal years, chlorophyll *a* concentrations were 16 to 175% higher than the mean for most stations (Fig. 4). During wet years, however, chlorophyll *a* concentrations were lower than the mean upstream but higher than the mean downstream. Chlorophyll *a* concentrations during wet years were opposite to those during critical years, which were higher than the mean at the eastern margin of the upper estuary and decreased to below the mean downstream. During dry years. chlorophyll *a* concentrations were lower than the mean for most stations, but values were highly variable. Positive and negative deviations alternated among stations with distance downstream.

Seasonal Variation. Spring and summer had high chlorophyll *a* concentrations during wet and normal years. Chlorophyll *a* concentrations were higher than the mean during the spring in all water years, but concentrations were significantly lower in critical years (Fig. 5; Table 3). Concentrations were also higher than the mean in the summer during wet and normal years. Summer differed from spring, however, by having only low positive deviations for dry years and negative deviations for critical years.

Unlike the spring and summer, fall was characterized by higher chlorophyll *a* concentrations than the mean during dry years. Otherwise, the pattern of deviations among water years was similar in the fall to those in the spring and summer. Chlorophyll *a* concentrations were not significantly different between normal and wet years and the lowest concentrations occurred during critical years. During the winter, chlorophyll *a* concentrations were lower than the mean for all water years. However, chlorophyll *a* concentrations in critical years, which usually had the

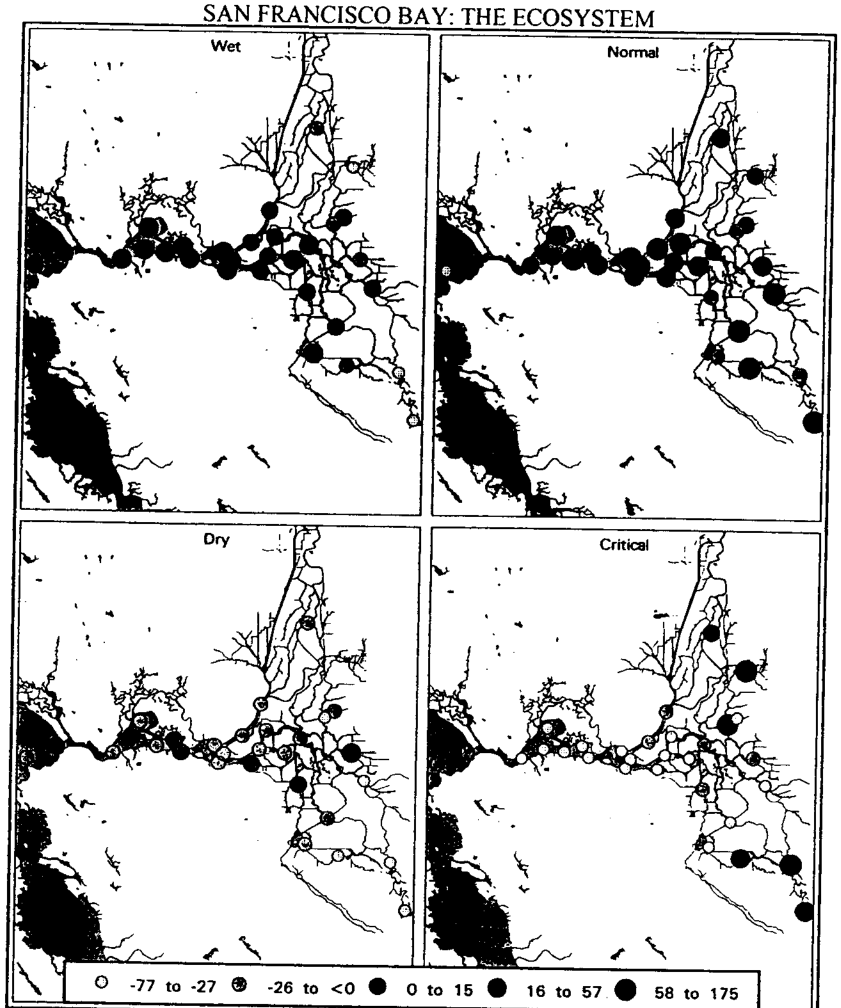

FIGURE 4. Percent deviation of monthly chlorophyll *a* concentration from the long-term mean for water-year types at sampling stations throughout the upper San Francisco Bay estuary.

lowest chlorophyll *a* concentrations among water years, were equal to those in normal and wet years.

Regional Variation. Upstream and downstream chlorophyll *a* concentrations differed among water-year types during the spring and summer. Normal and wet years had higher chlorophyll *a* concentrations than the mean in the spring or summer for all regions except San Pablo Bay Fig. 6, Table 4). These concentrations were significantly higher upstream in normal years and downstream in wet years. Critical years were characterized by chlorophyll *a* concentrations that were higher than the mean upstream but lower than the mean downstream during the spring. During the summer of critical years, however, chlorophyll *a* concentrations were lower than the mean at most upstream and downstream regions. Dry years had

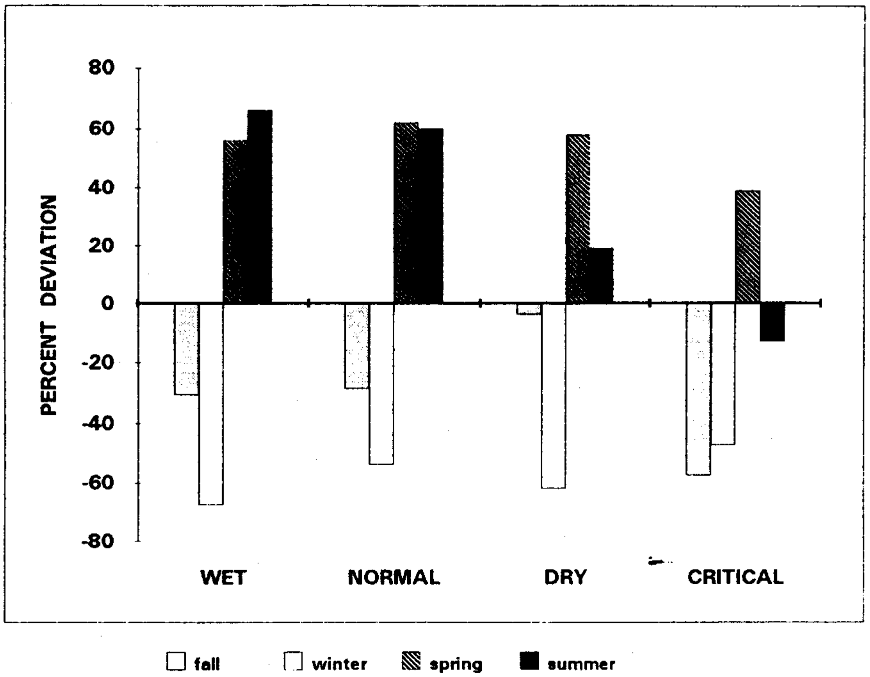

FIGURE 5. Seasonal average percent deviation of monthly chlorophyll *a* concentration from the long-term mean among water-year types.

higher chlorophyll *a* concentrations than the mean for some upstream and downstream regions during the spring and summer. However, these concentrations were only occasionally higher than those for critical years.

For both upstream and downstream regions, differences in chlorophyll *a* concentrations among water-year types were few during the fall and winter. During the fall, negative deviations for normal and wet years were not significantly different for most upstream and downstream regions (Fig. 6; Table 4). Normal years, however, had relatively higher chlorophyll *a* concentrations upstream and downstream in Suisun Bay than in critical years. Only in dry years were chlorophyll *a* concentrations higher than the mean. Positive deviations, combined with low

TABLE 3. Seasonal differences in chlorophyll *a* concentrations among water-year types. Statistical significance at the .05 level or higher was determined using the Kruskal-Wallis Test and is indicated by an 'X'.

	Fall	*Winter*	*Spring*	*Summer*
Wet/Normal		x		
Wet/Dry	x			x
Wet/Critical	x		x	x
Normal/Dry	x			x
Normal/Critical	x		x	x
Dry/Critical	x		x	x

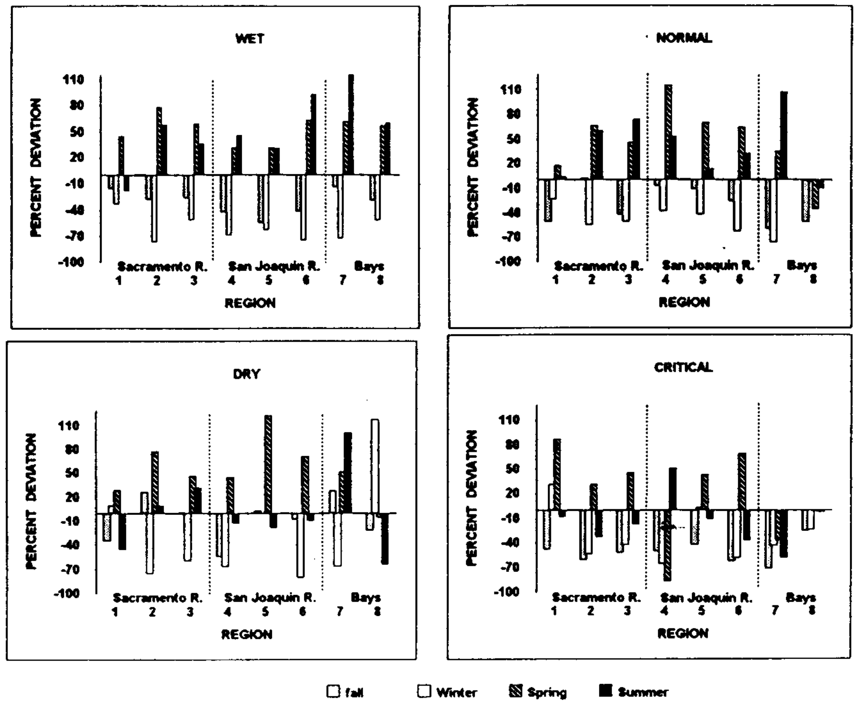

FIGURE 6. Regional average percent deviation of monthly chlorophyll *a* concentrations from the long-term mean among water-year types by season.

negative deviations, often gave dry years the highest chlorophyll *a* concentrations at both upstream and downstream regions. During the winter, chlorophyll *a* concentrations were consistently higher in normal years at both upstream and downstream regions.

Phytoplankton Community Composition

Long-term Trend. Phytoplankton community composition between 1975 and 1993 was characterized by a decrease in the percentage of diatoms. Diatoms comprised approximately 80-100% of the phytoplankton community between 1975 and 1979 (Fig. 7). Greens, which were the second most abundant group of phytoplankton, comprised up to 30% of the community. The phytoplankton community shifted to a more mixed assemblage, with fewer diatoms and more greens and flagellates, between 1980 to 1983. Diatoms reached a minimum during the 1987 to 1990 drought before returning to 1981-1986 levels in the early 1990s. The large decrease in the percentage of diatoms over time was a function of both a decrease in diatoms and an increase in other types of phytoplankton (Fig. 8). Changes in phytoplankton community composition for the entire upper estuary were similar to those for each region (not shown).

Water-Year-Type Variation. Most phytoplankton increased during normal and critical years, but diatoms increased only in normal years (Fig. 9, Table 5). Diatoms

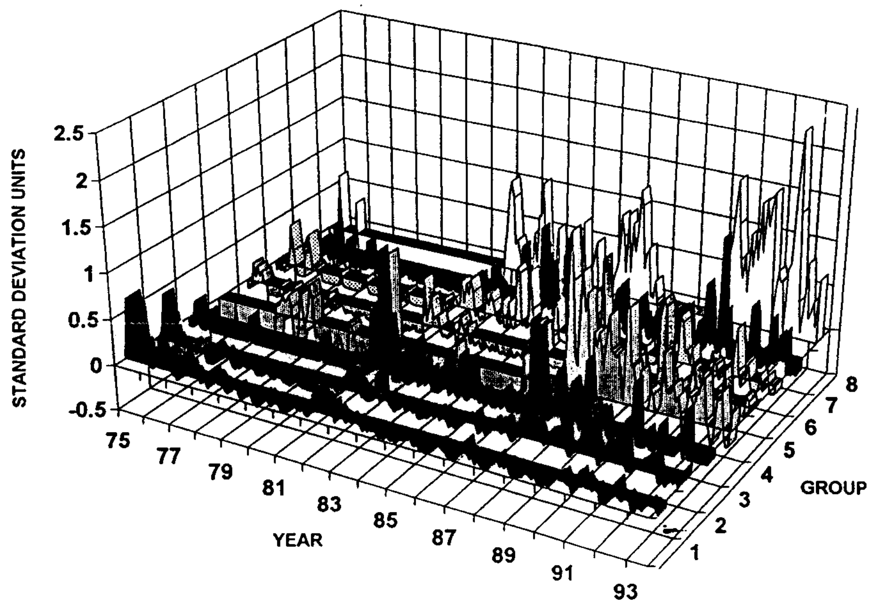

FIGURE 8. Monthly average standard deviation of phytoplankton group density from the long-term mean. Phytoplankton groups are described in Fig. 7.

flagellates increased more in the summer during critical and wet years. For the spring, diatoms and greens increased in normal years. Diatoms and greens, along with cryptophytes, also increased more during critical years than wet years. For the fall and winter, normal years had more greens, bluegreens and cryptophytes in the fall, and diatoms in the winter.

Regional variation. Phytoplankton community composition in upstream and downstream regions varied with water-year type during the spring and summer. During normal years, diatoms and greens increased upstream and downstream, as far as Suisun Bay (Fig. 11, Table 7). Diatoms and greens in the upstream regions were also accompanied by bluegreens and cryptophytes. The second largest positive deviations occurred during critical years, when diatoms, greens and bluegreens increased upstream and cryptophytes increased downstream. For wet years, miscellaneous flagellates had positive deviations upstream, but these were rarely different among water years. In contrast, miscellaneous flagellates, green flagellates and dinoflagellates increased more downstream during wet years than during normal or critical years. None of the positive deviations calculated for phytoplankton groups in dry years exceeded those of other years.

Phytoplankton community composition in upstream and downstream regions also varied with water-year type in the fall and winter. During normal years, diatoms, greens and cryptophytes increased upstream, while diatoms increased downstream in Suisun Bay (Fig. 12; Table 7). During critical years,·bluegreens,

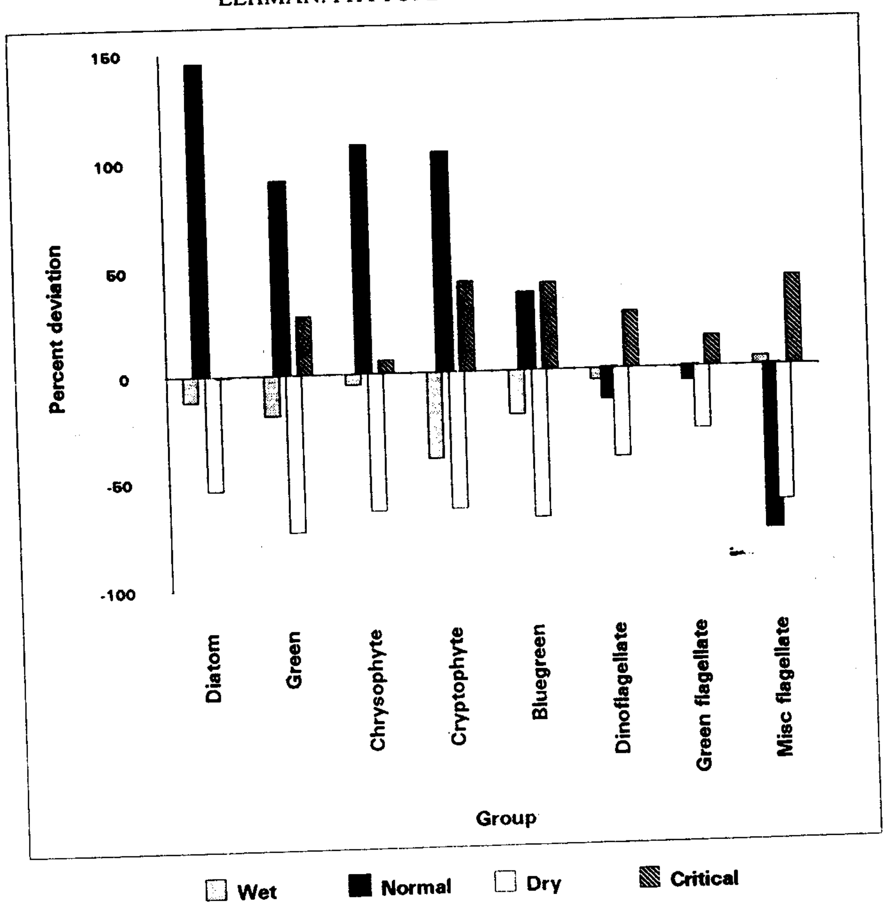

FIGURE 9. Average percent deviation of monthly phytoplankton density from the long-term mean among water-year types.

miscellaneous flagellates and green flagellates increased in both upstream and downstream regions. In wet and dry years, negative deviations characterized most phytoplankton upstream, with the exception of diatoms and cryptophytes. Downstream phytoplankton communities had more diatoms during both wet and dry years and more miscellaneous flagellates during wet years.

Phytoplankton Community Size Structure and Carbon Content. Changes in phytoplankton community composition with water-year type affected the size structure and carbon content of food particles. The average cell diameter of single-celled diatoms was significantly larger than other single-celled phytoplankton (Table 8). Green flagellates had the second largest cell diameter. Both diatoms and green flagellates contrasted with miscellaneous flagellates, which had the smallest diameter cells. Differences in cell diameter were also significant among most of the other single-celled phytoplankton, with the exception of the pairs bluegreens/chrysophytes and cryptophytes/dinoflagellates. Differences in size

TABLE 5. Differences in phytoplankton group densities from the long-term mean among water-year types. Significant differences at the .05 level or higher were determined using the Kruskal-Wallis Test and are marked with an 'X'. Water-year types are indexed as Wet (W), Normal (N), Dry (D) and Critical (C).

	W/N	*W/D*	*W/C*	*N/D*	*N/C*	*D/C*
Diatom	x	x	x	x	x	
Green	x	x	x	x	x	x
Chrysophyte		x		x		
Cryptophyte	x		x	x		x
Bluegreen	x	x	x	x	x	x
Dinoflagellate		x				
Green flagellate	x		x			
Misc flagellate	x	x			x	x

structure among phytoplankton groups were accompanied by changes in cellular carbon content, despite adjustments for plasma volume. Dinoflagellates, cryptophytes, green flagellates and diatoms had the highest cellular carbon content among groups.

Diatoms probably had the largest influence on the spatial and temporal variation of food particle size and nutrition. About 94% of the diatoms had cell diameters within the 10 *u*m or larger size range consumed by adult zooplankton. Although dinoflagellate, bluegreen and green flagellate cells were also larger than 10 *u*m in diameter and had high cellular carbon content, they occurred less frequently and differed less spatially and temporally among water-year types.

TABLE 6. Seasonal differences in phytoplankton group densities from the long-term mean among water-year types. Significant differences at the .05 level or higher were determined using the Kruskal-Wallis Test. Only Seasons with significant differences are listed. Seasons are Fall (f), Winter (w), Spring (sp) and Summer (sm). Water-year types are Wet (W), Normal (N), Dry (D) and Critical (C).

	W/N	*W/D*	*W/C*	*N/D*	*N/C*	*D/C*
Diatom	f,w	f	f,w	f	f,w	f,w
	sp,sm		sp	sp,sm	sp,sm	
Green	f,w	f	f	f,w	f,w	f,w
	sp,sm	sp,sm	sp,sm	sp,sm	sp,sm	sp,sm
Chrysophyte						
				sp,sm		
Cryptophyte	f		w	f	f	w
			sp,sm	sp,sm		sp,sm
Bluegreen	f		f	f,w	f	f
	sp,sm	sp		sp,sm	sp,sm	sm
Dinoflagellate						
		sm				
Green Flagellate		f	f		f,w	
	sm		sm		sp,sm	sm
Misc Flagellate	f,w	f,w	f			f,w
	sp,sm	sp,sm				sp,sm

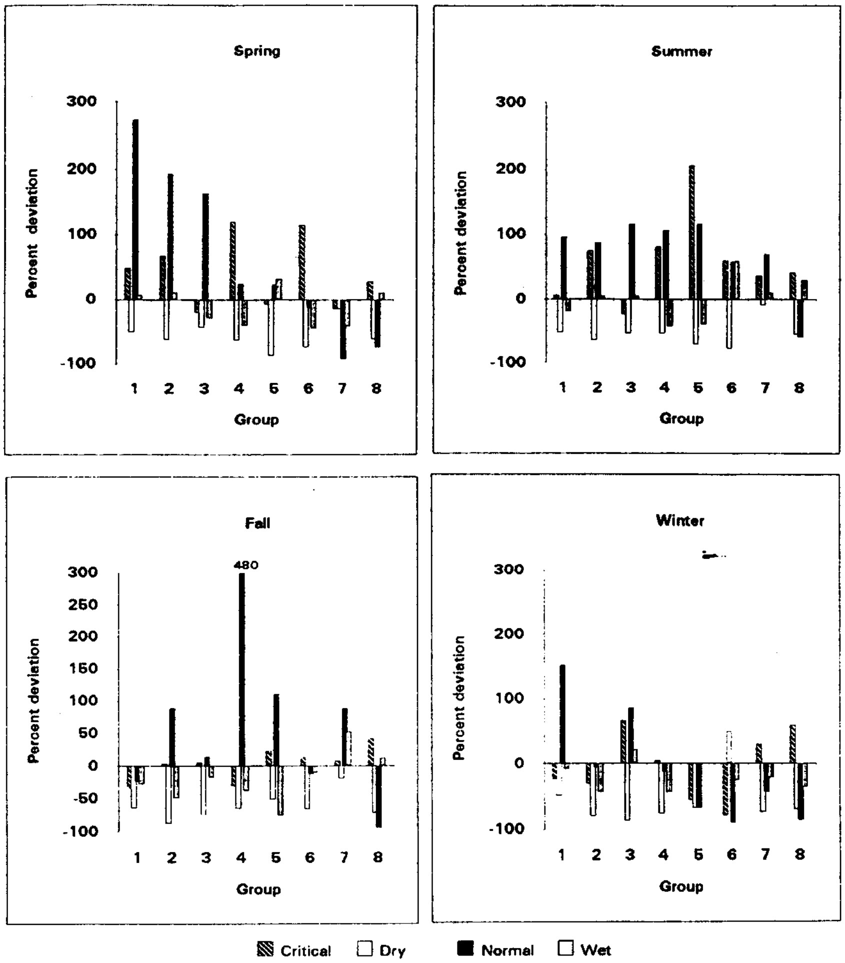

FIGURE 10. Seasonal average percent deviation of monthly phytoplankton group densities from the long term mean among water-year types. Phytoplankton groups are described in Fig. 7.

DISCUSSION

The spatial and temporal variation of chlorophyll *a* concentration with water-year type differed for upstream and downstream regions. During normal and critical years, high chlorophyll *a* concentrations upstream were a function of low or moderate streamflows, which allowed accumulation of phytoplankton biomass upstream (Conomos 1979; Peterson *et al.* 1989; Lehman 1992). Lower chlorophyll *a* concentrations during critical years were probably caused by reduced transport of phytoplankton biomass throughout the upstream region with low streamflows.

Upstream regions contrasted with downstream regions where higher chlorophyll *a* concentrations occurred during wet and normal years. During these years, phytoplankton biomass is transported downstream with high to moderate stream-

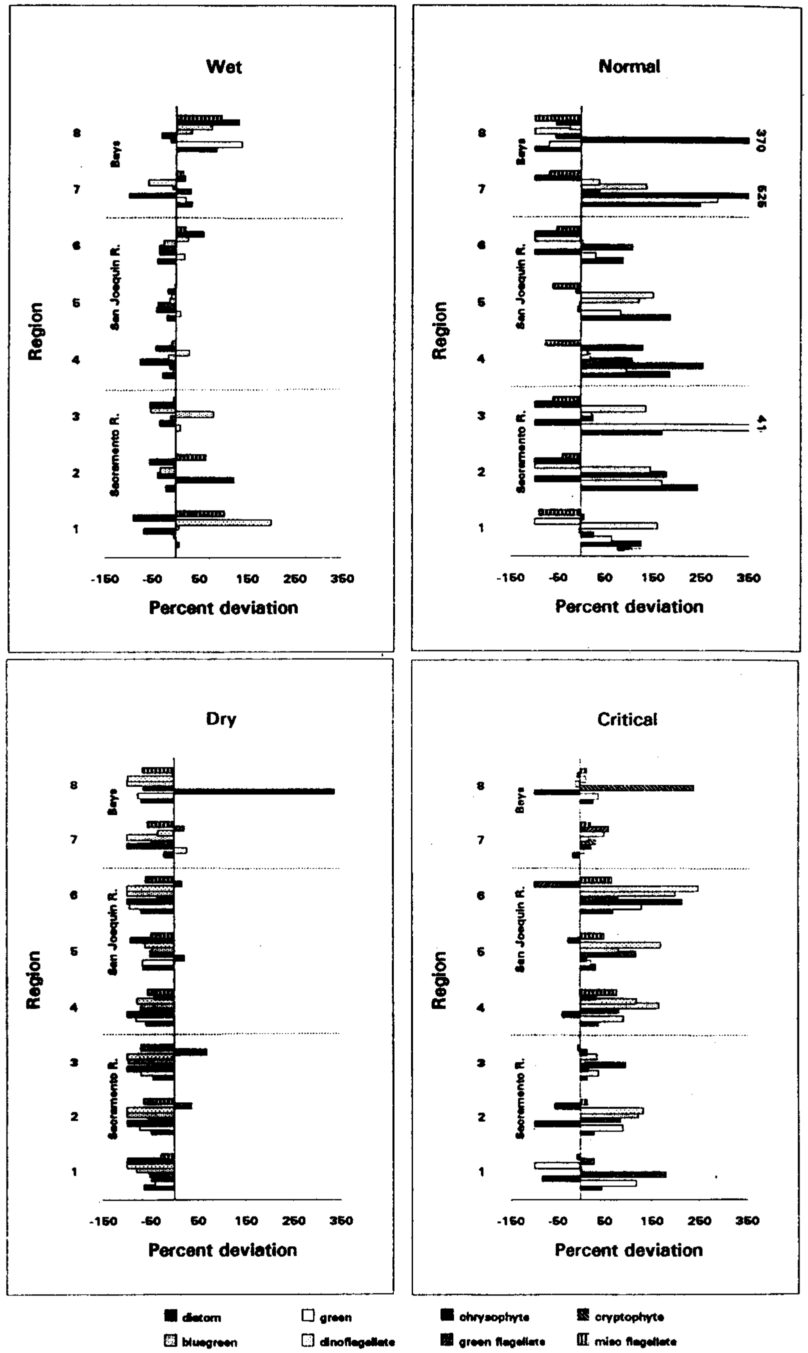

FIGURE 11. Regional average percent deviations of monthly phytoplankton group densities from the long-term mean among water-year types during the spring and summer.

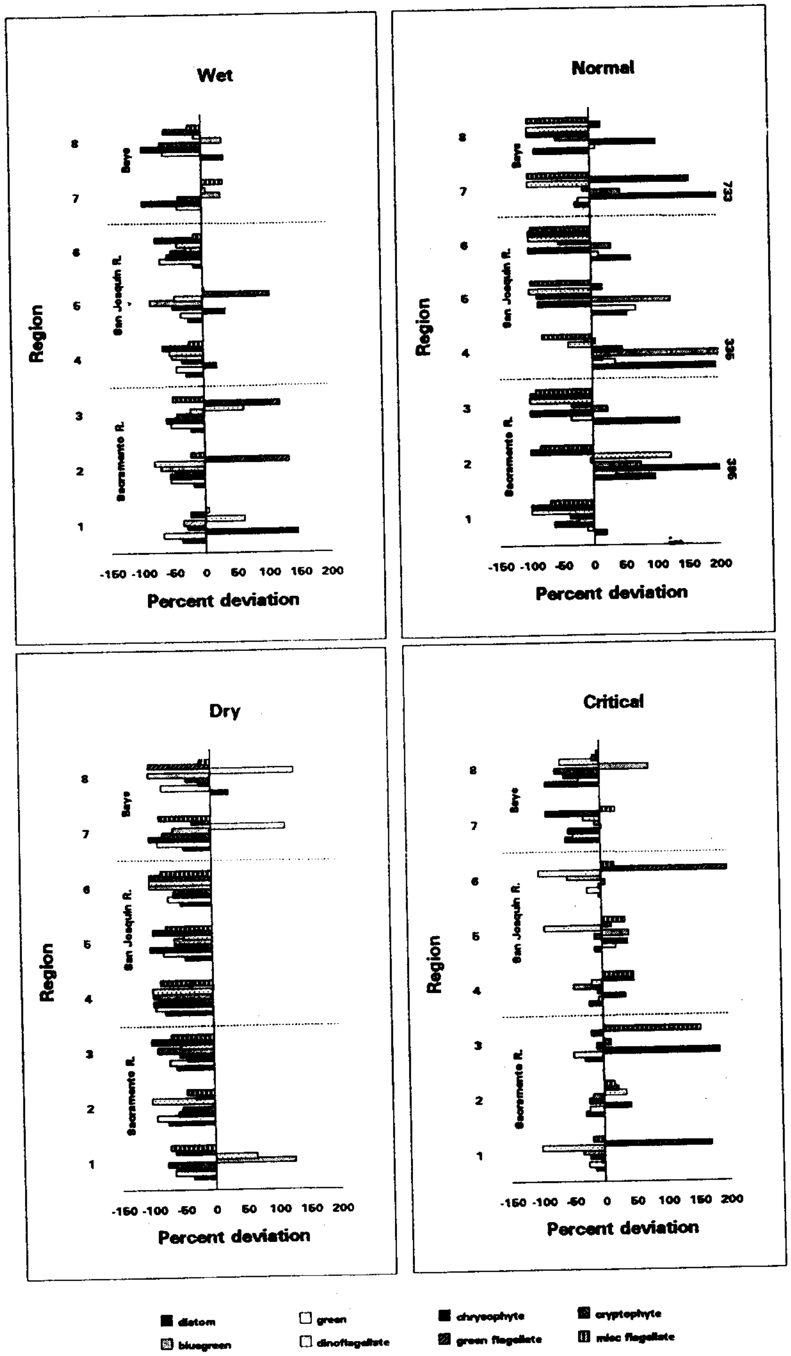

FIGURE 12. Regional average percent deviations of monthly phytoplankton group densities from the long-term mean among water-year types during the fall and winter.

TABLE 7. Regional differences in phytoplankton group densities from the long-term mean among water-year types by season. Significant differences at the .05 level were determined using the Kruskal-Wallis Test. Only regions with significant differences are listed. Water-year types are Wet (W), Normal (N), Dry (D) and Critical (C).

	W/N	*W/D*	*W/C*	*N/D*	*N/C*	*D/C*
			Fall			
Diatom	1,3,5,7,8		1,3,7,8	7	7	7
Green	3,4,5	4	4	1,3,4,5	4,5	4
Chrysophyte						
Cryptophyte	4,5			4,5,7	4,5	
Bluegreen	4		2,5	4	4	4,6
Dinoflagellate						
Green flagellate			3,7			
Misc flagellate		4,7	4,5		4,5	4,7,5
			Winter			
Diatom	4,8		3,7,8	4,8	2,3,4,7	3,7,8
Green	4,5			4		
Chrysophyte						
Cryptophyte			4			
Bluegreen	4		7	4	4	
Dinoflagellate						
Green flagellate			7			
Misc flagellate	7				7	4
			Spring			
Diatom	2,4,5,6,7,8		7,8	2,3,4,5,6,7	2,4,5,7	4
Green	2,3,4,5,7	6,4	4	2,3,4,5,6,7	2,3,4,5,7	4
Chrysophyte				4	1	
Cryptophyte			3,4		8	3,4
Bluegreen	2,3,4,5	3,7	3,7	2,3,4,5	2,3,4,5	
Dinoflagellate						
Green flagellate						
Misc flagellate		2,4				4
			Summer			
Diatom	4,8	8	4,7,8	4,5	2,3,4,7	4,7
Green	2,3,4,7	8	4,8	2,3,4,5	2,3,7	4,5
Chrysophyte						
Cryptophyte	2,4		2,3,4,5	2,4		2,3,4
Bluegreen	2,4,5		2,4,6	2,4		4,6
Dinoflagellate		8	8			
Green flagellate	7		7,8			
Misc flagellate	1,2,8	1,2,3,8	1		4	3,4,8

flow (Peterson *et al.* 1989). Once downstream, high to moderate streamflows plus tides may enhance the accumulation of phytoplankton biomass near the turbidity maximum (Peterson *et al.* 1975; Arthur & Ball 1979). During dry and critical years, low chlorophyll *a* concentrations in the downstream region were probably also affected by the turbidity maximum. The turbidity maximum is located farther upstream during dry and critical years where biomass accumulation and shoal to channel transport are reduced and net productivity is low (Cloern *et al.* 1983). The reason for lower phytoplankton biomass during dry years compared with critical years is unclear, but may be related to water management practices. The larger

TABLE 8. Average cell dimensions and cellular carbon for phytoplankton groups. (The letters s and f indicate single and filamentous forms.)

Group	n	Length µm	SD	Width µm	SD	Depth µm	SD	Log cell carbon pg	SD	% > or = 10 µm
Diatoms - s	10995	29.19	22.11	8.73	5.37	4.18	4.60	1.85	0.28	94
Diatoms - f	7932	5.94	3.60	6.62	2.50	21.20	34.94	1.50	0.50	7
Green - s	6602	14.66	13.50	5.97	3.33	1.27	1.83	1.63	0.28	42
Green - f	6	29.33	39.26	29.66	39.02	98.19	108.38	2.25	0.83	33
Chrysophytes	185	9.88	8.16	5.25	3.19	0.52	1.97	0.17	0.30	27
Cryptophytes	3838	14.01	4.24	7.22	1.04	3.89	2.62	1.83	1.27	69
Bluegreen - s	640	8.50	7.10	5.59	5.66	1.82	1.57	1.30	0.57	15
Bluegreen - f	455	4.76	0.62	4.76	0.62	67.71	14.15	2.46	0.13	0
Dinoflagellates	402	15.60	11.68	11.23	4.89	0.04	0.71	1.11	0.28	100
Green Flagellates	554	21.25	11.52	9.83	3.48	0.53	1.63	0.93	0.31	85
Misc. Flagellates	2182	6.43	0.55	4.24	0.10	0.06	0.25	0.07	0.05	0.05

percentage of inflow diverted for agriculture during dry years than critical years removes phytoplankton biomass and decreases residence time.

The spatial and temporal variation of phytoplankton community composition at upstream and downstream regions was also a function of changes in water-year type. During normal and critical years, diatoms and greens increased upstream during the spring and summer. Diatoms commonly occur early in the year when water temperature is low, turbidity is high and wind mixing is sufficient to prevent cells from settling to the bottom. Greens increase later in the spring when water temperatures are warmer. Their increase was facilitated in both normal and critical years by low to moderate streamflows which enabled the accumulation of cells. Moderate streamflows during normal years also dispersed these phytoplankton throughout the upstream regions. The coincident increase of cryptophytes upstream during critical years was probably a direct response to increased phytoplankton biomass, since they often function as mixotrophs. In addition, their buoyancy and mobility may protect them from sinking in the slow moving waters of critical years when they would otherwise settle on the bottom or be removed by benthic herbivores. Flagellates usually occur in warm and slow moving waters where their ability to migrate vertically allows them to avoid high light near the surface and access nutrients near the bottom. During wet and dry years, negative and small deviations from the mean for most phytoplankton were probably a function of the flushing of cells downstream with high streamflow or export of cells due to water management practices.

Downstream, diatoms and greens increased during normal and wet years. High streamflows transport cells downstream to Suisun Bay in normal years and to San Pablo Bay in wet years. Once these cells are downstream, they may be retained by tidal or gravitational circulation patterns (Peterson *et al.* 1975; Arthur & Ball 1979). In contrast, diatoms and greens were few downstream during critical years when low streamflows reduce the transport of cells downstream. Factors other than streamflow may contribute to the decrease of diatoms and greens downstream during critical years. Cells are lost from sedimentation by reduced turbulence (Thompson *et al.* 1981), increased benthic grazing by marine species (Nichols 1985) and increased retention of cells in deep channels upstream where net primary productivity is low (Arthur & Ball 1979; Cloern *et al.* 1983). In contrast, these factors probably contribute to the increase of flagellates downstream during critical years, since flagellates are mobile. The decrease of most phytoplankton groups during dry years is probably related to water management practices that result in export of phytoplankton-rich San Joaquin River water.

Spatial and temporal differences in the upstream and downstream distribution of chlorophyll *a* concentration with water-year type are important factors controlling the estuarine food web. Phytoplankton biomass can be an important source of carbon to the upper estuary (Jassby *et al.* 1993), where it is correlated with zooplankton biomass (Lehman 1992). Accumulation of phytoplankton biomass upstream during critical years provides food for the survival of freshwater and freshwater-tolerant species. However, accumulation of phytoplankton biomass upstream reduces the amount of phytoplankton biomass transported to the food web downstream. During wet years, the transport of phytoplankton biomass downstream provides food at the base of the food web in downstream nursery areas for fish, but leaves little for upstream organisms. Mass balance calculations suggest that Delta phytoplankton provide about 38% of the carbon load to Suisun Bay (Jassby & Powell 1994). Normal years probably provide the best combination of conditions for both upstream and downstream components of the food web. Moderate streamflows enable accumulation of phytoplankton biomass for use upstream and yet are high enough to transport some of that biomass downstream for use in Suisun Bay. In contrast, dry years appear to provide the poorest conditions for the food web, since both upstream and downstream chlorophyll *a* concentrations are low.

Changes in phytoplankton community composition with water-year type are important for understanding the ecology of the upper estuary because they affect the quality and size structure of food particles available at the base of the food web. Phytoplankton are not used equally by zooplankton in the aquatic food web. Although adult zooplankton can consume phytoplankton of varying cell size, they often feed selectively on phytoplankton larger than 8 to 11 *u*m in diameter (Paffenhoffer & Knowles 1978; Peterson *et al.* 1991: Kiorboe *et al.* 1990).

Availability of phytoplankton of the appropriate cell diameter and composition influences zooplankton population survival through intra- and inter-species competition for food quantity (Paffenhoffer & Knowles 1978) and quality (Peterson *et al.* 1991).

The linear size ratio between predators and their optimal prey is 18:1 for copepods (Hansen *et al.* 1994). This ratio is similar to the 22:1 ratio calculated for the copepod *Eurytemora affinis*, an important zooplankton food for juvenile fish in this estuary, and an average sized diatom in the upper estuary. Because of this size relationship, diatoms, which have large cell diameters and high cellular carbon content, may influence the food quality of large zooplankton among water-year types. In fact, the decrease of diatoms in the early 1980s coincided with the decline in abundance of many large zooplankton during the same period (Obrebski *et al.* 1992). A decrease in the average size of food particles may also have contributed to the success of introduced zooplankton species during the 1987 to 1992 drought (Orsi & Walter 1991). The influence of phytoplankton size structure on food quality is probably not through differences in phytoplankton growth rates, since growth rates do not differ among phytoplankton size classes (Cole & Cloern 1986).

Because of the strong influence of water-year type on phytoplankton, the long-term sequence of changes in water-year types was an important factor controlling the long-term trends in chlorophyll *a* concentration and phytoplankton community composition. Normal and wet years were associated with high chlorophyll *a* concentrations and diatom densities in the early 1970s. In contrast, wet and dry years coincided with low chlorophyll *a* concentrations and diatom densities between 1978 and 1986. Chlorophyll *a* concentrations and diatom densities continued to decrease downstream after 1986 when critical years were common. The magnitude of the decrease in critical years was enhanced downstream by the loss of phytoplankton to grazing by the clam *Potamocorbula amurensis*, which became established in the estuary in 1987 (Nichols 1985). Average chlorophyll *a* concentrations and diatom densities increased in the early 1990s in association with critical and wet years.

The long-term trend in chlorophyll *a* concentration and phytoplankton community composition with water-year type was partly a function of long-term climate change. World-wide climate is a function of the frequency and intensity of El Niño and southern oscillation (ENSO) events (Quinn & Neal 1985; Horel & Wallace 1981). Climatic conditions affect precipitation patterns in western North America (Cayan & Peterson 1989), which influence biological and environmental factors in San Francisco Bay (Peterson *et al.* 1989).

Determining the effect of individual ENSO events is often difficult because ENSO events in the upper estuary are associated with both wet and critical water-year types. The difficulty of determining their effects is compounded by the fact that the frequency and intensity of ENSO events have increased since 1977 (Quinn & Neal 1985). In the upper estuary, this 1977 climate shift resulted in an increase in the number of wet and critical water years. It also coincided with the decline in chlorophyll *a* concentration and diatom density in the early 1980s. Previous research has also demonstrated a correlation between the 1977 climate shift and phytoplankton community composition, chlorophyll *a* concentration and environmental variables in the upper estuary (Lehman & Smith 1991; Lehman 1992) and environmental and biological variables in the nearby Pacific Northwest (Ebbesmeyer *et al.* 1991).

Understanding the influence of water-year type on phytoplankton biomass and community composition may provide a way to gain insight into past and future changes in the estuarine food web. The large number of normal years and small number of critical years before 1970 suggest that average chlorophyll *a* concentrations and diatom densities were high early in the 20th century. It is also possible that phytoplankton communities were more stable early in the century since the interval between normal years was smaller than after 1970. That past changes in phytoplankton biomass and community composition can be accurately inferred from water-year types is suggested by phytoplankton data collected by Allen in 1920. These data indicate diatoms comprised at least 80 to 90% of the phytoplankton community during the normal year of 1913. This is similar to the percent composition of diatoms measured for normal years in the early 1970s. Similarly, it should be possible to use projected changes in water-year types to determine how the estuarine food web will be affected by climate and water management practices in the future.

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