Verh. Internat. Verein. Limnol. | 24 | 302–308 | Stuttgart, September 1990

III. Lakes. 1. North America

Limnology of Walker Lake and comparisons with other lakes in the Brooks Range, Alaska (USA)

John R. Jones, Jacqueline D. LaPerriere and Bruce D. Perkins

Introduction

This paper summarizes limnological data collected from Walker Lake, a deep arctic lake within the Brooks Range, Alasaka. Our purpose was to document conditions in this remote waterbody with particular emphasis on chemical content, distribution of algal biomass within the photic zone and nutrient limitation of the phytoplankton. Also, we present data from lakes located nearby and draw comparisons.

Site description

Walker Lake (67 ° 08′ N 154 ° 21′ W) is located on the south facing slope of the Brooks Range in the Gates of the Arctic National Park and Preserve. It is impounded by terminal moraines of the Itkillik II glaciation (Fernald 1964) at an altitude of 194 m in the headwaters of the Kobuk River (Fig. 1, after Reanier 1986). It lies in a steep NW-SE directed valley and has two major basins, each 120 m deep, separated by a shallow sill. The northern basin is elongate and symmetrical; the southern basin is complex with several ridges and troughs (Reanier & Anderson undated). The lake is 21 km long, with a surface area of 3751 ha, volume of $2.3 \cdot 10^9\,m^3$, maximum depth of 122 m, mean depth of 61.4 m, and shoreline length of 94 km (calculated from Reanier 1986). The Brooks Range in the vicinity of Walker Lake is formed of sedimentary rock of Paleozoic age and includes limestone, shale, chert conglomerate, and sandstone (Nelson & Grybeck 1980). Walker lake lies near the transition of the boreal forest and alpine tundra.

Methods

Samples collected from Walker Lake during 6 to 11 July 1988 at five sites and all inflowing streams (Fig. 1) were processed in a field camp by taking aliquots for chemical and chlorophyll measurements; most analyses were conducted in duplicate or triplicate at the University of Missouri (APHA 1985). Total nitrogen was measured on acid-preserved samples by persulfate digestion (D'Elia et al. 1977) followed by cadmium reduction. Total phosphorus was measured by persulfate digestion followed by the molybdosilicate method. Chlorophyll-*a* (Chl-*a*) and phaeophytin were determined by fluorometry (Knowlton 1984) after extraction in hot ehtanol (Sartory & Grobbelaar 1984). Cations were determined on acid-preserved samples by using a flame photometer or atomic absorption spectrophotometer.

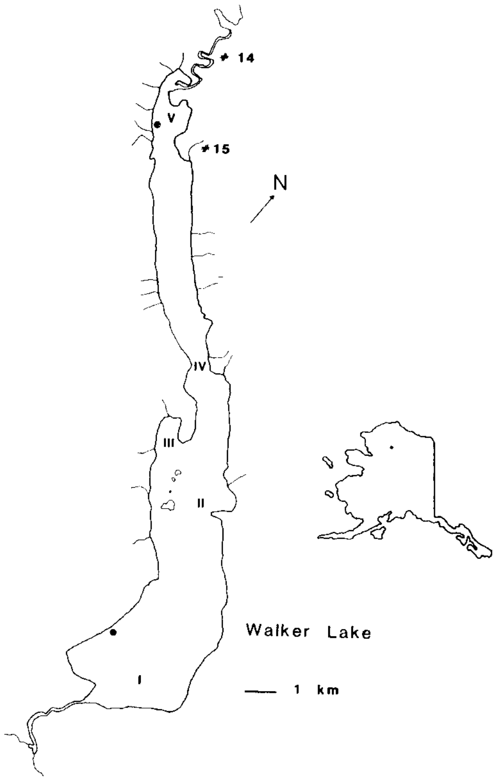

Fig. 1. Map of Walker Lake, Brooks Range, Alaska, showing the general position of the lake within the state, location of the five sampling sites (I to V), locations of the Nutrient Enrichment Experiments (darkened circles in the north and south basins), and locations of 21 tributaries we sampled. The map was modified from Reanier 1986.

0368-0770/90/0024-0302 $ 1.75

Table 1. Salinity and chlorophyll values for lakes in the Brooks Range, Alaska during summer 1987 and 1988. Values from the literature are also included. In the text, reference is made to the proportion of HCO_3 among the anions; this value was calculated by difference, we subtracted equivalents for SO_4 and Cl from the total equivalents of cations.

Lake	Year or Reference	Cations meq · l^{-1}	Ca	Mg	Na	K	HCO_3	SO_4	Cl	Chla[a]
						mg · l^{-1}				μg · l^{-1}
Walker	1987	1.42	22.9	2.8	0.45	1.10	–	–	–	0.27
Walker	1988	1.43	22.9	2.9	0.50	1.19	72	9.9	0.5	0.28
Nutuvukti	1988	0.68	9.8	1.9	0.77	0.25	29	6.9	0.4	0.96
Amiloyak	1987	0.21	1.5	1.4	0.47	0.15	–	3.0	0.3	0.95
Chandler	1987	0.50	3.4	3.3	1.15	0.32	–	6.6	0.3	1.21
Little Chandler	1987	0.47	3.5	2.9	1.05	0.33	–	6.3	0.3	1.16
Round	1987	0.48	4.2	2.7	0.95	0.29	–	5.4	0.3	0.70
Peters	Livingstone 1963[b]	0.58	8.2	1.9	0.2	0.1	25	9.4	0.3	–
Schrader	Brown et al. 1962[c]	0.64	7.2	2.7	0.1	2.3	–	–	–	–
Toolik	Cornwell 1983 Whalen 1986	0.60	9.2	1.4	0.51	0.31	24	–	–	1.8

[a] Chlorophyll-*a* values from the surface.

[b] Data taken from Table 20.1.

[c] Data taken from Table 2.

We also collected samples from the surface of Lake Nutuvukti in July 1988. Personnel of the U.S. Fish and Wildlife Service collected samples from five lakes in the Brooks Range during summer 1987 (Table 1) and samples were analyzed at the University of Missouri.

Results

Salinity

Waters of Walker Lake (Table 1) were of the bicarbonate type, characterized by a predominance of Ca among the cations (80 %) and HCO_3 among the anions (84 %). On average, Mg comprised 16 %, and the monovalent alkali metals constituted <4 % of the cation equivalents. Among the anions, sulfate accounted for 15 % and Cl made up <1 %. Concentrations and ionic proportions of each major element in the lake water were similar to values in the discharge-weighted average of inflowing streams (Table 2).

Salinity in Walker Lake matched the world average for freshwaters (cation equivalents = 1.42 meq · l^{-1}, Wetzel 1983) but was some 2–7 times greater than the other lakes sampled in the Brooks Range (Table 1). Composition of cations in Walker Lake was most similar to Lake Nutuvukti (Ca = 71 % and Mg = 23 % of cations) which also lies in the Kobuk River drainage and is influenced by the Walker Lake glaciation. In contrast, in the Chandler chain of lakes (Amiloyak through Round, Table 1) located on the north slope of the Brooks Range, Mg equivalents equaled or exceeded Ca, while Na comprised 9–10 % of the cations – this formulation is characteristic of water draining sedimentary rock (Wetzel 1983). Ionic composition in Walker Lake undoubtedly reflects the presence of extensive limestone deposits in the basin (Nelson & Grybeck 1980). In all these lakes (Table 1), however, HCO_3 dominated the anions and sulfate comprised 15–32 % of the negative equivalents. This proportion of sulfate is usual in freshwaters (Wetzel 1983) and other surface waters in the Brooks Range (Livingstone et al. 1958, Slack 1979) but not of the Arctic Slope where waters are low-sulfate (Kalff 1968).

Nutrients

Within Walker Lake, concentrations of TP averaged 2 μg · l^{-1} (n = 79, range 1 to 4 μg · l^{-1}) and TN averaged 379 μg · l^{-1} (n = 77, range 250 to 510 μg · l^{-1}). This TN value was virtually identical to the discharge-weighted average in the inflows (Table 2) but lake TP values were typically higher than measured in streams. This difference could partly be a function of our mid-summer sampling program; presumably stream phoshorus concentrations would be greater at the initiation of stream flow following breakup when most annual loading to the lake would occur (Whalen & Cornwell 1985).

Overall, the ratio of TN/TP within the lake was 209 and the discharge-weighted value of this ratio in the streams was 317; these ratios, along with the

Table 2. Limnological characteristics of 21 streams draining into Walker Lake, Alaska measured on 7 and 8 July 1988. Data are presented as the range of values, arithmetic mean and discharge-weighted mean among the 21 streams. Also, data from the two largest streams [numbers 14 (Kaluluktok Creek) and 15, Fig. 1] are presented – at the time of sampling, flow in these two streams exceeded flows in the other 19 streams by 4 to 125-fold.

Parameter		Range		Arithmetic[a] mean	Discharge-weighted[a] mean	Stream # 14	Stream # 15
		Lowest value	Highest value				
Temperature	°C	2 –	9.5	6.5	7.3	9.5	4.5
Dissolved Oxygen	$\mathrm{mg \cdot l^{-1}}$	8.8 –	12.6	11.4	11.2	11.6	12.1
Calcium	$\mathrm{mg \cdot l^{-1}}$	14.8 –	47.9	33.8	29.8	19.1	38.3
Magnesium	$\mathrm{mg \cdot l^{-1}}$	1.2 –	5.4	3.6	3.3	2.7	3.7
Sodium	$\mathrm{mg \cdot l^{-1}}$	0.28 –	1.16	0.46	0.48	0.59	0.34
Potassium	$\mathrm{mg \cdot l^{-1}}$	0.09 –	1.63	0.64	1.00	1.63	1.19
Chloride	$\mathrm{mg \cdot l^{-1}}$	0.2 –	0.4	0.3	0.3	0.3	0.3
Sulfate	$\mathrm{mg \cdot l^{-1}}$	7.2 –	51.0	19.5	14.7	9.3	13.2
Conductivity	$\mathrm{\mu mhos \cdot cm^{-1}}$	90 –	260	187	167	113	210
SiO_2	$\mathrm{mg \cdot l^{-1}}$	18 –	46	27	23	22	20
Total Phosphorus	$\mathrm{\mu g \cdot l^{-1}}$	1 –	2	1.2	1.4	2	1
Total Nitrogen	$\mathrm{mg \cdot l^{-1}}$	0.22 –	1.24	0.49	0.38	0.26	0.52
Chlorophyll-*a*	$\mathrm{\mu g \cdot l^{-1}}$	0.04 –	0.54	0.16	0.14	0.09	0.07
Phaeo Pigments	$\mathrm{\mu g \cdot l^{-1}}$	0.0 –	0.18	0.05	0.02	0.02	0.0
Total Fixed Solids	$\mathrm{mg \cdot l^{-1}}$	0.2 –	1.6	0.7	0.7	0.4	1.2
Total Volatile Solids	$\mathrm{mg \cdot l^{-1}}$	0.0 –	0.4	0.1	0.1	0.0	0.1

[a] All means are based on samples from 21 streams except for measurements of suspended solids which are based on samples from 20 streams.

nutrient values, are indicative of phosphorus limitation. Silica averaged $>20\,\mathrm{mg \cdot l^{-1}}$ in the lake and inflows; evidence that not all Alaskan lakes have low silica content (LIVINGSTONE et al. 1958).

Algal biomass

Values of Chl-*a* averaged $0.60\,\mathrm{\mu g \cdot l^{-1}}$ within Walker Lake ($n = 79$) and spanned an order of magnitude between 0.13 to $1.32\,\mathrm{\mu g \cdot l^{-1}}$. Measurements at the lake surface averaged $0.28\,\mathrm{\mu g \cdot l^{-1}}$ ($n = 22$), which was lower than Chl-*a* in nearby lakes (Table 1). There were clear patterns in the distribution of Chl-*a* pigments within Walker Lake at the time we sampled. First, there was a general longitudinal gradient in Chl-*a* values downlake – Chl-*a* in the epilimnion at Site V in the northern basin averaged $0.45\,\mathrm{\mu g \cdot l^{-1}}$, while epilimnetic values were between 0.21 and $0.33\,\mathrm{\mu g \cdot l^{-1}}$ at sites downlake (Fig. 1). This pattern also was demonstrated by surface samples (<0.5 m) collected from both basins on 11 June 1988; Chl-*a* averaged $0.34\,\mathrm{\mu g \cdot l^{-1}}$ in the north and $0.19\,\mathrm{\mu g \cdot l^{-1}}$ in the south ($n = 7$ in each basin). We suspect this downlake gradient occurs because the major tributaries enter the northern basin and nutrients are somewhat higher than downlake.

Second, at all sites Chl-*a* values showed a subsurface maximum of about $1\,\mathrm{\mu g \cdot l^{-1}}$ at depths between 21 and 30 m (e.g. Fig. 2 a). Subsurface Chl-*a* maxima were not uniform in thickness or concentration at the five sampling sites. In each case, however, values approximately doubled at some depth within the metalimnion. A maximum of $1-1.3\,\mathrm{\mu g \cdot l^{-1}}$ was reached in a broad band in the upper hypolimnion and values decreased below 30 m. Despite minor variations in Chl-*a* distribution within the water column, the total amount of Chl-*a* pigment in the upper 30 m differed by only 25% among sites ($18.3\,\mathrm{mg \cdot m^{-2}}$ at IV and $24.8\,\mathrm{mg \cdot m^{-2}}$ at V), and at three of the five sites values were $21.5 \pm 0.5\,\mathrm{mg \cdot m^{-2}}$ Chl-*a*.

The algal peak was associated with a weak nutricline; based on TN and TP, the strata between 21 and 30 m at the five sampling sites contained some 12% more phosphorus and 6% more nitrogen than the lakewide average for these elements. In many instances, however, the TN and TP content of individual samples from the epilimnion or metalimnion was as great or greater than that measured within the algal peak. This slight trend for total nutrient content to increase with depth may result from plankton or detritus accumulating in this zone rather than a high nu-

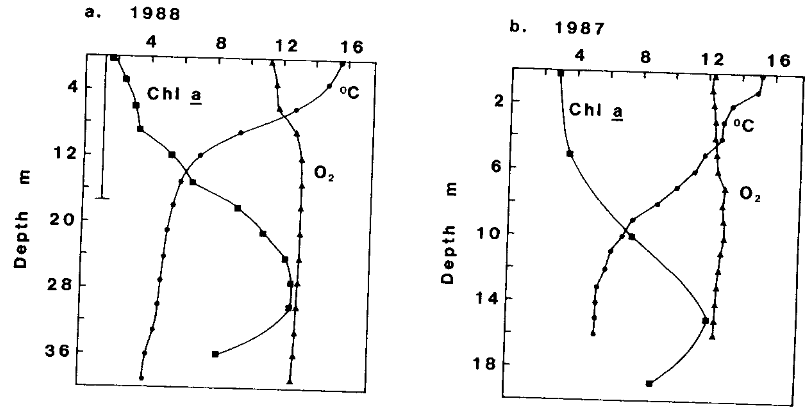

Fig. 2. Secchi depth (m) and distribution of chlorophyll-*a* ($\mu g \cdot l^{-1} \times 10$), temperature (°C), dissolved oxygen ($mg \cdot l^{-1}$) within the water column of Walker Lake at Site II on 10 July 1988 (panel a), and at a mid-lake near Site II on 3 July 1987 (panel b).

trient environment caused by dissolved nutrients.

Maximum Chl-*a* values were located at depths 1.3 to 2-times the Secchi transparency (14.5 to 17.5 m). Light measurements at Site I show the upper surface of the Chl-*a* maxima (21 m) was at about 5 % surface light. Based on the distribution of phaeopigments within the various samples we believe the subsurface maximum is composed of healthy algal cells (Kalff et al. 1972, Whalen & Alexander 1986 a). Overall, phaeophytin comprised on average 12 % of the total pigment in our Chl-*a* samples from the lake (n = 79, range 0 to 20 %) but within each site there was no apparent difference in the proportion of phaeopigments with depth. In fact, one of the lowest values measured (3 %) was at the Chl-*a* maxima (21 m) at Site IV. With minor exceptions, dissolved oxygen was at or near saturation within the subsurface Chl-*a* layer (e.g. Fig. 2 a).

A subsurface Chl-*a* peak of about 1 $\mu g \cdot l^{-1}$ was also present below a strong thermocline in Walker Lake during summer 1987 (Fig. 2 b). Values of Chl-*a* in July 1987 at the lake surface and within the hypolimnion were similar to measurements in July 1988; however, the maximum was some 10 m close to the surface in 1987 (Figs. 2 a and b).

Nutrient enrichment experiments

Phosphorus limitation was clearly demonstrated by the results of nutrient enrichment experiments conducted *in situ* in Walker Lake (Fig. 3). In both basins, chl-*a* was significantly greater than the control only in those treatments including phosphorus. Additions of nitrogen alone did not stimulate Chl-*a* growth over the controls, nor did additions of both nutrients together stimulate Chl-*a* growth over phosphorus alone (Fig. 3). Within the time frame of the experiment, there was no difference in algal response to two levels of phosphorus addition (5 and 10 $\mu g \cdot l^{-1}$). In both trials, phaeophytin was a significantly smaller proportion of total pigment in treatments with phosphorus (Fig. 4); evidence that algal chlorophyll was of higher quality than in controls and nitrogen alone (Kalff et al. 1972).

Discussion

Walker Lake is unquestionably oligotrophic as judged by phosphorus and algal Chl-*a*, but its nitrogen content was higher than expected in an unproductive waterbody (Wetzel 1983). Studies of surface water elsewhere in the Brooks Range also have shown nitrogen abundant relative to phosphorus (Slack et al. 1979, Whalen & Cornwell 1985). The source of nitrogen in Walker Lake was probably edaphic. This conclusion is based on our measurements in streams (Table 2) and measurements by Ugolini et al. (1987) of 1 $mg \cdot l^{-1}$ NO_3 in the soil solution of the organic layer in the Walker Lake watershed. Our present hypotheses are that part of the nitrogen in the tributaries originated with nitrogen-fixing lichens that were common within the watershed, and that alkalinity associated with limestone in the watershed caused high mobility of soil nitrogen (Haynes 1986). In

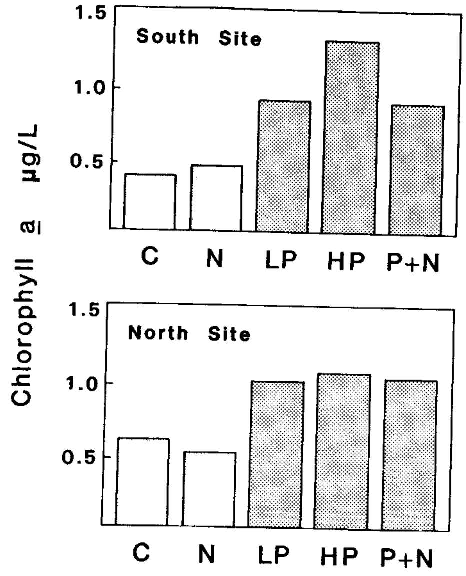

Fig. 3. Results of Nutrient Enrichment Experiments conducted between 6–11 July 1988 in the south basin, and 7–11 July 1988 in the north basin of Walker Lake (Fig. 1). At each site unfiltered surface water was divided among 10 l translucent polyethylene containers (Cubitainers) which were protected from direct sunlight (after WURTSBAUGH et al. 1985). Triplicate treatments received nutrient additions (as K_2HPO_4 or KNO_3) as follows: Low Phosphorus (LP) = 5 µg · l^{-1} P; High Phosphorus (HP) = 10 µg · l^{-1} P; Nitrogen (N) = 225 µg · l^{-1} N; and Nitrogen + Phosphorus (N + P) = 5 µg · l^{-1} P plus 225 µg · l^{-1} N. Nutrients were added only on the first day and were considered nominal additions above background. Three cubitainers received no nutrient additions and served as the controls (C). The containers were incubated at a depth of 5 m which was about one-third or less of the Secchi transparency at these two sites. At the end of the experiments algal growth was measured as chlorophyll-*a* (µg · l^{-1}). Statistical differences among treatments were analyzed on transformed data (inverse of the square root) by a one-way analysis of variance test followed by a TUKEY's HSD procedure (alpha = 0.05). At each site, phosphorus additions, alone or in combination with nitrogen significantly stimulated algal growth relative to the control and nitrogen alone treatment. Chlorophyll-*a* in the LP, HP, and N + P treatments (dark stippling) was significantly different from the controls and N alone treatment (light stippling). These latter two treatments did not differ in chl-*a*.

nearby regions of Alaska, it seems soil phosphorus is relatively immobile and efficiently retained (WHALEN & CORNWELL 1985).

High nitrogen and low phosphorus concentrations resulted in phosphorus being identified as the element restricting phytoplankton growth. Nutrient enrichment experiments clearly demonstrated planktonic algae at the lake surface were responsive to phosphorus additions and the nitrogen supply was adequate for growth. These findings differ from studies on Toolik Lake, Alaska (MILLER et al. 1986, WHALEN & ALEXANDER 1986 b) where both nitrogen and phosphorus are important. Overall, the ratio of Chl-*a*/TP averaged 0.3 in Walker Lake, which was identical to the ratio of these factors in a broad range of temperate lakes (VERDUIN 1988). This ratio varied from 0.1 at the surface to >0.6 within the Chl-*a* peak. An increase in this ratio with depth might result from low-light adaptation of the algae (PICK et al. 1984) and be a factor contributing to the observed subsurface maximum.

Our data do not permit us to judge whether settling or *in situ* growth also contribute to the

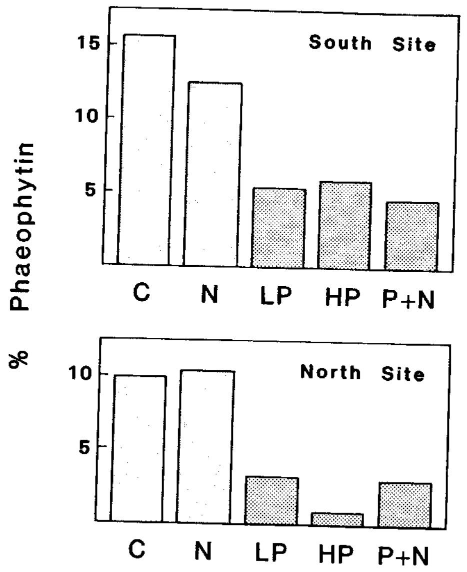

Fig. 4. Proportion of total chlorophyll as phaeopigment in the Nutrient Enrichment Experiment described in Fig. 3. Statistical differences among treatments were analyzed on transformed data (angular) by a one-way analysis of variance test followed by a TUKEY's HSD procedure (alpha = 0.05). At each site, phosphorus additions, alone or in combination with nitrogen showed a significantly lower proportion of phaeophytin relative to the control and nitrogen alone treatments. Phaeophytin (%) in the LP, HP, and N + P treatments (dark stippling) was significantly different from the controls and N alone treatment (light stippling). These latter two treatments did not differ in % phaeophytin.

Chl-*a* maximum in Walker Lake. Regardless of the major mechanism determining the formation and depth of this deep phytoplankton layer, inter-year variation in the onset or pattern of stratification might explain why it was not in the same position within the water column of Walker Lake in 1987 and 1988 (Fig. 2). In future studies, it would be worthwile to determine how this Chl-*a* maximum forms, its dynamics, taxonomic composition, and relative primary production occurring within this subsurface layer.

Acknowledgements

This research was supported by the Alaska Cooperative Fishery Research Unit, University of Alaska, Fairbanks, Missouri Agricultural Experiment Station, and Missouri Cooperative Fish and Wildlife Research Unit, University of Missouri-Columbia. We thank Mark Kaiser for help with statistical analyses, F. Jeffrey Adams and Reed Glesne for collecting samples in 1987, and Vicki Greer for calculating morphometric data from the bathymetric map.

References

American Public Health Association, 1985: Standard methods for the examination of water and wastewater. – 16th ed., New York, 1133 pp.

Brown, J., Grant, C. L., Ugolini, F. C. & Tedrow, J. C. F., 1962: Mineral composition of some drainage waters from arctic Alaska. – *J. Geophysical Res.* **67:** 2447–2453.

Cornwell, J. C., 1983: The geochemistry of manganese, iron and phosphorus in an arctic lake. – Ph. D. Dissertation. University of Alaska, Fairbanks, 233 pp.

D'Ellia, C. F., Steudler, P. A. & Corwin, N., 1977: Determination of total nitrogen samples using persulfate digestion. – *Limnol. Oceanogr.* **22:** 760–764.

Fernald, A. T., 1964: Surficial geology of the central Kobuk River valley, northwestern Alaska. – *U. S. Geolog. Survey Bull.* **1181-K.**

Haynes, R. J., 1986: Mineral nitrogen in the plant-soil system. – Academic Press, Inc. New York, 483 pp.

Kalff, J., 1968: Some physical and chemical characteristics of arctic fresh waters in Alaska and Northwestern Canada. – *J. Fish. Res. Bd. Canada* **25:** 2575–2587.

Kalff, J., Welch, H. E. & Holmgren, S. K., 1972: Pigment cycles in two high-arctic Canadian lakes. – *Verh. Internat. Verein. Limnol.* **18:** 250–256.

Knowlton, M. F., 1984: Flow-through microcuvette for fluorometric determination of chlorophyll. – *Water Resour. Bull.* **20:** 795–799.

Livingstone, D. A., 1963: Alaska, Yukon, Northwest Territories, and Greenland. – In: Frey, D. G. (Ed.): Limnology in North America: 559–574. – Univ. of Wisconsin Press, Madison.

Livingstone, D. A., Bryan Jr., K. & Leahy, R. G., 1958: Effects of an arctic environment on the origin and development of freshwater lakes. – *Limnol. Oceanogr.* **3:** 192–214.

Miller, M. C., Hater, G. R., Spatt, P., Westlake, P. & Yeakel, D., 1986: Primary production and its control in Toolik Lake, Alaska. – *Arch. Hydrobiol./Suppl.* **74:** 97–131.

Nelson, S. W. & Grybeck, D., 1980: Geologic map of the Survey Pass Quadrangle, Alaska. – U.S. Geological Survey Miscellaneous Field Studies Map MF-1176-A, scale 1 : 250,000.

Pick, F. R., Nalewajko, C. & Lean, D. R. S., 1984: The origin of a metalimnetic chrysophyte peak. – *Limnol. Oceanogr.* **29:** 125–134.

Reanier, R. E., 1986: Bathymetric map of Walker Lake, scale 1 : 26,316. – Available from the National Park Service, Fairbanks, Alaska, on request.

Reanier, R. E. & Anderson, P. M., undated: A bathymetric study of nine lakes in the south-central Brooks Range: A report to the National Park Service, 9 pp. – Unpublished report supplementing bathymetric map of Walker Lake by Reanier, R. E. 1986. Available from the National Park Service, Fairbanks, Alaska, on request.

Sartory, D. P. & Grobbelaar, J. U., 1984: Extraction of chlorophyll-*a* from freshwater phytoplankton for spectrophotometric analysis. – *Hydrobiologia* **114:** 177–187.

Slack, K. V., Nauman, J. W. & Tilley, L. J., 1979: Benthic invertebrates in a north-flowing stream and south-flowing stream, Brooks Range, Alaska. – *Water Resour. Bull.* **15:** 108–135.

Ugolini, F. C., Stoner, M. G. & Marrett, D. J., 1987: Arctic pedogenesis: 1. Evidence for contemporary podzolization. – *Soil Science* **144:** 90–100.

Verduin, J., 1988: The Baule-Mitscherlich limiting factor equation evaluated in freshwater habitats. – *Verh. Internat. Verein. Limnol.* **23:** 103–105.

Wetzel, R. G., 1983: *Limnology* (2nd ed.). – Saunders College Publishing, Philadelphia, 767 pp.

Whalen, S. C., 1986: Pelagic nitrogen cycle in an arctic lake. – Ph. D. Dissertation. University of Alaska, Fairbanks, 169 pp.

Whalen, S. C. & Alexander, V., 1986 a: Seasonal inorganic carbon and nitrogen transport by phytoplankton in an Arctic Lake. – *Can. J. Fish. Aquat. Sci.* **43:** 1177–1186.

– – 1986 b: Chemical influences on ^{14}C and ^{15}N Primary Production in an arctic lake. – *Polar Biol.* **5:** 211–219.

WHALEN, S. C. & CORNWELL, J. C., 1985: Nitrogen, phosphorus, and organic carbon cycling in an arctic lake. – *Can. J. Fish. Aquat. Sci.* **42:** 797–808.

WURTSBAUGH, W. A., VINCENT, W. F., ALFARO TAPIA, R., VINCENT, C. L. & RICHERSON, P. J., 1985: Nutrient limitation of algal growth and nitrogen fixation in a tropical alpine lake, Lake Titicaca (Peru/Bolivia). – *Freshwater Biology* **15:** 185–195.

Authors' addresses:

Dr. J. R. JONES and B. D. PERKINS, School of Forestry, Fisheries and Wildlife, University of Missouri, Columbia, Missouri 65211, U.S.A.
Dr. J. D. LAPERRIERE, U.S. Fish and Wildlife Service, Alaska Cooperative Fishery Research Unit, University of Alaska, Fairbanks, Alaska 99775, U.S.A.

This is a reprint of

Verhandlungen – Proceedings – Travaux

of the International Association for Theoretical and Applied Limnology, Congress in Munich 1989

If you are a member of this association you receive these "Proceedings" against your yearly membership fee of Swiss Francs 50.–

Please notice also the

Archiv für Hydrobiologie

an official organ of the International Association for Theoretical and Applied Limnology (SIL), and its Supplements.

Edited by: Prof. Dr. H. Kausch, Hamburg, Germany West and
Prof. Dr. W. Lampert, Plön/Holstein, Germany West.

Editorial Board: Prof. Dr. Carolyn W. Burns, Dunedin, New Zealand; Prof. Dr. Z. Maciej Gliwicz, Warszawa, Poland; Prof. Dr. J. Overbeck, Plön, Germany; Prof. Dr. Eric Pattée, Villeurbanne, France; Dr. Colin S. Reynolds, Ambleside, Great Britain; Prof. Dr. Robert G. Wetzel, Tuscaloosa, Alabama, USA.

As a member of SIL you are entitled to receive this important journal at a special membership price.

True to its tradition this periodical serves freshwater research in the widest sense, including treatment of problems of brackish and seawater as far as they bear a relationship to limnology. It is the editors' aim to devote increased attention to ecology in association with experimental, above all physiological works corresponding to the more recent developments in limnology. Finally, it is intended that the "Archiv" should continue to form a bridge between theoretical and applied water research.

For details please write to the Publishers E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Obermiller), Johannesstraße 3 A, D-7000 Stuttgart 1.

If you are interested in

Archiv für Hydrobiology, Supplements

and in the special issues

Ergebnisse der Limnologie/Advances in Limnology

these are available also against a special membership price; for details please ask the Publishers (for address see above).

If you are interested in being a member of the International Association for Theoretical and Applied Limnology, please write to the General Secretary-Treasurer:

Prof. Dr. R. G. Wetzel, Department of Biology,
The University of Alabama, Tuscaloosa, Alabama 35487-0344/USA