

Thermal stratification, nutrient dynamics, and phytoplankton productivity during the onset of spring phytoplankton growth in Lake Baikal, Russia

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Abstract

Lake Baikal, Russian Siberia, was sampled in July 1990 during the period of spring mixing and initiation of thermal stratification. Vertical profiles of temperature, dissolved nutrients (nitrate and soluble reactive phosphorus), phytoplankton biomass, and primary productivity were determined in an eleven-station transect encompassing the entire 636 km length of the lake. Pronounced horizontal variability in hydrodynamic conditions was observed, with the southern region of the lake being strongly thermally stratified while the middle and north basins were largely isothermal through July. The extent of depletion of surface water nutrients, and the magnitude of phytoplankton biomass and productivity, were found to be strongly correlated with the degree of thermal stratification. Horizontal differences likely reflected the contribution of two important factors: variation in the timing of ice-out in different parts of the lake (driving large-scale patterns of thermal stratification and other limnological properties) and localized effects of river inflows that may contribute to the preliminary stabilization of the water column in the face of intense turbulent spring mixing (driving meso-scale patterns). Examination of the relationships between surface water inorganic N and P depletion suggested that during the spring and early summer, phytoplankton growth in unstratified portions of the lake was largely unconstrained by nutrient supplies. As summer progressed, the importance of co-limitation by both N and P became more apparent. Uptake and regeneration rates, measured directly using the stable isotope ¹⁵N, revealed that phytoplankton in stratified portions of the lake relied primarily on NH₄ as their N source. Rates of NH₄ regeneration were in approximate equilibrium with uptake; both processes were dominated by organisms <2 μm. This pattern is similar to that observed for oligotrophic marine systems. Our study underscores the importance of hydrodynamic conditions in influencing patterns of biological productivity and nutrient dynamics that occur in Lake Baikal during its brief growing season.

Introduction

The conceptual framework for interpretation of phytoplankton dynamics and productivity in freshwater ecosystems has been linked to advances in the study of oceanic plankton systems. Two major contributions involve the roles of water column physical structure and the dynamics of nutrient utilization. The importance of certain chemical elements, particularly nitro-

gen and phosphorus, in potentially regulating phytoplankton abundance under favorable physical conditions and the role of the biota themselves in regulating the biogeochemical abundance of these elements in oceanic surface waters, was highlighted by the seminal work of Redfield (1958). The importance of hydrodynamics in controlling the timing and magnitude of spring phytoplankton blooms was emphasized by Sverdrup (1953). As appreciation increased for the magni-

tude of horizontal variation in phytoplankton abundance and productivity across the world's oceans, considerable emphasis was placed on the role of water column physical structure in understanding observed temporal and spatial variation in marine phytoplankton. Phenomena such as coastal upwelling zones (Smith et al. 1983), polar ice-edge blooms (Smith & Nelson 1985), and frontal boundaries in coastal oceans (Denman & Powell 1984) emphasize the dominant contribution of physical processes to large-scale patterns of phytoplankton in the oceans. Franks (1992) has recently reviewed this diversity of physical processes driving spatial variation in phytoplankton abundance.

Because of the greatly reduced spatial (both horizontal and vertical) scales characteristic of most lakes, the role of hydrodynamics in influencing phytoplankton in these systems has largely emphasized its influence on seasonal dynamics (e.g. Lund, 1965; Reynolds, 1990). While horizontal variation in phytoplankton abundance and productivity exists at many spatial scales (Powell, 1989), documentation of horizontal patterns is limited in freshwater systems and confined, quite naturally, to studies of relatively large lakes (Abbott et al., 1982; Harris, 1986). As a result, less is known about the potential of spatial variation in hydrodynamic structure for inducing variation in phytoplankton abundance and productivity in lakes.

To obtain preliminary answers regarding patterns among nutrient utilization, physical structure, and phytoplankton dynamics in a large lake, we intensively sampled the spatial distribution of selected physical, chemical and biological variables in Lake Baikal, Russia, during the period of early thermocline formation in 1990. Specific experiments using ^{15}N were conducted at a single site in the south basin to directly measure the transformations of nitrate and ammonium. These experiments were used to corroborate results from the spatial survey and for comparison with nutrient bioassays. Lake Baikal is particularly well-suited to evaluate applicability of concepts derived from marine studies to lakes because it shares several important features with oceans (Kozhov, 1963). These include (1) large horizontal dimensions (>600 km along its long axis) with distinct open-water, coastal and semi-isolated embayment regions, (2) extreme depth (>900 m) in each of its three sub-basins, and (3) an overall condition of low nutrient availability and biological productivity. Thus, it is an appropriate site to examine how macro- and meso-scale horizontal patterns of phytoplankton abundance, productivity, and nutrient utilization in large lakes relate to differences in physi-

cal structure that result from establishment of thermal stratification.

Materials and methods

Study site

Lake Baikal is the world's deepest (1637 m maximum depth, 740 m mean depth), largest in volume (23 000 km³), and oldest (25–30 My) freshwater body. It is located in an active rift basin at an elevation of 456 m above sea level amid several mountain ranges along the remote, northeastern borders of central Asia (51–56 ° N, 104–110 ° E). The lake is 636 km long, has an average width of 48 km and is divided into three distinct sub-basins (northern, central, and southern) with maximum depths of 920, 1637, and 1433 m, respectively (Martin, 1994). More than 330 rivers and streams drain Baikal's 540 000 km² watershed. The main inflowing rivers are the Selenga, the Upper Angara, and the Barguzin; of these, the Selenga has the largest flow, contributing 16.2–41.3 km³ yr⁻¹ on average, or ca. 50% of the total inflow to Lake Baikal (Sinyukovich & Sorokovikova, 1991).

In addition to its physical characteristics, Lake Baikal is also unique in the sense that it has an extraordinary biodiversity of plant and animal species. According to Martin (1994) at least 569 species of algae and 1825 species of animal have been recorded; however, new discoveries place the number of animal species at about 2000 (Timoshkin, 1994). Thirty-five percent of the algal species and 50–55% of the animal species are endemic. Endemism is most common within the invertebrates and the Gammaridae in particular (Kamaltynov, 1993). Cladocerans are largely absent from the water column and are replaced by the pelagic, predatory amphipod *Macrohectopus branickii* (Martin, 1994). Endemic fauna includes the freshwater seal, *Phoca sibirica*, and important commercial fisheries harvest large quantities of whitefish and grayling.

The climate of the Baikal region is severe, reflecting its latitude and continental location. Winters are long and cold and the lake surface annually freezes in its entirety. In mid-winter ice thickness may reach 80–120 cm. Ice break-up typically occurs in the southern regions of the lake at the beginning of May and in the northern part at the end of May. Ice-cover as late as June is not uncommon (Kozhov, 1963). Due to low temperatures and high winds, the spring mixing period in Baikal is prolonged; vertical mixing during this

period often extends to 700–800 m (Votintsev, 1986). As a result, summer thermal stratification develops in Baikal's open waters for a period of only 5–7 weeks during late July – early September. Autumn isothermy begins in early November when vertical transport of water masses extends to the bottom (Votintsev, 1986). Weiss et al. (1991) propose that deep ventilation in Baikal is the result of a thermobaric instability which depends on the combined effects of temperature and pressure on water density. However, complete annual temperature data from Baikal were not used to fully test this hypothesis and at this time the mechanisms of deep-water renewal are still not completely understood. Using measured profiles of dissolved atmospheric CFC-12, Weiss et al. calculated that the deep waters of Lake Baikal are ventilated on a time scale of approximately 8 years. Although the lake is considered oligotrophic on the basis of its deepwater oxygen concentrations and reports of high transparency, chlorophyll reaches very high levels in some areas of the lake at certain periods; the average transparency we encountered was not as great in comparison to classic oligotrophic conditions. Average annual primary production has been reported in the of range of 120 to 130 g C m⁻² (Moskalenko & Votintsev, 1972; Votintsev et al., 1975); however, it should be noted that these values are at least 25 years old and have likely risen since that time as more of the watershed has been developed.

Sampling

Research was conducted between 3 and 28 July 1990. Sampling was performed either from the R.V. Vereschagin, a 35 m oceanographic-class research vessel, or the R.V. Papania, a 20 m research vessel. Both ships were operated out of the town of Listvyanka (near the Angara River outflow) by the Academy of Sciences Limnological Institute at Irkutsk. A cruise track resulting in an 11-station transect was followed along the main axis of the lake, with stations separated by approximately 40–100 km (Figure 1). Stations were not visited in chronological sequence along the transect; sampling dates are indicated on Figure 1. A station in Lake Baikal's largest embayment: (Barguzin Bay) was also sampled.

Station coordinates were obtained either via LoranTM or via a MagellanTM portable navigation system that utilizes the Global Positioning System (GPS). Vertical profiles of temperature with depth were made at each station with an internally-recording

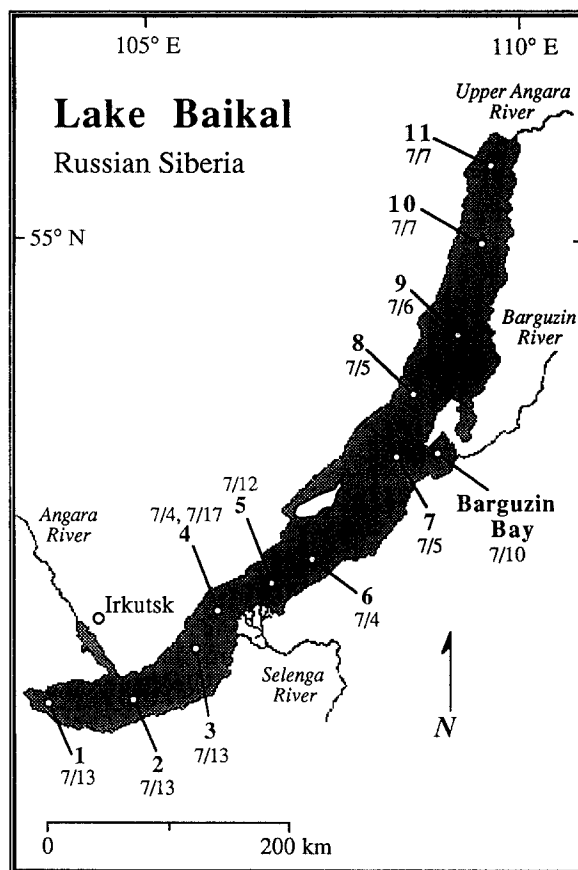


Figure 1. Map showing the locations of sampling stations, major inflowing rivers, and the lake's outflow (Angara River). Sampling dates are indicated for each station.

temperature-depth unit (accuracy: 0.02 °C) recording at 5 or 10 m intervals for the upper 250 m of the water column. For stations sampled during daytime, vertical light penetration was measured using a flat underwater light sensor (Licor, Inc.); Secchi transparency (using a 20 cm white disk) was also determined. Using the light penetration data, the depths of 100%, 50%, 30%, 10%, and 1% light penetration (relative to light intensity just below the surface) were determined (for stations sampled at night, data from a similar previous station were used). Water samples were obtained from those depths using Van Dorn bottles. At least two additional samples deeper in the water column (75–250 m) were also taken at each station. Deck-board solar radiation was continuously recorded with a BelfortTM recording pyrhelograph.

All ¹⁵N work was conducted at a central location within the south basin. Experiments were performed on samples collected at the 50% and 1% depths of light penetration.

Analytical methods

Water samples for spatial comparison were analyzed for dissolved nutrient levels (nitrate, NO_3 and soluble reactive phosphorus, SRP), phytoplankton biomass (particulate nitrogen), and primary productivity (PPR). NO_3 and SRP were determined on shipboard using fresh filtered (Whatman GF/F) samples using the hydrazine reduction method (Kamphake et al., 1967) and SRP by the ascorbic acid technique (APHA, 1976), respectively. Samples for analysis of particulate nitrogen were filtered onto pre-combusted glass-fiber (GF/F) filters. Filters were dried and returned to the United States for analysis on a Perkin-Elmer model 2400 elemental analyzer.

Primary productivity measurements were made using the ^{14}C method (Goldman, 1963) on samples collected from depths of 100% to 1% light penetration (as described above). For each depth, two clear and one dark 150 mL PVC bottles were filled, inoculated with ca. $2.75 \mu\text{Ci } ^{14}\text{C-HCO}_3$, and placed in an on-deck incubator. Light levels were simulated using punched stainless steel neutral-density screens; we confirmed the relative light penetration in each incubator compartment with the photometer. Clear weather dominated during the transect sampling and little day-to-day variation in light levels occurred in the incubator. Incubator temperatures were maintained close to surface lake temperature by continuously circulating lake water. PPR incubations were generally for 3–3.5 h between 0730 h and 2100 h local time. Incubations generally began immediately after sample collection; however, samples obtained from stations sampled at night were held in the dark at ambient surface temperature until morning. Incubations were ended by filtering bottle contents onto Millipore™ HA filters (pore size: $0.45 \mu\text{m}$). Filters were dried and returned to the United States for determination of sample radioactivity using a thin-window gas-flow Geiger-Mueller counter. Samples for analyses of total dissolved inorganic carbon (DIC) were placed in sterile evacuated blood collection tubes and preserved with chloroform (Roberts & Smith, 1988); these were also transported to the United States for analysis by infrared absorption (Infrared Industries IR-726 CO_2 monitor) against DIC standards.

^{15}N Experiments and methodology

Experiments which examined transformations of NO_3 and NH_4 were conducted at station 2 (see Figure 1) on water collected between the depths of 100% and

1% light penetration. Station 2 was selected for our nitrogen experiments because it represented a region of the lake where thermal stratification and nutrient depletion were most extreme. To support ^{15}N experiments, particulate carbon and particulate nitrogen were measured with a Carlo Erba model 1600 elemental analyzer. NH_4 was analyzed by the phenol hypochlorite method (Solorzano, 1969) on filtered (Whatman GF/F) samples at the limnology laboratory in Listvyanka, or on filtered and frozen samples at the Limnology Institute at the University of Constance, Germany.

NO_3 and NH_4 uptake kinetics experiments were conducted on water from 50% and 1% light penetration by dispensing water from the selected depths into 12 500-mL high density polyethylene bottles. Each bottle was then enriched with either $^{15}\text{NO}_3$ (99 atom-%) or $^{15}\text{NH}_4$ (99 atom-%) to yield final additions ranging from 2 to $112 \mu\text{g N L}^{-1}$. The samples were placed in a surface incubator and covered with neutral density screens to simulate *in situ* irradiance; samples were maintained near the temperature of collection with circulating lake water. Incubations began at mid-morning and lasted for approximately 10 h. Uptake was terminated by filtration through precombusted Whatman GF/F filters. The filtered samples were air dried and analyzed for ^{15}N content ($^{15}\text{N}: ^{14}\text{N}$ ratio) using emission spectrometry following Dumas combustion (Timperley & Priscu, 1986). Additional samples were collected at each depth for quantification of ambient NO_3 , NH_4 , particulate carbon, and particulate nitrogen using methods described previously.

Kinetic parameters for uptake (described here as the sum of transport and assimilation during the experimental time frame) were obtained with the Michaelis-Menten model fitted directly to the data with Mardquart's algorithm (Priscu et al., 1989; Robinson, 1985). NH_4 uptake was corrected for changes in specific activity during the incubation caused by internal NH_4 regeneration using data from the isotope dilution experiments (described below) as outlined by Priscu et al. (1989). The equation of Dugdale & Wilkerson (1986) was used to compute final uptake rates assuming no change in particulate nitrogen concentration during the experiments.

Water column NO_3 and NH_4 uptake was measured at the depths of 100%, 50%, 30%, 10% and 1% light penetration. Samples were placed in 500-mL PVC bottles, enriched with $100 \mu\text{g } ^{15}\text{NO}_3\text{-N L}^{-1}$ or $100 \mu\text{g } ^{15}\text{NH}_4\text{-N L}^{-1}$, covered with appropriate layers of neutral density screens (to simulate *in situ* conditions) and incubated under natural sunlight during

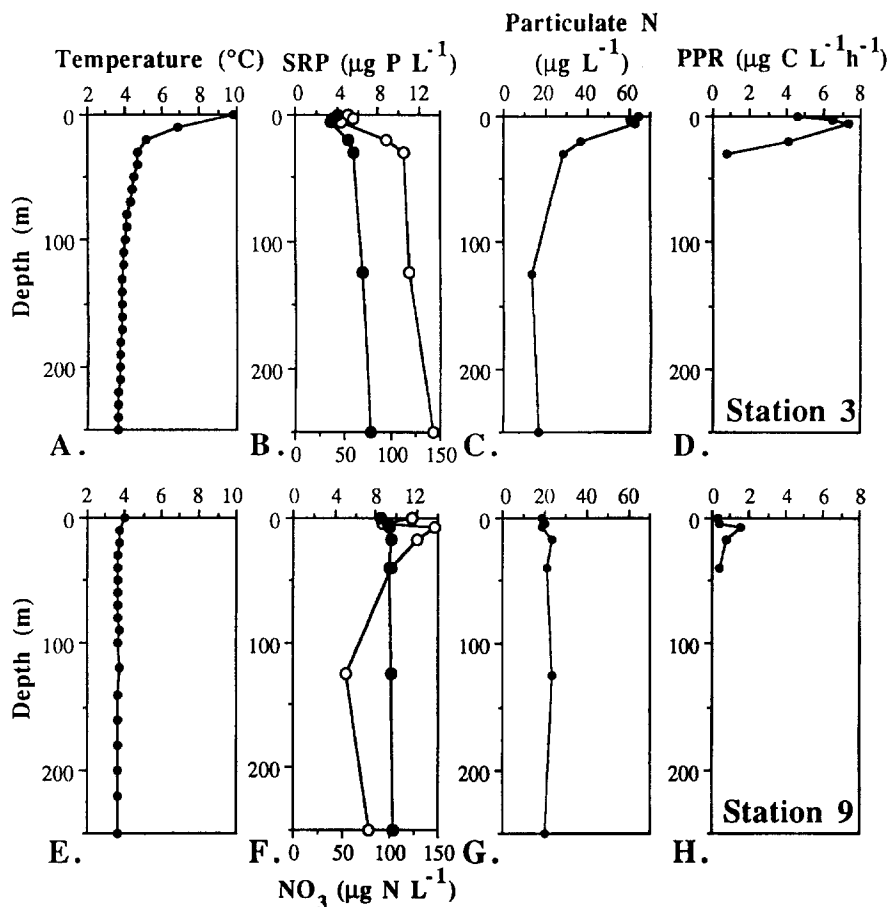


Figure 2. Illustrative vertical profiles of temperature ($^{\circ}\text{C}$), soluble reactive phosphorus (SRP; $\mu\text{g P L}^{-1}$; open circles), nitrate (NO_3 ; $\mu\text{g N L}^{-1}$; dark circles), particulate N ($\mu\text{g N L}^{-1}$), and primary productivity (PPR; $\mu\text{g C L}^{-1} \text{h}^{-1}$) at a stratified station (station 3, top panel) and an unstratified station (station 9, bottom panel).

mid-afternoon for approximately 5 h. Samples were maintained near the temperature of collection with circulating water. Uptake rates were determined as described above for the substrate kinetics experiments. Ambient uptake rates (i.e. at *in situ* nutrient concentration) for the samples from the 100% to 30%, and the 10% to 1% light depths were computed with the Michaelis-Menten model using parameters obtained from the uptake kinetics experiments at the 50% and 1% light depths, respectively.

Isotope dilution experiments were conducted essentially as outlined by Priscu et al. (1989) using activated zeolite to scavenge NH_4 from solution. Tests conducted on water from Lake Baikal showed that the zeolite extracted NH_4 from all sampling depths at >90% efficiency. Experiments were conducted in 2-L high density polyethylene carboys maintained near ambi-

ent light and temperature. The samples were enriched with $56 \mu\text{g NH}_4\text{-N L}^{-1}$ (20 atom-% ^{15}N) and subsampled 6 times over a 10 h incubation. These experiments were conducted on whole water, water screened through $20 \mu\text{m}$ nitex netting, and water gently filtered (<0.3 atm) through $2 \mu\text{m}$ Nuclepore filters. Fractionation allowed us to assess rates of NH_4 regeneration by various groups of the microbial community. Rates of uptake and regeneration were computed according to Laws (1984). Size fractionated particulate nitrogen and carbon were also measured on subsamples from each experiment. Experiments were conducted at both the 50% and 1% light depths; unfortunately, the ^{15}N samples for the 50% sample were contaminated during filtration and were not analyzed.

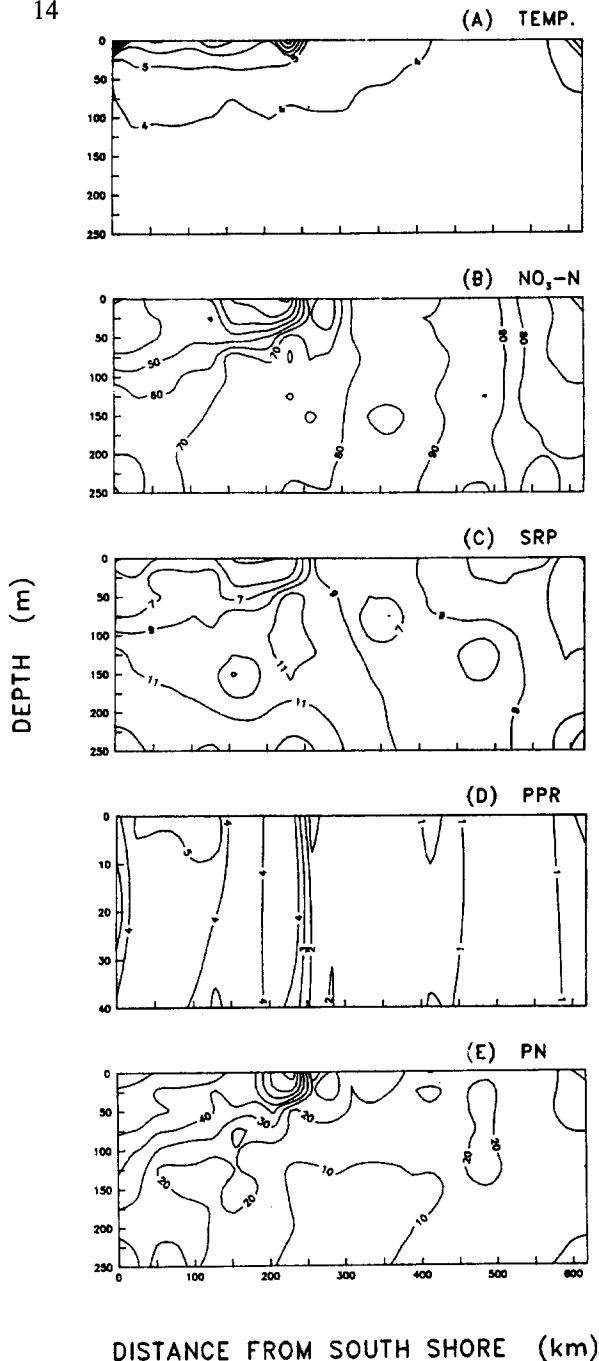


Figure 3. Isopleth diagrams of A, temperature; B, NO_3 ; C, SRP; D, primary productivity; and E, particulate N; illustrating the horizontal and vertical distribution of these parameters along the north-south axis of the lake moving from station 1 (south) to station 11 (north).

Results

Spatial variation

Vertical profiles of limnological properties differed dramatically from station to station along the lake-axis

transect. As examples, profiles of physical, chemical and biological variables for two stations are illustrated in Figure 2. Station 3, located in the northeast end of Baikal's southern basin, was strongly thermally stratified when sampled on 13 July (Figure 2A). There was a reduction of dissolved nutrient pools in the upper 25 m of the water column (Figure 2B), reflecting the higher biomass and productivity (Figures 2C, D). In contrast, at station 9, in the lake's northern basin, thermal stratification was poorly developed (Figure 2E), nutrient levels were uniform with depth (NO_3) or higher at the surface than below (SRP; Figure 2F), and biomass and productivity were low (Figures 2G, H). Isopleth diagrams illustrate the spatial extent of differences in the vertical distribution of these variables (Figure 3). They indicate a longitudinal pattern of relatively strong thermal stratification in the entire southern basin and in the extreme north of the transect (Figure 3A), with associated regions of lower dissolved nutrient levels (Figures 3B, C) and high biomass and productivity (Figures 3D, E).

Phytoplankton counts and taxonomic identification were made at 8 depths in the water column at station 5 (0–1000 m) and 9 depths at station 9 (0–400 m). The distribution of algae was similar at both locations with picoplankton forms of cyanobacteria completely dominant in terms of cell number. At station 5 in the southern portion of the central basin, *Synechocystis limnetica* was the most abundant species with counts from $2\text{--}9 \times 10^6$ cells L^{-1} . *S. limnetica* numbers were similarly high at station 9, in the north basin, at $2\text{--}7 \times 10^6$ cells L^{-1} . It is known that picoplankton cyanobacteria predominate over other species during the summer in Lake Baikal, and can account for up to 30% of the primary productivity during that time (Votintsev, 1986). In general phytoplankton biodiversity was low with a total of only 8 and 6 species identified within the euphotic zone at station 5 (0–50 m) and 9 (0–40 m), respectively. In addition to the abundant cyanobacteria, the majority of species belonged to the major taxonomic groups Chrysophyta and Cryptophyta. Other species identified at station 5 included *Chromulina* sp. ($2\text{--}25 \times 10^3$ cells L^{-1}), *Chroomonas acuta* ($3\text{--}36 \times 10^3$ cells L^{-1}), *Cryptomonas* sp. (3.6×10^3 cells L^{-1}), *Cyclotella minuta* (2×10^3 cells L^{-1}), *C. baicalensis* (1.5×10^3 cells L^{-1}), *Synedra acus* (2×10^3 cells L^{-1}), and the chlorophyte *Monoraphidium irregulare* (2×10^3 cells L^{-1}). Species composition in the station 9 euphotic zone (0–40 m) was very similar, *Chromulina* sp. ($2\text{--}10 \times 10^3$ cells L^{-1}), *Ochromonas* sp. (4×10^3 cells L^{-1}), *Dinobryon cylindricum* (4×10^3 cells L^{-1}), *Chryso-*

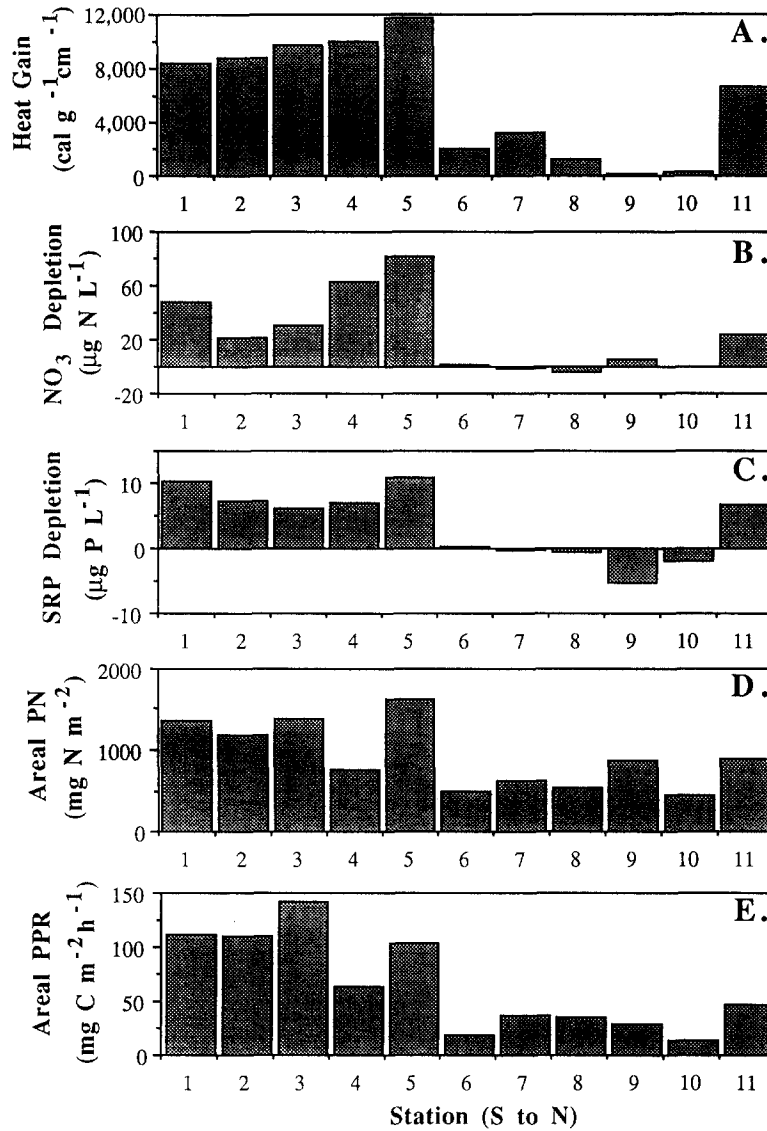


Figure 4. Summarized water column variables for the north-south lake transect. A. Net heat gain in the water column ($\text{cal g}^{-1} \text{cm}^{-2}$). B. Surface depletion of NO_3 ($\mu\text{g N L}^{-1}$). C. Surface depletion of SRP ($\mu\text{g P L}^{-1}$). D. Particulate N per unit area (mg N m^{-2}). E. PPR per unit area ($\text{mg C m}^{-2} \text{h}^{-1}$)

coccus sp. (2×10^3 cells L^{-1}), *Chroomonas acuta* (2×10^3 cells L^{-1}), and *Monoraphidium irregulare* (2×10^3 cells L^{-1}).

To further characterize these longitudinal patterns of physical, chemical and biological properties, we calculated summary variables for the vertical distributions at each station. For temperature profiles, we calculated the net heat gain (units: $\text{cal g}^{-1} \text{cm}^{-2}$) in the epilimnion since spring isothermy using the measured temperatures at a depth of 100–200 m as a reference for the minimum temperatures at each station. We

estimated the magnitude of net depletion of dissolved nutrient pools at the surface as the difference between the mean value for a nutrient in the 100%, 50%, and 30% depths and the mean value for the aphotic (<1% light) samples. The amount of phytoplankton biomass and productivity per unit surface area was calculated at each station by integrating the profiles of particulate N and PPR to the depth of 1% light penetration.

Water column summary indices calculated in this way further illustrate the distinct horizontal variation in limnological conditions along the length of Lake

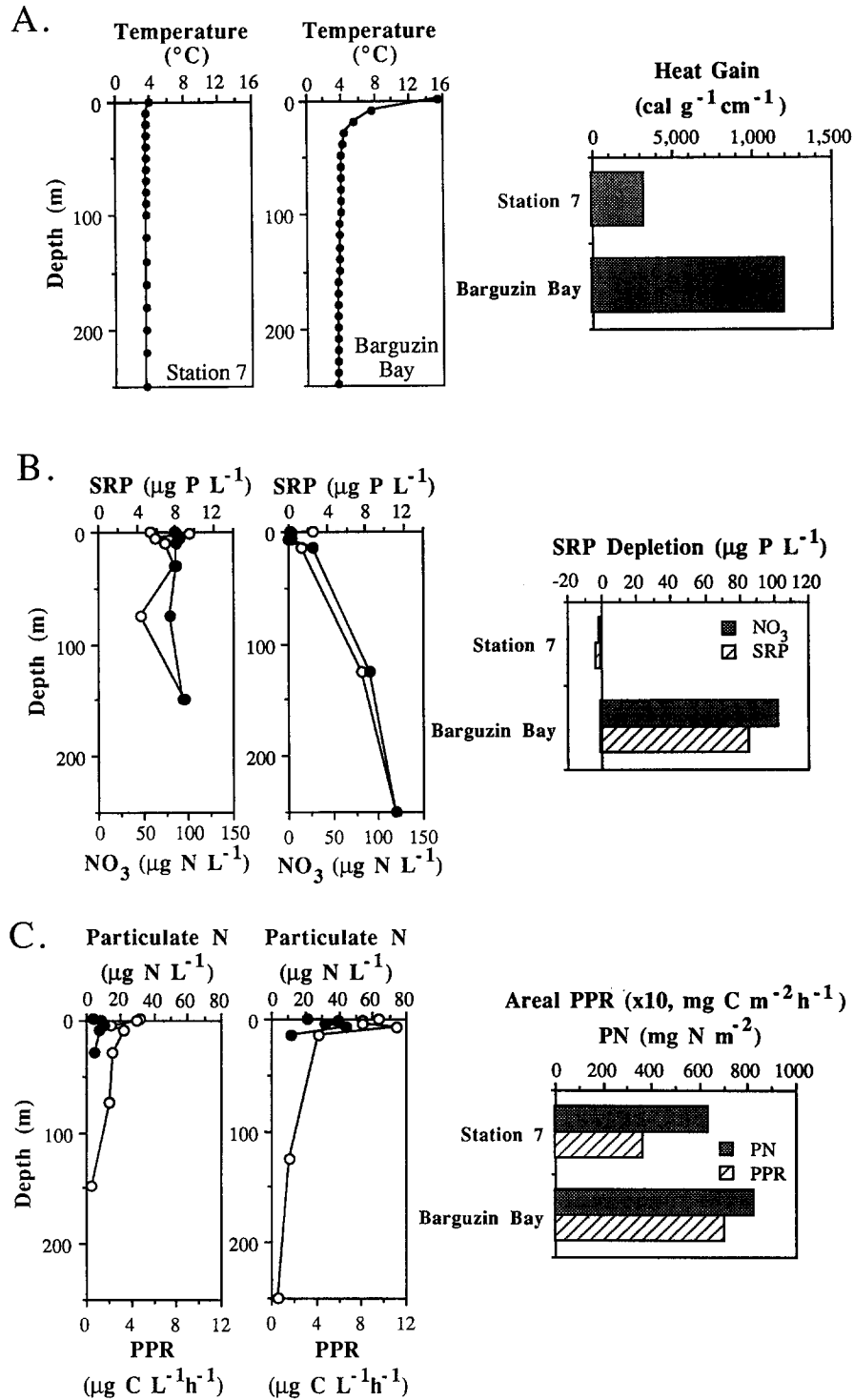


Figure 5. Comparison of limnological conditions in Barguzin Bay with nearby open-water station 7. A. Vertical profiles of temperature and degree of water column thermal stratification. B. Vertical profiles of NO_3 (dark circles; $\mu\text{g L}^{-1}$) and SRP (open circles; $\mu\text{g L}^{-1}$) and extent of surface water depletion ($\mu\text{g L}^{-1}$) of NO_3 and SRP. C. Vertical profiles of particulate N (open circles; $\mu\text{g L}^{-1}$) and PPR (dark circles, $\mu\text{g C L}^{-1} \text{h}^{-1}$), and areal particulate N (mg N m^{-2}) and areal PPR ($\text{mg C m}^{-2} \text{h}^{-1}$).

Baikal (Figure 4). Net heat gain was highest in the southern portion of the lake (Figure 4A; stations 1–5) but was also high at the most northerly station (station 11) sampled, which was only 25 km from the lake's northern shore. Depletion of surface nutrient pools was also highest at the southern stations, with enhanced depletion also observed at station 11 (Figures 4B, C). Regions of pronounced thermal stratification and increased nutrient depletion generally corresponded to regions of high phytoplankton biomass and productivity (Figures 4D, E). Because some stations were sampled at night, Secchi depth data are incomplete but illustrate that between-station differences in phytoplankton biomass were reflected in water transparency. For example, Secchi transparencies at stations 1, 2, 3, and 5 were 4–6 m, in contrast to stations 6, 9, and 10, where Secchi depths were >20 m.

Pronounced variation in limnological conditions was also observed between station 7 in the central basin and along the main transect and Barguzin Bay, located 40 km to the east (Figure 1). In the bay, thermal stratification was very strongly developed but in the open lake stratification was extremely weak (Figure 5A). Dissolved nutrient levels in Barguzin Bay surface waters were depleted nearly to detection limits but were high and uniform with depth at station 7 (Figure 5B), reflecting high biomass and productivity in the bay relative to the main basin (Figure 5C). The general patterns illustrated in Figure 4 suggest a close dependence between thermal stratification, nutrient utilization, and biological production during the beginning of the growing season in Lake Baikal. To evaluate this dependence, we examined correlations among water column properties for all stations sampled, including additional stations sampled in the northern basin but not shown in Figure 1. The magnitude of surface nutrient depletion was very closely correlated with the magnitude of the net heat gain ($p < 0.001$, $r^2 > 0.78$), for both NO_3 and SRP (Figures 6A, B). Both water column biomass (areal particulate N) and productivity (areal PPR) were also significantly correlated with thermal stratification (Figures 6C, D; $p < 0.001$, $r^2 > 0.57$); strongly stratified stations supported the highest phytoplankton biomass and high productivity.

The observed relationship between the development of thermal stratification, depletion of euphotic zone nutrients, and increases in phytoplankton biomass and productivity is further illustrated by comparison of water column profiles taken at station 4 on 4 July and then again, two weeks later, on 17 July. During this period surface water temperature increased by

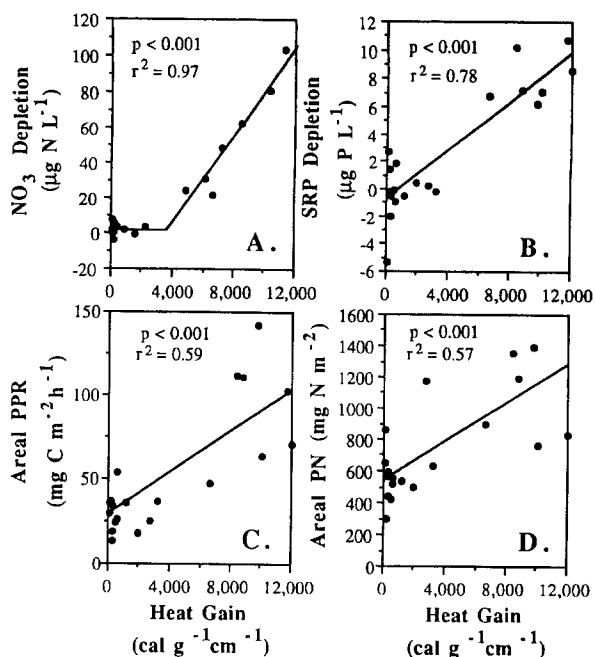


Figure 6. Relationships between chemical and biological parameters and net heat gain ($\text{cal g}^{-1} \text{cm}^{-2}$) for all stations sampled during the expedition. A. NO_3 depletion ($\mu\text{g L}^{-1}$). B. SRP depletion ($\mu\text{g L}^{-1}$). C. Areal PPR ($\text{mg C m}^{-2} \text{h}^{-1}$). D. Areal PN (mg N m^{-2}). Lines represent linear least-squares fits to the data; a piecewise linear regression was used to fit a threshold model to the NO_3 data.

3.5°C as stratification intensified (Figure 7A). During the same period, both phytoplankton biomass (as particulate N), and maximum primary productivity nearly doubled (Figures 7D, E). Nitrate depletion in the surface waters (100%, 50%, and 30% light depths) was dramatic (Figure 7B) as the mean concentration declined from $17 \mu\text{g L}^{-1}$ to $< 1 \mu\text{g L}^{-1}$. With the exception of the 0 m sample, SRP in the upper euphotic zone was low ($< 2 \mu\text{g L}^{-1}$) on both dates and so did not show appreciable additional depletion during the interval (Figure 7C).

To evaluate general patterns of phytoplankton utilization of N and P in Lake Baikal, we also examined relationships among biomass, productivity, nutrient concentrations, and nutrient utilization (again, defined as the difference between deep and surface water concentrations). Areal biomass and PPR increased with NO_3 depletion but these relationships became non-linear at depletion values > 60 , corresponding to stations with the highest degree of thermal stratification (Figure 8A, C; $p < 0.005$, $r^2 \geq 0.63$ for linear portion of the relationships). This divergence from linearity reflects data from stations 4 and 5 and Barguzin Bay,

Table 1. Rates of maximum uptake ($V_{\max} = \text{h}^{-1}$) and half-saturation constants ($K_s = \mu\text{g L}^{-1}$) for NO_3 and NH_4 computed with the Michaelis-Menten model fitted with Marquardt's algorithm. NH_4 data were corrected for isotopic dilution during the experiment. The coefficients of variation [(mean/SD) $\times 100$] for V_{\max} and K_s were $< 1\%$ for all experiments. Ambient N concentration represents levels in the water before ^{15}N enrichment. NO_3 uptake at the 1% light depth did not show first order kinetics; V_{\max} was computed as the y-intercept of a regression of uptake rate on NO_3 concentration.

Sample	V_{\max} (h^{-1}) ($\times 10^{-3}$)	K_s ($\mu\text{g L}^{-1}$)	Ambient N ($\mu\text{g L}^{-1}$)
50% light depth			
NH_4	7.5	2.5	1.5
NO_3	0.7	6.2	1.0
1% light depth			
NH_4	5.5	0.5	0.5
NO_3	0.5	–	5.0

where areal particulate N and PPR were low compared to NO_3 depletion. In contrast, areal biomass and PPR increased over the whole range of SRP depletion (Figure 8B, D; $p < 0.001$, $r^2 \geq 0.47$).

The stoichiometric nature of net nutrient utilization in the Baikal water column in the early phase of spring phytoplankton growth was evaluated by examining the relationship between NO_3 depletion and PO_4 depletion (Figure 9). The relationship appeared to be hyperbolic, with no further PO_4 depletion accompanying increases in NO_3 depletion greater than around $40 \mu\text{g L}^{-1}$. However, as only a few of our observations fell on the plateau region of this hyperbolic relationship, it appears that phytoplankton were largely growing unconstrained by external nutrient supplies at most stations in Lake Baikal during our primary study period. The hyperbolic nature of the SRP or NO_3 depletion relationship suggests that at the most strongly stratified stations, sustained phytoplankton development, with additional NO_3 depletion, was occurring using regenerated P. Rapid depletion of the NO_3 pool observed by our repeated sampling of station 4 as spring phytoplankton developed (i.e., 17 July vs. 4 July) underscores the likely importance of both N and P as co-limiting elements in Lake Baikal during most of the summer period.

Nitrogen uptake and regeneration

Nitrogen uptake in all samples, except for NO_3 at the 1% light level, increased hyperbolically as substrate

level was increased. V_{\max} for NH_4 uptake was more than an order of magnitude greater than for NO_3 at both the 50% and 1% light depths (Table 1). The half saturation constant was considerably lower for NH_4 than NO_3 in both experiments; NO_3 at the 1% light depth never showed first-order kinetics, presumably because saturation was reached at ambient NO_3 levels ($5 \mu\text{g NO}_3\text{-N L}^{-1}$). V_{\max} and K_s for NH_4 at the 50% light depth were greater than these same parameters at the 1% light depth corresponding to higher ambient NH_4 concentration at the former. In general, trends in these parameters indicate that the deep water populations were able to use NH_4 more efficiently at low levels, but not at saturating levels, than the shallow populations. Despite lack of first order kinetics for NO_3 at the 1% light level, kinetic parameters showed an overall preference for NH_4 uptake, relative to NO_3 , at both low and high light levels.

Rates of uptake and regeneration for all size fractions at the 1% light depth were within about 30% of each other (Table 2). Given the numerous sources of error associated with these types of measurement (Laws, 1984; Glibert et al., 1982), such variation should not be considered significant. Of interest, however, is the fact that both uptake and regeneration in the $< 2 \text{ m}$ fraction was within 30% of that in whole lake water, underscoring the importance of small organisms (picoplankton) in both uptake and regeneration of NH_4 in Lake Baikal during the period when sampling was conducted. Particulate carbon and nitrogen data show that the $< 2 \mu\text{m}$ size class also contributed significantly to total biomass (Table 2). Uptake to regeneration ratios were all greater than 1, but again, imprecision associated with isotope dilution experiments make it likely that these ratios were not significantly different than 1, particularly given the additional errors associated with error propagation of proportions (Fleiss, 1981).

The water column nitrogen uptake data allowed us to assess carbon to nitrogen uptake ratio at station 2. These data (Figure 10A) show that NH_4 uptake exceeded NO_3 uptake throughout the euphotic zone (i.e. to the depth of 1% light penetration) even below 10 m where NO_3 levels greatly exceeded NH_4 (Figure 10B). The ratio of PPR to total dissolved inorganic nitrogen uptake ($\text{DIN} = \text{NO}_3 + \text{NH}_4$) ranged from 8.7 to 25.2 (g:g) over the euphotic zone. Highest ratios occurred in the upper water column where DIN values were lowest. The overall average depth weighted PPR:DIN ratio was 20. This value is well above the Redfield ratio for balanced growth, suggesting potential N deficiency

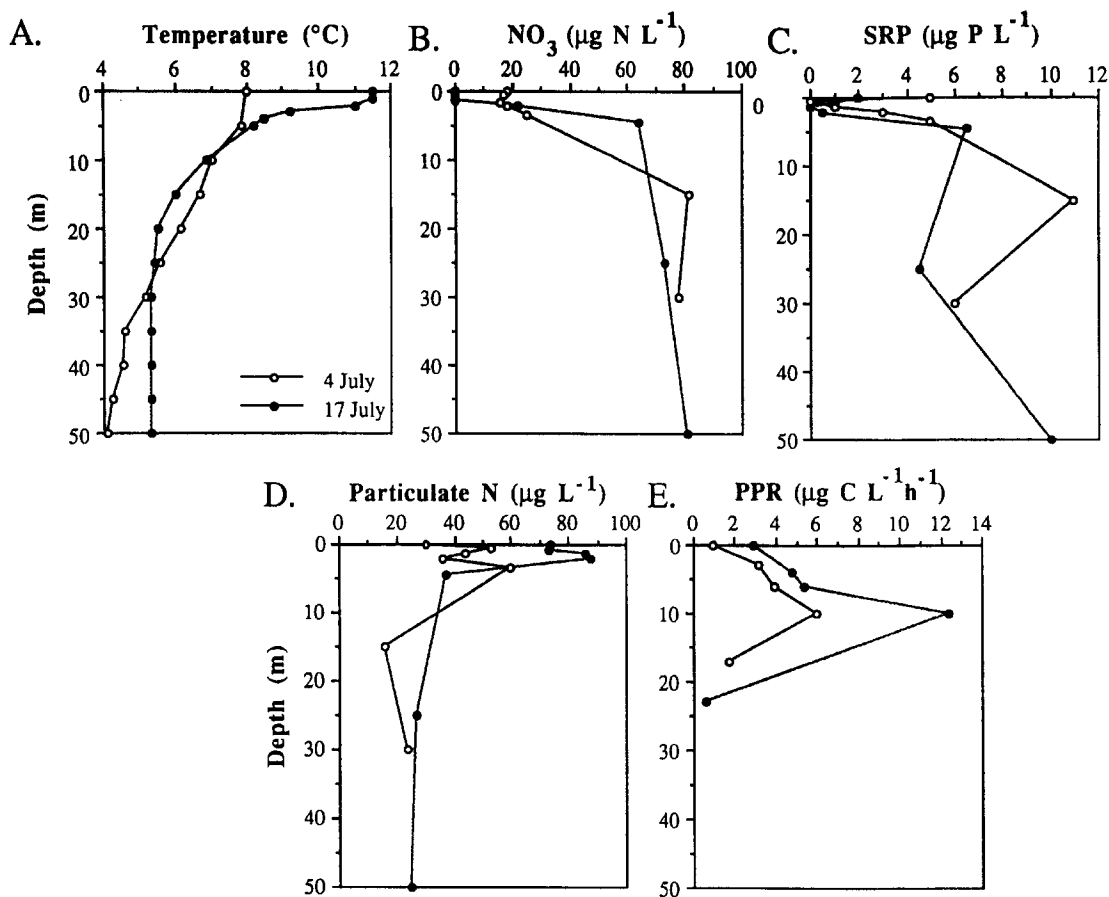


Figure 7. Changes in the vertical profiles of A, temperature ($^{\circ}\text{C}$); B, NO_3 ($\mu\text{g N L}^{-1}$); C, SRP ($\mu\text{g P L}^{-1}$); D, particulate N ($\mu\text{g L}^{-1}$); and E, primary productivity ($\mu\text{g C L}^{-1} \text{h}^{-1}$) between 4 July (open circles) and 17 July (dark circles) 1991, at station 4.

Table 2. Size fractionated NH_4 uptake (U) and regeneration (R) rates ($\mu\text{g NH}_4\text{-N L}^{-1} \text{h}^{-1}$) computed from an isotope dilution experiment at the depth of 1% light penetration. Size fractionated particulate carbon (PC = $\mu\text{g L}^{-1}$), particulate nitrogen (PN = $\mu\text{g L}^{-1}$) and the PC:PN ratio (g:g) from the 50% and 1% light depths are also given.

Sample	U R		U:R ($\mu\text{g L}^{-1}$)	PC ($\mu\text{g L}^{-1}$)	PN	PC:PN
	($\mu\text{g NH}_4\text{-N L}^{-1} \text{h}^{-1}$)					
50% light depth						
whole	—	—	—	413.6	58.0	7.1
<20 μm	—	—	—	371.5	54.1	6.9
<2 μm	—	—	—	242.5	36.1	6.7
1% light depth whole						
	0.84	0.76	1.10	418.2	65.6	6.4
<20 μm	1.19	1.00	1.19	385.6	62.3	6.2
<2 μm	0.96	0.68	1.40	208.2	32.0	6.5

on that date. It is important to realize, however, that the hourly rates used to obtain the PPR:DIN uptake ratio were obtained from daytime incubations. Since

inorganic nitrogen uptake continues in the dark whereas photosynthesis ceases, daily PPR:DIN uptake ratio, which is the most relevant time frame for phytoplank-

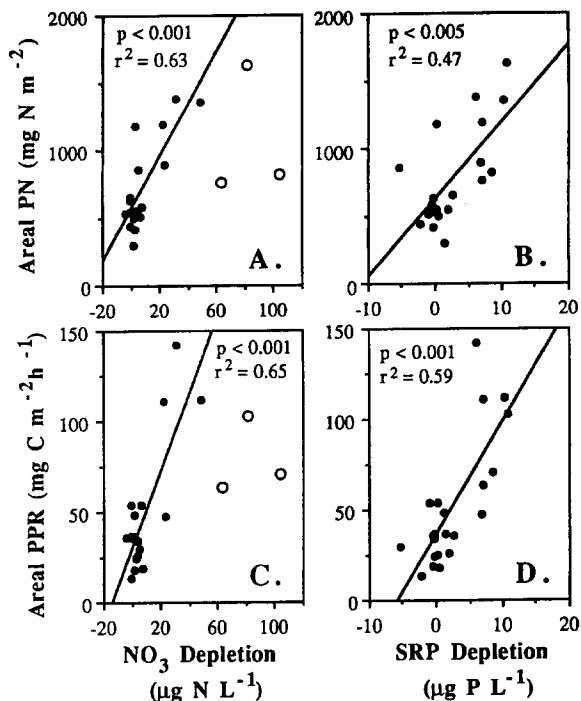


Figure 8. Relationships between areal PN (mg N m^{-2}) and A, NO_3 depletion ($\mu\text{g L}^{-1}$), and B, SRP depletion ($\mu\text{g L}^{-1}$) for all stations sampled. Relationships between areal PPR ($\text{mg C m}^{-2} \text{h}^{-1}$) and C, NO_3 depletion ($\mu\text{g L}^{-1}$), and D, SRP depletion ($\mu\text{g L}^{-1}$) for all stations sampled. Open circles correspond to data for the most strongly stratified stations; these data were not included in correlation analysis.

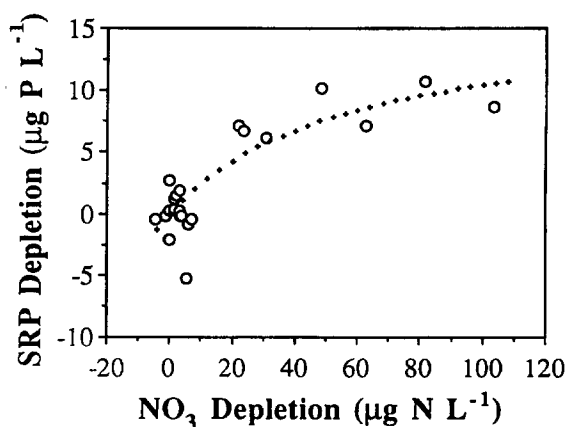


Figure 9. Relationship between surface water depletion of NO_3 and SRP ($\mu\text{g L}^{-1}$) for all stations sampled.

ton growth, will probably be half (or lower) of those based on hourly rates (see Priscu et al., 1991).

Discussion

Results from our study illustrate the large influence of hydrodynamic conditions on the spatial distribution of phytoplankton productivity and nutrient utilization in Lake Baikal during the onset of its brief summer growing season. In central to northern lake locations (such as stations 6, 7, 8, 9, and 10), the water column was largely isothermal and cold, surface nutrient concentrations high, and algal productivity and biomass low. However, at all stations where thermal stratification had become established, enhanced levels of phytoplankton biomass and productivity were observed, accompanied by lower concentrations of nutrients in the surface waters. More specifically, phytoplankton biomass and productivity, and net nutrient depletion were quantitatively associated with the magnitude, and therefore perhaps the duration, of water column thermal stratification (Figure 6), although for NO_3 depletion it appeared that a threshold level of heat gain was required before appreciable depletion occurred. These differences in water column properties occurred over both relatively short and large spatial scales. For example, Figure 5 contrasts conditions found in Barguzin Bay, which has a strongly stratified water column along with high levels of nutrient depletion and phytoplankton biomass, and station 7, with a nearly isothermal water column, little nutrient depletion, and very low phytoplankton, located in the central basin of the lake less than 40 km from the Barguzin Bay sampling station. At the same time, the data in Figure 4 clearly show the large-scale north-south gradient in physical, chemical, and biological parameters. In this sense the spatial distribution of phytoplankton productivity and nutrient utilization in Lake Baikal resembles phytoplankton blooms in marine systems where localized favorable physical conditions promote rapid phytoplankton growth under nutrient-sufficient conditions (Smith & Nelson, 1985). The high concentrations of dissolved nutrients in the 'blue-water' stations of Lake Baikal support the contention that in these regions phytoplankton growth in the early spring was constrained by light limitation induced by wind-driven mixing that transports cells below the photic zone.

The importance of spatial variation in water column thermal stratification in determining phytoplankton abundance and productivity in Lake Baikal during the onset of the summer growing season leads naturally to questions regarding the factors causing this spatial variation in hydrodynamic conditions. In the oceans, variation in water column stratification can

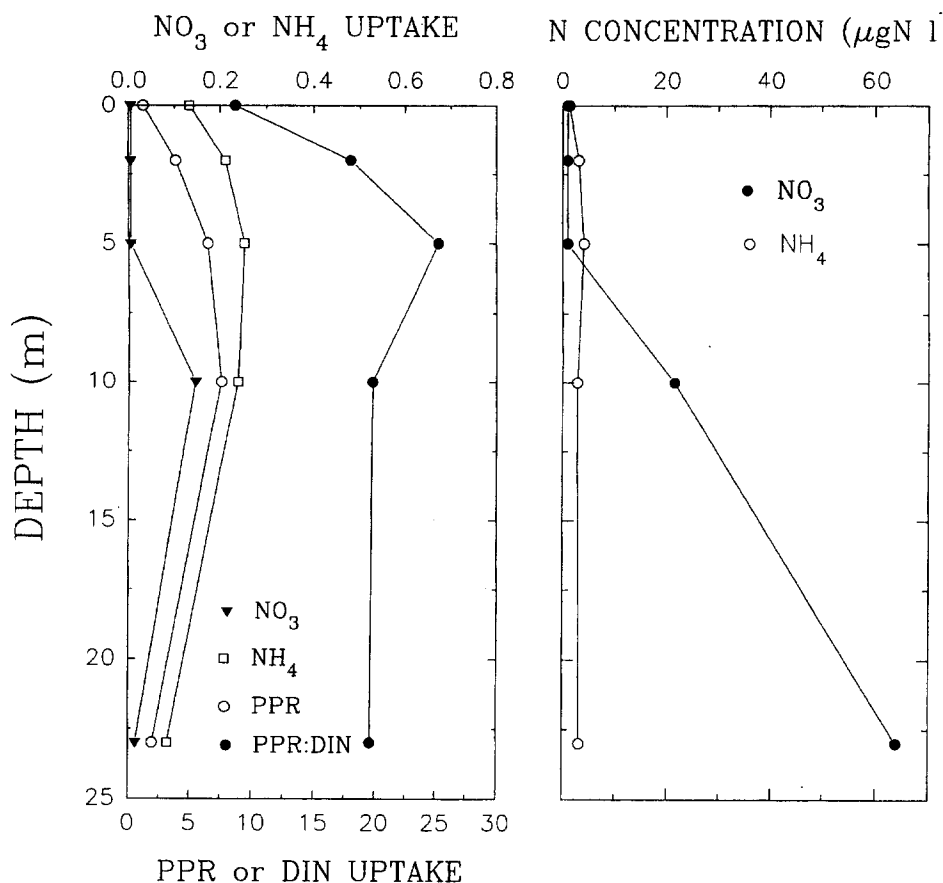


Figure 10. A. Vertical profiles of NO₃ uptake ($\mu\text{g N L}^{-1} \text{h}^{-1}$), NH₄ uptake ($\mu\text{g N L}^{-1} \text{h}^{-1}$), PPR ($\mu\text{g C L}^{-1} \text{h}^{-1}$), and the ratio of PPR to DIN (NO₃+NH₄) uptake (g:g). B. Vertical profiles of ambient NO₃ and NH₄ concentration ($\mu\text{g N L}^{-1}$) at the depths of rate measurements. All N uptake values represent rates at ambient N concentration; NH₄ uptake was corrected for isotopic dilution (see text for details). All data were collected from the south basin of Lake Baikal near station 2.

be caused by differences in temperature, salinity and advection; in lakes, only temperature and advection generally needs to be considered. Given Lake Baikal's large size and its north-south orientation, a natural hypothesis to explain spatial variation in thermal stratification would be that it is driven by differences in climate (insolation, air temperature, winds) along its very long north-south axis. This factor is certainly important in determining the distribution in spring bloom development in Lake Baikal, as there are differences in the dates of ice-out in different parts of Lake Baikal. Typically, the southern end tends to be ice-free many weeks sooner (Kozhov, 1963); however, we have no specific information on spatial variation in the timing of ice-out in Lake Baikal during spring 1990. The importance of the elapsed time since development of thermal stratification in determining levels of nutrient

depletion and phytoplankton biomass and productivity is clearly demonstrated by our repeated sampling of station 4, where nitrate depletion and phytoplankton biomass and productivity change significantly over a 2-week period (Figure 7).

Our observations also suggest that, in addition to spatial differences in the timing of ice-out, other factors may contribute to the initiation and development of thermal stratification at specific locations in Lake Baikal. First, while many of the thermally stratified stations lie in the southern basin and in the southern end of the central basin, the most northerly station (station 11) was quite strongly thermally stratified (Figure 4). Second, there were pronounced differences in thermal stratification between stations located near each other. Again, station 7 and the Barguzin Bay station lie at the same latitude and presumably experience

approximately the same climatic conditions; however, the water column at station 7 was strongly mixed and unproductive while in Barguzin Bay the water column was stratified and productive.

Many of the stations where the water columns thermally stratified were located in areas affected by Baikal's three main rivers. Stations 1–6, while in the southern part of lake and therefore ice-free earlier in the season, are also under the influence of Baikal's major tributary, the Selenga River. According to Kozhov (1963) this influence begins as early as April–May when warmer inflow from the river contributes to the heat gain in the open waters in the vicinity of the Selenga Delta. Further, Kozhov reports that in the summer the warm waters carried in by the Selenga are transported by lake currents and contribute to an increase in temperature in the open lake. Indeed, a permanent current is known to extend from the Selenga Delta in a southwest direction towards the Angara River outflow. Similarly, the influence of tributary inflow on the thermal regime in adjacent regions of the lake have been noted for Barguzin Bay (which receives direct drainage from the Barguzin River) and the Upper Angara River near station 11 (Kozhov, 1963). The influence of wind induced currents in Barguzin Bay also contribute to the redistribution of warmer inflowing waters and the establishment of thermal stratification within the approximately 500 km² geographic confines of the Bay. In addition, these riverine inflows of warmer and less dense water create a sufficient degree of stability so that thermal inputs from solar radiation can accumulate in the surface layer instead of being mixed into the colder, underlying waters. Consequently, both the inflow of relatively warmer water and the subsequent further warming of the lighter, surface water by solar radiation appear to be important contributors to regions in the vicinity of river inputs and can influence smaller scale spatial differences in thermal stratification. Despite the observations that hydrothermal vents contribute to the heat flow into certain regions of the lake, thermal discharge typically results in temperature anomalies in the near-bottom water or in lenses of similar density in the water column (Golubev et al., 1993). It is highly unlikely that such thermal inputs were responsible for the surface thermal structure observed at station 11 in the north basin. When the first author dove on these vents in the Russian *Pisces* submersible, the temperature increases encountered over the vents were extremely slight.

Our studies of Lake Baikal encompassed the dynamic period of mixing and initiation of thermal

stratification. Therefore, it is not surprising that the relationships among net N and P depletion and algal biomass and productivity (Figure 8) suggest that Baikal phytoplankton growth in the weakly-stratified northern portion of the lake was largely unconstrained by external nutrient concentrations during the onset of spring phytoplankton growth. Evidence regarding the identity of the primary limiting element (N or P) likely to eventually limit bloom development and phytoplankton productivity in Lake Baikal is equivocal, but suggestive. Weiss et al. (1991) suggested, based on molar relationships between nitrate and phosphate in surface samples, that nitrogen most likely limits phytoplankton in Lake Baikal given suitable physical conditions. Our survey data suggest that both N and P are likely to be in short supply upon the initial thermal stabilization of the Baikal water column. For example, during the period 4–17 July, high values of NO₃ depletion were not accompanied by increases in SRP depletion at the most strongly stratified stations. This occurred primarily because levels of SRP were already low and remained so throughout this two-week period. Since the SRP pool was depleted first upon water column stratification, regenerated P must have been important in sustaining spring phytoplankton growth (Figure 9). At the same time, results of a nutrient enrichment bioassay we conducted in mid-July showed a significant ($p < 0.05$) stimulation in growth when N and P were added in combination (Goldman, unpublished data). Single additions of either N or P were much less stimulatory, implying co-limitation by both N and P. Later in July when the period of summer growth was becoming more established, a second nutrient enrichment bioassay suggested that while co-limitation was still significant, the importance of nitrogen as a limiting factor may have been increasing.

Despite results from bioassay experiments, our repeated sampling of station 4 (Figure 7) indicates that the period between initial depletion of surface SRP pools and later depletion of surface NO₃ is probably quite short. Thus, it is likely that through most of Baikal's brief summer stratified season, both N and P are likely to be in short supply, potentially leading to close coupling between biological production and regeneration rates of these elements. The silicon level in Baikal is low at an average of 1.5 mg L⁻¹ (Votintsev, 1986). While the influence of silicon depletion on diatom growth is likely to be important during certain periods, diatoms did not dominate the phytoplankton community at the time of our study and measurements of water column silicon were not made.

In summary, our study, which combined intensive spatial sampling with experimental data, points to the overwhelming dominance of hydrodynamic conditions, and the resulting nutrient regime, in determining phytoplankton growth during the onset of spring phytoplankton growth. In another deep lake, Lake Tahoe, physical conditions also dominate since the level of annual primary productivity is largely determined by the depth of mixing (Goldman & Jassby, 1990). We contend that during the period of pre-stratification, phytoplankton growth in Lake Baikal is limited by physical factors (temperature and light) resulting from deep mixing; nutrient depletion begins to predominate once thermal stratification begins. The onset of spring phytoplankton growth along the north–south axis of the lake clearly showed spatial-temporal trends. Because of the earlier ice-out in the southern basin, this region of the lake was more strongly influenced by nutrients, whereas physical conditions predominate at more northerly locations where ice-out had been more recent and stratification was absent or very weak. This pattern is dependent to a large degree on meteorological conditions which dictate the spatial distribution and extent of wind and riverine forced water column mixing. More intensive studies that follow spatial and temporal patterns of nutrient utilization and phytoplankton nutrient deficiency as they develop during the summer season in Lake Baikal are needed to resolve the many questions raised by our study.

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