

Limnology of lakes in Katmai National Park and Preserve, Alaska: nutrients and plankton

J. D. LaPerriere[†] and J. R. Jones

Introduction

Two lakes in Katmai National Park and Preserve, Brooks and Naknek, were among the first examined for phytoplankton productivity and nutrient limitation (GOLDMAN 1960). This information was ancillary to studies of sockeye salmon in the Naknek River drainage, a component of the Bristol Bay fishery (BUCK et al. 1978). GOLDMAN (1960) found that both lakes were exceptionally clear (except the Iliuk-Arm of Naknek Lake which receives ash and pumice from the volcanic area, the Valley of Ten Thousand Smokes, and glacial flour from meltwater), phytoplankton grew deep within the water column, and nutrient bioassays showed a positive response to nitrogen.

This project established baseline water quality in major lakes within the Katmai National Park and Preserve (LAPERRIERE 1997, LAPERRIERE & EDMUNDSON 2000). In this paper information on the trophic state and nutrient limitation of the Katmai lakes is presented. In addition, we determined how measurements from these remote lakes on the Alaskan Peninsula compare to various published empirical plankton–nutrient relations.

Methods

Lakes were sampled at a central location from a floatplane on one occasion during early August 1990–1992; Battle, Brooks, Coville, Grosvenor, Kulik and Nonvianuk Lakes were also sampled in 1993 (see LAPERRIERE (1997) for site descriptions and map). Idavain Lake was sampled once in 1990 and weather conditions allowed sampling of Hammersly Lake only in 1991 and 1992. Data from these lakes are presented in Table 1 for documentation but they were not included in the analysis.

Nutrient samples were taken in triplicate with a Van Dorn sampler at a depth of 2 m and delivered into Cubitainers and placed in an insulated cooler.

To determine the vertical distribution of phytoplankton, triplicate samples were taken at depths of 1 m, the Secchi depth, and twice the Secchi depth. Triplicate vertical hauls with a 20- μ m mesh zooplankton net (0.235 \times 1 m) were made from just above the bottom of each lake and these samples were stored in 60-mL Nalgene bottles with 3 mL of buffered formalin.

At the field lab in 1990, samples for total phosphorus (TP) were poured into 50-mL acid-washed Nalgene bottles, frozen, and analyzed at the University of Alaska Fairbanks (UAF) using persulfate digestion (EISENREICH et al. 1975). After 1990, triplicate samples for both TP and TN (total nitrogen) were transferred to screw-cap culture tubes, and TN samples were preserved with sulfuric acid. Persulfate digestion and analyses of TP (PREPAS & RIGLER 1982) and TN (CRUMPTON et al. 1992) were performed in the original culture tube at the University of Missouri.

In 1990, triplicate composite samples for chlorophyll (Chl) were prepared by filtering equal sample volumes from the three depths through a single Gelman A/E glass fiber filter (ca. 1- μ m pore size). In 1991 and 1992, two to three 1-L samples from each depth were filtered separately and results were averaged. Filters were made alkaline with 1 mL of saturated MgCO₃ and stored frozen over desiccant until processed. Chlorophyll filters were ground with an electric pestle and analyzed for total chlorophyll *a* (Chl, uncorrected) on a fluorometer (APHA 1989). Samples from 1991 were not successfully read because of a laboratory error. Zooplankton samples were washed to remove preservative and analyzed for dry weight and ash-free dry weight (organic content) using pre-ignited glass fiber filters (APHA 1989).

Data were averaged across samples in a given summer to arrive at a summer mean, and these were averaged over time to arrive at the lake mean used in the analyses. Lake means were normalized (log)

[†]Deceased.

Table 1. Lake mean total phosphorus (TP), total nitrogen (TN), TN:TP values, total chlorophyll and zooplankton as ash-free dry weight ($\mu\text{g/L}$) for Katmai lakes, 1990–1993. Number of summer mean values used to calculate the lake mean are given in parentheses. Data from Lakes Hammersly and Idavain are included but were not part of this analysis. Missing data indicated by a dash.

Lake	TP $\mu\text{g/L}$	TN $\mu\text{g/L}$	TN:TP	Total chlorophyll $\mu\text{g/L}$	Zooplankton $\mu\text{g/L}$
Battle	2 (4)	222 (3)	99	0.1 (3)	0.9 (3)
Brooks	5 (4)	92 (3)	18	0.5 (3)	25 (3)
Coville	10 (4)	146 (3)	15	1.3 (3)	25 (3)
Grosvenor	4 (4)	223 (3)	52	0.7 (3)	18 (3)
Kukaklek	4 (3)	118 (2)	30	0.6 (2)	28 (3)
Kulik	4 (4)	377 (3)	94	0.7 (3)	4 (3)
Murray	4 (2)	149 (2)	33	0.4 (2)	11 (3)
Naknek	5 (3)	164 (2)	33	0.7 (2)	15 (3)
Novianuk	4 (4)	206 (3)	46	0.6 (3)	50 (2)
Hammersly	4 (2)	185 (2)	46	0.6 (1)	9.5 (2)
Idavain	22 (1)	—	—	1.0 (1)	144 (1)

when appropriate, and significance was set at 0.05.

Nutrient stimulation bioassays (JONES *et al.* 1990) were conducted on Coville and Grosvenor Lakes in 1992, and on Brooks and Kulik Lakes in 1993. Near-surface water (-0.5 m) was placed into 10-L Cubitainers. Triplicate containers were treated with N (adding $75 \mu\text{g N/L}$ as ammonium nitrate), with P (adding $5 \mu\text{g P/L}$ as sodium orthophosphate), with both N and P together at these concentrations, and with no additions as controls. In Coville Lake, $10 \mu\text{g P/L}$ were added in each P addition to double lake values. Cubitainers were suspended at one-half the Secchi depth for 4 or 5 days. Triplicate samples of each were filtered through GF-C glass fiber filters ($1.2\text{-}\mu\text{m}$ pore size) and stored in desiccant. They were extracted in hot ethanol and analyzed for Chl using a fluorometer (KNOWLTON 1984, SATORY & GROBBELAAR 1984). Statistical differences among treatments were analyzed by a one-way analysis of variance followed by a least significant difference test ($\alpha = 0.05$).

Results

Nutrient and chlorophyll values were uniformly low in the Katmai lakes (Table 1), suggesting oligotrophic conditions. Lake mean values of TP ranged between 2 and $10 \mu\text{g/L}$, TN ranged between 92 and $377 \mu\text{g/L}$ and Chl was $\leq 1.3 \mu\text{g/L}$.

The strength of an empirical Chl–TP relation ($R^2 = 0.78$) and its steep slope (>1.3) largely

stem from the position of Battle Lake at the lower end of the distribution and Colville Lake at the upper end of this narrow range of values (Fig. 1, Table 1). Comparisons with published empirical Chl–TP relations, adjusted to this same TP range ($2\text{--}10 \mu\text{g/L}$), show that the Katmai lakes behave similarly to other Alaskan lakes (Table 2). Collectively the Katmai data fit within the empirical Chl–TP relation for clear Alaskan lakes of varying typology (Fig. 1, data from EDMUNDSON & CARLSON 1998). In a combined dataset, 66% of Chl variance is explained by TP. The Chl–TP relation from lakes near Cook Inlet, Alaska (single sample survey data collected by BELL *et al.* 1993) also provides reasonable Chl predictions (Table 2). In these Alaskan lakes the Chl:TP ratio averaged ≤ 0.15 , and Chl–TP models have slopes ≥ 1 and small intercepts (Table 2).

Within this narrow TP range, global lake datasets have Chl:TP ratios between 0.22 and 0.5 (Table 2) and Chl–TP models fitted to these data overestimate Katmai Chl (Table 2) by $0.3 \mu\text{g/L}$ (JONES & BACHMANN 1976) to $1.3 \mu\text{g/L}$ (WATSON *et al.* 1992, NÜRNBERG & SHAW 1998). Interestingly, when limited to this P range, global data taken from WATSON *et al.*

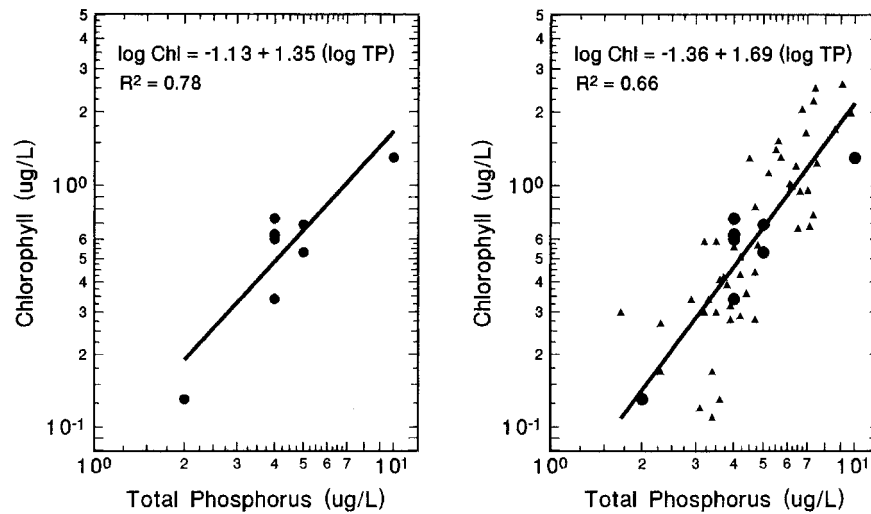


Fig. 1. Relationship (log scale) between chlorophyll and total phosphorus in the Katmai lakes (left panel), and the Katmai data combined with data from clear Alaskan lakes (right panel) from EDMUNDSON & CARLSON (1998).

Table 2. Chlorophyll–phosphorus models for the Katmai lakes and datasets from the literature limited to TP values from 2 to 10 $\mu\text{g/L}$. The mean ratio of Chl:TP is presented in the original dataset in addition to comparisons of predicted and observed Chl values in the Katmai lakes (bias) for each model. Mean square error was calculated as the sum of the mean difference squared and the variance.

Model for data limited to TP = 2–10 $\mu\text{g/L}$	Equation for log Chl		Chl:TP ratio in date set (mean)	Mean difference between predicted and observed chlorophyll (bias)	Mean square error
	Intercept	Slope for log TP			
Katmai, Fig. 1, n = 9	-1.13	1.35	0.13	-0.001	0.036
Alaskan Lakes, Fig. 1 (EDMUNDSON & CARLSON 1998), n = 48	-1.4	1.76	0.15	0.005	0.146
Katmai and Alaskan Lakes, Fig. 1, n = 57	-1.36	1.69	0.15	0.034	0.111
Cook Inlet Lakes, (AK unpublished), n = 156	-0.91	1.02	0.14	-0.026	0.018
(PIENITZ et al. 1997) Yukon and NWT, n = 22	-0.45	0.55	0.20	0.19	0.062
(JONES & BACHMANN 1976) global data, n = 54	-0.75	1.08	0.22	0.33	0.162
(WATSON et al. 1992) Global data, n = 150	-0.05	0.505	0.53	1.28	1.66
(NÜRNBERG & SHAW 1998) Global data, n = 111	0.02	0.42	0.49	1.34	1.82
(STOCKNER & SHORTREED 1985) British Columbia, n = 52	-0.13	1.02	0.83	2.95	10.76

(1992) and NÜRNBERG & SHAW (1998) resulted in weak Chl-TP models ($R^2 = 0.1$), with large intercepts ($>0.9 \mu\text{g/L}$) and slopes of around 0.5 (Table 2).

A Chl-TP model from lakes in the Yukon and Northwest Territories, Canada (mean Chl:TP = 0.2, PIENITZ et al. 1997) predicts Katmai Chl reasonably well, while predictions based on data (mean Chl:TP = 0.83) from fertilized lakes in coastal British Columbia (STOCKNER & SHORTREED 1985) greatly overestimate observed Chl (Table 2).

With two exceptions (Brooks and Coville Lakes) weight ratios of TN:TP were ≥ 30 (Table 1), suggesting phosphorus limitation. The correlation between mean TN and TP was not significant among these lakes, nor was the correlation between Chl and TN. The ratio of

Chl:TN (as $\mu\text{g/mg}$) averaged 3.9 in the Katmai lakes. This value closely matches other Alaskan lakes considered, and lakes in the Yukon and Northwest Territories (Table 2). It is, however, much smaller than ratios within the other datasets considered (Table 2), and expected values based on empirical Chl-TN models (CANFIELD 1983, PRIDMORE et al. 1985).

Nutrient stimulation bioassays reconfirmed N limitation in Brooks Lake when the lake water had a TN:TP ratio of 8, and was demonstrated in Coville Lake when TN:TP was 15 (Fig. 2). Phosphorus limitation was demonstrated in Grosvenor and Kulik Lakes (Fig. 2) when TN:TP was >60 . There was a secondary response in most of these experiments to the nutrient that was not, by itself, stimulating. In Kulik Lake, where N was highest and P was

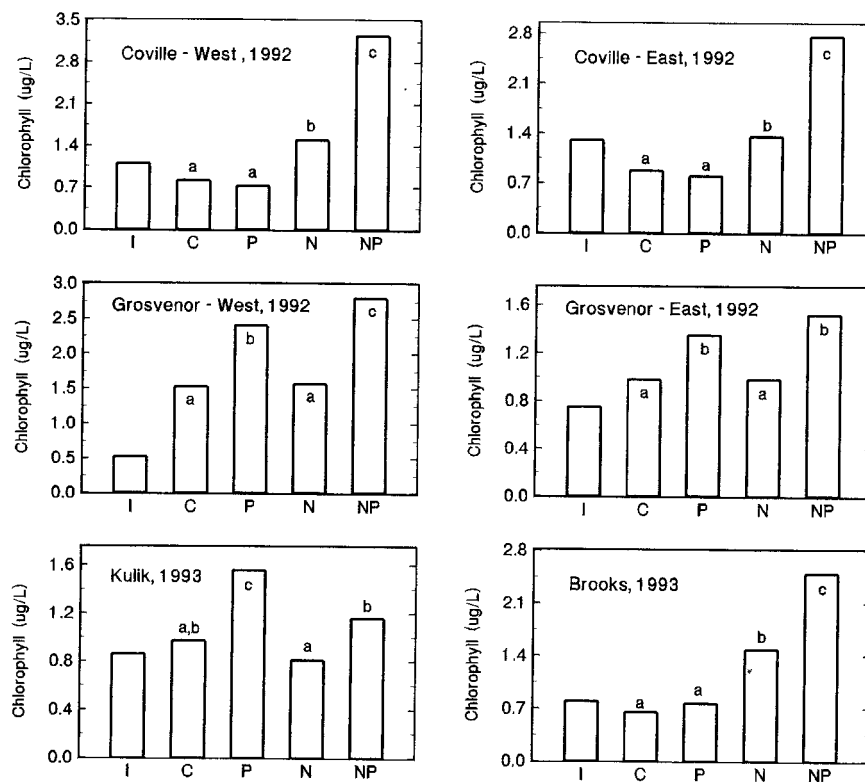


Fig. 2. Nutrient enrichment bioassays conducted in Colville, Grosvenor, Kulik and Brooks Lakes. Initial values are shown for reference, differences among treatments ($\alpha = 0.05$) are indicated by letters, treatments with the same letter were not statistically different.

stimulating, additional N depressed growth alone and in combination with P.

Zooplankton biomass ranged from 0.9 $\mu\text{g/L}$ in Battle Lake to 50 $\mu\text{g/L}$ in Novianuk Lake, with an overall mean of 20 $\mu\text{g/L}$ (Table 1). Katmai lakes behave similarly to the empirical equations of HANSON & PETERS (1984); zooplankton biomass predicted with TP_{\log} averaged 23 $\mu\text{g/L}$ (range 11–46 $\mu\text{g/L}$) and predictions using Chl_{\log} averaged 21 $\mu\text{g/L}$ (range 9–32 $\mu\text{g/L}$). In both cases, biomass estimates were overpredicted for Battle Lake by about 10-fold. The empirical equations of PACE (1984) or SHORTREED & STOCKNER (1986) overpredicted zooplankton biomass in all lakes by at least 3- to 4-fold. Zooplankton biomass exhibited little vertical heterogeneity in the detailed samples from Coville and Grosvenor Lakes, probably because of deep circulation.

Discussion

In all cases, nutrient and Chl values from the Katmai lakes (Table 1) closely match or are below the typical cut points for oligotrophic lakes (NÜRNBERG 1996). Orthograde oxygen profiles within each lake (LAPERRIERE 1997), and Secchi measurements between 5 and 17 m (LAPERRIERE & EDMUNDSON 2000), also support this classification. These pristine lakes, located near Bristol Bay of the Pacific Ocean, are discontinuous cold polymictic, mixing occasionally to great depth due to coastal storms (LAPERRIERE 1997).

The slope of the Chl–TP relation for these clear Katmai lakes suggests that algal biomass is exponentially responsive to increases within this low and narrow P range (Fig. 1). Deep mixing may contribute to this pattern. MAZUMDER (1994) found that the Chl increase per unit TP is greater (larger slope) in mixed systems than in stratified systems. Values of Chl and TP in the Katmai lakes are below the range of MAZUMDER'S (1994) values so the present data may expand this generalization. A strong Chl–TP response was also found among warm polymictic reservoirs in Thailand (JONES et al. 2000).

The steep Chl–TP slope in the Katmai lakes contrasts with the weak Chl–TP response

found in some heterogeneous databases with $<10 \mu\text{g/L}$ TP (WATSON et al. 1992, Nürnberg & Shaw 1998, Table 2).

Low Chl:TP in the Katmai lakes (small intercept) is consistent with the finding that deep lakes support low levels of Chl per unit of P (PRIDMORE et al. 1985). Low Chl:TN ratios in the Katmai lakes are also consistent with this conclusion. The expectation that mixed systems support high Chl:TP ratios (MAZUMDER 1994) is not supported by data from these oligotrophic lakes. Low Chl:TP is also associated with the effect of large grazers on algal biomass, considered strongest in oligotrophic lakes (MCQUEEN et al. 1986). Information was not available on zooplankton community structure to directly test the importance of herbivory on algal biomass (MAZUMDER 1994), but theory suggests that intense predation by juvenile sockeye salmon in some of these lakes would result in small grazers and thereby favor high, rather than low, Chl yields.

Naknek and Brooks Lakes were among the first evaluated as N limited (GOLDMAN 1960). This evaluation was reconfirmed for Brooks Lake by the bioassay (Fig. 2), and the TN:TP ratio herein (Table 1). Coville Lake was also evaluated as N limited by both methods. Probable P limitation was suggested by TN:TP in Naknek Lake, where GOLDMAN (1960) found N limiting (Table 1). The difference can be attributed to differences in sampling locations in the two studies. In the present study, Naknek Lake, where the clear waters of the North Arm mixed with the turbid Iliuk Arm, was sampled whereas GOLDMAN (1960) sampled the turbid Iliuk Arm. An incidental sample from this location in 1992 suggested potential N limitation. Most Katmai lakes showed potential P limitation based on TN:TP, and bioassays confirmed this in Grosvenor and Kulik Lakes (Fig. 2).

The question arises: why are both N- and P-limited lakes found in this region? Sustained P loading to some lakes could possibly be from ash from volcanic eruptions which, in this area, tends to contain P and no N (MATHISEN & POE 1978). The patterns of ashfall near Katmai Park and Preserve are complex, as are tephra layers in the soil profile (FIRESTEIN & HILDRETH 1992),

making it difficult to quantify present-day P fertilization from this source. Ash-laden waters fertilize the Iliuk Arm of Naknek Lake where GOLDMAN (1960) found N limitation. Spawned out sockeye salmon carcasses undoubtedly bring marine-derived nutrients into the Katmai lakes at an N:P ratio of about 6 (MATHISEN et al. 1988). Coville and Brooks Lakes are known to support large salmon runs and this source may help explain N limitation. Extensive wetlands within the watersheds of Colville and Brooks Lakes may also contribute to N limitation by denitrification of inflows (VYMAZAL 1995). Several large lakes in the study also have extensive wetlands but these may be unimportant because of other watershed influences. For example, N-limited Colville Lake drains into P-limited Grosvenor Lake, and it is assumed that inflows to the lower lake account for this difference. GUNTHER (1989) reported that nitrogen fixation by lichens was low in the watershed of Brooks Lake relative to atmospheric inputs in this remote location. Collectively, this information suggests that nutrient limitation in the Katmai lakes results from complex factors.

Zooplankton biomass data match expected values using the empirical equations of HANSON & PETERS (1984) but the values were much lower than predictions based on PACE (1984) or SHORTREED & STOCKNER (1986). Grazing pressure by juvenile sockeye salmon probably determines the crustacean biomass in some of these systems. Low zooplankton biomass in Battle Lake (Table 1) may be a response to low pH in the inflow or aluminum values above the chronic criterion for the protection of aquatic life (LAPERRIERE 1997).

Acknowledgements

The National Park Service, Water Resources Division, funded this project. We thank those who provided logistic, technical and laboratory support. We greatly appreciate the data from WATSON et al. (1992) supplied by JOHN DOWNING, data from NÜRNBERG & SHAW (1998) supplied by GERTRUD NÜRNBERG, and unpublished data from Cook Inlet lakes supplied by JOHN BAKER, JEFF KOENINGS and MIKE BELL, collected as part of a National Science Foundation grant BSR8905758 to M. BELL. We thank BRUCE PERKINS for sample processing and

MATT KNOWLTON for helpful comments.

References

- APHA, 1989: *Standard Methods for the Examination of Water and Wastewater*, 17th ed. – American Public Health Association, New York.
- BELL, M. A., ORTI, G., WALKER, J. A. & KOENINGS, J. P., 1993: Evolution of pelvic reduction in threespine stickleback fish: a test of competing hypotheses. – *Evolution* 47: 906–914.
- BUCK, E. H., BOWDEN, C., BALDRIDGE, J. & WILSON, W. J., 1978: *Bibliography, Synthesis and Modeling of Naknek River Aquatic System Information*. – Report for U.S. Department of the Interior, National Park Service, Pacific Northwest Region, Seattle, Washington. Arctic Environmental Information and Data Center, University of Alaska, Anchorage, 244 pp.
- CANFIELD JR., D. E., 1983: Prediction of chlorophyll *a* concentrations in Florida lakes: the importance of phosphorus and nitrogen. – *Water Resour. Bull.* 19: 255–262.
- CRUMPTON, W. G., ISENHART, T. M. & MITCHELL, P. D., 1992: Nitrate and organic N analysis with second-derivative spectroscopy. – *Limnol. Oceanogr.* 37: 907–913.
- EDMUNDSON, J. A. & CARLSON, S. R., 1998: Lake typology influences on the phosphorus-chlorophyll relationship in subarctic, Alaskan Lakes. – *Lake Reserv. Manage.* 14: 440–450.
- EISENREICH, S. J., BANNERMAN, R. T. & ARMSTRONG, D. E., 1975: A simplified phosphorus analysis technique. – *Environ. Lett.* 9:45–53.
- FIRESTEIN, J. & HILDRETH, W., 1992: The Plinian eruptions of 1912 at Novarupta, Katmai National Park, Alaska. – *Bull. Volcanology* 54:646–684.
- GOLDMAN, C. R., 1960: Primary productivity and limiting factors in three lakes of the Alaska Peninsula. – *Ecol. Monogr.* 30:207–230.
- GUNTER, A. J., 1989: Nitrogen fixation by lichens in a subarctic Alaskan watershed. – *Bryologist* 92: 202–208.
- HANSON, J. M. & PETERS, R. H., 1984: Empirical prediction of crustacean zooplankton biomass and profundal macrobenthos biomass in lakes. – *Can. J. Fish. Aquat. Sci.* 41: 439–445.
- JONES, J. R. & BACHMANN, R. W., 1976: Prediction of phosphorus and chlorophyll levels in lakes. – *J. Water Pollut. Control Fed.* 48: 2176–2182.
- JONES, J. R., LAPERRIERE, J. D. & PERKINS, B. D., 1990: Limnology of Walker Lake and comparisons with other lakes in the Brooks Range, Alaska (USA). – *Verh. Internat. Verein. Limnol.* 24: 302–308.
- JONES, J. R., PERKINS, B. D., WITT JR., A., KAISER, M. S., THAMASARA, S., SIRIWORAKUL, M. & BENYASUT, P., 2000: Limnological characteristics of some reservoirs in Thailand. – *Verh. Internat. Verein. Limnol.* 27: 2158–2166.
- KNOWLTON, M. F., 1984: Flow-through microcuvette for fluorometric determination of chlorophyll. – *Water Resour. Bull.* 20: 795–799.
- LAPERRIERE, J. D., 1997: Limnology of two lake systems of

- Katmai National Park and Preserve, Alaska: physical and chemical profiles, major ions, and trace elements. – *Hydrobiologia* 354: 89–99.
- LAPERRIERE, J. D. & EDMUNDSON, J. A., 2000: Limnology of two lake systems of Katmai National Park and Preserve, Alaska: Part II. Light penetration and Secchi depth. – *Hydrobiologia* 418: 209–216.
- MATHISEN, O. A. & POE, P. H., 1978: Effects of volcanic ash deposits on sockeye salmon lakes. – *Verh. Internat. Verein. Limnol.* 20: 165–172.
- MATHISEN, O. A., PARKER, P. L., GOERING, J. J., KLINE, T. C., POE, P. H. & SCALAN, R. S., 1988: Recycling of marine elements transported into freshwater systems by anadromous salmon. – *Verh. Internat. Verein. Limnol.* 23: 2249–2258.
- MAZUMDER, A., 1994: Phosphorus–chlorophyll relationships under contrasting herbivory and thermal stratification: Predictions and patterns. – *Can. J. Fish. Aquat. Sci.* 51: 390–400.
- MCQUEEN, D. J., POST, J. R. & MILLS, E. L., 1986: Trophic relationships in freshwater pelagic ecosystems. – *Can. J. Fish. Aquat. Sci.* 43: 1571–1581.
- NÜRNBERG, G. K., 1996: Trophic state of clear and colored, soft- and hardwater lakes with special consideration of nutrients, anoxia, phytoplankton and fish. – *Lake Reserv. Manage.* 12: 420–431.
- NÜRNBERG, G. K. & SHAW, M., 1998: Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. – *Hydrobiologia* 382: 97–112.
- PACE, M. L., 1984: Zooplankton community structure, but not biomass, influence the phosphorus–chlorophyll relationship. – *Can. J. Fish. Aquat. Sci.* 41: 1089–1096.
- PIENITZ, R., SMOL, J. P. & LEAN, D. R. S., 1997: Physical and chemical limnology of 59 lakes located between the southern Yukon and the Tuktoyaktuk Peninsula, Northwest Territories (Canada). – *Can. J. Fish. Aquat. Sci.* 54: 330–346.
- PREPAS, E. E. & RIGLER, F. A., 1982: Improvements in quantifying the phosphorus concentration in lake water. – *Can. J. Fish. Aquat. Sci.* 39: 822–829.
- PRIDMORE, R. D., VANT, W. N. & RUTHERFORD, J. C., 1985: Chlorophyll–nutrient relationships in North Island lakes (New Zealand). – *Hydrobiologia* 121: 181–189.
- SATORY, D. P. & GROBBELAAR, J. V., 1984: Extraction of chlorophyll-*a* from freshwater phytoplankton for spectrophotometric analysis. – *Hydrobiologia* 114: 177–187.
- SHORTREED, K. S. & STOCKNER, J. G., 1986: Trophic status of 19 subarctic lakes in the Yukon territory. *Can. J. Fish. Aquat. Sci.* 43: 797–805.
- STOCKNER, J. G. & SHORTREED, K. S., 1985: Whole-lake fertilization experiments in coastal British Columbia lakes: empirical relationships between nutrient inputs and phytoplankton biomass and production. – *Can. J. Fish. Aquat. Sci.* 42: 649–658.
- VYMAZAL, J., 1995: *Algae and Element Cycling in Wetlands*. – Lewis Publishers, Boca Raton 689 pp.
- WATSON, S., MCCAULEY, B. E. & DOWNING, J. A., 1992: Sigmoid relationships between phosphorus, algal biomass and algal community structures. – *Can. J. Fish. Aquat. Sci.* 49: 2605–2610.

Authors' addresses:

J. D. LAPERRIERE (Deceased), J. R. JONES, Fisheries and Wildlife Sciences, School of Natural Resources, 302 Anheuser-Busch Nat. Res. Bldg., University of Missouri-Columbia, Columbia, MO 65211–7240, USA.
E-mail: jonesj@missouri.edu