

**Growth Patterns of Juvenile Sockeye Salmon
in Different Thermal Environments
of Alaskan Lakes**

A Thesis
for the Degree of
Master of Science

by
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University of Alaska Fairbanks
Fairbanks, Alaska

December 1997

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Presented to the Faculty

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in Partial Fulfillment of the Requirements

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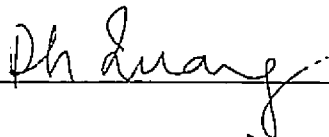
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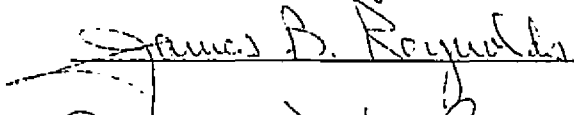
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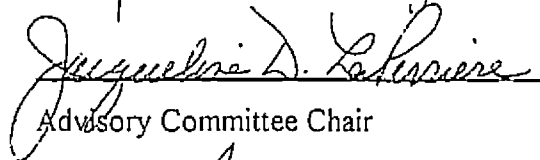
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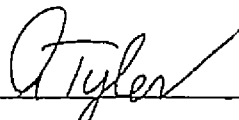


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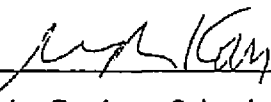


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ABSTRACT

Rearing conditions imposed on juvenile salmonids in lakes are important determinants of freshwater growth patterns. In Alaska, sockeye salmon (*Oncorhynchus nerka*) nursery lakes exhibit a wide range in thermal characteristics. Compared to clear lakes, stained lakes are warmer and have longer growing seasons, whereas glacial lakes are colder and have shorter growing seasons. In stained lakes, a shallow thermocline restricts most of the heat to the surface layers. Deep mixing in glacial lakes, concomitant with meltwater intrusion, keeps much of the water column near 4 °C. Mean depth accounts for 77% of the among-lake variation in the seasonal average water temperature (*TS*). Length of growing season is dependent on latitude and altitude; however, water temperature is not. Taken together, the factors *TS*, zooplankton biomass, and sockeye fry density accounted for 70% of the variation in age-1 sockeye smolt size. This limnological information can be included in stock-recruit models of sockeye salmon to improve assessments for management.

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INTRODUCTION

Temperature is one of the most important physical factors affecting overall lake metabolism. Temperature is the primary density-determining factor of the water column and it exerts a fundamental influence on water movement and stratification (Hutchinson 1957). Thermal stratification and shallow depth of mixing reduce heat transport from the surface layers to the hypolimnion (Michalski and Lemmin 1995), regulate nutrient cycling (Fee 1979; Osgood 1988; Fee et al. 1994; Guy et al. 1994), limit the vertical distribution of dissolved oxygen (Schindler 1971), control phytoplankton production (Nalewajko and Voltolina 1986; Stauffer and Lee 1987; Brooks 1994), and define the habitat for many aquatic organisms (Talling 1971; Webster and Hutchinson 1994).

Relationships between lake thermal environment and freshwater production have been viewed in the context of changing meteorological conditions and broad latitudinal (temperature) gradients. For instance, Scavia et al. (1986) associated lower phytoplankton densities (chlorophyll *a* concentration) in Lake Michigan to a protracted winter and subsequent delay in vernal heating of the water column. Species composition, size distribution, and biomass of pelagic zooplankton in Lake Windermere were also strongly influenced by climatic changes (George and Harris 1985). In particular, spring epilimnetic temperatures, not grazing by planktivorous fish, determined zooplankton abundance. On a global scale, primary production (Brylinski and Mann 1973; France 1992) and fish yield (Schlesinger and Regier 1982) have been correlated with mean annual air temperature. Although there is a close correlation between mean air and lake surface temperatures, the particular relevance of atmospheric temperature to biological standing stock is obscure (Hartman 1995). Moreover, correlations between climate and fish (e.g., year class strength) may be unpredictable because of density-dependent factors such as predation and competition (Lehtonen and Lappalainen 1995). Thus, lake-heat budgets may represent a more comprehensive and perhaps integrative view of thermal response to

penetrating solar radiation, morphometry, and climatic forces, thereby providing a more fundamental link to changes in freshwater production.

Heat budgets refer to the difference in heat content over a specified time interval (Ragotzkie 1978). For any given lake, the magnitude of the annual heat budget is related to depth and volume (Birge 1915; Gorham 1964; Timms 1975; Patalas 1984; Hanna 1990), as well as to geographic location (Arai 1981), climate changes (Owens and Effler 1989), and elevation (Larson et al. 1994). Since much of the absorbed solar radiation becomes heat, water clarity is another important factor affecting heat uptake and thermal structure (Koenings et al. 1986; Bowling and Salonen 1990; Mazumder 1994).

Specifically, humic (organic) stained lakes tend to absorb a greater proportion of the incident light, whereas glacially (inorganic) turbid lakes reflect a greater proportion (Koenings and Edmundson 1991; Kirk 1994). Thus, heat budgets vary tremendously as evidenced by the comparison of about 100 worldwide lakes presented in Hutchinson's (1957) limnological treatise. Because temperature and stratification govern virtually all physical, chemical and biological processes in lakes, my idea that variation in water temperature, heat content, and thermal structure across morphologically different lakes may account for differences in productivity and growth of juvenile sockeye (*Oncorhynchus nerka*) seems well founded.

Distribution and age at maturity of sockeye salmon are inversely related to sea surface temperatures of the North Pacific (Welch et al. 1995). These studies suggested that warmer temperatures at sea increased metabolic demand or altered food resource availability, thereby leading to slower growth rates. Plante and Downing (1993) derived an inverse relationship between mean annual air temperature and adult sockeye salmon production (biomass) for a number of Pacific northwest and British Columbia lakes. That oceanic temperatures strongly influence the physiology and ecology of adult sockeye salmon is not in question. The upper oceanic thermal limit to sockeye salmon abundance

and distribution is being defined. Compared to northern Pacific Ocean waters, however, temperate and sub-arctic lakes have much more extreme temperatures; i.e., temperatures in lakes are warmer in the summer and colder in the winter than in the ocean. Lakes also experience larger seasonal temperature fluctuations compared to the ocean. In addition, coastal lakes, strongly influenced by oceanic winds, can exhibit different mixing patterns and stratification compared to interior lakes. For example, coastal lakes influenced by the Pacific Ocean tended to be monomictic (stratified in summer), whereas interior lakes were generally dimictic (stratified in summer and winter) among sockeye lakes of British Columbia (Stockner 1987). Yet, despite the significance of temperature and heat as physical factors in lakes, use of temperature/stratification and heat budget variables to characterize juvenile sockeye growth patterns has not been fully explored, probably because the interrelations between temperature, plankton, and fish growth are largely indirect or viewed as unimportant.

Considering juvenile sockeye salmon, most temperature related work to date has focused on metabolic efficiency, feeding, and reproduction. Brett (1971) found that growth rates of underyearling sockeye were directly proportional to temperature when food was unlimited; however, as food resources became limited, optimal growth rates shifted to lower temperatures. In addition, diel vertical migration patterns exhibited by juvenile sockeye have been related to growth rates and bioenergetic efficiency through temperature selection (Levy 1990; Bevelhimer and Adams 1993). Therefore, the interaction(s) between food and temperature may underlie the variation observed in juvenile sockeye salmon population characteristics and growth patterns. Indeed, Stockner (1987) speculated that differences in epilimnetic temperatures, heat content, and plankton abundance between coastal and interior lakes of British Columbia accounted for some of the variation in age-1 sockeye salmon smolt size; however, this variation was not quantified.

Specific to Alaska sockeye nursery lakes, the emphasis on factors limiting freshwater production has focused on lake fertility (nutrients) and available forage (zooplankton) (Koenings et al. 1986; Koenings and Burkett 1987; Kyle 1994; Kyle et al. 1997). This in turn led to the development of various lake-carrying capacity models for sockeye salmon (Koenings and Burkett 1987; Kyle et al. 1997). However, considerable inter-annual and inter-lake variation exists in juvenile sockeye abundance, size, and age composition that cannot be explained by recruitment (escapement or stocking) or lake fertility (Schmidt et al. 1997). Alaska sockeye salmon producing lakes span a broad geographic range, extending from the southeast panhandle westward to the Alaska Peninsula and Bristol Bay, and they exhibit a variety of limnological characteristics (Koenings et al. 1986; Koenings et al. 1990; Koenings and Edmundson 1991; Kyle 1994).

Objective

Given the wide diversity of lakes, and obvious differences in regional climatic conditions (Milner et al. 1997), I expect that there is substantial variation in mean water temperatures, stratification, length of the growing season, and heat content. Thus, I hypothesize that the in-lake thermal environment is a strong determinant of juvenile sockeye salmon growth patterns. Specifically, my objective in this paper is to determine (quantify) the relative influence of temperature, as a density-independent factor, in conjunction with food resource availability, and density-dependent growth factors on size of age-1 sockeye salmon smolt by evaluating temperature regimes across a variety of sockeye nursery lakes.

Description of Study Areas

The 60 Alaskan lakes in my study encompass a broad geographic gradient extending from about 55° to 65° N latitude and from 130° to 145° W longitude. Most of the study lakes within southeast and southcentral Alaska, and the Kodiak Archipelago lie within the maritime zone (Milner et al. 1997). In the southeast panhandle area, several southeast lakes receive up to 500 cm precipitation per year, whereas lakes influenced by the coastal mountains surrounding Prince William Sound receive a mean annual precipitation of around 400 cm (Anonymous 1979). Average air temperatures in this zone range from 13° C in July to -3° C in January (Milner et al. 1997). On the Kenai Peninsula, lakes have a more transitional type of climate with an annual rainfall ranging from 20 to 60 cm (Anonymous 1979). Average temperatures on the Kenai Peninsula range from 12°C in July to -11° C in January (Milner et al. 1997). A few lakes included in my study are part of the Copper River drainage. This area is in the continental zone (Milner et al. 1997) where the average annual rainfall is about 30 cm (Anonymous 1979) and average air temperatures range from -23° C in January to 17° C in July (Milner et al. 1997). The two northernmost lakes included in the study are located on the Seward Peninsula, near the village of Nome and fall within the transitional/continental zone (Milner et al. 1997). This area receives an average yearly rainfall estimated at 60 cm and average temperatures range from -20° C in January to 11° C in July (Milner et al. 1997).

The study lakes also exhibit a wide range in morphometric characteristics. There are deep, fjordlike lakes, some with glacially scoured U-shaped basins, and there are a few shallow lakes that have a more extensive littoral zone. Tustumena Lake is the largest of the study lakes with a surface area of 294.5 km²; Cunningham Lake has the smallest area, only 0.2 km². Tustumena Lake is also the deepest with a mean depth of 124 m; however, Deer Lake has the greatest maximum depth at 304 m. Tustumena Lake with its large surface area and great depth is the most voluminous (36,600 x 10⁶ m³). Speel Lake is the

shallowest of the study lakes with an average depth of only 3.0 m and a total volume of $4.4 \times 10^6 \text{ m}^3$. Geographic location and lake morphometrics for the 60 study lakes are summarized in Table 1.

Salient water chemistry and plankton characteristics of the 60 lakes are summarized in Table 2. A very distinguishing feature among many of these lakes is the presence of color or turbidity caused by different water sources. That is, stained lakes are brownish or yellowish from the presence of high concentrations of dissolved organic material. In contrast, glacial lakes are heavily turbid from large inputs of silty meltwater. Clear lakes lack appreciable amounts of color and turbidity. Across 60 lakes, seasonal mean water color ranged from 2 to 55 platinum-cobalt (Pt) units and turbidity from 0.2 to 49 nephelometric turbidity units (NTU). According to trophic classifications, most of the study lakes are considered oligotrophic (nutrient poor) or mesotrophic (moderate nutrients) (Koenings and Edmundson 1991). That is, seasonal mean total phosphorus concentration averaged $9.2 \mu\text{g L}^{-1}$ and nitrogen concentration $195 \mu\text{g L}^{-1}$. Chlorophyll *a* levels are quite low with an overall mean value of about $1.0 \mu\text{g L}^{-1}$. Seasonal mean macrozooplankton biomass levels ranged from 11 to 3,878 mg m^{-2} and averaged 602 mg m^{-2} .

Table 1. Location and morphometric parameters of the 60 Alaskan study lakes.

Lake	Latitude (°N)	Longitude (°W)	Altitude (m, a.s.l)	Area (km ²)	Mean depth (m)	Maximum depth (m)	Volume (×10 ⁶ m ³)
Afognak	58.07	152.55	21	5.5	8	23	43
Akaŕura	57.08	154.15	30	6.7	10	22	67
Auke	58.22	134.38	3	0.9	19	34	17
Badger	55.12	130.45	103	2.0	69	146	139
Bakewell	55.17	130.38	51	2.9	24	59	69
Banner	56.34	134.41	58	0.7	51	119	34
Bear	60.14	149.20	10	1.8	10	17	18
Chelatna	62.29	151.27	422	11.1	60	122	661
Chenik	59.10	154.10	46	1.2	29	57	33
Chilkat	59.19	135.53	53	9.8	33	57	319
Chilkoot	59.21	135.35	9	7.0	55	89	382
Coghill	61.04	147.29	18	11.9	47	78	563
Crescent	58.12	133.20	53	3.2	29	67	95
Crescent	60.22	152.56	183	13.6	23	32	313
Crosswind	62.20	146.00	644	38.2	16	39	626
Cunningham	57.49	136.17	290	0.2	26	74	5
Deer	56.31	134.43	114	4.0	110	304	455
Delight	59.34	150.15	15	2.8	22	40	60
Desire	59.35	150.15	15	1.8	14	27	25
Elfendahl	57.50	136.20	87	3.2	63	136	214
Esther Pass	60.52	148.12	70	0.8	13	27	11
Falls	56.49	134.42	6	1.0	32	75	33
Farragut	57.15	132.58	135	4.8	67	108	321
Frazer	57.15	154.10	108	16.6	33	59	554
Glacial	64.52	165.42	393	4.0	6	22	23
Hetta	55.10	132.33	9	2.6	48	92	124
Hidden	58.23	152.42	68	1.9	11	49	21
Hidden	60.29	150.15	86	10.9	18	45	193
Hugh Smith	55.06	130.42	15	3.0	71	121	215
Jennifer	58.11	152.18	33	0.4	11	23	4
Karluk	57.24	154.05	106	39.4	49	126	1,920
Kenai	60.25	149.35	133	55.9	91	165	5,087
Kirschner	59.22	154.00	20	1.3	17	37	22
Klutina	61.44	145.43	524	67.1	45	90	3,019

Table 1. -continued.

Lake	Latitude (°N)	Longitude (°W)	Altitude (m, a.s.l)	Area (km ²)	Mean depth (m)	Maximum depth (m)	Volume (×10 ⁶ m ³)
Kook	57.40	135.00	14	2.4	30	44	72
McDonald	55.55	131.47	15	3.5	45	112	158
Osprey	56.23	134.39	58	1.0	60	118	57
Port Dick	59.15	151.15	144	1.0	21	45	20
Packers	60.28	151.55	15	2.0	12	32	25
Paxson	62.55	145.30	778	15.7	11	27	172
Portage	58.16	151.37	17	1.6	9	23	15
Ptarmigan	60.25	149.15	230	3.0	36	75	107
Red	57.15	154.20	62	8.4	25	48	208
Redoubt	56.53	135.15	4	11.2	73	90	819
Salmon	64.54	165.00	135	7.5	13	40	95
Salmon	55.34	132.38	36	5.0	28	63	141
Skilak	60.24	150.15	63	99.0	73	160	7,213
Speel	58.12	133.34	30	1.7	3	9	4
Spiridon	57.45	153.35	136	9.2	35	80	318
Summit	63.06	145.29	914	10.1	13	52	135
Sweetheart	57.58	133.35	166	4.9	74	155	364
Tazlina	62.00	148.13	544	155.9	68	110	10,584
Tokun	60.24	144.17	54	1.8	21	32	38
Tonsina	61.31	145.29	575	13.7	53	90	726
Tumakof	56.21	134.51	9	1.0	50	99	48
Tustumena	60.10	150.55	33	294.5	124	290	36,600
Upper Russian	60.20	149.50	210	4.7	27	81	127
Upper Trail	60.32	149.20	144	7.1	16	45	142
Upper Station	57.05	154.20	33	7.9	26	80	208
Virginia	56.20	132.10	32	2.6	29	54	76

Table 2. Means, ranges, and standard deviations for selected water chemistry characteristics and zooplankton biomass for the 60 study lakes. Summary statistics are based on the number of lake years (N).

Parameter	N	Minimum	Mean	Maximum	Standard deviation
Conductivity ($\mu\text{mohs cm}^{-1}$)	240	7	60	169	38
Turbidity (NTU)	193	0.2	5.5	48.6	11.4
Color (Pt units)	193	2	11	55	9
Total phosphorus ($\mu\text{g L}^{-1}$) ^a	244	1.6	9.2	39.9	7.5
Total nitrogen ($\mu\text{g L}^{-1}$)	243	39	195	664	124
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	245	0.02	1.13	6.35	1.09
Macrozooplankton biomass (mg m^{-2})	233	11	602	3,878	710

^aCorrected for turbidity interference

METHODS

Data Acquisition and Standardization

As with many empirical studies, numerous workers were involved in generating the data for my analysis. However, all field and laboratory methodologies used standardized procedures after Koenings et al. (1987). I compiled my database from lake surveys carried out during the 1980s and 1990s by the statewide limnology program of the Alaska Department of Fish and Game (ADF&G). Surveys of sockeye nursery lakes, as well as some non-anadromous systems that are annually or intermittently stocked with fry, were conducted throughout the state. Data are also included for two lakes located on the Seward Peninsula. For analysis of thermal conditions and heat budgets, I selected lakes which were sampled a minimum of four times per year at approximately one-month intervals through the ice-free season (usually May through October); however, most of the lakes included in my analysis were sampled on 6 or more occasions per ice-free season. Permanent sampling sites were established at each lake in order to characterize the major basins or bays. Included in the study are 18 lakes sampled for a single season, but several were surveyed over a span of years: 28 lakes for 2-5 years, and 14 lakes for more than 5 years. Thus, my temperature database comprises 60 lakes for a total of 248 lake years.

Surface area, mean depth, maximum depth, and volume were taken mostly from an ADF&G compilation of bathymetric maps (Spafard and Edmundson 1997), from the general literature, and from various ADF&G data reports and data archives. General water chemistry and nutrient data were obtained from the ADF&G water chemistry database. These analyses were carried out solely by the ADF&G limnology laboratory, Soldotna, Alaska. All laboratory methodologies are described in detail by Koenings et al. (1987). A HF Scientific, DRT digital turbidimeter was used to measure turbidity. The turbidimeter was routinely checked against EPA approved Formazin reference standards.

True water color was calculated from the spectrophotometric absorption readings on filtered (GFF) samples at 400 nm and converted to equivalent platinum-cobalt (Pt) units using an established linear relationship between absorbance and known Pt units (Koenings et al. (1987). Total phosphorus concentration was determined in duplicate using the molybdenum-blue method after persulfate digestion as described by Eisenreich et al. (1975). Analysis of Kjeldahl nitrogen utilized the acid block digestion and automated phenate methodology as devised by Crowther et al. (1980). Nitrate+nitrite was measured as nitrite after cadmium reduction and diazotization with sulfanilamide (Stainton et al. 1977). I calculated total nitrogen (TN) as the sum of Kjeldahl and nitrate+nitrite nitrogen. Chlorophyll *a* concentration, an index of algal biomass, was determined by direct fluorometric analysis of Strickland and Parsons (1972) using a Turner 111 or 112 fluorometer calibrated with pure chl *a* extract (*Anacyctis nidulans*, Sigma Chemical).

Zooplankton were collected with either a 0.2 or 0.5-m diameter, 153- μm mesh, conical net. The nets were hoisted manually at a constant speed (approximately 0.5 m s^{-1}) from just off the lake bottom or from a maximum depth of 50 m to the surface.

Macrozooplankton were enumerated and measured in triplicate 1-ml sub-samples taken with a Hensen-Stemple pipette and placed in a Sedgwick-Rafter counting chamber.

Species were identified using various taxonomic keys. Lengths of 15 or 30 animals of each species were measured to the nearest 0.01 mm and the mean body length for each taxon was calculated. Length estimates were converted to mass (dry weight) using appropriate species-specific conversion equations derived by Koenings et al. (1987). To calculate species biomass concentration, the mean dry weight is multiplied by the number of zooplankters in the sample divided by the net area (m^2). Summing the biomass of each species yields the total dry weight biomass concentration (mg m^{-2}) of the macrozooplankton. I used seasonal mean total macrozooplankton biomass (*ZB*) estimates as my index of food resource availability for rearing sockeye juveniles (fry). *ZB* estimates are assumed to be on a per-unit-lake area basis (i.e., mg m^{-2}).

I gathered information on age-1 smolt size and abundance from various studies dealing with sockeye adult returns, juvenile stocking, and lake fertilization. Smolt counts or estimates (\pm 95% confidence intervals) were made at smolt fences, fyke nets, and inclined plane traps (Todd 1994) over the entire outmigration. Mark and recapture efficiencies were determined using Bimark Brown stained smolts (Rawson 1984). During the outmigration, smolt were sub-sampled for age, length, and weight. Standard fork length was measured from the tip of snout to the fork of the tail to the nearest 0.1 mm, and mass was measured to the nearest 0.1 g. Sizes were weighted by time period to give mean age-1 smolt length and weight after Rawson (1984). Smolt abundance estimates were standardized to a common spatial unit, (lake surface area, km^{-2}). The total smolt abundance estimate per lake-surface area is defined as the fry density index (*FDX*). Thus, *FDX* represents my density-dependent (predation and competition) factor on juvenile sockeye growth. Age-1 smolt data were lagged by one year to correspond with the limnological data describing the environmental conditions during their year of lake residence.

Juvenile sockeye salmon information, however, was not available for all lake years nor for each lake for which I had limnological (temperature, water chemistry, and plankton) data. For 35 lakes, I compiled age-1 smolt size (length and weight) data (131 lake years) and of these, I acquired total smolt outmigration (abundance) estimates for 21 lakes (89 lake years). The smolt data originated from a variety of published ADF&G regional information and technical data reports, as well as unpublished ADF&G data.

Vertical profiles of temperature were measured *in situ* at 1-m increments from the surface to the bottom of the lake or to a maximum depth (cable length) of 50 m. For most surveys, temperature was measured using a portable YSI model 53 or 57 dissolved oxygen analyzer equipped with a thermistor which provides temperature readout. The model 53 and 57 instruments have a manufacturer's reported sensitivity of ± 0.1 °C. On some

occasions, a Leeds and Northrope temperature/oxygen analyzer or a Hydrolab multi-sensor was employed. The Leeds and Northrope thermistor has a stated sensitivity of ± 0.3 °C, and that of the Hydrolab probe of ± 0.15 °C. Prior to the field season, all thermistors were calibrated against a mercury thermometer immersed in a 0 °C ice/water bath. When necessary, calibrator readings were used as a correction factor. Although temperature data were collected from more than one sampling station in many of the lakes, I used vertical temperature profiles measured over the deepest part of the lake basin to characterize growing season trends, construct lake heat budgets, and to determine mean and maximum water temperature.

Growing Season and Maximum Temperature

I constructed temperature versus time plots to evaluate seasonal lake heating and cooling patterns (Figure 1). For each lake and year (lake year), I plotted temperatures (°C) for selected depths (Y-axis) by Julian day (X-axis). The date when 1-m stratum temperature reached 4 °C in the spring is defined as the initiation of lake heating (*HI*). Thus, *HI* or onset of heating represents spring (4° C) isothermy. The date of maximum heat content (*HM*) is taken as the point of maximum temperature of the 1-m stratum. The date when the temperature of the 1-m stratum cooled to 4 °C in the fall (*HF*) marks the termination of the growing season and represents fall (4 °C) isothermy.

To obtain reasonably unbiased estimates of *HI*, *HM* and *HF*, I fit a low (3 to 5) order polynomial to the measured temperatures for the 1-m stratum. However, when the number of sample dates was small ($n=4$), a 3rd order polynomial has insufficient degrees of freedom to fit the data at every point. For these few cases I fit a quadratic function to the data points. *HI* and *HF* were calculated as the projected value (Julian day) of the respective X-intercepts of the polynomial regression where $f(x) = 4.0$ °C. I obtained *HM*

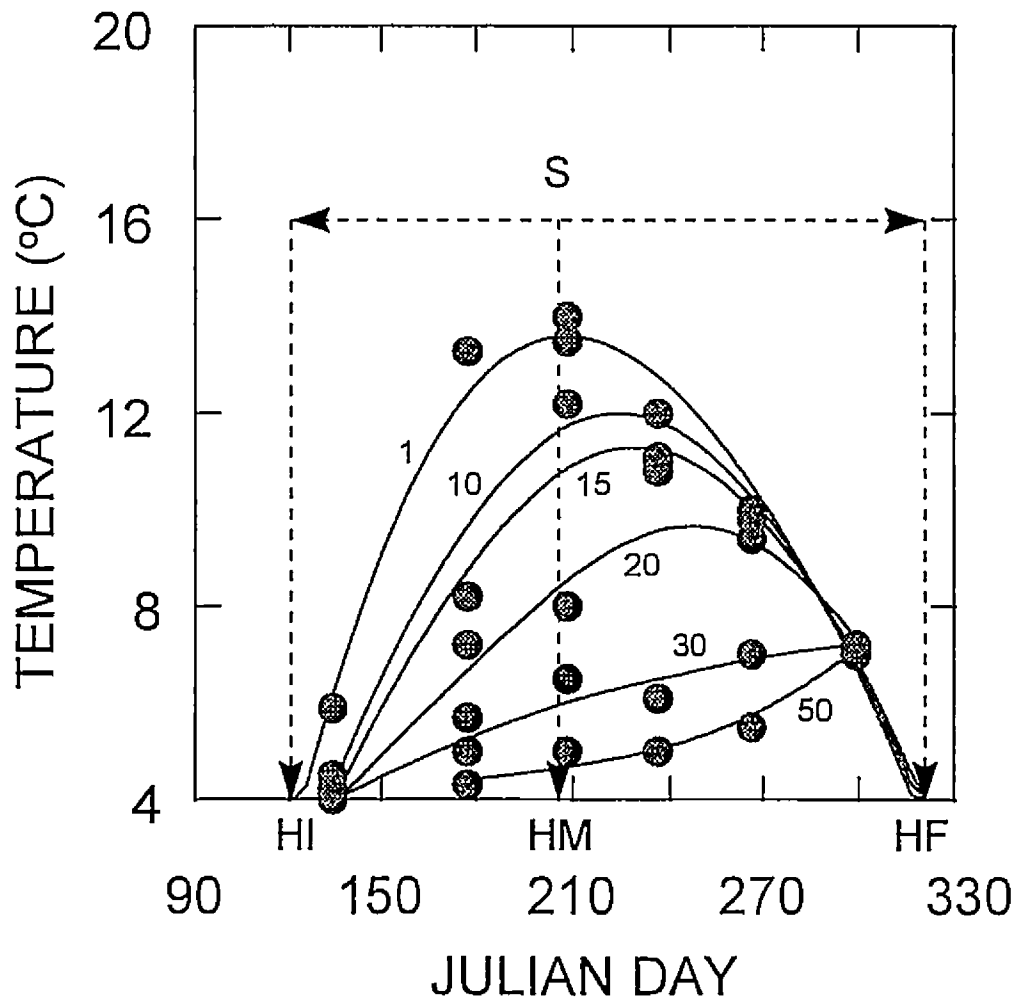


Figure 1. Plot of temperature at selected depths during the ice-free season in hypothetical Jackie Lake, showing the projected date of spring (4°C) isotherm (HI), date of maximum heat content (HM), and date of fall (4°C) isothermy. Also shown is the duration of the growing season (S) defined as the number of days between HI and HF . Individual temperature contours were obtained by fitting a polynomial function. Number adjacent to each contour indicates depth (m).

by taking the first derivative of the function, setting the solution equal to zero (i.e., where $f(x)$ is maximum), and then solving for X . Derivatives were taken using a central difference combined with the Richardson extrapolation technique using CurveExpert (Hyams 1995). Given HM , the corresponding predicted maximum temperature (T_{max}) is easily solved by substitution. The number of days between HI and HM and between HM and HF are referred to as the duration of the heating (HD) and cooling (CD) periods, respectively. The duration of the growing season (S) is simply the number of days between HI and HF .

Summer Lake Heat Budget

The entire heat content of a lake on any occasion is given by the product of temperature and volume (Ragotzkie 1978). Heat content of water is commonly expressed in terms of calories or gram-calories. Since it requires approximately 1 calorie to raise 1 gram of water by 1 °C, the product of volume and temperature (ml x °C) is equivalent to gram-calories (g-cal) or heat (Manahan 1993). For example, 5 ml of water having a temperature of 10 °C has a heat content (volume x temperature) of 50 g-cal. The difference in heat content (storage) over a specified time interval is referred to as a heat budget. Hence, the difference between the minimum and maximum heat content represents a lake's annual heat budget (Hutchinson 1957; Wetzel 1975). However, a lack of winter temperature information precluded me from calculating the annual heat budget. Alternatively, I computed the summer heat budget (θ_s) which is defined as the amount of heat required to raise the lake from spring isothermy at 4 °C to the time of maximum observed heat content (Hutchinson 1957; Wetzel 1975). Since deeper strata contain less volume of water compared to the upper layers, proper calculations of heat budgets require not only measured temperatures, but also water volume distributions (Birge 1915). The Birgean

heat budget incorporates the change in volume with depth (hypsographic data), so it is essentially unbiased by the depth of the lake (Hutchinson 1957).

I obtained hypsographic information from existing bathymetric maps. I plotted the area (m^2) of each depth contour (Y-axis) against the depth (Z , m) of that contour (X-axis) and then fit the data to a 5th order polynomial function as shown for hypothetical Jackie Lake (Figure 2). The lake volume (m^3) is estimated by the total area beneath the curve (Wetzel and Likens 1991). The volume of water contained within any interval (v) was estimated by integrating the function between two specified depths (a , b):

$$v = \int_{z_a}^{z_b} (a + bx + cx^2 + dx^3 \dots fx^5) dx$$

I partitioned the water column into several intervals based on the nature of the vertical temperature profile. I used smaller intervals (e.g., 2 to 5 m) to characterize thermal conditions for that portion of the water column exhibiting a rapid change in temperature with depth ($\geq 1 \text{ }^\circ\text{C m}^{-1}$), i.e. to represent the thermocline, and larger intervals (e.g., 10 to 20 m) for strata that were essentially isothermal. Nonetheless, the particular depths selected were not necessarily the same for all of the lakes. However, I used the same depth intervals for a given lake. Because of the large number of lakes and years sampled, I limited the number of intervals used in the heat budget analysis to about 8 per lake.

To obtain the temperature of a specified volume of water (T_v), I used the mean temperature of the upper and lower bounds for that depth interval. Simply put, a measured temperature of $12 \text{ }^\circ\text{C}$ for the 1-m depth and $9.0 \text{ }^\circ\text{C}$ for the 5-m depth yields an average temperature of $10.5 \text{ }^\circ\text{C}$ for the volume of water contained within the 1 to 5 m interval. For any occasion, totaling the product of temperature ($^\circ\text{C}$) and volume (ml) for each interval (i) through the whole water column gives lake heat content (g-cal). However, for comparative purposes, lake heat budgets are usually expressed on a per-

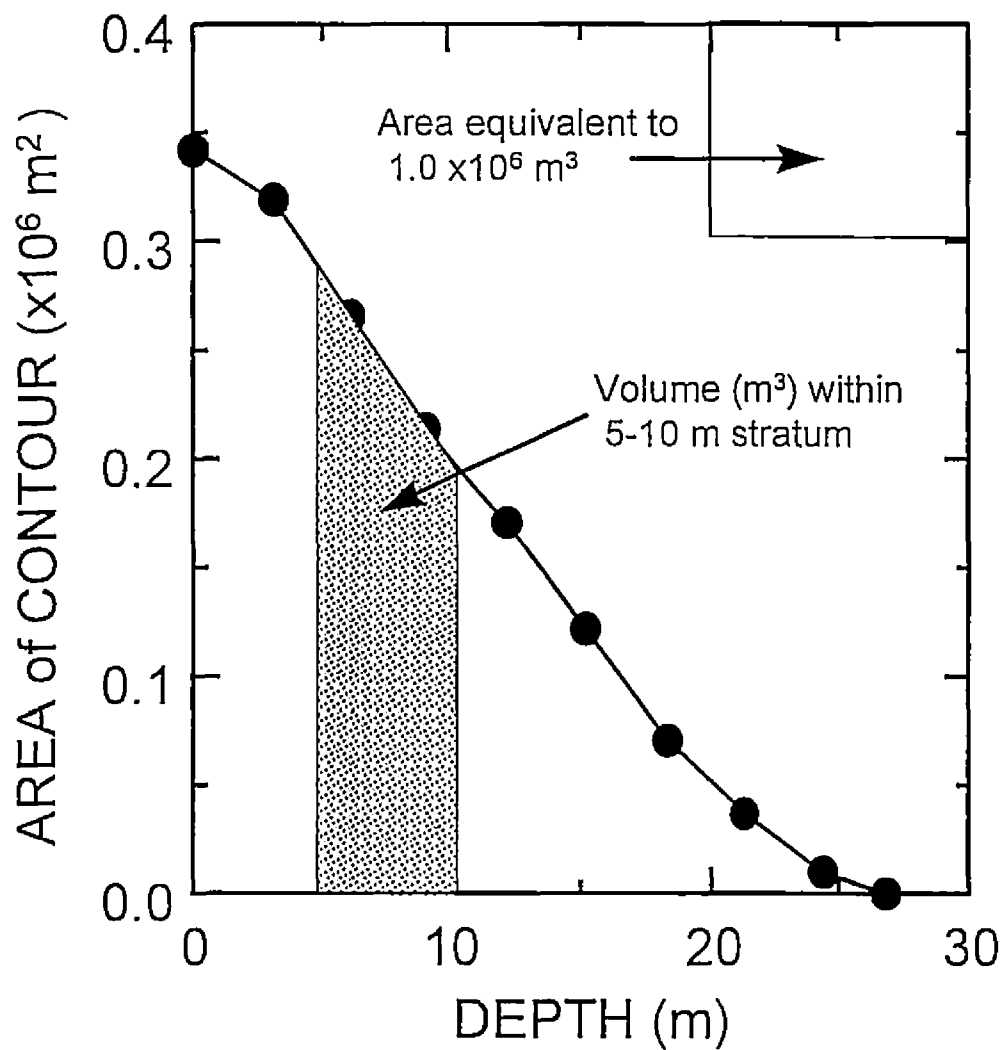


Figure 2. Hypsographic curve for hypothetical Jackie Lake. Area bounded by the curve and the lake surface is equivalent to the total lake volume. Shaded area represents a depth-interval volume (modified from Cole 1979).

unit-area basis (Birge 1915; Hutchinson 1957; Gorham 1964). Thus, heat content (HC) is divided by the lake surface area (SA , cm^2) to give the results in g-cal cm^{-2} :

$$HC = SA^{-1} \sum_{i=1}^{i=n} v_i T_{v_i}$$

The difference in heat content between HI and maximum observed heat content was taken as the estimate of the summer heat budget (θ_s).

Mean Water Temperatures

I also considered the seasonal average water-column temperature (TS) as an alternative means of comparing lake thermal conditions. Since the time interval between sampling surveys for any lake was not always consistent, taking the arithmetic mean of temperature for a specified depth over the course of the season is not appropriate for calculating its seasonal mean temperature. To avoid any temporal bias due to sampling protocol, I calculated the day-weighted average temperature for selected depths. That is, the area beneath the temperature-time plot for a specified depth (Figure 1) is given by $^{\circ}\text{C} \times \text{Julian day}$ (degree-days). Integrating the polynomial function on the interval $[HI, HF]$, the period between spring and fall 4°C isothermy, yields the total number of degree-days over the duration of the growing season (S). Dividing this estimate by S gives the seasonal mean temperature for that depth (\overline{T}_z):

$$\overline{T}_z = S^{-1} \int_{HI}^{HF} (a + bx + cx^2 + dx^3 \dots) dx$$

However, temperatures in a vertical profile must also be properly weighted by volume. I averaged \bar{T}_z of an upper and lower depth increment to determine the average temperature for the specified volume of water (\bar{T}_v). TS was then calculated using interval volumes (v) as the weighting factor:

$$TS = V^{-1} \sum_{i=1}^{i=n} \bar{T}_{v_i} v_i$$

where, V is total lake volume (i.e., $\sum v_i$). Electronic spreadsheets facilitated computations of θ_i and TS as shown for Jackie Lake (Table 3).

Statistical Analysis

For each lake, I summarized water chemistry and zooplankton data as seasonal mean values. Prior to analysis, I screened both limnological and fish data for normality by evaluating boxplots and calculating the g_1 and g_2 statistics to test for symmetry and kurtosis, respectively. In cases of skewness parameters were normalized, prior to statistical analysis, with a base 10 logarithmic (\log_{10}) transformation. The following variables were \log_{10} transformed: elevation, mean depth, surface area, turbidity, color, chlorophyll a, zooplankton biomass, age-1 smolt length and weight, and fry density index.

I initially partitioned the data set ($N=60$ lakes) into 26 clear (turbidity <5 NTU, color <10 Pt units), 20 stained (color ≥ 10 Pt units, turbidity <5 NTU), and 14 glacial lakes (Color <10 Pt units, turbidity ≥ 5 NTU) using the criteria proposed by Koenings and Edmundson (1991). I used one-way analysis of variance (ANOVA) with lake type as a categorical variable followed by Tukey's pairwise comparisons to test for differences in thermal characteristics among lake types. To meet the empirical requirements of residual

Table 3. Sample spreadsheet for the calculation of the summer heat budget and maximum volume-weighted temperature.

Depth (m)	Temperature (°C)	Interval (m)	Interval volume, v_i (ml $\times 10^{12}$)	Average temperature, Tv_i (°C)	Heat content, $v_i \times Tv_i$ (cal $\times 10^{12}$)
0	12.1	0 - 5	71.2	11.9	847
5	11.7	5 - 10	52.4	11.0	574
10	10.2	10 - 15	37.9	9.1	345
15	8.0	15 - 20	26.7	7.1	189
20	6.2	20 - 30	29.7	6.0	176
30	5.7	30 - 40	10.8	5.5	60
40	5.3	40 - 43	6.2	5.3	33
43	5.3				

$$\text{Maximum heat content, } HC_{max} = \left(\sum v_i Tv_i \right) = 2,224 \times 10^{12} \text{ cal}$$

$$\text{Heat content at } 4^\circ\text{C isothermy, } HC_{hi} = \left(\sum v_i, 4 \right) = 940 \times 10^{12} \text{ cal}$$

$$\text{Surface area, } SA = 4.8 \times 10^{10} \text{ cm}^2$$

$$\text{Heat budget, } \theta_s = \left(\frac{HC_{max} - HC_{hi}}{SA} \right) = 26,750 \text{ cal cm}^{-2}$$

$$\text{Maximum volume-weighted temperature, } T_{max} = \left(\frac{\sum v_i Tv_i}{\sum v_i} \right) = 8.3^\circ\text{C}$$

normality and constant variance, appropriate \log_{10} transformations of the data were performed prior to analysis.

Least squares regression analysis was used to test the functional relationship between two variables (Neter et al. 1994). All simple regression coefficients are presented with standard error estimates. I used analysis of covariance (ANCOVA) to test for differences in slope and intercepts among lake types using a significance level of $\alpha = 0.05$ (Neter et al. 1990). For a variable considered to be functionally dependent on more than one other variable, I used backward elimination, a stepwise regression technique (Neter et al. 1990). The significance for retaining variables was $\alpha=0.1$ and the partial coefficient of determination (r^2) was calculated for each selected variable. The partial- r^2 measures the contribution of an independent variable while holding the other independent variables constant. To develop the multivariate models to predict smolt size, I initially used the best-subsets regression approach (Neter et al. 1990) to select a small group of best subsets for further statistical analysis. After specifying the variables, the procedure provides a comparison of models with different numbers of predictors. Goodness-of-fit (adjusted- R^2) was used to compare models of the same size and both adjusted- R^2 and Mallows C_p statistic were used to compare models of different sizes. I considered a model adequate when the adjusted- R^2 was high and the C_p close to the number of parameters in the model (Neter et al. 1990). I conducted all statistical tests using SYSTAT version 6 (SPSS 1996), SAS/STAT version 6 (SAS Institute), and MINITAB (Minitab, Inc. 1995). The following list of notation gives definitions and units.

Notation

<i>HI</i>	Projected date of spring heating above 4° C, Julian day
<i>HM</i>	Projected date of maximum heat content, Julian day
<i>HF</i>	Projected date of fall cooling below 4° C, Julian day
<i>HD</i>	Duration of heating, d
<i>CD</i>	Duration of cooling, d
<i>S</i>	Duration of growing season, d
T_{1m}	Mean temperature of the 1-m depth, °C
T_{max}	Maximum temperature of the 1-m depth, °C
<i>TS</i>	Seasonal mean water column temperature, °C
θ_s	Summer heat budget, g-cal cm ⁻²
<i>LAT</i>	Latitude, °N
<i>ELEV</i>	Elevation, m
<i>SA</i>	Lake area, km ²
<i>Z</i>	Mean depth, m
Z_{max}	Maximum depth, m
<i>V</i>	Lake volume, m ³
<i>ZB</i>	Seasonal mean macrozooplankton biomass, mg m ⁻²
<i>FDX</i>	Fry density index, total annual smolt abundance km ⁻²
<i>SL</i>	Mean age-1 smolt length, mm
<i>SW</i>	Mean age-1 smolt weight, g

RESULTS

Characterization of Lake Thermal Regimes

In this section I examine growing season characteristics and temperature data from the 60 study lakes (Table 1) in order to define empirical bounds on the range of natural temperature regimes in which young sockeye salmon are likely to encounter. Summary statistics for all temperature and heat budget variables are presented in Table 4. In addition, I describe and quantify various factors that influence lake thermal environments.

Multi-Lake Variation

The side-by-side boxplots of Figures 3 show the distribution of the growing season variables for all lakes and years sampled by lake type. The distributions reveal an apparent association between the onset, termination, and duration of the growing season and lake typology. Based upon median values, the onset of spring heating (*HI*) or when the lake reaches 4° C isothermy occurs approximately three weeks earlier in stained lakes (117 d, 27 April) compared to clear lakes (134 d, 14 May) and one month earlier than glacial lakes (144 d, 24 May). In addition, the inter-quartile ranges for the stained and glacial lakes do not overlap. The date of maximum heat content (*HM*) appears to be the same in clear and glacial lakes (220 d, 08 August), which is one week later compared to the stained lakes (212 d, 31 July). In comparison, fall (4° C) isothermy (*HF*) occurs about one week later in stained lakes (312 d, 08 November) compared to clear lakes (303 d, 30 October) and 2 weeks later than glacial lakes (296 d, 23 October). For length of growing season (*S*), the median value is 195 d in stained lakes compared to 173 d in clear lakes and 153 days in

Table 4. Means, ranges, and standard deviations for various thermal characteristics for the 60 study lakes. Statistics are based on the number of lake years (N).

Parameter	Symbol	N	Minimum	Mean	Maximum	Standard deviation
Projected date of spring heating above 4° C, (Julian day)	<i>HI</i>	247	78	131	180	18
Projected date of maximum heat content (Julian day)	<i>HM</i>	245	192	218	247	10
Projected date of fall cooling below 4° C (Julian day)	<i>HF</i>	247	257	305	349	16
Duration of heating (days)	<i>HD</i>	245	30	87	141	18
Duration of cooling (days)	<i>CD</i>	245	45	87	157	20
Duration of the growing season (days)	<i>S</i>	247	101	174	252	29
Mean temperature of the 1-m depth (°C)	<i>T_{1m}</i>	245	6.5	10.4	15.0	1.7
Maximum temperature of the 1-m depth (°C)	<i>T_{max}</i>	246	7.8	13.9	22.5	2.6
Mean water column temperature (°C)	<i>TS</i>	236	4.4	7.3	12.5	1.8
Summer heat budget (g cal cm ⁻²)	<i>θ_s</i>	238	2,340	12,521	32,767	4,966

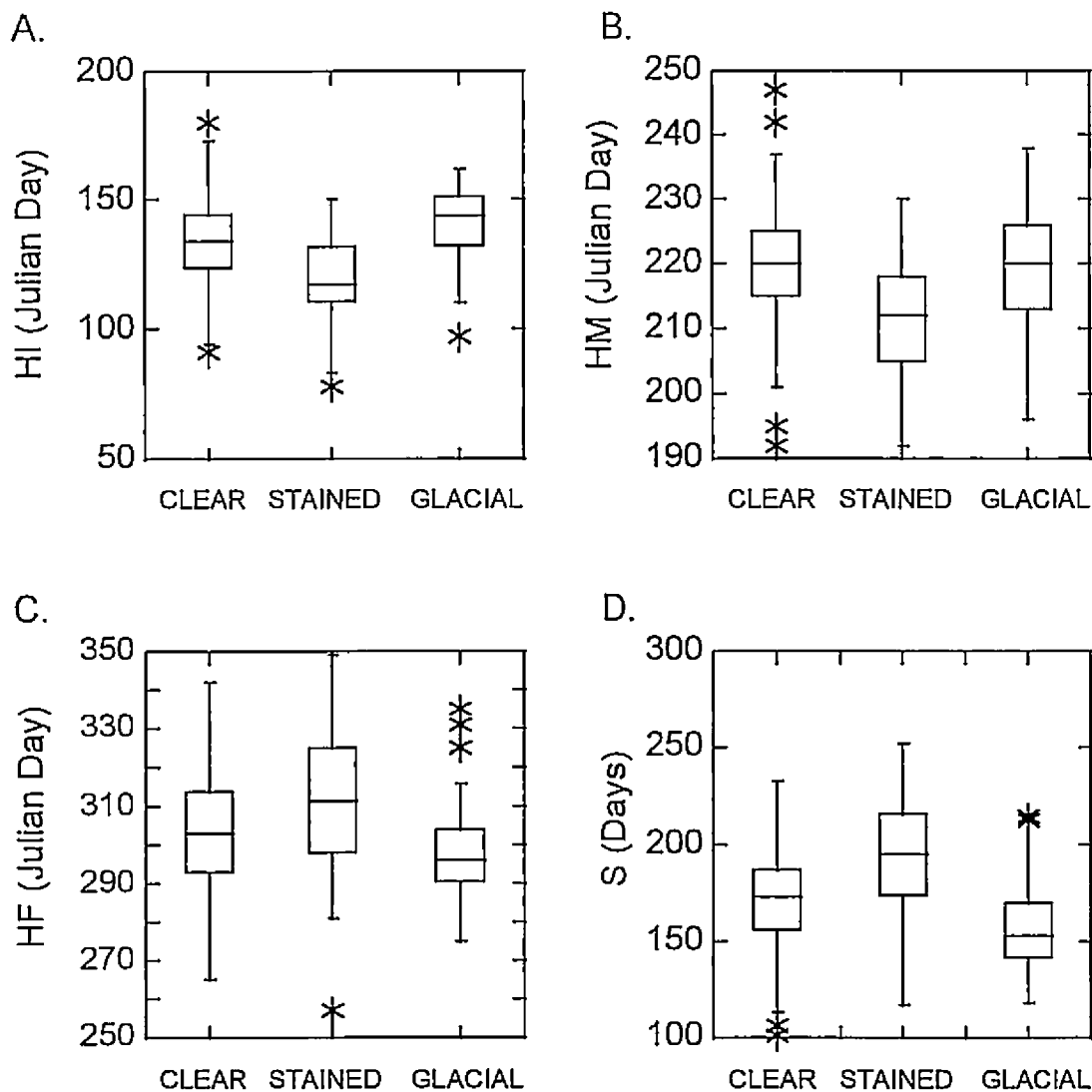


Figure 3. Boxplots of the date of spring isothermy (*HI*), date of maximum heat content (*HM*), date of fall isothermy (*HF*), and length of growing season (*S*) for clear, stained, and glacial lakes. Asterisks denote values greater than 1.5 times the interquartile range. Open circles denote values greater than 3.0 times the interquartile range.

glacial lakes. The inter-quartile ranges for S in stained and glacial lakes do not overlap, whereas the range overlap between clear and glacial lakes is considerable.

As to lake temperatures, the box-plots of Figure 4 indicate there is also a very strong association between mean temperature of the 1-m stratum (T_m) and lake type. In particular, the inter-quartile ranges for the three lake types do not overlap at all. The stained lakes median (11.9 °C) is about 2° C higher compared to the clear lakes median (10.3 °C) and 3° C higher compared to the glacial lakes median (8.5 °C). For maximum temperature of the 1-m stratum (T_{max}) variable, the median values are highest in stained lakes (16.2° C), lowest in glacial lakes (10.9° C), and intermediate in clear lakes (13.7° C). There is very little overlap in terms of the inter-quartile ranges for the T_{max} variable. In contrast, the median value for the mean water column temperature (TS) for clear lakes is highest (7.9 °C) followed by the stained (6.7 °C) and glacial lakes (5.5 °C). TS has a much narrower range in glacial lakes compared to clear and stained lakes. Surprisingly, there seems to be little if any association between the summer heat budget (θ_s) and lake type. The median values of θ_s is 13,831 cal cm⁻² for clear, 10,730 cal cm⁻² for stained, and 11,831 cal cm⁻² for the glacial lakes.

To determine whether the three lake types have the same means, I performed a separate one-way analysis-of-variance (ANOVA) on each of the temperature variables using lake type (clear, stained, and glacial) as the categorical or treatment variable (Table 5). However, I used lake means (n=60) instead of lake years in the ANOVA testing to better assess the variation attributed to lake typology, without the influence of inter-annual variability and possible bias due to unequal weighting by lake. That is, some lakes were sampled for a span of 10 years or more while others were sampled for just a single season. ANOVA indicates HI is earlier in stained lakes compared to both clear lakes ($P=0.0061$) and glacial lakes ($P=0.0007$), but there is no significant difference between clear and glacial lakes ($P=0.4222$). On average, HI occurs on 29 April in stained lakes, whereas HI

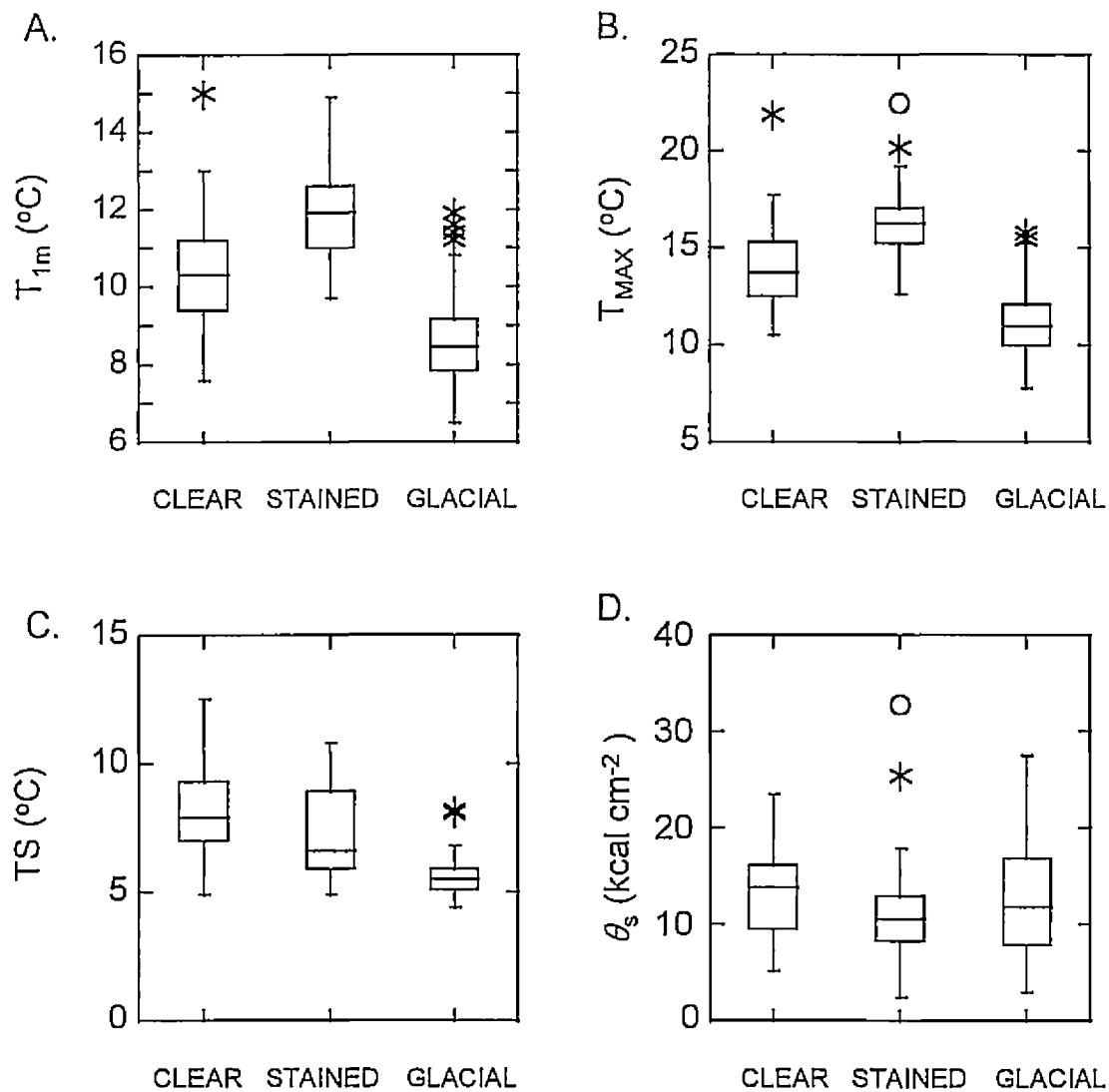


Figure 4. Boxplots of the seasonal mean temperature of the 1-m stratum (T_{1m}), maximum temperature (T_{max}), mean water column temperature (TS), and the summer heat budget (θ_s) for clear, stained, and glacial lakes. Asterisks denote values greater than 1.5 times the interquartile range. Open circles denote values greater than 3.0 times the interquartile range.

Table 5. Results of one-way analysis of variance for ten temperature responses using lake type (clear, stained, and glacial) as the treatment. Means that share the same letter do not significantly ($P > 0.05$, Tukey) differ.

Variable	Clear			Stained			Glacial		
	Mean	SE*	N	Mean	SE	N	Mean	SE	N
<i>HI</i>	134.3 ^a	3.2	26	118.9 ^b	3.6	20	141.0 ^a	4.3	14
<i>HM</i>	219.1 ^a	1.5	26	213.4 ^b	1.6	20	219.0 ^{ab}	2.0	14
<i>HD</i>	87.3 ^a	2.9	26	94.4 ^{ab}	3.2	20	78.0 ^b	3.8	14
<i>HF</i>	304.3 ^{ac}	3.0	26	312.3 ^{ab}	3.4	20	296.7 ^c	4.1	14
<i>CD</i>	84.5 ^a	3.4	26	98.9 ^b	3.8	20	77.8 ^a	4.5	14
<i>S</i>	170.1 ^a	5.2	26	193.5 ^b	5.9	20	155.6 ^{ac}	7.0	14
<i>T_{max}</i>	14.0 ^a	0.3	26	16.2 ^b	0.4	20	11.0 ^c	0.4	14
<i>T_{1m}</i>	10.3 ^a	0.2	26	11.8 ^b	0.3	20	8.6 ^c	0.3	14
<i>TS</i>	7.8 ^a	0.3	26	6.9 ^{ac}	0.3	20	5.9 ^{bc}	0.4	14
<i>θ_s</i>	11,783 ^a	845	26	10,815 ^a	926	20	11,637 ^a	1,107	14

*/standard error

does not occur until mid-May in clear and glacial lakes. The occurrence of *HM* seems to be very similar among the three lake types (01 - 07 August), ANOVA indicates it is slightly earlier ($P=0.0308$) in stained lakes compared to clear and glacial lakes. The one week difference does not seem to be biologically significant. The growing season ends approximately two weeks earlier in glacial lakes (October 29) compared to stained lakes ($P=0.0137$); however, ANOVA indicates there is no difference in *HF* between glacial and clear lakes ($P=0.3045$) nor between clear and stained lakes ($P=0.1915$). The duration of the growing season is 23 days longer ($P=0.0116$) in stained lakes compared to clear lakes, whereas *S* is nearly 6 weeks longer in stained lakes compared to glacial lakes ($P=0.0004$). There is no significant difference ($P=0.2428$) in *S* between the clear (170 d) and glacial (156 d) lakes.

ANOVA also indicates T_{max} is significantly different in the three lake types (Table 5). Specifically, maximum surface temperatures are about 2 °C warmer in stained lakes compared to clear lakes ($P=0.0001$) and 6° C warmer than glacial lakes ($P<0.0001$). In addition, T_{max} is significantly higher in clear lakes compared to glacial lakes ($P<0.0001$) and the difference in the means is about 4° C. As to average water temperatures, T_{Im} also differs significantly being highest in stained lakes, lowest in glacial lakes and intermediate for clear lakes. For each of the lake types, T_{Im} is about 3-5° C less than the maximum lake temperature. In contrast, there is no significant difference ($P=0.1932$) in *TS* between clear and stained lakes or between stained and glacial lakes ($P=0.1184$); however, glacial lakes are significantly colder than clear lakes ($P=0.0009$). Finally, stained lakes have the lower mean θ_s value of 10,815 cal cm⁻², whereas clear and stained lakes produced θ_s means of 11,783 cal cm⁻² and 11,637 cal cm⁻², respectively. However, ANOVA indicates that the differences in θ_s are not significant ($P>0.05$). Thus, there is a strong dependence of lake type on the growing season and water temperature, but apparently not on heat content.

Annual Variation

Between 1980 and 1995, temperature data were collected from a number of lakes representing each of the three lake types, though the particular set of lakes sampled differed from year to year. In order to examine the yearly variation, I plotted the annual means for near-surface temperatures by lake type for the 16-yr period (Figure 5) for three lakes representing each type which are located within the same geographic area. Hidden Lake (clear), Packers Lake (stained), and Tustumena Lake (glacial) are situated on the Kenai Peninsula and lie within a 20 km radius and are all at about the same altitude. Lakes Hidden and Tustumena were sampled regularly from 1980 to 1995. Except for 1980, 1982, and 1985, Packers Lake was sampled annually over the same time period. Hence, a reasonably consistent time series is available for the three lakes to qualitatively detect similarities and possible trends during this 16-yr time period. There is no apparent increasing or decreasing trend over the span of years in any of the three lakes though the annual changes in θ_s largely coincide, particularly between Hidden and Packers lakes. For these two lakes, the largest positive change is between 1986 and 1987; the largest negative change between 1987 and 1988. As to Tustumena Lake, there are several abrupt annual shifts in θ_s , e.g., between 1988-1989 (+ 16 kcal cm⁻²) and 1992-1993 (-15 kcal cm⁻²). Thus, fluctuations in θ_s appear to be larger in Tustumena Lake; however, this lake has a much greater (2 to 3 orders of magnitude) volume than the other two lakes. Thus, I considered whether the annual variation in θ_s has more to do with lake size or lake typology.

To assess the extent of annual fluctuations in θ_s as a function of lake size, I compared the coefficient of variation (standard deviation/mean) or CV for lakes that were sampled for 4 or more consecutive years (Table 6). For the 25 lakes meeting this criterion, CV values ranged from 2.7% to 47.9%. There appears to be a general tendency for lakes with larger volumes to have more variable summer heat budgets, though there are certainly

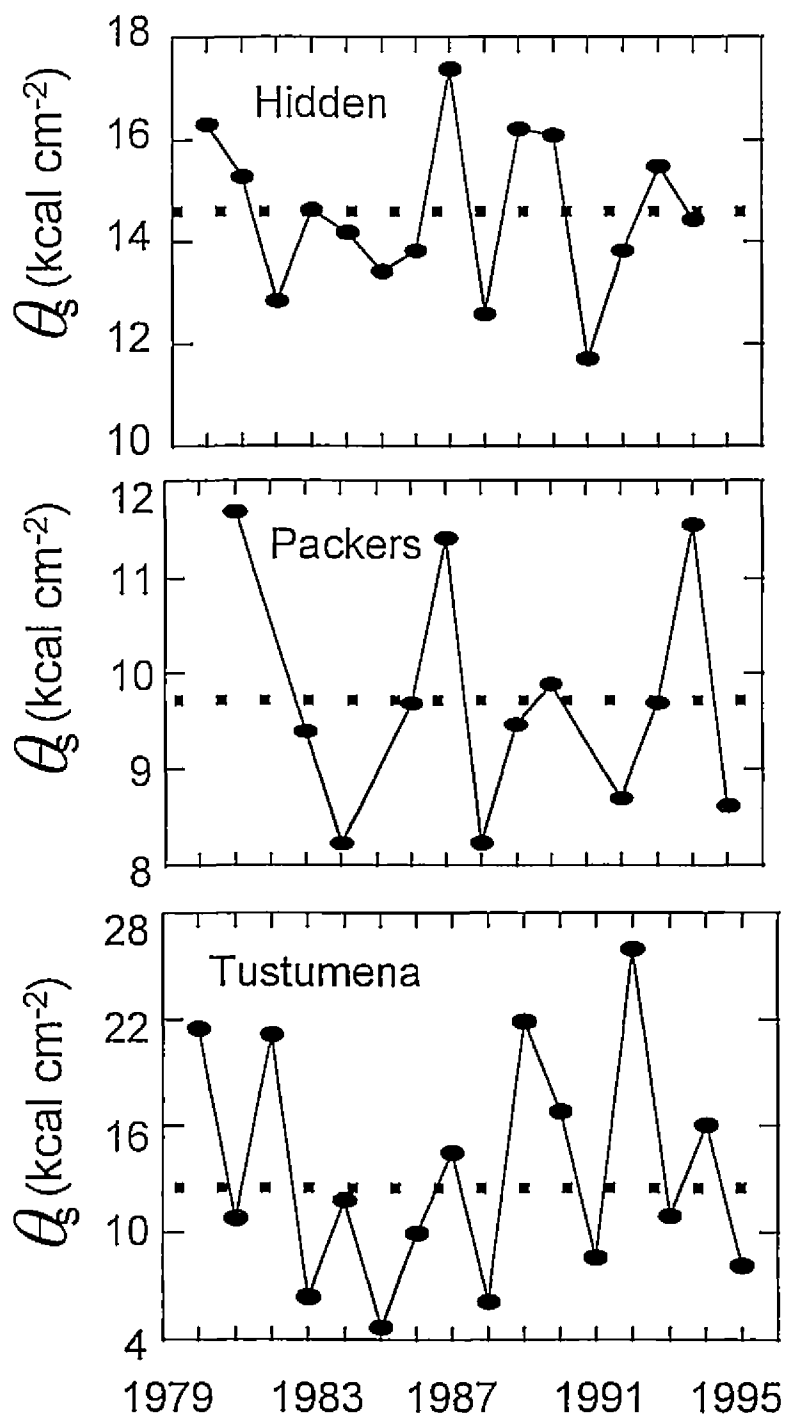


Figure 5. Interannual variation in summer heat budget (θ_s) for Hidden Lake (clear), Packers Lake (stained), and Tustumena Lake (glacial), 1980-1995. Dotted lines indicate the 16-year mean.

Table 6. Morphometry, summer heat budget (θ_s), and the extent of annual fluctuation in θ_s as measured by the coefficient of variation (CV) for 25 Alaskan lakes.

Lake	Type	Years of Data	Mean Depth (m)	Volume ($\times 10^6$ m ³)	Mean θ_s (cal cm ⁻²)	CV (%)
Portage	Stained	5	9.3	15.2	8,087	2.7
Red	Clear	6	24.7	207.7	14,758	5.7
Banner	Clear	4	51.2	33.5	9,515	7.4
Akalura	Clear	5	9.8	66.5	9,731	7.7
Upper Station	Clear	4	26.2	207.5	15,315	7.7
Spiridon	Clear	7	34.7	318.0	16,890	7.8
Afognak	Clear	6	7.9	43.2	9,348	10.4
Hidden	Clear	15	17.7	192.9	14,549	10.9
Bear	Clear	10	9.8	17.7	7,856	11.1
McDonald	Stained	13	44.9	157.9	12,799	11.7
Falls	Stained	4	32.0	33.0	7,653	12.4
Packers	Stained	12	12.4	24.5	9,710	12.8
Karluk	Clear	11	48.6	1920.0	18,749	13.2
Auke	Stained	4	19.4	17.4	6,009	16.3
Summit	Clear	5	13.4	134.9	7,385	16.8
Frazer	Clear	10	33.2	554.1	16,713	17.8
Kirschner	Clear	4	17.0	22.3	12,568	18.8
Coghill	Glacial	6	47.4	562.7	7,745	19.8
Skilak	Glacial	7	73.0	7212.5	16,961	23.0
Chenik	Clear	8	28.7	33.3	14,420	24.5
Crescent	Glacial	5	29.4	95.0	6,658	26.8
Hugh Smith	Stained	5	70.6	214.5	11,498	33.4
Kenai	Glacial	8	90.7	5086.9	18,469	33.9
Redoubt	Stained	4	72.9	818.5	19,578	46.5
Tustumena	Glacial	17	124.3	36600.0	14,071	47.9

exceptions. For instance, Chenik Lake has a large CV value, yet in terms of volume it is one of the smallest in this group. On the other hand, Karluk Lake is one of the more voluminous lakes, but annual fluctuations in θ_s are relatively small. What is also obvious is that lakes with the largest CV values (>20%) tend to be either glacial or stained. However, as a group glacial lakes typically have larger volumes compared to clear and stained lakes. In addition, the two stained lakes with large CV values (Hugh Smith and Redoubt lakes) also have fairly large volumes. Thus, it is not clear from these data whether the annual variation in θ_s is more influenced by morphometry or the nature (turbidity and color) of the water source.

Influence of Latitude and Altitude Gradients

Factors that might be expected to affect the growing season are latitude and elevation. My cursory evaluation of the data revealed that lakes in southeastern Alaska seemed to have a longer growing season compared to more northern lakes. For example, all lakes (n=11) with a growing season greater than 200 days are located in southeast Alaska. In comparison, lakes with a growing season of less than 150 days (n=11) are situated within the southcentral region of the state. Salmon Lake, which is on Prince of Wales Island in southeast Alaska, has the longest growing season which averaged 266 days. In contrast, Chelatna Lake, located in the upper Susitna River drainage, has an average growing season of only 135 days; a difference of more than 4 months compared to Salmon Lake. Since the initiation of spring warming (HI) and the onset of fall ($4^\circ C$) isothermy (HF) define the extent of the growing season (S), I tested the relationship between latitude and each of the growing season parameters.

For the 60 lakes, a significant ($r^2 = 0.54$, $P < 0.0001$) linear relationship exists between latitude (LAT) and HI (Figure 6A). Least squares regression (shown with standard error of the coefficients) produces

$$HI = -202.0 \pm 40.5 + (5.67 \pm 0.69)LAT.$$

In contrast, there is no linear relationship ($r^2 < 0.01$, $P = 0.799$) between latitude and date of maximum heat content, HM (Figure 6B). However, HF is inversely related ($r^2 = 0.36$, $P < 0.0001$) to latitude though the relationship is fairly weak (Figure 6C). This relationship is best described by the equation

$$HF = 549.4 \pm 42.4 + (-4.16 \pm 0.72)LAT.$$

Because latitude is positively related to HI and negatively related to HF , a significant ($r^2 = 0.60$, $P < 0.0001$) inverse relationship exists between LAT and S (Figure 6D);

$$S = 749.4 \pm 62.2 + (-9.8 \pm 1.06)LAT.$$

Thus, lakes at higher latitudes reach 4° C isothermy later in the spring and earlier in the fall than lakes at lower latitudes. The net result is that the length of the growing season decreases northward by about 10 days per 1 degree of latitude. Although the relationships between latitude and the various growing season variables (excluding HM) are significant, there is considerable unaccounted for variation about the regression lines.

As a group, the lakes range in elevation from just above sea level to more than 900 m. Therefore, I considered altitude or elevation ($ELEV$) relative to the various parameters which define the growing season. A semi-logarithmic function best describes the

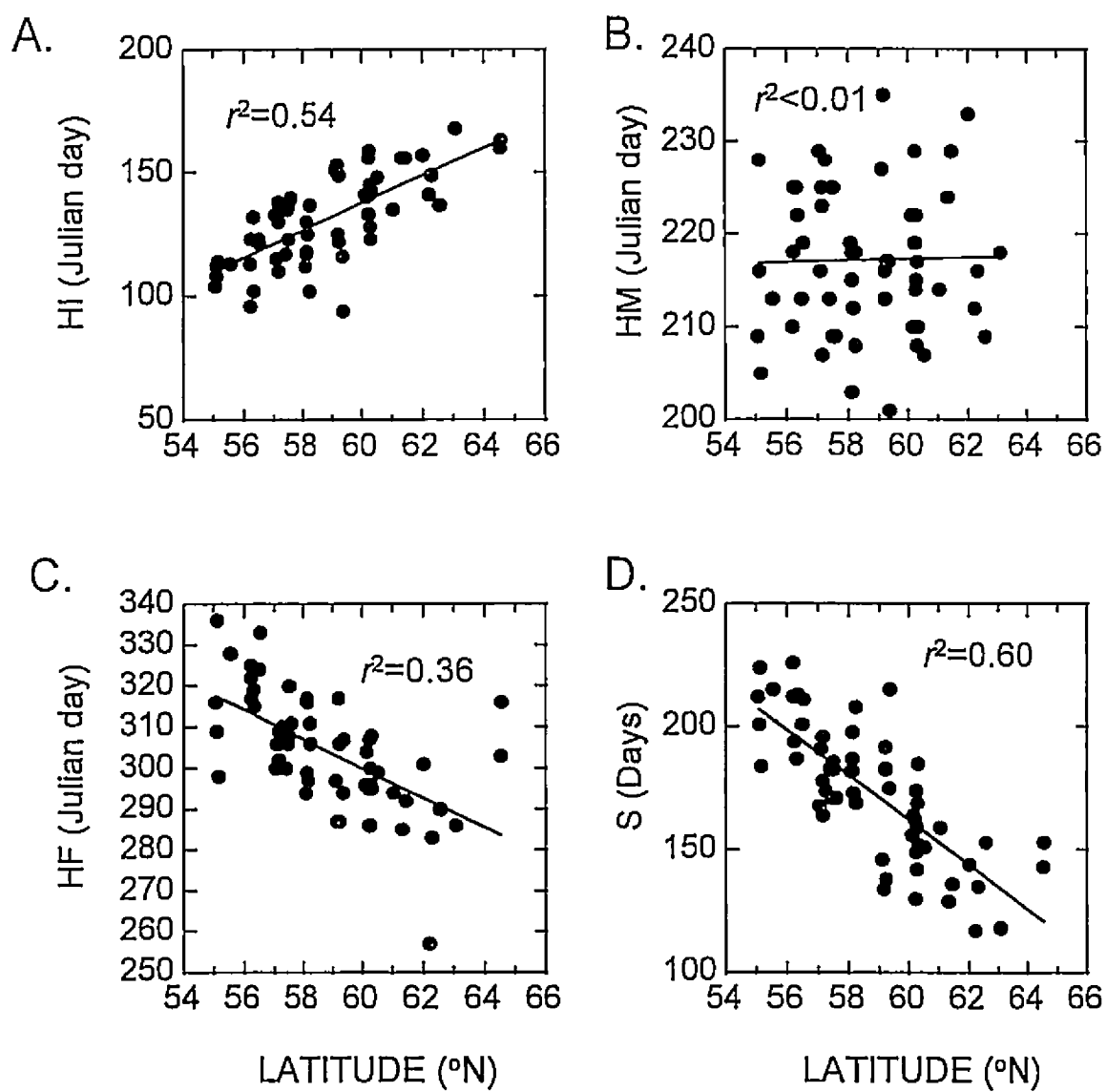


Figure 6. Fitted regression lines for the date of spring (4° C) isothermy (HI), date of maximum heat content (HM), date of fall (4° C) isothermy (HF), and duration of the growing season (S) versus latitude.

relationship (Figure 7A) between the onset of spring heating (*HI*) and *ELEV* ($r^2=0.39$, $P<0.0001$); the regression equation is

$$HI = 96.92 \pm 5.80 + (19.07 \pm 12.85)\log_{10}ELEV.$$

Although a positive ($P=0.0347$) relationship exists between the date of maximum heat content (*HM*) and *ELEV* (Figure 7B), the model has very little predictive power ($r^2=0.08$). In addition, fall 4° C isothermy (*HF*) is inversely related to *ELEV* ($r^2=0.18$, $P=0.0009$), though the response is not particularly strong (Figure 7C). This relationship is best described by the equation

$$HF = 325.35 \pm 6.04 + (-11.38 \pm 3.23)\log_{10}ELEV.$$

One of the points, corresponding to Salmon Lake, appears to be an extreme outlier. Excluding this data from the regression analysis results in only a slight improvement in the linear fit ($r^2=0.22$). A significant ($r^2=0.37$, $P<0.0001$) inverse relationship also exists between length of growing season and *ELEV* (Figure 7D). The regression equation is

$$S = 228.05 \pm 9.75 + (-30.19 \pm 5.22)\log_{10}ELEV.$$

Salmon Lake again appears as an obvious outlier in the scatter plot. Re-analyzing the data without Salmon Lake results in a similar slope and increases the variation explained by only 4%. Hence, Salmon Lake does not exert much leverage in the regression model.

In order to assess the combined effects of climate and topographic characteristics on the growing season and to better estimate each of the growing season characteristics, I carried out a stepwise multiple regression analysis (Table 7). Taken together, the factors *LAT* and *ELEV* account for an additional 5% and 8%, respectively of the variation in the onset of

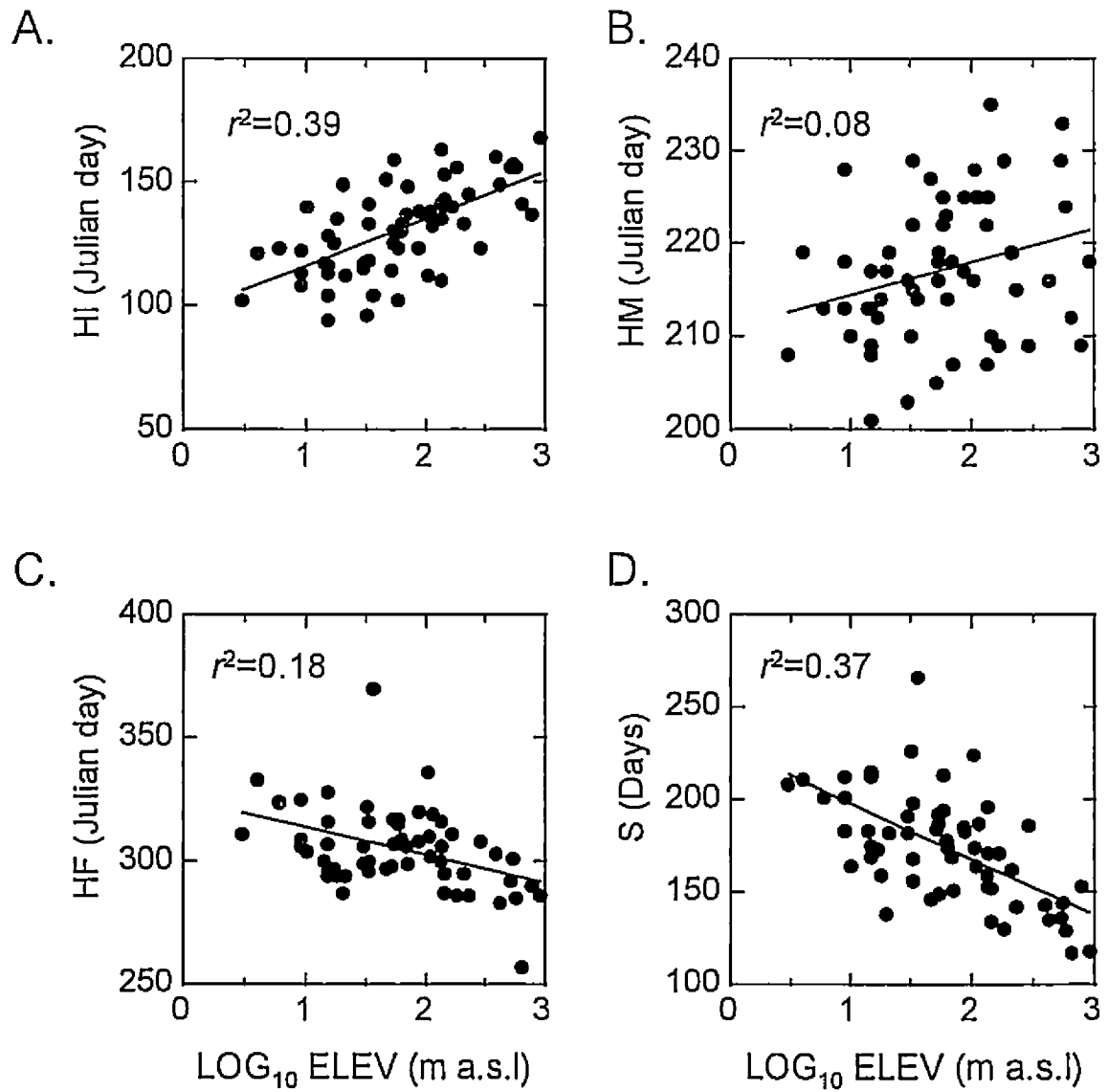


Figure 7. Fitted regression lines for the date of spring (4° C) isothermy (*HI*), date of maximum heat content (*HM*), date of fall (4° C) isothermy (*HF*), and duration of the growing season (*S*) versus elevation (*ELEV*).

Table 7. Multiple regression statistics for the dependence of the date of spring (4° C) isothermy (*HI*), date of maximum heat content (*HM*), date of fall (4° C) isothermy (*HF*), and duration of the growing season (*S*) on latitude (*LAT*) and elevation (*ELEV*).

Model	N	Variable	Coefficient	SE ^a	P-value	R ²
<i>HI</i>	60	y-intercept	-139.76	41.6	0.0014	0.62
		<i>LAT</i>	4.30	0.75	<0.0001	
		Log ₁₀ <i>ELEV</i>	9.99	2.96	0.0013	
<i>HM</i>	58	y-intercept	210.81	3.07	<0.0001	0.08
		<i>LAT</i>	ns ^b			
		Log ₁₀ <i>ELEV</i>	3.60	1.66	0.0347	
<i>HF</i>	60	y-intercept	549.37	42.42	<0.0001	0.36
		<i>LAT</i>	-4.16	0.72	<0.0001	
		Log ₁₀ <i>ELEV</i>	ns			
<i>S</i>	60	y-intercept	666.07	65.43	<0.0001	0.65
		<i>LAT</i>	-7.96	1.18	<0.0001	
		Log ₁₀ <i>ELEV</i>	-13.37	4.65	0.0057	

a/ standard error

b/ not significant ($P > 0.05$)

heating and length of growing season compared to latitude alone. As to *HI*, the regression coefficients are positive and in agreement with sign as in the simple regression models. As for *S*, the coefficients are appropriately negative. Multiple regression also established a dependence of *HM* on *ELEV*, but *LAT* ($P=0.3209$) failed the minimum criteria to remain in the model. For *HF*, the multiple regression has a poorer fit ($r^2=0.38$) compared to the single factor models. Thus, both latitude and elevation are significant determinants of the length of the growing season; however, based upon the goodness-of-fit criterion (r^2), latitude appears to be more important than elevation among the 60 lakes.

Influence of Morphometry

In view of the large number of lakes in my study and their different sizes, I tested the relationship between the summer heat budget (θ_s) and various lake dimensions. Although there is a significant ($P<0.0001$) relationship between θ_s and mean depth (Z) (Figure 8A), the response is uncharacteristically weak ($r^2=0.27$). The relationship is best described by the equation (shown with standard error of the coefficients)

$$\theta_s = 2183.8 \pm 2093.1 + (6310 \pm 1395.3)\log_{10}Z.$$

Seemingly, the change in θ_s per unit depth is more variable in stained and glacial lakes compared to clear lakes. However, there are also a few clear lakes in which θ_s is lower than expected, yet they have considerable depth and volume. Since mean and maximum depth (Z_{max}) is are highly correlated ($r^2=0.89$), regressing θ_s on Z_{max} also produces a significant ($r^2=0.25$, $P<0.0001$) relationship (Figure 8B), but the regression explains 2% less of the variation in θ_s compared to Z .

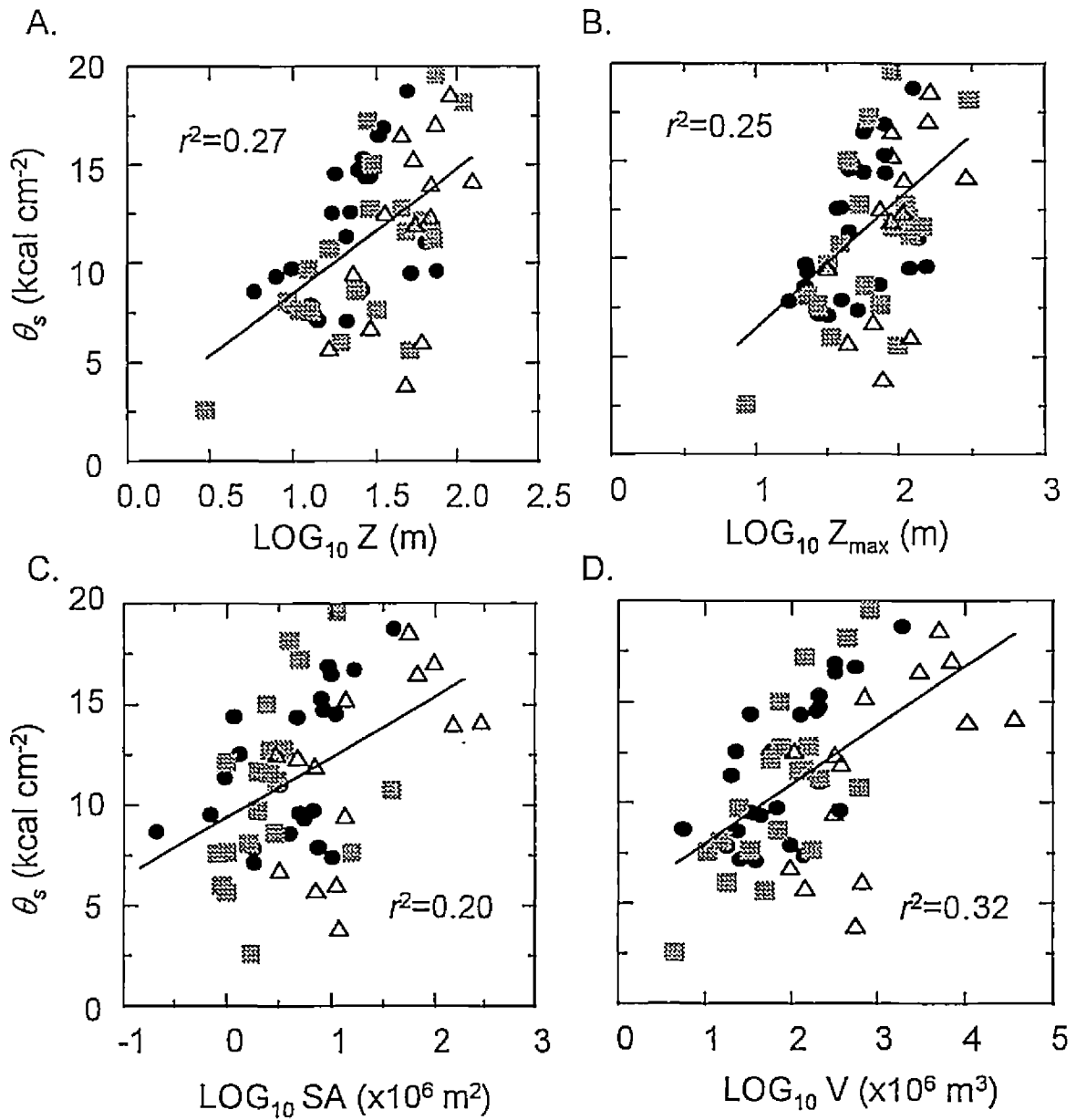


Figure 8. Fitted regression lines for the dependence of summer heat budget (θ_s) on mean depth (Z), maximum depth (Z_{max}), surface area (SA), and volume (V). Regressions are derived by pooling data across lake type. Circles are clear lakes, squares are stained lakes, and triangles are glacial lakes.

A significant ($P=0.0005$) relationship also exists between surface area and θ_s (Figure 8C), but the linear fit is poorer ($r^2=0.20$) compared to either Z or Z_{max} . Because both Z depth and area are related significantly to θ_s , I assumed their product (i.e., volume) would be a better predictor of θ_s (Figure 8D). Indeed, θ_s is somewhat better correlated with volume (V) ($r^2=0.32$, $P<0.0001$); the regression equation being

$$\theta_s = 5066.1 \pm 1313.2 + (2930.6 \pm 570.1)\log_{10}V;$$

However, the additional (5%) variation explained is relatively small. Nonetheless, these relationships strongly suggest that θ_s is under effective morphometric control. However, given the large unaccounted for variation in the regression models, there obviously must be some other factors that influence or modify heat uptake.

I considered mean water column temperature (TS) as an alternative method for comparing heat content. In contrast to θ_s , there is a much stronger curvilinear relationship between mean depth (Z), and TS (Figure 9A). That is, TS is inversely related to Z ($r^2 = 0.77$, $P<0.0001$). After logarithmic transformation of the data, least squares regression produces the equation

$$\log_{10}TS = 1.22 \pm 0.03 + (-0.26 \pm 0.02)\log_{10}Z.$$

The plot of the data shows that the decrease in TS with Z begins to lessen at a depth of about 25 m. Although the relationship appears to be largely independent of lake typology, results of analysis of covariance (ANCOVA) with lake type as a category variable and Z as a covariate indicated unequal slopes ($P=0.0092$) and y -intercepts ($P=0.0304$). That is, the negative response is greater in clear lakes (slope = -0.305 ± 0.038 , $r^2 = 0.76$) compared to stained lakes (slope = -0.235 ± 0.027 , $r^2 = 0.81$), whereas TS decreases the least as a function of increasing depth (slope = -0.143 ± 0.032 , $r^2 = 0.62$) in the glacial

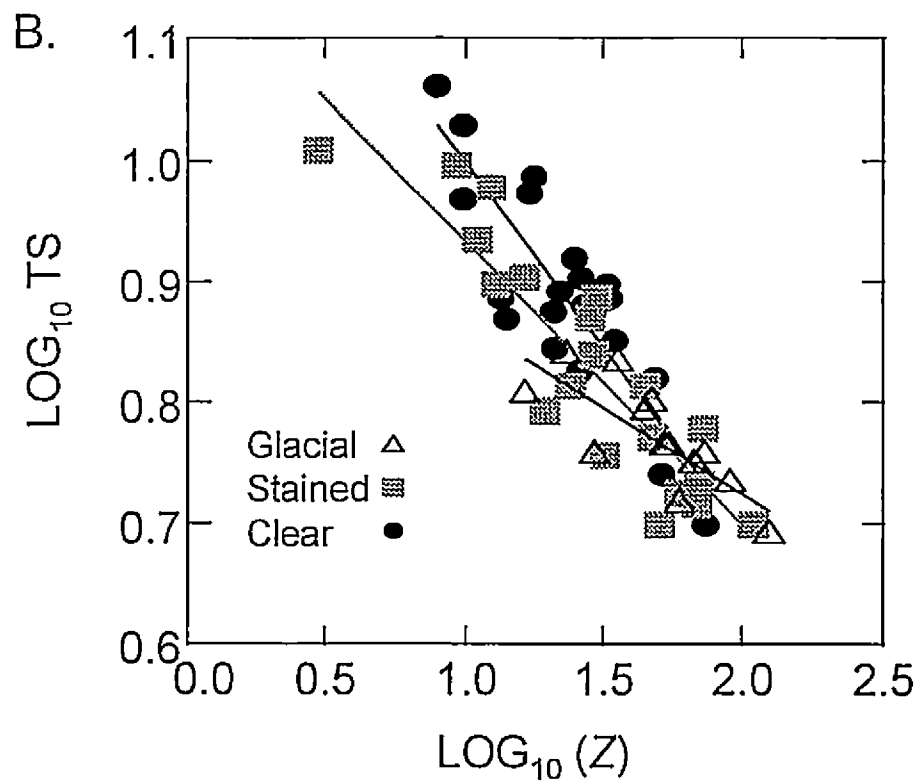
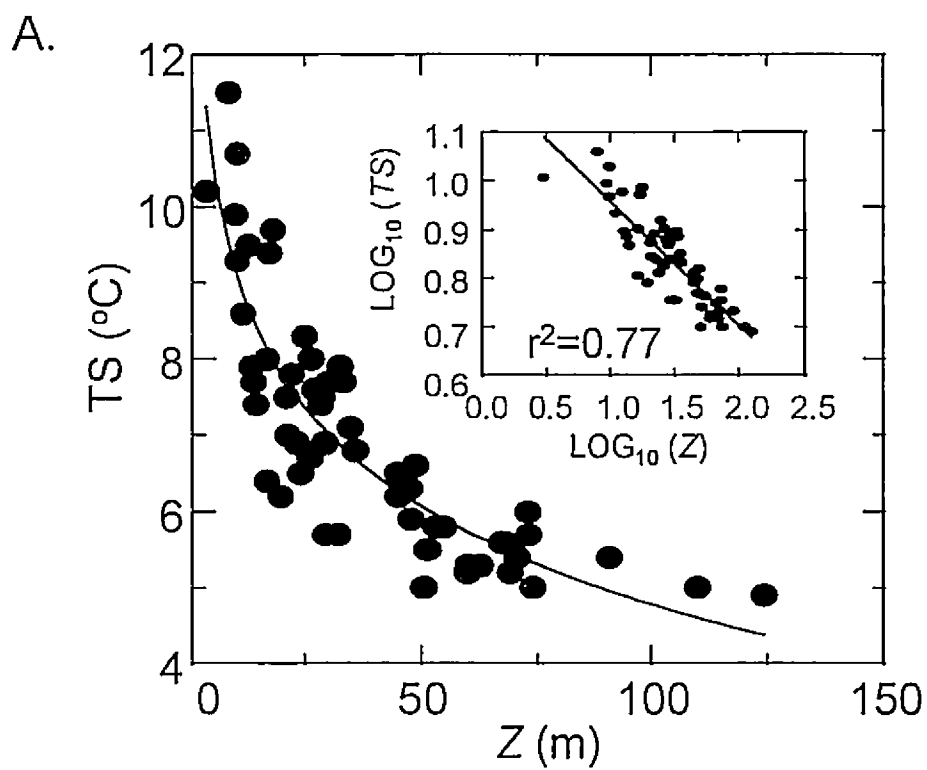


Figure 9. The inverse relationship between mean water column temperature (TS) and mean depth (Z) (A); and separate regression plots after log_{10} transformation, for clear, stained, and glacial lakes (B).

lakes (Figure 9B). Thus, TS appears to be less influenced by changes in depth in lakes with elevated amounts of color or turbidity.

Influence of Color and Turbidity

Considering clear and stained lakes together, a significant relationship exists between the average temperature of the 1-m stratum (T_{1m}) and color (Figure 10A). A curvilinear relationship results in the best fit ($r^2=0.42$, $P<0.0001$) and is described by the equation (shown with standard error of the coefficients)

$$T_{1m} = 7.97 \pm 0.31 + (2.97 \pm 0.30)\log_{10} \text{COLOR}.$$

In contrast, T_{1m} is inversely related to turbidity (Figure 10B), but the negative response is not quite as strong ($r^2=0.23$, $P<0.0001$) compared to color. Considering clear and glacial lakes together, linear regression produces the equation

$$T_{1m} = 10.10 \pm 0.12 + (-1.13 \pm 0.17)\log_{10} \text{TURBIDITY}.$$

Thus, T_{1m} increases nearly 3 °C for every 10 Pt unit increase in color, whereas T_{1m} decreases by about 1 °C for every 10 NTU increase in turbidity. It seemed reasonable to assume the differential effect of color and turbidity on lake surface temperatures might also influence heat accumulation and depth of mixing.

Figure 11 shows the temperature profiles at the time of maximum heat content (late July - early August 1993) for three lakes representing each of the three lake types. Although these lakes have similar summer heat budget (θ_s) values (i.e., 18,749 cal cm⁻² for Karluk, 12,799 cal cm⁻² for McDonald and 16,961 cal cm⁻² for Skilak), the pattern of stratification

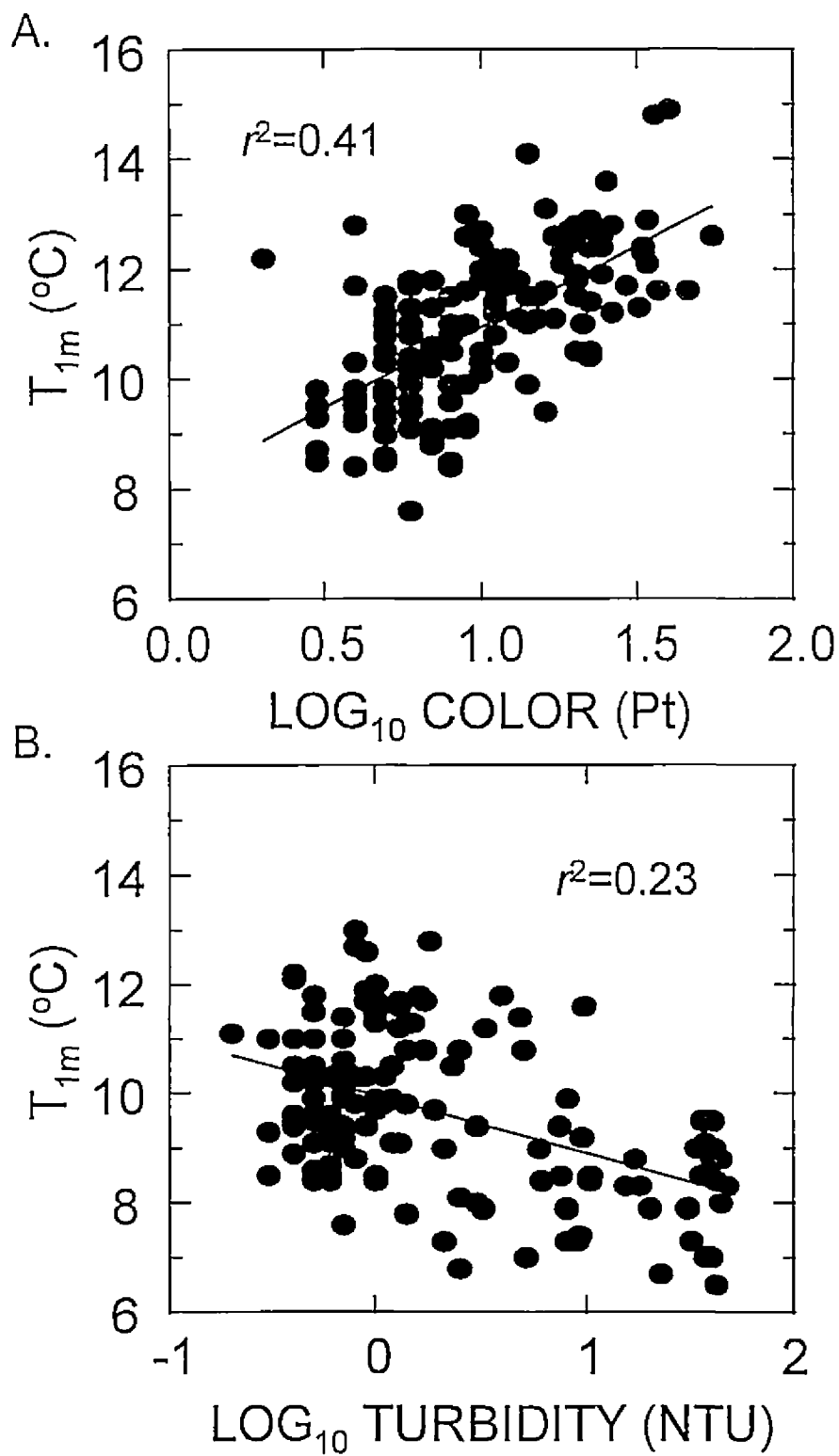


Figure 10. The relationship between seasonal mean temperature of the 1-m stratum (T_{1m}) and color (A); and the inverse relationship between T_{1m} and turbidity (B).

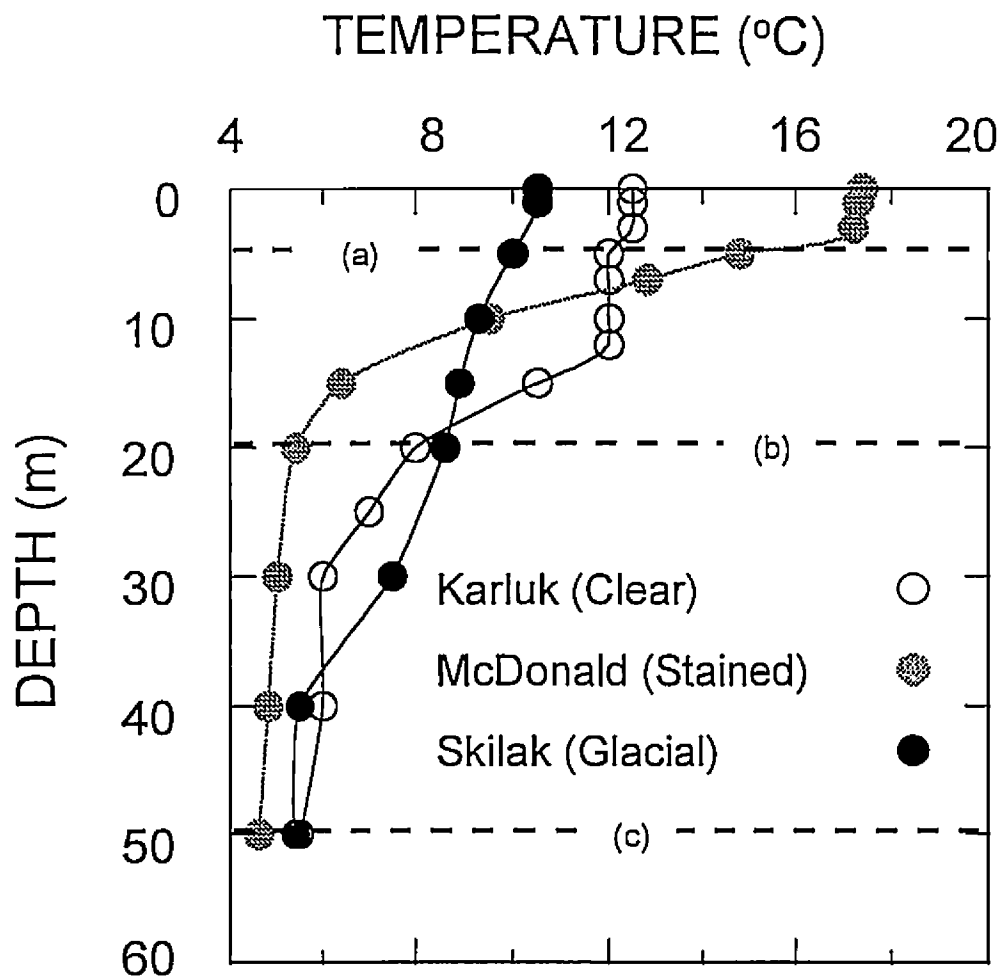


Figure 11. Vertical temperature profiles for three lakes of different typology during time of maximum heat content, August 1993. Mixing depths are shown by the dotted lines for McDonald (a), Karluk (b), and Skilak lakes (c).

is not at all the same. For example, Karluk Lake, which lacks appreciable color and turbidity, exhibits a distinct summer thermocline. During mid-summer, temperatures are isothermal at about 12 °C between the surface and 15 m. A strong temperature gradient ($\geq 1 \text{ }^\circ\text{C m}^{-1}$) is obvious between 15 and 20 m wherein temperatures decrease to about 6 °C. Below 20 m, the water column is essentially isothermic at about 5 or 6 °C. As such, the mixing depth for Karluk Lake is equivalent to 30% of the mean depth. In contrast, surface temperatures in organically stained McDonald Lake are much warmer and reach nearly 18 °C. However, temperatures begin to decrease very rapidly below 3 m cooling to about 5 °C at 15 m. Temperatures of the underlying water mass hover just above 4 °C. Thus, the mixing depth in this lake is about 3 m, which equates to only 7% of the mean depth. In glacially turbid Skilak Lake, thermal stratification usually does not occur at least for any prolonged (2-3 wk) period. Surface temperatures in this lake are much colder than Karluk and McDonald lakes. Maximum temperatures reach only about 10 °C; however, temperatures decrease very gradually through the water column cooling to about 5 °C at a depth of 50 m or about $0.1 \text{ }^\circ\text{C m}^{-1}$. Although, temperature measurements were not available below 50 m, the profile indicates that the lake presumably mixes at least down to a depth 50 m which represents 66% of the mean depth. Thus, water clarity appears to have some effect on the vertical temperature structure which might influence heat content.

Chlorophyll, Zooplankton Biomass, and Temperature

Correlations between the temperature variables and chlorophyll *a* (*CHL*) concentration were mixed (Table 8). *CHL* was negatively correlated with *HI* ($P < 0.05$) indicating phytoplankton standing stock tends to decrease as the onset of spring heating latens. *CHL* was not significantly correlated ($P > 0.37$) with any of the other growing season variables or the summer heat budget. As to water temperatures, the positive correlation between *CHL* and mean water column temperature (*TS*) was the strongest ($P < 0.0001$); however,

CHL was also highly and positively correlated with maximum (T_{max}) and average (T_{1m}) 1-m temperatures ($P < 0.001$). Of the 10 correlations between zooplankton biomass (*ZB*) and the temperature variables 8 were nonsignificant ($P = 1.000$). The correlation between *ZB* and θ_t was also insignificant, however the probability value ($P = 0.081$) was only slightly above my significance criterion for statistical testing. *ZB* was positively correlated with *TS* ($P = 0.017$), though the association was relatively weak ($r = 0.25$). Finally, the correlation between *ZB* and *CHL* was nonsignificant ($P = 1.000$). Thus, given the degree of association between *TS* and *CHL*, and *TS* and *ZB*, I considered *TS* to be an important variable in fish growth models as it might indirectly influence growth by regulating the forage base of rearing sockeye juveniles.

Factors Affecting Smolt Size

In this section, I examine food resource availability, competitive effects, and temperature as relevant parameters influencing and the size of sockeye salmon smolt. Initially, I examined whether algal (chlorophyll *a*) and zooplankton biomass levels varied systematically with temperature. I then used simple regression analysis to test for linkages between age-1 smolt size (mean length and weight) and the independent variables zooplankton biomass (*ZB*), fry density index (*FDX*), mean water column temperature (*TS*) and length of growing season (*S*). Subsequently, I combine all factors into a single model of mean age-1 smolt size and the population's biological and temperature environment.

Single Factor Models

Alaskan sockeye nursery lakes exhibit a tremendous amount of variation in smolt size. Across 35 study lakes, mean age-1 smolt length (*SL*) ranged from 52 mm to 145 mm and

averaged 87.1 mm. In comparison, mean age-1 smolt weight (*SW*) ranged from 1.0 g to 30.0 g and averaged 7.6 g. *SL* and *SW* are strongly correlated ($r^2=0.99$) and the curvilinear relationship conforms well to a power function (Figure 12). Age-1 smolt size tends to be larger in the clear lakes compared to stained and glacial lakes. Specifically, the clear lakes medians are 95.0 mm and 7.9 g, the stained lakes medians are 71.0 mm and 3.3 g, and the glacial lakes medians are 68.8 mm and 2.6 g. For 23 lakes, annual smolt (all age classes) outmigration estimates ranged from 952 to more than 9.8 million.

The independent variable zooplankton biomass (*ZB*) accounted for 52% of the variation in *SL* and 51% of the variation in *SW* (Table 9). The slopes of the two regression models are appropriately positive; i.e., increases in the amount of available forage for rearing sockeye juveniles tend to result in larger sized smolt. Both *SL* and *SW* are also positively and significantly related to water temperature. That is, *TS* explains about 20% of the variation in age-1 smolt size. However, duration of the growing season is not a significant factor affecting *SL* ($P=0.44$) or *SW* ($P=0.99$). In contrast, *SL* and *SW* are inversely related to the fry density index (*FDX*), which is expected under density dependent growth. That is, increasing fry densities have the same effect on age-1 smolt size as decreasing temperature. Nonetheless, *FDX* accounts for only about 10% of the variation in age-1 smolt size. Thus, both *SL* and *SW* increase with increasing food resources and temperature, but decrease with increasing fry population density which is in agreement with biological or management principles concerning juvenile sockeye growth.

Because the single factor models included different lake types, I considered that the responses might be different within each lake group. Results of analysis of covariance (ANCOVA) with *SL* as the response variable, lake type as a category variable, and *ZB* as a covariate indicated equal slopes ($P=0.06$) and *y*-intercepts ($P=0.23$) (Table 10). However, the reported *P*-value for the cross-product interaction term is only slightly greater than the significance level ($\alpha=0.05$) for rejection of the null hypothesis. Thus, that a lake type

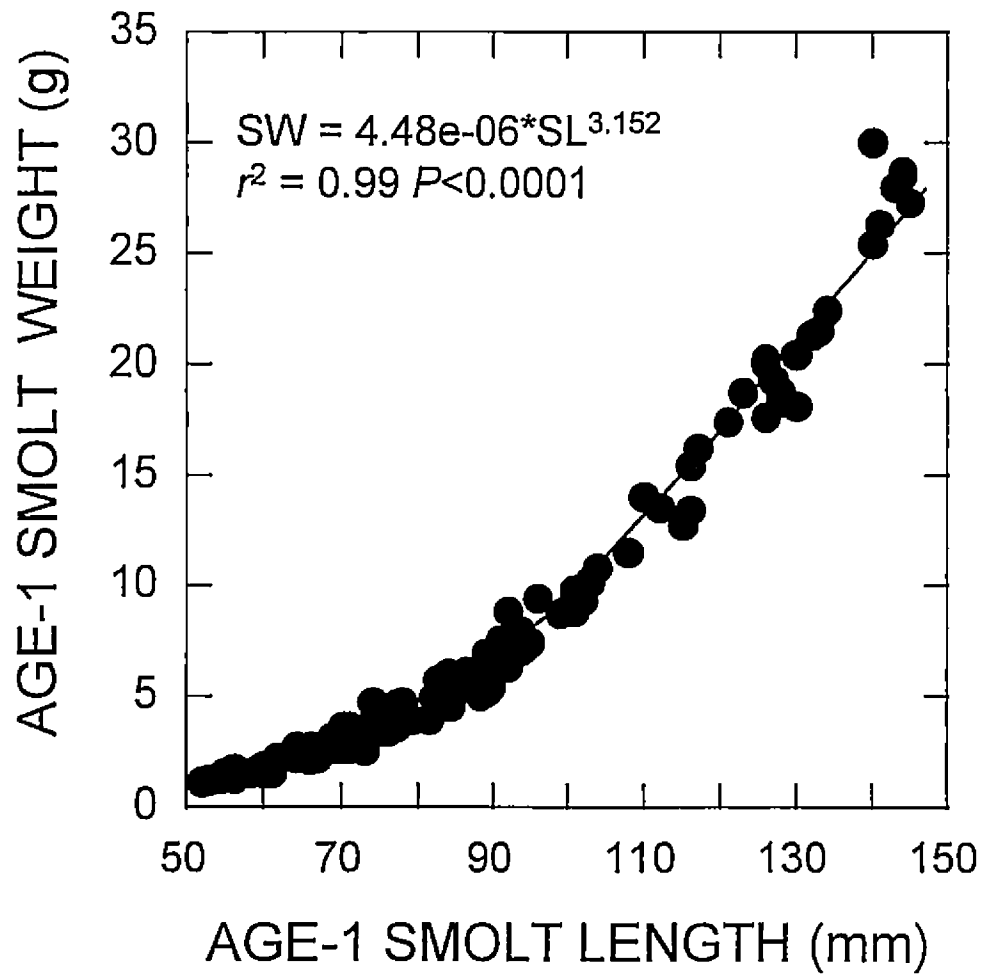


Figure 12. The relationship between age-1 sockeye smolt length and weight for 35 Alaska lakes (130 lake years).

Table 9. Comparison of simple linear regression models for the dependence of age-1 smolt length (SL) and weight (SW) on zooplankton biomass (ZB), fry density index (FDX), length of growing season (S), and mean water column temperature (TS) for all lake types combined.

Dependent variable	N (lake years)	Model	Coefficient	SE	P-value	r^2
$\text{Log}_{10} SL$	127	y-intercept	1.544	0.034	<0.0001	
		$\text{Log}_{10} ZB$	0.148	0.013	<0.0001	0.52
	88	y-intercept	2.217	0.093	<0.0001	
		$\text{Log}_{10} FDX$	-0.058	0.019	0.0038	0.09
130	y-intercept	1.710	0.036	<0.0001		
	TS	0.029	0.005	<0.0001	0.24	
133	y-intercept	0.886	0.201	<0.0001		
	S	-0.001	0.001	0.4409	<0.01	
$\text{Log}_{10} SW$	125	y-intercept	-0.519	0.112	<0.0001	
		$\text{Log}_{10} ZB$	0.477	0.042	<0.0001	0.51
	89	y-intercept	1.666	0.296	<0.0001	
		$\text{Log}_{10} FDX$	-0.190	0.062	0.0030	0.10
	128	y-intercept	0.085	0.120	0.4815	
		TS	0.085	0.015	<0.0001	0.19
		y-intercept	1.926	0.060	<0.0001	
		S	0.000	0.000	0.9995	<0.01

Table 10. ANCOVA indicating lack of a lake type (clear, stained, and glacial) effect on age-1 sockeye smolt length (SL) and weight (SW) with zooplankton biomass (ZB), fry density index (FDX), and mean water column temperature (TS) as covariates.

Dependent variable	Model	<i>df</i>	<i>F</i> -ratio	<i>P</i> -value	R^2
$\text{Log}_{10}SL$	$\text{Log}_{10}ZB$ (covariate)	1	11.9	0.0008	0.45
	Type (category)	2	1.5	0.2348	
	$\text{Log}_{10}ZB * \text{Type}$	2	2.9	0.0584	
	Error	121			
$\text{Log}_{10}SL$	$\text{Log}_{10}FDX$ (covariate)	1	1.7	0.2011	0.61
	Type (effect)	2	2.9	0.0616	
	$\text{Log}_{10}FDX * \text{Type}$	2	1.3	0.2868	
	Error	83			
$\text{Log}_{10}SL$	TS (covariate)	1	1.1	0.2933	0.32
	Type (effect)	2	0.4	0.6433	
	$TS * \text{Type}$	2	0.1	0.9434	
	Error	124			
$\text{Log}_{10}SW$	$\text{Log}_{10}ZB$ (covariate)	1	30.8	0.0000	0.64
	Type (effect)	2	0.3	0.7517	
	$\text{Log}_{10}ZB * \text{Type}$	2	1.9	0.1524	
	Error	119			
$\text{Log}_{10}SW$	$\text{Log}_{10}FDX$ (covariate)	1	1.1	0.2965	0.61
	Type (effect)	2	3.3	0.0428	
	$\text{Log}_{10}FDX * \text{Type}$	2	1.5	0.2196	
	Error	82			
$\text{Log}_{10}SW$	TS (covariate)	1	0.0	0.8946	0.50
	Type (effect)	2	1.0	0.3798	
	$TS * \text{Type}$	2	1.8	0.1725	
	Error	122			

effect does not exist cannot be emphatically declared. With TS as the covariate, ANCOVA also showed equivalent slopes ($P=0.94$) and y -intercepts ($P=0.64$) for the three lake types. Similar results were obtained with FDX as the covariate, in that the three regression lines have the same slope ($P=0.29$) and y -intercept ($P=0.20$). Considering SW as the dependent variable, lake type as the category variable, and ZB as the covariate, ANCOVA again indicates equal slopes ($P=0.15$) and y -intercepts ($P=0.75$). In addition, there is no significant difference in slope ($P=0.17$) nor y -intercepts ($P=0.38$) when TS is a covariate. Finally, with SW as the response variable, lake type as the category variable, and FDX as a covariate, ANCOVA also indicates there is no statistical difference in slope ($P=0.22$) and y -intercept ($P=0.29$) among clear, stained, and glacial lakes. Therefore, pooling the data across different lake typologies in the single factor regression models as I did is appropriate.

Combined Biological and Temperature Model

Given that mean age-1 smolt size (SL and SW) is significantly related to zooplankton biomass, fry density, and lake temperature, I attempted to develop a more accurate model for estimating smolt size through multivariate regression analysis. As with the single factor regressions above, I included zooplankton biomass (ZB), fry density index (FDX), mean water column temperature (TS), and length of growing season (S) in the pool of potential independent variables. Initially, I used the best subsets regression procedure to identify subsets of independent variables which provided a good fit of the underlying structure of the data (Table 11). The criterion for variable selection is based on adjusted R^2 values and Mallows' C_p statistic. For SL , the subset (ZB, FDX, TS) has the smallest (preferred) C_p value (3.2) and a high (preferred) adjusted R^2 (0.68). Although the C_p value is slightly below the number of parameters in the model, the magnitude of the C_p statistic indicates little if any bias from peculiarities in the data. Although the subset ($ZB,$

Table 11. Comparison of best subsets regression using age-1 smolt length (*SL*) and weight (*SW*) as response variables and zooplankton biomass (*ZB*), fry density index (*FDX*), mean water column temperature (*TS*), and duration of the growing season (*S*) as model predictors for all lake types combined.

Dependent Variable	N (lake years)	Number of Variables	R^2_{adj}	C_p	Model Predictors
$\text{Log}_{10} SL$	83	1	0.48	55.0	$\text{Log}_{10} ZB$
		2	0.58	29.0	$\text{Log}_{10} ZB \text{ Log}_{10} FDX$
		3	0.68	3.2	$\text{Log}_{10} ZB \text{ Log}_{10} FDX \text{ TS}$
		4	0.69	5.0	$\text{Log}_{10} ZB \text{ Log}_{10} FDX \text{ TS } S$
$\text{Log}_{10} SW$	84	1	0.46	58.5	$\text{Log}_{10} ZB$
		2	0.58	28.9	$\text{Log}_{10} ZB \text{ Log}_{10} FDX$
		3	0.69	3.1	$\text{Log}_{10} ZB \text{ Log}_{10} FDX \text{ TS}$
		4	0.68	5.0	$\text{Log}_{10} ZB \text{ Log}_{10} FDX \text{ TS } S$

SPSA, *TS*, *S*) does improve the goodness of fit by 1% and C_p is equal to the number of parameters in the model, the additional variability explained is trivial. Hence, from this variable selection method, I prefer the parsimonious subset (*ZB*, *FDX*, *TS*). As to *SW*, the subset (*ZB*, *FDX*, *TS*) also has the smallest C_p value (3.1) which closely approximates the number of parameters and has the highest adjusted R^2 (0.69). The four variable subset (*ZB*, *FDX*, *TS*, *S*) decreases the adjusted R^2 by 1%. Thus, for both *SL* and *SW*, the best subset (*ZB*, *FDX*, *TS*) is suggested.

Having established the best subset, I used stepwise regression analysis with backward elimination attempting to relate age-1 smolt size to biological variables (zooplankton biomass and smolt abundance) and lake temperatures. Taken together, the factors *ZB*, *FDX*, and *TS* (after appropriate transformation) accounted for 70% of the variation in *SL* and *SW* (Table 12). No other variables met the statistical criterion for remaining in the model. Thus, the explanatory variables retained by the stepwise procedure is in exact agreement with that using the best subset regression approach. The regression coefficients have the expected sign (i.e., positive for *ZB* and *TS*; negative for *FDX*) and their magnitude is similar to the coefficients in the single factor models presented earlier. In both models, the independent variables are all highly significant and have the same *P*-value. In addition, the *SL* multiple regression has a significant intercept, but the *SW* model does not. The coefficients of partial determination (r^2) indicate that *TS* reduces a significant amount (30%) of the variation in *SL* and *SW* when *ZB* and *FDX* are included in the models. In comparison, the partial- r^2 value indicates *ZB* reduces the variation in the models by about 40% when the variables *TS* and *FDX* are included in the model. Finally, when both *ZB* and *TS* are in the models, *FDX* reduces the variation by nearly 30% or about the same amount as does *TS*.

Examination of the residuals plotted against the fitted values shows both smolt size models are diagnostically well behaved, in that the data appear randomly distributed above and

Table 12. Multiple regression models for the dependence of age-1 smolt length (SL) and weight (SW) on zooplankton biomass (ZB), fry density index (FDX), and mean water column temperature (TS) for all lake types combined.

Model	N (lake years)	Model	Coefficient	SE	P -value	Partial r^2	R^2
$\text{Log}_{10} SL$	83	y -intercept	1.722	0.069	<0.0001	--	0.70
		$\text{Log}_{10} ZB$	0.121	0.018	<0.0001	0.36	
		$\text{Log}_{10} FDX$	-0.062	0.011	<0.0001	0.27	
		TS	0.024	0.005	<0.0001	0.26	
$\text{Log}_{10} SW$	84	y -intercept	0.122	0.216	0.5750	--	0.70
		$\text{Log}_{10} ZB$	0.385	0.056	<0.0001	0.37	
		$\text{Log}_{10} FDX$	-0.207	0.036	<0.0001	0.28	
		TS	0.077	0.014	<0.0001	0.26	

below zero. This pattern indicates no apparent bias by lake type nor presence of influential outliers, which is confirmed by the plots of predicted versus observed $\log_{10} SL$ and $\log_{10} SW$ (Figure 13A, B). However, after fitting the multiple regression, I was concerned with possible collinearity among ZB , FDX , and TS . Fortunately, in both models the partial correlation coefficient (r) between ZB and TS ($r < 0.10$) is negligible (Figure 14). In comparison, the partial- r value between TS and FDX is somewhat higher ($r = 0.27$), but I still considered this to be small. Also, the partial- r between ZB and FDX is not too large being $r = 0.29$ in the SL model and $r = 0.32$ in the SW model. Thus, I considered collinearity among the independent variables to be slight and of little consequence.

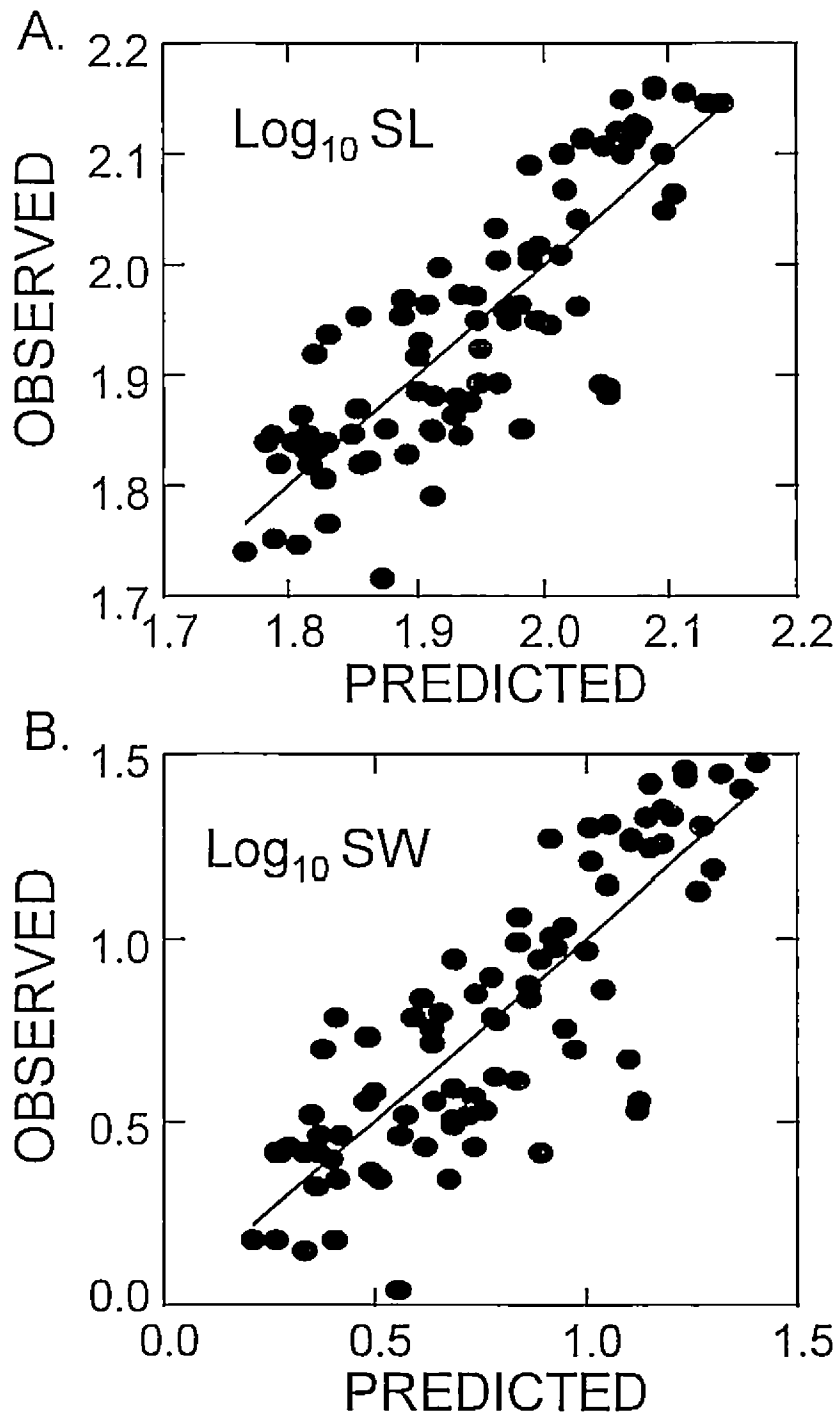


Figure 13. Plot of observed versus predicted values from multiple regression of log₁₀ age-1 smolt length (*SL*) versus log₁₀ zooplankton biomass (*ZB*), log₁₀ fry density index (*FDX*), and mean water column temperature (*TS*) (A); as for A except with log₁₀ age-1 smolt weight (*SW*) as the dependent variable (B).

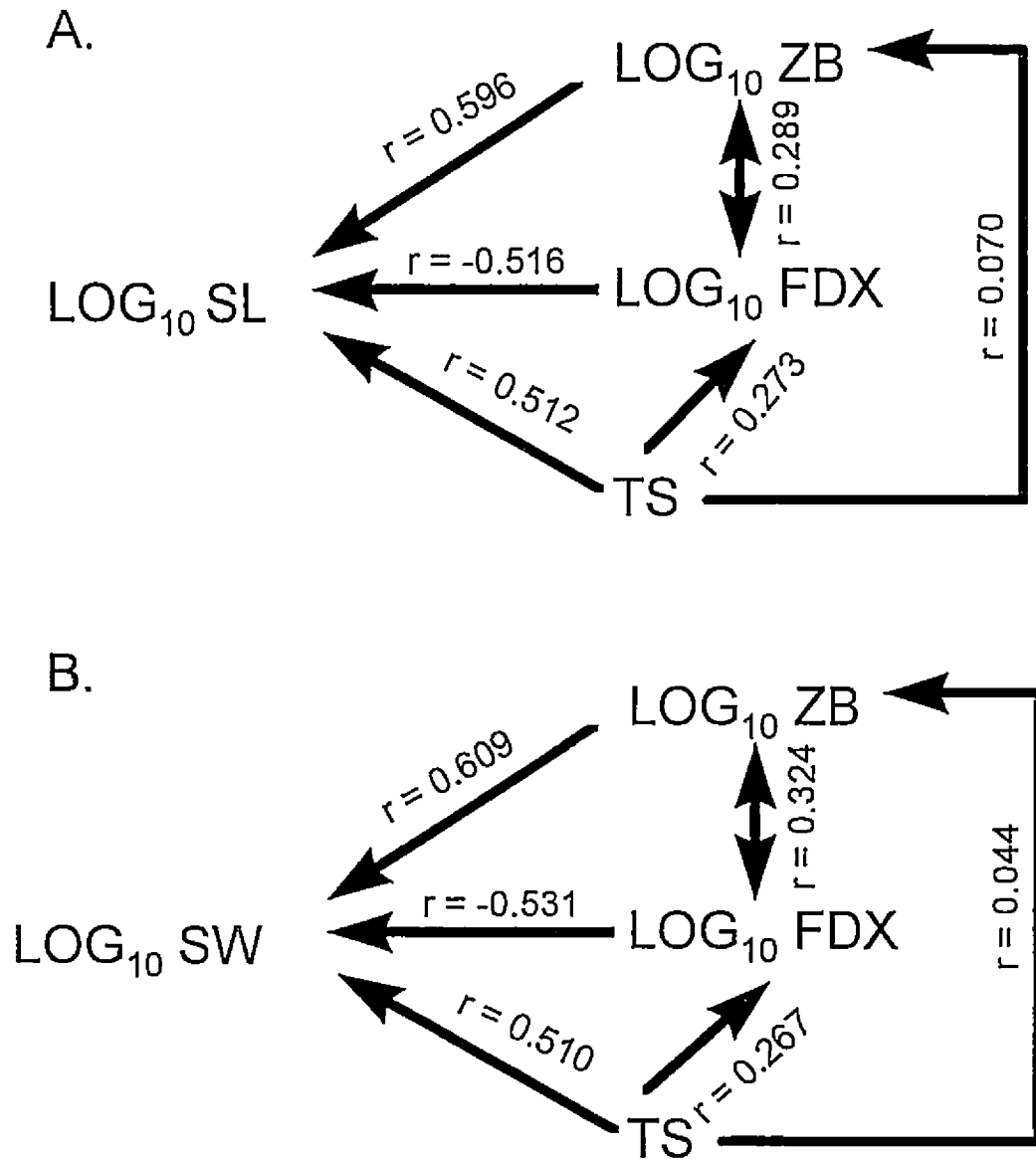


Figure 14. Path analysis with partial correlation coefficients (r) among age-1 smolt length (SL), zooplankton biomass (ZB), fry density index (FDX), and mean water column temperature (TS) for 83 lake years (A); as in A, except for age-1 smolt weight (SW) and 84 lake years (B). Arrows indicate the direction of effect.

DISCUSSION

Habitat temperature has a profound impact on organisms by affecting physiological rate processes and growth. For young sockeye salmon, their nursery habitat is that of freshwater lakes where they typically reside for 1 to 3 years feeding on plankton (crustaceans) prior to migrating out to sea as smolt. Rearing sockeye juveniles commonly exhibit rhythmic diel vertical migration (Narver 1970). That is, sockeye fry generally feed in the warmer surface waters at night and descend to cooler deeper waters during the day for digestion. Thus, quantifying the relative effect of temperature on juvenile sockeye growth in natural populations is problematic. Ideally, one would seek to know the amount of time sockeye spend at selected temperatures (depths) during their freshwater life history, along with detailed information on food (zooplankton) availability and distribution. Recent bioenergetic efficiency studies have shown the complex interaction among foraging behavior, predator avoidance, and temperature selection by salmon (Bevelhimer and Adams 1993; Lin and Regier 1995). However, this kind of sockeye distribution data are seemingly rare, at least for a broad number of lakes. Thus, the initial question raised is, how can we more easily define and quantify the thermal habitat or temperature regime experienced by rearing sockeye juveniles? In order to assess the potential temperature niche available for young salmon relative to their size at smoltification, I considered lake heat budgets and associated temperature-related variables as a reasonably sound alternative to obtaining specific rearing temperatures.

Hierarchical Governance of Variability in Thermal Regimes

For a given latitude, the primary factor controlling seasonal changes in water temperatures, stratification, and heat accumulation is the annual cycle of insolation received at that latitude (Hutchinson 1957). Insolation generally decreases with increasing

latitude resulting in cooler mean air temperatures and shorter growing seasons. Altitude generally has the same effect on temperature as does latitude. That is, air temperatures decrease with altitude. Because the lakes in my study are distributed over a relatively wide range in latitude and elevation (Table 1), quantification of a latitude-altitude (climate) gradient is important in understanding the hierarchical control of growing season trends, temperature cycles, and heat budgets even on a regional basis. For the Alaska lakes investigated here, the effect of a latitude-climatic gradient (55°-65° N) on length of growing season is obvious. Lakes in lower latitudes have earlier springs (Figure 6A) and longer growing seasons (Figure 6D) compared to higher latitudes. Altitude shows the same tendency (Figure 7A, B); however, its effect does not appear to be as strong as that of latitude (i.e., a poorer goodness-of-fit). Given the significance of both latitude and altitude, climatic influences were better assessed by multiple regression (Table 7). The multivariate model adheres to principle (i.e., the regression coefficients are of appropriate sign and magnitude), and more adequately ($r^2=0.65$) predicts growing season length. Although Geller (1992) established empirical relationships between latitude/elevation and surface temperatures for a group of Chilean lakes, average water temperatures (e.g., T_{1m} and TS) in the Alaska study lakes were unrelated to latitude or altitude. That neither latitude or altitude were strongly related to temperature or heat content suggested a more direct influence by other factors on heat uptake and temperature regimes.

Empirical studies have shown that morphometry (e.g., mean depth and volume) is a major factor influencing heat retention and the nature and extent of thermal stratification (Gorham 1964; Schindler 1971; Patalas 1984; Hanna 1990). The general rule-of-thumb is that larger deeper lakes store more heat than smaller shallower lakes. However, the findings of my empirical analysis do not seem, at least upon initial observation, to be entirely consistent with known physical principles governing temperature cycles and heat budgets. For instance, I found a very poor relationship between the summer heat budget and lake size in terms of mean depth (Figure 8A, 8B), area (Figure 8C) and volume

(Figure 8D), even though among this group lake volume varies by four orders of magnitude. That is, many of the stained and glacial lakes have much smaller heat budgets than expected for their size. Although heat uptake occurs primarily through absorption of solar radiation by the water, the proportion of incident light penetrating the water surface is dependent upon the nature and concentration of the principle light-attenuating component (Kirk 1994). Therefore, I considered lake typology differences as a causative factor for the large unaccounted for variation in the summer heat budget versus morphometry regressions.

Particulate or suspended materials in the upper layers can produce sharp thermal gradients as well as increasing density. For instance, Bowling and Salonen (1990) described steep shallow (1-3 m) summer thermoclines in several humic stained lakes in Finland. In a fish manipulation study, a decrease in zooplankton grazing pressure resulted in higher densities of phytoplankton which subsequently decreased light penetration, reduced the mixing depth, and lowered the heat content of the water column (Mazumder et al. 1990). Koenings et al. (1986) suggested backscattering by inorganic suspended silt particles decreased light penetration and lowered mean water temperatures in glacial lakes. A major difference among the Alaskan lakes in this study is that while many of them are clear (good water clarity) and have deep light penetration, the waters of stained and turbid lakes have comparatively shallow light penetration. Thus, I hypothesized that varying amounts of color (Pt units) or turbidity (NTU) might influence the rate of heating and thereby modify water temperatures and the summer heat budget (θ_s).

It is quite clear from my analysis that varying concentrations of organic stain (color) and glacial silt (turbidity) differentially influence surface temperatures (Figure 10A, B). This also implies higher heating rates in stained lakes and reduced heating rates in glacial lakes. The analysis seems to support this notion in that the onset of spring heating is 2 to 3 weeks earlier in stained lakes compared to clear and glacial lakes, though all lakes achieve

maximum temperatures at about the same time (Table 5). Bowling and Salonen (1990) also showed that rapid heat uptake promoted early and more stable thermal stratification in humic lakes compared to non-humic lakes of similar size. However, for the Alaska stained lakes the higher surface temperatures do not necessarily enhance the heat content. Instead, rapid spring warming tends to create a relatively steep thermal gradient thereby increasing resistance to wind-induced mixing, but most of the heat in stained lakes is stored in the first few meters. On the other hand, glacial lakes typically do not stratify in the summer, at least for prolonged periods. Yet, despite their deep mixing and heat potential, much of the water column remains near 4 °C from coldwater entering the basin at depth. Thus, stained and glacial lakes have large volumes of water that do not contribute significantly to the summer heat budget (Figure 11). The lack of correlation between mean depth and summer heat budget for the Alaska lakes now has a plausible explanation. However, cold isolated hypolimnia or cold water entering the basin at depth reduces the volume weighted temperatures, particularly so in deep lakes such as McDonald and Skilak lakes (Figure 11). Hence, as many of the stained and glacial lakes are deep (Table 1), mean water column temperature (*TS*) is strongly dependent upon lake depth (Figure 9A). Therefore, I conclude that *TS* is a more appropriate method for assessing thermal regimes across different lake types.

Defining Juvenile Sockeye Thermal Habitat

Because of the close correlation between air and surface water temperatures, thermal indices based on mean air temperature have been used to assess variation in freshwater fish species distribution (Shuter et al. 1980; Minns and Moore 1995), reproductive success (Serns 1982; Sabo and Orth 1995), and abundance (Kallemeyn 1987). The general conclusions reached in these studies are that colder temperatures have an indirect effect by reducing the growing season length (Sabo and Orth 1995) or temperature influences the

amount of accumulated energy (e.g., lipids) necessary for overwinter survival (Shuter et al. 1980). Unfortunately, detailed water temperature data are seldom available to assess the potential mechanisms of the meteorological-fish relationships. In addition, fish generally select the habitat temperature at which they carry out physiological functions with relatively high efficiency (Wootton 1990). That is, many freshwater fishes experience changes in water temperature because they migrate between the littoral and limnetic zones or between the epilimnion and profundal zone. As such, climate variables such as air temperature may not reflect a fish's thermal environment. For salmonids, density independent growth depends on the length of the growing season and water temperatures (Thorpe 1994).

It has been shown that length of growing season indirectly affects growth and survival of juvenile fish by controlling the rate of embryonic development (Sabo and Orth 1995). Hubert (1988) found that the distribution of small and largemouth bass in Wyoming was related to length of growing season, in that the species were not present in lakes with a growing season less than 100 d or lakes above 1900 m in altitude. For the Alaska lakes, climatic factors (latitude and altitude) explained much of the variation in length of growing season (S) (Table 7). However, I found no significant relationship between S and age-1 smolt size (Table 9). This is not entirely unexpected given the lack of correspondence between S and any of the water temperature variables. The effect of temperature on juvenile growth is hypothesized herein as being direct through metabolic influences or indirect through its effects on lake productivity (zooplankton). Although S might provide a reasonable means for assessing regional and annual variation in thermal regimes among lakes, it apparently does not summarize very well the in-lake rearing conditions imposed on juvenile sockeye salmon.

It is well known that sockeye salmon demonstrate diel vertical migration in response to a combination of foraging opportunities (Brett 1971), predator avoidance (Narver 1970),

and for reasons of bioenergetic efficiency (Bevelhimer and Adams 1993); however, there are certainly exceptions. In particular, water clarity has a profound effect on the amplitude of the diel vertical movement (Yanusz 1989). For instance, in Alaska, Schmidt et al. (1994) found that juvenile sockeye in moderately turbid Skilak Lake exhibited highly exaggerated diel migration extending from the just below the surface to depths of 80 m or more. In contrast, fry remain near the surface (5-10 m) throughout the summer in nearby and heavily turbid Tustumena Lake. On the other hand, sockeye fry preferred the 7° C isotherm just below the thermocline throughout the summer in stained Hugh-Smith Lake (Peltz and Koenings 1989). As a result, smolt size was smaller than expected based upon the large amount of zooplankton in the lake. Although I could not determine the average temperature experienced by rearing juvenile salmon for specific lakes, mean water column temperature (*TS*) incorporates both length of growing season and corresponding seasonal changes in temperatures at different depths (*see* methods). In addition, *TS* is strongly related to morphological characteristics (Figure 9A) and it is significantly influenced by varying amounts of color (Figure 10A) and turbidity (Figure 10B). That is, *TS* is constrained within definable bounds of climate, morphometry, and lake typology. My point is that *TS* probably captures much of the spatial and temporal ranges in temperature experienced by rearing juvenile fry. Therefore, I suggest the variable *TS* is a good index of the overall thermal conditions imposed on lake rearing fry.

Model Evaluation and Applications

To isolate the effect of temperature on fish growth, one also needs to consider the concomitant effects of the biotic factors such as food abundance and density dependent forces (Lehtonen and Lappalainen 1995). In my analysis, I examined these factors expressed as *TS* (habitat temperature), *ZB* (food), and *FDX* (sockeye fry density). Of the three variables, *ZB* is the strongest single predictor of smolt size (mean length and weight)

followed by *TS* and *FDX* (Table 9). Despite lake type differences in temperature regimes (Table 5), the nature of the response between age-1 smolt size and each of the independent variables is consistent with respect to sign and magnitude across the lake type (Table 10), so pooling the data across lake types in the single factor regression analysis was appropriate. From the standpoint of the goodness-of-fit criterion (r^2), the influence of *TS* is relatively weak (20%, Table 9). However, the interaction(s) between food and temperature may underlie the variation observed in juvenile sockeye salmon growth patterns. Thus, I considered a multiple regression approach to better assess temperature effects relative to food resource availability and fry density.

In developing my multivariate models predicting age-1 smolt length (*SL*) and weight (*SW*), I limited the pool of independent variables to four: *ZB*, *FDX*, *TS*, and *S* (Table 11). Although I derived several other temperature variables, some of which were well correlated with each other (Table 8), including them along with *TS* and *S* might have invoked collinearity, a condition that can lead to spurious correlations and improper conclusions (Neter et al. 1994). That is, correlations among the independent variables can create the potential for confounding effects in the model. The empirical models I derived for Alaskan lakes predict smolt size with a relatively high degree of accuracy ($r^2 = 0.70$). There is no apparent covariation in the model because the partial regression coefficients are of similar magnitude as in the single factor regressions. Despite the significance of temperature in the models, the idea that *TS* might affect smolt size indirectly by limiting zooplankton production seems a reasonable assumption. That is, unfavorable climatic conditions not only decrease water temperatures, but lower primary production (Nalewajko and Voltolina 1986) and zooplankton densities (Shuter and Ing 1997). For the Alaska lakes in this study, there is little association between *ZB* and any of the other thermal characteristics (Table 8). Moreover, there is no collinearity between zooplankton biomass and *TS* in either of the multivariate models as evidenced by the small partial- r values (Figure 14). This apparent lack of correlation suggests that the influence of

temperature has more of a direct effect on juvenile fry growth by affecting vital metabolic rates. Therefore, I reject my null hypothesis that there is no effect of temperature on the growth of sockeye fry. The fact that it was possible to demonstrate a temperature relationship, despite the confounding variables of zooplankton biomass and fry density, indicates that temperature has a major effect on the growth of rearing sockeye fry as indexed by age-1 smolt size (Figure 14).

It is not my intention, however, to discuss the mechanisms behind the rate of physiological processes in response to temperature in conjunction with food resource availability and fish density. The literature is replete with both laboratory experiments, field studies and computer simulations dealing with this subject (e.g., Brett 1971; Serns 1982; Bellhaver and Adams 1993; Lin and Regier 1995). Instead, the models I developed here provide some ecological insight as to the combined effect of food assimilation, bioenergetics, migration behavior, and thermal conditions on juvenile sockeye growth which may have some application in fishery enhancement and management programs. Our empirical knowledge of how food acquisition, predation and competition, and temperature interact to affect the growth of sockeye smolt could lead to improved efforts in managing and enhancing this species, particularly along a regional basis or in the context of multiple lake types. There are practical applications for such a device.

Alaska's sockeye salmon fisheries are managed using defined spawner-escapement goals and stock-recruitment analysis. However, to assume that factors regulating salmon populations in their natal lakes remain relatively constant is naïve (Rigler 1982; Schmidt et al. 1997). That is, recruitment into stock is not independent of other biotic and abiotic components. For example, large escapements can decrease a lake's productivity, and subsequent adult returns, through excessive grazing on the zooplankton forage base (Kyle et al. 1988; Schmidt et al. 1995). In addition, acceleration or deceleration of fry emergence due to annual temperature variations could place rearing juveniles in an

unfavorable environment that is offset from peak zooplankton abundance (Koenig and Burkett 1987). There is also strong evidence that marine survival increases with increasing size of juvenile Pacific salmon at their time of entry into the ocean. Koenigs et al. (1993) showed that smolt-to-adult survival of smaller sockeye smolts (<90 mm) increased with size, but survival of larger (>90 mm) smolts did not for a number of Alaska, Canada, and Russia fish stocks. Thus, the dependence of sockeye smolt size on temperature, as well as density dependent factors (Figure 14) argues for including limnological data in standard stock-recruit (e.g., Ricker) models. In particular, juvenile salmon growth and survival should be used in conjunction with lake physical characteristics (i.e., temperature) and other biotic components to develop or refine escapement goals. I believe this approach will lead to improvements in the ability to predict future fish stocks.

Conclusion

The present data show that latitude, altitude, morphometry, and water clarity affect the variation in length of growing season, water temperature, summer stratification and heat content in sockeye salmon nursery lakes. Seasonal mean water column temperature is the most appropriate method of comparing lake thermal regimes among different lake types. Mean water column temperature accounts for a substantial amount of the variation observed in age-1 sockeye smolt size (length and weight); however, smolt size cannot be predicted on the basis of water temperature alone. The obvious importance of food resource availability (zooplankton) and density-dependent forces must be included when forecasting smolt size. The multivariate models appear to have good explanatory capabilities with respect to physiological responses to temperature. However, more research is needed to shed light on the particular causal mechanisms for the direct relationship between water temperature and juvenile sockeye growth.

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