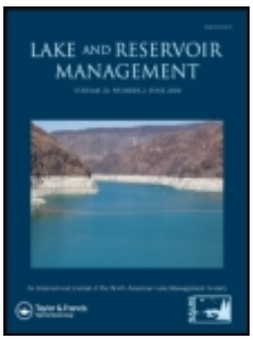

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Variation in Water Quality and Phytoplankton Nutritional Status in an Urbanized Lake System (Lake Merced, California, USA)

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Abstract

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Lake chemistry is influenced by land use in the surrounding watershed, particularly in complex urban landscapes, which are commonly subjected to an increase in material loadings. Because land use is rarely uniform, individual ecosystems embedded within the landscape may reflect varying water quality conditions. The Lake Merced system is composed of three lake basins with watersheds (surface area = 13 km^2) residing entirely within the city of San Francisco, California. On nine occasions from January-June 1995 we sampled the two main lakes (North and South Lake Merced) within the system to evaluate their relative productivity and nutrient status. On each date, several physical-chemical conditions were measured, and nutrient enrichment bioassays were performed to evaluate the nutritional status of the phytoplankton (nitrogen (N) and phosphorus (P) enrichment in a 2 x 2 factorial experimental design). All the parameters tested except temperature were higher in the north lake compared with the south (pair-wise Wilcoxon Ranked sums), and common trophic state variables were more than 2-fold higher in the north lake. Phytoplankton growth in North Lake Merced was N-limited while growth in South Lake Merced was co-limited by N and P. In sum, our data indicate that differences among these lakes may be explained by simple volume differences between lakes (with the smaller North Lake Merced being more eutrophic), and heavy stocking of fishes to the north lake. Particulate nutrient ratios (N:P) were good indicators of phytoplankton nutritional status throughout the system, while N:P ratios based on total nutrient concentrations gave misleading results.

Lake chemistry often reflects land use in the surrounding watershed (Bormann and Likens 1967, Dillon and Kirchner 1975), and urbanized systems are particularly subjected to enhanced material loading from land clearance, concentrated use of domestic chemicals and impervious surfaces that expedite runoff (Pickett *et al.* 1997, Sorrano *et al.* 1999). Because land use is rarely homogenous within a given watershed, the structure and function of aquatic subsystems within the watershed can vary as well (Gibson *et al.* 1995, Kratz *et al.* 1997). Thus, comparative studies on systems distributed within landscapes are required to adequately understand, predict and manage the full scope of ecological change (McDonnell and Pickett 1993, Gutzwiller 2002).

Nitrogen (N) and phosphorus (P) have been most frequently identified as limiting resources to phytoplankton growth (Hecky and Kilham 1988, Elser *et al.* 1990), and in turn these nutrients regulate the rate of eutrophication in many lakes (Schindler 1978, Schelske *et al.* 1986). Ambient nutrient concentrations can be used to assess the trophic status of ecosystems (Carlson 1977); however, these measures are not always the best predictors of system limitation, because the total nutrient pool is rarely accessible for phytoplankton growth (Lean and Pick 1981, Thompson *et al.* 1994). Instead, phytoplankton are capable of storing phosphorus in excess of immediate growth requirements (Rhee and Gotham 1981, Lean and Pick 1981). This is particularly true in eutrophic lakes, where ambient nutrient concentrations can be large and fuel luxury storage, thereby complicating the relationship

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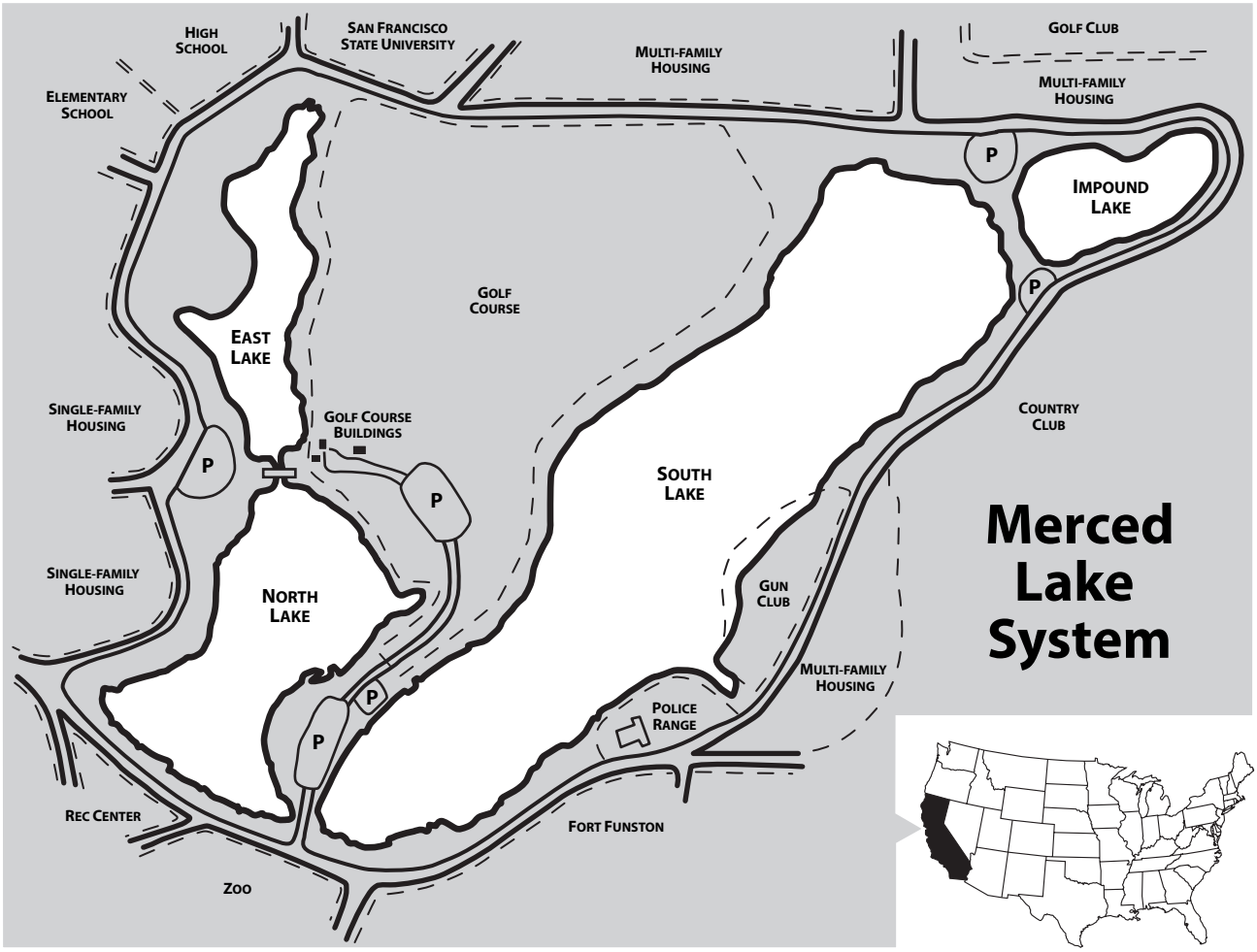

Figure 1.-A map of the Lake Merced system with locations of lakes and impoundments, as well as the general land-use within the watershed.

between ambient nutrients and phytoplankton standing stocks (Paerl and Bowles 1987 Carrick *et al.* 1993b).

The Lake Merced system is, in many respects, a typical urban ecosystem where resources are managed for multiple purposes, such as recreation, drinking water and emergency reserves (Woodward 2003). The lake system consists of three lake basins and one impoundment with watersheds (surface area = 13 km^2) residing entirely within the city of San Francisco, California (Fahy 1974). Lake Merced was once thought to be a physically and chemically homogeneous set of lakes (Adams 1978, Geo Consultants 1993); however, more recent information suggests that limnological differences do exist among basins (Marchi 1998). In this paper we compare phytoplankton nutrient limitation within this urbanized lake system to evaluate simple predictors of lake trophic state. The specific objectives of our study were: (1) to compare the limnological conditions (chlorophyll, water transparency, basic chemistry) between the two largest basins, both North and South Lake Merced, (2) to determine the degree and pattern of nutrient limitation within each lake, and (3) to evaluate simple predictors of phytoplankton nutrient status for the Lake Merced system as potential performance measures to evaluate system change.

Methods

Study Site

The Lake Merced system experiences a Mediterranean-type climate with mild winters and summers, characteristic of San Francisco region on the west coast of the United States (Fig. 1). Two centuries ago, Lake Merced was a single-lake system with a direct connection to the Pacific Ocean (Fahy 1974). During the early 1800s, Lake Merced became intermittently separated from the ocean by the formation of sand spits along the coast. In 1852, an earthquake caused a breach in the sand spit, forming a channel connection to the ocean. This channel

was subsequently filled by long-shore sediment transport and human intervention, and by 1880 Lake Merced was completely isolated from the Pacific Ocean. Shortly thereafter, the construction of berms around the lakeshore permanently isolated the three lakes and a single impoundment from the ocean. A strip of land (approximately 25 m wide at its narrowest point) currently separates the two largest lakes (North and South Lake Merced; Fig. 1). A culvert was installed to allow flow between North and South Lake Merced (denoted NLM and SLM, respectively); however, declining water levels during the last four decades have dropped lake levels well below the height of these pipes, preventing direct water exchange (Adams 1978).

Both lakes have shallow (mean depth of 3-4 m), saucer-shaped basins that are isothermal most of the year, despite the fact the NLM is considerably smaller compared with SLM (Adams 1978). Moreover, the NLM is stocked with trout that represent a put-and-take recreational fishery (Marchi 1998). Both lakes support limited littoral areas dominated by *Typha*, and the entire watershed contains a mix of urban centers that surround a narrow corridor of steep sloping coastal scrub vegetation (Geo Consultants 1993).

Sampling Scheme

We sampled both NLM and SLM on nine occasions (approximately monthly) in 1995 to determine ambient limnological conditions and the nutritional status of the phytoplankton. Single lake stations were visited on nine occasions January-June. Previous research shows that environmental variation within this timeframe (January-June) captures the bulk of seasonal variation in this coastal, Mediterranean climate (Smith *et al.* 1987, Hollibaugh *et al.* 1988). Single sampling stations were chosen in each basin because preliminary studies show that biological conditions were fairly homogenous among several sites within each basin (Marchi 1998).

All biological and chemical nutrient analyses were conducted on raw lake water collected from a depth of 0.5 m using an acid-washed 2-L Niskin bottle. Water samples were transferred from the Niskin sample bottle into a clean, acid-washed 5-L polyethylene bottle (amber to prevent photo-shock) and a shaded acid-washed 20-L carboy. These samples were then transported back to the laboratory and processed within two hours of collection to determine ambient nutrient concentrations, phytoplankton biomass and species composition, and phytoplankton nutrient limitation (see sections below).

Limnological Measurements

Temperature, conductivity and salinity were measured at 0.5 m intervals (surface to sediments) using a YSI-33 meter. Dissolved oxygen concentrations were measured using the YSI-57 oxygen meter. Photosynthetic active radiation (PAR) was measured using a LiCor LI-1000 datalogger fitted with upwelling and downwelling submersible sensors. Light extinction coefficients were calculated using a standard formula (Wetzel and Likens 2000). Hydrogen ion concentrations (pH) were measured at depths of 0.5 m and 1.0 m using a Fisher Accumet 955 pH meter and Secchi depth transparency was determined using a 25-cm disk.

Ambient N and P nutrient concentrations were separated into three chemical constituents (dissolved organic, dissolved inorganic, and particulate phases) using filtration under low vacuum (<10 mm Hg) pressure (Carrick *et al.* 1993b). Concentrations of dissolved inorganic nutrients were measured on water filtered through a 0.45-µm filter. Dissolved inorganic nitrogen (DIN) included nitrate nitrogen (NO_3-N), nitrite nitrogen (NO_2-N) and ammonium nitrate (NH_4-N), while dissolved inorganic phosphorus was measured as soluble reactive phosphorous (SRP). Total concentrations of N and P were measured on raw lake water, while the N and P retained on the filters were assumed to be in the particulate phase (Carrick *et al.* 1993b). The concentrations of both dissolved organic nitrogen (DON) and phosphorus (DOP) were determined by subtracting dissolved inorganic and particulate fractions from total nutrient concentrations.

All nutrient concentrations were determined using standard colorimetric reactions. Total N was determined by the methods outlined in Solorzano and Sharp (1980). TN standards and urea standards were treated exactly as field samples and read at 543 nm. NH_4 was analyzed by the annotated salicylate method (Joye *et al.* 1996); NO_3-N was analyzed in a similar fashion to TN using cadmium reduction tubes (Solorzano and Sharp 1980); and NO_2-N was analyzed by mixing 5 ml of sample and 0.25 ml of color reagent in a 20 ml scintillation vial (Parsons *et al.* 1984). Standards and samples were allowed to react for 10 minutes before being read on a spectrophotometer at the 543 nm wavelength. TP and SRP were determined using the ammonium molybdate colorimetric reaction; all samples were read on a spectrophotometer at the wavelength of 885 nm (Solorzano and Sharp 1980).

Phytoplankton Biomass and Composition Determinations

Phytoplankton biomass was estimated by determining the concentration of chlorophyll *a* in water samples. Duplicate samples of raw lake water were filtered onto EPM 2000 glass-fiber filters under gravity or low vacuum pressure (<10 mm Hg). Chlorophyll *a* was extracted from the filters using the acetone:DMSO procedure (Shoaf and Lium 1976, Carrick *et al.* 1993a). Extracted pigments (before and after acidification) were then read on a Turner 10-AU fluorometer. Phytoplankton biomass was also estimated by measuring *in vivo* fluorescence (Vincent 1979). Raw lake water was poured into cuvettes, allowed to dark adapt for 20 minutes,

and then measured using a Turner 10-AU fluorometer. *In vivo* fluorescence readings were strongly correlated with extracted chlorophyll *a* concentrations, and thus appear to be reasonable estimates of phytoplankton biomass ($r=0.88$, $p<0.01$, $n=27$). The relative abundance of dominant and subdominant phytoplankton was determined using light microscopy. Lake water samples were thoroughly mixed, and 20-ml aliquots were drawn off into scintillation vials and preserved with a 2% acid Lugol's solution. Aliquoits were dispensed into a Palmer-Maloney counting chambers (0.1 ml) and analyzed using a Zeiss Axioskop Research Microscope. Our taxonomic determinations conform to those outlined in Whitford and Schumacher (1973) and Prescott (1973).

Nutrient Enrichment Bioassays (NEB)

Nutrient enrichment bioassays were conduct on each sampling data (January-June) to evaluate the nutrient status of phytoplankton in the Lake Merced system. The growth of phytoplankton to additions of N and P in a 2 x 2 factorial experiment was assessed to determine their nutritional status (Schelske 1984). Bioassays were initiated by filling 8 clean, acid-washed 500-ml flasks with 400 ml of lake water from the shaded, 20-L carboy that contained raw lake water (including the natural zooplankton assemblage). Two replicate treatment flasks were inoculated with soluble inorganic nitrogen (as $NaNO_3$, final concentration of 300 µg/L), soluble inorganic phosphate (as NaH_2PO_4, 30 µg/L), both N and P, or no nutrients (control). The quantity of nutrients added to bottles was chosen to enrich the phytoplankton with approximately a 2-fold increase in particulate N and P (at the Redfield ratio assuming a carbon to chlorophyll ratio of 50:1; see Carrick *et al.* 1993a); therefore, a similar increase in algal growth was expected (Schelske 1984).

All flasks were then incubated for 5-7 days under light, temperature and day length conditions representative of ambient lake conditions at the time of collection (0.5 m depth). Light levels were set at 100 µEinsteins/m^2/s, while temperatures ranged from 12-19°C. Photoperiods were set at 12:12 light-dark cycle during January to April and at 13:11 light-dark cycle during the May to June period. All experiments were initiated approximately one hour after collection. Phytoplankton biomass was determined daily (~1400 h) from each flask by measuring the *in vivo* fluorescence of subsamples (7-ml aliquoits) as described above. The maximum phytoplankton growth response usually occurred between hours 24-120 during the incubation period. Extracted chlorophyll *a* was measured at the beginning and end of each experiment

Our nutrient enrichment bioassay technique was calibrated against field conditions by conducting simultaneous field and laboratory experiments. In June, a standard laboratory bioassay was set-up and run on samples collected from NLM. In addition to the laboratory bioassay, 8 clean, acid-washed 300-ml BOD bottles were filled with raw lake water also collected from NLM. Replicate bottles were inoculated with N, P, N+P and no nutrients (control) at a final concentration identical to the lab bioassay. The bottles were incubated at a depth of 0.5 m on a floating rack in the lake with light exposures comparable to those used in our laboratory incubations. Samples were drawn off at 24-hour intervals over the same 6-day period as the lab NEB experiment, and the *in situ* samples were processed in the identical manner as those in the laboratory.

Data Analysis

Environmental differences between the two lakes were assessed by direct comparison. A Wilcoxon ranked sum test (two-tailed, $p<0.05$) was used to evaluate paired-wise differences in limnological parameters measured in NLM and SLM. Nine parameters were routinely surveyed over the study period that defined the physical (light penetration, Secchi Depth, temperature), chemical (pH, dissolved oxygen, conductivity, N and P concentrations) and biological (chlorophyll concentration) characteristics of each lake.

Phytoplankton nutrient limitation was determined by comparing the growth response among experimental treatments (Carrick *et al.* 1993b). Exponential growth rates were determined for each nutrient enrichment experiment by calculating the time-dependent change in the *in vivo* fluorescence readings of the phytoplankton in each of the treatment bottles using an exponential growth equation. Growth among lake basins and nutrient treatments was analyzed using a two-way ANOVA. Given the significant interaction term, one-way analysis of variance was applied where the lake sampled was considered a blocked factor (ANOVA, $p<0.05$), and specific treatment effects were examined using a multiple comparisons test for main effects (two tailed with $p<0.05$). Estimates of algal yield for each treatment were calculated as the maximum biomass produced minus the initial biomass. All statistical analyses were performed using StatView 4.0 for the Macintosh.

Results

Limnological Variation

Limnological conditions in the Lake Merced system exhibited some predictable variation over the 6-month study. Water temperatures warmed from 12 to 19°C, over the January-June period, and the water column in both NLM and SLM were either isothermal or weakly stratified on each date ($n=9$). Light penetration (extinction coefficients and Secchi depth) decreased between January and June (Fig. 2). Both phytoplankton biomass and TN concentration showed little variation between January and May, followed by increases in both lakes (Fig. 3). Increases in water column dissolved

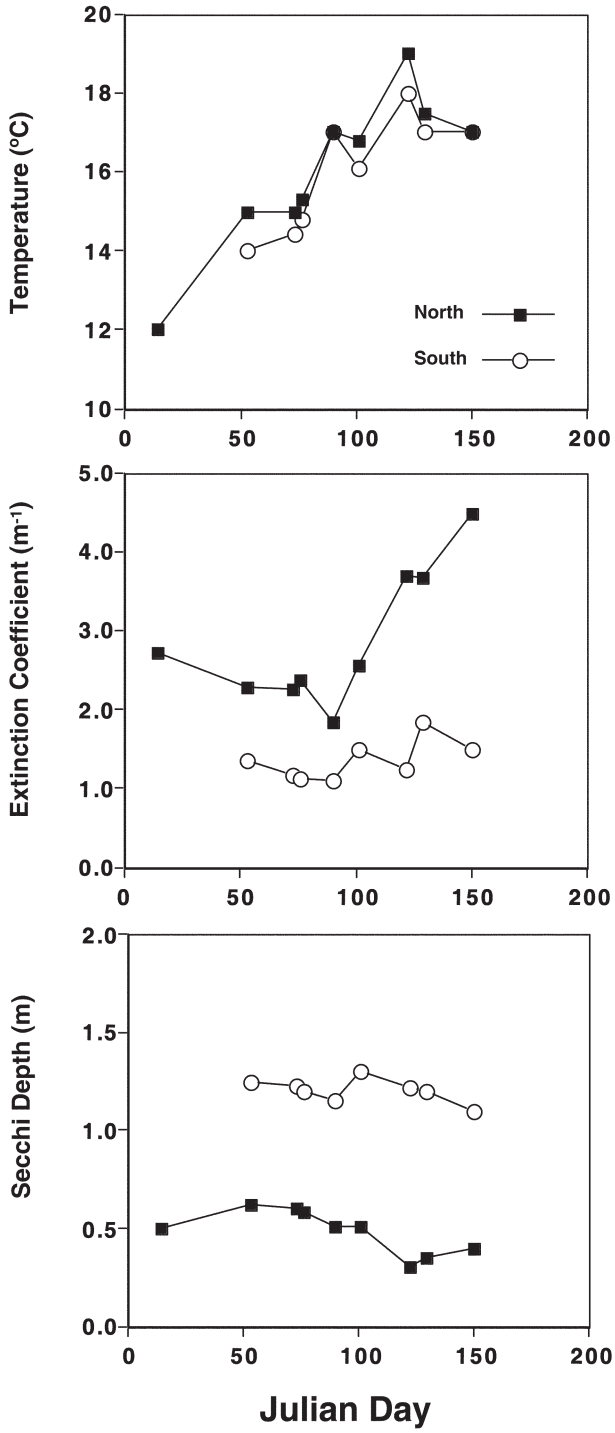

Figure 2.-Physical parameters measured during January-June 1995 in North and South Lake Merced. In most cases, standard error bars were smaller than figure symbols, and thus were not included.

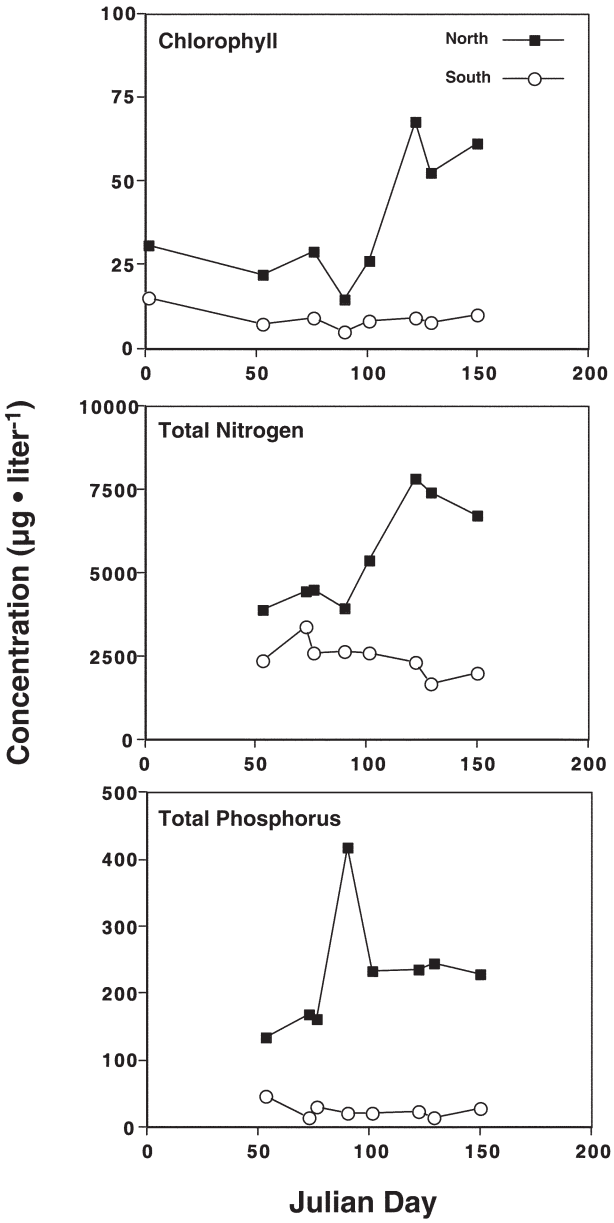

Figure 3.-Nutrient and chlorophyll concentrations measured in North and South Lake Merced. In most cases, standard error bars were smaller than figure symbols, and thus were not included.

Table 1.-Pair-wise comparisons for various biological, chemical and physical variables measured in South and North Lake Merced (Wilcoxon Ranked Sum). Lakes were sampled on nine occasions during January-June, 1995 (n=9 for most). Values are averages for each lake (**p<0.01).

Parameter, units	Lake		Result
	South	North	
Biological			
Chlorophyll *a*, µg/L	8.8 ± 2.9	37.9 ± 19.6	SLM < **NLM****
Chemical			
Conductivity, µ/S/cm	426 ± 24	649 ± 27	SLM < **NLM****
Oxygen, mg/L	7.2 ± 0.9	8.8 ± 1.8	SLM < **NLM****
pH, units	8.1 ± 0.1	8.7 ± 0.3	SLM < **NLM****
Total N, µg/L	2447 ± 515	5519 ± 1595	SLM < **NLM****
Total P, µg/L	25 ± 10	228 ± 87	SLM < **NLM****
Physical			
Temperature, °C	16.0 ± 1.5	16.1 ± 2.0	SLM = NLM
Light Extinction, 1/m	1.4 ± 0.3	2.9 ± 0.9	SLM < **NLM****
Secchi Depth, cm	1.2 ± 0.1	0.5 ± 0.1	**SLM** > NLM**

Table 2.-Distribution of phosphorus and nitrogen as soluble reactive P (SRP) or dissolved inorganic N (DIN as NO_2-N + NO_3-N), dissolved organic P (DOP) or dissolved organic N (DON), particulate P (PP) or particulate N (PN) components for water collected from South and North Lakes Merced on eight dates in 1995.

Lake	Phosphorus				Nitrogen			
Statistic	SRP (%)	DOP (%)	PP (%)	Total (µg/L)	DIN (%)	DON (%)	PN (%)	Total (µg/L)
South Lake								
Average	0.0	38.6	61.4	25	0.2	35.2	60.3	2447
SD	0.0	41.8	41.8	10	0.3	44.8	49.3	515
North Lake								
Average	2.1	34.0	66.0	228	1.8	41.5	56.9	5519
SD	3.9	9.4	9.4	87	1.5	7.0	7.4	1595

Table 3.-Results from two-way analysis of variance (ANOVA) comparing phytoplankton growth response to nutrient enrichment (C, P, N, and N+P treatments) in different lake basins (North and South lake basins) in the Lake Merced ecosystem. Treatments joined by underlining were not significantly different ($p < 0.05$).

Factor	df	F-statistic	p-value	Tukey's Pair-wise Comparison (Least to Greatest)	
Lake Basin	1	558.4	0.0001	South	North
Treatment	3	70.0	0.0001	C P	N N+P
Interaction	3	18.8	0.0001		
Residual	80				

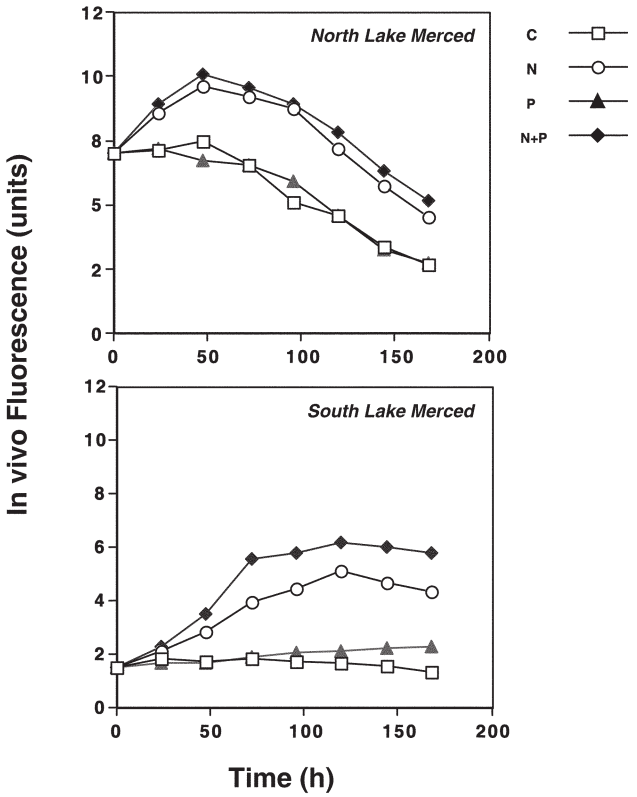

Figure 4.-Typical results for nutrient enrichment bioassays carried out in North and South Lake Merced (February 1995). Time courses of phytoplankton biomass (measured as *in vivo* fluorescence) were the average taken from duplicate bottles receiving one of four nutrient treatments (N, P, N+P, and C=control). Standard error bars were smaller than figure symbols, and thus were not included.

oxygen content and pH were also associated with enhanced phytoplankton biomass.

All parameters tested except temperature were different between basins (Wilcoxon pair-wise comparison, Table 1). Light penetration was 2- 3-fold lower in the NLM compared with that in the SLM (Fig. 2). Average chlorophyll *a* concentrations were significantly higher in NLM (37.9 µg/L) compared with those in the SLM (8.8 µg/L), and this difference was consistent throughout the study (Fig. 3). Distinct chemical differences were also observed between basins, with pH, TP, TN and conductivity estimates all higher in the NLM compared with SLM. A cursory observation of water samples indicated that phytoplankton composition in both basins was dominated by cyanobacteria, while other groups of algae (Bacillariophyta, Chlorophyceae, and Pyrrophyta) were rare.

Nutrient Concentrations

The concentration of total nutrients (TN and TP) was significantly higher in NLM compared to SLM (Table 1). Average TP concentrations in NLM (228 µg/L) were more than 9-fold higher compared with those in the SLM (25 µg/L). TN concentrations in the north lake were 2-fold higher than concentrations in south lake (5,519 and 2,447 µg/L, respectively). Nutrients in both lakes were distributed similarly among particulate, dissolved organic and dissolved inorganic chemical phases (Table 2). The majority of N and P found in each lake basin occurred in the particulate form, while the dissolved organic and inorganic components of N and P were found to make up roughly one third of the total. The organic nutrient fractions did not differ greatly between basins, with both DOP and DON constituting 30-41% of the total. The dissolved inorganic nutrient fractions in both basins were minor; both SRP and DIN constituted <2% of total nutrient concentrations. Ratios for TN and TP were high in both lakes relative to the Redfield ratio of 16:1. We measured molecular N:P ratios for total nutrients of 200 in SLM and 54 in NLM. The average N:P ratio of particulate nutrients indicated clear differences among basins, suggesting that the plankton were more P-limited relative to plankton in SLM (40:1) than in NLM (9:1).

Phytoplankton Response to Nutrient Enrichment

Phytoplankton growth was stimulated by nutrient additions, although the pattern of response differed among lakes (Table 3, Fig. 4). In NLM, phytoplankton showed the greatest growth response to both the N and N+P nutrient treatments, with maximum responses coming 48-72 hours after initial nutrient inoculation (Fig. 4). In SLM, the highest growth was achieved in the N+P addition, while little-to-no growth was observed in control and P treatments; the N treatment in this lake yielded an intermediate response. The growth response measured using *in vivo* fluorescence appeared to be a good proxy for phytoplankton biomass, as evidenced by the strong correspondence with paired extracted chlorophyll *a* values ($r=0.89$, $p<0.001$, $n=27$).

In NLM, nitrogen was considered the primary limiting nutrient for phytoplankton growth because there was no difference between the algal growth responses in the N and N+P enrichments (Table 4). The N and N+P treatments were never statistically significant from one another during this study (one-way ANOVA analysis, $p>0.05$, Table 4). Phosphorus enrichment alone did not stimulate algal growth, and the control and P treatments were never statistically different (Table 4). In contrast, both N and P were considered co-limiting to phytoplankton growth in SLM. The N+P treatment yielded significantly higher algal growth compared with all other treatments ($p<0.05$) on all dates (Table 4). N addition also

Table 4.-Results from one-way analysis of variance comparing average phytoplankton growth rates among nutrient treatments for both South and North Lake Merced (blocked factor). Treatments joined by underlining were not significantly different from one another when assessed using a Tukey's pair-wise comparison ($p < 0.05$). Where ***$p < 0.001$.

Lake	Date	F-statistic	Tukey's Pair-wise Comparison (Least to Greatest)	
South	22 Feb	145.0***	C P	N N+P
	17 Mar	378.0***	C P	N N+P
	11 Apr	2440.6***	C P	N N+P
	9 May	455.0***	C P	N N+P
	1 Jun	244.0***	C P	N N+P
North	4 Jan	387.8***	C P	N+P N
	22 Feb	120.8***	P C	N N+P
	17 Mar	66.2***	C P	N N+P
	11 Apr	218.8***	C P	N+P N
	9 May	53.1***	C P	N N+P
	1 Jun- Lab	85.0***	C P	N N+P
	1 Jun- *In situ*	27.7***	C P	N N+P

yielded significant increases above the controls, although these yields were consistently lower than those produced with N+P enrichment. P additions alone did not stimulate algal growth.

No differences were observed between nutrient bioassays conducted in the laboratory or *in situ* (Table 3). The relative response among all nutrient additions was the same between the laboratory and the *in situ* experiments, as was the ranking of nutrient importance (Table 4). The N and N+P treatments yielded the highest growth in both experiments, although the *in situ* incubation peaked at 72 hours and the lab incubation peaked at 48 hours. The control and P treatments did not stimulate appreciable growth, and these treatments were similar.

Discussion

Limnological Variation within the Lake Merced System

Within the context of our sampling, significant limnological differences were observed between the north and south lakes (see Table 1). Between-lake differences were particularly evident when the trophic state index (based on TP) was calculated for each lake (Carlson 1977). According to this, SLM was classified as mesotrophic-eutrophic and NLM was considered hypereutrophic (TSI values of 51 and 82, respectively). These differences are larger than those measured in earlier studies, where similar physical-chemical characteristics were measured between the two lakes (Adams 1978). We anticipate the differences to continue or perhaps become more pronounced throughout the second half of the growing season that followed the period sampled here, given that maximum temperatures and run-off (from rainfall) in the region occur between the January-June period (Smith *et al.* 1987, Hollibaugh *et al.* 1988).

TP and TN were both strongly correlated with chlorophyll ($r=0.88$, $p<0.001$; $r=0.93$, $p<0.001$, respectively), suggesting that nutrients could regulate phytoplankton biomass throughout the Lake Merced ecosystem (Dillon and Rigler 1974). For instance, total-N was 2-fold higher in NLM compared with SLM, and total-P was nearly 10-fold higher in the north lake. Interestingly, the between-basin nutrient differences bracket the 4-fold difference in chlorophyll that exists between the two lakes (9 versus 38 µg/L, respectively); this pattern seems to indicate that nutrient ratios may play a key role in shaping the nutrient status of the phytoplankton (see below).

The variation in water quality observed in the Lake Merced system is difficult to explain because material loadings to this system have not been measured, and these lakes are thought to be fed from a common aquifer (Fahy 1974, Geo Consultants 1993). Presumably, the system experiences considerable run-off from the highly urbanized watershed that completely encircles these water bodies (see Fig. 1), and the export of nutrients, particularly phosphorus, is enhanced by urban and agricultural land-use (Dillon and Kirchner 1975, Johnson *et al.* 1997). Because the capacity of any lake to assimilate

nutrient loading is a function of size and residence time (Vollenweider 1975, Janus *et al.* 1984), it is possible that some of the variation in water quality among lakes in the Merced system can be attributed to the smaller size and volume of NLM compared with SLM (surface area 0.23 versus 0.75 km^2, respectively; Fig. 1). However, internal nutrient cycling cannot be ruled out as a factor that could augment between-lake differences, particularly if P-rich particles accumulate in lake sediments and are reintroduced into the water column through resuspension (James *et al.* 1997, Havens 1991) or plankton migration (Barbiero and Welch 1992), or other disturbances related to differences in food web structure between lakes (Schindler *et al.* 1997, see below).

Importance of Secondary N-Limitation

The degree of N-limitation exhibited by phytoplankton corresponds with the current trophic state of each lake, and thus may reflect advancing eutrophication within the Lake Merced system. The greater degree of N-limitation in NLM indicates that phytoplankton there were more phosphorus-sufficient relative to SLM. Co-limitation of phytoplankton growth in SLM is consistent with this explanation, given its mesotrophic status. Along these lines, the ratio of particulate N to P in SLM (40:1) falls in the range where co-limitation is likely to occur, whereas the N:P ratio for NLM (9:1) is indicative of N-limited conditions (Tilman 1982). The occurrence and subsequent blooming of heterocystous, N-fixing phytoplankton (*i.e.*, *Anabaena* in April-May 1995) in NLM further indicates N was in short supply relative to conditions in SLM (Smith 1983). Together, these results (ambient nutrients and N:P ratios) correspond well with the nutrient status conditions derived from the nutrient bioassay experiments; the bioassays were further calibrated against field conditions to ensure that environmental realism was achieved through adequate control for key lake conditions (Schelske 1984).

While N can be a primary limiting nutrient to phytoplankton growth in some systems (Howarth 1988, Vitousek and Howarth 1991), phytoplankton growth is often driven toward secondary N-limitation in systems originally P-limited but subsequently exposed to large loads of P (Tilman 1982, Tyrell 1999). This phenomenon is particularly true of shallow, productive lakes like Lake Merced, where vascular plant growth is not prevalent. A review of nutrient limitation studies showed that 38 of 41 shallow lakes were either N or N+P limited (Henry *et al.* 1985), and the general frequency of N-limitation among lakes tended to increase with lake trophic status (Miller *et al.* 1974). In shallow, productive Lakes Apopka and Okeechobee (Florida, USA), excessive P-supply appears to cause phytoplankton growth to be nitrogen limited (Aldridge *et al.* 1993, 1995). Moreover, nutrient dilution experiments confirm that removal of P can relax the degree of secondary N limitation in Lake Apopka (Florida) and illustrate the potential of removing particulate P to remediate overloaded lakes (Carrick *et al.* 1993b).

Secondary limitation has been identified in many temperate lakes as well, where seasonal and historical changes in nutrient limitation correspond with increasing P-loads, thereby enhancing phytoplankton demand for additional nutrients (Lehman and Sandgren 1978, Sommer 1989). In the St. Lawrence Great Lakes, enriched growth eventually drives silicon to seasonal limitation more swiftly and severely in lakes (Erie and Ontario) that receive the highest loads of P (Schelske *et al.* 1986). Thus, the demand for silicon and nitrogen has been used as a measure of relative eutrophication in the Great Lakes system as a whole (Schelske 1975).

Management Implications

Lake Merced system water quality is of considerable regional importance, especially given its multiple use as resource. The lake system is currently used for irrigation, recreational fishing and boating, and emergency water needed to supply the city of San Francisco (Marchi 1998). Some assessments suggest that measures should be taken to improve water quality within this lake system, given that it may be relied upon heavily in the case of a catastrophe (Geo Consultants 1993). The city of San Francisco lies in proximity to the San Andreas geological fault line, one of the most active fault lines in the continental United States (Fahy 1974). Thus, seismic activity could disrupt the regular water supply and cause the city to rely on back up supplies like Lake Merced.

Our work indicates that while water quality is variable within the system, conditions in less productive SLM could likely degrade further toward the highly productive conditions now characteristic of NLM. Moreover, relatively simple water quality parameters (chlorophyll, nutrient concentrations, light penetration) are good indicators of phytoplankton nutritional status in heterogeneous systems like Lake Merced (Havens *et al.* 1999), as confirmed by our bioassay results. Our data indicate that particulate rather than total nutrient concentrations were better indicators of ecosystem trophic status because of the ability of some phytoplankton to maintain considerable internal stores. Particulate nutrients may be good predictors in lakes where P availability is large enough to illicit secondary nutrient limitation (Carrick *et al.* 1993b). Thus, simple measures of water quality in productive lake systems like Merced could be used to set target nutrient loads and evaluate ecosystem change, once calibrated against experimental results to determine nutrient limitation (Havens and Schelske 2001).

Improving the management efforts for the Lake Merced ecosystem would require a more in-depth understanding of the factors that influence water quality. While difficult to identify such factors in a preliminary study, it is likely that

fish stocking led to enrichment in NLM, because fish have been shown to alter nutrient cycling, and in some cases add nutrients (Vanni 2002). Fish (trout) are planted several times during the fishing season (April-June) to support a put-and-take recreational fishery (Lake Merced Fishing Club, personal communication). Nutrient excretion rates of fish can be comparable to external loads in lakes, such as inflow from tributaries (Persson 1997), atmospheric deposition (Wetzel 2001) or watershed inputs (Schaus *et al.* 1997). Thus, the introduction of stocked fish could represent an additional nutrient load to this lake. This condition could account for higher nutrient concentrations in NLM relative to SLM, particularly higher concentrations of P, because many fishes excrete nutrients at low N:P (ratios<20, Vanni 2002).

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References

Adams, T.L. 1978. Phytoplankton populations of Lake Merced including water quality data and physiology of select species. MS thesis, San Francisco State University, 74 p.

Aldridge, F.J., C.L. Schelske and H.J. Carrick. 1993. Nutrient limitation in a hypereutrophic Florida lake. Arch. Hydrobiol. 127:21-37.

Aldridge, F.J., E.J. Phlips and C.L. Schelske. 1995. Nutrient limitation in a hypereutrophic Florida lake. Arch. Hydrobiol. 45:177-190.

Barbeiro, R.P. and E.B. Welch. 1992. Contribution of benthic blue-green algal recruitment of lake populations and phosphorus translocation. Freshw. Biol. 27:249-260.

Bormann, F.H. and G.E. Lichens. 1967. Nutrient cycling. Science 155:424-429.

Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22:361-369.

Carrick, H.J., F.J. Aldridge and C.L. Schelske. 1993a. Wind influences phytoplankton biomass and composition in a shallow, productive lake. Limnol. Oceanogr. 38:1179-1192.

Carrick H.J., C.L. Schelske, F.L. Aldridge and M.F. Coveney. 1993b. Assessment of phytoplankton nutrient limitation in productive waters: Application of dilution bioassays. Can. J. Fish. Aquat. Sci. 50:2208-2221.

Dillon, P.J. and W.B. Kirchner. 1975. The effects of geology and land use on the export of phosphorus from watersheds. Water Res. 9:135-148.

Dillon, P.J. and F.H. Rigler. 1974. The phosphorus-chlorophyll relationship in lakes. Limnol. Oceanogr. 19:767-773.

Elser, J.J., E.R. Marzolf and C.R. Goldman. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. Can. J. Fish. Aquat. Sci. 47:1468-1477.

Fahy, N.E. 1974. Origin of Lake Merced. CGEOA 27:170-174.

Geo Consultants. 1993. Lake Merced Water Resource Planning Study Prepared for: San Francisco Water Department. GRC project no. 1756-000. 73 p.

Gibson, C.E., Y. Wu, S.J. Smith and S.A. Wolfe-Murphy. 1995. Synoptic limnology of a diverse geological region: catchment and water chemistry. Hydrobiologia 306:213-227.

Gutzwiller, K.J. 2002. Applying landscape ecology in biological conservation. Springer Press, New York. 518 p.

Havens, K.E. 1991. Fish-induced sediment resuspension: effects on phytoplankton biomass and community structure in a shallow, hypereutrophic lake. J. Plankton Res. 13:1163-1176.

Havens, K.E., H.J. Carrick, E.F. Lowe and M.F. Coveney. 1999. Contrasting relationships between nutrients, chlorophyll *a*, and Secchi transparency in two shallow subtropical lakes: Lake Okeechobee and Apopka (Florida, USA). Lake and Reserv. Manage. 15(4):298-309.

Havens, K.E. and C.L. Schelske. 2001. The importance of considering biological processes when setting total maximum daily loads (TMDL) for phosphorus in shallow lakes and reservoirs. Env. Pollution 113:1-9.

Hecky, R.E. and P. Kilham. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33:796-822.

Henry, R., K. Hino, J.G. Tundisi and J.S.B. Riberio. 1985. Responses of phytoplankton in Lake Jacaretinga to enrichment with nitrogen and phosphorus in concentrations similar to those of the River Solimoes. Arch. Hydrobiol. 103:453-477.

Hollibaugh, J.T., B.E. Cole, S.J. Dollar, S.W. Hager, W.J. Kimmerer, S. Obrebski, S.V. Smith, M. Valentino, S. Vink and T.W. Walsh. 1988. Tomales Bay, California: A macrocosm for examining biogeochemical coupling at the land-sea interface. EOS 69:843-845.

Howarth, R.W. 1988. Nutrient limitation of net primary productivity in marine ecosystems. Annu. Rev. Ecol. Syst. 19:89-110.

James, R.T., J. Martin, T. Wool and P.F. Wang. 1997. A sediment resuspension and water quality model of Lake Okeechobee. J. Am. Water Res. Assoc. 33:661-680.

Janus, L.L. and R.A. Vollenweider. 1984. Phosphorus residence time in relation to trophic conditions in lakes. Verh. Internat. Verein. Limnol. 22:179-184.

Johnson, L.B., C. Richards, G.E. Host and J.W. Arthur. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. Freshw. Biol. 37:193-208.

Joye, S.B., S.V. Smith, J.T. Hollibaugh and H.W. Paerl. 1996. Estimating denitrification rates in estuarine sediment: A comparison of stochiometric and acetyle based methods. Biogeochemistry 33:197-215.

Kratz, T., K.E. Webster, C.J. Bowser, J.J. Magnuson and B.J. Benson. 1997. The influence of landscape position on lakes in northern Wisconsin. Freshw. Biol. 37:209-217.

Lean, D.R.S. and F.R. Pick. 1981. Photosynthetic response of lake plankton to nutrient enrichment: A test for nutrient enrichment. Limnol. Oceanogr. 26:1001-1019.

Lehman, J.T. and C.D. Sandgren. 1978. Documenting a seasonal change from phosphorus to nitrogen limitation in a small temperate lake, and its impact on the population dynamics of *Asterionella*. Verh. Internat. Verein. Limnol. 20:375-380.

Marchi, A.M. 1998. An evaluation of phytoplankton nutrient limitation in an urbanized lake system. MS thesis, San Francisco State University, 68 p.

McDonnell, M.J. and S.T.A. Pickett. 1993. Humans as components of ecosystems. Springer Verlag Press, New York. 364 p.

Miller, W.E., T.E. Maloney and J.C. Greene. 1974. Algal productivity in 49 lake waters as determined by algal assays. Water Res. 8:667-679.

Paerl, H.W. and N.D. Bowles. 1987. Dilution bioassays: Their application to assessments of nutrient limitation in hypereutrophic waters. Hydrobiologia 146:265-273.

Parsons, T.R., Y. Maita and C.M. Lalli. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon Press: New York. 279 p.

Persson, A. 1997. Phosphorus release by fish in relation to external and internal load in a eutrophic lake. Limnol. Oceanogr. 42:577-583.

Pickett, S.T., W.R., Burch Jr., S.E. Dalton, T.W. Foresman, J.M. Grove and R. Rowntree. 1997. A conceptual framework for the study of human ecosystems in urban areas. Urban Ecosystems 1:185-199.

Prescott, G.W. 1973. Algae of the Western Great Lakes Area. 5th Ed. W.C. Brown, Dubuque. 977 p.

Rhee, G.Y. and I.J. Gotham 1981. The effects of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. Limnol. Oceanogr. 26:649-659.

Schaus, M.H., M.J. Vanni, T.E. Wissing, M.T. Bremigan, J.A. Garvey and R.A. Stein. 1997. Nitrogen and phosphorus excretion by detritivous grizzard shad in a reservoir ecosystem. Limnol. Oceanogr. 42:1386-1397.

Schelske, C.L. 1975. Silica and nitrate depletion as related to rate of eutrophication in Lakes Michigan, Huron, and Superior. P. 277-298. *In* A.D. Hasler (ed.). Ecological Studies, Vol. 10. Springer-Verlag Publ. New York, N.Y.

Schelske, C.L. 1984. *In situ* and natural phytoplankton assemblage bioassays. P 15-47. *In* L.E. Schubert (ed.). Algae as Ecological Indicators. Academic Press (London).

Schelske, C.L., E.F. Stoermer, G.L. Fahnenstiel and M. Haibach. 1986. Phosphorus enrichment, silica utilization, and biogeochemical silica depletion in the Great Lakes. Can. J. Fish. Aquat. Sci. 43:407-415.

Schindler, D.W. 1978. Factors regulating phytoplankton production and standing crop in the worlds freshwaters. Limnol. Oceanogr. 23:478-486.

Schindler, D.W., S.R. Carpenter, J.J. Cole, J.F. Kitchell and M.L. Pace. 1997. Influence of food web structure on carbon exchange between lakes and the atmosphere. Science 277:248-251.

Shoaf, W.T. and B.W. Lium. 1976. Improved extraction of chlorophyll *a* and *b* from algae using dimethyl sulfoxide. Limnol. Oceangr. 21:926-928.

Smith, S.V., W.J. Wiebe, J.T. Hollibaugh, S.J. Dollar, S.W. Hager, B.E. Cole, G.W. Tribble and P.A. Wheeler. 1987. Stoichiometry of C, N, P, and Si fluxes in a temperate-climate embayment. J. Mar. Res. 45:427-460.

Smith, V.H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. Science 221:669-671.

Sommer, U. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypereutrophic lake. Limnol. Oceanogr. 34:1162-1173.

Solorzano, L. and J.H. Sharp. 1980. Determination of total dissolved nitrogen in natural waters. Limnol. Oceanogr. 25:751-754.

Soranno, P.A., K.E. Webster, J.L. Riera, T.K. Kratz, J.S. Baron, P.A. Bukaveckas, G.W. Kling, D.S. White, N. Caine, R.C. Lathrop and P.R. Leavitt. 1999. Spatial variation among lakes within landscapes: Ecological organization along lake chains. Ecosystems 2:395-410.

Thompson, P.A., H.M. Oh and G.Y. Rhee. 1994. Storage of phosphorus in nitrogen-fixing *Anabaena Flos-Aquae* (Cyanophyceae). J. Phycol. 30:267-273.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ. 296 p.

Tyrell, T. 1999. The relative influences of nitrogen and phosphorus on oceanic primary production. Nature 400:525-531.

Vanni, M.J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu. Rev. Ecol. Syst. 33:341-370.

Vincent, W.F. 1979. Mechanisms of rapid photosynthetic adaptation in natural phytoplankton communities. I. Redistribution of excitation energy between photosystems I and II. J. Phycol. 15:429-434.

Vitousek, P.M. and R.W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87-115.

Vollenweider, R.A. 1975. Input-output models with special reference to the phosphorus loading concept in limnology. Schweiz. Zeit. Hydrol. 37:53-84.

Wetzel, R.G. and G.E. Likens. 2000. Limnological methods. Springer Verlag Publ. New York. 429 p.

Wetzel, R.G. 2001. Limnology. 3rd Edition, Academic press, New York, NY, 1006 p.

Whitford, L.A. and G.J. Schumacher. 1973. A manual of the freshwater algae. Sparks Press, Raleigh, NC. 324 p.

Woodward, S.L. 2003. Biomes of earth: terrestrial, aquatic, and human-dominated. Greenwood Press, Westport, Conn. 435 p.