

General Limnology of Lakes Near Cook Inlet, Southcentral Alaska

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ABSTRACT

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Data from lakes on the Kenai Peninsula ($n = 111$) and in the Matanuska-Susitna Valley ($n = 108$) show that lakes near the Cook Inlet, Alaska are moderately stained, with low turbidity and are predominately oligotrophic with a potential for phosphorus limitation. In both locations measures of salinity (as measured by conductivity) and pH were heterogenous and tied to hydrologic flowpaths. Overall, seepage lakes had lower pH, salinity, alkalinity, Ca, Mg and Si than drainage lakes. In our data set, both seepage and drainage lakes on the Kenai had lower alkalinity, Ca, and Si than corresponding lake types in Mat-Su. Most zooplankton biomass (ZB) measurements in the Cook Inlet lakes were $<100 \mu\text{g} \cdot \text{L}^{-1}$ and over one-third were $<10 \mu\text{g} \cdot \text{L}^{-1}$. Values of ZB were low relative to empirical models and did not increase with lake trophic state. Each of these lakes supports a fish community and the well-known effects of food web structure via grazing by planktivorous fish likely account for the observed ZB values. Environmental measurements and their patterns match earlier studies and collectively describe extant features of lake resources in this region of the southern boreal forest in southcentral Alaska.

Key Words: Alaskan lakes, nitrogen, phosphorus, plankton, seepage lakes, drainage lakes.

Lake resources in Alaska have been studied for a century (Hobbie 1997) with information coming from detailed investigations of individual lakes (e.g., Alexander and Bardsate 1971, O'Brien et al. 1997, LaPerriere 2003), regional surveys of lake resources (e.g., LaPerriere 1997, Kling et al. 2000) and statewide

transects in varying climatic zones (Sato et al. 1992, Gregory-Eaves et al. 2000). Collectively these studies have documented the variety of lake types within the state, and characterized regional patterns and processes.

This paper presents the general limnology of lakes from two lowland regions near Cook Inlet, Alaska within the Southern Boreal Forest ecozone (Fig. 1). These lakes on the Kenai Peninsula and the Matanuska-Susitna (Mat-Su) Valley north of Anchorage were samp-

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led by Bell et al. (1993) as part of a study of adaptation and natural selection in the threespine stickleback (*Gasterosteus aculeatus*). The ion chemistry of lakes in the southern lowland region on the Kenai Peninsula has been studied by Eilers et al. (1993) and several Kenai lakes were included in statewide surveys by Satoh et al. (1992) and Gregory-Eaves et al. (2000). Lakes in the Mat-Su Valley, located north of Anchorage (Fig. 1), are less-well studied but several were included in the inventory by Gregory-Eaves et al. (2000). Approximately half of the Cook Inlet lakes selected for study are seepage lakes with no visible outlets and the rest were drainage lakes with outlet streams. Predatory fishes (salmonids) were present in about one-half the lakes (Bell et al. 1993). Our analysis emphasizes general water chemistry, nutrient status, plankton and trophic state of lakes in this ecozone.

Site Description

Lakes on the Kenai Peninsula were largely within or adjacent to the Kenai National Wildlife Refuge (Fig. 1). Sedimentary bedrock in this glaciated area is overlain with glacial, aeolian (volcanic ash) and fluvial deposits (Reger and Pinney, 1996, Milner et al. 1997). Poor drainage in lowland areas results in extensive areas of muskeg and bog vegetation (Eilers et al. 1993). Upland moraines and unsorted glacial drift are composed of gravel, sand, silt and clay. Water chemistry information was collected from 111 lakes (Table 1) varying in size from 1-322 ha (median 21 ha) and located at elevations from 5-198 m (median 54 m). About half ($n = 58$) were seepage lakes, without an active outlet, with muskeg vegetation. The others ($n = 53$) were drainage lakes, with discharge streams. Lakes were selected in these proportions non-randomly to facilitate the study by Bell et al. (1993).

Lakes in the Matanuska-Susitna (Mat-Su) Valley included samples from within the Nancy Lake State Recreation Area where some information exists on lake water chemistry (Maurer 1988). The Talkeetna Mountains dominate the central region of the Mat-Su Valley with the Matanuska River receiving drainage to the south and the Susitna River receiving drainage from the north and west. This glaciated region is characterized by glacial moraines and outwash with aeolian and fluvial deposits (Reger and Pinney 1996, Milner et al. 1997). Water chemistry information was collected from 108 lakes (Table 2) varying in size from 1-1136 ha (median 20 ha) and located at elevations from 8 to 265 m (median 68 m). About one-third ($n = 39$) were seepage lakes and the remainder drainage lakes. The lakes were selected non-randomly.

Methods and Materials

Lakes on the Kenai Peninsula and in the Mat-Su Valley (Fig. 1) were sampled between 26 May and 16 August 1990. Sampling alternated between the two regions every 1 to 14-days to avoid confounding spatial and seasonal variation (Bell et al. 1993). Water samples were collected from a boat using a 1-L Van Dorn sampler from a 1-m depth (0.5 m in shallow lakes). Samples were held in the field up to 8 h at ambient temperature (15-22°C) and refrigerated before processing (within 48 h of collection). Sample collection techniques and laboratory methods of Koenings et al. (1987) were followed. An Orion model-399A/ion analyzer was used to measure pH within 24 h after arrival in the laboratory. Conductivity was measured using a YSI model-32 instrument. Alkalinity was measured by titration with sulfuric acid and a pH meter. Turbidity was measured

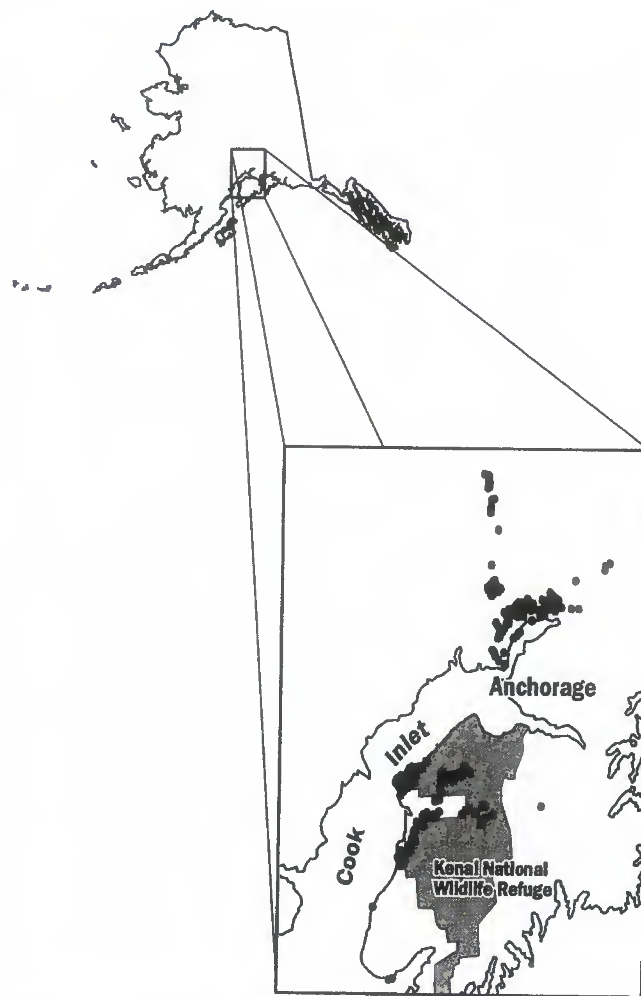


Figure 1.—Location of the study lakes in Alaska. Lakes on the Kenai Peninsula are in and adjacent to the Kenai National Wildlife Refuge, and lakes in the Mat-Su Valley are located north of Anchorage and the Cook Inlet.

Table 1.—Summary statistics for lakes sampled on the Kenai Peninsula, Alaska. Single asterisk indicates $p < 0.05$ and double asterisk indicates $p \leq 0.01$.

Parameter	Units	n	mean	Percentiles					Median Values	
				0	25th	50th	75th	100th	Seepage	Drainage
Lake Area	ha	110	36	1	9	21	47	322	15	33**
Lake Elevation	m	111	52.5	5	32	54	72	198	43	54
pH	—	107	7.0	5.5	6.6	6.8	7.3	8.8	6.7	7.25**
Conductivity	μS	107	53	11	22	39	61	245	25	56**
Alkalinity										
$\mu\text{eq} \cdot \text{L}^{-1}$	107	391	20	100	160	480	1800	120	420**	
Ca	$\mu\text{eq} \cdot \text{L}^{-1}$	109	308	35	115	180	377	1457	130	329**
Mg	$\mu\text{eq} \cdot \text{L}^{-1}$	109	138	16.5	41	115	210	469	99	173**
Fe	$\mu\text{g} \cdot \text{L}^{-1}$	106	159	5	36	78	214	1499	69	101
Si	$\mu\text{g} \cdot \text{L}^{-1}$	111	1089	0	90	461	1323	7438	169	1022**
Color	Pt	111	15	4	8	13	19	50	9.5	17**
Turbidity	NTU	107	1.3	0.4	0.7	1.2	1.6	6.6	1.2	1.2
TP	$\mu\text{g} \cdot \text{L}^{-1}$	111	11	4	7	8	11	82	7.5	9*
TN	$\mu\text{g} \cdot \text{L}^{-1}$	111	330	163	257	303	372	854	302	310
TN/TP	—	111	32	5	22	27	33	113	26	28
Chla	$\mu\text{g} \cdot \text{L}^{-1}$	103	1.9	0.3	0.75	1.1	1.8	39.8	1.1	1.2
Phaeo	$\mu\text{g} \cdot \text{L}^{-1}$	103	0.9	<0.1	0.4	0.65	1.1	9.6	0.67	0.64
Chla/TP	—	103	0.15	<0.1	0.1	0.13	0.19	0.75	0.15	0.13
Chl _a /TP	—	103	0.24	<0.1	0.15	0.22	0.29	0.75	0.24	0.20
Zooplankton - B	$\mu\text{g} \cdot \text{L}^{-1}$	72	108	0.3	3.2	16	80	1467	13	19

Table 2.—Summary statistics for lakes sampled in the Mat-Su Valley, Alaska. Single asterisk indicates $p \leq 0.05$ and double asterisk indicates $p \leq 0.01$.

Parameter	Units	n	mean	Percentiles					Median Values	
				0	25th	50th	75th	100 th	Seepage	Drainage
Lake Area	ha	108	43	1	7	20	40	1136	13	21
Lake Elevation	m	108	77	8	53	68	99	265	63	72
pH	—	108	7.3	5.4	6.9	7.4	7.7	8.5	7.1	7.5**
Conductivity	μS	108	76	6	32	57	106	282	41	61**
Alkalinity	$\mu\text{eq} \cdot \text{L}^{-1}$	107	709	20	260	520	1040	2700	360	580**
Ca	$\mu\text{eq} \cdot \text{L}^{-1}$	108	522	15	209	384	768	1846	235	454**
Mg	$\mu\text{eq} \cdot \text{L}^{-1}$	108	212	17	66	140	307	1745	82	189**
Fe	$\mu\text{g} \cdot \text{L}^{-1}$	108	115	3	21	49	133	1166	42	64
Si	$\mu\text{g} \cdot \text{L}^{-1}$	108	2028	23	553	1810	3124	6730	788	2082**
Color	Pt	105	18	4	9	14	24	74	12	17
Turbidity	NTU	108	1.1	0.2	0.6	1	1.2	8.4	0.9	1.0
TP	$\mu\text{g} \cdot \text{L}^{-1}$	104	8	2	6	7	9	22	7	7
TN	$\mu\text{g} \cdot \text{L}^{-1}$	105	327	121	221	284	366	2773	322	268*
TN/TP	—	104	26	7	21	24	30	57	23	26*
Chla	$\mu\text{g} \cdot \text{L}^{-1}$	104	1.0	0.2	0.5	0.8	1.2	4.6	0.7	0.9
Phaeo	$\mu\text{g} \cdot \text{L}^{-1}$	104	0.8	0.1	0.4	0.5	0.7	5.4	0.5	0.5
Chla/TP	—	100	0.13	<0.1	0.1	0.12	0.17	0.47	0.10	0.13*
Chl _a /TP	—	100	0.22	<0.1	0.15	0.20	0.29	0.69	0.17	0.20
Zooplankton - B	$\mu\text{g} \cdot \text{L}^{-1}$	57	63	0.2	7.6	19	56	1084	26	13.5

using an HF Instruments model-DRT 100 turbidimeter with reference standards. Color was determined on filtered lake water (Whatman GFF filters) by comparing spectrometric absorbance at 400 nm to a platinum cobalt standards. [Ca] was estimated colorimetrically with glyoxal indicator, and [Mg] was measured colorimetrically with Brilliant Yellow dye. Total iron was measured at 562 nm using Ferrozine iron reagent (Hach Chemical Company). Reactive silicon was measured at 810 nm using the ammonium molybdate method. A Technicon Autoanalyzer I equipped with a 630 nm filter and a block digester was used to measure Total Kjeldahl nitrogen. Cadmium reduction was used to measure nitrate-nitrite nitrogen at 543 nm and these values were combined with total Kjeldahl nitrogen and reported as total nitrogen (TN) in the text. Total phosphorus (TP) was determined using the molybdenum-blue method after persulfate digestion. Acetone extraction and a Turner model 111 or 112 fluorometer were used to measure chlorophyll-*a* (Chl_a) and pheophytin on a known volume of lake water filtered through GFF filters. Measurements of Chl_a were combined with pheophytin values to represent total chlorophyll (Chl_T).

Zooplankton samples were collected from 0.5 m above the bottom to the surface using a net with a mouth diameter of 20 cm and 153 μm mesh, and 100% net efficiency was assumed. Zooplankton were enumerated in the taxonomic groups within the rotifers, copepods and cladocerans and up to 30 lengths were measured (copepods and cladocerans only). Dry weight biomass as $\mu\text{g} \cdot \text{L}^{-1}$, was calculated with length:weight equations of Dumont et al. (1975) and McCauley (1984). We assumed a size of 3 mm for *Leptadorea* and 0.18 mm for nauplii.

Statistical analyses were conducted using SPSS software. Comparisons were made using the Mann-Whitney U-Test with probability of <0.05 . Values were log transformed when appropriate for correlation and regression analyses and significance was set at <0.05 . Principal Components Analysis was run using the Multivariate Statistical Package for Windows, version 3.11, Kovach Computing Services, Wales, U. K.

Results

Kenai Peninsula Lakes

Most Kenai lakes were moderately stained (>10 Pt units), with near-neutral pH (few values were <6 or >8) and low turbidity (Table 1). Similar to the earlier survey of Eilers et al. (1993), Kenai lakes exhibited a broad range in salinity, as measured by conductivity

(11-245 μS), alkalinity (20-1800 $\mu\text{eq} \cdot \text{L}^{-1}$), and the divalent cations (35-1457 $\mu\text{eq} \cdot \text{L}^{-1}$ Ca and 16.5- 469 $\mu\text{eq} \cdot \text{L}^{-1}$ Mg). Among these lakes, alkalinity, conductivity and calcium were strongly inter-correlated (log transformed, $r \geq 0.86$, $n = 106$). Reactive Si (0-7438 $\mu\text{g} \cdot \text{L}^{-1}$, Table 1) encompassed the broad range measured by Eilers et al. (1993), and was strongly correlated with conductivity (log transformed, $r = 0.74$, $n = 106$).

Lake water chemistry on the Kenai Peninsula is closely tied to hydrologic patterns (Eilers et al. 1993). Our data show (Table 1) seepage lakes ($n = 58$), relative to drainage lakes ($n = 53$), had significantly lower color (median 9.5 vs. 17 Pt units, respectively), pH (median 6.7 vs. 7.25), conductivity (median 25 vs. 56 μS), alkalinity (median 120 vs. 420 $\mu\text{eq} \cdot \text{L}^{-1}$), Ca (median 130 vs. 329 $\mu\text{eq} \cdot \text{L}^{-1}$), Mg (median 99 vs. 173 $\mu\text{eq} \cdot \text{L}^{-1}$), and Si (median 169 vs. 1022 $\mu\text{g} \cdot \text{L}^{-1}$). Seepage lakes also had significantly smaller surface areas than drainage lakes (median 15 vs. 33 ha) but did not differ in elevation.

Eilers et al. (1993) found cations in seepage lakes, on average, were composed of near equal proportions Ca, Mg and Na with $\sim 10\%$ K, and anions were dominated by inorganic carbon ($>55\%$) and Cl ($\sim 40\%$). In contrast, high-alkalinity lakes, many with active outlets, were dominated by Ca ($\sim 65\%$) and inorganic carbon ($\sim 95\%$). We lack data to directly compare major ion composition of these two lake types but found seepage lakes had significantly lower ratios of Ca:Mg (median 1.7 vs. 2.4 as $\mu\text{eq} \cdot \text{L}^{-1}$), Ca:conductivity (median 4.6 vs. 5.7 as $\mu\text{eq} \cdot \text{L}^{-1} : \mu\text{S}$) and alkalinity:conductivity (median 4.5 vs. 8 as $\mu\text{eq} \cdot \text{L}^{-1} : \mu\text{S}$) than drainage lakes in our study suite. These ratios are consistent with lower proportions of Ca and alkalinity among the total ion content of seepage lakes as compared to drainage lakes. Analysis of the data set of Eilers et al. (1993) also shows significant differences in these same ratios between lake groups representing seepage and drainage lakes.

Values of pH and alkalinity showed a strong curvilinear relation (Fig. 2) which matches the pattern described by Eilers et al. (1993). Values of pH increased rapidly with alkalinity to a value of $\sim 150 \mu\text{eq} \cdot \text{L}^{-1}$ and the rate of increase declined thereafter, consistent with known carbon equilibria (Stumm and Morgan 1996). Among the Kenai lakes, pH was strongly correlated with log transformed values of alkalinity ($r = 0.90$, $n = 107$), conductivity ($r = 0.88$, $n = 107$) and Ca ($r = 0.86$, $n = 106$). However, pH was not significantly related to TN_{\log} and was weakly correlated with TP_{\log} ($r = 0.3$, $n = 107$).

Among seepage lakes, TP values were slightly less than drainage lakes (median 7.5 vs. 9 $\mu\text{g} \cdot \text{L}^{-1}$, Table 1). The two lake types, however, did not significantly differ in fertility as measured by TN and Chl_a, in the yield of chlorophyll per unit of phosphorus (Chl_a/TP or Chl_T/TP) or in TN/TP.

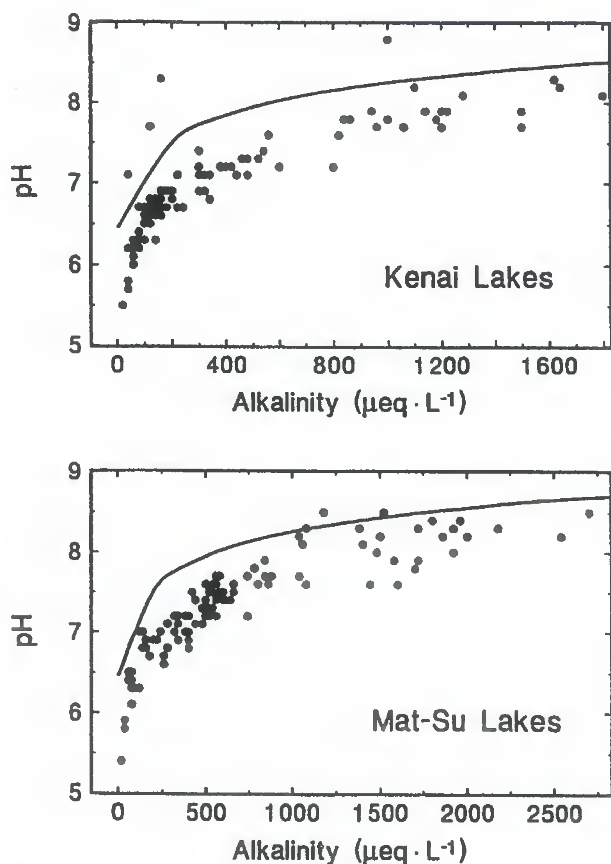


Figure 2.—Upper Panel: Values of pH from lakes on the Kenai Peninsula plotted against alkalinity ($\mu\text{eq}\cdot\text{L}^{-1}$). The solid line represents expected values based on carbon equilibria using equations from Stumm and Morgan (1996). Lower Panel: Values of pH from the Mat-Su lakes against alkalinity, with the same carbon equilibria.

Among all Kenai lakes, TN_{\log} and TP_{\log} were correlated ($r = 0.56$, $n = 111$). Based on TN/TP these lakes were primarily limited by P (Smith 1982); this ratio was <10 in one lake, and $\sim 12\%$ of the sampled lakes had $\text{TN}/\text{TP} >10 < 20$. Among all lakes, TP_{\log} was correlated with both conductivity and alkalinity (log transformed, $r = 0.37$ and 0.25 , respectively, $n = 107$) but correlations with TN and other measures of salinity were not significant. Using criteria by Nürnberg (1996) some 68% of the Kenai lakes were oligotrophic based on TP ($<10 \mu\text{g}\cdot\text{L}^{-1}$) and TN ($<350 \mu\text{g}\cdot\text{L}^{-1}$), $\sim 28\%$ were mesotrophic ($\text{TP} >10\text{--}30 \mu\text{g}\cdot\text{L}^{-1}$ and $\text{TN} >350\text{--}650 \mu\text{g}\cdot\text{L}^{-1}$) and $<5\%$ were eutrophic. Based on Chl_a all but a few lakes were oligotrophic, but on the basis of Chl_T $\sim 16\%$ were mesotrophic. Log transformed values of Chl_a were strongly correlated to TP_{\log} and TN_{\log} ($r = 0.7$ and 0.61 , respectively, $n = 103$), and both correlations were improved slightly by using Chl_T . The ratio of Chl_a/TP averaged 0.15, and Chl_T/TP averaged 0.24 (Table 1).

Zooplankton biomass (ZB) data in a sub-set of the

Kenai lakes (Table 1) ranged from 0.3 to $1467 \mu\text{g}\cdot\text{L}^{-1}$ ($n = 72$). Only five lakes had ZB values $>400 \mu\text{g}\cdot\text{L}^{-1}$ and the median value was $16 \mu\text{g}\cdot\text{L}^{-1}$. There was no difference between ZB measurements in seepage ($n = 37$) and drainage lakes ($n = 35$). Empirical equations, based on Chl_a and TP, predict ZB would range between 15 and $500 \mu\text{g}\cdot\text{L}^{-1}$ in most Kenai lakes (Hanson and Peters 1984, Pace 1984, Shortreed and Stockner 1986), however, nearly half the lakes in our data set had ZB below the predicted minimum. Among Kenai lakes ZB_{\log} was not significantly correlated with any of the trophic state metrics (TP_{\log} , TN_{\log} or $\text{Chl}_{a,\log}$).

For these Kenai lakes, ZB_{\log} entered as significant variable, with a negative coefficient, in the regression of $\text{Chl}_{T,\log}$ on TP_{\log} ($R^2 = 0.55$ with ZB and 0.52 without, $n = 68$). Large *Daphnia* (>1 mm) which are known to reduce Chl yields (Mazumder 1994) were present in 10% of these lakes but collections from 45% of the lakes contained no *Daphnia*.

Matanuska-Susitna Valley Lakes

Overall the Mat-Su lakes (Table 2) were similar to those sampled on the Kenai Peninsula – most were stained (>10 Pt units), with approximately neutral pH (only 3 lakes had values <6) and low turbidity (only 1 lake had >3 NTU). Salinity ($6\text{--}282 \mu\text{S}$), alkalinity ($20\text{--}2700 \mu\text{eq}\cdot\text{L}^{-1}$), and the divalent cations ($15\text{--}1846 \mu\text{eq}\cdot\text{L}^{-1}$ Ca and $17\text{--}1745 \mu\text{eq}\cdot\text{L}^{-1}$ Mg), varied over a broad range (Table 2). The Alaskan lake study of Gregory-Eaves et al. (2000) included four drainage lakes in the Mat-Su Valley that ranged in conductivity from 15 to $100 \mu\text{S}$ with cations dominated by Ca (61–77%) and anions

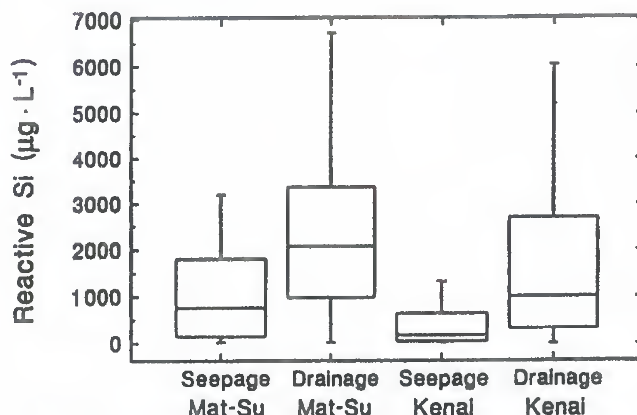


Figure 3.—Box plots of reactive silica ($\mu\text{g}\cdot\text{L}^{-1}$) in seepage and drainage lakes in Mat-Su and on the Kenai Peninsula. In the box plot the horizontal line represents the median, the box represents the interquartile range, and the solid lines represent a distance 1.5 times the interquartile range.

dominated by inorganic carbon (85-96%). Among the Mat-Su lakes we sampled, alkalinity, conductivity and Ca were strongly intercorrelated (log transformed, $r \geq 0.91$, $n=107$) and all three measures of salinity were correlated with Si (log transformed, $r \geq 0.65$, $n=107$). Mg was less strongly correlated with conductivity and alkalinity (log transformed, $r \geq 0.65$, $n=107$) than Ca.

As was found on the Kenai Peninsula, seepage lakes ($n=39$), relative to drainage lakes ($n=69$) in the Mat-Su Valley (Table 2), had significantly lower pH (median 7.1 vs. 7.5, respectively), conductivity (median 41 vs. 61 μS), alkalinity (median 18 vs. 29 $\mu\text{eq} \cdot \text{L}^{-1}$), Ca (median 235 vs. 454 $\mu\text{eq} \cdot \text{L}^{-1}$), Mg (median 82 vs. 189 $\mu\text{eq} \cdot \text{L}^{-1}$), and Si (median 788 vs. 2082 $\mu\text{eq} \cdot \text{L}^{-1}$). The lake types did not differ in surface area (median 13 vs. 21 ha), elevation (median 63 vs. 72 m) color (median 12 vs. 17 Pt units) or turbidity (~ 1 NTU in each). The ratio of Ca:conductivity differed between seepage and drainage lakes (median 6.2 vs. 6.9) but ratios of Ca:Mg and alkalinity:conductivity were not different between these lake types. Overall, these analyses suggest seepage lakes in the Mat-Su Valley are more dilute with lower pH and Si than drainage lakes, but that color and ion composition did not appreciably differ between the two types.

The curvilinear relation between pH and alkalinity found in Kenai lakes also applied among Mat-Su lakes (Fig. 2). Values of pH were strongly correlated with log transformed measurements of alkalinity ($r = 0.94$, $n = 107$), conductivity ($r = 0.88$, $n = 108$) and Ca ($r = 0.90$, $n = 108$), but not with TN or TP.

Seepage lakes in the Mat-Su Valley (Table 2) did not differ from drainage lakes in TP but had somewhat greater TN levels (median 322 vs. 268 $\mu\text{g} \cdot \text{L}^{-1}$) and, therefore, marginally lower TN:TP ratios (median 23 vs. 26). Values of Chla did not differ between the two lake types but seepage lakes had lower ratios of Chla/TP than drainage lakes (median 0.1 vs. 0.13).

Among all Mat-Su lakes, TN and TP were correlated (log transformed, $r = 0.63$, $n = 104$). Mat-Su lakes were primarily limited by P (Smith 1982), only two lakes had TN:TP ratios < 10 , and in $\sim 20\%$ of the lakes this ratio was $> 10 < 20$. Among seepage lakes, TN_{\log} was correlated with conductivity and alkalinity (log transformed, $r = 0.39$, $n = 36$), but TP was not. Among drainage lakes, neither nutrient was significantly correlated with measures of salinity. Using Nürnberg's (1996) trophic state criteria most Mat-Su lakes were oligotrophic ($\sim 80\% < 10 \mu\text{g} \cdot \text{L}^{-1}$ TP and $\sim 70\% < 350 \mu\text{g} \cdot \text{L}^{-1}$ TN) and with the exception of one large TN value (2772 $\mu\text{g} \cdot \text{L}^{-1}$) the rest were mesotrophic. Using Chla, all but one lake was oligotrophic and based on Chl_T $\sim 8\%$ were mesotrophic. Log transformed values of Chla were correlated with both TP_{\log} and TN_{\log} ($r = 0.53$ and 0.33 ,

respectively, $n = 100$), and correlations improved somewhat using Chl_T . The ratio of Chla/TP averaged 0.125 across all lakes, and based on Chl_T it averaged 0.22 (Table 2).

Zooplankton biomass (ZB) data in a sub-set of the Mat-Su lakes (Table 2) ranged from 0.2 to 252 $\mu\text{g} \cdot \text{L}^{-1}$, with an outlier of 1084 $\mu\text{g} \cdot \text{L}^{-1}$ ($n = 57$) and a median of 19 $\mu\text{g} \cdot \text{L}^{-1}$. ZB did not differ between seepage ($n = 26$) and drainage ($n = 31$) lakes (Table 2). Empirical equations using TP and/or Chla predict that ZB would range between ~ 15 and 280 $\mu\text{g} \cdot \text{L}^{-1}$ (Hanson and Peters 1984, Pace 1984, Shortreed and Stockner 1986). As with lakes in the Kenai Peninsula, nearly one-half of the Mat-Su lakes had ZB values below this minimum. ZB_{\log} was not correlated with TP_{\log} or TN_{\log} but was negatively correlated with Chla_{\log} ($r = -0.35$). Based on this comparison, ZB was low in most Mat-Su lakes and there was no cross-system positive response of ZB to trophic state metrics.

Within this sub-set, ZB_{\log} entered as significant variable with a negative coefficient in the regression of Chl_{\log} on TP_{\log} ($R^2 = 0.56$ with ZB and 0.48 without, $n = 53$). Some 28% of the lakes had large *Daphnia* (> 1 mm) which are known to reduce Chl yields (Mazumder 1994) and 25% of the lakes had no *Daphnia*.

Regional Comparison of Seepage and Drainage Lakes

Seepage lakes on the Kenai Peninsula, relative to those in Mat-Su, had significantly lower color (median 9.5 vs. 12 Pt units), pH (median 6.7 vs. 7.1), alkalinity (median 120 vs. 360 $\mu\text{eq} \cdot \text{L}^{-1}$), Ca (median 130 vs. 235 $\mu\text{eq} \cdot \text{L}^{-1}$), Si (median 169 vs. 788 $\mu\text{eq} \cdot \text{L}^{-1}$), but more Fe (median 68.5 vs. 42 $\mu\text{g} \cdot \text{L}^{-1}$) and a greater yield of Chl per unit TP (median 0.15 vs. 0.1). Whereas comparisons between drainage lakes showed that Kenai lakes had significantly lower alkalinity (median 420 vs. 580 $\mu\text{eq} \cdot \text{L}^{-1}$), Ca (median 329 vs. 454 $\mu\text{eq} \cdot \text{L}^{-1}$), and Si (median 1022 vs. 2082 $\mu\text{g} \cdot \text{L}^{-1}$) but were marginally more fertile as measured by TP (median 9 vs. 7 $\mu\text{g} \cdot \text{L}^{-1}$), TN (median 310 vs. 268 $\mu\text{g} \cdot \text{L}^{-1}$), and Chla (median 1.2 vs. 0.9 $\mu\text{g} \cdot \text{L}^{-1}$) than drainage lakes sampled in Mat-Su. Zooplankton biomass did not differ between seepage lakes or drainage lakes in the two study regions.

Differences in Si among the Cook Inlet lakes (Fig. 3) explained $> 98\%$ of among lake variance in the first axis of a Principal Components Analysis. Differences in TN among lakes loaded as the variable in the second axis, and explained an additional 1.5% of the variance.

Discussion

Lakes on the Kenai Peninsula and Mat-Su Valley, near Cook Inlet, Alaska (Tables 1 and 2) were moderately stained, with low turbidity and fertility such that ~70% were oligotrophic (as ranked by nutrients). With the exception of a small number of eutrophic Kenai lakes (~3%), the remaining lakes were mesotrophic. Ratios of TN:TP were >20 in ~80% of study suite, suggesting potential phosphorus limitation (Smith 1982) which is considered characteristic of many Alaskan lakes (Gregory-Eaves et al. 2000).

As found in other unproductive Alaskan lakes (Edmundson and Carlson 1998, LaPerriere and Jones 2002) the Chl_a/TP ratio in the Cook Inlet lakes averaged ≤0.15 (Tables 1 and 2) whereas in several global data sets this ratio in oligotrophic lakes is much larger (LaPerriere and Jones 2002). Low yields of Chl per unit of plant nutrients have been observed in lakes with aquatic vegetation (Scheffer 1998) and this may be a factor in some study lakes. Invertebrate grazers reduce algal biomass (Pace 1984, Hansson 1992, Mazumder 1994) and the negative coefficient and modest, but significant, improvement in the Chl_T-TP models afforded by zooplankton biomass suggests grazing modestly reduced Chl_T yields in both Kenai and Mat-Su lakes. Available data indicate phaeophytin was an important component of the planktonic pigment content of Cook Inlet lakes during summer, although delays in sample processing and analysis may have contributed to this finding. Phaeophytin averaged 77% of the Chl_a concentration in our lake samples and Gregory-Eaves et al. (2000) found similar levels in several regional lakes. The ratio of Chl_T/TP averaged 0.23 (Tables 1 and 2) and this value closely matches ratios for uncorrected Chl/TP in Interior Alaskan lakes (LaPerriere et al. 2003). The Chl-TP model of Jones and Bachmann (1976) limited to the range of TP values in Cook Inlet lakes, provided reasonable estimates of Chl_T (mean and median of observed/predicted = ~1). The inference is that the relation between planktonic Chl and the limiting nutrient in Cook Inlet lakes fits the general pattern found in temperate lakes.

Most zooplankton biomass values in the Cook Inlet lakes were < 100 μg · L⁻¹ and over one-third were < 10 μg · L⁻¹ (Tables 1 and 2). These values are low relative to published studies. Empirical models, based on lake trophic state characteristics (Hanson and Peters 1984, Pace 1984, Shortreed and Stockner 1986) over-predicted observed values in most study lakes. Each of these lakes supports a fish community (Bell et al. 1993) and the well-known effects of food web structure via grazing by planktivorous fish likely account for the observed ZB values (Northcote 1988).

Chemical differences (Table 1) between seepage and drainage lakes dominate our analysis, and confirm the earlier findings of Eilers et al. (1993) in the Kenai lakes. On the whole, seepage lakes had lower pH, color, and ion content, including Si (Fig. 3), than drainage lakes. There was a lower proportion of Ca and alkalinity among the total ion content of seepage lakes as compared to drainage lakes in both data sets. Chemical differences between seepage and drainage lakes have long been recognized and characterized in various lake regions (Birge and Juday 1934, Gorham et al. 1983, Saunders et al. 2000). Eilers et al. (1993) suggested that seepage lakes on the Kenai Peninsula do not receive substantial groundwater or surface water input, as indicted particularly by low Si levels in seepage lakes relative to the content found in local groundwater and rivers. Our data support this pattern, but do not provide additional hydrologic evidence for the causal mechanism. Eilers et al. (1993) proposed that hydrologic flowpaths differed between high- and low-alkalinity lakes because of slight differences in lake elevation, but our data did not show similar differences, and did not lend support to this explanation (Table 1). Lakes on the Kenai Peninsula (n = 107) showed a similar range in pH and salinity measurements as were reported by Eilers et al. (1993, n = 59). Their randomized survey design did not detect any lakes in the 300-700 μeq · L⁻¹ alkalinity range, whereas our sampling showed ~20% of our suite had values between 300-600 μeq · L⁻¹, and none in the 600-800 μeq · L⁻¹ range. Collectively, these two studies suggest there are a reduced number of lakes within this general alkalinity range and that some threshold of abundance may be tied to lake types and regional hydrologic patterns.

Among lakes in the Mat-Su Valley, seepage lakes were more dilute with lower pH and Si than drainage lakes, but color and major ion composition did not appreciably differ between them. These differences, particularly differences in Si (Fig. 3), point towards hydrologic differences in the inflow to these two lake types in Mat-Su, as suggested by Eilers et al. (1993) for the Kenai. Overall, lakes on the Kenai Peninsula have lower Ca, alkalinity and Si than lakes in Mat-Su, when comparing seepage and drainage lakes in both regions. This difference likely reflects greater bicarbonate materials in the parent materials of the Mat-Su Valley.

A conceptual framework in limnology holds that within specific lake districts weathering of regional geologic materials largely determines ion chemistry which, in turn, is closely tied to the levels of plant nutrients and overall lake fertility. Simply put, measures of salinity, such as conductivity or alkalinity, are typically good surrogates for TP and TN in lakes within a given region. Lake morphometry also has a role as a surrogate for hydrological characteristics. These concepts have

been reviewed by Duarte and Kalff (1989) and Chow-Fraser (1991). In Alaska correlations between conductivity and plant nutrients, TN and TP, have been found among lakes on the Yukon Flats (Heglund and Jones 2003), and among lakes within the Interior (LaPerriere et al. 2003) but not across lakes along a statewide north-south transect (Gregory-Eaves et al. 2000). Nor was the signal strong in the Cook Inlet lakes; in the Kenai lakes TP showed a weak correlation with measures of salinity, and in Mat-Su seepage lakes only TN was correlated with salinity. The lack of correlation for Cook Inlet lakes may be related to complex surface and groundwater hydrologic flowpaths that result in highly variable salinity and nutrient concentrations. Spatial heterogeneity could mask or attenuate the linkage between salinity and nutrients. Biotic processes associated with the extensive wetlands and muskeg vegetation in the study area may also contribute to the observed pattern. Certainly, denitrification in wetlands (Vymazal 1995) would be a factor reducing catchment-derived TN inputs. Uptake of plant nutrients by macrophytes and associated periphyton (Scheffer 1998) could also contribute to blunting a potential correspondence between salinity and nutrients in pelagic lake samples.

Our pH and alkalinity data from both regions near Cook Inlet (Fig. 2) follow the general pattern expected based on inorganic carbon equilibria, as did data from Eilers et al. (1993). In Alaskan lakes catchment-derived inputs and within-lake alkalinity generation largely determine surface water pH (Gregory-Eaves et al. 2000). Colored bog waters, enriched with DOC (dissolved organic carbon), have relatively high pH measurements relative to lakes located elsewhere (Satoh et al. 1992). Eilers et al. (1993) found DOC values between 2-17 mg · L⁻¹ in the Kenai lakes and Gregory-Eaves et al. (2000) found DOC values between 6-168 mg · L⁻¹ in their suite of lakes in the Southern Boreal Forest. In neither of these previous studies was the cross-system correlation between pH and DOC significant. Nevertheless, variation in the pH-alkalinity relationship among Cook Inlet lakes could be locally influenced by dissolved organic carbon (DOC) and by organic inputs from spodic soils and bog vegetation (Eilers et al. 1993). Productivity-mediated increases in pH (Stumm and Morgan 1996) may also contribute to variation in the pH-alkalinity relationship (Fig. 2) and would include the influence of macrophytes and associated periphyton not directly measured in our pelagic samples.

Like other large-scale lake studies conducted recently in the Cook Inlet area (Satoh et al. 1992, Eilers et al. 1993, Gregory-Eaves et al. 2000) our survey was based on a single sample event during summer. Several lakes were common to at least two of these sampling efforts and the outcomes showed general agreement

in lake water chemistry. The overall range of pH and parameters representing salinity in our study suite (Table 1) were virtually identical to that found by Eilers et al. (1993). Our data set extends the limnological characterization of the Kenai Peninsula to include lake trophic state. The limited sampling by Satoh et al. (1992) and Gregory-Eaves et al. (2000) also fit within our distribution of salinity and trophic state characteristics. Collectively these data provide a satisfactory estimate of extant lake conditions in these regions of Southern Boreal Forest of southcentral Alaska and are an overall contribution to regional and high latitude limnology.

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