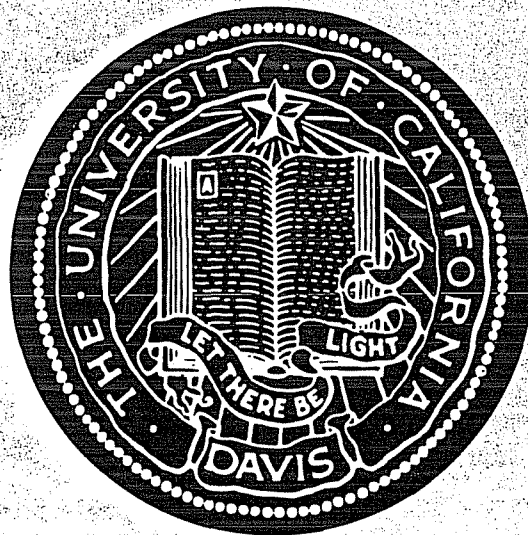# LIMNOLOGY AND NUTRIENT CYCLING IN PYRAMID LAKE, NEVADA 1989-1991

Interim results of an ongoing water quality study
at Pyramid Lake, Nevada
in conjunction with Pyramid lake Fisheries and
the United States Environmental Protection Agency

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Report Summary

In September 1989, the University of California at Davis was contracted by the Pyramid Lake Paiute Tribe - Pyramid Lake Fisheries to conduct a one year study on nutrient cycling and limnology in Pyramid Lake, Nevada. This initial study was part of an intended four year study to develop scientifically sound water quality standards for the lake and the lower section of the Truckee River. Funding for the initial year of the study was provided by a Lake Water Quality Assessment Grant (Section 314(a) of Clean Water Act) from the United States Environmental Protection Agency (US EPA) to the state of Nevada. The remainder of the study is being funded by the US EPA under section 106 of the Clean Water Act. This report summarizes data collected at Pyramid Lake mainly during the second year of the current four year study.

Nutrient concentrations during 1989-1991 were consistent with the previous description of Pyramid Lake as a phosphorus-rich, nitrogen-deficient lake. Dissolved inorganic phosphorus concentration was >47 μg L^{-1} throughout the first two years of the study and generally 60-80 μg L^{-1}. Similarly, dissolved silicate concentration was also relatively high at 75-827 μg L^{-1}. In contrast to silicate and phosphate, dissolved inorganic nitrogen was generally low with concentrations <20 μg L^{-1} throughout spring-fall. The dominant nitrogen pool in Pyramid Lake at all times was dissolved organic nitrogen (DON). Throughout 1989-1991, DON was 532-734 μg L^{-1} accounting for >80% of total nitrogen.

Examination of seasonal variability of nutrients during 1990 in the northern, deep basin revealed two general patterns. Nitrate, phosphate, and silicate concentrations were all maximal during winter mixing and decreased in surface waters during spring. Concurrent

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with the surface depletion of these nutrients was their enrichment in bottom waters presumably through the mineralization of organic matter in the sediments. In contrast to these nutrients, ammonium and total Kjeldahl nitrogen showed localized peaks mainly in surface waters. At all times of year, the dominant nitrogen fraction was dissolved organic nitrogen.

Particulate organic matter (POM) showed seasonal peaks in the spring and summer during 1990-1991. The spring peak coincided with maximal chlorophyll concentration in surface waters following the mixing of nutrients accumulated in the hypolimnion into surface waters. The summer peak coincided with the seasonal maximum in areal phytoplankton production. During the spring, the chemical composition of POM (e.g. C:N:P) suggested balanced growth of phytoplankton under nutrient sufficient conditions. This was one of only two occasions when the phytoplankton assemblage in the lake was not significantly stimulate by nitrogen addition in laboratory bioassays. After this spring bloom in 1990, the elemental C:N ratio of POM continued to increase suggesting nitrogen deficiency. By August 1990, C:N ratio was >18 suggesting extreme nitrogen deficiency.

Dissolved nutrient ratios, laboratory bioassay experiments, and the chemical composition of POM all suggest that nitrogen is the most important nutrient limiting phytoplankton growth. Throughout 1990-1991, the elemental ratio of dissolved inorganic N:P was <2 suggesting strongly that nitrogen should limit growth. Low nitrogen availability was supported by laboratory bioassays in which phytoplankton were stimulated 169, 346, and 365% over controls by the addition of 20, 50, and 100 μg N L^{-1} respectively. The strong positive response to nitrogen addition was only absent during winter overturn when surface nitrate concentrations were high and when nitrogen fixing cyanobacteria were a large component of the phytoplankton assemblage. The chemical composition of POM (e.g. C:N) suggested moderate to extreme nitrogen deficiency throughout summer-fall.

Report Summary

Below normal air temperatures in December 1990 coupled with a 5% surface enrichment of total dissolved solids in surface waters caused winter overturn during winter 1990-1991 to begin in January. This is one month earlier than in 1989-1990. The effect of the early mixing was that the winter-spring phytoplankton bloom stimulated by high nitrate concentration in surface waters peaked in March 1991 as compared with April 1990. One consequence of this change in timing was that more nutrients were stripped from the water column during 1991. In addition to surface waters (0-20 m), nitrate concentration was partially depleted below winter concentrations down to a depth of 60-75 m rather than 30 m observed during 1990. The greater stripping of nutrients during 1991, however, did not lead to higher chlorophyll concentration in surface waters. This lack of increased accumulation of phytoplankton biomass in surface waters during 1991 relative to 1990 can be attributed to a lack of stratification of the water column during the bloom.

In May 1991, an extensive synoptic survey of the lake was done to assess spatial variability of nutrients and particulate matter (POM). Examination of nitrate, ammonium, and silicate distributions in surface waters suggested that nutrient concentrations are higher in shallow regions of the lake and lower in the middle of the deep, northern basin. Chlorophyll, particulate carbon, particulate nitrogen, and particulate phosphorus were also higher in shallow regions. The elevated nutrient concentrations in the north end of the lake suggests that upwelling of deeper waters may be important in this region. Overall, the relative spatial variations in nitrate, ammonium, chlorophyll, and POM across and along the lake were 15-40% suggesting some patchiness in these parameters. The largest variations along transect lines occurred in the deep basin where transects were >10 km in length.

N-fixation was detected in the lake between 21 August and 19 September 1991 with the maximum rate measured on 5 September. The spatial distribution of nitrogen fixation rate was "patchy"; measured rates for individual stations varied by over three orders of magnitude on several sampling dates. Overall, total nitrogen input to Pyramid Lake during 1991 through

fixation was estimated to be 69 metric tones of nitrogen which is a little less than the bloom in 1990 (88 metric tons).

Preliminary data from sediment traps deployed in the middle of the deep basin suggest that seasonal variations in the flux of particles from surface waters was large. The amount of material caught in the surface trap (30 m) during May 1991 was sixfold higher than in September 1991. This suggests that the degree of stratification strongly affects the fraction of surface production exported to deeper waters. The proportion of surface production exported during May and September 1991 were 45 and 9% respectively; the lake was weakly stratified in May and strongly stratified in September. However, part of the higher flux of particulate matter in May can be attributed to inorganic particles. The organic content of sediment trap material was higher in September (30-34%) than in May (14-16%) suggesting a lower relative contribution of inorganic particles during summer.

Truckee River flow was extremely low in 1990-1991 at 5% of mean flow for 1972-1987. Low flow during the first two years of our study reduced nutrient loading to the lake. The input of dissolved nitrogen and phosphorus to Pyramid Lake during 1989-1991 was extremely low at only 4.6 and 1.4 mg m^{-2} yr^{-1} respectively. It also appears that under low flow conditions (<5 m^3 s^{-1}) nitrate may be effectively stripped within the Truckee River during spring-fall. During 1989-1991, nitrate concentration near the mouth of the Truckee was above detection (>0.005 mg L^{-1}) only during December-April.

SECTION 1

Introduction

Background

Water quality monitoring of Pyramid Lake was minimal prior to 1975 and consisted of occasional grab samples and profiles of physicochemical parameters (temperature, salinity, dissolved oxygen, etc.). In 1975, the Bureau of Indian Affairs contracted W.F. Sigler to conduct an ecological study of Pyramid Lake. This initial study, completed in 1978, consisted of sampling 19 stations on a monthly basis including measurement of physicochemical parameters (temperature, dissolved oxygen, turbidity, pH, and conductivity), major ions (chloride, sulfate, potassium, calcium, and magnesium), and nutrients (total Kjeldahl nitrogen, ammonium, nitrate, nitrite, total phosphorus, orthophosphorus, and silica).

Following this initial study, D.L. Galat continued routine monitoring of the lake between 1976-1979 as part of his Doctoral research. D.L. Galat and co-workers also conducted a comprehensive base-line limnological study including algal primary productivity, algal species composition, zooplankton species composition, periphyton and macrophyte growth, nitrogen fixation, microbial standing crop, and a carbon budget (Galat et al. 1981; Hamilton-Galat and Galat 1983; Horne and Galat 1985; Galat 1986).

Pyramid Lake Fisheries (PLF), the Pyramid Lake Paiute Indian Tribe's resource management agency, began a water quality sampling program in 1985. In this program samples were collected quarterly at three stations (southern, shallow basin; near Anaho Island; and northern, deep basin). Monitoring included Hydrolab profiles of temperature, dissolved

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oxygen, pH, and conductivity, measurement of chlorophyll a as an indicator of phytoplankton biomass, and nutrient analyses for total Kjeldahl nitrogen, nitrate, nitrite, ammonium, soluble reactive phosphorus, total soluble phosphorus, total reactive phosphorus, and total phosphorus. Generally, samples were collected at the station in the northern basin on a monthly basis.

In September 1989, PLF contracted the Limnological Research Group at University of California-Davis (UCD) to conduct a four year study to determine the potential effects of nutrient loading to Pyramid Lake. The initial year (1 September 1989 to 31 August 1990) of the study was supported by a Section 314(a) grant to the State of Nevada. Funding for the second year of the study was provided by the United States Environmental Protection Agency under Section 106 of the Clean Water Act to the Pyramid Lake Paiute Tribe.

The basic monitoring program established by PLF in 1985 was modified in 1989 to provide better information for nutrient modeling. The station west of Anaho Island was dropped in favor of collecting more samples at the remaining two stations (e.g. depths sampled in the deep, northern basin was increased from four to 11). In addition, biweekly synoptic sampling of eight stations (including the two index stations) along a north-south transect was initiated during May-October.

Limnological research during the PLF-UCD study was also expanded to routinely examine phytoplankton production, biomass, species composition, and growth potential. In addition to basic monitoring samples, particulate matter was collected from each depth during monthly samplings at the two index stations for the determination of particulate carbon, nitrogen, and phosphorus. Sampling depths for the measurement of chlorophyll and phytoplankton species composition were established in surface waters (0-30 m) at 10 and 6 depths in the deep and shallow basins respectively. Concurrent with the collection of these samples was the measurement of phytoplankton production at the deep-basin station using water collected at the 10 depths sampled for chlorophyll. During May-October, algal growth potential (AGP) was determined in the laboratory monthly using water collected at the depth

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of expected maximum phytoplankton biomass at the deep-basin station. Growth potential was determined by comparing the response of the natural phytoplankton assemblage to additions of nitrogen, phosphorus, and iron. AGP was determined bi-monthly October-May.

The goals of the PLF-UCD cooperative project are: (1) to develop sound water quality standards for Pyramid Lake and the portion of the lower Truckee River located on the Paiute Reservation, (2) to obtain a better understanding of the limnological processes which operate to determine water quality (with particular emphasis on the coupling of external and internal nutrient cycling), and (3) to increase the institutional capability of the Pyramid Lake Paiute Tribe - Pyramid Lake Fisheries to monitor effectively water quality conditions. These goals will be reached by using extensive monitoring data, specific limnological research, and mathematical modeling techniques. To obtain a more comprehensive view of lake dynamics, present observations will be coupled with historic data. Lebo et al. (1991) summarizes preliminary results for the first year of the study (1989-1990).

Project Activities

YEAR 1 (1 September 1989 to 31 August 1990)

During the first year of the study, the basic monitoring program established by Pyramid Lake Fisheries (PLF) in 1985 was expanded to provide more information on spatial and seasonal variations in nutrient concentrations and physicochemical parameters (described in Section 2). Algal growth potential experiments were conducted, and these experiments supported nitrogen limitation of phytoplankton in Pyramid Lake. During August-September 1990, the rate of nitrogen fixation was estimated during a period when the lake phytoplankton assemblage included blue-green algae. Data collected during the initial year of the study were used to estimate nutrient release from bottom sediments and water column remineralization.

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YEAR 2 (1 September 1990 to 31 August 1991)

Routine monitoring was continued for water quality. Extensive synoptic sampling of the whole lake was conducted during May 1991 to examine spatial variability of temperature, conductivity, dissolved oxygen, nutrients, and particulate matter. A preliminary survey of the lake revealed low aquatic macrophytes. Therefore, more extensive surveys were not conducted. Data collected for the Lower Truckee River for 1989-1991 were examined and summarized.

Much of the work during the second year focused on the fate of primary production. Sediment traps were deployed at the deep basin index station at three depths for a month in April and August 1991. Sediment cores were collected from both the deep and shallow basins for analysis of pore water chemistry and solid phase composition. Using these sediment cores, historical lake water quality conditions will be examined.

The final objective for the second year of the project was to form a conceptual model describing nutrient and production relationships in the lake. Since river inflow and nitrogen fixation were low during 1989-1991, the data for the first two years of the study provided valuable information about internal nutrient cycling in Pyramid Lake.

Future Work

YEAR 3 (1 September 1991 to 31 August 1992)

Routine water quality sampling and algal growth potential assays will continue. Modeling will focus on control of production by two distinct algae assemblages: (1) diatom and green algae and (2) blue-green algae. These two algal groups are treated separately since previous research at Pyramid Lake and in other systems suggests that the processes controlling production of each group are different. A considerable effort will focus on the

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issue of nitrogen regeneration and its importance to annual production. Nitrogen fixation will be estimated throughout summer-fall when phytoplankton capable of fixation are present in the lake. If a large bloom occurs, experiments examining controls of blue-green algal production will be conducted. A preliminary nutrient budget will be constructed and the importance of in-basin nutrient loading will be evaluated.

YEAR 4 (1 September 1992 to 31 August 1993)

The routine water quality sampling and algal growth potential assays will continue. Most of the effort during this year will be directed toward development of water quality standards for Pyramid Lake and the Lower Truckee River. A final project report will be produced which presents these water quality standards and provides a comprehensive presentation and discussion of all monitoring and research conducted during the entire four year study. Empirical and mechanistic techniques will be used to: (1) predict changes in Pyramid Lake water chemistry as a function of both external and internal nutrient sources, (2) relate in-lake nutrient levels to phytoplankton productivity, and (3) determine the influence of any change in productivity on beneficial uses of the lake. Of particular interest is the impact of increased nutrient loading on the magnitude and distribution of hypolimnetic oxygen, vis-a-vis, impacts on fish populations.

SECTION 2

Methods and Study Site

Description of Study Site

Pyramid Lake is located in northwest Nevada entirely within the boundaries of the Pyramid Lake Paiute Indian Reservation (Fig. 2-1). It has a surface area of 446 km^2, has a volume of 26.4 km^3, and is a slightly saline (4.0-4.2 ppt), warm monomictic lake (Galat 1986). The lake has an average depth of 59 m and a maximum depth of 103 m. It is 40 km long, and its width varies from 16 km in the north to 6.5 km in the south. There are two basins in the lake: a smaller (90 km^2), shallower (<50 m) basin in the south and a larger (356 km^2), deeper (maximum depth 103 m) basin in the north.

The principal ions contributing to salinity in Pyramid Lake are sodium, chloride, bicarbonate-carbonate, and sulfate. The lake is highly alkaline at 23.0-23.6 meq L^{-1}, and pH is generally 9.1-9.3 (Galat et al. 1981). At all times, surface waters are supersaturated with respect to aragonite (Galat and Jacobsen 1985). Pyramid Lake exhibits moderately high epilimnetic phosphorus concentrations (soluble reactive phosphorus >50 µg L^{-1}; total phosphorus >70 µg L^{-1}) and low epilimnetic nitrogen concentrations (dissolved inorganic nitrogen <100 µg L^{-1}; total nitrogen <1000 µg L^{-1}) (Galat and Verdin 1988).

The headwaters of the only permanent water source to Pyramid Lake, Truckee River, arise in the Sierra Nevada mountains of eastern California and western Nevada (Fig. 2-1). Its mainstream begins at the outlet of oligotrophic Lake Tahoe and descends 715 m in a generally northeasterly direction for 192 km until forming a delta at the south end of Pyramid
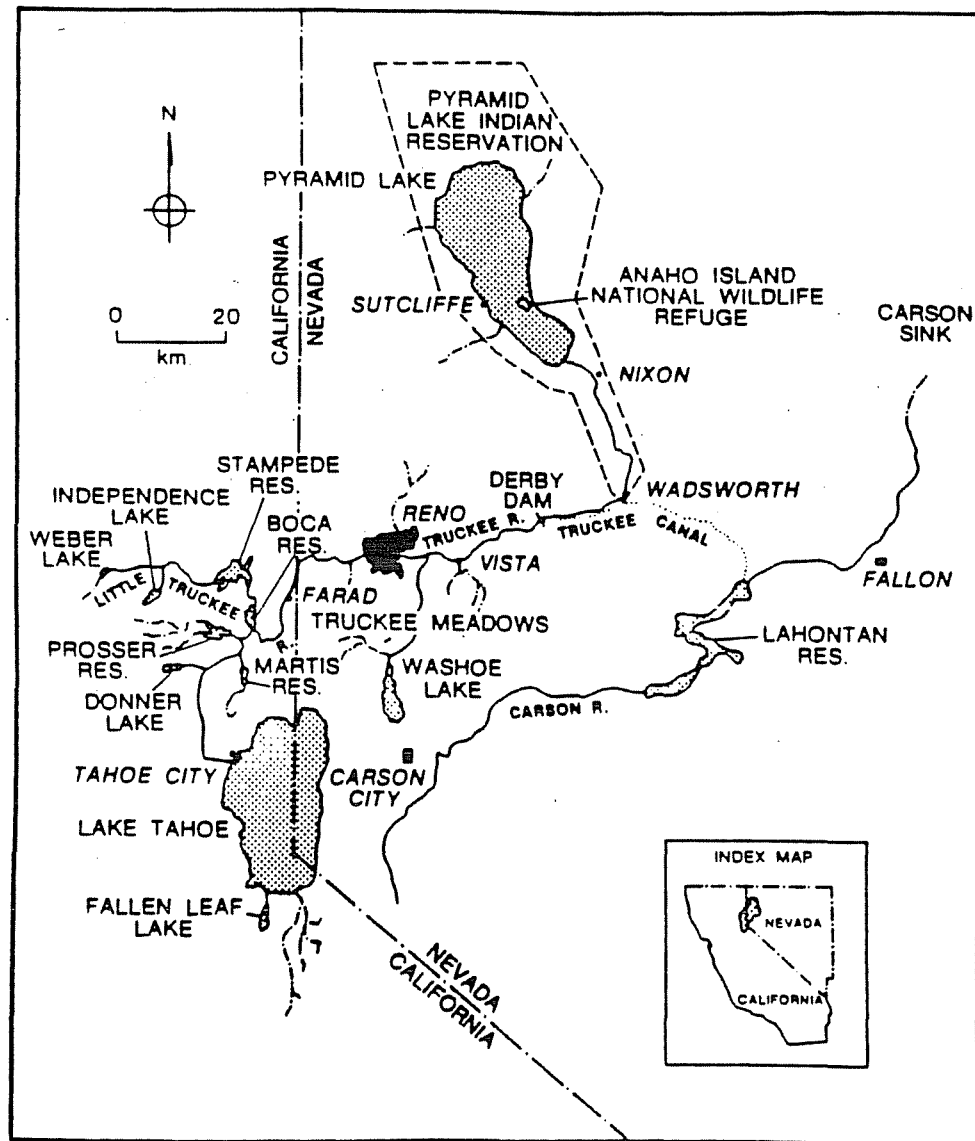
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Figure 2-1. Map of Pyramid Lake Watershed (Galat 1990).

Methods and Study Site

Lake. The Truckee River passes through the City of Reno en route to Pyramid Lake, and effluent from the Reno-Sparks wastewater treatment facility is discharged into the river. Currently, this effluent receives tertiary treatment for both nitrogen and phosphorus. Since 1973, water discharge to Pyramid Lake from the Truckee River has ranged from 0.4 (1977) to 24.2 (1983) 10^8 m^3 yr^{-1}. During the same period, loading of total phosphorus and total nitrogen to the lake have ranged from 28-882 mg P m^{-2} yr^{-1} and 126-3775 mg N m^{-2} yr^{-1} (Galat 1990).

Compared to other saline lakes, Pyramid is oligotrophic with mean chlorophyll a concentration of 3.3 μg L^{-1} (Galat et al. 1981). Phytoplankton production accounts for a majority of the carbon budget contributing approximately 83% of annual carbon inputs to the lake (Galat 1986). The phytoplankton assemblage is generally dominated by diatoms during the early spring, a mixed assemblage of diatoms and green algae during the summer, and in certain years blooms of *Nodularia spumigena* during summer-fall (Galat et al. 1981; Galat and Verdin 1989).

A community of endemic Lahontan Basin fish occurs in Pyramid Lake. One species, the cui-ui (*Chasmistes cujus*), is listed by the US Department of the Interior as endangered while another, the Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*), which was reintroduced after its disappeared from the lake, supports a nationally recognized trophy sport fishery which provides the Pyramid Lake Paiute Tribe with significant income and employment. Shifts in community structure of the zooplankton forage base, direct toxicity and hypolimnetic oxygen depletion are potential negative consequences affecting the Pyramid Lake fish community if frequency, magnitude or duration of *N. spumigena* blooms increase (Galat and Verdin 1989).

Methods and Study Site

Sampling program

Previous Sampling Program

The previous program at Lake Pyramid included the collection of samples at selected locations at quarterly or monthly intervals. From 1985-1989 (prior to the involvement of the U.C. Davis Limnology Group), water samples were collected quarterly at three stations (near the Truckee River inflow, west of Anaho Island, and at the deepest point in the lake). In addition to quarterly samples, efforts were made to take monthly samples at the deep station.

At each station, vertical profiles of temperature, dissolved oxygen, electrical conductivity, and pH were measured and discrete samples were collected for chemical analyses. The number of discrete samples for chemical analyses taken at each station depended on the season. During summer stratification, water was taken at the surface, in the epilimnion, near the thermocline, in the hypolimnion, and near the bottom. When the lake was mixed (January-March), sampling was reduced to surface, mid-depth, and deep. The following chemical parameters were measured: nitrate, nitrite, ammonium, total Kjeldahl nitrogen, total phosphorus, total dissolved phosphorus, dissolved inorganic phosphorus, and phytoplankton chlorophyll (only at surface).

Modifications to Routine Sampling

The routine sampling program, 1985-1989, was expanded in September 1989 and now includes the following features:

a) The sampling station west of Anaho Island is no longer sampled and data collection at the deep (station 96) and shallow (station 92) stations is greatly expanded (Fig. 2-2).

b)   Samples at these two locations are taken at least monthly.

c)   Complete water column profiles for light penetration (photosynthetically active radiation) are taken to a depth of approximately 0.1% of the surface light intensity with measurements every meter.

d)   Complete water column profiles for temperature, pH, dissolved oxygen, and electrical conductivity are taken with measurements every 1-5 m.

e)   At the deep station (bottom depth = 103 m), discrete water samples are collected at 11 depths: 0, 5, 10, 20, 30, 45, 60, 75, 90, 100, and 102 m. At the shallow station (bottom depth = 46 m), discrete water samples are collected at six depths: 0, 10, 20, 30, 40, and 45 m.

f)   Each of these discrete water samples is analyzed for the following water quality parameters: nitrate+nitrite, ammonium, total Kjeldahl nitrogen (TKN), particulate carbon and nitrogen, total phosphorus, total reactive phosphorus, dissolved reactive phosphorus,
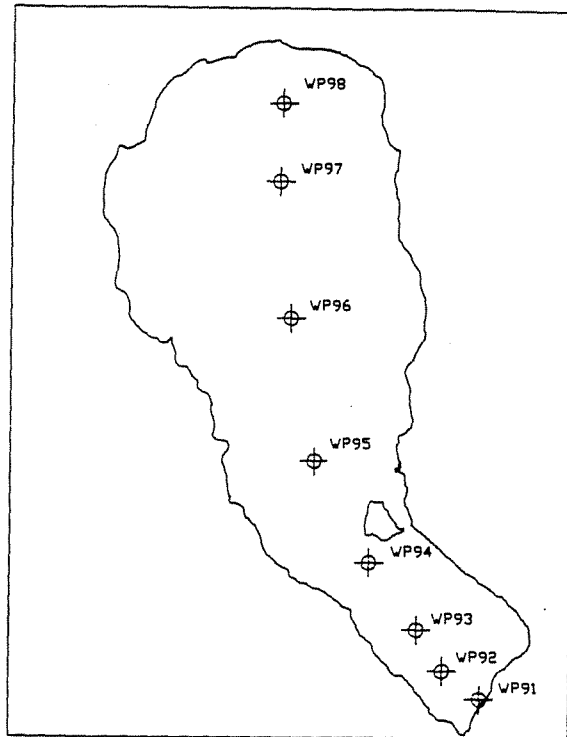

Figure 2-2. Map of Pyramid Lake showing station locations for bi-weekly synoptic samplings. Monthly index stations are 92 and 96.

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particulate phosphorus, silicon, and total reactive iron. Dissolved organic nitrogen is calculated by subtracting particulate nitrogen and ammonium from TKN.

g)   At the deep station (station 96), ^{14}C-primary productivity is measured monthly at 0, 2.5, 5, 7.5, 10, 12.5, 15, 20, 25, and 30 m (maximum depth of euphotic zone). At each of these depths, a subsample is taken for chlorophyll $\underline{a}$ and phaeopigments, dominant phytoplankton species, and alkalinity (required for productivity calculations).

h)   At the shallow station (station 92), samples are taken for chlorophyll and phaeopigments at 0, 5, 10, 15, 20, and 25 m. A composite sample from all these depths is collected for dominant phytoplankton species.

i)   Vertical tows of surface waters are made at each station for zooplankton species counts.

j)   Algal growth potential bioassays are run at least bimonthly and often on a monthly schedule.

k)   During the biologically active months (May-November), eight stations along a transect are sampled twice each month (Fig. 2-2). At each station, composite samples are collected from the upper 0-5 m (0, 2.5, 5 m) for nutrient analyses. Additional samples are collected at stations 92 and 96. Vertical profiles of dissolved oxygen, temperature, and electrical conductivity are measured as well as secchi depth.

Methods and Study Site

Sample Collection and Analyses

Temperature, conductivity, pH, and dissolved oxygen are measured *in situ* with a Hydrolab Surveyor II. Dissolved solids (TDS) and salinity are estimated from measured conductivity. Salinity is calculated using the 5th order polynomial for seawater. Since the ionic composition of Pyramid Lake is different from seawater (Galat et al. 1981), salinity values are only approximate. TDS is calculated using an empirically derived relationship between TDS and conductivity for Pyramid Lake (Lockheed Ocean Science Laboratory unpubl.). Light profiles are measured using a LI-COR 1925A underwater Quantum Sensor (2π) with a surface reference cell.

Light extinction coefficients are calculated using measured light profiles by plotting the natural logarithm of light intensity/surface intensity versus depth. The slope of this line (determined through linear regression) is the extinction coefficient.

Discrete water samples are collected with Van Dorn samplers lowered on either a calibrated hand line or a hydrowire. Sonar is used to locate desired sampling depths.

Nutrient concentrations are measured using standard colorimetric methods with the absorbances determined spectrophotometrically. Table 2-1 lists the limits of detection (LOD) for each analysis for Pyramid Lake Fisheries (PLF) and U.C. Davis (UCD) laboratories. Ammonia is measured in unfiltered samples by a modified indophenol reaction method (Solorzano 1969; Liddicoat et al. 1975). Nitrate concentration is also determined in unfiltered samples using a modified cadmium reduction method (Jones 1984). Total and dissolved reactive phosphorus are measured as soluble reactive phosphorus (SRP, Strickland and Parsons 1972) in unfiltered samples and 0.45 μm filtrate respectively. Phosphorus methods are modified to remove arsenic interference (Johnson 1971). Silicate is measured as reactive silicate in 0.45 μm filtrate (Strickland and Parsons 1972).

Total nitrogen is determined as the sum of total Kjeldahl nitrogen (TKN) and nitrate. TKN is determined by mineralizing organic nitrogen compounds in an unfiltered sample with sulfuric acid in the presence of mercuric sulfate (catalyst) and potassium sulfate. Digested nitrogen is measured as ammonia. Dissolved organic nitrogen is calculated from TKN by subtracting particulate nitrogen (see below) and ammonia.

Table 2-1. Limit of detection (LOD) for nutrient analyses at Pyramid Lake Fisheries (PLF) and U.C. Davis (UCD) laboratories. Values are in μg L^{-1}.

Parameter	PLF	UCD
Nitrate	1.7	1.0
Ammonium	3.3	2.1
Total Kjeldahl Nitrogen	15	--
Dissolved Reactive Phosphorus	2.0	--
Total Reactive Phosphorus	--	0.9
Total Phosphorus	1.8	0.8
Silicate	51	--
Total Reactive Iron	--	1.2

Total phosphorus (TP) is determined as SRP after acid-persulfate digestion of unfiltered samples (Strickland and Parsons 1972).

Total reactive iron is measured by a modified ferrozine method after acid hydrolysis with $NH_2OH \cdot HCl$ of a raw water sample (Stookey 1970).

Biological Parameters

Particulate matter is collected on precombusted GF/F filters for analysis of chlorophyll, particulate carbon (PC) and nitrogen (PN), and particulate phosphorus (PP). Chlorophyll a, corrected for phaeopigments, is measured fluorometrically after extraction into cold 90% acetone (Strickland and Parsons 1972). PC and PN are measured with a Perkin Elmer model 2400 CHN analyzer. PP is measured by high temperature combustion (450°C) followed by acid hydrolysis (Solorzano and Sharp 1980). The water filtered for PC/PN and PP is prescreened through 80 μm Nitex mesh to remove zooplankton and large debris.

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Therefore, concentrations of particulate carbon, nitrogen, and phosphorus do not include larger phytoplankton cells such as *Botryococcus sp.* or *Nodularia spumigena*. The LOD for PC, PN, and PP are 10 µg C, 2 µg N, and 0.02 µg P respectively.

Primary productivity (PPr) is estimated by the incorporation of ^{14}C-HCO_3^- into particulate matter during *in situ* incubations under natural light conditions (Goldman 1960). Since Wetzel and Likens (1979) caution the use of the light-dark bottle oxygen technique when PPr is <10 µg-C L^{-1} hr^{-1} (Pyramid Lake is generally 1-10 µg-C L^{-1} hr^{-1}), we use the more sensitive ^{14}C methodology. To estimate PPr, water is dispensed into 125 mL quartz bottles, incubated at the depth of collection for 4 hours at mid-day, and then filtered onto GF/F filters. Residual bicarbonate is driven off by acidifying filters with 1 mL of 0.5 N HCl for 12 hours (Jellison and Melack 1988). Areal production is calculated by integrating production over the ten depth intervals sampled. Daily production is calculated from areal production by dividing by the fraction of total daily insolation during the incubation period.

Algal growth potential (AGP) bioassays are commonly used to evaluate the response of phytoplankton to changes in nutrient supply (US EPA 1973; Maloney and Miller 1975) and are used here to evaluate potential nutrient limitation of phytoplankton growth. Rather than employing the standard US EPA 'Algal Assay Procedure: Bottle Test' (US EPA 1978) where an inoculum of a single test species such as *Selenastrum capricornutum* is used, our assays use the phytoplankton communities present in Pyramid Lake. In this manner, our results are directly applicable to evaluating nutrient controls of natural populations in Pyramid Lake.

AGP bioassays are conducted on a monthly schedule whenever possible. For each assay, sample water is collected at 5 m in the deep basin (station 96) and brought back to UCD for processing. Experiments are run in a random block design (6 treatments x 3 replicates) at ambient lake temperature. Treatment flasks are inoculated with 450 ml of prescreened (80 µm) lake water, and nutrients are added to 5 sets of flasks leaving one set as controls. Samples for chlorophyll and nutrients are taken at the beginning and end of 5-6 day

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incubations. Final chlorophyll concentration in treatments is compared with controls to determine whether there was a stimulation of phytoplankton biomass.

Sediment Samples

Sinking particulate organic matter (POM) is collected in sediment traps deployed at three depths at the index station (96) in the deep basin. The traps are located to catch POM sinking from surface waters (30 m), reaching the mid-hypolimnion (50 m), and material reaching bottom waters (80 m). Following the recommendations of Bloesch and Burns (1980), the aspect ratio (height/width) of traps is 10 using a diameter of 10 cm and POM in traps is not preserved. Tubes are deployed in triplicate at each depth. To sample traps, water in the upper 90 cm of each tube is drained off without disturbing material in the bottom, and the remaining volume (approximately 650 ml) is retained for analysis. POM is concentrated by centrifugation at 10,000 RPM and dried at 60°C for several days.

Sediment cores were obtained using a gravity corer at the index station in the deep basin (96) and from station 93 in the middle of the shallow basin. Cores were sectioned at 1-2 cm intervals. Pore water was obtained from core subsections through centrifugation within a few hours. Core material was stored wet at 4°C for several days before being dried at 60°C.

Sediment trap samples are analyzed for total weight, organic content, carbonate content, and elemental composition (e.g. PC, PN, and PP). Methods for sediment elemental composition are given above. Total mass collected in sediment traps is determined by filtering 5-20 ml of homogenized sediment trap solution onto pre-weighed GF/F filters. These filters are dried for several days (60°C) and reweighed to determine mass. The carbonate content of sediment trap material is determined by filtering 5-20 ml of solution onto pre-weighed GF/F filters as with total weight. Filters are then soaked for 15 minutes in 1 N HCl, dried for several days at 60°C, and reweighed. The organic content of sediment trap

material is determined by heating samples used for total mass and carbonate content at 500°C for >12 hours. The filters are then reweighed to determine Loss on Ignition (LOI).

Methods used to determine the organic and carbonate content of sediments are similar to those used on sediment trap material. For organic content, LOI is determined for a known weight of sediment. The carbonate content of sediment is determined by soaking a known weight of sediment in 1 N HCl for 2 hours. The solution is then filtered onto a pre-weighed GF/F filter, dried, and reweighed.

Quality Control

The precision of measurements at Pyramid Lake Fisheries (PLF) and U.C. Davis (UCD) laboratories is evaluated on a regular basis. For colorimetric analyses, concentrations for each parameter are determined from a standard curve with at least three concentrations in addition to a blank. All standards and blanks are run in duplicate. Problems related to sample matrixes are evaluated by spiking a sample from each station with a known concentration and comparing the concentration calculated from the standard curve with the expected concentration. The precision of each analysis is evaluated by analyzing laboratory splits (i.e. aliquots from the same sample bottle) on >30% of field samples. For particulate analyses, filter blanks are run with each set of samples to account for any contamination during handling.

The accuracy of analyses at both laboratories are evaluated by blind internal test samples and participation in the testing program of the United States Geological Survey.

The results of quality control procedures for the current project year are summarized in a separate report released in December 1991. Information is given on parameters derived from standard curves and spike recoveries for analyses performed at both UCD and PLF

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laboratories. Included is an evaluation of the status and reliability of the different analyses
performed at both labs.

SECTION 3

Meteorological and General Information

Lake Elevation

The surface elevation of Pyramid Lake is affected by the balance between Truckee River inflow and evaporative losses (Milne 1987). After the construction of Derby Dam in 1905, transbasin water diversions began from the Truckee River to Lahonton Reservoir for the Newlands Irrigation Reclamation Project (Galat et al. 1981). This diversion of Truckee River water had a profound affect on the water balance of Pyramid Lake. With drastically reduced freshwater inputs, the elevation of the lake surface decreased rapidly. Figure 3-1 shows the elevation of the surface of Pyramid Lake over the past century (USGS, Carson City, Nevada). Following the closure of Derby Dam, the surface of Pyramid Lake dropped almost 90 vertical feet over six decades to a minimum elevation of approximately 3784 feet (1153 m) in 1967. Some of the water lost over this period was replenished during the mid-1980s due to heavy precipitation in the mountains; lake elevation increasing nearly 30 feet during 1983-1986.

Since the temporary water gain of the mid-1980s, drought has afflicted the California-Nevada region causing the elevation of Pyramid Lake to once again decrease. Figure 3-2 shows lake elevation during the past two decades. Lake elevation reached a relative maximum of 3817 feet (1163 m) above sea level in June 1986 before continuing to decline. By July 1991, the elevation of the lake surface was 3802 feet (1159 m) above sea level reflecting the lack of substantial freshwater input over the past five years. The decrease in elevation during the study period to date (October 1989 - July 1991) has been approximately 5 feet (1.5 m). Discussion of Truckee River flow is given in Section 10.
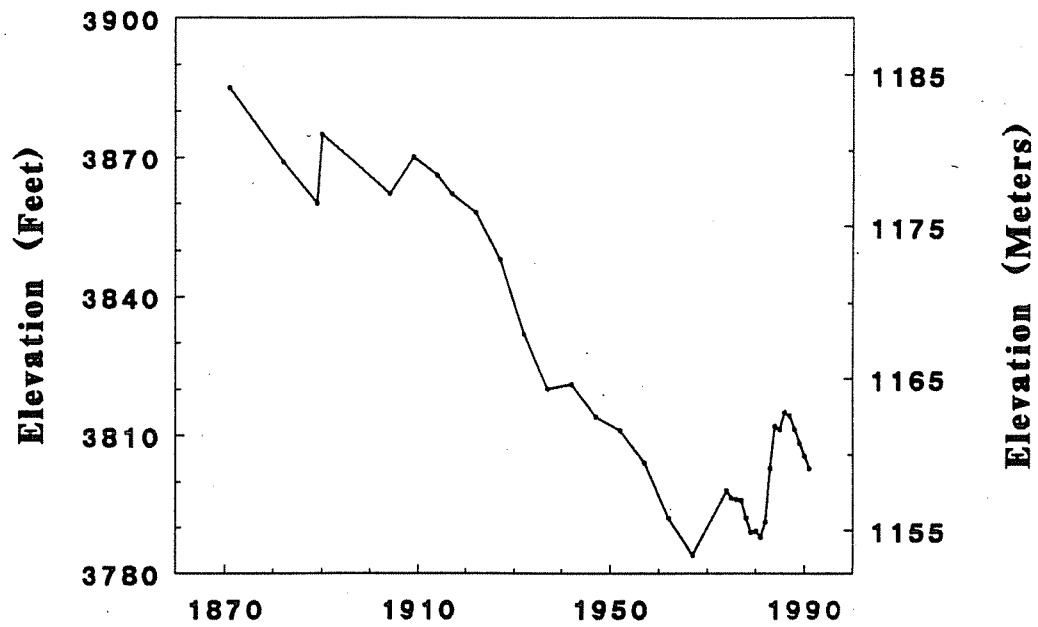
18

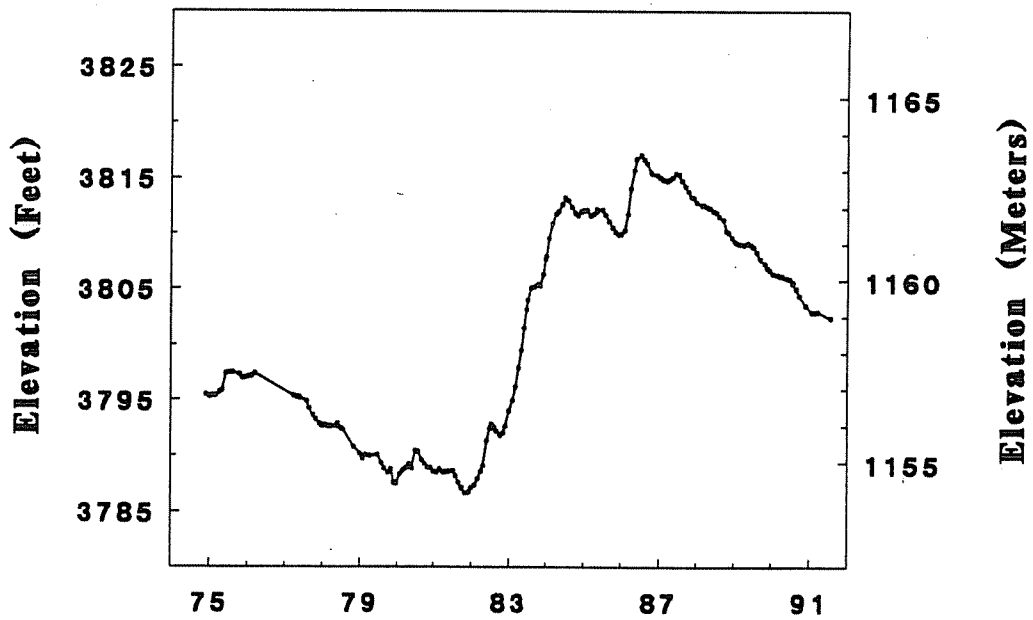Figure 3-1. Surface elevation of Pyramid Lake plotted for 1870-present.

Figure 3-2. Surface elevation of Pyramid Lake plotted for 1974-present.

General Information

Air and Water Temperatures

Seasonal variations in temperatures were typical for the Northern Hemisphere. Figure 3-3 shows mean monthly maximum and minimum air temperatures recorded at Pyramid Lake 1986-1991. As expected, highest mean maximum temperature of 30-31°C occurred during summer in July-August. The lowest temperatures occurred in winter when mean monthly minima were -2 to -3°C during January-February. Daily maximum and minimum temperatures during 1989-1991 are shown in Figure 3-4. The range of values for the study period were similar to the monthly means that were shown in Figure 3-3 with mean high temperatures of 27-38°C during July-August of 1990 and 1991. One notable exception between the monthly means presented in Figure 3-3 and daily means for 1989-1991 was the colder temperatures recorded during December 1990. On several days in December 1990, maximum temperatures were only -15°C which was much colder than mean values.

Surface water temperatures reflected the seasonal changes in air temperature. Figure 3-5 shows surface water temperature (1-2 m) for October 1989 through July 1991 for both index stations (92 and 96) plotted against time of year. As with air temperature, maximum values occurred during the summer with surface waters >20°C throughout July-September. Conversely, minimum temperatures occurred in January-March when values were 6±1°C. Figure 3-6 shows the same data plotted against date. Data for both 1989-1990 and 1990-1991 showed the same general pattern. Indeed, seasonal variations in surface water temperature during 1986-1991 (not shown) were similar during all years. One difference between winter 1989-1990 and 1990-1991 was a longer duration of minimum surface temperature during the latter year. Because of colder air temperatures during December 1990 (Fig. 3-4), surface waters reached a minimum temperature earlier in the winter. Minimum temperature for 1990-1991 occurred in January-March compared with February-March during 1989-1990.
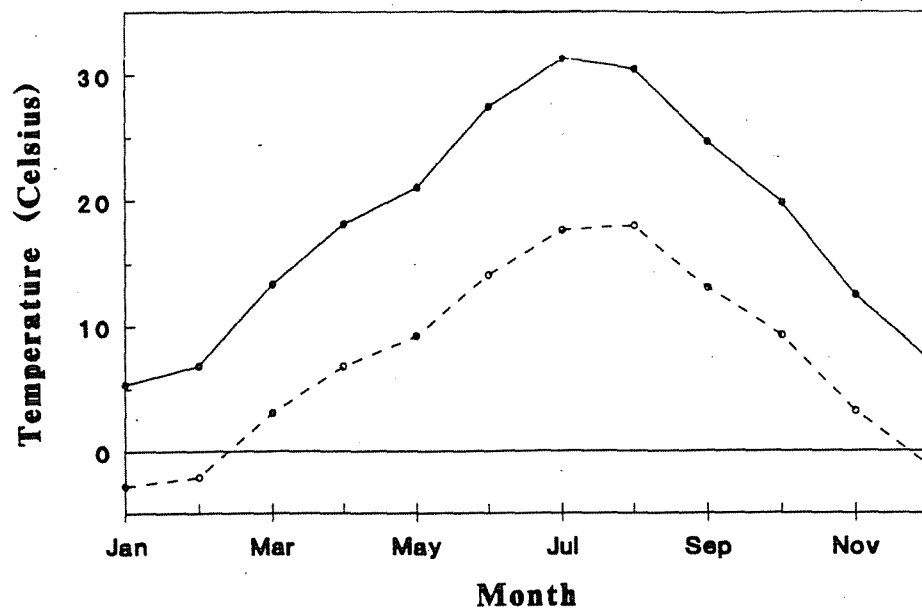
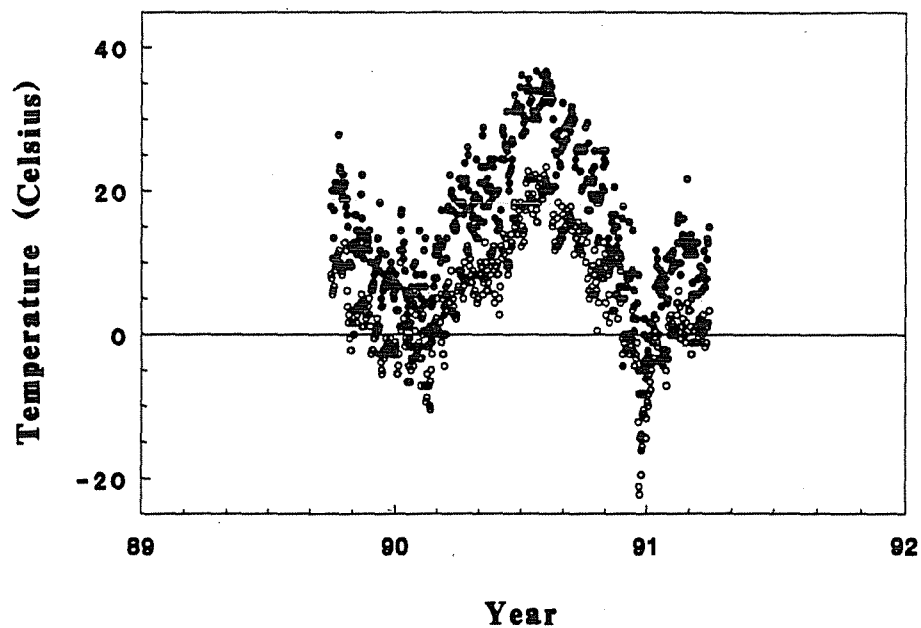Figure 3-3. Mean monthly maximum and minimum air temperatures at Pyramid Lake for 1986-1991.

Figure 3-4. Daily maximum and minimum temperature at Pyramid Lake for 1988-1992.
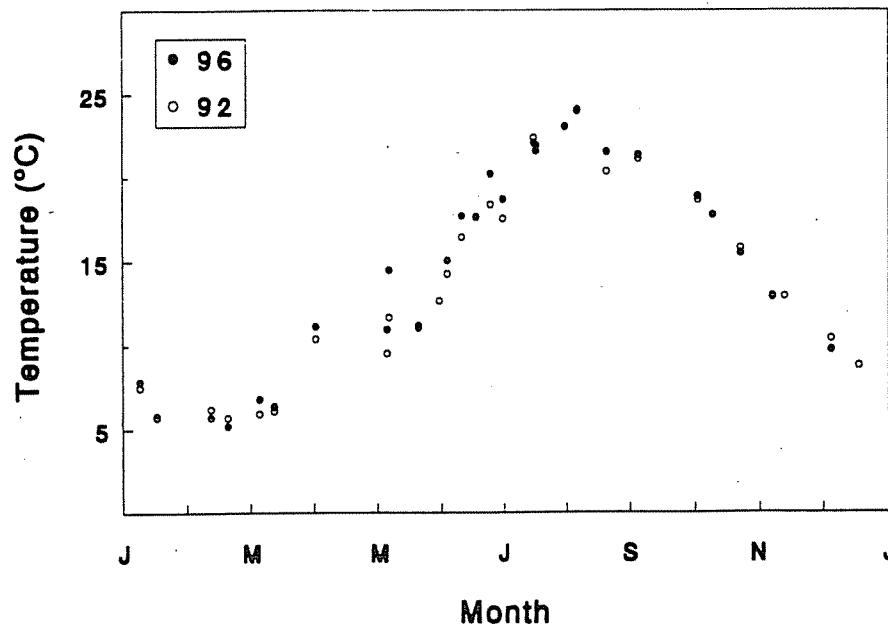
General Information

Figure 3-5. Surface (1-2 m) water temperature of Pyramid Lake for 1989-1991 plotted by time of year.
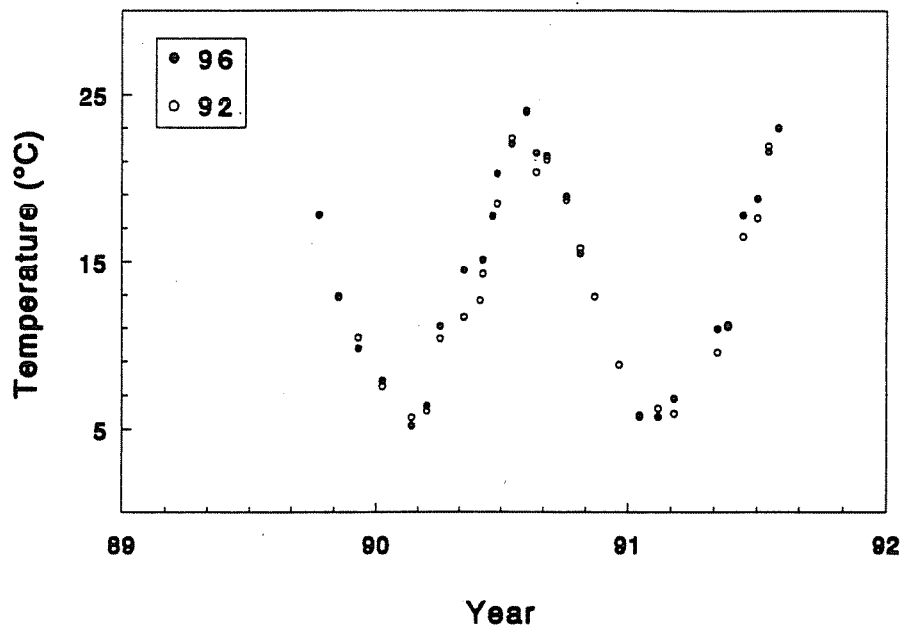

Figure 3-6. Surface (1-2 m) water temperature of Pyramid Lake 1988-1992.

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General Information

Wind

       Pyramid Lake experiences strong winds throughout the year that are highly variable. For example, daily recorded winds were 1.5, 9, 3, 7.5-8, and 4 m s^{-1} (1 m s^{-1} = 1.94 miles hr^{-1}) on successive days during 11-15 February 1990 demonstrating the wide daily variations in wind speed that occurred at the lake. Figure 3-7 shows monthly-average mean wind speed reported at Sutcliffe, Nevada on the western shore of the lake for October 1989 through August 1991. Values are the average of single daily observations taken in the morning, and, therefore, represent a biased estimate of daily wind speed. During 1989-1991, monthly mean wind speed varied from a minimum of 1.7 m s^{-1} in November 1989 to maximum mean speed of 4.9 m s^{-1} in March 1991. Stronger winds (>5 m s^{-1}) were observed during all seasons with the strongest values (>10 m s^{-1}) recorded fall, winter, and spring. Overall, wind speeds 5-10
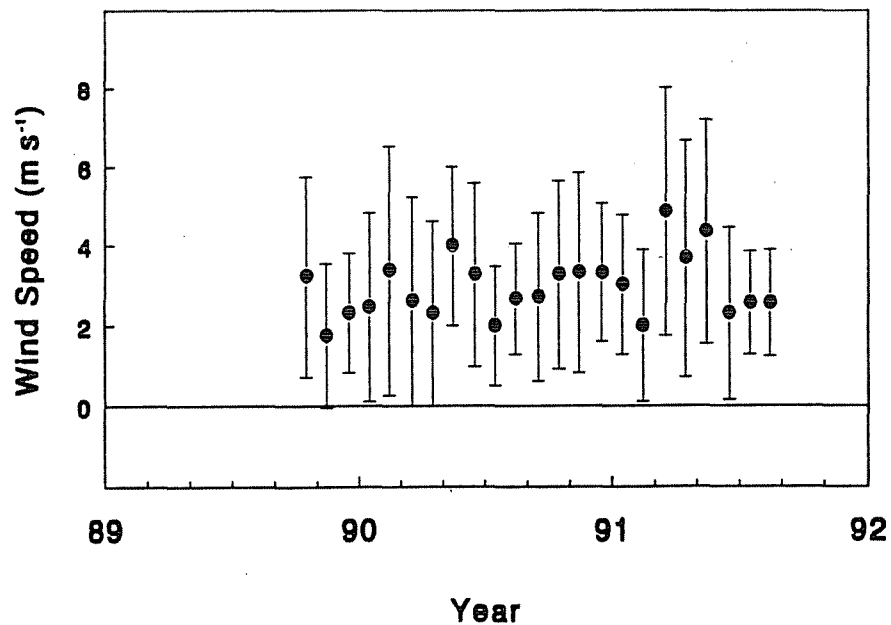

Figure 3-7. Mean monthly wind speed at Sutcliffe, NV for 1989-1991. Values are the average of single daily observations. Error bars indicate one standard deviation of the mean.

General Information

and >10 m s^{-1} comprised 17% and 1% of total days recorded respectively. The remaining days were equally divided between days when winds were <2 (40%) and 2-5 m s^{-1} (42%).

Monthly mean wind speeds were averaged by season to discern seasonal patterns in wind speed. Generally, winds were strongest during spring (e.g. March-May) with a seasonal average of 3.7±1.0 m s^{-1}. During the spring, strong winds (>5 m s^{-1}) were recorded 27% of the time compared with 17% for the entire year. The proportion of days with winds >5 m s^{-1} was even higher during March-May 1991 when a series of spring storms occurred in the region. Strong spring winds at Pyramid Lake were also observed by Galat et al. (1981). In contrast to spring, the calmest season at the lake was summer. Although calm months (winds <2.5 m s^{-1}) occurred during all seasons (Fig. 3-7), average wind speed was lowest at 2.6±0.4 m s^{-1} during the summer. Average wind speed during fall and winter were intermediate at 2.9±0.7 and 2.8±0.6 respectively. Overall, the seasonally-weighted annual average wind speed at Pyramid Lake during 1989-1991 was 3.0 m s^{-1}.

Light Availability

Light available for phytoplankton photosynthesis varied seasonally due to changes in total insolation and clarity of the water. As expected in the Northern Hemisphere, maximum light intensities at Pyramid Lake occurred during June-July of each year. Light intensity at the lake surface during these months was 2000-2200 μE m^{-2} s^{-1} compared with lower daily maximum values of <1200 μE m^{-2} s^{-1} during December-February (Fig. 3-8). The availability of incident light for photosynthesis was modified by seasonal changes in the clarity of the water. Figure 3-9 shows the extinction coefficient for light in surface waters of Pyramid Lake during 1987-1991. The extinction coefficient indicates how rapidly light entering surface waters is either scattered or absorbed. For example, a coefficient of -0.25 m^{-1} indicates that light intensity decreases by approximately 22% with each meter of depth. Extinction coefficients varied from -0.18 to -0.36 m^{-1} during the past five years indicating that
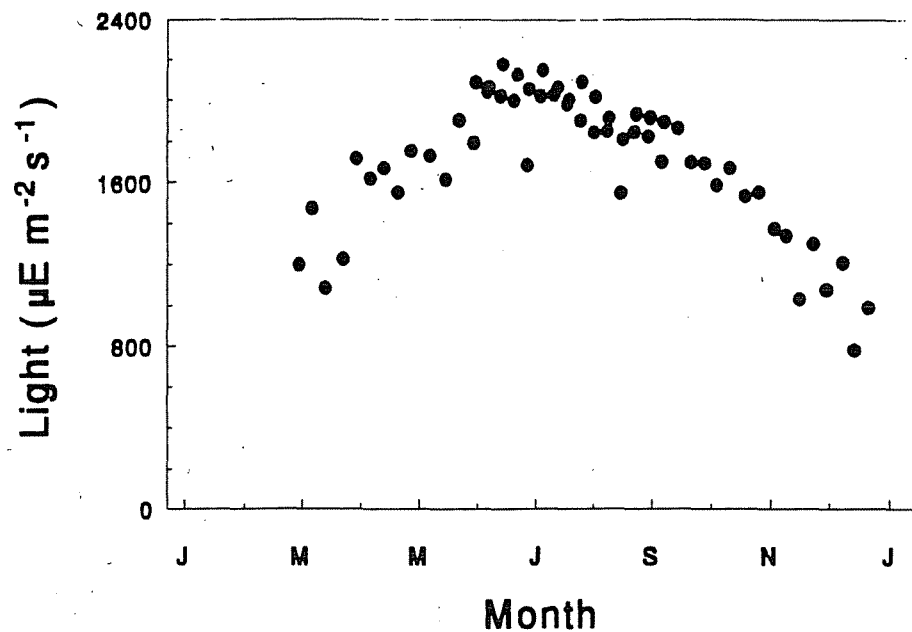
Figure 3-8. Maximum insolation at Pyramid Lake during 1989-1991 plotted by time of year. Values are weekly averages.
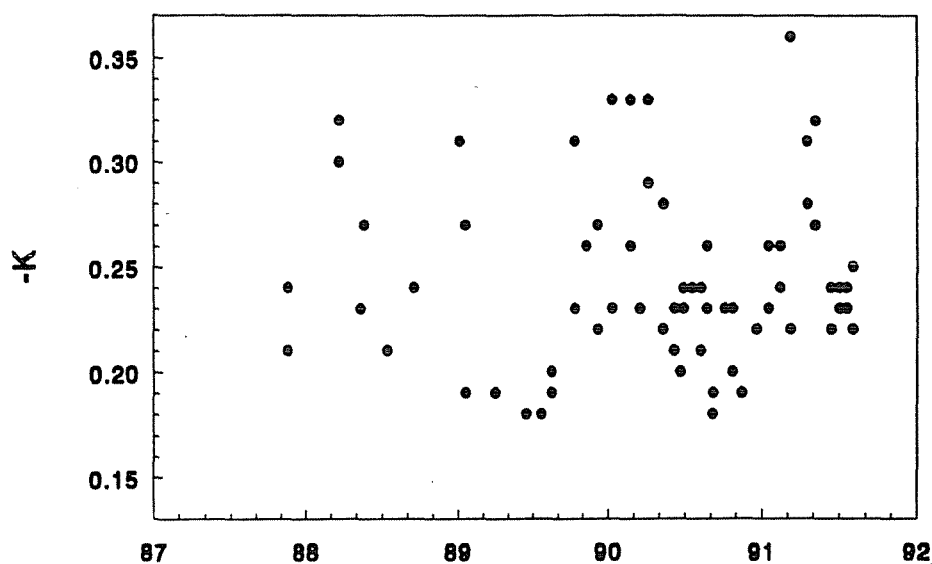

Figure 3-9. Light extinction coefficient in surface waters of Pyramid Lake for 1987-1992. Values are calculated from profiles of light intensity.

light penetrated to a depth of 12-25 m. When photic depth (1% of incident light) was plotted against time of year (Fig. 3-10), there was a clear decrease in light penetration during winter-spring. This decrease in the availability of light was due to greater turbidity probably associated with wind transport of dust (Galat et al. 1981) and the spring chlorophyll maximum (Lebo et al. 1991). Therefore, light was more available for photosynthesis during summer when incident light intensity was maximal and light penetration was great and less available during winter when turbidity was higher and incident light intensity was lowest.

Comparison of the clarity of surface waters at stations 92 and 96 suggests that the shallow basin is more turbid than the deep basin. Figure 3-11 shows bi-monthly mean extinction coefficients separated by location for data collected 1987-1991. Clearly, light extinction was higher in the shallow basin during fall-spring, but both basins were similar during summer. Overall, the non-weighted average values were -0.26±0.05 m^{-1} (n=28) and
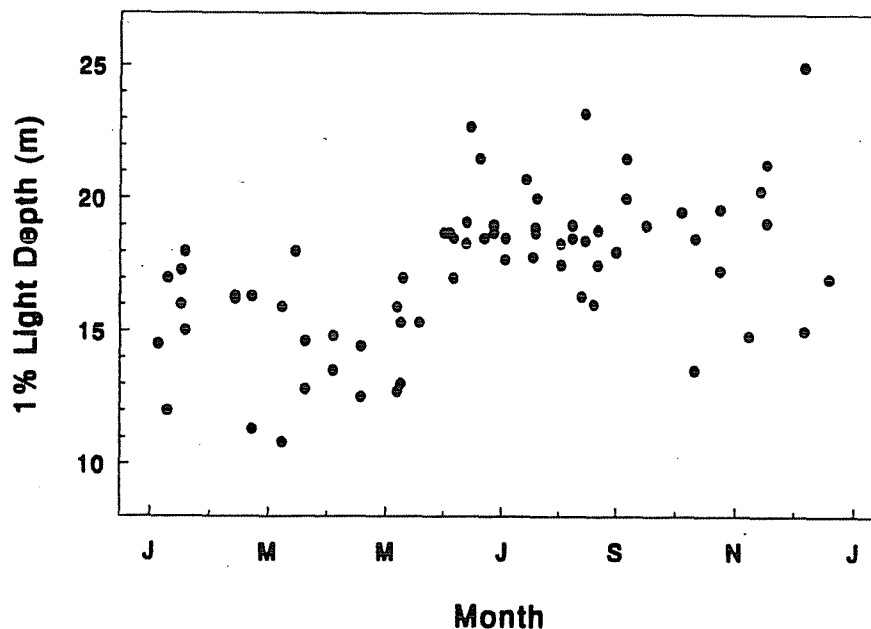

Figure 3-10. Depth of 1% incident light plotted by time of year for 1987-1991.
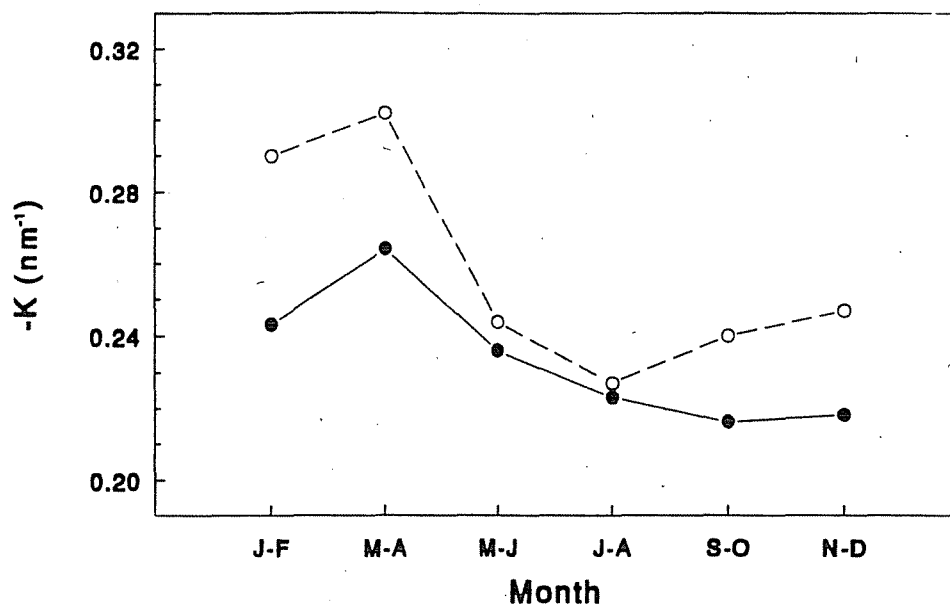
Figure 3-11. Mean light extinction coefficient for stations 92 and 96 plotted bimonthly for 1987-1991. Values are the mean of 3-9 discrete points. Average standard deviation for the bimonthly means are 0.037 and 0.027 for stations 92 and 96 respectively.

-0.23±0.03 m^{-1} (n=38) at stations 92 and 96 respectively. This difference is significant at α=0.01 and translates into a decrease in the depth of 1% light penetration of 2.2 m at station 92 (16.8 m) relative to 96 (19.0 m).

SECTION 4

Observations from 1990: A Dry, Low-Productivity Year [1]

Abstract

Seasonal variability of nutrients and productivity are examined at station 96 in the middle of the deep basin of Pyramid Lake during 1990, a dry period. River inflow and N-fixation during 1990 were minimal allowing internal nutrient cycling to be more closely studied. Nutrient cycling was strongly affected by seasonal thermal stratification that was typical for a warm monomictic lake. Concentrations of nitrate, phosphate, and silicate in surface waters were highest during winter mixing and decreased rapidly in the spring due to a diatom bloom. Maximum average chlorophyll concentration in surface waters was 2.7 ± 1.2 μg L^{-1} and occurred in April while surface nutrients were being depleted. In contrast to chlorophyll, maximum particulate carbon in surface waters occurred in July-August when areal productivity was highest (367-398 mg C m^{-2} day^{-1}). Concurrent with nutrient depletion in surface waters was N-deficiency in the plankton. After the spring bloom dissipated in May, particulate matter (POM) became increasingly N-deficient reaching maximum elemental C:N of >18 during summer-fall. Profiles of the C:N ratio of POM were nearly constant with depth for individual sampling dates suggesting that the residence time of POM in the water column was short (<1 month). While surface waters were nutrient depleted during summer stratification, nutrient concentrations of bottom waters progressively increased, presumably through the oxidation of POM sinking to the bottom (103 m). The conversion of the rate of oxygen depletion in bottom waters to carbon equivalents of POM suggests that 42% of mean annual phytoplankton production during 1990 was mineralized in bottom waters.

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[1] This section has been accepted for publication in Hydrobiologia

Observations from 1990

Introduction

Saline lakes are among the most productive aquatic ecosystems in the world with high maximum chlorophyll (Chla) concentrations (2-2170 μg L^{-1}) and carbon fixation (38-2601 g C m^{-2} yr^{-1}) (Hammer 1986). In most of these lakes, a few dominant species usually contribute most of production, and algal blooms can be more or less continuous in some very productive systems. Even in lakes where overall production is only modest, such as Pyramid Lake, Nevada (149-236 g C m^{-2} yr^{-1}, Galat 1986), productivity can be greatly increased during bloom periods (Galat and Verdin 1988). Mean lake Chla concentrations in Pyramid Lake during summer-fall blooms of *Nodularia spumigena* can exceed 70 μg L^{-1} (Galat and Verdin 1988) compared with an annual mean value of 3.3 μg L^{-1} for 1976-1977 (Galat et al. 1981). During years with larger *N. spumigena* blooms, the lake's nutrient budgets and annual production are dominated by production associated with the bloom. For example, a large *N. spumigena* bloom in 1979 accounted for 44% of annual production (Galat et al. 1981) and 81% of N inputs to the lake (Horne and Galat 1985).

In 1990, the *N. spumigena* bloom in Pyramid Lake was relatively small with N-fixation <15 mmol-N m^{-2} (Lebo et al. 1991) or approximately 13% of the large bloom reported for 1979 (Horne and Galat 1985). River discharge to the lake was also very low; surface freshwater inflow for 1990 was 0.30 x 10^8 m^3 (See Section 10) or only 5% of mean annual inflow for 1972-1987 (6.54 x 10^8 m^3 yr^{-1}, Galat 1990). This absence of a large bloom in 1990 coupled with low river inflow allows internal nutrient cycling and seasonal variations in production under N-limiting conditions to be examined more closely. The purpose of this section is to look at physical mixing, nutrient cycling, oxygen consumption, and phytoplankton production at station 96 during a non-bloom year. Using salinity profiles, we estimate evaporative loss from the epilimnion during summer stratification. Although seasonal variations in salinity in Pyramid Lake are small, these salinity gradients may be important in regulating mixing.

Observations from 1990

Methods

Section 2 gives a description of samples that were collected and analytical methods used.

Results

Physical Parameters

Seasonal variations in water density demonstrated profiles typical of a warm monomictic lake. Figure 4-1 shows sigma-t (σ_t) plotted against depth and date for 1990. Deep vertical mixing occurred in January-March as σ_t was uniform throughout the water column at >3.2 mg L^{-1}. The densest water (σ_t > 3.3 mg L^{-1}) during the study period occurred in the late winter below 20 m suggesting that there was a net loss of heat from bottom waters during winter mixing in 1990. Throughout the year, the density of deeper waters (>40 m) remained relatively constant at a σ_t of approximately 3.2-3.3 mg L^{-1}.

Surface waters, after winter mixing, became progressively warmer and reached maximum temperature (T>20°C) during July-September (Fig. 4-1). During this period of increasing thermal stratification, there was a concomitant decrease in the density of surface waters to a σ_t of <1.5 mg L^{-1} during summer. During July-September, the upper water column was highly stratified with a strong thermocline and pycnocline (density gradient) at 20-25 m. The close correspondence between σ_t and temperature indicates that temperature was the primary factor regulating σ_t. After this summer period, stratification broke down during November-January as surface temperature decreased. By late December, surface temperature was <8°C and σ_t was approximately 3.2 mg L^{-1} throughout the water column.

The influence of seasonal variations in salinity on density was more subtle. Figure 4-1 shows total dissolved solids (TDS) contoured against depth and date for 1990. When

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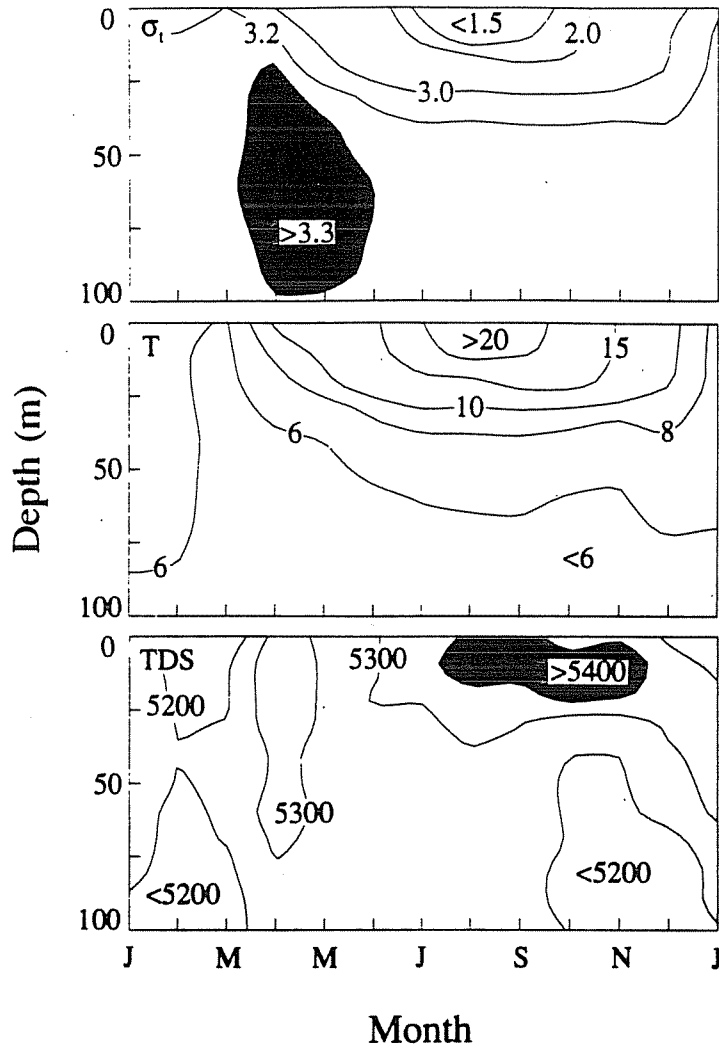Figure 4-1. Density (σ_t in mg L^{-1}), temperature (T in °C), and total dissolved solids (TDS in mg L^{-1}) contoured versus depth and date for January 1 - December 31, 1990. Data used to draw the isopleths were collected on 12 monthly samplings at 11 depths.

compared with temperature variations (6-24°C), seasonal variations in TDS are small at 5100-5500 mg L^{-1}. Figure 4-2 shows TDS profiles for May and November 1990; due to instrumental problems in May and lost data in November, data from 0-20 m in June were used for May surface waters and data from 60-100 m in December were used for bottom waters in November. Clearly, the profiles indicate an increase of 127 mg L^{-1} in surface water (0-30 m) TDS concentration during this period. When data for all months between June and November were included, TDS increased by 28 mg L^{-1} month^{-1} on the average during June-November (r=0.85; n=6; P=0.03). This relative increase of 2.6% suggests that 0.78 m of surface waters (0-30 m) were lost through evaporation during May-November 1990 which is similar to the recorded decrease in lake elevation for this period (-0.74 m, Fig. 3-2). Profiles of TDS in Figure 4-2 also indicate a decrease of 74 mg L^{-1} in bottom water TDS concentration between May and December. However, the corresponding salt balance
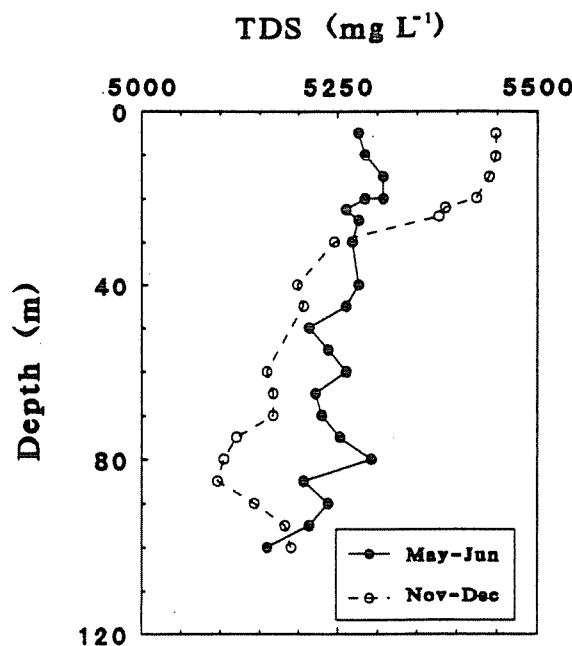

Figure 4-2. Profiles of total dissolved solids (TDS) showing surface enrichment during fall.

Observations from 1990

estimating the apparent decrease in TDS concentration in deep waters (60-100 m) proved to be invalid due to complex deep water circulation. Regression analysis using data from all months revealed no significant trend in bottom water TDS (r=-0.36; P=0.5).

Oxygen

Dissolved oxygen (DO) concentration was highest (>9 mg L^{-1}) throughout the water column during winter overturn (Fig. 4-3). After overturn, there was a progressive decrease in DO until mixing resumed again in the late fall (November). In surface waters, the decrease in DO can be attributed to a lower solubility of oxygen in warmer waters. The minimum in surface DO (<8 mg L^{-1}) in July-August corresponds to annual maximum temperatures (Fig. 4-1). Surface waters were always >88% of saturation and generally >100% (Fig. 4-3). The undersaturated values during the winter are due to disequilibrium between surface waters and the atmosphere; although DO increased during this period, the solubility of oxygen also increased due to the rapid cooling of the water (Fig. 4-1). Vertical mixing during the winter also transferred oxygen to deeper waters contributing to the undersaturation of surface waters.

There was a seasonal decrease in DO below the thermocline (20-25 m) due to the consumption of oxygen. After winter overturn, DO in the hypolimnion progressively decreased from >9 mg L^{-1} in February-April to <5 mg L^{-1} at the bottom (>90 m) during October-November (Fig. 4-3). Minimum DO concentration during the fall corresponds to <50% of saturation. DO depletion also occurred in the metalimnion and upper hypolimnion (20-40 m) during the stratified period. This layer of reduced DO was probably due to the regeneration of slowly sinking surface production.

Nutrients

Pyramid Lake is P-rich with relatively high P concentrations throughout the year. Table 4-1 lists the range of nutrient concentrations during 1990 in the epilimnion and
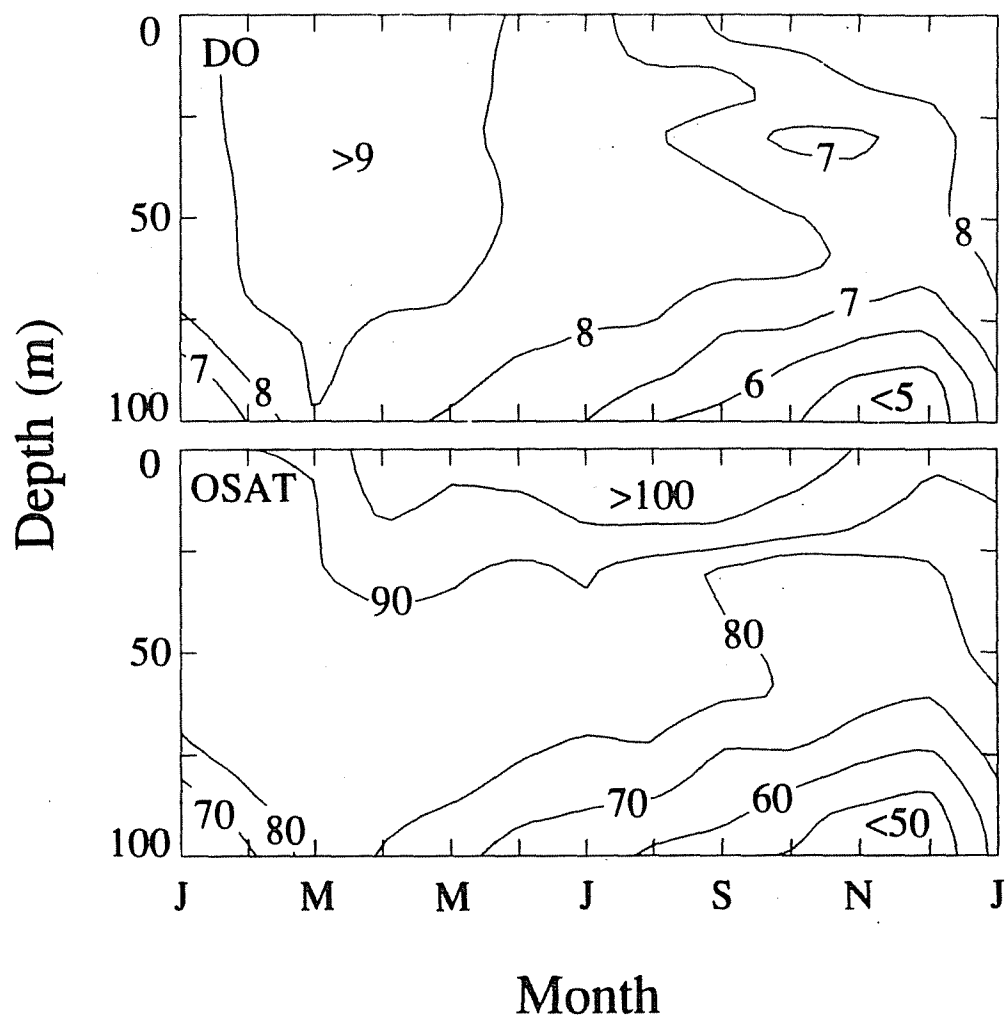
Figure 4-3. Dissolved oxygen (DO) in µg L^{-1} and percent oxygen saturation (OSAT) contoured against depth and date for 1990. See Fig. 4-1 for samples used.

Observations from 1990

hypolimnion. Total reactive P (TRP) and total P (TP) were always >47 µg L^{-1}. In contrast to P, dissolved inorganic N (DIN) concentration was often much lower (NO$_3$-N+NH$_4$-N <10 µg L^{-1}). Using maximum DIN concentration observed in surface waters (approximately 60 µg L^{-1}), the maximum elemental ratio of dissolved N:P is <2 (1.9, DIN:TRP) which is well below the Redfield ratio of 16 for

Table 4-1. Range of nutrient concentrations in Pyramid Lake for 1990. Surface and deep samples represent 0-30 and >30 m respectively. Values are in µg L^{-1}. Dissolved organic nitrogen (DON) is TKN minus PN and NH$_4$-N.

Parameter	Surface	Deep
TRP	47-69	55-107
TP	56-87	58-120
NO$_3$-N	4-57	14-139
NH$_4$-N	<1-28	<1-17
TKN	471-737	445-811
DON	425-696	408-618
SiO$_2$-Si	156-532	436-2733

plankton biomass (Redfield et al. 1963). Low N:P has been consistently shown in previous studies in Pyramid Lake (Hutchinson 1937; Galat et al. 1981; Hamilton-Galat and Galat 1983). Despite low DIN, dissolved N was always relatively high due to high concentrations of dissolved organic N (DON), the dominant N fraction in the lake. Figure 4-4 shows profiles of DON in March, July, and October 1990. During 1990, DON was high (>400 µg L^{-1}) throughout the water column and accounted for >80% of total N.

Seasonal variations in nutrient concentrations are shown in Figure 4-5. During winter overturn (January-March), concentrations of all fractions of N, P, and Si were relatively constant. In February, TP and TRP were 85 and 68 µg L^{-1} respectively, dissolved SiO$_2$-Si was 500 µg L^{-1}, and total Kjeldahl N (TKN), NO$_3$-N, and NH$_4$-N were approximately 470, 55, and 5 µg L^{-1} respectively. After winter overturn, there was a progressive depletion of NO$_3$-N, TRP, and SiO$_2$-Si in surface waters from these maximum concentrations. The depletion of NO$_3$-N (<10 µg L^{-1}) and SiO$_2$-Si (<200 µg L^{-1}) was rapid during early spring (February-April) when diatoms have been shown to dominate the phytoplankton assemblage (Galat et al. 1981). TRP (<55 µg L^{-1}) was depleted more gradually during February-June. Concentrations of NO$_3$-N, TRP, and SiO$_2$-Si increased again in the late fall (November) as stratification was breaking down. The minimum concentrations of 47 and 156 µg L^{-1} for TRP and SiO$_2$-Si

respectively (Table 4-1) are relatively high suggesting phytoplankton growth is never limited by P or Si.

Seasonal variations in NO_3-N, TRP, and SiO_2-Si in bottom waters (>75 m) showed a progressive buildup of nutrients (Fig. 4-5). After winter mixing, NO_3-N increased from 55 μg L^{-1} in March to 130 μg L^{-1} by October. Similar increases occurred for TRP (68 to 100 μg L^{-1}) and SiO_2-Si (500 to 2300 μg L^{-1}). The increase in TP concentration in bottom waters (85 to >110 μg L^{-1}) was due mainly to the increase in TRP. The correspondence between DO depletion (Fig. 4-3) and nutrient enrichment (Fig. 4-5) suggests that these seasonal patterns are due to the remineralization of organic matter in bottom waters and the sediments. After October, concentrations of these three nutrient fractions in deep waters decreased as vertical mixing throughout the water column increased.
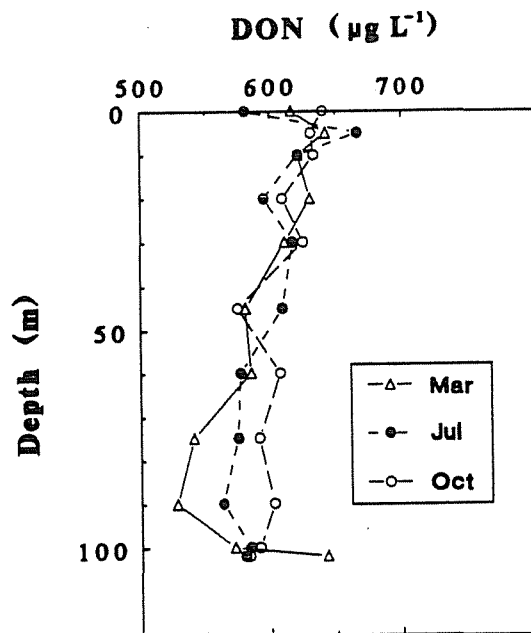

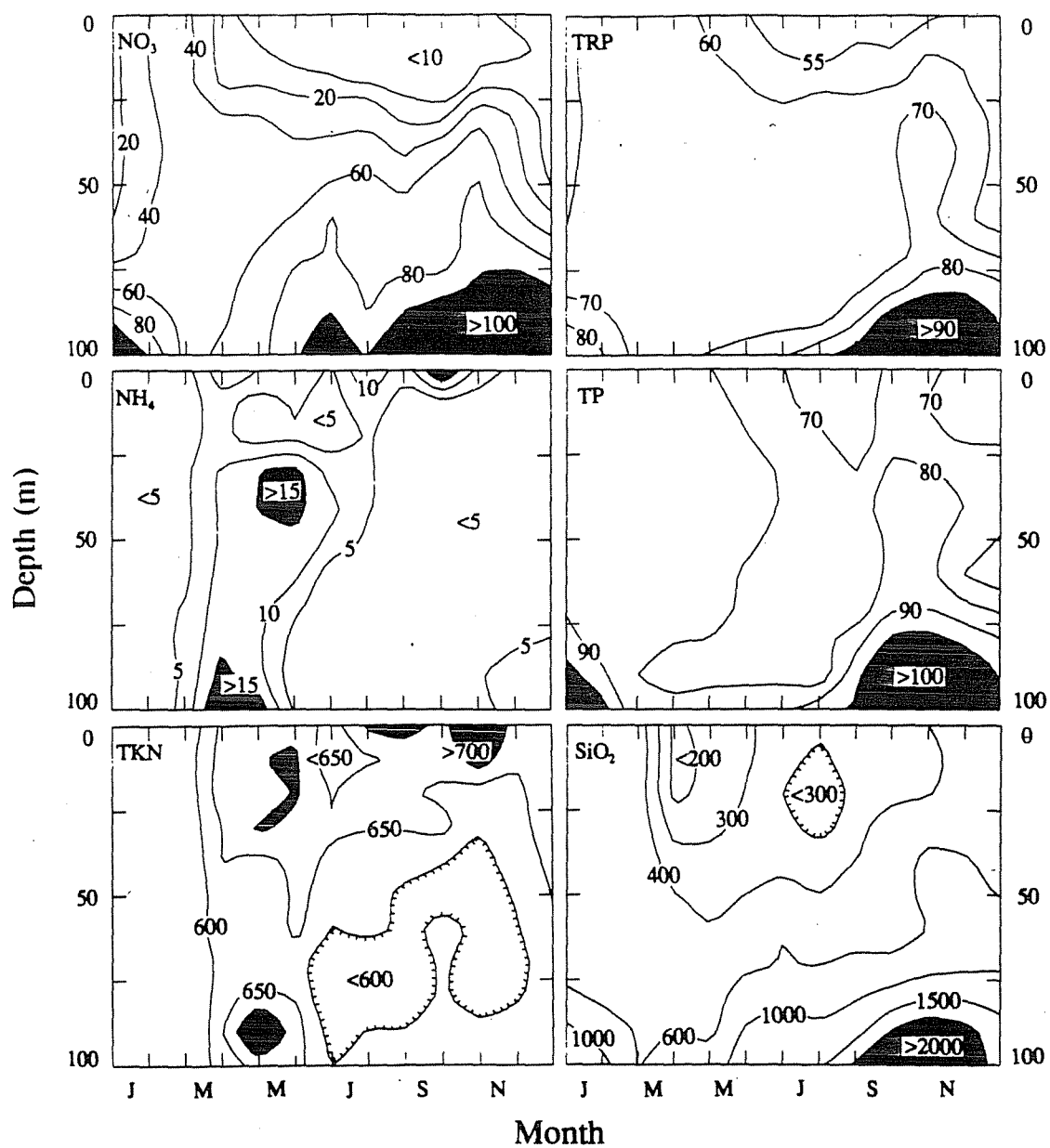Figure 4-4. Profiles of dissolved organic nitrogen (DON) during spring (March), summer (July), and fall (October 1990).

Figure 4-5. Nitrate (NO₃), ammonium (NH₄), total Kjeldahl N (TKN), total reactive P (TRP), total P (TP), and silicate (SiO₂) contoured in μg L⁻¹ against depth and date for 1990. See Fig. 4-1 for samples used.

Observations from 1990

TKN and NH_4-N showed different seasonal patterns from NO_3-N, TRP, and SiO_2-Si (Fig. 4-5). Rather than progressive surface depletion and bottom water buildup, TKN and NH_4-N demonstrated localized maxima in the spring, summer, and fall. These maxima were usually at the surface, although both TKN (>700 $\mu g\ L^{-1}$) and NH_4-N (>15 $\mu g\ L^{-1}$) were high in the lower epilimnion (20-40 m) and at the bottom (>80 m) in the spring. The close correspondence between peaks in TKN and NH_4-N suggests that seasonal changes in both N fractions are linked.

Particulate Matter

Seasonal variations in particulate C, N, and P (PC, PN, PP) are shown in Figure 4-6. For 1990, there was a surface enrichment in particulate organic matter (POM) throughout the stratified period (April-November). Highest concentrations of PC, PN, and PP all occurred during July-August with a smaller peak in April-May. During the summer peak, concentrations of PC, PN, and PP were >800, >60, and >10 $\mu g\ L^{-1}$ respectively. Maximum concentrations of PC (400-600 $\mu g\ L^{-1}$) and PN (>40 $\mu g\ L^{-1}$) during the spring peak were slightly lower while PP concentration was similar (>10 $\mu g\ L^{-1}$). The lowest concentrations of POM occurred in the hypolimnion during the stratified period (April-November) when PC, PN, and PP concentrations were generally <200, <20, and <2 $\mu g\ L^{-1}$ respectively. PN concentration was particularly low (<10 $\mu g\ L^{-1}$) during fall when N availability in surface waters reached its seasonal minimum (Fig. 4-5).

The elemental composition of POM suggests a progressive increase in N-deficiency for phytoplankton growth during summer-fall stratification. Figure 4-7 shows the molar C:N ratio of POM contoured against depth and date. During the spring when nitrate was available for growth (Fig. 4-5), the C:N ratio of POM was 7-8 which is similar to the Redfield ratio of 6.6 (Redfield et al. 1963). This suggests that phytoplankton growth during spring was balanced. After the onset of stratification in April, there was a progressive increase in the C:N ratio suggesting greater N-deficiency during summer-fall. The highest C:N ratio of >18

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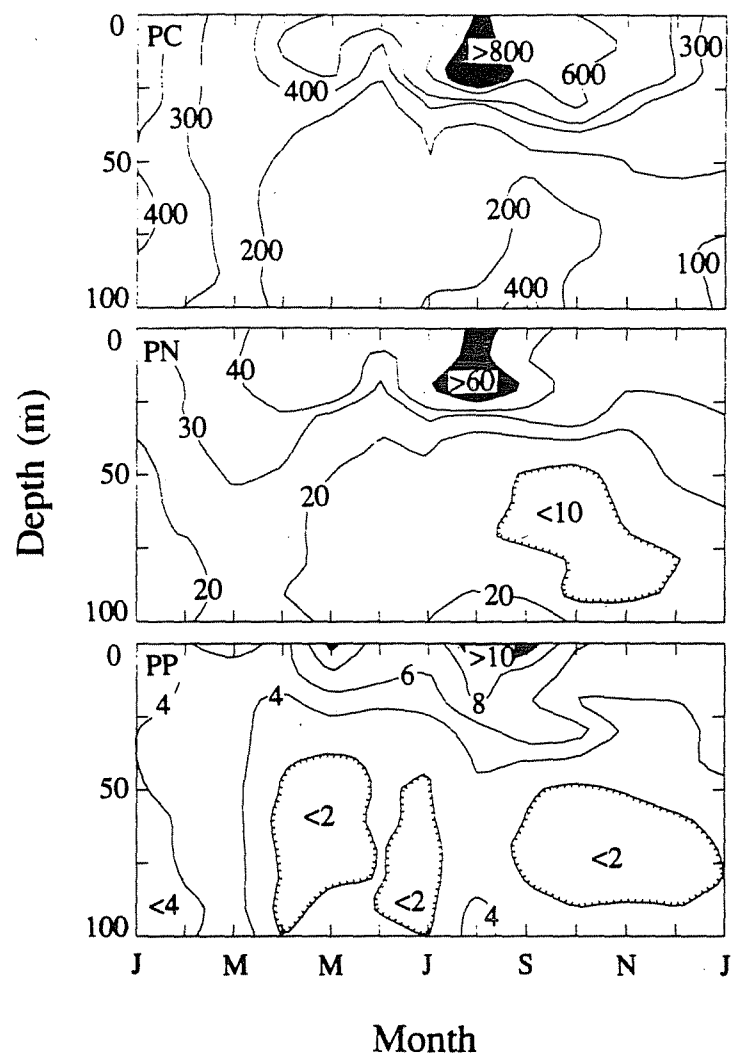
Figure 4-6. Particulate carbon (PC), nitrogen (PN), and phosphorus (PP) contoured in µg L⁻¹ against depth and datet for 1990. See Fig. 4-1 for samples used.
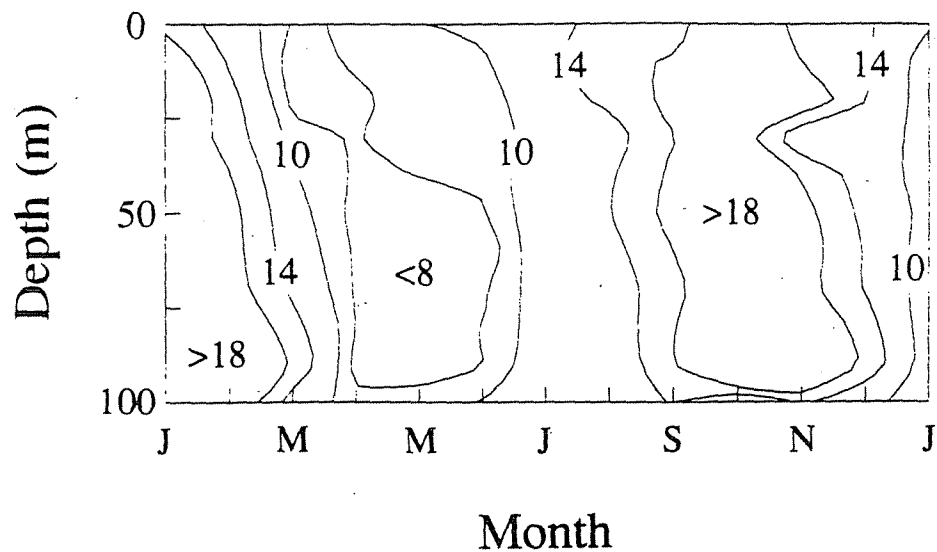
Figure 4-7. Elemental carbon:nitrogen ratio contoured against depth and date for 1990. See Fig. 4-1 for samples used
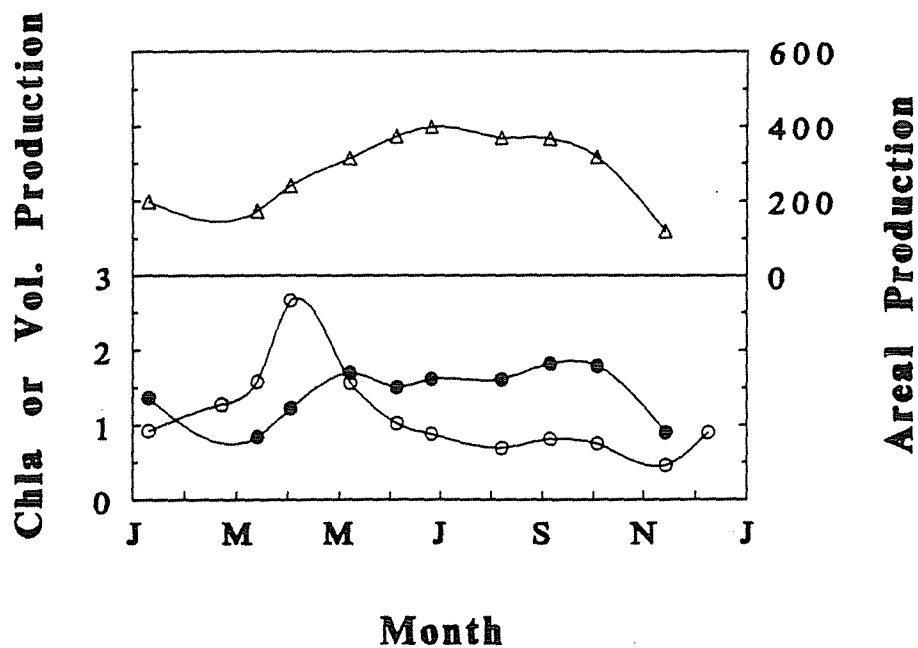
Figure 4-8. Seasonal variation in areal phytoplankton production in mg C m^{-2} day^{-1} shown in upper frame. Lower frame shows seasonal variations in chlorophyll (O) in μg L^{-1} and volumetric phytoplankton production (•) in μg C L^{-1} hr^{-1} for surface waters (0-25 m). Values in lower frame are non-weighted means of nine depths.

Observations from 1990

occurred during fall indicating severe N-deficiency during September-November (Healey and Hendzel 1980). With increased mixing in the late fall, the C:N ratio of POM decreased again, presumably through the greater availability of DIN (Fig. 4-5). By December, values were <10 indicating more balanced growth.

Phytoplankton

Average Chla concentration is shown in Figure 4-8 for surface waters (0-25 m) of Pyramid Lake during 1990. Chla was highest in April (2.7 ± 1.2 μg L^{-1}) after winter overturn. This peak in Chla during the early spring followed the period when nutrient concentrations in surface waters were maximal (Fig. 4-5). In Pyramid Lake, the spring bloom is composed predominantly of diatoms (Galat et al. 1981) causing the depletion of N, P, and Si. After April, there was a continual decrease in Chla to a minimum in November. The exception to this monotonic trend is a small increase in September relative to August. In September, *N. spumigena* was present in the phytoplankton assemblage and N-fixation was measured in the lake (Lebo et al. 1991).

In contrast to Chla, areal primary production was highest during summer (Fig. 4-8). Between June-September, areal production was >365 mg C m^{-2} day^{-1} with a peak of 398 mg C m^{-2} day^{-1} in July. This summer peak corresponds to the seasonal maximum in solar radiation at Pyramid Lake (Galat 1986). Production was lower during October-May at 118-316 mg C m^{-2} day^{-1}. The monthly weighted annual average for 1990 was 269 mg C m^{-2} day^{-1}. It should be noted that this estimate of annual phytoplankton production does not include any major *N. spumigena* blooms which would increase the average substantially. In 1979, Galat et al. (1981) reported average production to be 505 mg C m^{-2} day^{-1} when there was a large bloom. In contrast to areal production, mean volumetric production in surface waters (0-25 m) was high (>1.50 μg C L^{-1} h^{-1}) throughout May-October with a peak in September (1.81 μg C L^{-1} h^{-1}).

Observations from 1990

Discussion

Importance of 1990

The lack of a large bloom of *N. spumigena* during summer-fall 1990 coupled with low Truckee River discharge allows the dependence of phytoplankton production on internal nutrient cycling within Pyramid Lake to be more closely examined. In years with large *N. spumigena* blooms and/or high runoff, more subtle processes within the lake are overshadowed by nutrient inputs associated with these events. The effect of low *N. spumigena* production on total annual carbon production can be seen when production during 1990 is compared with previous estimates. In 1990, annual carbon production was 98 g C m^{-2} compared with 149-236 g C m^{-2} for 1976-1979 (Galat 1986). Since *N. spumigena* blooms can account for >40% of annual production (Galat et al. 1981), lower production in 1990 can be attributed to the small bloom. Another impact of low *N. spumigena* production is a large reduction in nitrogen inputs to the lake. During 1979 when the bloom was large, N-fixation accounted for 86% of nitrogen inputs to the lake (Horne and Galat 1985). Without these connections between Pyramid Lake and its surroundings (e.g. atmospheric N_2), the lake can be treated as an isolated box depending on internal cycling.

POM Cycling

Depth distributions and elemental composition of particulate organic matter (POM) suggest that the residence time of POM within the water column of Pyramid Lake is relatively short (<1 month). When the elemental composition of POM is plotted against time and depth (Fig. 4-7), isopleths of constant C:N ratio are nearly vertical. This suggests that changes in C:N ratio occur throughout the water column at roughly the same time. For example, C:N ratio of POM in deeper waters (>40 m) decreased within one month of balanced growth (lower C:N) in surface waters during spring. The similarity between the

elemental composition of seston in surface and deep waters suggests that POM in deeper waters is of recent surface origin.

Distributions of PC, PN, and PP also suggest that the residence time of POM within the water column is short. Following the August peak in PC concentration in surface waters, there were relative peaks in PC, PN, and PP in bottom waters. Concentrations of PC, PN, and PP were >300, >20, and >4 respectively at the bottom in August-September compared with lower values before and after this period (Fig. 4-6). The rapid turnover of POM in the water column suggests that the elemental composition of POM throughout the water column should reflect recent growth conditions of surface waters.

Maximum bottom water concentrations of PC, PN, and PP following the summer surface peak in POM suggest that some fraction of surface production is rapidly transferred to bottom waters. Preliminary sediment trap data revealed that the carbon content of material leaving surface waters (at 30 m) was 55.6 mg C g^{-1} during April-May 1991. Since the carbon content of atmospheric fallout is low (3 μg C g^{-1}, Galat 1986), POM flux at 30 m should be entirely autochthonous. Total mass flux out of surface waters during April-May 1991 was 1.81 g m^{-2} day^{-1} yielding an epilimnetic carbon loss of 0.101 g C m^{-2} day^{-1}. This flux is equivalent to 40% of areal phytoplankton production during this period (0.251 g C m^{-2} day^{-1}) suggesting a large fraction of spring surface production is exported to deeper waters. During the summer (July-September) when stratification is stronger, the proportion of surface production sinking to deep waters will probably be lower. In studies of POM flux in several large lakes (z_{max} > 30 m), the majority (>70%) of surface production during the summer stratified period was regenerated within the epilimnion (Eadie et al. 1984; Quay et al. 1986; Hama et al. 1990). Additional sediment trap data will elucidate seasonal variations in POM flux to deep waters (>30 m).

The elemental composition of regenerated POM in bottom sediments and deep waters can be estimated from seasonal changes in nutrient and oxygen profiles. Table 4-2 lists

Observations from 1990

volume weighted average bottom water (60-100 m) concentrations for nitrate (NO_3-N), total reactive phosphorus (TRP), silicate (SiO_2-Si), and oxygen (DO) in February and October 1990. With the beginning of partial stratification in March, average concentrations of nutrients in bottom

Table 4-2. Average concentrations of nitrate (NO_3-N), reactive phosphorus (TRP), silicate (SiO_2-Si), and dissolved oxygen (DO) in bottom waters (60-100 m). Nutrient values are in μg L^{-1} while DO is in mg L^{-1}. Values are volume-weighted means based on a single profile of five points.

Parameter	Feb 1990	Oct 1990	Change
NO_3-N	56.5	88.4	+32.1
TRP	66.7	78.2	+11.5
SiO_2-Si	509	1171	+662
DO	9.29	6.92	-2.37

waters increased monotonically while DO decreased. The elemental ratio of this nutrient buildup in bottom waters during February-October was 6.2 N : 1 P : 64 Si while consuming 400 O. This calculation assumes that changes in nutrient and DO concentrations in bottom waters are entirely due to *in situ* processes such as the breakdown of POM and dissolution of particulate Si. Clearly, POM reaching bottom waters is enriched in P relative to N since the stoichiometry of bottom water nutrient increase is well below the Redfield ratio of 16 for N:P (Redfield et al. 1963). This is expected since Pyramid Lake is P-rich. POM reaching the bottom is also greatly enriched in SiO_2-Si relative to both N and P since regenerated nutrient stoichiometry is far in excess of utilization by diatoms (e.g. Si:P of 16, Broecker and Peng 1982). This suggests that a large fraction of the latter elements are mineralized higher in the water column.

The average amount of surface production regenerated in the sediments can be estimated by converting DO consumption in bottom waters to carbon equivalents. Using the stoichiometry of the Redfield ratio (106 C : 138 O_2), the consumption of 2.37 mg O L^{-1} in deep waters (60-100 m) would require the breakdown of 114 mg C m^{-2} day^{-1} or 36% of mean areal production for February-October 1990. If we assume that DO consumption in bottom waters is constant throughout the year (temperature is nearly constant, Fig. 4-1), bottom water regeneration of POM can account for 42% of annual mean areal production for 1990.

Observations from 1990

The proportion of annual phytoplankton production reaching bottom waters can be estimated by adding POM buried in the sediments to the value determined above for regenerated POM. Assuming the organic content of surface sediments (<10 cm) is in steady state with the present supply rate of POM to bottom waters, POM buried in the sediment can be determined if the efficiency of regeneration is known. This efficiency can be estimated by comparing material caught in a sediment trap deployed in bottom waters with surface sediments. In April-May 1991, material caught in a sediment trap deployed at 80 m in the deep basin was 16% organic matter while the carbon content of bottom sediments was reported to be 2-2.5% (Meyers et al. 1980). This suggests that approximately 13-16% of POM reaching bottom waters is buried within the sediments. Applying this burial efficiency to the amount of regenerated POM determined above suggests that 48-50% of surface production may have reached bottom sediments.

However, this simple estimate of the proportion of overlying production regenerated in bottom waters and the sediments may be an overestimate due to sediment focusing. If the flux of POM reaching bottom waters in the deep basin is a combination of overlying surface production and the redistribution of POM from shallower regions of the lake, this simple balance will overestimate the proportion of surface production reaching bottom waters. Preliminary sediment trap data from April-May 1991 suggest sediment focusing may be a problem in Pyramid Lake; there was a twofold increase in the amount of POM caught in the trap deployed at 80 m (3.87 g m^{-2} day^{-1}) relative to the one at 30 m (1.81 g m^{-2} day^{-1}). Hilton (1985) lists several processes contributing to sediment focusing in lakes including slumping/sliding of sediments on steep slopes and peripheral wave action in shallows. Both of these processes could be important in Pyramid. Seasonal variations in POM flux are needed to better address the importance of sediment focusing.

Another source of POM to the lake, although small compared with phytoplankton production, is eolian transport of vegetation in the form of tumbleweeds. Galat et al. (1981) reported that the input of tumbleweeds accounted for 2.5% of the carbon budget in 1977.

Observations from 1990

Comparison of PC concentrations during January and December shows higher values during winter 1989-1990 relative to 1990-1991 (Fig. 4-6). In January 1990, PC concentration was >400 μg L^{-1} compared with <300 μg L^{-1} in December. However, PN and PP concentrations were similar in both months suggesting a source of carbon-rich material in January 1990. This PC enrichment during winter 1989-1990 may be due to the input of tumbleweeds. Since the measured elemental composition of tumbleweeds entering Pyramid Lake is carbon-rich (C:N = 44, Horne and Galat 1985), high tumbleweed input during winter 1989-1990 could explain the higher PC and C:N ratio observed relative to 1990-1991. Field observations during sampling reported extensive surface rafts of tumbleweeds during winter 1989-1990, but minimal tumbleweed debris was observed during 1990-1991.

Importance of Mixing

Regenerated nutrients in deeper waters are returned to surface waters during winter mixing. Since Pyramid Lake is N-deficient, N inputs to surface waters have the greatest impact on production. Stimulation of phytoplankton by N addition (50 μg N L^{-1}) was significant ($\alpha = 0.05$) relative to controls in laboratory bioassays throughout most of the year (Reuter et al. in press; See Section 7). In February 1990, there was a threefold increase in surface NO_3-N concentration from 17 μg L^{-1} to 55 μg L^{-1} during overturn. This input of N immediately stimulated phytoplankton and Chla increased to a maximum in April (Fig. 4-8).

Winter mixing also replenishes bottom water DO consumed during the preceding year through the remineralization of organic matter in bottom waters and the sediments. After the replenishment of bottom water DO during winter overturn, there was a continual decrease in DO during February-December (Fig. 4-3). The rate of depletion suggests that annual deep water mixing is critical to maintaining aerobic bottom waters. For 1990, bottom water DO at 100 m decreased by 3.6 mg L^{-1} (8.4 to 4.8 mg L^{-1}) between April-December. Assuming DO would continue to decline if winter overturn did not occur, bottom waters would go anoxic in approximately 19 months (-0.45 mg L^{-1} month^{-1}). This requirement of annual mixing to

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Observations from 1990

maintain aerobic bottom waters is supported by hydrodynamic date collected in 1985-1987 when winter overturn was incomplete. During this period, bottom waters (100 m) were anoxic until deep mixing occurred in February 1988.

Winter mixing is affected strongly by vertical gradients in salinity. Although seasonal variations in temperature are the primary factor controlling water density (Fig. 4-1), variations in salinity can influence the timing of winter mixing. In November-December 1990, total dissolved solids (TDS) in surface waters, on the average, were enriched by 250 mg L^{-1} (5%) relative to bottom waters (Fig. 4-2). This relatively small gradient in salinity translates to a temperature increase of 2.4°C for isopycnal mixing of surface and bottom waters. Practically, surface waters only needed to cool to within 2.4°C of bottom water temperature for vertical mixing to commence. This example, for a dry year, illustrates how seasonal salinity increase in surface waters due to evaporation can facilitate mixing and contribute to an early overturn of the water column (January 1991). During wet years, dilution of surface waters with freshwater input from the Truckee River will hinder mixing. In October 1986, bottom water (>75 m) TDS was higher than surface waters (0-30 m) by 228 mg L^{-1}. This salinity gradient would require the temperature of surface waters to be lower than bottom waters for mixing to occur. In fact, cooling of surface waters in 1986 would not be sufficient to initiate mixing. The maximum possible density of surface water was σ_t = 3.18 mg L^{-1} at a temperature of 3.6°C given that mean TDS was 4966 mg L^{-1}. Since σ_t for bottom water was 3.24 mg L^{-1}, deep mixing is physically impossible and temporary meromixis was observed (1985-1987, unpubl.).

Since processes affecting salt balances within the lake are important in controlling mixing, it is important to quantify their magnitude. The validity of our estimate for evaporative loss can be assessed by comparing it to previous estimates. For evaporative loss, previous estimates for the Pyramid Lake region of Nevada range 1.20-1.37 m yr^{-1} from measured pan evaporation (Galat et al. 1981; Milne 1987) and 1.31 m yr^{-1} from a heat balance climatic model (Hostetler and Bartlein 1990). Extrapolating our estimate of 0.78 m

Observations from 1990

from a salt balance for surface waters during May-November gives an annual rate of approximately 1.3 m yr^{-1} which is consistent with these independent estimates of evaporation. Therefore, evaporative loss calculated by salt balance for 1990 appears valid. The similarity between estimated evaporative loss (0.78 m) and reported decrease in lake surface elevation (0.74 m) suggests freshwater inputs to the lake were minimal.

Controls of Production

Low N-fixation during 1990 provides an opportunity to examine factors controlling the size of the bloom. Galat and Verdin (1988) point out that years with large blooms fall into two categories: high flow years with July blooms and low flow years with August-September blooms. This suggests that several factors may be important in regulating bloom size. Large, early blooms during wet years suggests that water stability near the surface may contribute to bloom size, which has been suggested for cyanobacteria by Reynolds (1984). A second factor may be average wind speed. Horne and Galat (1985) suggest that the capacity for *N. spumigena* to bloom in Pyramid Lake may be inversely related to wind speed with larger blooms during calm periods. In addition, Galat and Verdin (1988) suggest that increased wind was an important factor contributing to the collapse of a large *N. spumigena* bloom in 1986. A small bloom in 1990 is consistent with this observation since wind speeds were continually high all summer-fall. Examination of control of bloom magnitude is an area of ongoing research.

The obvious factor controlling diatom and green algae production is N availability. Dissolved nutrients, the elemental composition of particulate matter (POM), and laboratory nutrient enrichment bioassays all support the importance of N-limitation (Reuter et al. in press). Dissolved nutrients (e.g. N:P always <2) always suggest N should be limiting. However, POM showed a gradual increase in N-deficiency. Phytoplankton growth in early spring was near Redfield ratio of 6.6 (Redfield et al. 1963) indicating a lack of N-deficiency. During June-November, the C:N ratio of POM continually increased with values >16 by

August indicating severely N-deficient growth at that time (Healey and Hendzel 1980). This gradual transition from balanced growth during spring to severe N-deficiency during summer indicated by POM is less dramatic than seasonal variations in algal response to N-additions in laboratory bioassay. During April-October 1990, N-addition (50 μg L^{-1}) significantly stimulated phytoplankton growth in all months except September when N-fixers were present in the lake (Reuter et al. in press). The appearance of N-fixers in the lake during September coincided with maximal C:N ratio of POM.

The source of N for growth during the spring bloom was almost exclusively provided by NO$_3$-N injected into surface waters during winter mixing. During February-April 1990, the change in mean volume weighted NO$_3$-N in surface waters (0-30 m) was 19 mg N m^{-2} day^{-1}. The corresponding N-demand of phytoplankton during this period was 26.7 mg N m^{-2} day^{-1}. N-demand for this period is calculated from average areal production (206 mg C m^{-2} day^{-1}) assuming an elemental C:N of 9 (Fig. 4-7). Clearly, the decrease in NO$_3$-N concentration in surface waters (0-30 m) fulfilled most (71%) of the N-demand of phytoplankton during the early spring. Hamilton-Galat and Galat (1983) reached this same conclusion based on data collected in 1979. Concomitant with this decrease in NO$_3$-N was an increase in particulate N (PN) concentration in surface waters. During February-April, mean volume weighted PN concentration increased by 11.5 mg N m^{-2} day^{-1} accounting for 61% of the observed decrease in NO$_3$-N. This suggests that there is an efficient transfer of winter NO$_3$-N to spring algal biomass in surface waters. However, PN decreased after April to values similar to February by June. Since this decrease did not result in an increase in available (NO$_3$-N, NH$_4$-N, Fig. 4-5), it appears that NO$_3$-N input to surface waters during winter overturn is returned to deep waters (>30 m) by June.

Phytoplankton production during the summer, in contrast to the spring, is not supported through depletion of epilimnetic NO$_3$-N. During April-November 1990, monthly weighted mean N-demand for surface waters was 31 mg N m^{-2} day^{-1} (taking into account increasing C:N of POM). However, decrease in surface water NO$_3$-N concentration during

this period was only 0.4 mg N m^{-2} day^{-1}. This slow decrease in NO$_3$-N concentration can only fulfill about 1% of phytoplankton N-demand during this stratified period. Clearly, other sources of N fuel phytoplankton production. In many N-deficient aquatic systems, phytoplankton mainly use "regenerated" N (Dugdale and Goering 1967; Axler et al. 1982; Harrison 1978). The fact that epilimnetic NO$_3$-N declined slowly but was not completely exhausted (NO$_3$-N > 5.5 μg L^{-1}) supports the availability of additional sources of N. Recent work in N-deficient systems suggests that dissolved organic N (DON) may also be utilized by phytoplankton (Ward et al. 1989). Since DON is the dominant N fraction in Pyramid Lake (Table 4-1), it is potentially a large source of N.

Potential sources of new N to the euphotic zone during the stratified period are through N-fixation, NO$_3$-N mixing through the thermocline, eolian transport of dust, and river inflow. Horne and Galat (1985) estimated the input of N through eolian transport of dust to the surface of the entire lake for 1979 to be 1270 kg N yr^{-1}. Converting this total value to a daily rate yields a flux of 7.9 μg N m^{-2} day^{-1} or <0.03% of N-demand. Since there is no reason to believe that dust transport during 1990 is dramatically different than 1979, this source of N can be assumed to be negligible. The input of N from the Truckee River can be estimated from mean monthly discharge to the lake and measurements of dissolved inorganic N (DIN) near the mouth of the Truckee (See Section 10). Like eolian dust transport, the input of DIN from the Truckee River was negligible averaging only 7.8 μg N m^{-2} day^{-1} during April-November 1990. The input of N from the Truckee, therefore, can also be dismissed as negligible during 1990.

N-fixation was measured in the lake during August-September when blue-green algae were present in the phytoplankton assemblage (Lebo et al. 1991). Figure 4-9 compares the magnitude of N-fixation and diffusion of NO$_3$-N through the thermocline during the stratified period of 1990. Although the *N. spumigena* bloom was small in 1990, measured N-fixation was 198 mg N m^{-2} for the year with a peak of 60.9 mg N m^{-2} day^{-1} on September 10. During this short two week period in early September, N-fixation provided 14 mg N m^{-2} day^{-1} to

surface waters or 3% of N-demand for April-November. N-fixation during 1990, therefore, was a relatively minor source of new N to surface waters. It should be pointed out that in years of large *N. spumigena* blooms N-fixation can be a large source of new N to surface waters, and it can stimulate a secondary diatom bloom during fall (Galat and Verdin 1989).

The importance of NO_3-N mixing across the thermocline as a source of new N to surface waters can be estimated from vertical gradients in NO_3-N concentration. To translate NO_3-N gradient into transport of N across the thermocline, the rate of diffusion during the period of interest must be known. This constant can be determined indirectly using a relatively conservative tracer. Since SiO_2-Si is far in excess of phytoplankton demand, change in SiO_2-Si concentration of surface waters (0-20 m) can be used to empirically determine the apparent eddy diffusion coefficient (D) for vertical mixing. D for SiO_2-Si and NO_3-N should be almost identical due to similar molecular weights and, therefore, directly
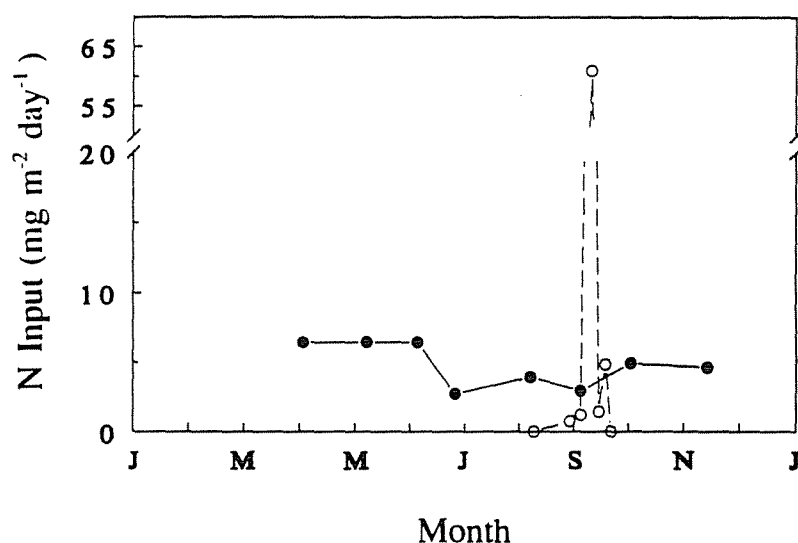

Figure 4-9. Estimated input of "new" nitrogen to surface waters through cross-pycnal mixing (•) and nitrogen fixation (o) during stratified period of 1990.

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transferrable. The determination of D was done for partially stratified (April-June) and fully stratified (July-November) periods since the degree of stratification should affect mixing. During these periods, SiO_2-Si in surface waters increased by 43 and 9.5 μg L^{-1} $month^{-1}$ during partial and full stratification respectively. These increases suggest values of 5.3 and 1.7 m^2 day^{-1} for D, with a higher rate of diffusion under partial stratification.

Using the eddy diffusion coefficients estimated above, the average flux of NO_3-N into surface waters was 6.4 during April-June and 3.8 mg N m^{-2} day^{-1} during July-November (Fig. 4-9). Therefore, it appears that NO_3-N mixing through the thermocline was the dominant source of new N to surface waters during April-November except during the small *N. spumigena* bloom in early September. Overall, eddy diffusion of NO_3-N through the thermocline supplied 1146 mg N m^{-2} during April-November 1990. This corresponds to approximately 17% of phytoplankton N-demand in surface waters during this period. Hama et al. (1990) reported a similar proportion (20%) of N-demand as new production in Lake Biwa.

The balance of N-demand for phytoplankton production during the stratified period is probably supplied by N regenerated within surface waters. Overall, N-fixation (3%) and eddy diffusion through the thermocline (17%) can fulfill approximately 20% of N-demand. The remaining 80% must come from rapid recycling of N in surface waters. These proportions of internal and external N-loading to Pyramid Lake, however, must be kept within the context of a low production and low flow year. The proportion of N supplied by N-fixation would be much higher during years with large *N. spumigena* blooms. For example, N-fixation during 1979 supplied 1.7 g N m^{-2} (Horne and Galat 1985) or approximately 26% of phytoplankton N-demand for April-November 1990. DIN input from the Truckee River would also increase during years with more "normal" flow. Galat (1990) reported DIN loading to the lake to be 0.13-6.0 mg N m^{-2} day^{-1} for 1973-1987. Although N removal in the municipal effluents of Reno-Sparks initiated in 1987 would reduce the magnitude of DIN loading, N input from the Truckee would be an important source to the lake during wet years.

Observations from 1990

Conclusions

Low flow and productivity during 1990 allow internal nutrient loading in Pyramid Lake to be more closely examined. Clearly, the source of N for phytoplankton during the spring bloom is hypolimnetic nitrate (NO_3-N) mixed to the surface during the winter. During February-April 1990, the decrease in surface NO_3-N fulfilled 71% of phytoplankton N-demand, and 61% of NO_3-N removed was accumulated as phytoplankton biomass in surface waters. This winter increase in surface N was only temporary as biomass accumulated during the bloom was lost from surface waters by June.

Seasonal changes in the elemental composition of particulate matter (POM) suggest that the residence time of POM in surface waters is short. After spring production was lost from surface waters, POM became increasing N-deficient reaching maximal elemental C:N of >18 during summer-fall, with similar values in surface and deep waters. This suggests that POM in deep waters (>45 m) is of recent surface origin. The conversion of bottom water oxygen depletion to apparent POM suggests that as much as 48-50% of surface production may reach bottom waters. However, sediment focusing may have caused an overestimate of sediment regeneration of surface production.

The main source of new N to surface waters during 1990 after the onset of stratification was eddy diffusion of NO_3-N through the thermocline. During April-November, eddy diffusion of NO_3-N supplied 17% of phytoplankton N-demand and was the dominant input of N to surface waters. One exception was during a small *N. spumigena* bloom in September when N-fixation, for a brief period, was relatively high. N-fixation during this small bloom provided an additional 3% of phytoplankton N-demand during the summer-fall stratified period. Since the input of N through river inflow and eolian dust transport were estimated to be low (<8 μg N m^{-2} day^{-1}), the balance (80%) of phytoplankton N-demand during 1990 must be fulfilled by surface water regeneration of N.

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SECTION 5

Limnology of Pyramid Lake during 1990-1991

Introduction

Data collected during September 1990 - August 1991 (1990-1991 in succeeding references) offers a chance to examine interannual variability of internal nutrient loading. The drought that has plagued the California-Nevada region over the past five years continued during 1990-1991 diminishing fluvial nutrient loading. During the second year of the current study, Truckee River flow was 0.27×10^8 m^3 s^{-1} or only 4% of mean flow during 1972-1987 (Galat 1990, see section 10). N-fixation, the dominant source of external nitrogen to the lake (Horne and Galat 1985), was also relatively low during 1990-1991 (see section 8). Therefore, external nutrient inputs to Pyramid Lake were minimal in 1990-1991, and productivity must have depended on internal sources of nutrients for growth as was the case for 1990 (see section 4). Although there is some overlap between the time periods discussed in this section and the previous one, a comparison of these two time periods allows us to examine variability in internal nutrient loading patterns to the lake.

One difference in nutrient cycling between the first two years of the study was the timing of winter overturn which was earlier in 1990-1991 than in 1989-1990. Due to elevated surface water total dissolved solids (TDS) during fall 1990 (Fig. 4-2) and several weeks of cold temperatures during December 1990 (Fig. 3-4), the lake was completely mixed by January 1991 (Fig. 3-6). The supply of nutrients to surface waters, therefore, occurred one month earlier in winter 1991 than in 1990. The timing of mixing of nutrients to surface waters during winter holomixis should have profound effects on phytoplankton production in

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the lake. Since the winter-spring diatom bloom depends on winter nitrate (NO_3-N) for growth (see discussion in section 4), the timing of the bloom should be affected by the timing of winter mixing.

This section summarizes limnological data collected during September 1990 - August 1991. As in section 4, data are presented mainly for station 96 in the deep basin. Spatial differences in nutrients, particulate matter, and physicochemical parameters are examined in section 6. Since seasonal variations in limnological parameters during 1990-1991 are similar to the pattern described in section 4, this section focuses on the impact of the timing of winter holomixis on nutrient cycling. We also examine seasonal variations in the elemental composition of particulate matter during 1990-1991.

Methods

A description of samples collected and analytical procedures are given in section 2.

Results

Physical Parameters

Thermal stratification during 1990-1991 broke down in fall as air temperatures decreased (see Fig. 3-4). Figure 5-1 shows temperature and sigma-t (σ_t) profiles during fall-winter. In September 1990, surface temperature was >20°C, and there was a pronounced thermocline and pycnocline (density gradient) at 15-30 m. Temperature decreased in this region from >20 to <10°C while σ_t, a measure of density, increased from 1.48 to 3.04 mg L^{-1}. By November, surface waters had cooled to <13°C causing σ_t to increase to approximately 2.8 mg L^{-1} reducing the difference in density of surface and bottom waters to <0.5 mg L^{-1}. Between November and January, the thermocline continued to weaken and become deeper until the water column was homogeneous. Thermal stratification was very
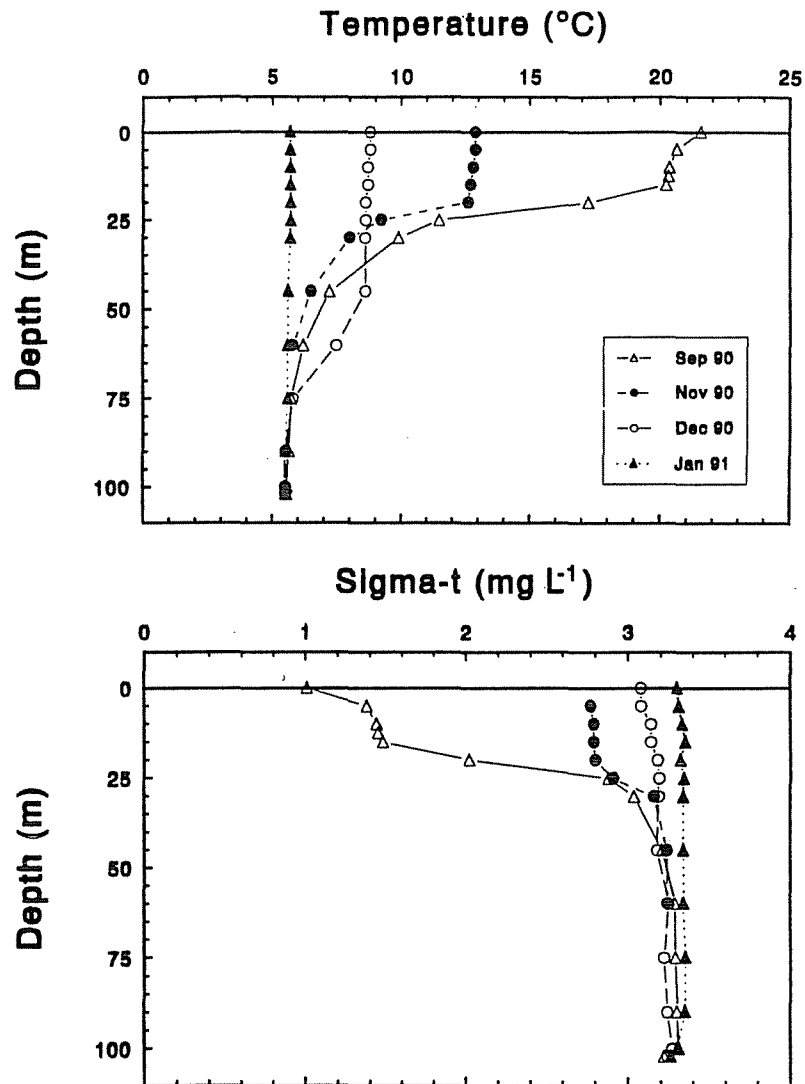
Figure 5-1. Temperature and sigma-t profiles at station 96 during fall-winter 1990-1991. Sigma-t is a measure of the density of water.

weak by December 1990 with a small gradient in temperature (<3°C) between 45-75 m. In early January 1991, temperature and σ_t were <6°C and 3.30-3.35 mg L^{-1} respectively throughout the water column suggesting complete vertical mixing. Vertical profiles of temperature and σ_t remained homogeneous until March.

Thermal stratification of the water column was reestablished during the spring with the warming of surface waters beginning after March. Figure 5-2 shows temperature profiles for March-July 1990 in the deep basin. In March, the water column was uniformly cold at 5.2-5.9°C suggesting minimal impedance to vertical mixing. After March, temperature in surface waters increased concurrent with the seasonal increase in solar insolation (see Fig. 3-8). Surface water temperature (0-10 m) was already >9°C by May with a gentle gradient in the upper 60 m of the water column. By June, thermal stratification was pronounced with surface
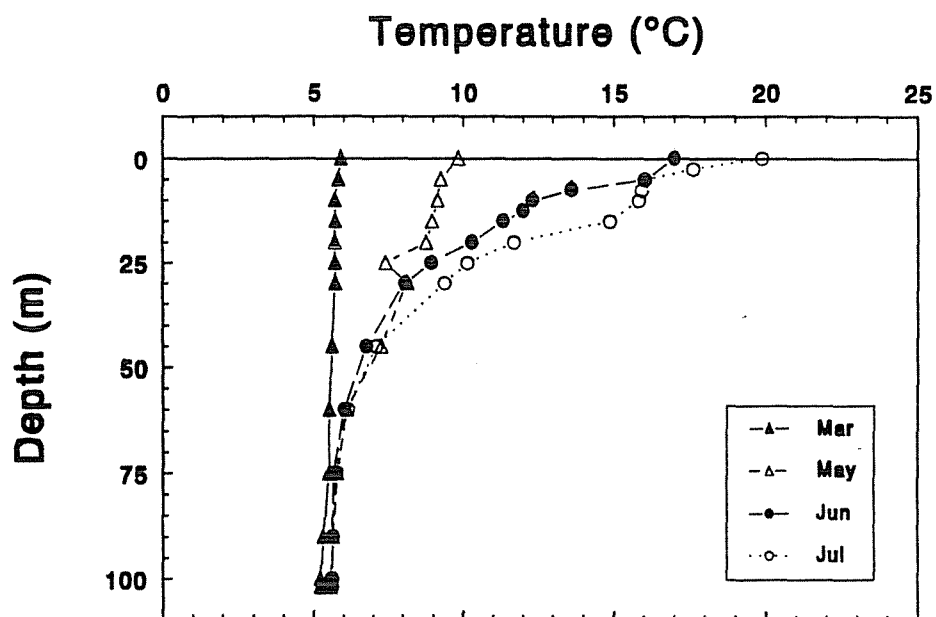

Figure 5-2. Temperature profiles at station 96 during spring-summer 1991.

temperature >12°C and a shallow gradient between 5-25 m. This shallow thermocline was deeper (15-25 m) by July as surface water temperature increased to >15°C.

As thermal stratification increased during spring-summer, there was a concurrent increase in the concentration of total dissolved solids (TDS) in the epilimnion due to evaporation at the lake surface. Figure 5-3 shows volume weighted mean TDS in surface waters (0-20 m) at stations 92 and 96 during 1990-1991. At both stations, there was a decrease in TDS during fall-winter as surface waters mixed with deeper waters with lower TDS (e.g. see Fig. 4-2). The seasonal minimum in TDS concentration in surface waters occurred during the period of winter mixing (January-March) at 5150-5200 mg L^{-1}. After winter mixing ceased in March, there was a gradual increase in mean TDS concentration of surface waters at both stations. Linear regression of TDS vs. month for March-August yielded increases of 41.0 (r=0.96; P<0.01) and 35.9 mg L^{-1} month^{-1} (r=0.89; P=0.04) for
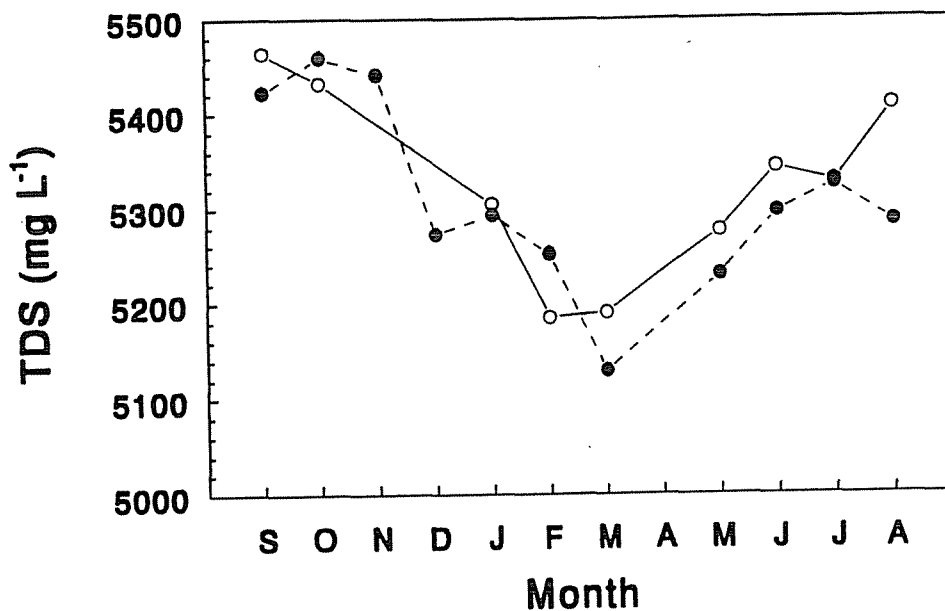

Figure 5-3. Mean concentration of total dissolved solids (TDS) in surface waters at stations 92 (o) and 96 (●) during 1990-1991. Values are volume weighted averages of samples collected 0-20 m.

stations 92 and 96 respectively. Assuming a simple salt balance for surface waters, these increases in TDS concentration translate to evaporation rates of 0.16 and 0.14 m month^{-1} with higher evaporation at 92. Since river inflow during this period was negligible (see section 10), the evaporative losses from the epilimnion should contribute to an overall drop in lake elevation. Indeed, the observed drop in lake elevation was 0.145 m month^{-1} during March-July which is similar to our estimates of evaporative loss through simple salt balances of surface waters.

In contrast to pronounced seasonal variations in surface waters, the physical properties of bottom waters were relatively constant throughout 1990-1991. At all times, bottom waters (>60 m) were cold (<6°C) and dense (σ_t = 3.3±0.1 mg L^{-1}). Hypolimnetic TDS concentration, in contrast to surface waters, was also relatively constant with time. At both stations 92 and 96, there was no significant (P>0.50) trend in TDS concentration in the hypolimnion (>25 m). Indeed, volume weighted mean TDS concentration at station 96 varied 5186-5326 mg L^{-1} during 1990-1991 with the maximum in January and minimum in October. The lack of a trend was also evident at station 92 where hypolimnetic TDS concentration varied 5193-5333 mg L^{-1}. The physical properties of bottom waters for 1990-1991 were identical to those observed during 1989-1990.

Oxygen

Seasonal variations in dissolved oxygen (DO) concentration of surface waters (0-20 m) during 1990-1991 were similar to 1989-1990. During fall, DO increased as water temperature cooled due to the higher solubility of oxygen in cold water relative to warm water. In September, DO was 7.75-8.42 mg L^{-1} in surface waters or 101-113% of saturation. DO concentration was 8.36-9.20 mg L^{-1} (85-94%) in December and >9.3 mg L^{-1} (88-97%) by February with the numbers in parentheses indicating percent of saturation. Two factors probably contribute to the undersaturation of surface waters with respect to the atmosphere during winter: (1) the mixing of surface waters with low DO bottom waters and (2) a

disequilibrium between surface waters and the atmosphere as the solubility of oxygen rapidly increased due to decreasing surface water temperature.

Conversely, DO concentration of surface waters decreased during spring-summer as surface waters became warmer (see Fig. 5-2). Although always near saturation (91-103%), DO concentration decreased from >9.8 mg L^{-1} in May to 8.36-9.07 mg L^{-1} in June to 8.04-8.67 mg L^{-1} by July. This continual decrease during spring-summer can be attributed to the decrease in solubility of oxygen as water temperature increases. This pattern is identical to the one shown in Fig. 4-3 for spring-summer 1990.

More important than the seasonal variations in DO concentration in surface waters was a continual decrease in bottom water (60-100 m) DO concentration at station 96. Figure 5-4 shows volume weighted mean DO concentration in bottom waters during 1990-1991. Throughout most of the year, DO concentration continually decreased over time. The one
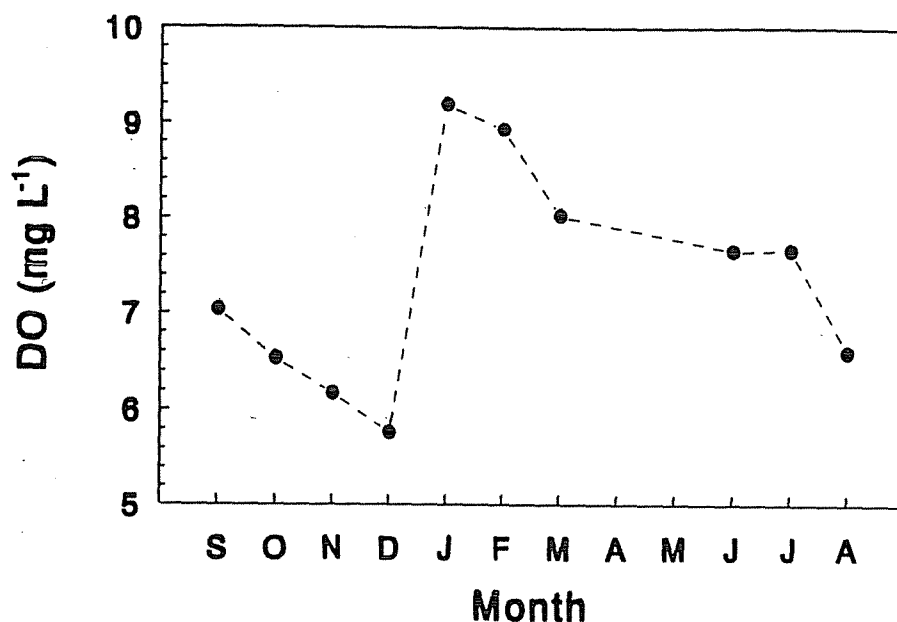

Figure 5-4. Mean dissolved oxygen (DO) concentration in deep waters at station 96 during 1990-1991. Values are volume weighted averages of samples collected 60-100 m.

exception was during December-January when lake overturn occurred and bottom water DO
was replenished. During overturn, mean bottom water DO concentration increased from 5.76
to 9.19 mg L^{-1}. After overturn, DO decreased to a relative minimum of 6.59 mg L^{-1} in
August, and presumably it would continue to decrease until the next overturn. The rate of
decrease in mean bottom water DO concentration during September-December and February-
August were -0.42 (r=1.00; n=4; P<0.005) and -0.29 mg L^{-1} month^{-1} (r=0.90; n=5; P=0.04)
respectively. The slower rate of oxygen loss during winter-summer suggests that some
additional oxygen may have been supplied to deep waters during partial stratification.

Nutrients

Nutrient concentrations measured during 1990-1991 support potential N-limitation of
phytoplankton in Pyramid Lake. Table 5-1 lists the range of nutrient concentrations in
surface and deep waters at station 96 during 1990-1991. The most available forms of N for
phytoplankton are nitrate (NO_3-N) and ammonium (NH_4-N) which were low throughout the
year. As in shown in section 4, maximum concentration of dissolved inorganic N (DIN) in
surface waters occurred during winter mixing; DIN was approximately 60 µg L^{-1} in January.
A comparison of this maximum concentration of DIN with winter dissolved phosphate (DRP)
and silicate (SiO_2-Si) suggests N should become depleted first. The mass ratios for DIN:DRP
and DIN:SiO_2-Si were 0.75 and 0.072
respectively in January compared with
approximate stoichiometry of 7.2:1:14.4 for
utilization of N:P:Si by phytoplankton
(Redfield et al. 1963). The minimum
concentrations for DRP and SiO_2-Si of 49
and 75 µg L^{-1} respectively support the
absence of P- and Si-limitation in Pyramid
Lake during 1990-1991.

Table 5-1. Range of nutrient concentrations for 1990-1991. Values are in µg L^{-1} and are given for station 96 surface (0-20 m) and deep (≥30 m) waters.

Parameter	Surface	Deep
SiO_2-Si	75-827	106-2733
NO_3-N	2-58	10-139
NH_4-N	<1-22	<1-18
TKN	595-789	542-766
DON	532-734	533-720
TP	56-90	86-103
DRP/TRP	49-80	49-100
TR-Fe	7-77	4-51

The dominant form of N in Pyramid Lake during 1990-1991 was always dissolved organic N (DON). Throughout the year, DON was always >532 $\mu g\ L^{-1}$ accounting for >85% of total N However, a large pool of DON does not affect the above conclusion regarding the strong potential for N-limitation of phytoplankton in Pyramid Lake. Lean et al. (1989) noted that most of the large DON pool in lakes is refractory and not readily available for phytoplankton use.

Seasonal changes in nutrient concentrations of surface waters (0-20 m) are shown in Figure 5-5. Values in the graph are volume weighted means of four discrete depths. DIN concentration (NO_3-N + NH_4-N) in surface waters was generally low (<20 $\mu g\ L^{-1}$) throughout the year except during January-March. During this period when the water column was vertically homogeneous and bottom waters with high DIN concentration were being mixed throughout the water column, there was a considerable increase in DIN from 14 $\mu g\ L^{-1}$ in December to 57 $\mu g\ L^{-1}$ by January. This large increase was mainly due to an increase in NO_3-N (13 to 55 $\mu g\ L^{-1}$). After maximum concentration in January, there was a rapid decrease in NO_3-N during January-April with NO_3-N concentration only 3 $\mu g\ L^{-1}$ by April. Concurrent with this winter-spring NO_3-N decrease, SiO_2-Si and DRP concentrations also decreased. However, minimum DRP (58 $\mu g\ L^{-1}$) and SiO_2-Si (75 $\mu g\ L^{-1}$) concentrations were much higher than NO_3-N. The decrease in DRP during this period was more gradual than both NO_3-N and SiO_2-Si occurring March-July. Surprisingly, NO_3-N concentration increased again during May and was 10-15 $\mu g\ L^{-1}$ throughout June-August (see discussion).

Contrasting this pattern of maximum winter concentrations of NO_3-N, DRP, and SiO_2-Si in surface waters followed by rapid decline was the seasonal pattern in NH_4-N concentration. NH_4-N concentration was highest during April (8 $\mu g\ L^{-1}$) and July (7 $\mu g\ L^{-1}$) and lowest during November-January (<2 $\mu g\ L^{-1}$). The peak in NH_4-N concentration during April follows the period of rapid utilization of NO_3-N by phytoplankton. Since the main source of NH_4-N should be through mineralization of organic matter, the source of this peak is probably breakdown of spring production.
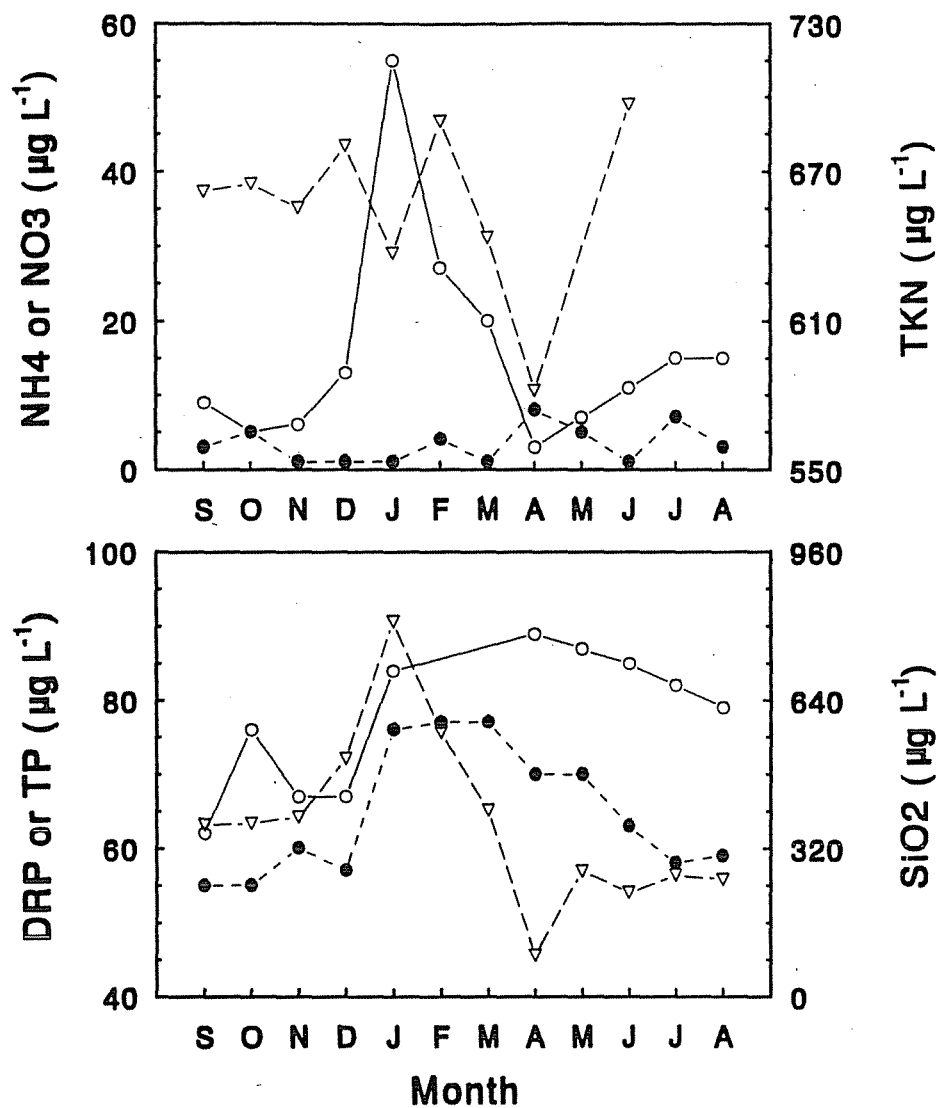
Figure 5-5. Mean nutrient concentrations in surface waters at station 96 during 1990-1991. In the upper frame, symbols indicate: (▼) total Kjeldahl nitrogen, (○) nitrate, and (●) ammonium. Symbols in the lower frame indicate: (▲) silicate, (○) total phosphorus, and (●) dissolved reactive phosphorus. Values are volume weighted averages of samples collected 0-20 m.

Seasonal changes in the concentration of nutrients in bottom waters were opposite of surface waters. Figure 5-6 shows mean volume weighted nutrient concentrations in bottom waters (60-100 m). In contrast to winter maxima in NO_3-N, DRP, and SiO_2-Si in surface waters, minima in the concentrations of these constituents occurred during winter-spring. After these minima during the spring, concentrations of NO_3-N, DRP, and SiO_2-Si generally increased, although the patterns are not as well-defined as in 1989-1990 (see Fig. 4-5). NH_4-N concentration, in contrast, was highest in bottom waters (11 µg L^{-1}) during April when maximal surface water concentration was observed.

Particulate Matter

Seasonal variations in particulate carbon (PC), nitrogen (PN), and phosphorus (PP) are shown in Figure 5-7. Values are volume weighted means for surface (0-20 m) and bottom (>45 m) waters of station 96. For all three elements, there was a relative maximum in particulate concentration in surface waters during the spring (April-May) following the decline in NO_3-N, SiO_2-Si, and DRP (January-April, Fig. 5-5). During this spring period, concentrations of PC, PN, and PP were 369-462, 44-47, and 6.5-7.2 µg L^{-1} respectively. After this spring peak, concentrations of all three parameters decreased to lower values during June-July before increasing again in August, especially PC and PN. High concentrations of particulate matter were also evident during fall 1990 when relative maxima occurred for all three elements. The lowest concentration of particulate matter occurred during winter overturn in January. At that time, the concentration of PC, PN, and PP were 244, 22, and 3.7 µg L^{-1} respectively.

The exception to this simple picture of two peaks in spring and summer-fall is a peak in PP during the late winter; PP concentration reached a maximum at 8.2 µg L^{-1} in March two months before the spring peak in all elements (Fig. 5-7). This increase in PP, which occurred in both basins of the lake, without corresponding increases in PC and PN suggests a source of P-rich particulate matter that is deficient in C and N. The source of this peak in PP
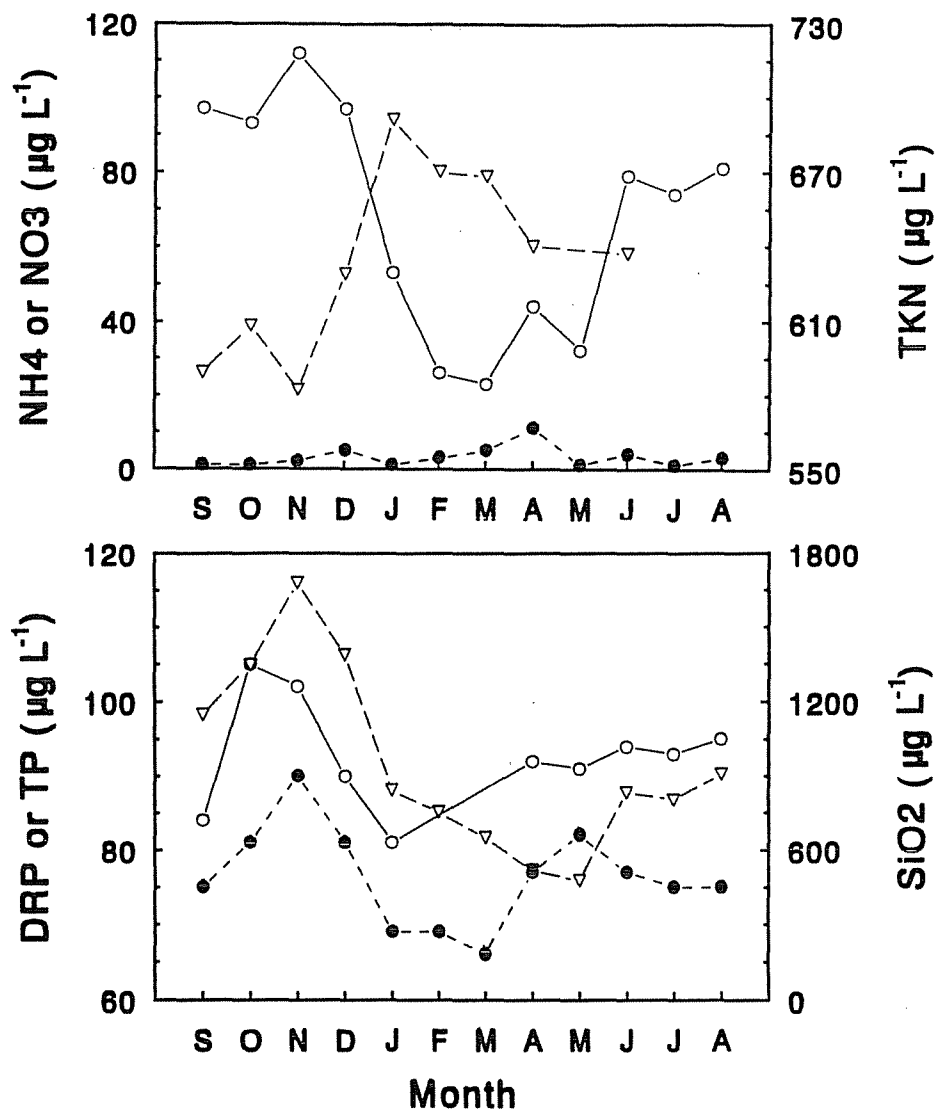
Figure 5-6. Mean nutrient concentrations in bottom waters at station 96 during 1990-1991. In the upper frame, symbols indicate: (▼) total Kjeldahl nitrogen, (O) nitrate, and (⬤) ammonium. Symbols in the lower frame indicate: (▲) silicate, (O) total phosphorus, and (⬤) dissolved reactive phosphorus. Values are volume weighted averages of samples collected 60-100 m.
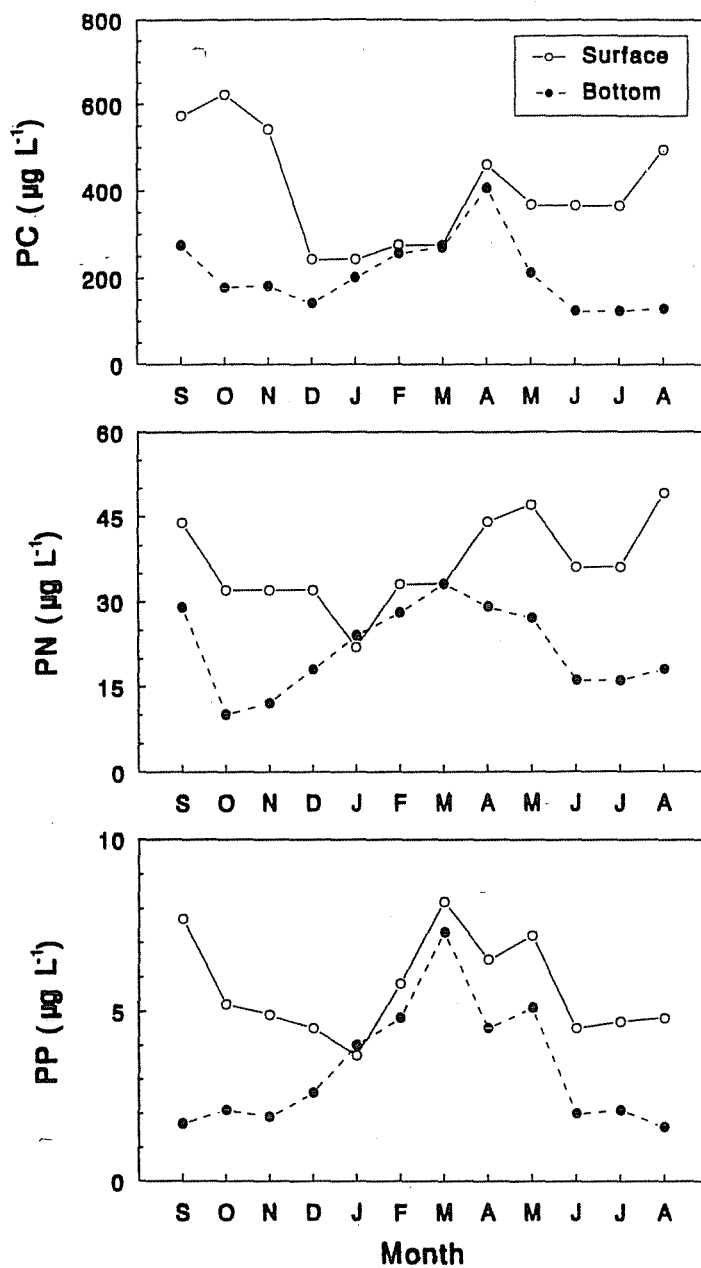
Figure 5-7. Mean concentrations of particulate carbon (PC), nitrogen (PN), and phosphorus (PP) in surface and deep waters at station 96 during 1990-1991. Values are volume weighted averages of samples collected 0-20 and ≥45 m for surface and deep waters respectively.

may be eolian input of dust to the lake during winter-spring storms. In March 1991, mean wind speed was 4.9 m s^{-1} compared with an overall annual average of 3.0 m s^{-1}. The hypothesis of high dust input during the spring is supported by previous work at the lake. Galat et al. (1981) reported that dust storms were frequent at the lake and were generally more severe during spring. The P content of dust in soils surrounding the lake will be measured to assess the validity of the proposed source in PP concentration during early spring.

Particulate matter was consistently higher in surface waters relative to bottom waters during periods of thermal stratification (Fig. 5-7). During 1990-1991, the average difference between mean surface and bottom water concentrations of PC, PN, and PP were 277±114, 20±5, and 3.1±1.3 μg L^{-1} respectively during stratified periods. These values are the non-weighted average for all months when the lake was thermally stratified and include September-December and May-August. These average differences can be compared with a similar computation for January-April, the unstratified or weakly stratified period. During January-April, the average differences between surface and bottom waters were 31±22, 5±8, and 0.9±0.9 μg L^{-1} for PC, PN, and PP respectively. The differences observed during the stratified period (n=8) were significantly different from the values during the unstratified period (n=4) at α = 0.01. The difference between these two periods is that particulate matter is concentrated in surface waters during stratified periods while it mixes freely during winter overturn.

The composition of particulate matter (POM) during 1990-1991 reflected nutrient availability in the lake. Figure 5-8 shows seasonal changes in the elemental composition of POM. In fall 1990, C:N ratio was maximal at >15. This high C:N ratio of POM during September-November indicates severe N-deficiency (Healey and Hendzel 1980). As the lake began to mix, the C:N ratio of POM decreased responding to a greater availability of N for phytoplankton. During winter mixing, the elemental composition of POM reached a minimum C:N ratio of 8.9 reflecting higher concentrations of NO$_3$-N (Fig. 5-5). Seasonal

variations in N:P ratio support N-deficiency; during all months except August, the N:P ratio of POM was <18 which is similar to the Redfield ratio of 16. This lack of P-deficiency is expected since Pyramid Lake is P-rich.

The ratio of C:P of particulate matter suggests that POM is carbon-rich. During most of 1990-1991, the C:P ratio of POM was 124-211 which is high relative to the Redfield ratio of 106 (Redfield et al. 1963). This suggests that POM is carbon-rich and contains a large fraction of structural material (e.g. cell wall). The minimum in C:P ratio of POM occurred in March when there was a peak in PP without a corresponding increase in PC (see above). Surprisingly, the C:P of POM increases during fall to values >250. Since there is no reason to suspect that phytoplankton growth is P-deficient during fall (DRP > 50 μg L^{-1}), this increase in C:P (and N:P) may indicate the accumulation of detrital material in the lake or species with heavy gelatinous coverings. Seasonal changes in phytoplankton species
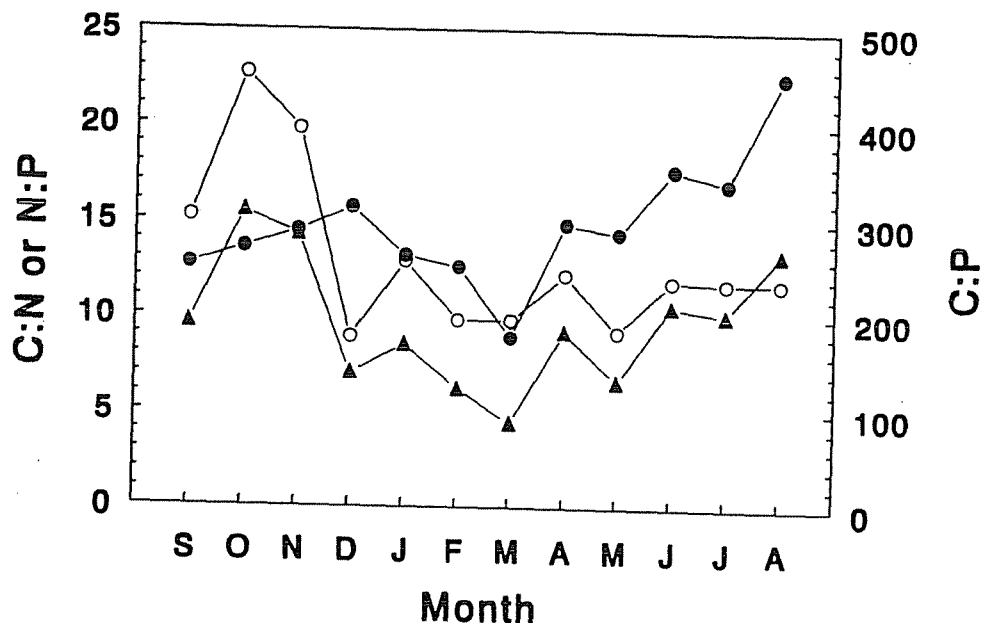

Figure 5-8. Mean elemental ratios of particulate matter in surface waters during 1990-1991. Symbols indicate (o) C:N, (●) N:P, and (▲) C:P. Values are derived from mean concentrations of PC, PN, and PP (see Fig. 5-7).

composition will be examined to differentiate between these alternatives. Previous work by Hamilton-Galat and Galat (1983) reported that 38% of particulate matter in Pyramid Lake during January 1979 was detrital supporting the accumulation of detrital matter during winter. The observed increases in C:P and N:P ratio of POM during the fall suggest that the accumulation of detrital carbon reported for winter may occur during fall-winter.

Plankton

The patterns of seasonal change in phytoplankton biomass and production were similar in 1990-1991 to observations presented in section 4. Figure 5-9 shows seasonal changes in mean chlorophyll (chla) concentration, mean rate of phytoplankton production per unit volume, and phytoplankton production per unit surface area. All three values are based on measurements in surface waters (0-30 m). Overall, annual mean areal production and mean chla were 273 mg C m^{-2} day^{-1} and 1.0 µg L^{-1} for 1990-1991 respectively.

The maximum concentration of chla was 2.6 µg L^{-1} and occurred in March during the spring bloom. During this period of relatively high phytoplankton biomass, there were also relative peaks in volume production (1.34 µg C L^{-1} h^{-1}) and areal production (325 mg C m^{-2} day^{-1}). After this spring peak in chla, concentration decreased continually during spring-summer to a minimum of 0.39 µg L^{-1} in July. Chla concentration was also low the previous fall with a mean concentration of 0.53 µg L^{-1} in November 1990. During this fall minimum in chla concentration, phytoplankton production was also low with rates of 118 mg C m^{-2} day^{-1} and 0.67 µg C L^{-1} h^{-1} for areal and volumetric production respectively.

Phytoplankton production was highest during the summer when areal production was >400 mg C m^{-2} day^{-1} (Fig. 5-9). In contrast to the minimum in chla concentration observed during July, areal and volumetric production were highest during the summer (July-August) at 441-444 mg C m^{-2} day^{-1}. Relatively high volumetric production (1.57-1.76 µg C L^{-1} h^{-1}) during this period despite low chla suggests phytoplankton were rapidly growing under high
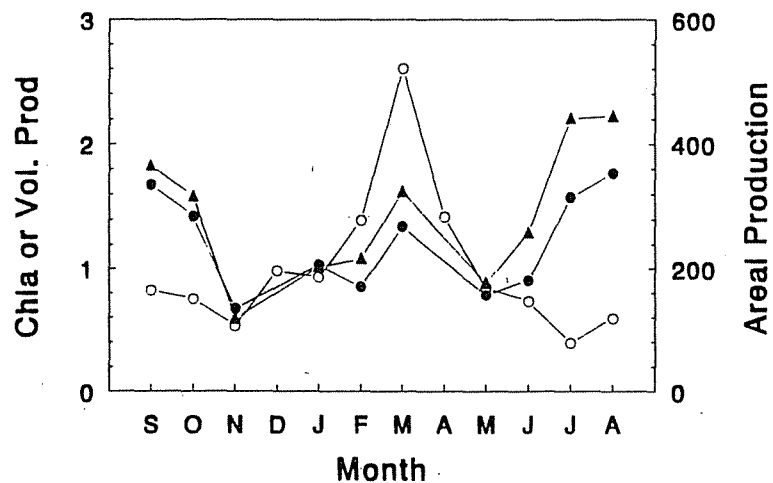
Figure 5-9. Chlorophyll (Chla, ○), phytoplankton production per unit volume (Vol. Prod., ●), and phytoplankton production per unit surface area (Areal Production, ▲) during 1990-1991. Chla and Vol. Prod. are volume weighted averages of samples collected 0-30 m.
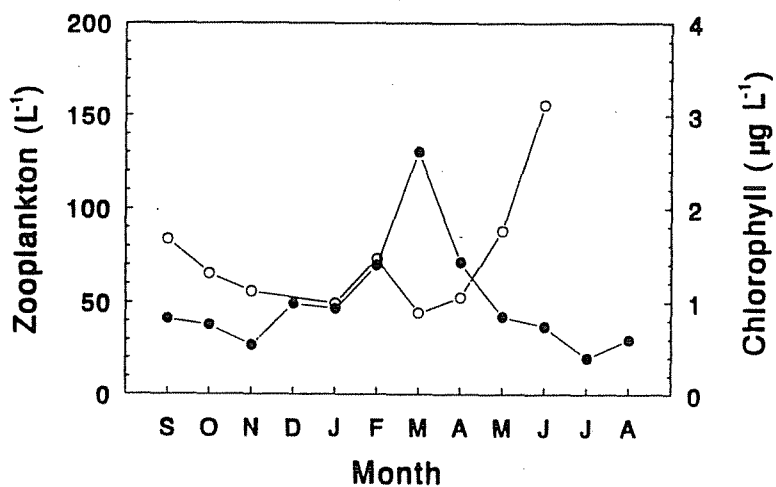

Figure 5-10. Zooplankton abundance (○) and mean chlorophyll concentration (●) in surface waters during 1990-1991.

summer insolation. We will be examining factors controlling phytoplankton growth and biomass, such as zooplankton grazing, during the coming year.

Seasonal changes in the zooplankton abundance were opposite of chla concentration. Figure 5-10 shows mean zooplankton abundance in surface waters (0-25 m) during 1990-1991. In contrast to chla, the maximum in zooplankton abundance (156 L^{-1}) occurred in June when chla was decreasing to a minimum (July). The minimum in zooplankton abundance was 44-56 L^{-1} and occurred November-April with the exception of February (73 L^{-1}). High zooplankton abundance when chla is low during summer suggests that grazing pressure may have some influence in controlling phytoplankton biomass during summer.

Discussion

Comparison of data for 1990-1991 with 1990 suggests that annual mean phytoplankton production and biomass were the same during both years. Comparing monthly weighted averages, mean annual phytoplankton production was 273 mg C m^{-2} day^{-1} in 1990-1991 compared with 269 mg C m^{-2} day^{-1} in 1990 (phytoplankton production measurements began in January 1990). Similarly, chlorophyll (chla) concentrations were also the same for both years with a slightly lower value during 1990-1991; annual mean chla was 1.0 μg L^{-1} in 1990-1991 compared with 1.1 μg L^{-1} in 1990. Clearly, overall production and biomass were the same for both years. Not surprisingly, maximum mean chla concentration in surface waters (0-25 m) was also nearly identical at 2.7 and 2.6 μg L^{-1} during spring of 1990 and 1991 respectively.

The similarity between external nutrient inputs during 1989-1990 and 1990-1991 allows the impact of the timing of winter mixing on phytoplankton production to be examined. Since Truckee River discharge into Pyramid Lake during 1989-1991 was low (<5% of 1972-1987), spring production during both years should be entirely dependent on internal nutrient loading. However, the supply of nutrients to surface waters occurred one

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month earlier in the year during 1990-1991 than the previous year. This difference in the timing of winter mixing should affect the timing of the winter-spring bloom and consequently nutrient cycling and availability after the bloom.

The winter-spring diatom bloom in Pyramid Lake was directly affected by the timing of winter overturn. As in winter 1989-1990, nutrient depletion of nitrate (NO_3-N) mixed to the surface during the winter began immediately. However, the timing of this input was one month earlier in 1990-1991 than the previous year. This earlier start for the bloom in 1990-1991 resulted in a chla maximum in March 1991 compared with April 1990. The similarity in maximum chla concentration between years suggests that the magnitude of the bloom is controlled by the initial concentration of NO_3-N during overturn (55 μg L^{-1} during both years) rather than timing.

The timing of the bloom did affect the accumulation of particulate nitrogen (PN) in surface waters during the spring. In 1990-1991, the early bloom occurred mainly during the unstratified period causing a lower efficiency in the transformation of NO_3-N into PN. The increase in PN during 1990-1991 was only 42% of the decrease in NO_3-N concentration compared with 61% during 1989-1990. This difference between years may be due to a greater retention of particulate matter in surface waters during the partially stratified bloom period in 1989-1990 compared with the unstratified bloom period in 1990-1991.

There also was a greater stripping of nutrients from the entire water column in 1990-1991 compared with 1989-1990. Figure 5-11 shows profiles of NO_3-N for May 1990 and April 1991. These two months are compared since they are the month following maximum chla during both years. In 1990, NO_3-N concentration was approximately 10 μg L^{-1} in surface waters (0-20 m) during May with higher concentrations by a depth of 30 m (>40 μg L^{-1}). The concentration of NO_3-N was similar to values during winter overturn at depths >45 m (values in deep water actually show the beginning of annual buildup (see section 4). In comparison, NO_3-N concentrations during April 1991 were much lower. The mean NO_3-N

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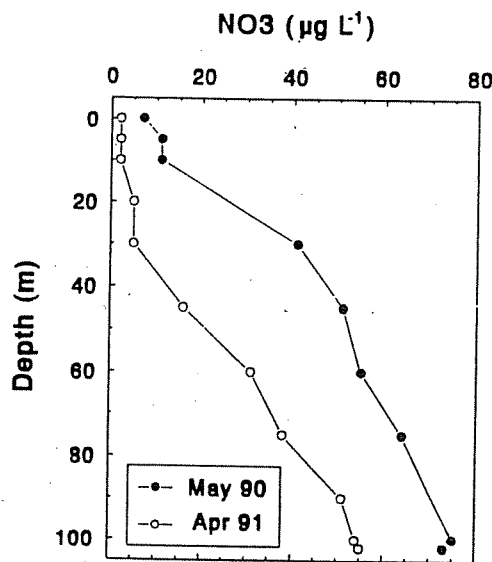
Figure 5-11. Nitrate profiles at station 96 following spring
maximal chlorophyll for 1990 and 1991.

concentration in surface waters at that time was 3 $\mu g\ L^{-1}$ with concentrations depleted down
to 75 m. In the deeper waters (60-75 m), NO_3-N concentration was 31-38 $\mu g\ L^{-1}$ in April
1991 compared with values of 55 $\mu g\ L^{-1}$ during overturn.

The greater stripping of NO_3-N during the winter-spring bloom should affect the
availability of N for phytoplankton during spring-summer. Lower NO_3-N concentration in
intermediate waters (30-60 m) should reduce the resupply of NO_3-N into surface waters
following the bloom as the gradient in NO_3-N concentration occurs deeper in the water
column. With this hypothesized lower input of "new" nitrogen to surface waters, N
availability for phytoplankton growth should be reduced causing the rate of growth to be
reduced. Comparison of areal phytoplankton production of >300 and 177-258 mg C m^{-2} day^{-1}
during May-June of 1990 and 1991 respectively supports this scenario. However, the

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elemental C:N ratio of phytoplankton biomass during May-June 1991 was 9.2 to 11.9 indicating only moderate nitrogen-deficiency rather than a more severe limitation.

Comparison of particulate matter (POM) in summer 1991 with 1990 suggests that N availability may have actually been greater during 1991 than the previous year. Indeed, the maximum C:N ratio of POM during summer 1991 was only 11.9 compared with >18 in 1990. The greater availability of N for phytoplankton during 1991 is supported by higher summer NO_3-N concentrations. In 1991, mean NO_3-N concentration in surface waters was >10 μg L^{-1} during June-August despite very low spring concentrations. Higher NO_3-N concentrations during summer 1991 may have contributed to higher areal productivity during July-August 1991 (441-442 mg C m^{-2} day^{-1}) compared with the same period in 1990 (367-398 mg C m^{-2} day^{-1}). The apparent higher NO_3-N concentrations during 1991 may also be a laboratory artifact. We are currently examining this possibility.

Summary

The timing of winter mixing had a direct effect on the timing of the winter-spring bloom. As soon as NO_3-N is mixed to surface waters, phytoplankton utilize it and accumulate biomass (chlorophyll). The beginning of the bloom during winter overturn despite active vertical mixing reinforces the supply of NO_3-N to surface waters as the primary factor triggering the winter-spring bloom in Pyramid Lake. When the bloom is early, such as in 1990-1991, NO_3-N is more efficiently stripped from deeper in the water column. However, the accumulation of particulate N in surface waters is actually less efficient as surface production is mixed deeper in the water column.

SECTION 6

Spatial Variability of Nutrients and Particulate Matter

Introduction

Knowledge of spatial variability of nutrients and particulate matter (POM) concentrations is important to our understanding of lake processes. Generally, monitoring of water quality in lakes consists of sampling a few fixed locations at different times of year. The validity of trends determined from these sparse data sets is constrained, to some extent, by a knowledge of the variability or "patchiness" of the parameters of interest. For example, is an observed increase in chlorophyll during one time of year due to a phytoplankton bloom throughout the lake or just in the parcel of water sampled at a specific location? Knowledge concerning how variable chlorophyll is in different regions of the lake on the same sampling date would help answer this question. Alternatively, an understanding of the spatial variability of nutrients and POM can help to identify sources of these parameters and help to define an appropriate sampling strategy (e.g. number and locations of sampling stations).

An understanding of the spatial variability of nutrients and POM is also critical in the design of computer models to represent and predict water quality conditions. In the construction of models, it is desirable to reduce the number of spatial dimensions that are included. This comes both from large increases in computational time and complexity with the addition of each length dimension (i.e. depth, length, and width). It is not necessarily true that more complex models are more accurate. Indeed, the opposite may be true. The addition of each length scale increases the amount of data that is needed to calibrate and validate any model. When the spatial variability of model parameters is known, decisions

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concerning the need for additional spatial dimensions can be made with greater confidence. Knowledge about spatial variability will also help identify the processes that contribute to changes in nutrient and POM concentrations. For example, higher nutrient concentrations in shallow regions may indicate more vertical exchange of nutrients in these areas of the lake.

This section of the report provides an initial examination of the spatial variability of nutrients and POM in Pyramid Lake. A more extensive evaluation of spatial variability will be conducted during the coming year. In this preliminary investigation, spatial variability is examined in three ways: an extensive synoptic sampling during May 1991, comparison of monthly monitoring data collected at stations 92 and 96, and bi-weekly transects along the north-south axis of the lake conducted during spring-fall. Data used for these comparisons are confined to 1989-1991. These data provide information concerning spatial variability throughout the lake (May 1991) and whether there are consistent differences in nutrients and POM concentrations along the north-south axis of the lake.

Methods and Sampling

The extensive synoptic sampling conducted in May 1991 included depth profiles for physicochemical parameters, nutrients, and POM at 19 stations around the lake over a three day period. The stations that were sampled are shown in Figure 6-1 with the approximate bathymetry of the lake. Stations were selected to ascertain variability along the north-south axis of the lake and across the lake (three east-west transects). In this preliminary treatment of spatial variability, data presented are restricted to surface waters (5 and 15 m) for nitrate (NO_3-N), ammonium (NH_4-N), silicate (SiO_2-Si), chlorophyll (5 m only), and particulate matter (PC, PN, and PP). A more extensive analysis of data collected in May 1991 will be conducted during the third year of the study including phosphorus and total Kjeldahl N as analyses are completed.
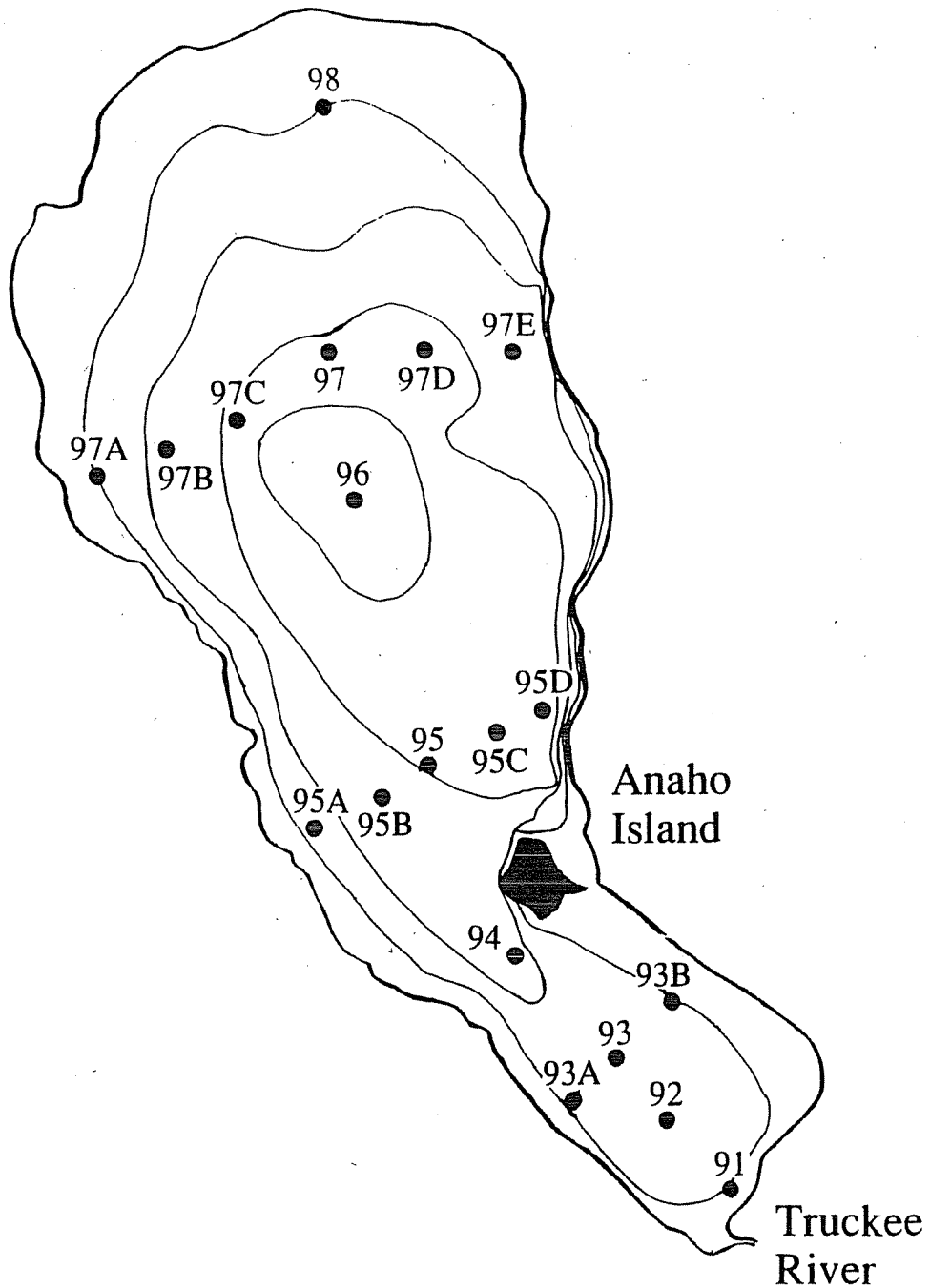
Figure 6-1. Map of station locations for 21-23 May 1991 synoptic sampling. Approximate bathymetry of Pyramid Lake is included.

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Analytical methods for nutrient, particulate matter, and chlorophyll concentrations are given in section 2.

The purpose of this section is to examine how variable nutrients and POM are along north-south and east-west transects of the lake. To determine spatial heterogeneity, surface concentrations of parameters during May 1991 are contoured by concentration interval. We also use data along transect lines across (east-west) and along (north-south) the lake to quantify spatial variability by calculating relative standard deviation of mean concentrations. Mean values reported in the text are given as the mean ± one standard deviation. Finally, we examine whether there are consistent differences in nutrient concentrations and POM in different regions of the lake by comparing data collected around the lake to the index station in the middle of the deep basin.

Results

Spatial Distributions in May 1991

The concentration of nutrients in surface waters during May 1991 are shown in Figure 6-2 with contours based on concentrations at the 19 sampling stations (see Fig. 6-1). Values presented are averages for water collected in the photic zone (5 and 15 m). NO_3-N concentration only varied 13.5-25 μg L^{-1} throughout most of the lake, but it was 32 μg L^{-1} at one station in the southern basin. The higher average concentration at that station was due to high nitrate concentration (44 μg L^{-1}) at 15 m compared with 14-25 μg L^{-1} at the other stations. Spatially, NO_3-N was higher in the shallow regions (bottom depth <50 m) of the lake (north and south) at 23.7±4.8 μg L^{-1} (n=6) compared with 17.3±2.4 μg L^{-1} for deeper regions. Even if the station on the western margin of the shallow basin (93A) was excluded, NO_3-N concentration at shallow stations was still 22.0±2.8 μg L^{-1}. Whether data for 93A was included or excluded from the calculation of mean NO_3-N concentration in the shallow basin, the difference between shallow and deep stations was significant at α=0.02. Indeed, the

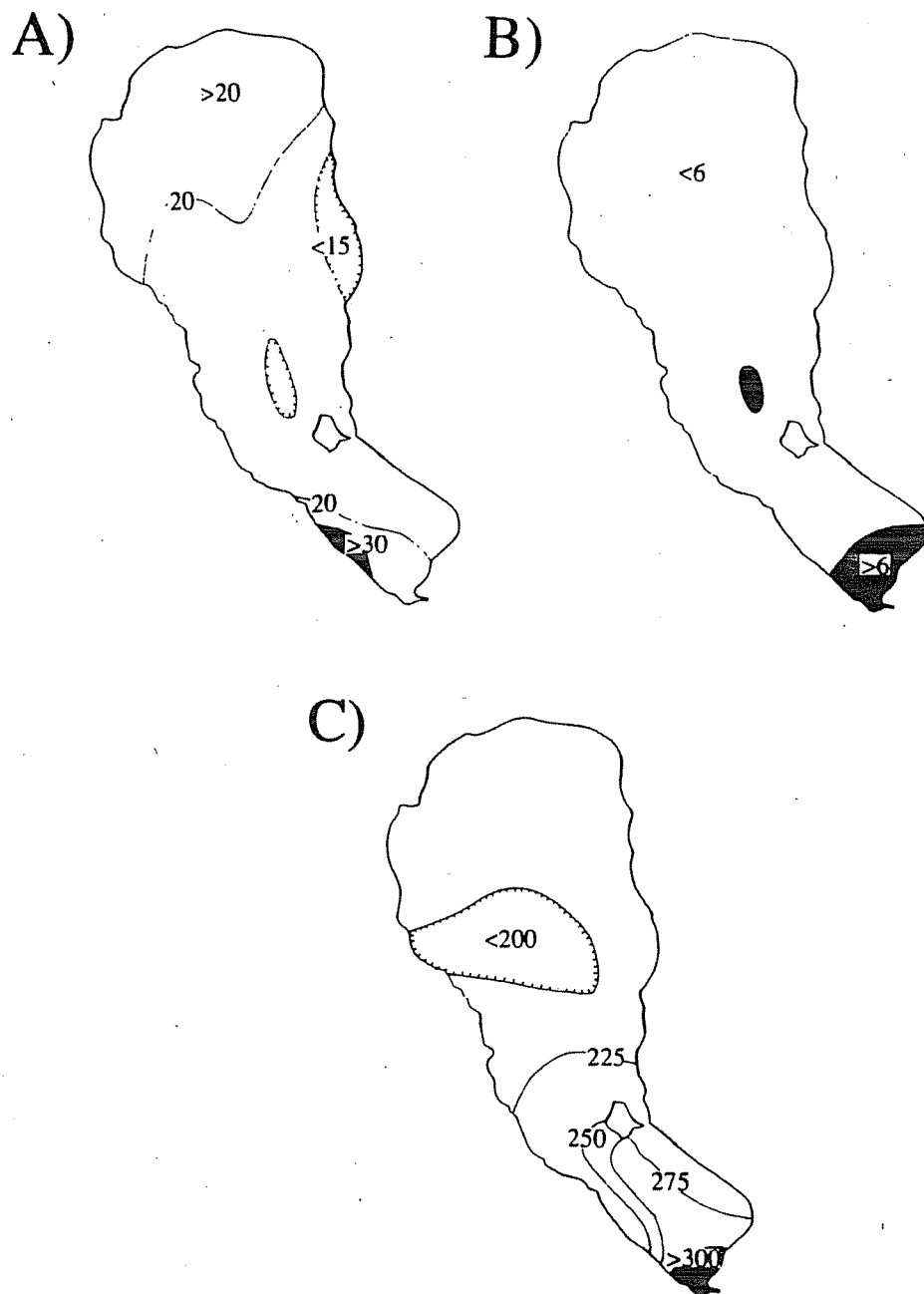Figure 6-2. Distributions of (A) NO₃-N, (B) NH₄-N, and (C) SiO₂-Si in surface waters during 21-23 May 1991. Contours are based on the 19 stations identified in Figure 6-1.

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regions of the lake where NO_3-N concentration was lowest occurred on the eastern side and in the middle of the deep basin.

Ammonium concentration was low throughout the lake with 84% of stations sampled at concentration <5 µg L^{-1}. Mean NH_4-N concentration during the May 1991 synoptic sampling was only 3.5±1.2 µg L^{-1} with small peaks of 6-7 µg L^{-1} west of Anaho Island and in the south end of the shallow basin. Since our limit of detection for NH_4-N is approximately 2 µg L^{-1}, a large fraction of the apparent variability in lake concentrations may be due to analytical variability. It is interesting that the peak in NH_4-N near Anaho Island was at the same station where NO_3-N concentration was lowest.

Spatial variations in SiO_2-Si concentration were generally small with higher concentration in the shallow basin. The range of concentrations for the synoptic sampling was 179-326 µg L^{-1} with values in the deep basin only varying from 179-234 µg L^{-1}. Generally, SiO_2-Si concentration decreased south to north with the highest concentration (326 µg L^{-1}) near the mouth of the Truckee River and lowest values (<200 µg L^{-1}) in the middle of the deep basin.

Lake-wide distributions of chlorophyll and particulate matter are shown in Figure 6-3. Chlorophyll concentrations varied from 0.41 µg L^{-1} in the middle of the lake to 1.56 µg L^{-1} south of Anaho Island with mean concentration for the lake being 0.94±0.37 µg L^{-1}. This corresponds to a relative standard deviation (RSD) of 39% for chlorophyll. Relative standard deviation is the standard deviation of the mean divided by the mean, and it is usually expressed as a percent. The RSD of 39% for chlorophyll is high compared with 23 and 16% for NO_3-N and SiO_2-Si respectively. Generally, chlorophyll was higher (>1 µg L^{-1}) in the north and south ends of the lake and lower (<0.6 µg L^{-1}) in the middle, deep region of the lake. This pattern of higher concentrations in the shallow regions of the lake was also true for PC, PN, and PP with values of >450, >40, and >7 µg L^{-1} respectively. However, the variations in PC, PN, and PP were much smaller than chlorophyll at a relative standard
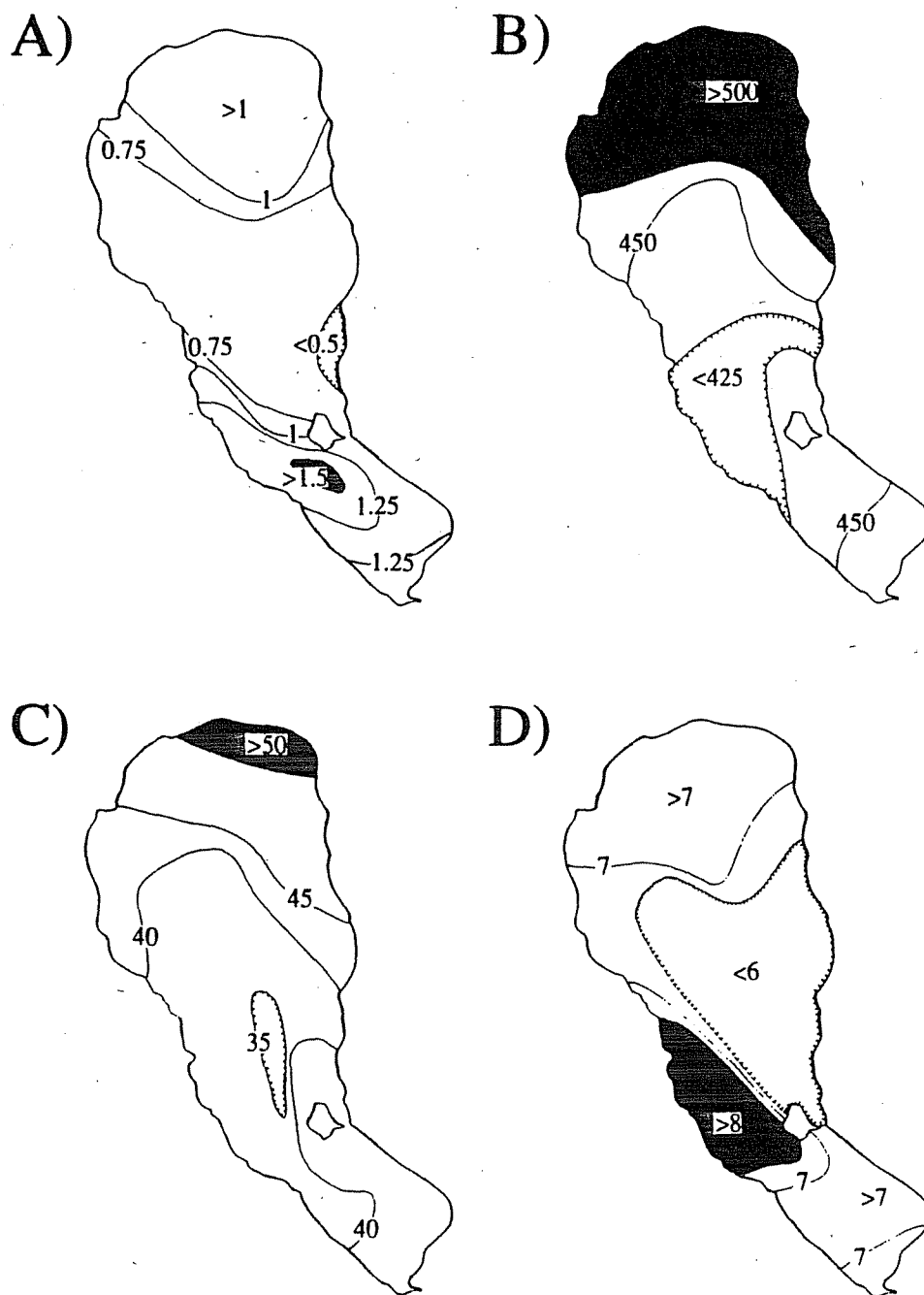
Figure 6-3. Distributions of (A) chlorophyll, (B) PC, (C) PN, and (D) PP in surface waters during 21-23 May 1991. Contours are based on the 19 stations identified in Figure 6-1.

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deviations of 9-19%. Spatial distributions of PC, PN, and PP were not identical; PC and PN were similar but PP showed a broad peak west of Anaho Island absent in both PC and PN distributions. PP concentration in this region increased from 5-7 μg L^{-1} in the main body of the lake to 8.6-9.8 μg L^{-1} (LOD = 0.2 μg L^{-1}) indicating the input of of P-rich, C- and N-poor material to this region.

Comparison of the elemental composition of particulate matter revealed that variations in C and N were similar while variations in chlorophyll and P were more independent. Figure 6-4 shows distributions of PC:chlorophyll (C:Chla), PC:PN, PN:PP, and PC:PP. Values contoured on the maps are elemental ratios derived from averages for surface waters (See Fig. 6-3). All plots reflected variations in either chlorophyll or PP rather than PC or PN. For example, C:Chla, N:P, and C:P were all high in the middle of the lake reflecting low concentrations of chlorophyll and PP in this region. Variations in C:Chla, N:P, and C:P were 41, 20, and 19% (RSD) for the whole lake respectively compared with only 6% for C:N. The distributions of elemental composition revealed two regions where PP apparently increased relative to PC and PN. These two regions were the northwest corner of the deep basin and the middle to western shore of the lake near Anaho Island. In these region, C:P and N:P ratios decreased to <150 and <12 respectively.

Variability Along Transects in May 1991

The relative variability of nutrients, chlorophyll, and POM along the four transects sampled in May 1991 are shown in Figure 6-5. Values represent the relative standard deviation (RSD) of 3-8 samples sampled in either a north-south (91-98) or east-west (93, 95, & 97) orientation. Variability of NO$_3$-N and SiO$_2$-Si were generally low (<21%) except for the 93 transect where NO$_3$-N variability was 33% due to one high value and a low number of samples (n=3). The higher (>40%) RSD observed for NH$_4$-N along two transects was due to low concentrations. Mean NH$_4$-N concentration on all transects was 3.5-4 μg L^{-1} with standard deviations of 0.6-1.8 μg L^{-1}. These standard deviations for mean concentration along
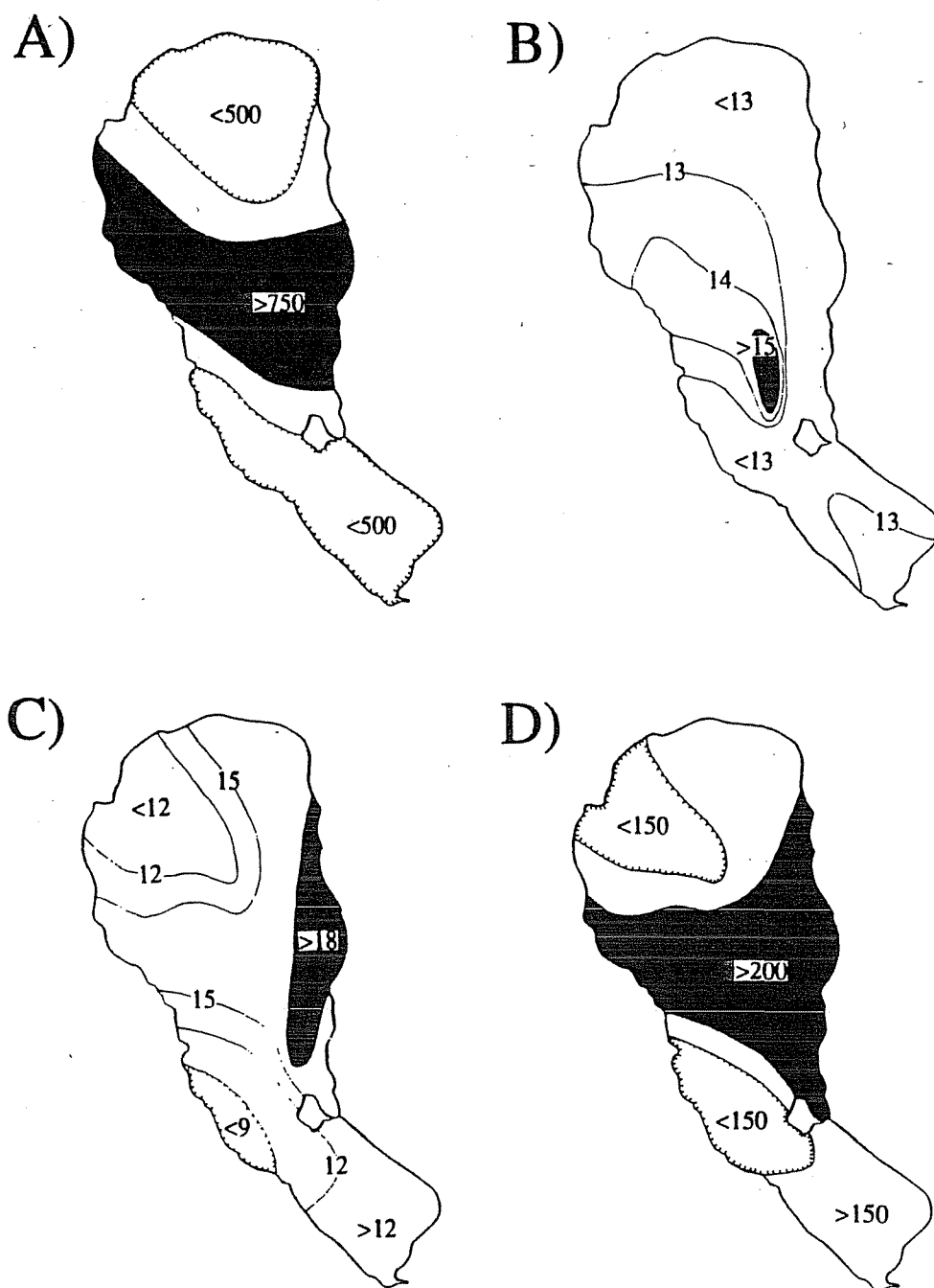
Figure 6-4. Distributions of (A) C:Chla, (B) C:N, (C) N:P, and (D) C:P in surface waters during 21-23 May 1991. Contours are based on values derived from mean parameter concentrations for data collected at the 19 stations identified in Figure 6-1.
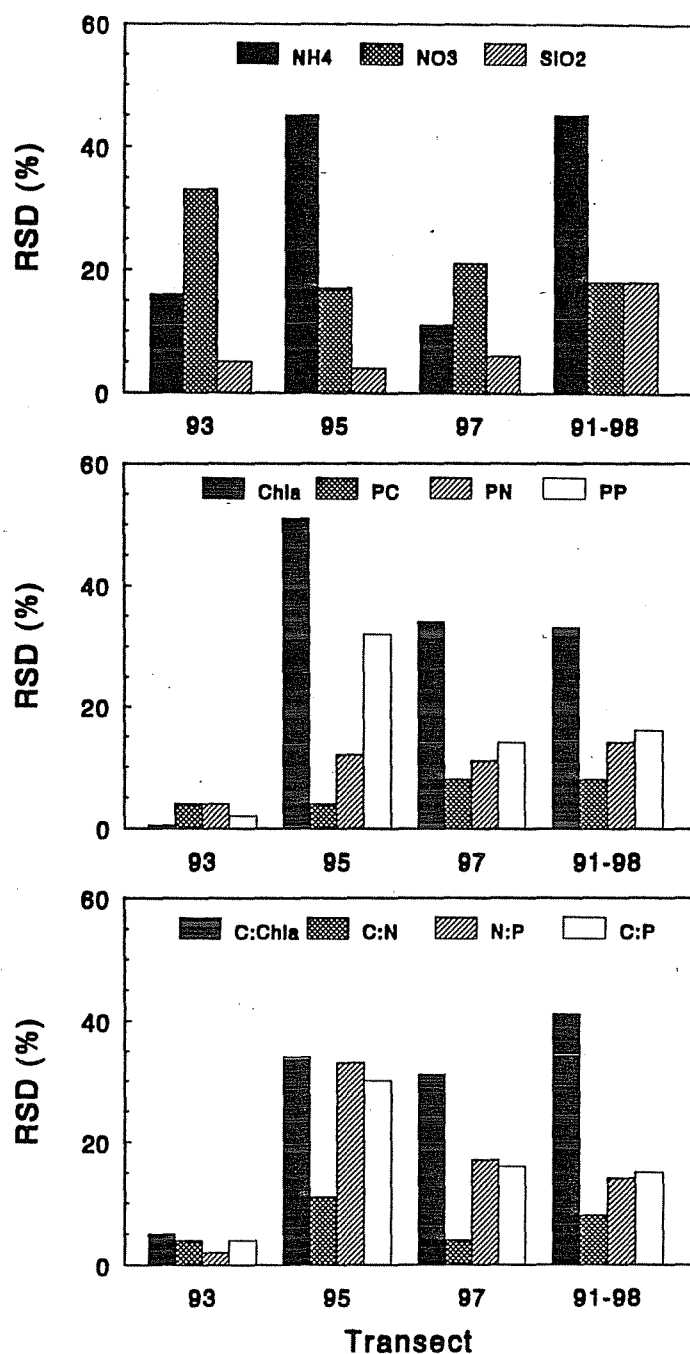
Figure 6-5. Relative standard deviation (RSD) along four transects sampled during 21-23 May 1991 for nutrients, chlorophyll, and POM. Transects 93, 95, and 97 are east-west while 91-98 is north-south (see Fig. 6-1).

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the transects were similar to precision estimates for NH_4-N analysis at concentrations of 1-10 $\mu g\ L^{-1}$ (1.3 $\mu g\ L^{-1}$, n=103, Lebo et al. 1991) indicating the higher variability may be largely analytical.

The parameter with the largest variability along transects was chlorophyll (Fig. 6-5). Except in the shallow basin (93 transect), RSD for chlorophyll was >30% with a maximum of 51% for the 95 transect across the southern portion of the deep basin. This suggests that chlorophyll concentrations around the lake exhibited patchiness. The higher spatial variation in C:Chla (31-41%) was due to these variations in chlorophyll concentration.

The variability of POM along transects was generally similar to that observed for nutrients (4-16%, Fig. 6-5). The one exception was PP along the 95 transect. Along that transect, regions of maximum and minimum PP were sampled causing RSD to be similar to chlorophyll at 32%. Lower RSD (14%) for the 97 transect suggests that the higher east-west variability observed on the 95 transect is not universally true for the whole deep basin. When the elemental composition of POM was examined (C:N:P), variations in elemental ratios were due mainly to higher variability of PP; variations in N:P and C:P were similar in relative magnitude (RSD) to variations in PP, which were always higher than RSD for PC and PN. This indicates that processes contributing to the enrichment in PP relative to PC and PN dominated the variability of the elemental composition of POM during May 1991.

Comparison of Basins

Potential differences in nutrient and POM concentrations between the shallow and deep basins of Pyramid Lake were examined using data from the May 1991 synoptic sampling and monthly monitoring samplings from 1989-1991 (n=23). These two data sets provide information concerning: (1) whether there were differences between parameter concentrations in each basin during May 1991 and (2) whether there were consistent differences between the basins over the first two years of our study. For example, were

nutrients consistently higher in the shallow basin? The comparison between values at stations 92 and 96 also provides information concerning the interbasin patchiness of nutrients and POM. If the difference in the concentration of a parameter, such as NO_3-N concentration, between basins is generally large but not consistently higher in either basin the mean difference will be small but RSD of the mean will be high. Therefore, high RSD indicates a large degree of patchiness for a parameter.

Table 6-1 lists mean nutrient, chlorophyll, and POM concentrations for the deep (n=13) and shallow (n=6) basins during the May 1991 synoptic sampling. The values presented are the average of all values within each basin with the dividing line separating basins assumed to be at Anaho Island (See Fig. 6-1). Parentheses around the probability indicate that higher concentrations occurred in the shallow basin. For the synoptic sampling, chlorophyll and nutrients were generally higher in the shallow basin, but only the differences for chlorophyll and SiO_2-Si were significant at $\alpha < 0.05$. The concentration of particulate matter was, in contrast, identical in both basins (P>0.50). For PC, PN, and PP, the

Table 6-1. Comparison of deep and shallow basins of Pyramid Lake for data collected during 21-23 May 1991. Values shown are the mean, standard deviation of the mean (s), and the number of samples from each basin (N). The probability that there was no difference between basins for each parameter (P) is given in the last column with significant differences highlighted with an asterisk.

Parameter	Deep Basin			Shallow Basin			P
	Mean	s	N	Mean	s	N	
NH_4-N	3.4	1.3	13	4.3	1.0	6	(>0.1)
NO_3-N	18.3	3.7	13	21.6	5.3	6	(>0.1)
SiO_2-Si	211	16	13	295	49	6	(<0.01) *
Chla	0.76	0.31	12	1.29	0.17	6	(<0.01) *
PC	455	45	13	452	25	6	>0.5
PN	40.4	5.4	13	40.8	1.8	6	(>0.5)
PP	6.6	1.4	13	6.9	0.9	6	(>0.5)
C:Chla	667	209	12	354	49	6	<0.01 *
C:N	13.2	0.9	13	12.9	0.5	6	>0.2
N:P	14.4	3.2	13	13.2	1.3	6	>0.2
C:P	189	39	13	170	20	6	>0.1

differences between basins were small (<4%) compared with overall concentrations. Although the elemental composition ratios of POM showed more difference than concentrations with higher values in the deep basin, the relative percent differences between basins were only 2-11%. The significantly lower mean value for C:Chla in the shallow basin was due to significantly higher chlorophyll concentration in that region, as previously noted.

The difference between concentrations of nutrient, chlorophyll, and POM for monthly monitoring samplings at stations 92 and 96 are shown in Table 6-2. In this comparison, volume weighted mean parameter concentrations in surface waters (0-20 m) were used. The mean value reported in the table is the average of the difference between station 96 and 92 (e.g. 96-92). For all parameters except SiO_2-Si, the mean difference in parameter concentrations between basins was not significantly difference from zero (Student's t-test, α=0.05). Figure 6-6 plots the mean difference between basin concentrations for each parameter normalized to the midpoint of its range of values (i.e. maximum+minimum/2) during 1989-1991. The error bars denote RSD for the mean difference in parameter concentration between basins. For P (total and dissolved) and total Kjeldahl N concentrations, both mean differences (0.2-1%) and RSD of the difference (2.5-6.8%) were small relative to concentrations in the lake, which were always high (See Tables 4-1 and 5-1). The deviations in the relative differences for NH_4-N, NO_3-N, chlorophyll, and POM between basins were higher (17-21%) indicating a greater patchiness for these parameters.

Table 6-2. Comparison of nutrient chlorophyll, and particulate matter concentrations collected monthly at stations 92 and 96 during 1989-1991. Values used in the comparison are the volume weighted average of surface waters with statistics on the <u>difference</u> reported in this table (see text). Reported parameters are the mean, standard deviation (s), number of samples in the comparison (N), and the probability of no difference between stations. The only significant difference is indicated with an asterisk.

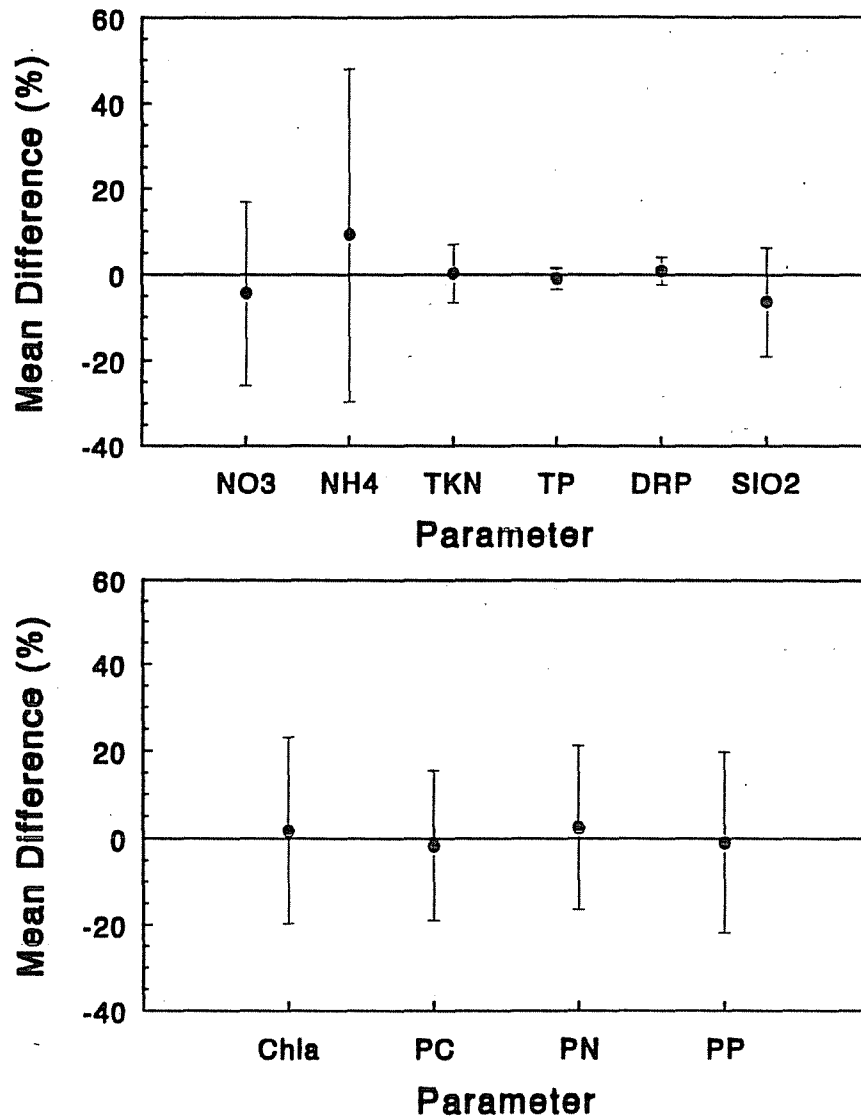| Parameter	Mean	s	N	P
NO_3-N	-1.3	6.2	21	>0.2
NH_4-N	0.6	2.6	21	>0.2
TKN	1.1	40.7	18	>0.5
DRP/TRP	-0.7	2.0	16	>0.2
TP	0.5	1.7	15	>0.1
SiO_2-Si	-29	57	21	<0.05 *
Chla	0.02	0.35	19	>0.5
PC	-11	110	21	>0.5
PN	1.2	9.4	20	>0.5
PP	-0.7	1.5	11	>0.5

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Figure 6-6. Mean difference between stations 96 and 92 for nutrients, chlorophyll, and POM expressed in percent for 1989-1991. Error bars denote one relative standard deviation of mean difference.

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Comparison of Bi-weekly Transects

The spring-fall bi-weekly transects (n=10) along the north-south axis of the lake were used to compare concentrations of nutrients in different regions. In this comparison, NH_4-N, NO_3-N, SiO_2-Si, total Kjeldahl nitrogen (TKN), and total phosphorus (TP) concentrations at transect stations were compared with the concentrations measured at station 96 in the middle of the deep basin for the same transect. The means and standard deviation of these differences between concentrations at transect stations and 96 were computed and compared with zero using the Student's t-test to ascertain whether concentrations were consistently different. Table 6-3 lists the mean differences between basins for parameters listed above. Generally, the positive values for mean difference between transect stations and the middle of the deep basin indicated that the concentrations of nutrients were consistently higher in all regions of the lake relative to station 96. When values for all stations (91-95, 97-98) were included, concentrations at transect stations were higher than the middle of the deep basin 79% (NH_4-N), 71% (TKN), 64% (SiO_2-Si), 74% (TP), and 82% (NO_3-N) of the time.

Table 6-3. Comparison of bi-weekly transect stations along the north-south axis of the lake to station 96 in the middle of the deep basin. Values are mean difference between each station and 96 (e.g. 96-station). The number in parentheses after each parameter is the number of transects for which data was available.

Parameter	91	92	93	94	95	97	98
NO_3-N (10)	2.0	1.2	1.4	1.0	0.7	1.9	1.3
NH_4-N (7)	5.3	1.4	1.7	0.7	1.0	1.7	0.6
TKN (6)	177	23	98	96	31	88	86
TP (7)	3.7	0.4	1.9	2.7	-0.5	2.9	2.1
SiO_2-Si (4)	4.0	17	34	17	21	8	0

Table 6-4. Probability of no difference between transect stations and 96 for mean values listed in Table 6-3. Significant differences are highlighted with an asterisk.

Parameter	91	92	93	94	95	97	98
NO_3-N	<0.05 *	>0.1	<0.05 *	>0.1	>0.2	<0.05 *	>0.2
NH_4-N	<0.01 *	0.05-0.01	>0.1	>0.5	>0.5	>0.1	>0.2
TKN	<0.05 *	>0.5	>0.1	>0.2	>0.5	>0.1	>0.2
TP	0.05-0.1	>0.5	>0.2	>0.2	>0.5	>0.2	>0.1
SiO_2-Si	>0.1	>0.2	>0.1	>0.5	>0.2	>0.2	>0.5

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The probability of a significant difference between the transect stations and the middle
of the deep basin is listed in Table 6-4 for all nutrients included in this comparison. Despite
the large number of samples with a higher concentration relative to station 96 values, mean
values were only significantly different from zero for N species for five comparisons at three
locations. These were at station 91 (NH_4-N, NO_3-N, and TKN) and NO_3-N at stations 93 and
97. SiO_2-Si concentrations were consistently different at stations in the shallow basin, but the
low number of transects with SiO_2-Si data (n=4) limited the power of the present comparison
to detect differences.

Discussion

A knowledge of the spatial variability of nutrients, chlorophyll, and particulate matter
(POM) concentrations in lakes is important to the overall understanding of nutrient cycling
and productivity. It is also essential in interpreting sparse data sets with any confidence.
Extensive synoptic sampling is an important component of any field sampling program and
provides a large amount of information concerning spatial heterogeneity of nutrients and POM
over a short period of time. It also can help identify sources of nutrients to the lake or
regions where concentrations are higher than index stations. However, synoptic samplings do
not supplant less intensive efforts on regular intervals, but they provide a good compliment.
Information from both sources contribute to the framework for the construction of models to
describe and predict nutrient cycling and productivity.

Nutrient concentrations that remained relatively high during all times of the year
showed low spatial variability. Spatial variability of SiO_2-Si, total phosphorus (TP), and total
Kjeldahl N (TKN) were all low during 1989-1991 with the relative deviation of the difference
between stations 96 and 92 being 2.5, 3.2, and 12.6% for TP, TKN, and SiO_2-Si respectively.
The higher variability of SiO_2-Si relative to TP and TKN was due to the enrichment of
SiO_2-Si in the southern basin near the Truckee River. Despite low flow in 1991 (See Section
10), SiO_2-Si at station 91 to increase to 326 µg L^{-1} relative to 271-278 µg L^{-1} at stations

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92-93 due to high SiO_2-Si concentration in the Truckee River (18.1 mg L^{-1}). During years with more normal river inflow, SiO_2-Si concentrations should be more variable reflecting high Truckee River inputs of this parameter, and in years with high flow, SiO_2-Si should be greatly elevated. The concentration of SiO_2-Si at station 92 during April 1986 was >14 mg L^{-1} supporting this hypothesis.

High spatial variability (RSD=15-40%) of POM, chlorophyll, and dissolved inorganic N fractions indicates that these parameters exhibit patchiness in Pyramid Lake. Higher NO_3-N, POM and chlorophyll in shallow regions of the lake suggests that these regions may be more productive than deeper regions of the lake. The supply of "new" sources of nutrients to surface waters in these regions needs to be more closely examined. It is interesting that minimum NO_3-N, maximum C:N, and maximum NH_4-N all occurred at the same location. This suggests that patches of water may be somewhat isolated during transport around the lake causing phytoplankton production to respond to local nutrient conditions.

One source of regional enrichment of PP appears to be the input of dust through wind transport. This input appears to be confined to two regions in May 1991: the northwest portion of the deep basin and west of Anaho Island. Since the prevailing wind pattern for several days prior to the synoptic sampling in May 1991 was out of the northwest, both of these regions are downwind from sources of dust on the western shore of the lake. The importance of eolian P loading to the lake will be more closely examined during the coming year.

The locations of nutrient enrichment during May 1991 suggests that upwelling was occurring in the north end of the lake and on the western side of the shallow basin. Upwelling of nutrient-rich deeper waters in these regions is consistent with the pattern of surface transport and wind direction at the time of the synoptic sampling; northwest winds caused surface currents to move toward the south end of the lake during May 1991. The transport of surface waters toward the south required (by conservation of water mass) that

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deeper waters come to the surface in the north end of the lake to replace waters moving to the south. Indeed, the folklore of the Pyramid Lake Paiute Indians expressed by tribal elders suggests that prevailing surface currents at the lake are toward the south and that waters are returned to the north end of the lake through northward subsurface flow.

Physicochemical data collected during sampling of the north-south transect of the lake during August 1990 support northward subsurface flow. Figure 6-7 shows dissolved oxygen and sigma-t, a measure of water density, contoured against distance and depth. Both parameters suggest that intermediate depth water (20-40 m) in the shallow basin (0-10 km distance from the Truckee River) was being transported into the deep basin. Generally, water mixes down isopleths of constant sigma-t under the acceleration of gravity. In the plot of sigma-t, isopleths of constant density are sloped from a depth of 30-40 m at station 92 (4 km) toward a depth of approximately 60 m at station 96 (23 km). The occurrence of subsurface exchange between the basin and upwelling in the north will be examined further in the coming year.

Models constructed to examine nutrient cycling and productivity in Pyramid Lake must account for several sources of nutrients identified in the synoptic sampling of the lake. These include: (1) wind induced surface transport to the south of the lake and subsurface return flow toward the north, (2) eolian input of P in dust, and (3) Truckee River inputs at the south end of the lake.

The patterns of spatial variability discussed in this section probably represent a conservative estimate of true variability in the lake. This is due to the minimal influence of two of the main sources of variability in Pyramid Lake: river inflow and large blooms of *Nodularia spumigena*. In years when river flow is high or the *N. spumigena* bloom is large, variability should be much higher. We will be examining the importance of these additional sources of variability to the overall variability of parameters in Pyramid Lake during the coming year.
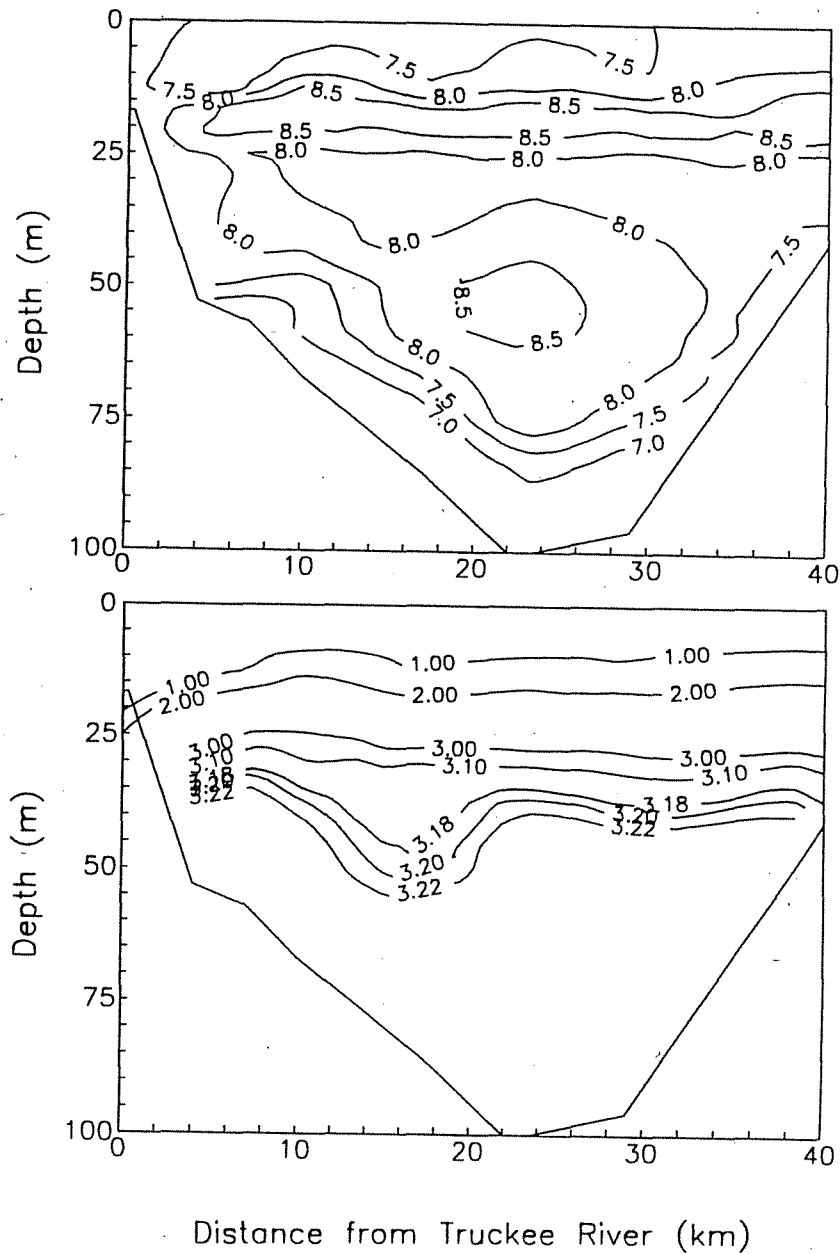
Figure 6-7. Dissolved oxygen (upper) and sigma-t (lower) in mg L^{-1} contoured versus depth and distance from the Truckee River for August 1990. Contours are based on depth profiles of temperature, conductivity, and dissolved oxygen measured at stations 91-98. As a reference, stations 92 and 96 are located at 4 and 23 km respectively.

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Conclusions

The spatial variability of P, total Kjeldahl nitrogen, and SiO_2-Si were relatively small, although variations in silicate would be much greater during years with more normal river inflow. Small variations in these parameters were contrasted by larger variations (15-40%) in NO_3-N, NH_4-N, particulate matter (POM), and chlorophyll concentrations. The higher variability in chlorophyll and POM can be attributed to patchiness of these parameters around the lake. Generally, the variations of these parameters was greater in the larger, deep basin where transect distances were longer.

Although nutrients were generally higher in the shallow basin, only SiO_2-Si was consistently different between the two index stations (station 92 and 96). A comparison of nutrient concentrations along the north-south transects of the lake during spring-fall indicated that concentrations were lowest at the center of the deep basin and higher in all regions of the lake. However, only N fractions for five comparisons and three locations were significant at $\alpha=0.05$. The power of these comparisons will improve when more data is available with which to make comparisons.

SECTION 7

Nitrogen Limitation in a Saline, Desert Lake [1]

Abstract

The increase in human development in the downstream portion of the Pyramid Lake drainage basin has resulted in increased nutrient loading to the lake. Since this is a deep, terminal lake, concern exists over nutrient build up and a change in trophic status. On the basis of lake chemistry which shows consistently high concentrations of total reactive P (40-70 μg P L^{-1}) and variable low concentrations of dissolved inorganic N (DIN), it has been hypothesized that Pyramid is N-limited, however, no systematic study of nutrient limitation had been undertaken. Nutrient enrichment bioassays conducted throughout the past two years showed that additions of DIN dramatically stimulated chlorophyll production; addition of 20 to 100 μg L^{-1} of nitrate caused mean stimulation of chlorophyll production to be 169 to 365% relative to controls. Phosphate or dissolved iron, when added singly or in combination with DIN, had no effect. This positive response to N addition was significant at all times of year except: (1) immediately after complete lake mixing in February when a large pool of hypolimnetic nitrate was mixed into the euphotic zone and (2) when N-fixing blue-green algae comprised a large fraction of the phytoplankton assemblage. The stimulatory response to N addition was strong during all other times of year. However, the seston exhibited a gradual depletion of N relative to C after winter overturn. In 1990, C:N ratios of seston suggested no N-deficiency in phytoplankton biomass during February-April, moderate deficiency in May-July and severe deficiency from August until winter overturn. The

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depletion of N in seston during 1991 was less dramatic with elemental C:N only increasing to 12 during summer compared with >18 the previous year. Overall, dissolved nutrients, bioassays results, C:N ratio of seston, and a high affinity of plankton for NO_3-N all support N-limitation in Pyramid Lake with limitation being less severe in 1991 compared with 1990.

Introduction

The relationship between nutrient availability and algal growth represents a cornerstone in limnological research over the past 50 years (e.g. Goldman 1960; Edmondson 1972; Vollenweider 1976; Schindler 1988). In particular, considerable emphasis has been placed on the importance of P in lake eutrophication. This conclusion has largely been based on the following: (1) the popular empirical models of Vollenweider (1968, 1976) and Rast and Lee (1978) which provide strong statistical relationships between lake P concentration and chlorophyll in a variety of lakes, (2) experimental evidence showing that changes in P loading and concentration can affect phytoplankton productivity and biomass (Schindler 1974; Edmondson and Lehman 1981), (3) the fact that removal of P from wastewater is much easier to achieve than N-removal (Wetzel 1983), and (4) the hypothesis that lakes can respond to N reduction by increasing N-fixation (Schindler 1977). While there is little doubt that P is an important limiting nutrient in freshwaters, the role of N in lake eutrophication has also been documented (Goldman 1981) and may be especially important on a regional basis. Recently, Elser et al. (1990) reviewed the existing bioassay literature on P and N in lakes of North America and concluded that, in freshwaters, N as a limiting factor may have a more important role than previously recognized.

Pyramid Lake, Nevada is one of the largest semi-arid, saline lakes in North America and is located in the desert environment of the Great Basin. It occupies a closed basin (i.e. without a channelized outflow) and receives 84% of its annual water input from a single major tributary, the Truckee River (Van Denburgh et al. 1973). Development and urbanization in the immediate upstream drainage basin influences water quality in the Truckee

Nitrogen Limitation

River and consequently, Pyramid Lake. There is increased nutrient loading from regional wastewater treatment facilities as well as non-point source discharges from local agricultural land. Galat (1990), notes that this is becoming particularly critical to lakes and reservoirs in the arid western United States, where population growth is accelerating and demand for water is intense. Management of nutrient inputs to terminal lakes like Pyramid is especially important since these systems must rely primarily on sedimentation and permanent burial for nutrient removal.

In desert environments, terrestrial plant production is classically limited by N (Hadley and Szarek 1981). Since transport of allochthonous organic matter to desert lakes is low, the amount of terrestrial N-loading to these waters will also be reduced (Galat 1986; Galat and Verdin 1988). Furthermore, higher rates of erosion from sparsely vegetated soils in these regions carry increased sediment and associated P. In mountainous areas, such as the basin occupied by Pyramid Lake, this condition will be exaggerated. These conditions result in the characteristically low N and high P content in Pyramid Lake and in arid and semi-arid lakes in general (Goldman and Horne 1983). Given this, and the observation that N-fixation by the blue-green alga *Nodularia spumigena* can account for 80% of the annual combined N input, Pyramid Lake should be N-deficient (Horne and Galat 1985; Galat and Verdin 1988).

In this section we report the results of nutrient limitation studies performed in Pyramid Lake between October 1989 and August 1991. We have: (1) examined water column ratios of dissolved and total N and P, (2) conducted monthly nutrient enrichment bioassays using natural phytoplankton populations, (3) compared seston ratios of C and N, and (4) measured seasonal rates of N-fixation, and (5) conducted preliminary experiments to determine the kinetic parameters of N-uptake. We examine data in an attempt to distinguish between nutrient stimulation, deficiency, and limitation.

Nitrogen Limitation

Materials and Methods

See Section 2 for a complete description of the study site, sampling, chemical analyses, and bioassay design.

Results

The existence of N-limitation was not suggested by the ratio of total N (TN) to total P (TP). Potential N-limitation is often evaluated by comparing the concentrations of N and P in the lake to the Redfield ratio for average phytoplankton biomass (106:16:1 for C:N:P atoms, Redfield et al. 1963). In Pyramid Lake, mean TN:TP in surface waters (0-20 m) was 19.2±3.2 (n=14) during 1989-1991 and ranged 14.2-23.9 (Fig. 7-1). This ratio indicated balanced growth with respect to these two nutrients and even potential P-limitation. However, the ratio of dissolved inorganic N (DIN) to total reactive P (TRP) was very low with a mean of only 0.8±0.5 and a range of 0.3-2.0 (Fig. 7-1). The discrepancy between the ratios calculated on the basis of TN and DIN was due to the large contribution of dissolved organic N (DON) to the TN pool. Even if the mean ratio of inorganic N:P (DIN:TRP) is modified to include all sources which are likely contribute to the biologically available pool (DIN + 40% of particulate N (PN) + 15% of DON, Harrison 1978), it would still be only 3-5. Given the low bioavailability of PN and DON for algal growth, use of the inorganic N:P ratio is more logical, and in Pyramid Lake this ratio strongly suggested potential N-limitation.

Natural phytoplankton assemblages from Pyramid Lake showed a dramatic response to the addition of N. When 20, 50, and 100 µg N L^{-1} of DIN were added to lake water, there was a statistically significant (α<0.05) increase in algal chlorophyll, relative to controls, during 9 of 14, 9 of 14, and 4 of 5 monthly experiments respectively (Table 7-1). Figure 7-2 plots the relative response (enrichment factor) of the natural plankton assemblage to additions of N, P and iron (Fe) during October 1989-August 1991. In the context of this discussion, the enrichment factor is the final chlorophyll concentration in each treatment divided by the
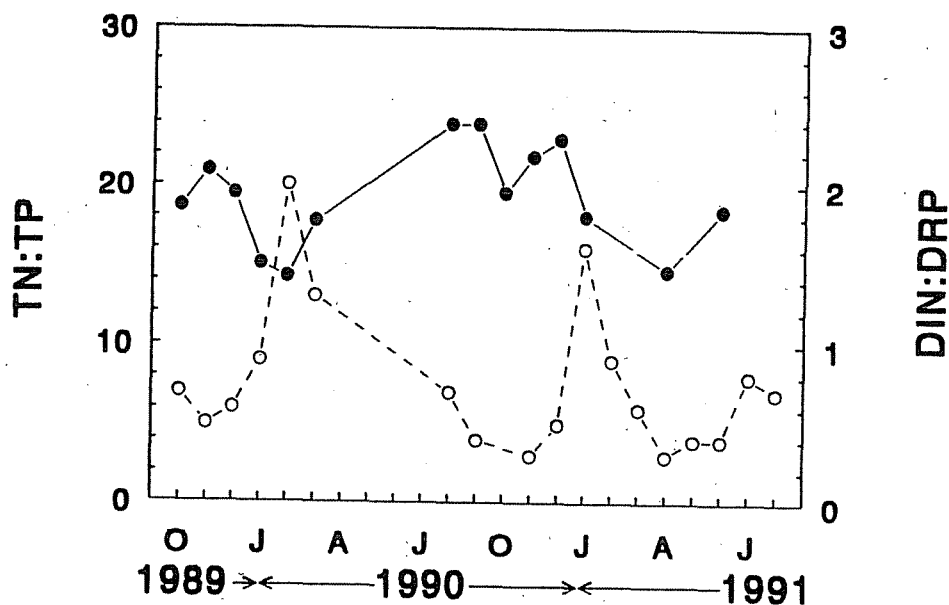
Figure 7-1. Elemental nutrient ratios for surface waters (0-20 m) during 1989-1991. Symbols indicate: (●) TN:TP and (o) DIN:DRP.

Table 7-1. Probability of treatment response being the same as the control. Parentheses indicate treatment response less than the control while n.s. indicates a probability >0.05.

Date	+20 µg N L⁻¹	+50 µg N L⁻¹	+100 µg N L⁻¹	+20 µg P L⁻¹	+50 µg Fe L⁻¹
11/89	<0.01	<0.01		n.s.	
2/90	n.s.	n.s.		n.s.	
3/90	<0.01	<0.05		n.s.	
4/90	<0.01	<0.01		n.s.	
5/90	<0.05	n.s.		(<0.05)	
6/90	<0.01	<0.01			(<0.01)
7/90	<0.01	<0.01			n.s.
8/90	<0.01	<0.01			n.s.
9/90	n.s.	n.s.			n.s.
10/90	<0.01	<0.01	<0.01		n.s.
2/91	n.s.	n.s.	n.s.		n.s.
5/91	<0.01	<0.01	<0.01		n.s.
6/91	n.s.	n.s.	<0.01		n.s.
7/91	n.s.	<0.05	<0.01	n.s.	n.s.

Figure 7-2. Bioassay response to nutrient additions by treatment for 1989-1991. Symbols in upper frame indicate nitrogen additions of: (●) 20, (o) 50, and (▲) 100 µg L^{-1}. In the lower frame, symbols indicate response to the addition of: (●) 20 µg P L^{-1} and (o) 50 µg Fe L^{-1}. The enrichment factor is the final chlorophyll concentration in each treatment divided by the control.

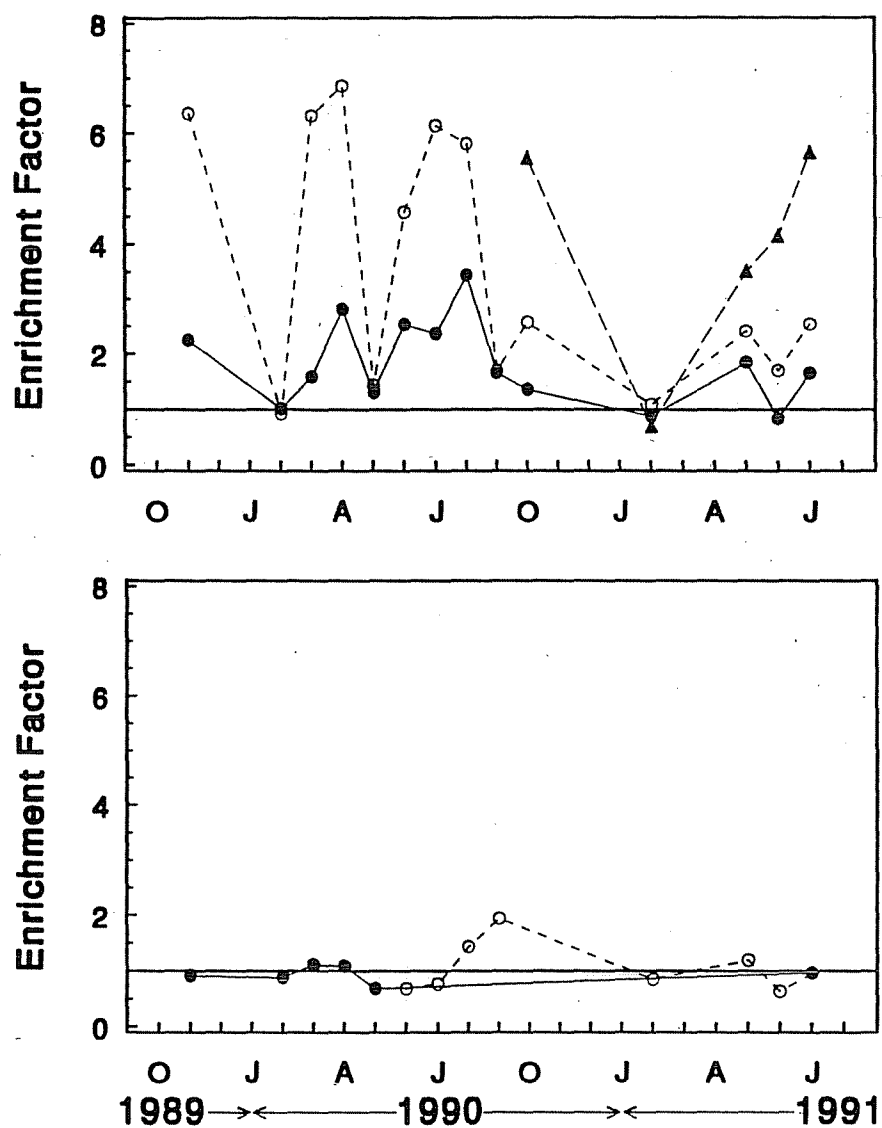control. The average stimulation of phytoplankton during the study period was striking at 169 (n=15), 346 (n=15), and 365% (n=6) over controls for the addition of 20, 50, and 100 µg N L^{-1} respectively. Additions of 20 µg P L^{-1} or 50 µg Fe L^{-1} to lake water did not significantly stimulate phytoplankton on any occasions (Table 7-1). Furthermore, the addition of either element (P or Fe) in combination with 20 µg L^{-1} N did not enhance the stimulatory effect of adding N alone (unpubl.).

Nitrogen addition (as NO_3-N) did not lead to a stimulation of chlorophyll concentration relative to controls during February of either year, when the lake was vertically mixing. Nitrate was the most abundant form of DIN throughout most of the year, with concentrations in the epilimnion generally 5-15 µg L^{-1} (Fig. 7-3). The periods of holomixis, February 1990 and January-February 1991, resulted in large increases in NO_3-N concentration of surface waters as nitrate-rich waters mixed upward from the deep hypolimnion (125-150 µg L^{-1}, see sections 4 and 5). During these times, NO_3-N concentrations were 55-60 µg L^{-1} throughout the water column. When this source of DIN was provided, phytoplankton did not respond to experimental additions of N. In fact, growth in the control during February 1991 was quite dramatic at 500% of initial chlorophyll concentration (Fig. 7-4). The percent increase of chlorophyll relative to the unamended controls during February of each year was minimal at <9% for all treatments.

The only other time when N addition did not significantly stimulate chlorophyll accumulation was in September 1990, when heterocystous blue-green algae comprised a large fraction of the phytoplankton assemblage (C.L. Rhodes unpubl.). In September, *N. spumigena* was present in the lake, fixing atmospheric N. Appreciable rates of N-fixation were first measured in the lake on 29 August (0.77 mg N m^{-2} day^{-1}), with a maximum rate (60.9 mg N m^{-2} day^{-1}) occurring on 10 September (Fig. 7-5). While the September bioassay (5 September) showed a 65-69% increase over the controls (Fig. 7-2), this response was not statistically significant (P>0.18). The lack of statistical significance in the September bioassay was in part due to a higher degree of variation between replicate flasks in this
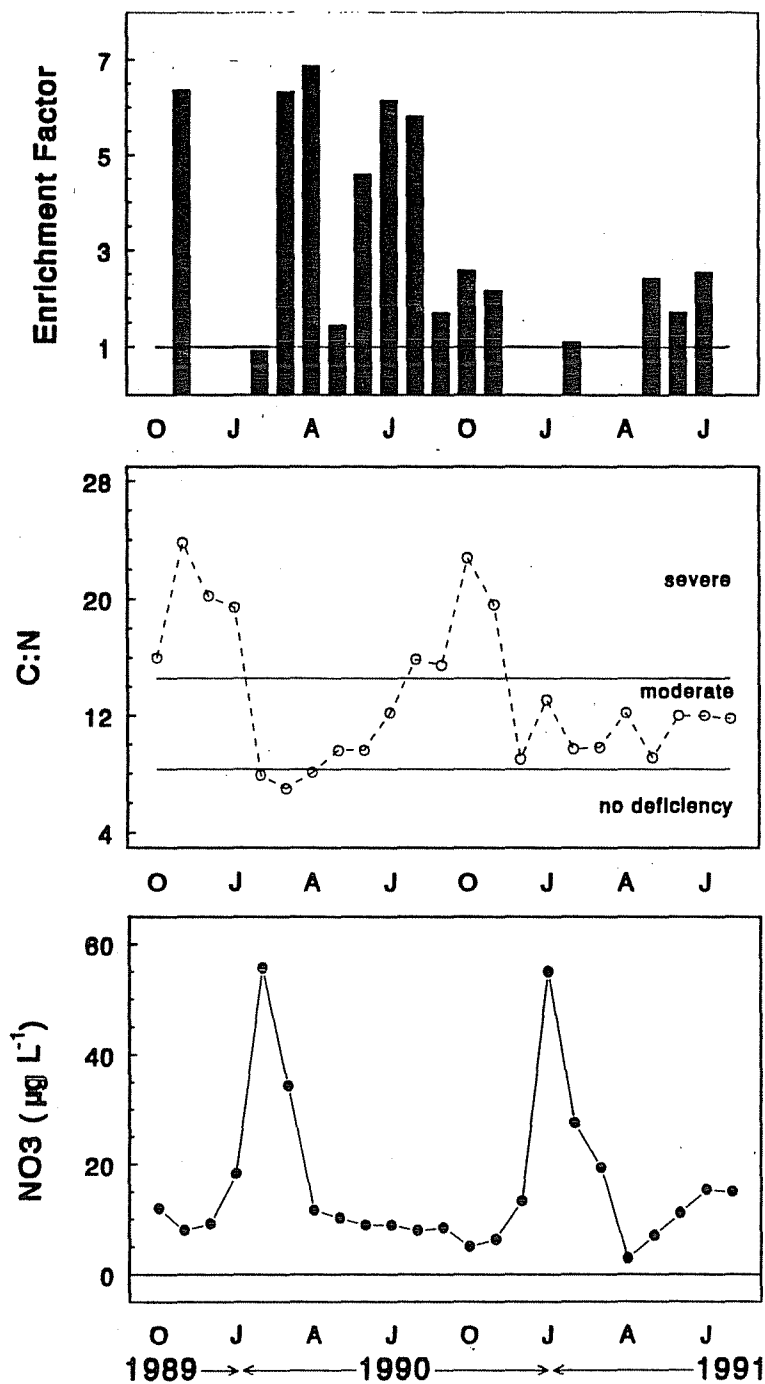
Figure 7-3. Bioassay response to the addition of 50 μg N L^{-1}, C:N of surface waters (0-20 m), and NO$_3$-N concentration in surface waters (0-20 m) during 1989-1991. Horizontal lines in the middle panel are from Healey and Hendzel (1980) (see text).
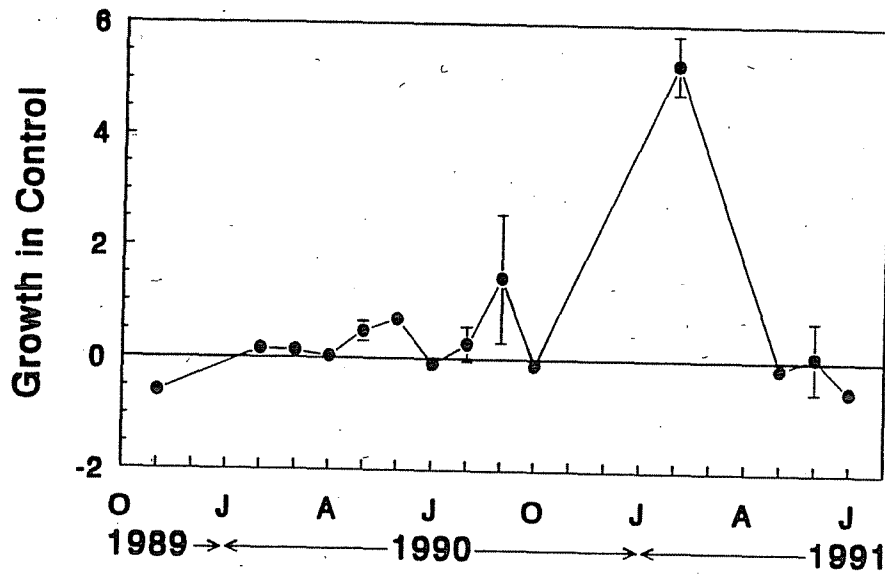
Figure 7-4. Growth in bioassay controls. Values are final chlorophyll concentration for control flasks divided by initial chlorophyll. Error bars denote one standard deviation of mean values.
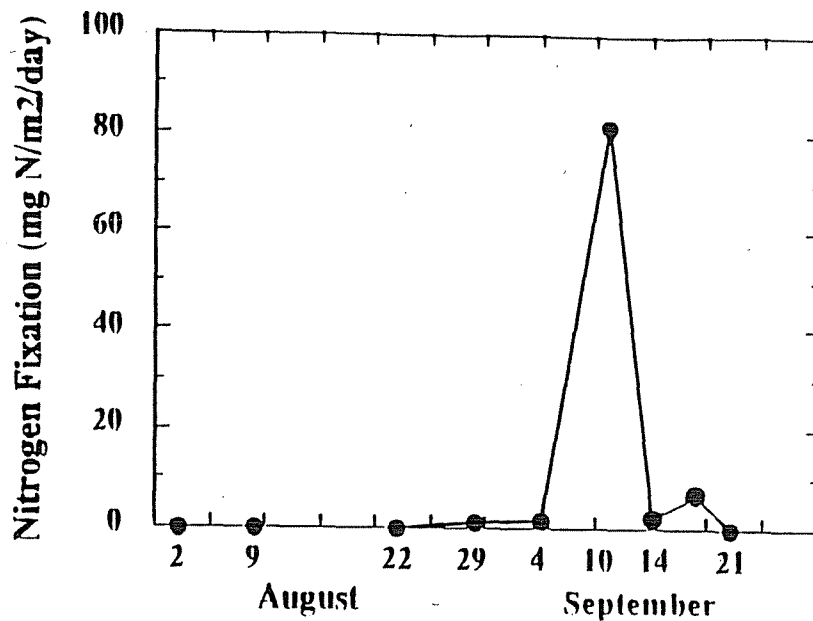
Figure 7-5. Nitrogen fixation during August-September 1990.

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experiment. The coefficient of variation for control, +20 μg N L^{-1}, and +50 μg N L^{-1} were 47, 17, and 27% respectively. A non-homogeneous distribution of *N. spumigena* filaments between flasks may have contributed to this variability; since vigorous shaking disrupts these fragile filaments and can affect the physiology of N-fixation, only gentle mixing was used.

A condition of N-deficiency in the phytoplankton is also supported by data on the chemical composition of seston. Figure 7-3 shows mean elemental seston C:N ratio for surface waters (0-20 m) during the study period. Based on both laboratory culture and field studies with natural communities, Healey (1975) and Healey and Hendzel (1980) suggested using C:N as an indicator or N-deficiency. A ratio >14.6 indicates severe N-deficiency, while intermediate (8.3-14.6) and low (<8.3) ratios indicate moderate and no deficiency respectively. The presence of detrital and non-algal material can interfere with these interpretations. However, Hamilton-Galat and Galat (1983) reported that epilimnetic particulate carbon in Pyramid Lake was primarily living phytoplankton.

The elemental composition of seston suggests that N-deficiency was severe during fall-winter of 1989-1990 and 1990-1991 with C:N ratio exceeding 14 (Fig. 7-3). These periods correspond to the times when NO$_3$-N concentration in surface waters was low <10 μg L^{-1}.

With the onset of complete mixing and the resulting increase in NO$_3$-N concentration of surface waters, there were dramatic decreases in C:N ratio from 19 to 8 in 1990 and 20 to 9 in 1991 when vertical mixing commenced. Similar to bioassay results, this ratio indicated phytoplankton were not N-deficient at that time. Following holomixis in 1990, the elemental composition of seston revealed a progressive change as evidenced by the uniform increase in C:N ratio. Between March and September 1990, this ratio increased by approximately 1.5 per month. However, this continual increase in seston C:N ratio observed for summer 1990 was not repeated in 1991. Seston C:N ratio remained in the region of moderate deficiency between November 1990 and August 1991 indicating N-limitation was probably less severe during the second year of the study.

The kinetics of NO_3-N uptake indicated that Pyramid Lake phytoplankton had a high physiological capacity to utilize nitrate when this substrate was present at low ambient concentrations. While the results of uptake kinetic experiments are not a direct measure of nutrient limitation, a low half-saturation constant (K_s) can be ecologically advantageous in an environment where specific nutrients are in short supply (Axler et al. 1982). Nitrate uptake kinetics were investigated in November 1990 when epilimnetic concentrations were at an annual minimum. At that time, measured rates of NO_3-N depletion approached a level of saturation by 20 $\mu g\ L^{-1}$ and were relatively uniform for 20, 40, and 80 $\mu g\ L^{-1}$ (Fig. 7-6). The estimated K_s for this experiment was very low, 5 $\mu g\ N\ L^{-1}$, and approximated the ambient NO_3-N concentration at that time. The absolute value of K_s determined in this fashion should be viewed cautiously, and we only include it here to emphasize the apparent conditioning of Pyramid Lake plankton to chronic low DIN concentration.
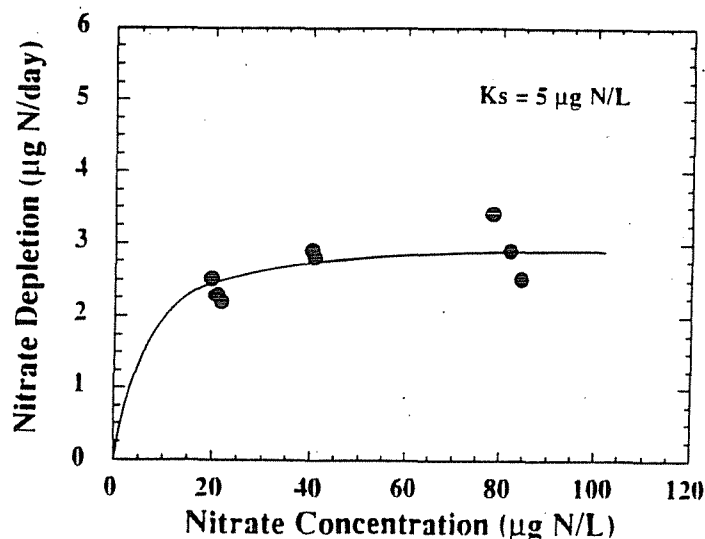

Figure 7-6. Rate of NO_3-N depletion during November 1990 bioassay plotted against initial NO_3-N concentration. The line shown on the graph was derived from the data assuming Michaelis-Menton kinetics for NO_3-N uptake.

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Nitrogen Limitation

Discussion

The first measurements of nutrient concentrations in Pyramid Lake were made in July 1933. In this initial survey, ammonium was below detection in surface waters while soluble reactive P was much higher at 85 μg L^{-1} (Hutchinson 1937). Hutchinson also observed that there were no obvious terrestrial sources of combined N within the basin, which led him to conclude that N should be the most important chemical factor restricting the growth of phytoplankton in this lake. Our present studies confirmed this hypothesis by showing that additions of dissolved inorganic N nearly always stimulated algal chlorophyll production, and that seston C:N ratios were generally sufficiently high to indicate N-deficient growth.

A reliable indicator of N-deficiency was the ratio of the dissolved inorganic pools, i.e. DIN:TRP which ranged from 0.3-2.0. Using lakewater TN:TP ratio as an indicator of nutrient deficiency was clearly misleading. The TN:TP ratio in Pyramid Lake surface waters indicated balanced growth throughout the year despite contrary evidence from the bioassay experiments and the chemical composition of seston. Dissolved organic N, which is largely refractory, comprised >80-95% of TN, while organic P accounted for <40% of TP (Lebo et al. 1991). Thus, the TN:TP ratio poorly represented the pool of biologically available nutrients and was an invalid measure of seston composition.

Water column nutrient concentration ratios should be used with caution and in conjunction with other indicators of nutrient deficiency. For example, in February 1990, the DIN:TRP ratio was 2, suggesting strong N-limitation of growth, but the bioassay showed minimal stimulation by N addition. At this time, DIN increased to >50 μg N L^{-1} due to vertical mixing, and provided N for phytoplankton growth during winter months. Annual primary productivity reached its seasonal minimum at this time (see Fig. 4-8), largely due to low light and low temperature conditions and therefore algal N-demand was reduced. Even though the DIN:TRP was less than the Redfield ratio, the new input of NO_3-N from the hypolimnion during winter mixing was sufficient to meet physiological demands.

Consequently, experimental treatment of adding 50 μg L^{-1} had no effect. Apparently, the absolute abundance of biologically available N and P as well as their ratio is important.

Based on the data presented above, it appears that the level of N-stress on phytoplankton growth in the surface waters of Pyramid Lake can be divided into four distinct periods. The first period immediately followed turnover in February 1990 and January 1991, when levels of DIN in surface waters increased from 10-15 to 55-60 μg N L^{-1}. These were the only times during the study that such large increases in available N was observed. DIN was mainly input to surface waters as NO$_3$-N, since NH$_4$-N buildup in the deep hypolimnion was minimal (Lebo et al. 1991). Concomitant with this mixing of DIN into surface waters, the seston C:N ratio changed from a condition of severe N-deficiency to no deficiency. This large decrease in C:N was not due to N-enriched seston from the hypolimnion. During the fall-winter, C:N below the thermocline was >18. Clearly, N-starved cells were utilizing this newly available resource.

The second period was from March through August during which time N-stress became increasingly acute. The response to N additions was very large during this period and highly significant (P<0.01) while seston showed a more gradual increase in N-deficiency. Data from 1990 clearly showed this pattern. In March and April 1990, the C:N ratio of seston was low indicating that phytoplankton growth was not N-deficient. Furthermore, the C:N ratio of seston during these months was 7-8, close to the proportion of the Redfield ratio (6.6). After this period of balanced growth, there was a continual increase in C:N after April, at least in 1990, to values (>16) indicating severe N-deficiency by August. Carbon:nitrogen ratio of seston during summer 1991 remained relatively constant at approximately 12 indicating N-deficiency was less severe at that time. This conclusion was supported by less stimulation of phytoplankton by the addition of 50 μg N L^{-1} during summer 1991 (Fig. 7-3).

The third period of interest occurred in September when a bloom of N-fixing *N. spumigena* appeared. These annual blooms occur frequently in Pyramid Lake between early

Nitrogen Limitation

July and early October (Galat et al. 1990), but in some years, the magnitude of the bloom may be greatly reduced which appears to be the case in 1989 and 1990. While the growth of N-fixing organisms is not limited by N, low N environments offer a competitive advantage to these species. In the September 1990 bioassay, chlorophyll in the control flasks increased by 2.0 $\mu g\ L^{-1}$ (Fig. 7-4). Nitrogen fixation was clearly providing a temporary relief from N-stressed growth. The incorporation of this "new" atmospheric N into phytoplankton only caused a small decrease in C:N of seston (Fig. 7-3). This lack of a response in the chemical composition of seston to the *N. spumigena* bloom was probably due to the timing of the monthly sampling relative to the bloom; the September monitoring sample depicted in Fig. 7-3 was taken one week prior to the bloom maximum. During a large bloom in 1979, Hamilton-Galat and Galat (1983) reported a large drop in C:N from 9.3 to 5.8 for samplings before and during the bloom respectively.

The fourth period began after the *N. spumigena* bloom disappeared in the fall and continued until winter turnover. During this time, seston composition indicated severe N-deficiency and N additions stimulated chlorophyll production. However, years when blooms are high may be characterized by different N dynamics during fall than we observed in 1989-1991 when the magnitude of the *N. spumigena* bloom was either absent or low. Hamilton-Galat and Galat (1983) showed that C:N ratio during October-November 1979 remained low at 6-8 despite the disappearance of *N. spumigena* from the plankton assemblage. Therefore, large blooms may modify our results which strongly suggest N-limitation during this period.

These results highlight the need to distinguish between nutrient stimulation, deficiency, and limitation when assessing the status of lakes. Nutrient stimulation refers to the capacity for biomass accumulation as a consequence of external nutrient additions and is measured in enrichment bioassay experiments. Since these are typically done under controlled conditions, the response is related to the abundance of biologically available nutrients in the experimental vessel. Nutrient deficiency can pertain to either the nutrient content of the lake water itself or

nutrient composition of phytoplankton cells. As indicated by the data from Pyramid Lake, even though the accumulation of phytoplankton biomass can be stimulated by nutrient addition, the growth of the resident algae in the natural system can be nutritionally balanced with respect to N and P. The steady increase in C:N during the late spring to fall suggests that growth was less than optimal and that DIN was in increasingly short supply. Nutrient limitation refers to the ability of nutrient supply to regulate phytoplankton growth in nature and is a concept which be applied to whole-lake production rather than that of individual populations. Maximal growth rates are also limited by physical factors such as light and temperature. Our results indicate that during 1989-1991 N availability was an important factor limiting phytoplankton production, with N-limitation being stronger during 1990 compared with 1991.

Conclusions

Nitrogen is clearly the nutrient most limiting to plankton biomass in Pyramid Lake throughout the year. During 1989-1991, significant stimulation of phytoplankton chlorophyll production occurred with the addition of N at all times of year except following winter overturn and during a bloom of N-fixing *Nodularia spumigena* in September 1990. N-limitation was supported by low availability of dissolved inorganic N (e.g. DIN:TRP<2), large stimulation of chlorophyll production by addition of N to lake water, high C:N ratio of seston, and high affinity (e.g. low K_s) of plankton for nitrate. Lower response to N addition and higher nitrate concentration during 1991 suggests that limitation may have been less severe in the second year of the study compared with 1990.

However, the clear picture of N-limitation throughout most of the year observed during 1989-1991 must be viewed with caution. Our study period did not included years of high river flow or a large *N. spumigena* bloom. Data reported for a large bloom in 1979 suggest that N cycling during fall may be strongly affected in years of large blooms.

SECTION 8

Nitrogen Fixation during 1991

Introduction

Pyramid Lake experiences annual blooms of *Nodularia spumigena* during summer-fall of most years. Archeological data indicates the presence of these blooms for centuries (Galat et al. 1990). In years when there is a large bloom, the input of N to the lake through fixation of atmospheric N dwarfs all other external sources (Horne and Galat 1985) and can stimulate fall blooms of diatoms (Galat and Verdin 1989). Despite the overwhelming importance of N-fixation to N cycling in the lake, the factors regulating bloom size in any given year are poorly understood. Galat and Verdin (1988) suggested that bloom size was inversely related to the concentration of total N in surface waters during the preceding winter. However, using this criteria, the bloom during 1990 should have been very large. This was not the case. The bloom during 1990 was small with 14.1 mmol N m^{-2} fixed (using 4:1 conversion, see methods) during August-September (Lebo et al. 1991) or 13% of the large bloom reported for 1979 (Horne and Galat 1985).

This section presents a preliminary description of the *N. spumigena* bloom during August-September 1991. Additional information concerning this bloom and the one in 1990 will be included in later reports when data are available.
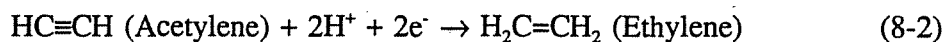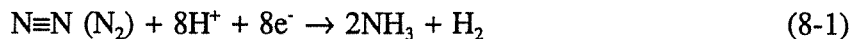
Nitrogen Fixation

Methods

Nitrogen fixation measurements were initiated on 18 July 1991 to detect the onset of N-fixation by blue-green algae in the lake. *N. spumigena* blooms in Pyramid Lake are extremely patchy (Galat and Verdin 1989), necessitating a synoptic sampling approach to adequately assess whole-lake N-fixation. Eleven synoptics were completed between 18 July and 19 September 1991. The number of stations sampled on each occasion was proportional to the apparent density of *N. spumigena*; more stations were sampled when the population was dense to improve our estimate of total N-fixation. A depth profile in the photic zone was also sampled along with each synoptic to assess the vertical distribution of N-fixation. Synoptic surface samples were taken with a 5 gallon bucket. While only semi-quantitative, this method helped overcome the small-scale patchiness of the algae (Horne and Galat 1985; Galat and Verdin 1989).

Nitrogen fixation was estimated by the acetylene reduction technique (Stewart et al. 1967; Hardy et al. 1968; Flett et al. 1976) using the protocol of Reuter (1983). Gas samples were analyzed by gas chromatography using a FID detector.

Two reactions are important in the acetylene reduction technique: N-fixation and acetylene reduction. These reactions are shown in equations 8-1 and 8-2.

$$N\equiv N\ (N_2) + 8H^+ + 8e^- \rightarrow 2NH_3 + H_2 \tag{8-1}$$

$$HC\equiv CH\ (Acetylene) + 2H^+ + 2e^- \rightarrow H_2C=CH_2\ (Ethylene) \tag{8-2}$$

The enzyme nitrogenase mediates both reactions. In the acetylene reduction technique, acetylene replaces dinitrogen as the substrate for nitrogenase. Because it binds more tightly to nitrogenase than N_2, acetylene is preferentially reduced to ethylene. Acetylene reduction provides an indirect estimate of N-fixation, but the ease of measuring acetylene and ethylene

by gas chromatography makes it the method of choice. While acknowledging that it is an indirect estimate, we express values calculated from acetylene reduction assays as N-fixation.

The rate of acetylene reduction is converted to N-fixation by dividing the measured rate by four; nitrogenase requires eight electrons to reduce one dinitrogen molecule to two ammonia molecules (reaction 8-1) but only two electrons to reduce one acetylene molecule to ethylene. This 4:1 conversion ratio is a theoretical maximum. The conversion of ethylene produced to N-fixed is complicated by production of H_2 in the N-fixation reaction. In reaction 8-1 above, only one H_2 is shown which is a minimum value. The number of H_2 molecules produced is a function of the physiological state of the alga. When more H_2 molecules are being produced, the conversion ratio between reactions 8-2 and 8-1 is higher (Sprent and Sprent 1990).

The 4:1 conversion ratio was used on the 1991 data to convert from ethylene produced to N-fixed. Previous N-fixation data reported for both 1979 (Horne and Galat 1985) and 1990 (Lebo et al. 1991) for Pyramid Lake used the traditional 3:1 ratio neglecting H_2 production. All values used in this report use the 4:1 conversion ratio with values from previous work transformed by multiplying by 0.75 (3/4).

Results

Eleven N-fixation synoptic samplings were conducted between 18 July 18 and 19 September 1991, and a total of 250 field samples were taken. Including these field samples, their laboratory split samples, associated standards, and experiments, a total of 500 samples were analyzed by gas chromatography.

As previous experience from the 1990 bloom indicated, rates of N-fixation were not detectable until filaments of *N. spumigena* were common and visually detectable in the

surface water. N-fixation was first detected on 21 August 1991 and the last synoptic was conducted on 19 September 1991 after a particularly windy week. In contrast to the 1990 bloom which disappeared after a large wind-storm, the 1991 bloom appeared to recover from the wind damage during mid-September and persist. Pyramid Lake Fisheries personnel reported the persistence of *N. spumigena* filaments at very low levels into November.

Figure 8-1 shows total N input to the lake through fixation by *N. spumigena* during August-September 1991 by sampling date. Peak fixation was observed on 5 September at >5 metric tons. Total N input to the lake during August-September was estimated to be 69 metric tons. It should be noted that this calculation does not include N-fixation occurring after 19 September 91.

As previously noted, the distribution of *N. spumigena* is extremely heterogeneous. The 1991 bloom displayed the same spatial patchiness as blooms studied previously (Galat and Verdin 1989). Figure 8-2 shows the depth integrated rates of N-fixation by *N. spumigena* for each sampling date when fixation was detected.

Discussion

No fixation was detected during the first four synoptics. Filaments were visible but not very common. We chose not to concentrate these samples by filtering through Nitex mesh due to potential errors associated with concentrating N-fixing blue-green algae by meshing (Leonardson 1983). It is difficult to concentrate blue-green algal cells without some filament breakage at the heterocysts. Since heterocysts are the sites of N-fixation, any heterocyst damage reduces N-fixation rates.

Like the 1990 bloom, the 1991 *N. spumigena* bloom was small in comparison to the 1979 bloom. Horne and Galat (1985) reported 900 metric tons of N were input to the lake during the 1979 bloom. Accounting for the different conversion ratios used on the 1979 and

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Pyramid Lake Nitrogen Fixation
Estimated Input Summer/Fall 1991

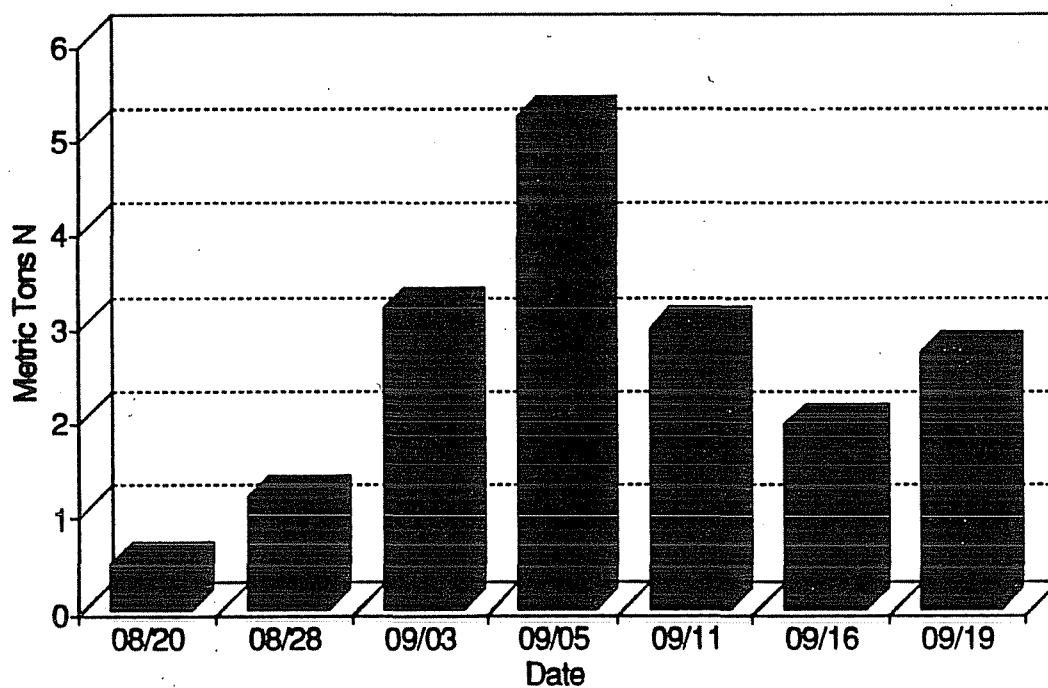

Figure 8-1. Total N input to Pyramid Lake through N-fixation during 1991 by sample date.
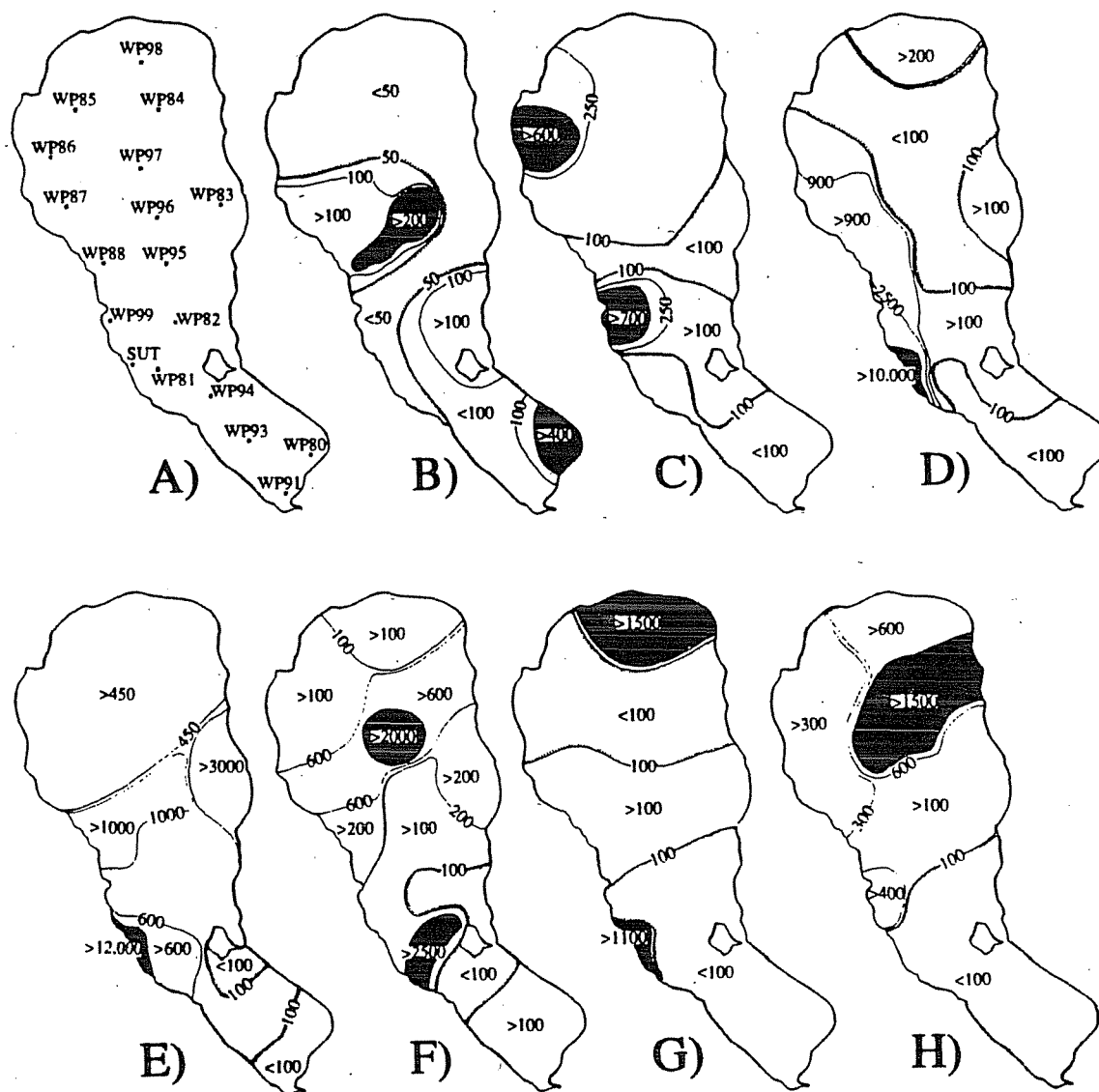
Figure 8-2. Synoptic sampling stations (A) and contours of N input rate (μmol-N m^{-2} day^{-1}) for synoptic dates: (B) 20 Aug, (C) 28 Aug, (D) 3 Sept, (E) 5 Sept, (F) 11 Sept, (G) 16 Sept, and (H) 19 Sept.

1991 data, we estimated the 1991 bloom to be only 10% the size of the 1979 bloom or similar in size to the one in 1990 (88 metric tons).

Previous work on the *N. spumigena* bloom (Horne and Galat 1985; Galat and Verdin 1989) showed that the spatial distribution of the alga was extremely heterogeneous. The 1991 bloom also displayed this pattern (Figure 8-2). By plotting the distribution of N-fixation for each sampling date, temporal changes in the distribution of fixation became apparent. The only easily interpretable trend in the spatial distributions of N-fixation was the presence of high fixation rates off the western shore of the lake, near Sutcliffe, Nevada. Presumably this area of high fixation was produced by prevailing northerly winds collecting the buoyant algal cells in this region.

Spatial patterns of *N. spumigena* distribution were previously investigated by remote sensing (Galat and Verdin 1989; Galat et al. 1990). This approach was a creative attempt to make up for the absence of a long-term data set. However, estimation of the 1991 bloom with LANDSAT 5 (Path 45, Row 30) satellite fly-overs would have missed the height of the bloom. During the period covered by synoptic sampling, fly-overs occurred 17 August, 2 September, and 18 September 91 while maximal fixation was measured on 5 September.

SECTION 9

Preliminary Sediment Trap and Sediment Core Data

Introduction

The loss of particulate matter (POM) from the water column and its ultimate burial in the sediments is an important component of all nutrient cycles. In terminal lakes, such as Pyramid, the burial of POM in the sediments can be the main sink for nutrients since there is no outflow to export nutrients in surface discharge. It is, therefore, important to know the rate of permanent loss of nutrients and organic matter to the sediments. To achieve a complete understanding of nutrient cycling, knowledge of the rate of total sedimentation, including material buried in the sediments and remineralized to the water column, is also necessary.

The rate of total sedimentation was estimated using sediment traps deployed at different depths within the water column. We deployed traps at station 96 in the center of the deep basin beginning in April 1991, with sediment collected in the traps retrieved every 3-4 weeks. The traps were deployed at three depths to determine particle flux out of surface waters (30 m), to deeper waters (50 m), and to the bottom sediments (80 m). The bottom trap was suspended 20 m off the bottom to minimize the trapping of resuspended bottom material. Comparison of material collected at the three depths allowed us to evaluate the importance of changes in composition during sinking to the bottom. Due to technological problems, traps were only deployed for two periods between April and September 1991: April-May and August-September.

Material permanently buried in the sediments was collected by obtaining sediment material from the bottom of the lake with a gravity coring device. To analyze permanent burial in Pyramid Lake, sediment cores were collected during 11-12 September 1991 at stations 96 and 93 at the centers of the deep and shallow basins respectively. Since we collected sedimentary material deposited over many decades, the time of year that the core was collected was not important (i.e. the impact of seasonal cycles on distributions will be minimal). Duplicate cores were collected at both locations to verify that changes in sediment composition with depth were not artifacts. Cores were subsectioned at 1-4 cm intervals to generate 7-20 samples for each core of 50-120 cm.

This section of the report presents preliminary data from sediment traps deployed April-May and August-September and the sediment cores collected in September. During the coming year, a more complete examination of seasonal changes in the amount and composition of material caught in sediment traps will be done as data becomes available. Traps will be deployed in the lake throughout the coming year with material collected on a monthly basis. We use the preliminary data available by September 1991 to provide some initial observations concerning changes in sedimentation rate and particulate material with depth and season. More information about sediment cores will also be forthcoming. We will be analyzing sediment material for: (1) percent organic matter, (2) percent carbonate content, (3) water content, and (4) elemental composition (e.g. C, N, and P). We will also be analyzing pore fluids extracted from the sediments for nutrient concentrations. Profiles of pore water nutrient concentration will allow us to estimate the flux of nutrients out of the sediments and compare these rates to observed seasonal buildup of nutrients in bottom waters.

Methods

See section 2 for a description of sample storage and analyses conducted on material caught in the sediment traps and bottom sediments.

Sediment Trap & Sediments

Results

Sedimentation Rate

The apparent sedimentation rate determined from material caught in traps deployed at the three depths during April-May and August-September are shown in Figure 9-1. For convenience, we will refer to the sediment trap data by the month (May or September) when material was removed from the traps. Clearly, apparent sedimentation in May was much higher than in September; sedimentation rate in May was 1.8-3.9 g m^{-2} day^{-1} compared with only 0.3-1.1 g m^{-2} day^{-1} during September. The error bars on the graphs indicate one standard deviation of replicate tubes at each depth. In September, mean values are based on three replicates at each depth while in May values are based on either two (30 and 50 m) or only one (80 m) sample due to the disturbance of several tubes by fish. Therefore, error bars
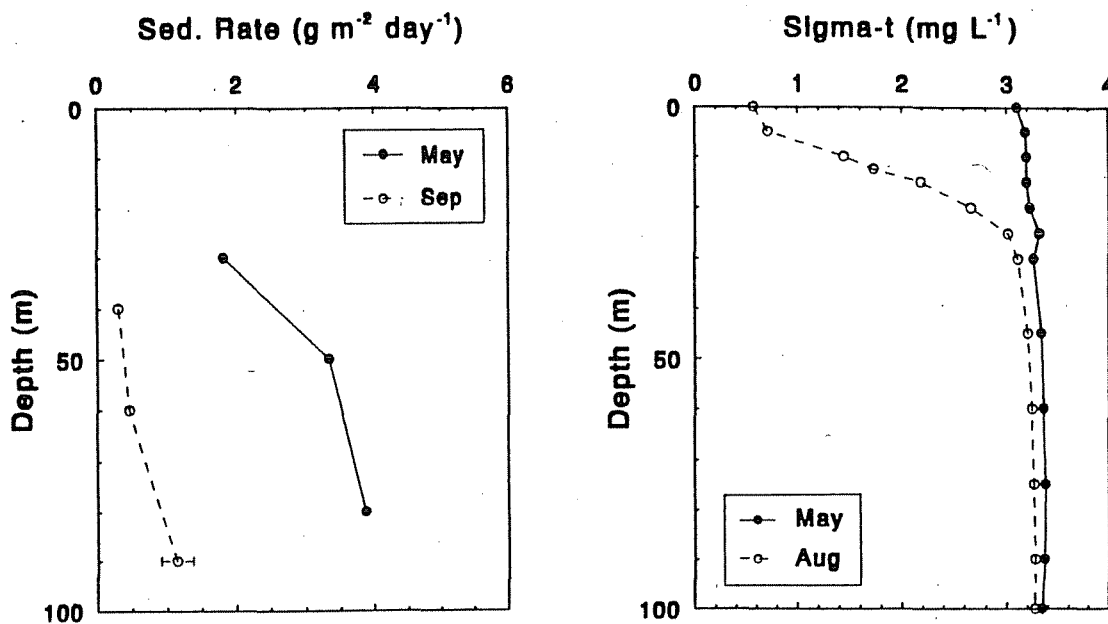

Figure 9-1. Sedimentation rate and profiles of sigma-t for April-May and August-September 1991 at Pyramid Lake.

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are plotted for all samples except the 80 m trap in May. The apparent lack of error bars on several of the mean values indicates that the bars fall within the marker for the mean value.

The dramatic decrease in sedimentation rate observed between May and September can be attributed to an increase in stratification during this period. Figure 9-1 shows profiles of sigma-t for May and August 1991. Clearly, surface waters during August were highly stratified with a strong density gradient between 5-25 meters; sigma-t increased from 0.6 to 3.0 mg L^{-1} in this region. This sharp density gradient during August provided a strong barrier in the lower epilimnion constraining the transport of particulate matter (POM) to deeper waters. Indeed, surface waters were enriched in POM during the summer stratified period of 1991 (see Fig. 5-7) supporting the trapping of POM in surface waters at that time. Stratification during May was, in contrast, less developed. Indeed, sigma-t was nearly uniform throughout the water column in May (Fig. 9-1) suggesting that particulate matter could sink unconstrained by density gradients.

In both months, there was an increase in the total flux of particulate matter with depth. The maximum sedimentation rate obtained for both dates was from the deep trap with transport increasing by a 200-300% relative to the surface trap. Tables 9-1 and 9-2 compare sedimentation rate with depth for May and September respectively. In the comparison for May, mid-depth and bottom samples were similar and grouped together due to the loss of replicates at the bottom depth through fish disturbance. In May, sedimentation rate increased from 1.80 to 3.51 g m^{-2} day^{-1} from surface to bottom while the relative increase in September was even more dramatic at 0.30 to 1.13 g m^{-2}

Table 9-1. May 1991 sediment trap data. Traps were deployed 22 April - 14 May 1991. Values reported are the mean of 2 (surface) or 3 (deeper) samples (See text). Units are the same as in Figures 9-1 and 9-2. P values indicate probability of no difference between surface and deep samples. Asterisks indicate significant differences.

Parameter	Surface	Deep (>50 m)	P
Sed. Rate	1.80	3.51	<0.01 *
PC	63.6	58.7	>0.5
PN	6.65	6.17	<0.1
PP	1.29	1.25	>0.2
Chl	1.38	3.03	>0.2
%Org	16.0	13.9	<0.05 *
%CaCO3	23.4	25.2	>0.5

day^{-1}. The increases observed for both dates are significant at α=0.01 with the apparent increase in sedimentation rate for deeper waters occurring at a deeper depth (>60 m) in September (Fig. 9-1).

Table 9-2. September 1991 sediment trap data. Traps were deployed 14 August - 11 September 1991 at 40 (S), 60 (M), and 90 m (B). Values are calculated t values for comparisons of three replicates per depth.

Comparison	Sed. Rate	%Org	Chl
S - M	-2.52	3.15 *	-2.22
S - B	-5.12 **	1.39	0.22
M - B	-5.00 **	-0.14	3.80 *

* = P<0.05; ** = P<0.01

Composition of Sediment Trap Material

Chemical composition of sediment trap material for May and September is shown in Figure 9-2. Data available in September 1991 are included. Clearly, the material from September was more organic-rich (30.3-33.8%) than material caught in May (13.9-16.0%). The higher organic content of material in September indicates that plankton cells comprised a larger fraction of total particle flux to deep waters during summer than in spring. However, the larger relative contribution of plankton to total particle flux in September compared with May does not indicate a larger flux of total organic matter. POM flux to the sediments in September decreased by a factor of 2.8 relative to May at 41 mg C m^{-2} day^{-1} compared with 114 mg C m^{-2} day^{-1}. The lower organic content of trap material in May was probably due to a large influx of inorganic particles during spring.

The chlorophyll content of sediment trap material showed a large increase at the bottom in May. This peak may be a remanent of the earlier winter-spring bloom (February-April, Fig. 5-9) reaching bottom waters. Since this peak is only based on a single sample, weighty conclusions concerning the fate of spring bloom production are not justified. However, attributing this peak to the demise of the winter-spring bloom is consistent with the timing of sinking spring production suggested by C:N data for 1990; there was a plume of low C:N ratio seston in deeper waters observed during May 1990 following the April bloom in surface chlorophyll concentration during that year (Fig. 4-7). Seasonal changes in the chlorophyll content of sediment trap material over the next year, based on three replicates per depth, will better examine the fate of spring production. The pattern with depth was different
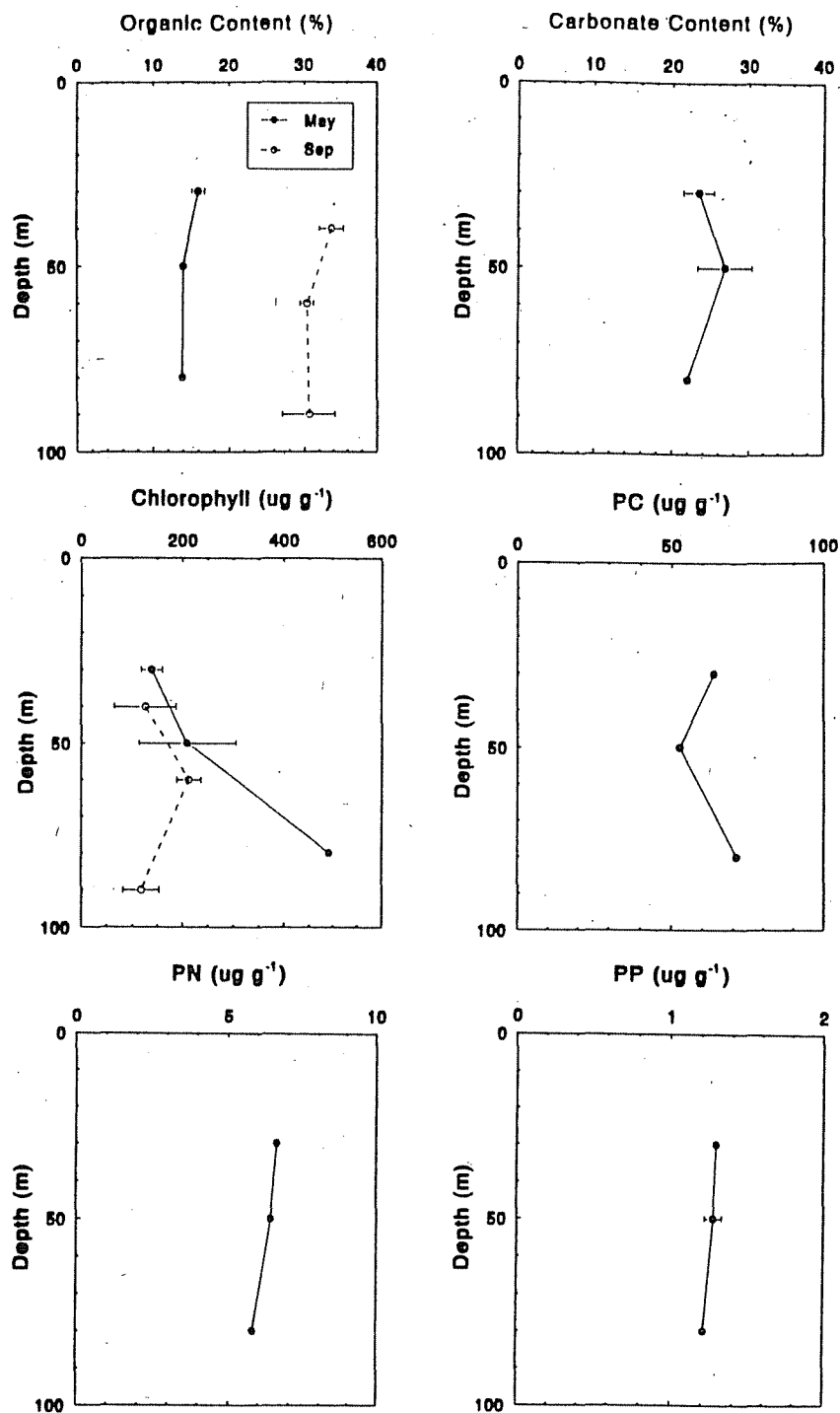
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Figure 9-2. Chemical composition of material caught in sediment traps during April-May and August-September 1991. Error bars indicate one standard deviation of the mean for traps with two or three replicates.

in September. In contrast to maximal chlorophyll content of trap material at the bottom in May, the chlorophyll content was highest in the middle trap in September (Fig. 9-2). This mid-depth peak in the chlorophyll content of sediment trap material during September was significantly (α=0.05) higher than the chlorophyll content of material caught in the bottom trap.

The elemental composition and carbonate content of particulate matter during May are also shown (Fig. 9-2). For PC, PN, PP, and carbonate content of particulate matter, material caught at all three depth at which traps were deployed was similar at 52-71 mg g^{-1}, 5.8-6.6 mg g^{-1}, 1.2-1.3 mg g^{-1}, and 22-27% respectively. This suggests that in May there was little modification of particulate matter as it sank to the bottom. As more data becomes available, changes in POM composition with depth will be more closely examined.

Sediment Cores

The only data that was available for sediment cores during the preparation of this report were changes in the water content of sediments. Figure 9-3 plots the water content of sediments at stations 93 and 96. For all cores, water content of sediments decreased with depth in the core indicating compaction of sediments over time. Comparison of cores taken in the deep and shallow basin showed that sediments at station 96 in the middle of the deep basin contained more water than at station 93. At the surface, sediments at station 96 were 87% water compared with only 78% at station 93. This 8-10% difference in the water content of sediments between locations was maintained throughout the depth profiles. This suggests that the sediments at each location may be composed of different material with finer material in the deeper basin. Further analyses will help to define differences in the sediments between the basins.
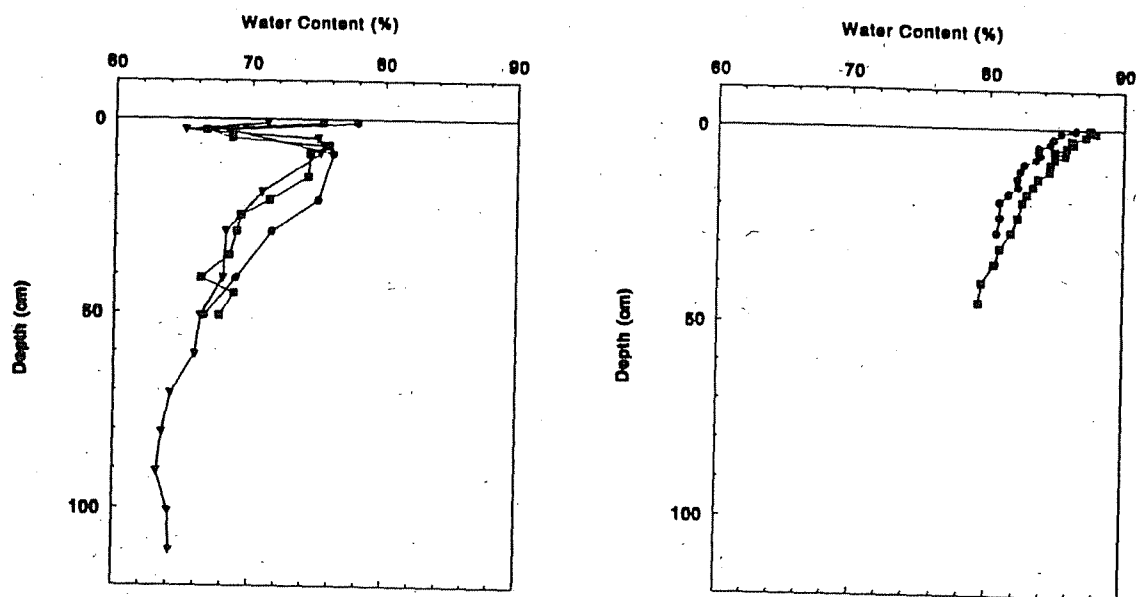
Figure 9-3. Sediment water content at stations 93 and 96 in Pyramid Lake.

Discussion

Preliminary sediment trap data for May and September 1991 suggest that there is a dramatic decrease in the total flux of particulate matter with the onset of stratification. Comparison of data for the surface trap revealed a decrease in total flux from 1.8 g m^{-2} day^{-1} in May to 0.3 g m^{-2} day^{-1} in September. A large fraction of this observed decrease in total particle flux can be attributed to a much lower flux of inorganic particles. Concurrent with this decrease in total flux, the relative contribution of plankton cells and other organic material actually increased from 14-16% in May to 30-34% in September. This suggests that there was a large decrease in the flux of inorganic particles out of surface waters between May and September. The balance of the observed sixfold decrease in total particle flux can be attributed to a threefold decrease in the flux of organic matter.

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A comparison of the flux of organic matter out of surface waters with total phytoplankton production suggests that more production is lost from the photic zone during unstratified periods. In May, 101 mg C m^{-2} day^{-1} of organic matter was caught in the upper sediment trap compared with 251 mg C m^{-2} day^{-1} fixed in surface waters by phytoplankton (Fig. 5-9). This suggests that 40% of the carbon fixed in surface waters during the spring was exported to deeper waters of the lake. In contrast, only 41 mg C m^{-2} day^{-1} were caught in the surface trap during September compared with 444 mg C m^{-2} day^{-1} fixed by phytoplankton. Therefore, it appears that only 9% of surface production was exported to deeper waters during September. This change in the proportion of surface production exported to deeper waters can be attributed to the increase in stratification. It appears, therefore, that strong stratification during summer-fall is an effective barrier trapping surface production in the epilimnion.

An important potential consequence of surface trapping of POM during summer-fall stratification is that *N. spumigena* production may be predominantly trapped in surface waters. Historically, the annual *N. spumigena* blooms in Pyramid Lake occur during summer-fall (Galat et al. 1990). Since this coincides with the period of strongest thermal stratification (see Fig. 4-1), the majority of production associated with *N. spumigena* blooms may be retained in surface waters with minimal impact on bottom waters. Examination of sediment trap material collected during summer-fall 1992 will help test this hypothesis.

The elemental composition of sediment trap material collected in May is compared with seston samples collected during trap deployment in Figure 9-4. For C:N, N:P, and C:P, the material collected in the traps was very similar to seston collected from the water column. This was especially true for the trap deployed at 50 m. The similarity between trap material and seston in the water column indicates that the bulk of the material collected in the traps was slowly sinking seston. Further, the lack of any vertical change in sediment trap material with depth revealed that minimal biological reworking of POM occurred as particles sink to
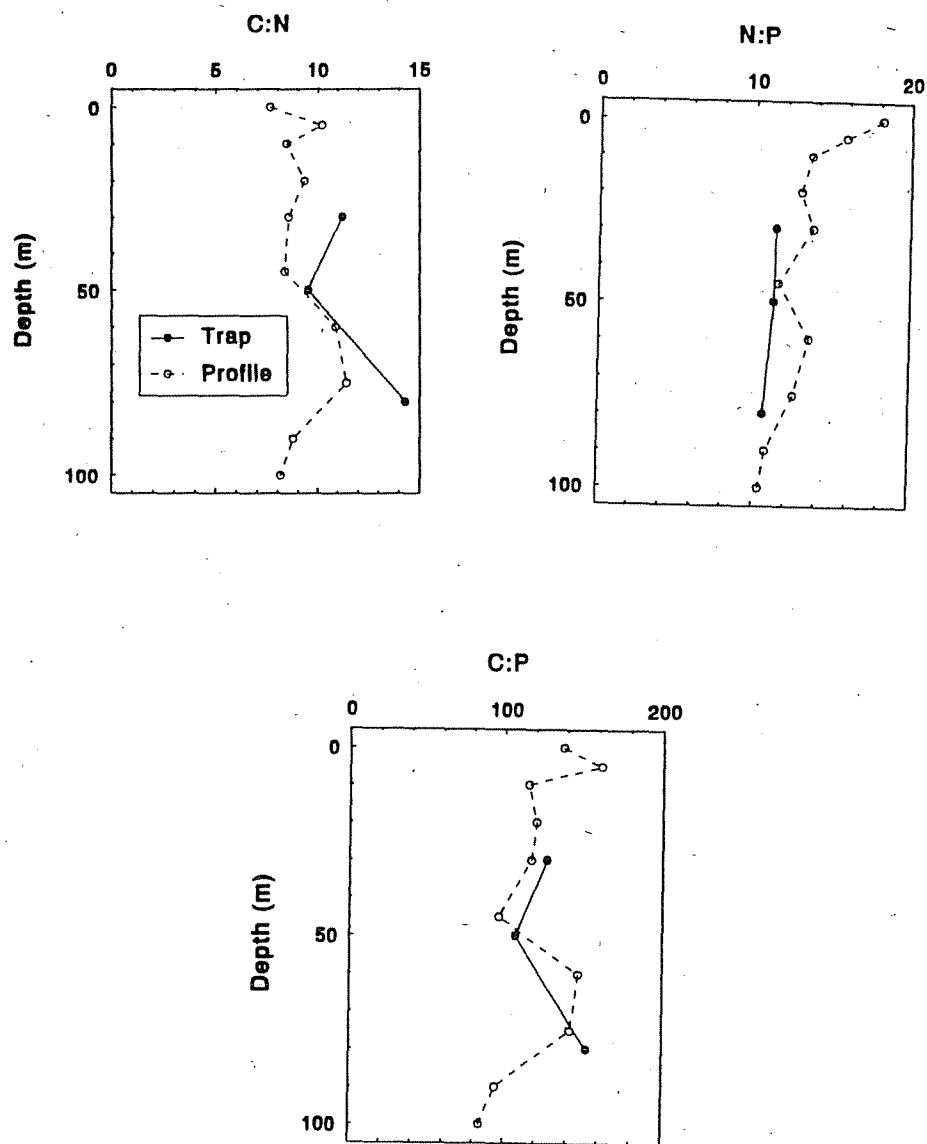
Figure 9-4. Sediment trap material and seston elemental ratios for April-May and May 1991 respectively.

the bottom. Continued deployment of traps over the coming year will help to better define this relationship.

Conclusions

Preliminary examination of material collected in sediment traps deployed in the deep basin suggested that the rate of sedimentation was affected by the strength of thermal stratification. The input of inorganic particles to surface waters during spring may also be an important source of sedimentary material. Deployment of traps over the coming year will better define seasonal changes in the rate of sedimentation and composition of material reaching bottom sediments. It appeared that little or no modification of particles occurred during sinking to the bottom.

SECTION 10

Truckee River Flow and Nutrient Loading

Introduction

The Truckee River is heavily modified due to man's activities over the past century. As the Truckee traverses the eastern Sierra Nevada Mountains between Lake Tahoe and Pyramid Lake, the quantity and quality of water is strongly affected. Beginning in 1905, agricultural water diversions claimed the majority of Truckee River water destined for Pyramid Lake. The profound effect of this diversion was a dramatic drop in the elevation of the lake surface (Fig. 3-1). The development within the watershed of the Truckee River has also affected the quality of the water. Historically, a large source of nutrients to the Truckee was through treated municipal effluent from Reno-Sparks treatment facility. Maximum annual loading of phosphorus (1980) and nitrogen (1987) from the treatment facility to the river were 177.8 and 656.6 Mg yr^{-1} respectively (Galat 1990). Since these peaks in nutrient loading, phosphorus (1982) and nitrogen (1988) removal have been implemented at the treatment facility.

Galat (1990) reviewed seasonal and long-term trends in Truckee River nutrient concentrations and loadings to Pyramid Lake between 1973-1987, and our observations build upon that foundation. More specifically, this section reviews flow (USGS, Carson City, Nevada) and nutrient concentration data (T. Swan unpubl.) near the mouth of the Truckee River during October 1989 - June 1991. We also estimate monthly nutrient loading rates to the lake and compare them with the previous estimates done by D.L. Galat.

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Methods

The data summarized in this section was collected at Nixon, Nevada along the portion of the Truckee River that is within the boundaries of the Pyramid Lake Paiute Indian Reservation. Flow data was provided by USGS (Carson City, Nevada) while nutrient concentration data was obtained from the Reno-Sparks treatment facility (T. Swan unpubl.). Nutrient loading rates to the lake were computed using monthly means for flow and nutrient concentrations. For nutrients, means were computed using 1-9 samples while mean flow was derived from average daily discharge measurements. This method of determining total annual nutrient load should be considered preliminary with a more sophisticated computation of loading rates to the lake done in the future.

Results

Flow

Truckee River discharge to Pyramid Lake has been inordinately low during the past five years of drought in the region. Figure 10-1 shows monthly mean flow for the Truckee at Nixon, Nevada during 1969-1991. Clearly, freshwater input into Pyramid Lake over the past five years has been almost non-existent. Throughout the present study (1989-1991), flow was as low as it has been over the past two decades (1969-1991). Flow is plotted on a logarithmic scale in the lower panel for emphasis. Mean flow for October 1989 - June 1991 was only 1.04 m^3 s^{-1} which translates to an annual rate of 0.33 x 10^8 m^3 yr^{-1}. Since Galat (1990) reported annual mean flow for 1973-1987 to be 6.54 x 10^8 m^3 s^{-1}, flow during 1989-1991 was only 5% of recent historical flow.

Figure 10-2 compares monthly mean flow during 1989-1991 with the mean values for each month over the past two decades (1969-1991). Clearly, flow from the Truckee River into Pyramid Lake was diminished during all times of year. However, the seasonal pattern of
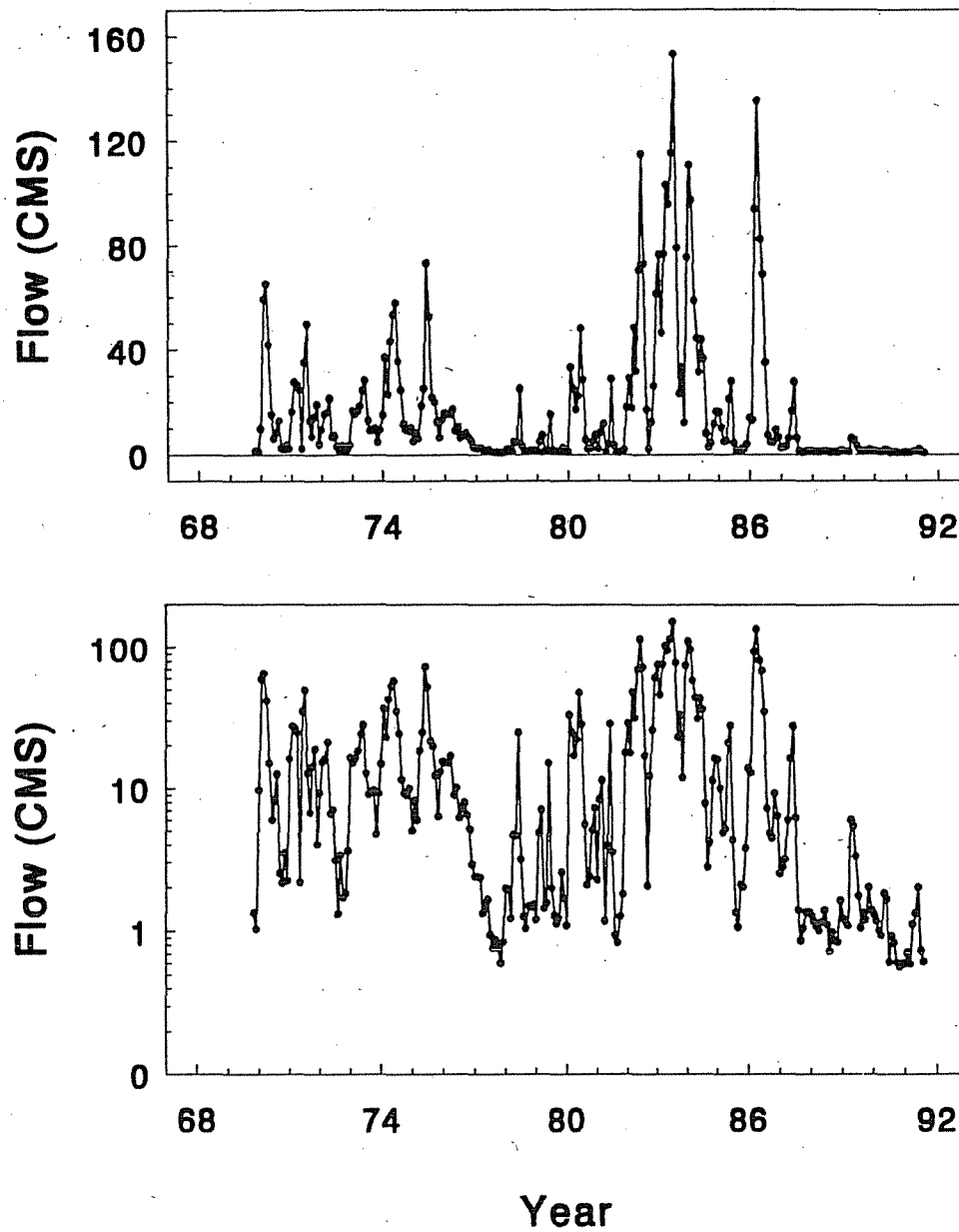
Figure 10-1. Mean monthly flow for the Truckee River at Nixon, Nevada 1968-1991. Data is plotted on a logarithmic scale in the bottom panel.
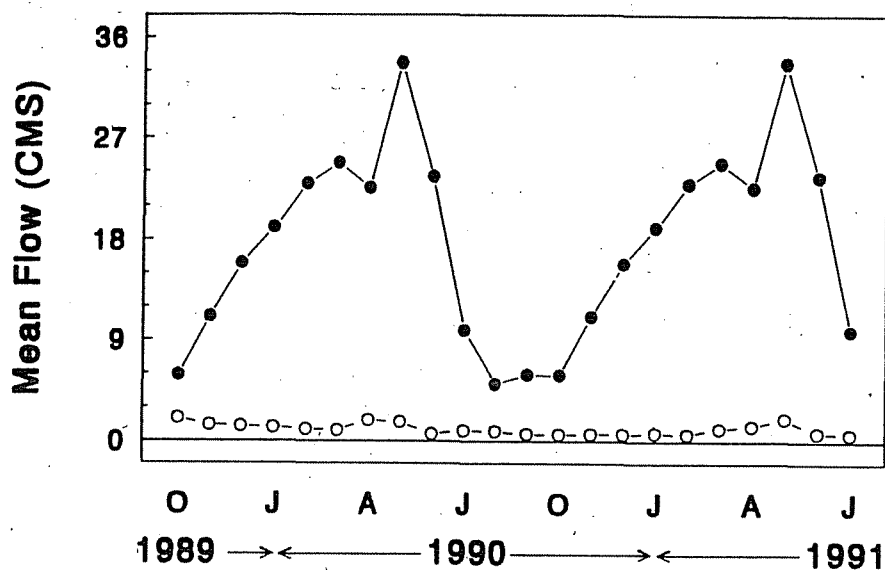
Figure 10-2. Mean monthly flow for the Truckee River at Nixon, Nevada during 1989-1991 (o) compared with the average for each month for 1969-1991 (●).

maximal flow during the spring and low flow during summer-fall (Galat 1990) was maintained. The highest flow during both years of our present study occurred in May (1.84 and 2.04 m^3 s^{-1}) at 5.5-6% of the mean for 1969-1991. This suggests that although total flow was greatly reduced during 1989-1991 the seasonal variations still occurred but at a much lower amplitude.

Nutrients and Organic Matter

Figure 10-3 shows nutrient and organic matter concentrations for the Truckee River at Nixon during October 1989 - June 1991. Phosphorus concentrations were relatively constant throughout this period with no apparent seasonal pattern. Generally, phosphate (DRP) and total P (TP) were 0.01-0.03 and 0.02-0.10 mg L^{-1} respectively with similar values during all seasons. The few sporadic high concentrations (>0.15 mg L^{-1}) reported for TP during fall 1989 were not repeated in 1990 and, therefore, may be anomalous. The monthly weighted

Figure 10-3. Nutrient and organic matter concentrations at Nixon, Nevada for 1989-1991.

mean concentrations of DRP and TP during this period were 0.018 and 0.057 mg L^{-1} respectively (Table 10-1).

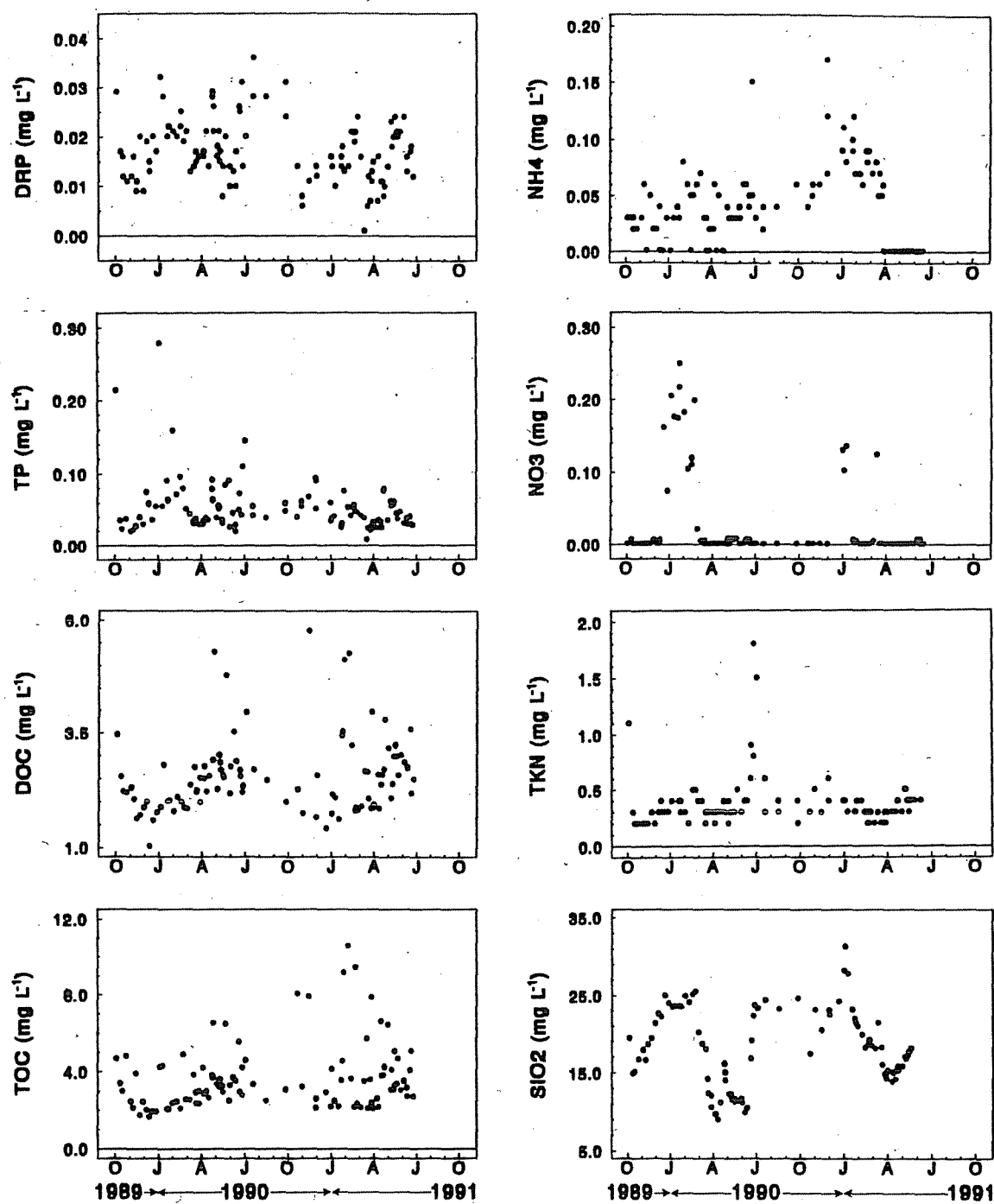Nitrogen fractions, in contrast to P suggest that seasonal variations in concentration are important. Figure 10-3 shows ammonium (NH_4-N), nitrate (NO_3-N), and total Kjeldahl N (TKN) at Nixon during October 1989 - June 1991. For the dissolved inorganic fractions (DIN, NH_4-N+NO_3-N), maximum concentrations occurred during the winter. Indeed, NO_3-N concentration was <0.01 mg L^{-1} at all times of year except during January-March of each year. The winter enrichment of NH_4-N was not as dramatic as NO_3-N, but seasonal changes in NH_4-N concentration definitely suggest higher concentrations during winter with lower values during summer. The anomalous high value in June 1990 is an exception to this general pattern and may be an artifact. Examination of additional data will help to better define seasonal variations in NH_4-N. However, Galat (1990) also reported higher winter concentrations of DIN for 1973-1987 supporting our observations from 1989-1991.

TKN data suggest that there may be two seasonal peaks in organic N concentration (Fig. 10-3). During 1989-1991, TKN concentration was generally higher during winter and summer with lower values in spring and fall. This seasonal pattern was apparent for both years of the present study. Generally, TKN concentration was 0.2-0.5 mg L^{-1} although values >1 mg L^{-1} occurred on two occasions.

Silicate (SiO_2-Si) concentrations were always high in the Truckee River at 10-25 mg L^{-1} (Fig. 10-3). Concentration was relatively constant throughout the year at 20-25 mg L^{-1} except during the spring of both years when SiO_2-Si concentration was

Table 10-1. Monthly weighted average nutrient concentrations (mg L^{-1}) and loading (mg m^{-2} yr^{-1}) in Truckee River October 1989 through June 1991. Loading values are the mean annual rate for the two year period.

Parameter	Mean	High	Low	Loading
DRP	0.018	0.031	0.010	1.37
TP	0.057	0.111	0.027	4.24
NH4	0.042	0.100	0.001	2.50
NO3	0.025	0.210	0.001	2.08
TN	0.47	1.08	0.24	33.4

Truckee River

lower. During March-May, SiO_2-Si concentration decreased to 10-15 mg L^{-1}. The timing of this seasonal minimum in SiO_2-Si concentration suggests that river flow may be an important factor influencing concentration. Since the seasonal minima for 1989-1991 coincide with relative maxima in river flow, there may be an inverse relationship between SiO_2-Si and river flow. The relationship between SiO_2-Si concentration and flow will be examined more closely in the coming year.

Concentrations of dissolved (DOC) and total (TOC) organic carbon at Nixon during 1989-1991 are shown in Figure 10-3. Concentrations of DOC and TOC were generally 1.5-3.5 and 2-6 mg L^{-1} respectively. Generally, concentrations of both fractions of organic matter were higher during summer and lower during winter. However, due to the scatter in the data, the strength of this seasonal pattern is weak and requires additional data for verification.

Loading to Pyramid Lake

The predominant forms of P entering Pyramid Lake from the Truckee River during 1989-1991 were particulate and dissolved organic. Figure 10-4 shows P loading from the Truckee River to Pyramid Lake between October 1989 - June 1991. In almost all months, TP loading was much greater than phosphate (DRP) suggesting that the input of DRP to the lake is small. Table 10-1 lists annual mean loading of TP and DRP to Pyramid from the Truckee during the past two years. During this period, DRP was 1.37 mg m^{-2} yr^{-1} or only 32% of TP loading (4.24 mg m^{-2} yr^{-1}). Galat (1990) reported an identical proportion of DRP to total phosphorus loading during 1982-1987, after phosphorus removal was implemented at Reno-Sparks treatment facility. This suggests that dissolved organic and particulate fractions contributed more to total phosphorus loading than DRP. Overall, P loading for 1989-1991 (4.2 mg P m^{-2} yr^{-1}) was extremely low compared with rates of 49-1021 mg P m^{-2} yr^{-1} reported by Galat (1990).
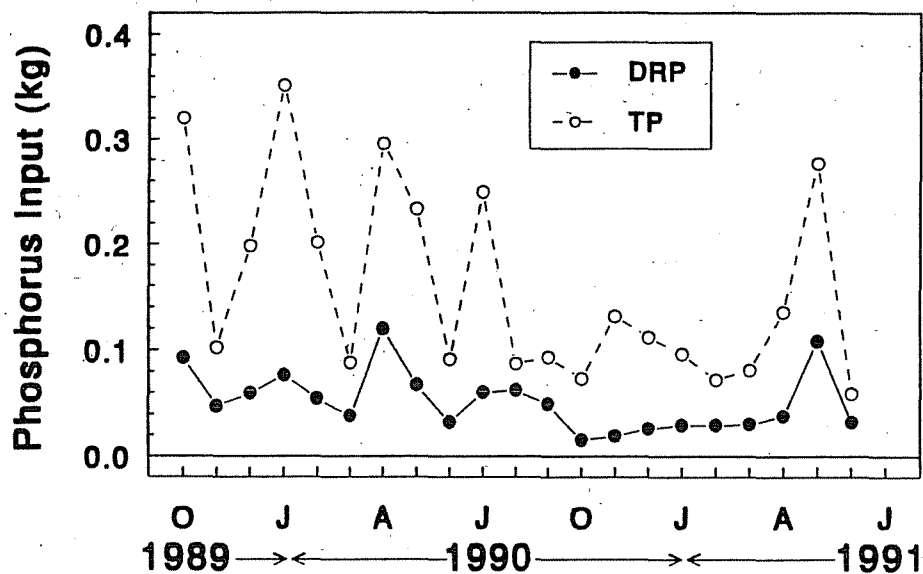
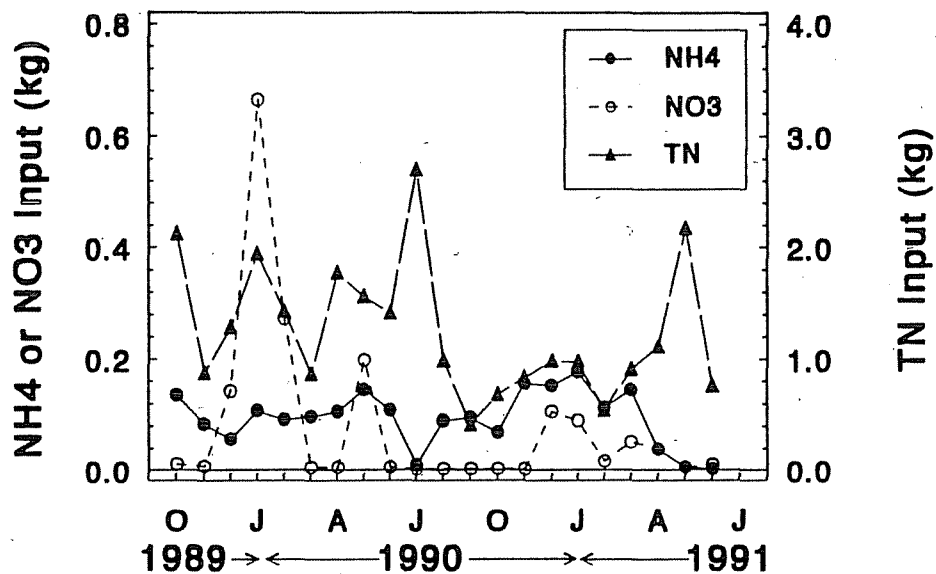Figure 10-4. Phosphorus loading from the Truckee River to Pyramid Lake 1989-1991.

Figure 10-5. Nitrogen loading from the Truckee River to Pyramid Lake 1989-1991.

Truckee River

Figure 10-5 shows N loading from the Truckee into Pyramid Lake during 1989-1991. Clearly, dissolved inorganic fractions contributed even less to total N loading than DRP did for P (notice change in axes scales for DIN and TN). Table 10-1 lists loading of NH_4-N, NO_3-N, and total N (TN) during 1989-1991. During this period, NH_4-N and NO_3-N contributed 2.5 (8%) and 2.1 mg N m^{-2} yr^{-1} (6%) to TN loading of 33.4 mg N m^{-2} yr^{-1}. Our findings of low contribution of DIN to TN loading are quite different from previous work. Galat (1990) reported that DIN contributed 44±9% of TN loading to the lake during 1973-1987.

Seasonal changes in NO_3-N and NH_4-N concentration in the Truckee had a great effect on N loading to Pyramid Lake. The influence of seasonal variations in NO_3-N concentration on loading rate was dramatic with extremely low input during summer-fall (<0.02 kg $month^{-1}$) and pronounced peaks during winter-spring. For NH_4-N, minima were observed each summer when concentration was lower than winter values (Fig. 10-3) and flow was low (Fig. 10-2). However, higher winter loading of NH_4-N was not well-defined.

Discussion

The continuing drought in the California-Nevada region strongly affected the flow and nutrient loading of the Truckee River. During 1989-1991, discharge from the Truckee into Pyramid Lake was extremely low at only 5% of average annual discharge for 1973-1987 (Galat 1990). Consequently nutrient loading to the lake was also low. This low input of nutrients from the Truckee into the lake, in effect, removed the second largest source of N to the lake (Horne and Galat 1985). Since N-fixation during this period was also low, phytoplankton in the lake depended mainly on internal sources of N during 1989-1991. This dependence was clearly demonstrated in section 4.

Nitrogen loading to Pyramid was further reduced through the efficient removal of N from the Truckee River before reaching the lake. Generally, dissolved inorganic nutrients of

anthropogenic origin are diluted by river water causing low concentrations at high flow and high concentrations at low flow. Since river flow during 1989-1991 was extremely low, nutrient concentrations are expected to be high due to the high contribution of effluents to total inputs (Galat 1990). This was not the case. For dissolved inorganic N (DIN), concentration was relatively low during spring-fall and higher in winter (Fig. 10-5). This seasonal pattern of lower DIN concentration during the "growing season" is indicative of biological processes and suggests that biological uptake within the river was an important process modifying DIN loading to the lake. The higher concentrations observed during winter can be attributed to minimal biological activity at low temperatures and low light increasing the proportion of DIN reaching the lake.

Figure 10-6 compares DIN loading to the lake with discharge for 1973-1991. Data for 1973-1987 were obtained from Galat (1990). Clearly, there is a direct relationship between DIN loading and discharge. For data from 1973-1987, the relationship is highly significant ($r=0.98$; $n=15$; $P<0.001$), and the regression line is shown on the graph. The bottom panel expands the region of the plot for low flow, which includes the data from our study. Data from 1989-1991 is indicated by open circles. When discharge was $<150 \times 10^6$ m^3 yr^{-1}, DIN loading to Pyramid Lake was lower than predicted by the loading-discharge relationship for 1973-1987. It should be pointed out that the general loading-discharge relationship presented on the graph is not valid for 1989-1991 since N removal was implemented at Reno-Sparks treatment facility in 1988. Even with this constraint, loading clearly decreases at low flow. This decrease in concentration with decreasing flow can be attributed to a longer travel time for water in the river and a greater relative contact of periphyton with bulk water when the river is shallow (Galat 1990). Therefore, it appears that loading-discharge relationships for N to Pyramid Lake must take into account biological removal at annual discharge rates $<150 \times 10^6$ m^3 yr^{-1}.

The importance of N removal in treated effluent from the Reno-Sparks treatment facility on loading to the lake can not be assessed directly given the continuous drought since
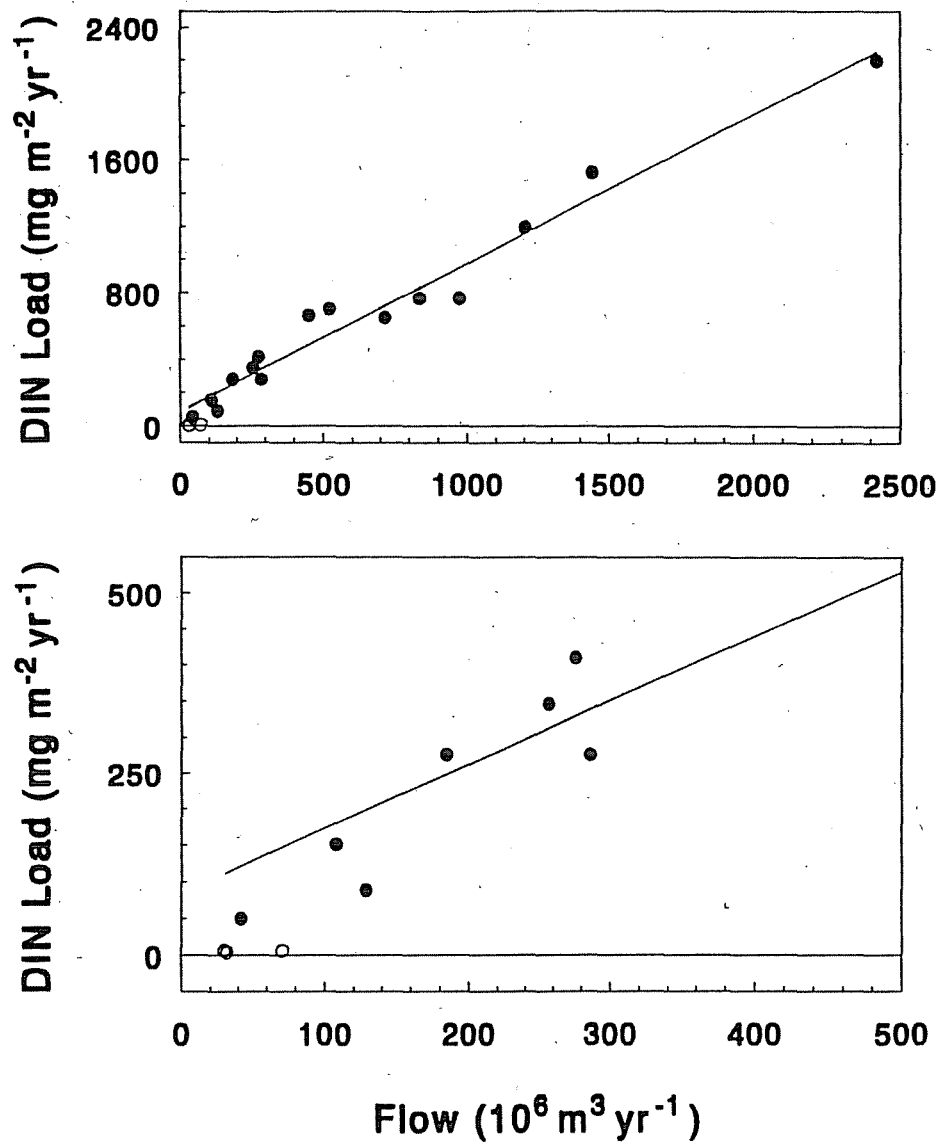
Figure 10-6. Dissolved inorganic nitrogen loading to Pyramid Lake versus annual discharge for 1973-1991. The bottom panel expands the region of the plot for low flow.

its implementation. We can infer a probable result from the impact of P removal on loading. Figure 10-7 compares DRP (SRP) loading to Pyramid Lake to annual discharge. When P removal was implemented (1982), there was a dramatic decrease in DRP loading to the lake. DRP loading in 1982 was only 151 mg P m^{-2} yr^{-1} for a total discharge of 1442 x 10^6 m^3 yr^{-1} compared with a predicted value of 552 using the loading-discharge relationship for 1973-1981. Clearly, the impact of P removal was felt immediately. The removal of N beginning in 1988 may have had a similar effect, but it was obscured by biological removal of DIN under low flow conditions. When more normal flow in the Truckee River returns at the conclusion of the present drought period, the true impact of N removal can be assessed more directly.

The elemental ratios of nutrient loading to Pyramid Lake suggest that inputs to the lake may contribute to N-deficiency. During 1989-1991, the elemental ratio of total N:P

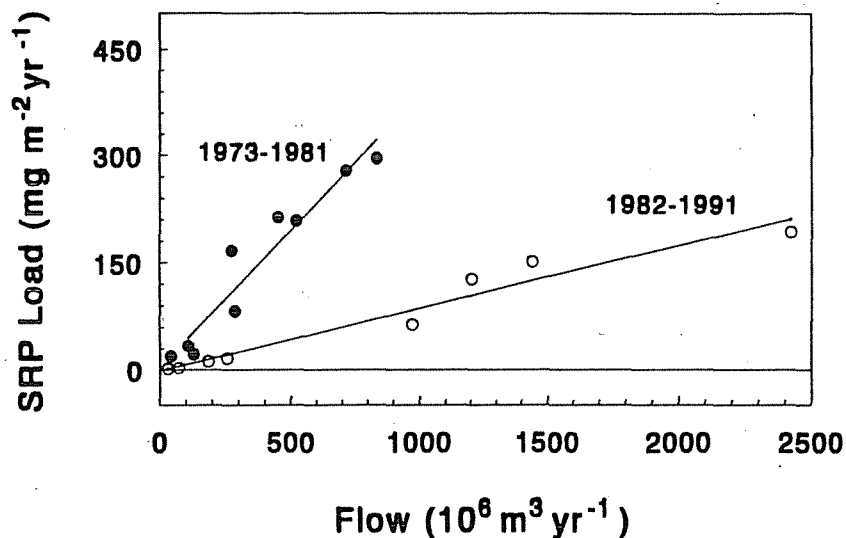

Figure 10-7. Phosphate loading to Pyramid Lake versus annual discharge for 1973-1991. Closed symbols indicate years before phosphorus removal was implemented at the Reno-Sparks treatment facility in 1982 while open symbols denote subsequent years. Lines drawn on the graph show the relationship between phosphate loading to Pyramid Lake and flow for the pre- and post-phosphorus removal periods.

inputs to the lake was approximately 17.4 indicating balanced growth. However, the ratio of DIN:DRP was much lower at 7.4. In section 7, we discussed the use of nutrient ratios to infer potential limitation of phytoplankton growth. The results of that discussion are also applicable to nutrient loading to the lake. Despite high TN:TP in Pyramid Lake throughout the year, enrichment bioassays and seston C:N ratio both suggest strongly that N was limiting growth. It is probable that like lake waters, which originate from the Truckee River, the potential for nutrient limitation is best assessed using dissolved inorganic fractions rather than total loads. Using this rationale, the DIN:DRP loading from the Truckee River to Pyramid Lake during 1989-1991 contributed to N-deficiency in the lake. A better assessment of N:P loading after N removal was implemented can be made with data for future years when flow is higher.

Conclusions

Truckee River water and nutrient inputs to Pyramid Lake during 1989-1991 were extremely small due to the continuing drought in the region. Examination of seasonal patterns of nutrient concentration near the mouth of the Truckee revealed that DIN was higher during the winter and lower during the summer. Indeed, NO_3-N concentration was >5 μg L^{-1} only during winter months. Silicate, in contrast, was lowest during the spring when flow was maximal. DRP concentration showed no discernible seasonal pattern.

Low DIN concentrations observed during summer suggests that biological uptake of N is an important process modifying DIN loading to Pyramid Lake during low flow. At annual flow rates <150 x 10^6 m^3 yr^{-1}, N-uptake within the Truckee River appears to reduce DIN loading rate to the lake. Since the first two years of this study were <<150 x 10^6 m^3 yr^{-1}, our data cannot be extrapolated to periods of higher flow. Therefore, the impact of N removal in treated effluent from the Reno-Sparks treatment facility cannot be assessed with our data. Several years of more normal flow are required before a definitive result is possible.

SECTION 11

Conceptual Model for Pyramid Lake

Background

Over the past two decades, the food chain for Pyramid Lake has been fairly well-defined through previous ecological research. Figure 11-1 shows generalized trophic relationships for Pyramid Lake proposed by Galat et al. (1981). This scheme includes four main trophic levels for the main food chain: plants, zooplankton, planktivorous fish, and the Lahontan cutthroat trout as a tertiary consumer. It also includes a detrital pathway where detrital C is consumed from sediments by benthic invertebrates and then incorporated back into the main food chain through the consumption of the invertebrates by fish. In the early 1980s, trophic interactions in Pyramid Lake were further examined by Estep and Vigg (1985) using stable isotopes of C and N. Figure 11-2 shows the results of this study. Generally, the ratios of stable isotopes in consumers are similar to their prey and, thus, provide a means of tracing trophic interactions in aquatic systems. The results of this later study supported the earlier observations made by Galat et al. (1981).

Previous research at Pyramid Lake by D.L. Galat and his co-workers has also established the main pathways by which C and N enter the lake. These observations are summarized in Galat (1986) and Horne and Galat (1985) for C and N respectively. In particular, D.L. Galat found that phytoplankton fixation was the dominant source of C to the lake with lesser contributions by Truckee River inflow and eolian transport of vegetation (Galat 1986). For N, the dominant input to the lake was also associated with planktonic production through the fixation of atmospheric N during annual blooms of *Nodularia*
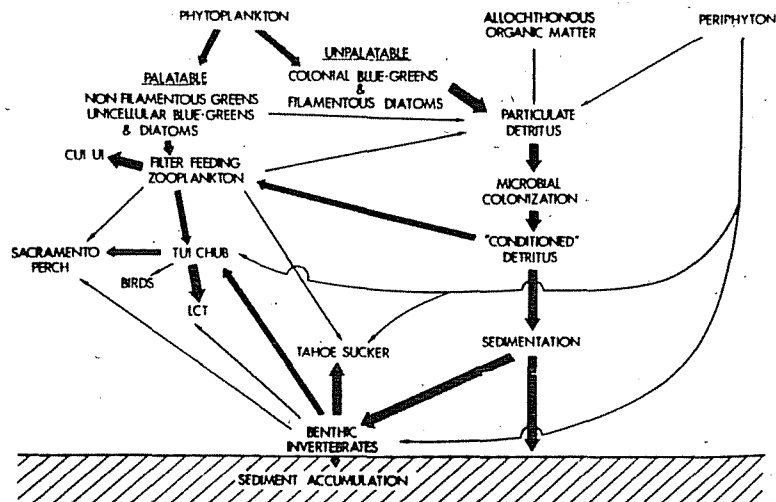
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Figure 11-1. Generalized trophic relationships for Pyramid Lake presented in Galat et al. (1981).
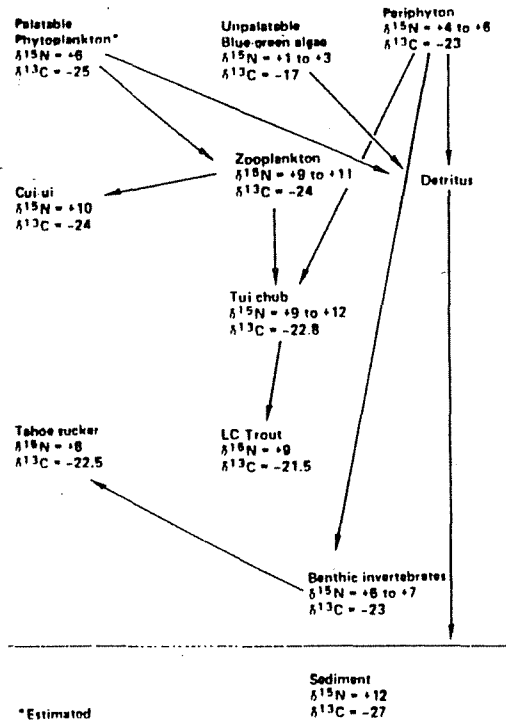

Figure 11-2. Relationships of food webs with isotopic compositions of organisms from Pyramid Lake (from Estep and Vigg 1985).

Conceptual Model

spumigena (Horne and Galat 1985). Our observations will help to define the interannual variability of these contributions to lake nutrient cycles building upon this previous work.

Conceptual Model

One goal of our project is to better define the interactions between nutrients and primary productivity in Pyramid Lake so that the impact of changes in the pattern of nutrient inputs to the lake can be better predicted. To achieve this goal, the processes controlling primary production need to be better understood so that they can be incorporated into simulation models. We also need to better understand nutrient cycles in the lake and the fate of surface production. For example, how much of surface production escapes the main food chain (e.g. plant-zooplankton-fish) and is exported to hypolimnetic waters as detritus? The ultimate fate of phytoplankton production in surface waters strongly affects how increases or decreases in the supply of nutrients to Pyramid will affect the overall production of the lake.

Modelling phytoplankton production in Pyramid Lake requires that phytoplankton be divided into two separate groups: diatoms/green algae and N-fixing blue-green algae. This division is necessary for several reasons. First, *N. spumigena* is generally not edible to many zooplankton eliminating the direct transfer of its fixed C to the main food chain. The two groups also appear to be controlled by different processes. Since the main limiting nutrient for diatoms and green algae in Pyramid Lake is N (section 7), it is expected that processes controlling growth for both groups be different; *N. spumigena* can fix atmospheric N. The exclusion of *N. spumigena* from the main food chain suggests that the fate of its production must be modelled in a different manner than diatoms and green algae that are grazed effectively by zooplankton. Table 11-1 lists processes that may be important in controlling the production of each group. Notice that diatoms/green algae include N availability and zooplankton grazing while factors controlling blue-green algal production are proposed to be physicochemical.

Conceptual Model

Incorporating nutrient limitation into limnological models requires that the sources of all parameters of interest be defined. This has been well-documented for N through the work of Horne and Galat (1985). However, P cycling has been largely ignored. Although Pyramid Lake is P-rich and never limiting to phytoplankton growth, the concentration of P could affect *N. spumigena* production. It is, therefore, important that we better define P cycling in Pyramid so that the impact of changes in P loading pattern can be predicted. Table 11-2 lists important sources and sinks for N and P in Pyramid Lake. Since the sediments are probably the main sink for both nutrients, we have collected sediment cores from the shallow and deep basins to better define the permanent loss of nutrients to the sediments.

Table 11-1. Hypothesized processes important in controlling primary production in Pyramid Lake.

Algal Group	Important Processes
Diatoms & Green Algae	light, temperature, nitrogen zooplankton
Blue-green Algae	light, temperature, wind, inorganic carbon

A conceptual representation of simplified N interactions in Pyramid Lake is given in Figure 11-3. Included in this scheme are the two groups of algae (diatoms/green algae and *Nodularia*), the main food chain of the lake, the mineralization of detritus in the sediments, and external and internal source of dissolved inorganic N (DIN) to surface waters. The final two years of this study will be focused on evaluating how to best represent the exchange of material between these different pools. The central component in this present scheme is clearly epilimnetic DIN. We will be examining how the availability of DIN for plankton affects C production.

Table 11-2. Nitrogen and phosphorus sources and sinks in Pyramid Lake.

Nutrient	Sources	Sinks
Nitrogen	N-fixation Truckee River Vegetation	Sediments Denitrification NH_4-N Loss
Phosphorus	Truckee River Dust	Sediments

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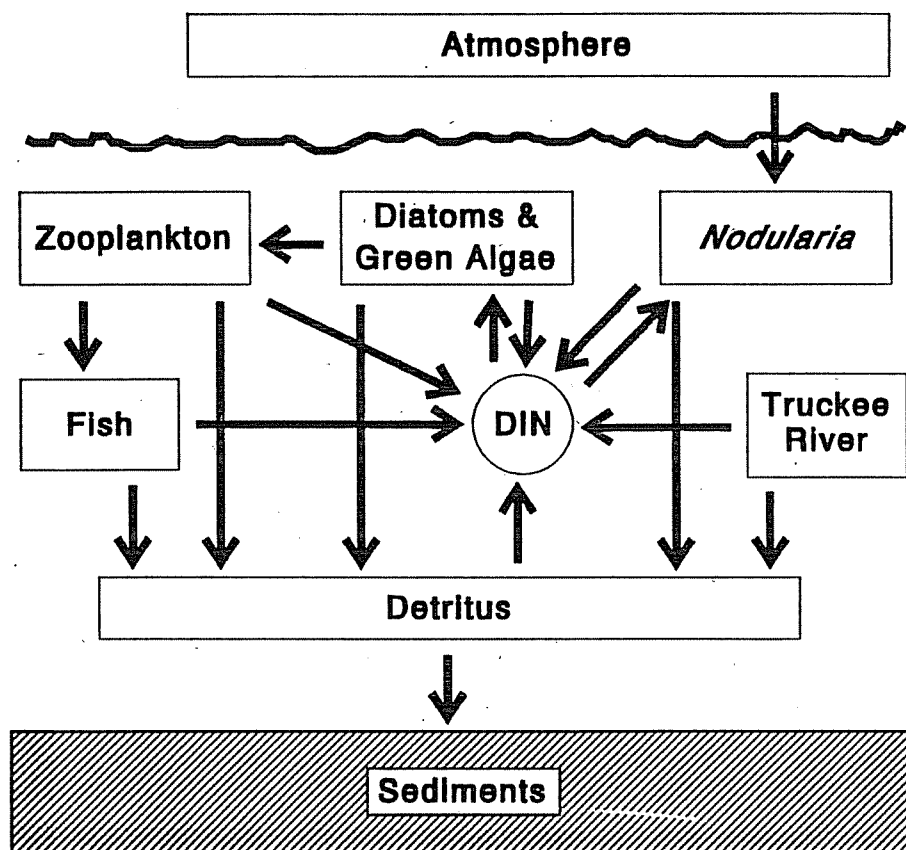
Figure 11-3. Simplified nitrogen interactions for Pyramid Lake.

SECTION 12

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APPENDIX A

Glossary of Terms

AOELIAN: See eolian.

AEROBIC: Describes life or processes that require the presence of molecular oxygen.

ALGAE: Small aquatic plants which occur as single cells, colonies, or filaments.

ALKALINE: Water bodies with pH higher than 7.

ALLOCHTHONOUS: Materials (e.g., organic matter and sediment) which enter a lake from atmosphere or drainage basin; see autochthonous.

AMBIENT: Concentration of a nutrient or temperature in the bulk water mass.

ANAEROBIC: Describes processes that occur in the absence of molecular oxygen.

ANOXIA: A condition of no oxygen in the water. Often occurs near the bottom of fertile stratified lakes in the summer and under ice in late winter.

ARAGONITE: Mineral form of calcium carbonate.

AREAL PHYTOPLANKTON PRODUCTION: The total amount of carbon fixed by phytoplankton throughout the photic zone. Areal production is expressed in amount of carbon per unit surface area per unit time (e.g. mg C m^{-2} day^{-1}).

AUTOCHTHONOUS: Materials produced within a lake; e.g. autochthonous organic matter from plankton versus allochthonous organic matter from terrestrial vegetation.

BENTHOS: Macroscopic (seen without aid of a microscope) organisms living in and on the bottom sediments of lakes and streams. Originally, the term meant the lake bottom, but it is now applied almost uniformly to the animals associated with the substrate.

BIOASSAY: Experiments where the growth of organisms is used to evaluate what nutrient is limiting plant growth.

BIOMASS: The weight of biological matter. Standing crop is the amount of biomass (e.g., fish or algae) in a body of water at a given time. Often measured in terms of grams per square meter of surface.

BIOTA: All plant and animal species occurring in a specified area.

BLOOM: When phytoplankton biomass becomes large in response to favorable growth conditions. For example, a peak in phytoplankton biomass is observed during the spring in many aquatic systems when there is an ample supply of nutrients and light.

C: Abbreviation for carbon.

CARBON FIXATION: Incorporation of inorganic carbon into organic molecules through photosynthesis of plants.

CHLOROPHYLL: A green pigment in algae and other green plants that is essential for the conversion of sunlight, carbon dioxide, and water to sugar. Sugar is then converted to starch, proteins, fats, and other organic molecules.

COLORIMETRIC METHOD: A method where the intensity of color development is used to measure the concentration of a parameter of interest.

COMPOSITE SAMPLE: When water collected at several depths or locations are combined to yield a single sample.

CONCENTRATION: Amount of a substance, such as nitrate, in a given volume of water. Common units of concentration are μg L^{-1} or mg L^{-1}.

DEFICIENCY: When algal biomass lacks some of an essential nutrient compared with normal growth conditions.

DELTA: The accumulation of sediments at the mouth of a river.

DIMICTIC: Lake that mixes twice each year. Usually spring and fall.

DISEQUILIBRIUM: When dissolved constituents in water are different from those expected from gas and mineral solubilities. For example, dissolved oxygen is higher than expected for equilibrium with the atmosphere.

DRP: Abbreviation for dissolved reactive phosphorus.

ECOLOGICAL STUDY: The investigation of an ecosystem designed to identify the animals and plants present and how they interact.

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Glossary of Terms

ECOSYSTEM: A system of interrelated organisms and their physical-chemical environment. In this report, the ecosystem is defined to include the lake and its watershed.

EDDY DIFFUSION: Random mixing of water parcels. Although there is no net exchange of water, nutrients will be transported from regions of high concentration to areas of low concentration. The eddy diffusion coefficient indicates how rapid this exchange is.

EFFLUENT: Liquid wastes from sewage treatment, septic systems, or industrial sources that are released to a surface water.

ELEMENTAL RATIO: A comparison of the number of atoms of each element present in compound of interest. For example, the nitrogen:phosphorus ratio of phytoplankton cells.

ENDEMIC: Species that are only found in a specific location such as a group of lakes in one region.

EOLIAN: Inputs to lakes from the atmosphere carried by wind.

EPILIMNION: Uppermost, warmest, well-mixed layer of a lake during summertime thermal stratification. The epilimnion extends from the surface to the thermocline.

EUTROPHIC: From Greek for "well-nourished," describes a lake of high photosynthetic activity and low transparency.

EUTROPHICATION: The process of physical, chemical, and biological changes associated with nutrient, organic matter, and silt enrichment and sedimentation of a lake or reservoir. If the process is accelerated by man-made influences, it is termed cultural eutrophication.

EXTERNAL NUTRIENT SOURCES: Nutients entering the lake from the outside through river inflow, atmospheric deposition, eolian transport, etc.

EXTINCTION COEFFICIENT: A way to express how rapidly light decreases with depth. It is derived from a plot of the logarithm of (light intensity at each depth/light at surface) versus depth. The slope of this plot is the extinction coefficient for light. Plankton, inorganic particles, dissolved organic matter, and water all contribute to the decrease in light with depth.

Fe: Abbreviation for iron.

FLUX: The rate at which a measurable amount of a material flows past a designated point in a given amount of time.

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FOOD WEB: Pattern of production and consumption of organic matter in an ecosystem. Green plants are an ultimate source of energy for all food chains.

GROWTH POTENTIAL: The potential or ability of a phytoplankton population to increase total biomass if the factor controlling growth is removed. For example, the ability of phytoplankton to growth if nitrogen is added.

HALF-SATURATION CONSTANT: Nutrient concentration (such as nitrate) when the uptake rate of that nutrient is half the maximum rate possible.

HEADWATERS: The upstream boundary of a watershed.

HOLOMIXIS: Complete mixing of top and bottom waters.

HYDROLOGIC CYCLE: The circular flow or cycling of water from the atmosphere to the earth (precipitation) and back to the atmosphere (evaporation and plant transpiration). Runoff, surface water, groundwater, and water infiltrated in soils are all part of the hydrologic cycle.

HYPOLIMNION: Lower, cooler layer of a lake during summertime thermal stratification.

INOCULUM: Addition of organisms in bioassay experiments.

INSOLATION: Light from the sun.

INTERFERENCE: In chemical analyses, when something in solution (e.g. dissolved ion) prohibits an accurate measurement of the concentration of the nutrient of interest. For example, Pyramid Lake contains arsenate which forms the same blue complex as phosphate in the colorimetric analysis of phosphate. The color development for a given sample will depend on the concentration of both parameters rather than just phosphate, the parameter we are interested in measuring.

INTERNAL NUTRIENT SOURCES: Nutrients released within the lake as opposed to those entering the lake from the outside.

ISOTHERMAL: The same temperature throughout; e.g. overturn.

ISOPLETH: Lines on a contour plot of constant concentration.

LIMIT OF DETECTION: The minimum concentration of a nutrient that can be measured with the technique being used.

LIMITATION OF GROWTH: When phytoplankton growth is reduced below its optimum due to the lack of something such as light or nutrients.

LIMNOLOGICAL STUDY: An investigation designed to identify physical, biological, and chemical interactions in lakes.

LIMNOLOGY: Scientific study of fresh water, especially the history, geology, biology, physics, and chemistry of lakes. Also termed freshwater ecology.

MACROPHYTE: Large aquatic plant that is rooted in the bottom.

MEROMIXIS: Condition when lakes do not mix from top to bottom.

MESOTROPHIC: Describes a lake of intermediate photosynthetic production; See oligotrophic and eutrophic.

METALIMNION: Layer of rapid temperature and density change in a thermally stratified lake. Resistance to mixing is high in the region.

MINERALIZE: Break down organic molecules into carbon dioxide and inorganic nutrients.

MONOMICTIC: Lakes that mix completely once during each year. Usually, during the winter.

MONOTONIC: A continuous increase or a continuous decrease in concentration over time.

N: Abbreviation for nitrogen.

NEW NITROGEN: Input of nitrogen to the photic zone from either external or internal sources to the lake. This term is in contrast to regenerated nitrogen which is derived from organic matter mineralized within the photic zone.

NITROGEN DEMAND: The amount of nitrogen required by phytoplankton for growth.

NITROGEN FIXATION: Use of atmospheric nitrogen gas (N_2) by plants to fulfill nitrogen requirements for growth. Most plants use nitrate-N and ammonium-N for growth.

NH_4-N: Abbreviation for nitrogen in the form of ammonium.

NO_3-N: Abbreviation for nitrogen in the form of nitrate.

NODULARIA: Blue-green algae genus that fixes atmospheric nitrogen. Common in late summer to early fall in Pyramid Lake.

NUTRIENT: An element or chemical essential to life, including carbon, oxygen, nitrogen, phosphorus, and others.

NUTRIENT BUDGET: A comparison of all sources and losses of a nutrient to a water body.

NUTRIENT CYCLING: The flow of nutrients from one component of an ecosystem to another, as when macrophytes die and release nutrients that become available to algae (organic to inorganic phase and return).

NUTRIENT LOADING: Amount of a nutrient that enters a lake over a given period of time.

OLIGOTROPHIC: "Poorly nourished," from the Greek. Describes a lake of low plant productivity and high transparency.

ORGANIC MATTER: Molecules manufactured by plants and animals and containing linked carbon atoms and elements such as hydrogen, oxygen, nitrogen, sulfur, and phosphorus.

OVERTURN: The mixing, top to bottom, of lake water caused by the formation of denser water at the surface due to cooling or warming and wind-derived energy. Can occur in fall, winter, and spring depending on the seasonal temperature range of the lake.

P: Abbreviation for phosphorus.

PATCHINESS: High degree of spatial variability where some regions of the lake have high concentration (patches) while other regions are low.

PC: Abbreviation for particulate carbon.

PERIPHYTON: Small plants that grow on the surface of rocks, sediment, or larger plants.

pH: A measure of the concentration of hydrogen ions of a substance, which ranges from very acid (pH = 1) to very alkaline (pH = 14). pH 7 is neutral and most lake waters range between 6 and 9. pH values less than 6 are considered acidic and most life forms can not survive at pH of 4.0 or lower.

PHOTIC ZONE: The lighted region of a lake where photosynthesis takes place. Extends down to a depth where plant growth and respiration are balanced by the amount of light available.

PHOTOSYNTHETICALLY ACTIVE LIGHT: Light in the range of 400-700 nm which can be utilized by plants for photosynthesis.

PHYSICOCHEMICAL PARAMETERS: Parameters that describe the physical and chemical nature of water such as temperature, salinity, dissolved oxygen, etc.).

PHYTOPLANKTON: Microscopic algae and microbes that float freely in open water of lakes and oceans.

PHYTOPLANKTON ASSEMBLAGE: All the phytoplankton species that are present in the photic zone.

PLANKTON: Planktonic algae float freely in the open water. Filamentous algae form long threads and are often seen as mats on the surface in shallow areas of the lake.

PN: Abbreviation for particulate nitrogen.

PORE WATER: The water filling the spaces between particles in bottom sediments.

PP: Abbreviation for particulate phosphorus.

PRESCREENED: When water is passed through a screen with larger holes (e.g. 80 μm) to remove large particles before being processed as a sample or before an experiment is setup.

PRIMARY PRODUCTIVITY: The rate at which algae and macrophytes fix or convert light, water, and carbon dioxide to sugar in plant cells. Commonly measured as milligrams of carbon per square meter per hour.

PYCNOCLINE: Density gradient where lighter waters overlie denser waters.

REDFIELD RATIO: The elemental ratio of phytoplankton biomass in the ocean reported by Redfield et al. 1963. Value for carbon:nitrogen:phosphorus was 106:16:1. This ratio is often used to determine if phytoplankton biomass is deficient in nitrogen or phosphorus.

REMINERALIZATION: Break down of organic matter into inorganic nutrients; e.g. ammonium, carbon dioxide, water, and phosphate.

RESPIRATION: Process by which organic matter is oxidized by organisms, including plants, animals, and bacteria. The process releases energy, carbon dioxide, and water.

SEDIMENT: Bottom material in a lake that has been deposited after the formation of a lake basin. It originates from remains of aquatic organisms, chemical precipitation of dissolved minerals, and erosion of surrounding lands.

SEDIMENT CORE: An intact section of bottom sediment.

SEDIMENT FOCUSING: When the amount of particulate matter sinking to the bottom increases with depth due to redistribution of material from shallow regions of the lake. When sediment focusing occurs in a lake, the amount of material deposited in the deepest region of the lake is higher than expected while minimal deposition occurs in shallow regions.

SEDIMENT TRAP: Device to catch particulate matter as it slowly sinks through the water column.

Si: Abbreviation for silicon.

SiO_2-Si: Abbreviation for silicon in the form of silicate.

SIGMA-T: An expression of water density. Sigma-t (mg L^{-1}) is density in (g L^{-1}) - 1000.

SOLUBILITY: The amount of a compound that can dissolve into water. Solubility can apply to dissolved gases such as oxygen or minerals such as aragonite ($CaCO_3$).

SPATIAL VARIABILITY: Variations in parameters around the lake (e.g. across and along the lake).

STANDING CROP: Another term for biomass.

STIMULATE: In the context of bioassay experiments, an increase in phytoplankton biomass due to the addition of a limiting nutrient that is higher than any increase observed when no nutrients are added.

STOICHIOMETRY: The ratio of atoms.

STRATIFICATION: Layering of water caused by differences in water density. Thermal stratification is typical of most deep lakes during summer. Chemical stratification can also occur.

SUPERSATURATE: When the concentrations of dissolved ions are higher than predicted. Saturation applies to gas solubilities (e.g. oxygen) relative to the atmosphere and to mineral precipitation.

SYNOPTIC SAMPLING: Collecting water quality samples at different locations around a water body within a short period of time. Sampling in this fashion indicates how spatially variable parameters are at any given point in time.

TERTIARY TREATMENT: Level of effluent treatment at municipal waste facilities where nitrogen, phosphorus, or both are removed before wastewater is discharged into surface waters.

THERMAL STRATIFICATION: Lake stratification caused by temperature-created differences in water density.

THERMOCLINE: A horizontal plane across a lake at the depth of the most rapid vertical change in temperature and density in a stratified lake. See metalimnion.

TKN: Abbreviation for total Kjeldahl nitrogen.

TN: Abbreviation for total nitrogen.

TP: Abbreviation for total phosphorus.

TRFe: Abbreviation for total reactive iron.

TROPHIC STATE: The degree of eutrophication of a lake. Transparency, chlorophyll-a levels, phosphorus concentrations, amount of macrophytes, and quantity of dissolved oxygen in the hypolimnion can be used to assess state; e.g. oligotrophic.

TRP: Abbreviation for total reactive phosphorus.

UPWELLING: Movement of deeper water from below the photic zone into surface waters. Generally, the upwelling of waters is a source of nutrients for phytoplankton growth.

VOLUMETRIC PRODUCTION: Amount of carbon fixation per volume of water over a period of time. Commonly expressed in mg C L^{-1} hour^{-1}.

WATER COLUMN: Water in the lake between the interface with the atmosphere at the surface and the interface with the sediment layer at the bottom. Idea derives from vertical series of measurements (oxygen, temperature, phosphorus) used to characterize lakewater.

WATER QUALITY STANDARD: A concentration of a given substance (e.g. dissolved phosphate) that should not be exceeded so that good water quality is maintained.

WATERSHED: A drainage area or basin in which all land and water areas drain or flow toward a central collector such as a stream, river, or lake at a lower elevation.

ZOOPLANKTON: Microscopic animals which float freely in lake water, graze on detritus particles, bacteria, and algae, and may be consumed by fish.

Note - many of these definitions are taken from Lake and Reservoir Restoration Guidance Manual prepared by the North American Lake Management Society (L. Moore and K. Thornton, eds.) for the Office of Research and Development Environmental Research Laboratory, Corvallis, Oregon and the Office of Water Criteria & Standards Division Nonpoint Sources Branch of U.S. EPA, Washington, D.C., 1988.

APPENDIX B

Seminars, Scientific Meetings, and Publications

Seminars

Lebo, M.E. 1991. Limnology and Nutrient Cycling in Pyramid Lake, Nevada 1989-1990. Pyramid Lake Technical Advisory Committee Meeting, 20 June 1991, Reno, Nevada.

Scientific Meetings

Lebo, M.E., J.E. Reuter, and C.L. Rhodes. 1991. Nutrient Cycling and Phytoplankton Productivity in a Saline Desert Lake. 11th International Symposium of the North American Lake Management Society, 11-16 November 1991, Denver, Colorado.

Rhodes, C.L., J.E. Reuter, M.E. Lebo, and C.R. Goldman. 1991. Indices of Nitrogen Limitation in Pyramid Lake, Nevada. 11th International Symposium of the North American Lake Management Society, 11-16 November 1991, Denver, Colorado.

Reuter, J.E., **C.L. Rhodes**, M.E. Lebo, M. Kotzman, and C.R. Goldman. 1991. Nitrogen Limitation in a Saline, Desert Lake. 5th International Symposium on Inland Saline Lakes, March 1991, La Paz, Bolivia.

Reuter, J.E. et al. 1990. Water Quality Issues at Pyramid Lake, Nevada. California Lake Management Society, October 1990, South Lake Tahoe, California.

Note - author in bold presented the paper

Publications

Lebo, M.E., J.E. Reuter, C.L. Rhodes, and C.R. Goldman. 1992. Nutrient cycling and productivity in a desert saline lake: observations from a dry, low-productivity year. Hydrobiologia (in press).

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Meetings and Publications

Reuter, J.E., C.L. Rhodes, M.E. Lebo, M. Kotzman, and C.R. Goldman. 1992. Nitrogen
limitation in a saline, desert lake. Hydrobiologia (in press).

Workshops

Grant Management Workshop. U.S. EPA Region IX, Grants Management Section, Policy and
Grants Branch. 13-14 May 1991. San Francisco, California.

The Stream Water Quality and Uncertainty Model - Qual2eu. U.S. EPA, Center for Exposure
Assessment Modeling, Office of Research and Development. 24-28 June 1991, Athens,
Georgia.

Water Quality Standards Multi Regional Workshop. U.S. EPA, 26-28 August 1991, Seattle,
Washington.

Lake Water-Quality Assessment and Modeling Workshop. 11th International Symposium of
the North American Lake Management Society, 15 November 1991, Denver, Colorado.