

Limnology of Shallow Lakes in the Yukon Flats National Wildlife Refuge, Interior Alaska

Patricia J. Heglund and John R. Jones

Department of Fisheries and Wildlife Sciences

University of Missouri

Columbia, MO 65211-7240

ABSTRACT

Heglund, P. J. and J. R. Jones. 2003. Limnology of shallow lakes in the Yukon Flats National Wildlife Refuge, Interior Alaska. *Lake and Reservoir Management*. 19(2):133-140.

Data from 129 shallow riverine lakes within the Yukon Flats National Wildlife Refuge (between 65° 45'N and 67° 30'N and 142° 30'W and 150° 00'W) are presented as a baseline contribution to the regional limnology of Alaska. Ion composition reflected the composition of carbonate alluvium within the region; in most lakes Ca > Mg and bicarbonate dominated the anions (~90%). In lakes where alkali deposits occurred, Na, Mg and bicarbonate were the principal ions. Some 25% of the lakes were slightly brackish (conductivity >500 µS) to brackish. The lakes are colored, with 18 to 447 Pt-units. And, they are fertile, with over 70% classified as eu- or hypereutrophic on the basis of their nutrient content. Ratios of N:P suggested nitrogen was potentially limiting in about half the study lakes and was increasingly important at high P values. The yield of algal chlorophyll (Chl) per unit of plant nutrient was low in these lakes and Chl-nutrient relations explained less of the variance relative to published models. Invertebrate grazing potentially regulates Chl in some lakes. Typically these lakes freeze to the sediments and most do not support a permanent fishery. High ratios of organic suspended solids to Chl indicate detrital carbon contributes to the filterable carbon pool of these shallow lakes.

Key Words: shallow lakes, water chemistry, colored lakes, nitrogen, phosphorus, algae.

Yukon Flats National Wildlife Refuge, located 120 km north of Fairbanks, encompasses the largest interior basin in Alaska (Fig. 1). It extends 360 km east-west along the Arctic Circle, between 65° 45' and 67° 30' north latitude and 142° 30' and 150° 00' west longitude. The refuge is bordered by the southern foothills of the Brooks Range to the north, the White-Crazy Mountains to the south, the Hodzanna Highlands to the west, and the Porcupine Plateau to the east (Williams 1962). It lies on a broad plain of poorly-drained deposits with a high water table and discontinuous permafrost within the boreal, coniferous forest biome. Elevation averages 180 m with local relief of <45 m (King 1962). Some 30,000 shallow lakes lie within the refuge boundary (King 1962).

This paper summarizes the limnological characteristics of 129 water bodies thought to represent extant conditions of the lentic aquatic resources within the refuge, and is a contribution to the general regional limnology of Alaska. These lakes match the definition of "shallow lake" by Scheffer (1998) in that they are colonized to some extent by macrophytes and do not

stratify for long periods in summer. The term wetlands, with deep water habitats, is also a valid characterization of them (Stewart and Kantrud 1971).

Study Area

Seven 11.2 km² plots within Yukon Flats National Wildlife Refuge were studied (Fig. 1). These had been identified previously in a waterfowl production survey. Of the 170 shallow lakes (herein called lakes) encompassed within these plots, 129 were sampled limnologically (Heglund 1988, 1992). Many were formed by movements of the Yukon River or its tributaries (lateral lakes and oxbows). Some lakes were created by the activities of beaver (*Castor canadensis*), some were formed through the accumulation of water in basins and others were formed and by cryogenic processes associated with thawing of the permafrost. Along the Yukon River floodplain, alluvial deposits create a mosaic of physically and chemically different lakes that reflect the complex

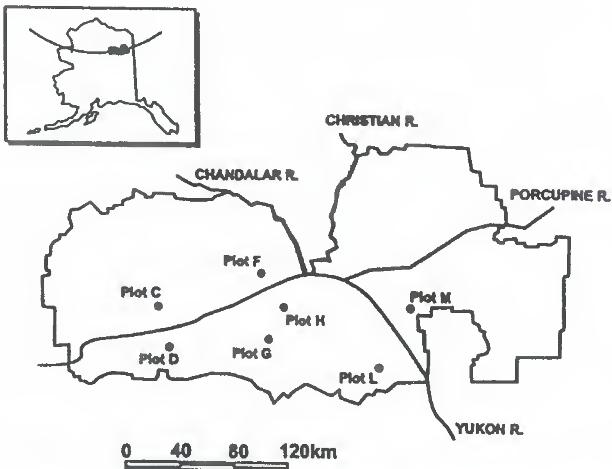


Figure 1.—Map of the Yukon Flats National Wildlife Refuge, Alaska, showing major rivers and the general location of the study plots.

surficial geology, changes in depth to permafrost, and subsurface movement of water (Williams 1962, Clautice and Mowatt 1981, Heglund 1988). Maximum depth ranged from <0.5 m to 6 m, with most lakes <2 m. Most were nearly circular, in >90 % shoreline development was <2. Thermal stratification was ephemeral, and the lakes often mixed diurnally. Both closed (no outlet) and open (with outlets) can be found on the Yukon Flats, and some have direct contact with the ground-water.

Samples were collected in 1985 (plots F, G, and H, $n = 26$), in 1986 (plots D, L, and M, $n = 847$), and in 1987 (plots C, D, and G, $n = 1637$), 1988 (plots H, G, D, M, $n = 9$). All plots and lakes were sampled again in 1989, and 5 lakes in Plot D were re-sampled in 1990. Overall, 117 lakes were sampled two seasons, 9 lakes one season and 3 lakes 3 seasons. Typically lakes were sampled on four occasions in a given season but there were some exceptions. The data were collected as part of a study of aquatic bird resources within the Yukon Flats (Heglund 1988, 1992). Macrophyte communities are described by Heglund (1992), and most are freshwater herb marsh wetlands.

Plot C ($n = 16$ sites) located west of the Hodzanna River, lies in stratified layers of silt, sand and gravel deposited by streams draining the adjoining upland (Williams 1962). The soil includes layers of peat and woody material with lakes formed by local thawing of the perennially frozen soil (Williams 1962). Over 75% of the area burned in 1979 and subsequently the vegetation was dominated by willow (*Salix* spp.), grasses (*Calamagrostis* spp. and *Hordeum jubatum*), and fireweed (*Epilobium angustifolium*).

Plot D ($n = 27$ sites) is located at the foot of the White Mountain marginal escarpment. Its western half

lies on silt, sand, and gravel deposited by Lost Creek from adjoining upland with frozen soils. The eastern section rests on sorted gravel.

Plot D ($n = 26$ sites) is located at the foot of the White Mountain marginal escarpment. Its western half lies on silt, sand and gravel deposited by Lost Creek as it drains out of the adjoining uplands. Soils in this region are frozen and wetland vegetation is characterized as floating mats of water arum (*Calla palustris*) and marsh cinquefoil (*Potentilla palustris*). The eastern section of the plot rests on sorted gravel overlying pockets of unfrozen soils. Wetland vegetation surrounding these lakes is dominated by freshwater sedges (*Carex aquatilis* and *C. rostrata*) and swamp horsetail (*Equisetum fluviatile*).

Plot F ($n = 8$ sites) is located north of the Arctic Circle and east of the Hadweenzic River. It rests on alluvial fan deposits from the Hadweenzic and Chandalar rivers. Numerous vegetated dunes comprised of Eolian sands mark the topography (Williams 1962). Shoreline vegetation of most ponds is predominantly composed of wet graminoids.

Plot G ($n = 8$ sites) is located near the south-central border of the Yukon Flats. Several lakes are connected via Big Creek to Birch Creek which ultimately drains into the Yukon River. The lakes rest on low-terrace alluvium of well-stratified layers of coarse to fine, well-sorted amounts of silt, sand, and gravel (Williams 1962). Water sedge (*Carex aquatilis*) and red-stem willow (*Salix arbusculoides*) dominate the vegetation of lake margins. Northern pike have been confirmed in the lakes on this plot connected to the river.

Plot H ($n = 10$) is located south of the Yukon River between Upper and Lower Birch Creek, in alluvial fan deposits composed of gravel layers containing silt, peat and woody material. Alkali (sodium and magnesium bicarbonate) deposits are also present (Clautice and Mowatt 1981) and several solution lakes lie within these materials. Lake margins are dominated by large, mesic to wet graminoid herbaceous meadows.

Plot L ($n = 27$) lies at the base of a marginal escarpment where Preacher Creek flows out of the Crazy Mountains on well-sorted gravel. The plot includes a number of oxbow lakes. Soils are saturated above, perennially frozen below and characterized by a polygonal network of willow dominated mounds surrounded by wet troughs. Isolated lakes are in various stages of bog development. Connected lakes have the potential to host predatory fish such as northern pike.

Plot M ($n = 33$) is located on alluvial deposits of the Little Black River. Soils have minor amounts of sand and silt. Soils are well-stratified layers of fine to coarse gravels with minor amounts of sand and silt. The site has many unfrozen zones and, like Plot H, is fairly well-

drained. Grasses (*Arctophila fulva*, *Alopecurus aequalis*, and *Glyceria* spp.), sedges (primarily *C. rostrata*, and *C. aquatilis*), and cattail (*Typha latifolia*) dominate the vegetation surrounding most lakes. Northern pike may occur in Lake 628.

Methods

Monthly water samples were collected on four occasions per sampling season (June-September). One 4 L plastic container was filled per lake by collecting a composite water sample from near the center of the water body and just below the surface with a 500 mL bottle. Conductivity (KSP, μS , Fisher meter), alkalinity (ALK, titration as $\text{mg} \cdot \text{L}^{-1} \text{CaCO}_3$), color (Pt-units, HACH comparator), and pH (HACH comparator) were measured on site. Total volatile suspended solids were measured on tared filters ($\text{mg} \cdot \text{L}^{-1}$, APHA 1981). Chlorophyll (Chl, $\mu\text{g} \cdot \text{L}^{-1}$) was filtered onto Gelman A/E filters and concentrations were determined with ethanol extraction (Knowlton 1984, Sartory and Grobbelaar 1984). Total phosphorus (TP, $\mu\text{g} \cdot \text{L}^{-1}$) was determined by colorimetric measurement of orthophosphate following persulfate oxidation (APHA 1981). Total nitrogen (TN, $\mu\text{g} \cdot \text{L}^{-1}$) was measured colorimetrically following persulfate oxidation and cadmium reduction (D'Elia et al. 1977). Sulfate ($\text{SO}_4\text{-S}$, $\text{mg} \cdot \text{L}^{-1}$) was determined with a Technicon Auto Analyzer II and the method of McSwain and Watrous (1974). Chloride (Cl, $\text{mg} \cdot \text{L}^{-1}$) was determined by titration with mercuric nitrate (APHA 1981). Cations (Ca, Mg, Na, K, $\text{mg} \cdot \text{L}^{-1}$) were determined on acid-preserved samples with an atomic absorption spectrophotometer or flame photometer (USEPA 1975).

Statistical analyses included correlation and regression on the arithmetic means of limnological values from each lake. Analyses were based on $n=129$ and significance of $p=0.01$, unless otherwise stated. Data were transformed to \log_{10} where appropriate.

Results

Ionic Salinity and Composition, and pH

Ionic salinity on the Yukon Flats, expressed as the sum of the cations, ranged from 0.22 to $123 \text{ meq} \cdot \text{L}^{-1}$, with a mean of $5.33 \text{ meq} \cdot \text{L}^{-1}$. Values exceeded the world average ($1.12 \text{ meq} \cdot \text{L}^{-1}$, Wetzel 2001) in $\sim 75\%$ of the lakes but the median value ($2.99 \text{ meq} \cdot \text{L}^{-1}$) approxi-

mates the average for waters associated with carbonate rock ($3.25 \text{ meq} \cdot \text{L}^{-1}$, Wetzel 2001). Cations were strongly correlated with anions ($r = \geq 0.98$, $n = 129$) and both measurements were strongly correlated with conductivity (KSP, $r = 0.99$, $n = 129$, Table 1). KSP ranged from 26 to $8200 \mu\text{S}$ with a mean of $442 \mu\text{S}$ (median $243 \mu\text{S}$). Some 25% of the lakes were slightly brackish (KSP $> 500 \mu\text{S}$, Stewart and Kantrud 1971), two sites were moderately brackish (KSP $> 2000 \mu\text{S}$) and one was brackish (KSP $> 5000 \mu\text{S}$, Table 1). Brackish sites were located in Plot H where alkali deposits occur (Clautice and Mowatt 1981), and within plots F and M where Mg was prevalent ($\sim 40\%$ of cations). Lakes with KSP $< 125 \mu\text{S}$ were located within plots D and L, both are at the base of escarpments where parent materials are from the uplands.

In $\sim 65\%$ of lakes $\text{Ca} > \text{Mg}$ (as % of cation equivalents) and bicarbonate dominated the anions (mean = 90%, median = 93%), which is indicative of waters from sedimentary materials (Wetzel 2001). Sodium accounted for $> 40\%$ of the cations in lakes where alkali deposits occur (Plot H). Among the anions, Cl was seldom $> 5\%$, and S was seldom $> 10\%$.

Values of pH ranged from 5.9 to 10 with a mean and median of 7.8 (Table 1). Consistent with carbon equilibria (Stumm and Morgan 1996), pH in the Yukon Flats lakes increased rapidly with alkalinity to a value of $\sim 100 \text{ mg} \cdot \text{L}^{-1}$ (Fig. 2a). In some lakes productivity mediated increases in pH (Stumm and Morgan 1996) may account for pH values exceeding the expected distribution with alkalinity (Fig. 2a). Among our measurements, pH showed a strong relationship with TN_{\log} ($r = 0.64$, Fig. 2b). Most lakes with $\text{pH} > 8.5$ had $\text{TN} > 1000 \text{ g} \cdot \text{L}^{-1}$. The correlation between TP_{\log} and pH was also significant ($r = 0.435$).

Color

All study lakes on the Yukon Flats were stained (Koenings and Edmundson 1991, Nürnberg and Shaw 1998). Values ranged from 18 to 447 Pt-units, with a mean and median of ~ 170 Pt-units (Table 1). Only 15% of the lakes had values < 80 Pt-units, and most lakes with < 50 Pt-units were isolated oxbows within Plot L where upland materials are prevalent. Values > 400 Pt-units ($n = 4$) were measured in isolated basins in Plot H where peat is a feature of the alluvial deposits. Correlations of color with TP_{\log} and TN_{\log} were significant ($r = 0.49$ and 0.375 , respectively) but there was not a strong relation between color and lake trophic state. The correlation between color and pH was not significant. Satoh et al. (1992) concluded that Alaskan colored water was not particularly acidic, and our data from the Yukon Flats are consistent with that finding.

Table 1.—Summary statistics for shallow lakes (n = 129) in the Yukon Flats National Wildlife Refuge.

Variable	Units	Mean	Median	Range
Area	ha	10.3	1.8	<0.1 - 247.3
Color	Pt-U	169	170	18 - 447
pH		7.8	7.8	5.9 - 10
Conductivity	μS	442	243	26 - 8200
Ca	$\text{mg}\cdot\text{L}^{-1}$	27.9	23.4	1.1 - 221
Mg	$\text{mg}\cdot\text{L}^{-1}$	20.6	10.3	0.5 - 153
Na	$\text{mg}\cdot\text{L}^{-1}$	45.9	4.4	0.6 - 2704
K	$\text{mg}\cdot\text{L}^{-1}$	10.0	3.4	0.5 - 114
Alkalinity	$\text{mg}\cdot\text{L}^{-1}\text{CaCO}_3$	253	144	9.3 - 5191
Cl	$\text{mg}\cdot\text{L}^{-1}$	3.6	1.7	0.6 - 21
S	$\text{mg}\cdot\text{L}^{-1}$	8.2	2.9	0.4 - 298
TP	$\mu\text{g}\cdot\text{L}^{-1}$	262	73	16 - 2532
TN	$\mu\text{g}\cdot\text{L}^{-1}$	1117	920	132 - 3969
TN:TP		12.3	11	0.6 - 56
Chl	$\mu\text{g}\cdot\text{L}^{-1}$	11.9	7.5	0.5 - 115
Chl:TP		0.11	0.09	<0.01 - 0.46
Chl:TN	$\mu\text{g}\cdot\text{mg}^{-1}$	12.1	8.6	1 - 107
VSS	$\text{mg}\cdot\text{L}^{-1}$	5.0	2.4	0.3 - 85
VSS:Chl	$\text{mg}\cdot\mu\text{g}^{-1}$	0.56	0.34	<0.1 - 8.5

Nutrients

Values of TN ranged from 132 to 3969 $\mu\text{g}\cdot\text{L}^{-1}$ with a mean of 1117 $\mu\text{g}\cdot\text{L}^{-1}$ (median 920 $\mu\text{g}\cdot\text{L}^{-1}$, Table 1). Values <350 $\mu\text{g}\cdot\text{L}^{-1}$ were found in isolated oxbows on Plot L where materials are from the uplands, and ~90% of values >1000 $\mu\text{g}\cdot\text{L}^{-1}$ were in sites with abundant fire scars (plots C, F, H, and M). Among the measured variables, TN showed a strong quadratic relation to KSP_{\log} ($R^2 = 0.71$, Fig. 3) which suggests N increases sharply among the slightly brackish lakes.

TP ranged from 16 to 2532 $\mu\text{g}\cdot\text{L}^{-1}$ with a mean of 262 $\mu\text{g}\cdot\text{L}^{-1}$ (median 73 $\mu\text{g}\cdot\text{L}^{-1}$, Table 1). The relation between TP_{\log} and KSP_{\log} ($R^2=0.59$, Fig. 3) was quadratic, with P increasing sharply among slightly brackish lakes. These cross-system patterns between nutrients and salinity were similar with ALK because of its strong correlation with KSP.

As is typical within lake districts, TN_{\log} was positively related with TP_{\log} ($R^2 = 0.47$) but the slope of the relationship is <1 (Fig. 4); therefore, among lakes in the Yukon Flats, the increase in P is accelerated relative to increases in N. Owing to this relation between the plant nutrients, the TN:TP ratio in Yukon Flats lakes declines sharply with TP (Fig. 4). Because of strong correlations with measures of salinity (Fig. 3), the declining pattern in TN:TP is similar when KSP or ALK is used as the independent variable. TN:TP

ranged from <1 to 56 with a mean and median of ~12 (Table 1).

Phytoplankton and Volatile Suspended Solids

Chlorophyll ranged from 0.5 to 115 $\mu\text{g}\cdot\text{L}^{-1}$ with a mean of 11.9 $\mu\text{g}\cdot\text{L}^{-1}$ (median 7.5 $\mu\text{g}\cdot\text{L}^{-1}$, Table 1). The ratio of Chl:TP averaged 0.11 (median 0.09) and the ratio of Chl:TN averaged 12.1 (as $\mu\text{g}\cdot\text{mg}^{-1}$, median 8.6). These ratios suggest Chl values are low relative to nutrient levels (Table 1). Measured Chl in the Yukon Flats is on average only 45% (median 36%) of predictions based on the worldwide TP-Chl model of Prairie et al. (1989) which spanned a similar TP range. Using their world wide TN-Chl model (similar TN range), however, measured Chl averaged 90% (median 55%) of predictions. Using their model with both TP and TN (Prairie et al. 1989), measured Chl averaged 55% (median 44%) of predicted values. Outcomes were similar using the world wide Chl-nutrient models of Nürnberg (1996).

Among the Yukon Flats lakes Chl was not particularly responsive to nutrients. The Chl_{\log} - TP_{\log} relation for all lakes is quadratic (Fig. 5); however, much less of the variance is accounted for relative to published models (Jones and Bachmann 1976, Smith 1982, Prairie

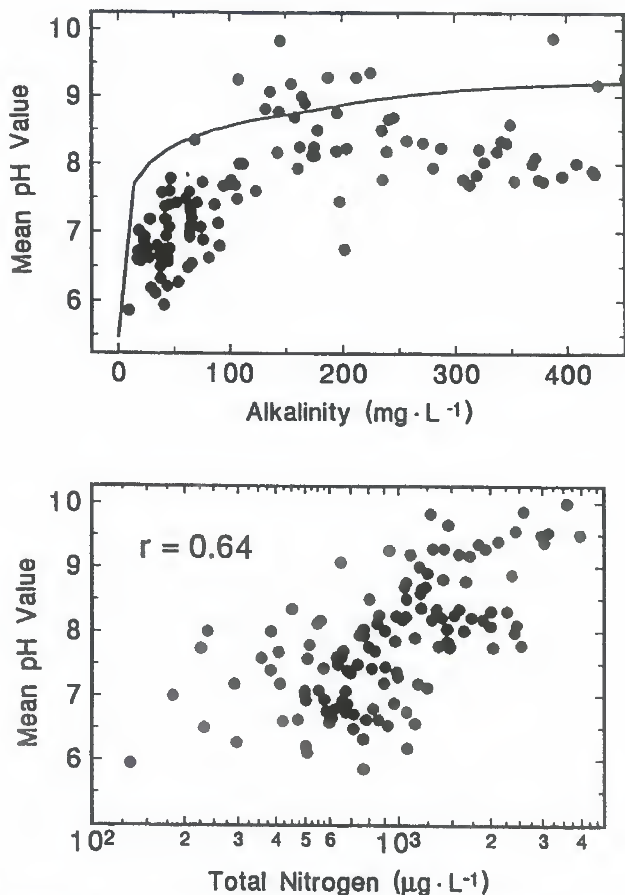


Figure 2.—Upper Panel: Mean pH of 129 shallow lakes on the Yukon Flats National Wildlife Refuge, Alaska plotted against alkalinity ($\text{mg} \cdot \text{L}^{-1}$). The solid line represents expected values based on carbon equilibria using equations from Stumm and Morgan (1996). Lower Panel: Values of pH correlated with log Total Nitrogen ($\mu\text{g} \cdot \text{L}^{-1}$).

et al. 1989, Nürnberg 1996). Similar to other studies (Prairie et al. 1989) an asymptote in the Chl_{\log} - TP_{\log} relation is reached in the Yukon Flats data at about $100 \mu\text{g} \cdot \text{L}^{-1}$ TP. Among lakes along the ascending limb of this relation, TN:TP averaged 17 and the Chl-TP relation was stronger ($R^2 = 0.49$, $n = 80$) than within the overall data set. The slope of the regression relation was 1.2, suggesting an accelerated increase in Chl relative to TP within this sub-set of lakes. The Chl_{\log} - TP_{\log} relation, however, was not significant among lakes beyond the asymptote ($n = 49$). The quadratic Chl-TP relation was not improved by adding TN_{\log} , $\text{TN}:\text{TP}_{\log}$ or color_{\log} . The Chl_{\log} - TN_{\log} relation was linear and explained less variation in Chl than the Chl_{\log} - TP_{\log} relation (Fig. 5); it was not improved by adding a quadratic term, $\text{TN}:\text{TP}_{\log}$ or color_{\log} . The correlation between Chl_{\log} and KSP_{\log} ($r = 0.33$) was weaker than the relations between KSP and nutrients (Fig. 3).

Volatile suspended solids (VSS), a measure of particulate organic carbon, ranged from 0.1 to

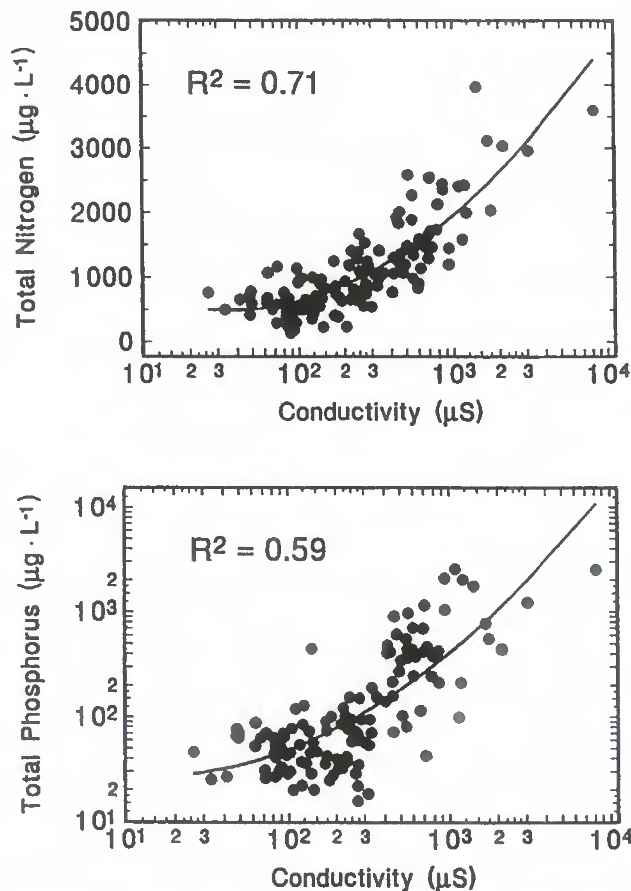


Figure 3.—Total nitrogen and Total phosphorus (log transformed) values from shallow lakes on the Yukon Flats National Wildlife Refuge, Alaska, regressed on conductivity (log transformed).

$85 \text{ mg} \cdot \text{L}^{-1}$, with a mean of $5 \text{ mg} \cdot \text{L}^{-1}$ (median $2.4 \text{ mg} \cdot \text{L}^{-1}$, Table 1). VSS_{\log} was strongly correlated with Chl_{\log} ($r = 0.70$). In the study lakes the ratio of $\text{VSS}:\text{Chl}$ averaged $0.56 (\text{mg} \cdot \mu\text{g}^{-1})$, median 0.34 , Table 1). Unpublished field and experimental data from lakes and wetlands in Missouri suggest that autochthonous

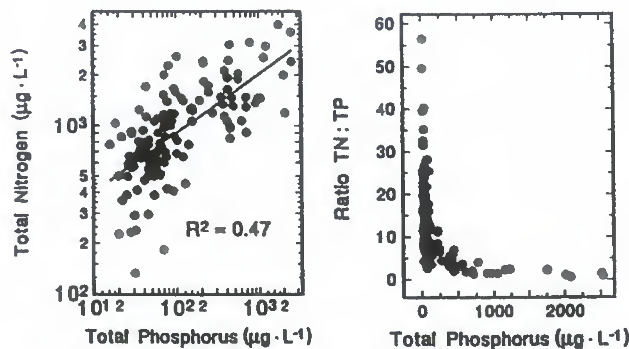


Figure 4.—Data from 129 shallow lakes on the Yukon Flats National Wildlife Refuge, Alaska. Left Panel: Total nitrogen regressed on Total phosphorus (both log transformed, $\mu\text{g} \cdot \text{L}^{-1}$). Right Panel: ratio of TN:TP regressed on Total phosphorus values.

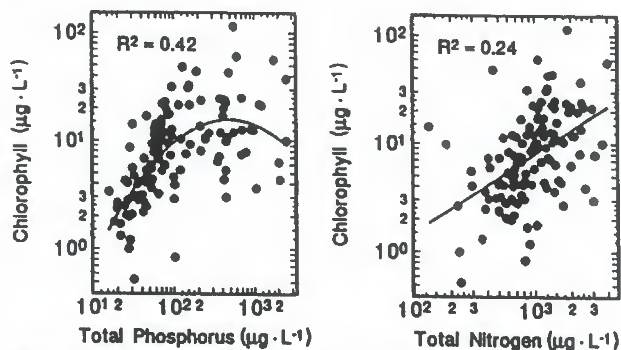


Figure 5.—Data from 129 shallow lakes on the Yukon Flats National Wildlife Refuge, Alaska. Left Panel: Chlorophyll regressed on Total phosphorus (both log transformed, $\mu\text{g} \cdot \text{L}^{-1}$). Right Panel: Chlorophyll regressed on Total nitrogen (both log transformed, $\mu\text{g} \cdot \text{L}^{-1}$).

systems dominated by algae have VSS:Chl ratios of ~ 0.18 . That ratios were double this level in nearly half of the Yukon Flats lakes suggests non-phytoplanktonic carbon sources were an important component of the seston.

Discussion

Nutrient concentrations in shallow lakes within the Yukon Flats National Wildlife Refuge are highly variable but most water bodies were either eutrophic ($\geq 40\%$) or hypereutrophic ($> 33\%$). Classifications varied somewhat depending on whether TP or TN was used for the assessment (Table 2). These lakes are naturally fertile. Like many naturally productive lakes they are located in alluvia rich in carbonates. Strong relations between plant nutrients and KSP and ALK (Fig. 3) in these water bodies support the conceptual framework that links parent geology and nutrients (Chow-Fraser 1991). And, like many shallow lakes they partly owe their nutrient status to their polymictic mixing pattern which promotes sediment-water exchange and internal

nutrient cycling, especially at high pH in lakes with macrophytes (Scheffer 1998). Fire history may also contribute to their nutrient content (Schindler et al. 1980, Bayley et al. 1992). Field observations suggest that plots with the most extensive fire scars had the highest levels of TN, these were also among the most saline within our suite of study lakes. Nitrogen fixation may also be important in some lakes (Alexander and Gu 1997). Lastly, colored lakes generally have high nutrient concentrations (Nürnberg and Shaw 1998).

Among lakes on the Yukon Flats, increases in TP are accelerated relative to TN (Fig. 4) resulting in a hyperbolic pattern with a sharp decline in TN:TP in those lakes with $< 100 \text{ g} \cdot \text{L}^{-1}$ TP and modest decrease thereafter (Fig. 4). Effectively, TN:TP decreased with lake trophic state; among mesotrophic lakes TN:TP averaged 26 (median 23), among eutrophic lakes the average was 14 (median 12.5) and among hyper-eutrophic lakes the average was 5 (median 4). This decline in TN:TP with TP is consistent, but more sheer in the mesotrophic range than the pattern described for the world's lakes by Downing and McCauley (1992).

It is common for lakes with high TP to have low TN:TP ratios. The nitrogen cycle has been studied extensively in Alaskan lakes (Alexander and Gu 1997) and is closely tied to N-fixation by terrestrial vegetation and in some cases cyanobacteria within lakes. High TN in lakes where fire scars occur raises the testable hypothesis that this disturbance increases loss from the surrounding basin or it increases the abundance of terrestrial N-fixers within those plots relative to the others. Also, N-loss by denitrification and uptake in these shallow lakes by macrophytes may contribute to this low ratio (Jensen et al. 1991, Scheffer 1998). Using TN:TP to judge potential nutrient limitation (Smith 1982), P-limitation (TN:TP > 20) was suggested in $\sim 20\%$ of the sites and either nutrient was possibly limiting in $\sim 30\%$ (TN:TP 10 to 20). In those remaining lakes where N-limitation was suggested (TN:TP < 10), half had TN:TP ratios < 5 . The analysis by Chow-Fraser

Table 2.—Trophic state of shallow lakes in the Yukon Flats National Wildlife Refuge. Criteria are from Nürnberg (1996).

Trophic State	Chlorophyll		Total P		Total N	
	Criterion	%	Criterion	%	Criterion	%
Oligotrophic	< 3.5	21	< 10	0	< 350	5
Mesotrophic	3.5 - 9	34	10 - 30	13	350 - 650	22
Eutrophic	9.1 - 25	37	31 - 100	49	651 - 1200	40
Hypereutrophic	> 25	8	> 100	38	> 1200	33

(1991) showed that N becomes the limiting element in saline lakes and data from slightly brackish lakes on the Yukon Flats supports this pattern.

Phosphorus limitation is considered prevalent in Alaska (Gregory-Eaves et al. 2000) and elsewhere at high latitude (Pienitz et al. 1997a and 1997b). There are increased reports, however, that nitrogen limitation occurs in the arctic (Lim et al. 2001, LaPerriere et al. 2003). The strength of our empirical Chl-nutrient relations were modest (Fig. 5) relative to the published literature, and Chl yields per unit of nutrient in the Yukon Flats lakes were one-third to one-half of levels commonly found in lakes. This outcome suggests an overall weak response of Chl to nutrients in these shallow lakes. Concurrent with this study, 74 nutrient stimulation bioassays (unpublished) were conducted on 15 lakes (after Jones et al. 1990). Half of those experiments showed either no measurable response to nutrient additions (35%) or a positive response to light during the incubation (16%), which further supports the view that algal Chl responded weakly to nutrients in these lakes. Phosphorus stimulated Chl in 11% of the trials in which TN:TP averaged 36 (median = 42). Nitrogen stimulated Chl in 38% of the incubations which is consistent with N limitation on the basis of TN:TP ratios. The cross-system correlation between pH and TN in the study lakes implies some contribution from productivity mediated increases in pH (from plankton, macrophytes and associated epiphytes) thereby providing additional support that lake productivity responds to the most prevalent limiting nutrient on the Yukon Flats (Fig. 2b).

The low yield of Chl per unit of plant nutrient in these systems (Table 1), and the modest among-lake response to nutrients (Fig. 5), is consistent with past findings in shallow lakes with aquatic vegetation (Scheffer 1998). Others have found ratios of Chl:TP were greatly reduced among saline lakes (Bierhuizen and Prepas 1985, Chow-Fraser 1991). In the Yukon Flats top-down control by invertebrate grazers likely contributes to the low Chl-nutrient yields and variation in their relationships. Most of these shallow lakes freeze to the sediments each winter. Therefore, they do not support a permanent fish community and field observations suggest they are dominated by large-bodied planktonic grazers (P. Heglund, pers. obs.). In such systems with two trophic levels – producers and invertebrate grazers – grazing by herbivore predators reduces algal biomass compared with systems with fish (Hansson 1992). Nutrient regeneration by zooplankton could also be a factor in reducing nutrient limitation of phytoplankton in these lakes (Moegenburg and Vanni 1991). Negative effects of color on nutrient-Chl relations by processes such as complexation of nutrients and reducing light (Jones 1992) were not apparent in our

empirical analyses, nor was the positive effect of color found by Nürnberg and Shaw (1998). However, a small number of our nutrient experiments did show a response to light, suggesting it may play a role that was not detected in among system analyses. An effect of color on Chl might not be observed in systems that are strongly regulated by grazing.

The high ratio of VSS:Chl (Table 1) suggests that detrital carbon contributes to the filterable carbon pool of these shallow lakes. Potential sources are planktonic invertebrates, benthic plant growth, bacterial activity and allochthonous materials from meadow and upland vegetation (Wetzel 2001). Our data do not identify the sources in the Yukon Flats lakes but non-phytoplanktonic carbon is prominent in the seston of other high latitude lakes (Hamilton et al. 2001, Lim et al. 2001).

The shallow, riverine, fresh to slightly brackish lakes on the Yukon Flats are among the most nutrient-rich and colored in Alaska (LaPerriere et al. 1998, 2003, Kling et al. 1992, Edmundson and Carlson 1998, Gregory-Eaves et al. 2000). Reasons are their geological setting in carbonate alluvium, polymictic thermal pattern and shallow morphology. These data provide a limnological characterization of a previously unstudied region of Alaska, and provide basis for comparisons with shallow, riverine lakes elsewhere in Alaska and in other high latitude locations.

ACKNOWLEDGMENTS: Funding was provided by the U. S. Fish and Wildlife Service - Region 7, Yukon Flats National Wildlife Refuge, Fairbanks, Alaska, and the Alaska Fish and Wildlife Research Center - Region 8, Anchorage Alaska. Numerous people provided encouragement and logistical support for this project, including Jacqueline D. LaPerriere. We particularly thank Bruce Perkins and Doug Helmers for laboratory analyses, and Leigh Fredrickson for his interest in this component of the project.

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