

Caveats on the use of paleolimnology to infer Pacific salmon returns

William O. Hobbs¹ and Alexander P. Wolfe

Department of Earth and Atmospheric Science, University of Alberta, Edmonton, Alberta T6G 2E3, Canada

Abstract

The ability of paleolimnology to reconstruct historical sockeye salmon (*Oncorhynchus nerka*) abundance was assessed at Fraser Lake, an important nursery lake in the interior of British Columbia (BC), Canada. Multiple sediment proxies of lake production, as well as nitrogen and carbon stable isotopes, all portray relatively complacent stratigraphies, despite well-monitored changes in salmon returns over the most recent 60 years. The separation of autochthonous from total sediment organic matter did not clarify the identification of the nitrogen isotopic fingerprint of marine-derived nutrients (MDN). Slight shifts in diatom assemblages are better interpreted as responses to either early human activities in the catchment or post–Little Ice Age climate warming. The low proportion of MDN in the lake’s annual budget (3% N and 7% P) is the probable reason their influence is not expressed in lake sediments. Thus, paleolimnology is incapable of providing unequivocal inferences concerning historical salmon abundances in Fraser Lake, in contrast to lakes from southern Alaska, where the same techniques have yielded unambiguous results. Sediment MDN proxies, together with catchment characteristics and escapement data, were collated for an additional nine sockeye nursery lakes spanning southern Alaska to southern BC. Primary production and biogeochemical cycling in Alaskan nursery lakes appears largely driven by MDN from sockeye returns, whereas BC lakes are more strongly influenced by allochthonous organic matter and lake-water residence times. Alaskan lakes possess the limnological features that are prerequisite for meaningful salmon reconstructions using paleolimnology, while lakes from southern BC do not. This does not suggest that MDN are unimportant in southern BC lakes but rather that they are not readily disentangled from other factors that shape the paleolimnological record.

Pacific salmon (*Oncorhynchus* spp.) are important elements of the natural, economic, and cultural fabric of British Columbia (BC). Changes in Pacific salmon populations have been attributed alternately to overfishing, habitat loss, and climate-driven oceanographic changes. Salmon life histories link marine and freshwater ecosystems, and thus they represent keystone organisms. For example, semelparous spawning salmon provide an essential source of marine-derived nutrients (MDN, mainly nitrogen [N] and phosphorus [P]) to nursery lakes and rivers (Finney et al. 2000; Naiman et al. 2002). The importance of these nutrient subsidies is sufficient to influence riparian and terrestrial production adjacent to salmon spawning habitats (Reimchen et al. 2002; Helfield and Naiman 2006). In the case of sockeye salmon (*Oncorhynchus nerka*), lakes are exclusively used as rearing habitat during the first year, where parr benefit from nutrients accrued by the disarticulation and decomposition of adult carcasses in upstream spawning reaches. Via these mechanisms, there is potential for positive feedback

between annual adult returns and eventual juvenile migration to the ocean as smolts.

Variability of sockeye MDN subsidies are tracked by lake phytoplankton production. Elevated MDN can induce dominance by eutrophic taxa such as diatoms of the genus *Stephanodiscus* (Finney et al. 2000). Because salmon accrue 95% of their biomass at sea (Groot and Margolis 1991), where they occupy an elevated trophic position, there is enrichment in their nitrogen stable isotopic composition (¹⁵N: ¹⁴N) relative to a purely freshwater life history. Dead salmon enrich the isotopic signature of N in spawning grounds, so that entire drainages, including nursery lakes, become geochemically distinct from non–salmon bearing counterparts, to degrees that are proportional to the numbers of salmon that return and die (Naiman et al. 2002). As a result, the combination of biological and geochemical proxies in lake sediments has been used successfully to reconstruct historical sockeye salmon abundance in a number of Alaskan lake basins (Gregory-Eaves et al. 2004; Schindler et al. 2005).

The applicability of paleolimnological techniques for inferring salmon populations has not been comprehensively assessed outside Alaska. Holtham et al. (2004) presented results from a nursery lake on Vancouver Island (British Columbia, Canada) that did not record the influence of MDN subsidies, leaving open the possibility that paleolimnology may not be universally applicable to the reconstruction of sockeye salmon abundances. There have been no prior studies from nursery lakes of the Fraser River drainage in the BC interior, where salmon travel up to 1,000 km to reach spawning habitat. The Fraser River is among the world’s most productive salmon fisheries (Groot and Margolis 1991). Here, we present results of paleosal-

¹ Corresponding author (whobbs@ualberta.ca).

Acknowledgments

We thank Lauren Walker for help with fieldwork and Margo French of the Carrier Sekani Tribal Council for logistical support at Fraser Lake. Comments by Dr. Mark Brenner and an anonymous reviewer greatly improved this manuscript. Stable isotope analyses were completed at the University of California, Davis, Stable Isotope Facility. ²¹⁰Pb analyses were performed by MyCore Scientific Ltd, Deep River, Ontario.

This research was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) through awards to both authors.

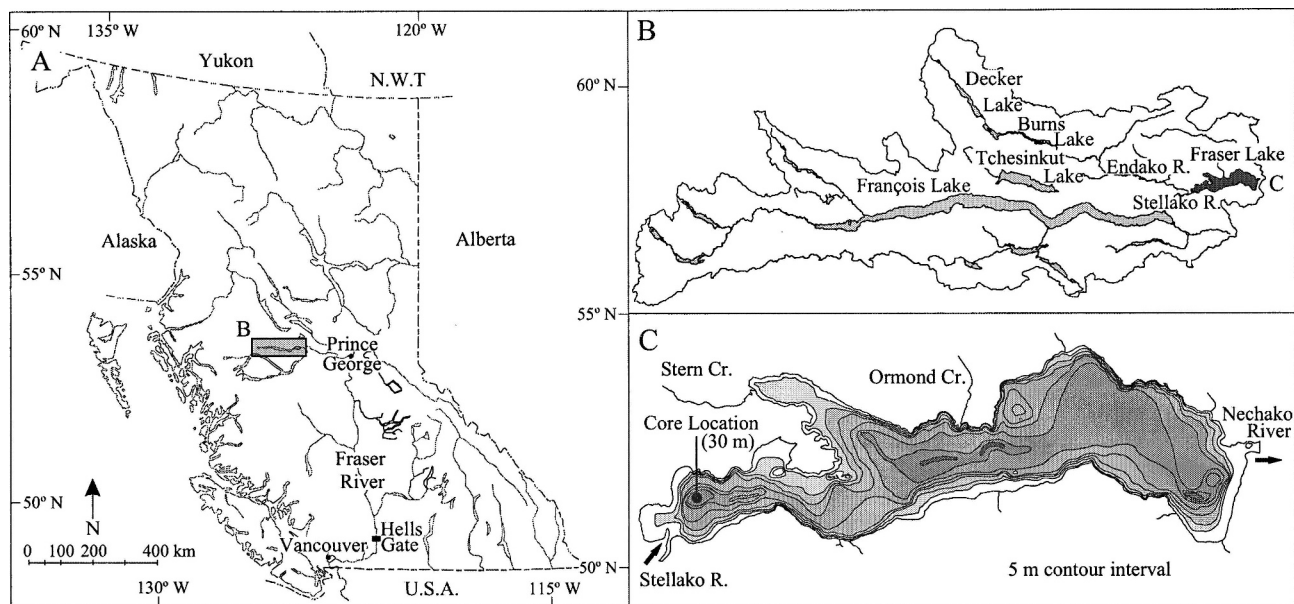


Fig. 1. (A) Site location map of Fraser Lake, British Columbia, Canada. (B) Fraser Lake catchment and (C) bathymetry of the lake showing location of the sediment core from the western basin.

on investigations from Fraser Lake, a large nursery lake near the distal range of sockeye migration in the Fraser River Basin (Fig. 1). These results are considered in the context of additional unpublished results from BC as well as previously published sites from Alaska and coastal BC. Together, these findings provide guidance for future investigations by specifying site characteristics that appear to maximize the probability that meaningful salmon signatures are preserved in lake sediments.

Study site

Fraser Lake ($54^{\circ}05'N$, $124^{\circ}45'W$) has a 6,707-km² catchment that incorporates several additional large lakes, namely, François, Decker, Burns, and Tchesinkut (Fig. 1). The entire region falls within the Sub-Boreal Spruce biogeoclimatic zone, characterized by englemann-white spruce, subalpine fir, and lodgepole pine. Approximately 92% of drainage into Fraser Lake is contributed by the Endako and Stellako rivers. The lake is dimictic and clear and has a photic zone of 12 m during summer stratification (Carmichael 1985). The residence time of lake water is less than a year (Table 1). Primary and secondary production in Fraser Lake is somewhat higher than other BC salmon nursery lakes. Fraser Lake is currently mesotrophic and experiences a depletion of N during the growing season, in addition to persistently high P concentrations and stable thermal stratification. Fraser Lake appears to have switched from P limitation to N limitation in the 1970s (Shortreed et al. 2001).

Of the 17 most important sockeye nursery lakes in the Fraser River basin, Fraser Lake has the fifth-highest mean number of returning salmon (escapement), and the second-highest spawner density behind Chilko Lake (Shortreed et al. 2001). Salmon migrate an estimated 820 km from the

mouth of the Fraser River to spawning grounds primarily in the Stellako River but also the Endako River and Ormond Creek (Fig. 1). Department of Fisheries and Oceans Canada records for the Stellako date back to 1938 and document an increase in escapement post-1970,

Table 1. Fraser Lake morphometry, water chemistry (1992–1993), and sockeye salmon escapement abundance (DFO, 1938–2004).

Lake morphometry	
Longitude	124°45'W
Latitude	54°05'N
Elevation (m a.s.l.)	670.0
Z _{max} (m)	30.5
Z _{mean} (m)	13.4
Lake volume (×10 ⁹ L)	725.3
Catchment area (km ²)	6,707.1
Lake area (km ²)	54.6
Catchment : lake ratio	121.8
Water residence time (yr)	0.8
Sockeye salmon escapement (10 ³ fish)	
Mean escapement	91.6
Minimum escapement	2.6
Maximum escapement	372.5
Spawner density (10 ³ km ⁻²)	1.7
Water chemistry ^a	
Mean NO ₃ ⁻ (μg L ⁻¹)	3.3
Spring overturn NO ₃ ⁻ (μg L ⁻¹)	3.0
Seasonal minimum NO ₃ ⁻ (μg L ⁻¹)	0.9
Mean TP (μg L ⁻¹)	15.4
Spring overturn TP (μg L ⁻¹)	17.8
Chlorophyll <i>a</i> (μg L ⁻¹)	4.2
pH	7.5

^a Shortreed et al. (2001), *n* = 12.

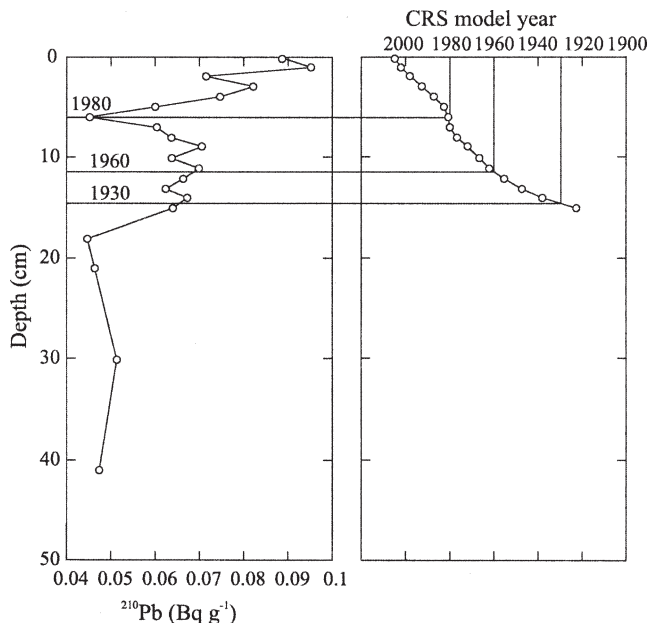


Fig. 2. ^{210}Pb chronology from the Fraser Lake gravity core. Sediment ages are estimated using the constant rate of supply (CRS) model.

with highs of $\sim 370,000$ fish in 1988 and 2000. Prior to 1938, significant impacts to the run occurred with the onset of commercial fishing and the establishment of Fraser River canneries in the late 1800s and following a series of catastrophic landslides at Hells Gate in 1913–1914 (Fig. 1). The first fishway that bypasses the Hells Gate slide was completed in 1917, allowing for slow recovery of all upstream runs in the Fraser River basin (Thompson 1945).

Methods

Core collection and chronology—A 41-cm sediment core was recovered from the western basin of Fraser Lake on 27 May 2004 (Fig. 1). A modified Kajak-Brinkhurst gravity corer was used to collect a continuous sediment record with an intact sediment–water interface (Glew et al. 2001). The core was extruded and subsampled at 0.25-cm intervals for the first 10 cm and 0.5 cm thereafter, using a high-resolution sectioning device (Glew et al. 2001). Core chronology was established using the inventory of unsupported ^{210}Pb activity measured by alpha spectroscopy, to which the constant rate of supply (CRS) model was applied (Appleby and Oldfield 1978). Because the inventory of unsupported ^{210}Pb becomes exhausted at 18 cm (Fig. 2), sedimentation rates from the lower dated portion of the core (10–15 cm) were extrapolated to predict the age of deeper sediments, resulting in an estimated age of about A.D. 1735 at 41-cm depth.

Sediment geochemistry—Isotopic ratios and elemental abundances of N and C were determined from 0.25-cm increments taken every 2 cm from the Fraser Lake core in order to ascertain the applicability of $\delta^{15}\text{N}$ as a proxy for

MDN in Fraser Lake and to provide indications of the source of organic matter from molar C:N ratios. This sampling provides approximately decadal temporal resolution for the core, which should be sufficient to identify impacts associated with major events, such as the legacy of the Hells Gate slides in 1913–1914, which depressed stocks for several decades. Natural abundances of stable carbon (^{13}C : ^{12}C) and nitrogen isotopes (^{15}N : ^{14}N) are reported as per mil (‰) using delta notation ($\delta^{13}\text{C}$; $\delta^{15}\text{N}$). $\delta^{15}\text{N}$ is reported relative to air ($\delta^{15}\text{N} = 0\text{‰}$) and $\delta^{13}\text{C}$ relative to the Vienna Pee Dee Belemnite (VPDB) marine-carbonate standard for carbon and oxygen. Samples were analyzed by continuous-flow isotope-ratio mass spectrometry, following pyrolysis and gas chromatographic separation in a coupled elemental analyzer. Analytical precision for isotopic analyses was $\pm 0.15\text{‰}$ ($\delta^{15}\text{N}$) and $\pm 0.03\text{‰}$ ($\delta^{13}\text{C}$), as calculated by the analysis of laboratory standards. In addition to %C and %N obtained from elemental analysis, total organic matter content (%OM) was estimated by loss on ignition following Heiri et al. (2001).

Organic matter separations—Following initial nitrogen isotopic measurements that failed to reveal an interpretable MDN signal in Fraser Lake bulk sediments, a density separation of sediment organic matter was undertaken to isolate a fraction representative of solely autochthonous sources. This was undertaken in an attempt to remove the potential overprinting of the aquatic isotopic signature, including that attributable to salmon, from terrestrial organic matter. The density separation protocol followed that of Hamilton et al. (2005), in which a slurry of sediment (100–200 mg) is slowly introduced to colloidal silica medium at a density 1.27 g cm^{-3} . The light organic matter (LOM) recovered from the supernatant, deemed to reflect primarily in-lake algal and microbial production, was then analyzed for $\delta^{15}\text{N}$. Both LOM and the remaining fraction were microscopically examined, which confirmed that different compositions were indeed separated from each other.

Diatom preparation, identification, and enumeration—For diatom analysis, aliquots of 100 mg dry sediment were oxidized with 30% H_2O_2 to remove organic matter in preparation for identification and enumeration. General slide preparation and diatom enumeration protocols are presented elsewhere (Battarbee et al. 2001). Microscope slides were permanently mounted using Naphrax[®]. Between 400 and 500 diatom valves were counted from each sample under oil immersion at $\times 1,000$, using differential interference contrast optics. Diatom taxonomy followed Krammer and Lange-Bertalot (1986–1991), Cumming et al. (1995), and Fallu et al. (2000), with genus-level nomenclatural revision according to Round et al. (1990). Diatom counts are expressed as frequencies (%) of taxa relative to the sum of valves counted in any one sample.

Spectrally inferred chlorophyll a—Fossil chlorophyll a (Chl a) in lake sediments provides an indication of total algal production within the lake. A nondestructive method of inferring Chl a concentrations from the spectral

properties of freeze-dried lake sediments was applied to Fraser Lake samples (Wolfe et al. 2006). This method exploits sediment red reflection (650–700 nm) to estimate concentrations of Chl *a* and its degradational pheopigments (primarily pheophytin *a* and pheophorbide *a*). The description and protocols of this method can be found in Wolfe et al. (2006).

Statistical methods—Diatom stratigraphic zones were determined objectively by stratigraphically constrained cluster analysis, using the squared chord distance metric. Compositional changes in diatom assemblages were summarized by ordination, using a detrended correspondence analysis (DCA) performed on the relative frequencies of each taxon >1% in any one sample (Hill and Gauch 1980). This amounts to the inclusion of between 8 and 15 taxa per sample, more than are illustrated for some intervals (Fig. 3). Plotted stratigraphically, the diatom DCA axis 1 sample scores graphically depict down-core diatom assemblage compositional changes (Birks et al. 2000). The sample scores are expressed in standard deviation (or turnover) units along the primary axis. Eigenvalues of the DCA axes 1 through 4 were 0.15, 0.06, 0.05, and 0.03, respectively. Prior to DCA, all data were square-root transformed, detrended by segments, and rare species were down-weighted.

A second ordination was undertaken to compare new results with previously published data pertaining to sediment MDN records in relation to lake features. For a series of 10 lakes in Alaska and BC, the following parameters were tabulated: catchment:lake ratio, catchment area, sockeye escapement, spawner density, mean sediment C:N, and $\delta^{15}\text{N}$. Data for five of these lakes are published (Finney et al. 2000; Gregory-Eaves et al. 2004; Holtham et al. 2004). The remaining lakes include Fraser and the authors' unpublished data from four additional lakes in the interior (N. Barrière and McKinley) and coast of BC (Nahwitti and Clayoquot). Principal components analysis (PCA) was applied to a correlation matrix based on these data, thereby providing a synthetic overview of how reliably the MDN signature is transferred to lake sediments. Lake parameters were centered and standardized, and ordinations were conducted with CANOCO v.4.

Results

^{210}Pb chronology—Supported levels of ^{210}Pb were attained in the Fraser Lake Glew core at a depth of 18 cm. However, the unsupported inventory does not decline exponentially with depth but rather contains several intervals of moderately to strongly diluted ^{210}Pb activity (Fig. 2). The most plausible explanation for these dilutions is short-lived events of accelerated inorganic sedimentation, given that the most pronounced depletions of the unsupported ^{210}Pb inventory (2 and 7 cm) coincide with reduction in sediment organic content (Fig. 3). Extensive land-use changes in the basin, coupled to exceptionally high fluvial discharges into Fraser Lake during several years in the 1980s and 1990s (Carmichael 1985), are the most likely causes of irregular sedimentation patterns at the coring site.

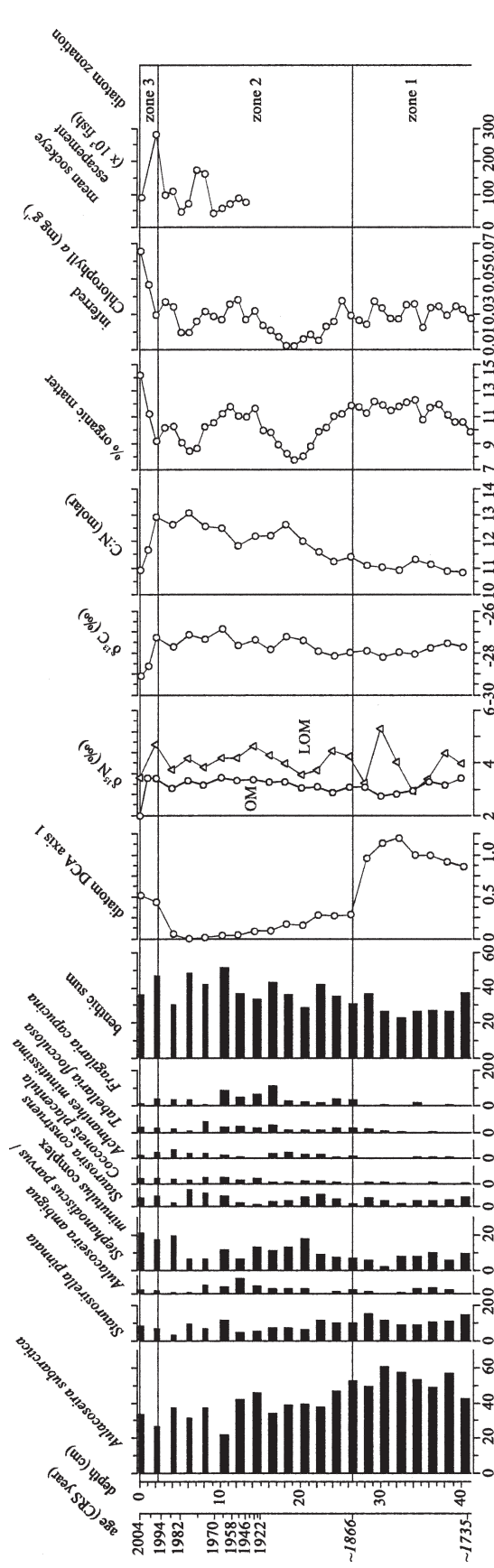


Fig. 3. Diatom and geochemical stratigraphy of the Fraser Lake sediment core. Relative abundances of diatom taxa are shown as black solid bars, where the thickness of the bars is proportional to sample thicknesses. DCA axis 1 scores summarize diatom compositional changes. $\delta^{15}\text{N}$ results from bulk OM (open circles) and LOM (open triangles) are shown on the same plot, alongside $\delta^{13}\text{C}$, C:N, %OM, inferred Chl *a*, and sockeye escapement (1938–2004) averaged over dated sediment intervals. Extrapolated CRS model ages are included in italics.

Nonetheless, the ^{210}Pb results can be accommodated by the CRS model to produce a realistic age model for the last ~ 75 yr. This model (Fig. 2) depicts a rapid increase in sediment accumulation rate after ~ 1980 . At this time, the average accumulation rate of 1.6 mm yr^{-1} for the 1930–1980 interval rose to 2.6 mm yr^{-1} for 1980–2005. Previous results from the west basin of Fraser Lake documented similar sedimentation increases in the uppermost 10 cm of core (Cumming 2001). Hydrological monitoring of the Stellako River by Environment Canada shows peak mean annual flows in 1976 that correspond to the estimated ^{210}Pb age (within 1σ) of the noted excursions.

Diatom stratigraphy—Diatom valves were well preserved in the sediments of Fraser Lake, with no indications of dissolution. A total of 195 diatom taxa were identified, of which only taxa exceeding 3% in any sample are illustrated (Fig. 3). Diatom assemblages show few major changes over the period of deposition. There is a clear dominance throughout the core by the planktonic diatom *Aulacoseira subarctica*, a meso- to eutrophic taxon (Fig. 3). Phytoplankton samples taken during the growing season from the water column of Fraser Lake show an early spring and late summer dominance of *A. subarctica* with *Asterionella* spp. and *Stephanodiscus* spp. (Carmichael 1985).

Despite the dominance by one species of diatom, there are subtle changes significant enough for a cluster analysis to define three zones of similarity. The first zone extends from the bottom of the core (41 cm) to 26 cm. Subdominant taxa include the planktonic diatoms *Stephanodiscus parvus* and *S. minutulus*, both eutrophic diatoms, and *Staurosirella pinnata*, a benthic species with a wide tolerance of nutrient conditions (Christie and Smol 1993; Reavie et al. 1995). The high percent abundance of *A. subarctica* ($>60\%$) translates into the low observed total benthic sum in zone 1. The second zone is essentially the remainder of the core, extending from 26 to 2.5 cm and starts at approximately the mid-1800s. At the bottom of this zone, *A. subarctica* declines in concordance with increases in the *S. parvus/S. minutulus* complex and other planktonic spp. (*Fragilaria capucina* and *Tabellaria flocculosa*). Optimum nutrient conditions for *F. capucina* and *T. flocculosa* are eutrophic; however, a large tolerance has also been observed suggesting more meso- to eutrophic conditions (Reavie et al. 1995). The percent abundance of the benthic taxa *Cocconeis placentula* and *Achnanthes minutissima*, which have a wide tolerance to nitrogen and phosphorus concentrations (Christie and Smol 1993; Stevenson 1995), also increase in zone 2. Diatom DCA scores show that the assemblages exhibit very low compositional changes throughout this zone (Fig. 3). The uppermost zone 3 (2.5 cm to surface) shows the largest percent abundance in the *S. parvus/S. minutulus* complex (21.6%), suggesting increasingly eutrophic conditions. Other planktonic diatoms (*A. subarctica*, *F. capucina*, and *T. flocculosa*) decrease in percent abundance during this time period, while the benthic taxa remain similar to zone 2. This zone represents an estimated age of 1997 to present.

Geochemistry, spectrally inferred chl a, and sockeye escapement—The $\delta^{15}\text{N}$ of organic matter from sediment core samples ranged from 2.02‰ to 3.44‰ (Fig. 3). There is only a subtle variation of $\sim 0.30\%$ throughout most of the core, with the exception of the uppermost surface sample, which is isotopically depleted by 1.4‰ relative to the underlying sample. In order to explore relationships between $\delta^{15}\text{N}$ and sockeye escapement, the annual sockeye escapement data were averaged over the intervals represented by individual sediment slices, according to the ^{210}Pb dating results (Fig. 2). In so doing, the escapement data represent integrations of time that are directly compatible with the resolution of the sediment record (multiannual to decadal). No clear relationship was found between $\delta^{15}\text{N}$ and salmon escapement.

The $\delta^{13}\text{C}$ of bulk organic sediment shows some variation down-core (-26.88% to -29.13% ; $\sigma = 0.48\%$), including a 1.87‰ depletion in the upper 2 cm of the core (Fig. 3). The C:N exhibits a range of 10.8–13.1, suggesting that Fraser Lake organic matter is mainly aquatically derived, which is also confirmed by the strong relationship between %OM and Chl *a* (Fig. 3; $n = 42$, $r = 0.77$, $p < 0.001$). The reliability of C:N as a proxy for organic matter source is also supported by the diatoms: DCA axis 1 scores are correlated to sediment C:N ($n = 21$; $r = -0.78$; $p < 0.001$), with the lowest C:N values associated with the greatest abundances of planktonic taxa.

Stratigraphically, geochemical variables vary very little in diatom zone 1 (26–40 cm) of the core, with the exception of the depletion of $\delta^{15}\text{N}$ synchronous to a positive excursion in the diatom DCA axis 1 (28–34 cm; Fig. 3). The second diatom zone (2.5–26 cm), beginning in approximately the mid-1800s, displays increased variation in %OM coincident with Chl *a* and an increase in C:N. The third diatom zone shows the greatest amount of change geochemically, evidenced by isotopic depletions and increased algal-derived OM.

Organic matter separations—Microscopic inspection of the LOM and remaining ($\rho > 1.27 \text{ g cm}^{-3}$) fractions revealed two different compositions; while LOM contained diatom frustules and green to gray amorphous organic matter, the denser fraction comprised charcoal, plant ligneous tissues, abundant pollen grains, and relatively few diatom frustules. These observations strongly suggest that the density separation was highly successful in separating aquatic from terrestrial sediment organic matter (Hamilton et al. 2005).

Isotopically, $\delta^{15}\text{N}_{\text{LOM}}$ is enriched on average 1‰ relative to $\delta^{15}\text{N}_{\text{BULK}}$, whereas $\delta^{13}\text{C}_{\text{LOM}}$ is depleted on average by 1‰ relative to $\delta^{13}\text{C}_{\text{BULK}}$. The coisotopic plot of LOM and BULK fractions reveals that they are indeed distinct (Fig. 4). Consistently low $\delta^{13}\text{C}_{\text{LOM}}$ values imply that primarily aquatic OM was recovered by the density separation, which is supported by the lower C:N of this fraction ($\Delta\text{C:N}_{\text{BULK-LOM}} = 1.0\text{--}2.1$; $n = 19$). The stratigraphic record of $\delta^{15}\text{N}$ for both fractions (Fig. 3) shows that, with the exception of three intervals (28, 34, and 36 cm), the $\delta^{15}\text{N}_{\text{LOM}}$ is significantly enriched (by

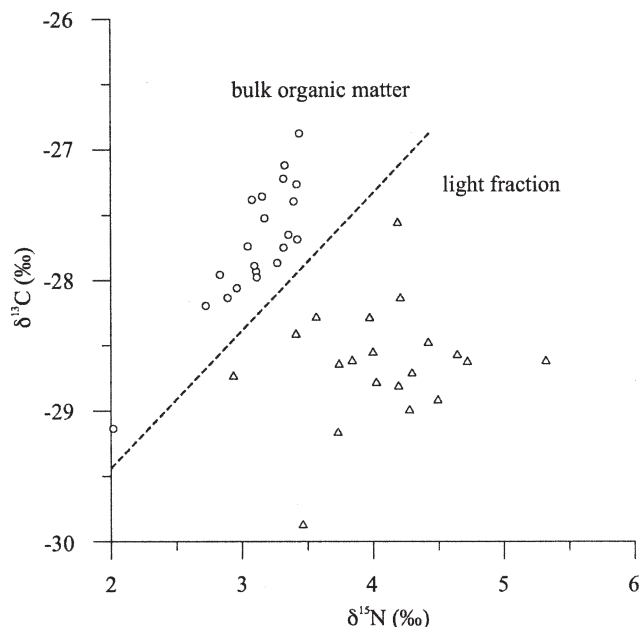


Fig. 4. Coisotopic plot ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of bulk organic matter (open circles) and the density-separated light fraction (open triangles) from the Fraser Lake core. The dashed line separates the two fractions.

$\geq 0.30\text{‰}$, or twice instrument precision) relative to $\delta^{15}\text{N}_{\text{BULK}}$. Neither the primarily aquatic LOM nor the bulk fraction produce N-isotopic results that can be interpreted with respect to salmon escapement (Fig. 3).

Discussion

Paleosalmon proxies—The use of lake-sediment $\delta^{15}\text{N}$ as a proxy of sockeye salmon abundance in nursery lake ecosystems has been applied with success in coastal Alaska (Finney et al. 2000; Gregory-Eaves et al. 2004; Schindler et al. 2005). The most striking difference between studies from Alaska and our data is the upper range of sediment $\delta^{15}\text{N}$ values. Finney et al. (2000) have reported $\delta^{15}\text{N}$ in sediment OM from Karluk Lake, Alaska ranging from 6.20‰ to 9.75‰, whereas Fraser Lake exhibits a narrower range of 2.02–3.44‰. The $\delta^{15}\text{N}$ of *O. nerka* is reported to be $11.2 \pm 0.45\text{‰}$ (Schindler et al. 2005). Studies have shown there is little diagenetic fractionation of the $\delta^{15}\text{N}$ of lake seston, indicating the sediments are reliable archive of $\delta^{15}\text{N}$ of primary OM (Hodell and Schelske 1998; Teranes and Bernasconi 2000). The more depleted $\delta^{15}\text{N}$ of Fraser Lake sediments, combined with the absence of correlation to sockeye escapement, suggests that variability of the MDN subsidy to this lake is not registered.

The most probable explanation for the absence of an MDN influence to Fraser Lake is the estimated proportion it contributes to the annual nutrient budget of the lake. An approximate annual nutrient budget from fluvial inputs to Fraser lake suggested that only 3% N and 7% P was attributable to sockeye salmon (Carmichael 1985). In comparison, sockeye contribute $>50\%$ N and $\sim 60\%$ P to

Karluk Lake (Koenings and Burkett 1987; Finney et al. 2000).

Summer lake-water chemistry shows complete utilization of the Fraser Lake N pool for much of the growing season (Shortreed et al. 2001). We thus consider the possibility that periodic N limitation may have stimulated cyanobacterial N fixation, in turn accruing isotopically light OM to sediments and inducing relatively low sediment $\delta^{15}\text{N}$ values (Peterson and Fry 1987). The main source of N for Fraser Lake is via the Endako–Stellako River basins, which are influenced by surrounding forests and agricultural land use. Nitrate and ammonium fertilizers tend to have a $\delta^{15}\text{N}$ ranging from -3‰ to 3‰ (Macko and Ostrom 1994), while the $\delta^{15}\text{N}$ of forest litter and surface soils are $\leq 0\text{‰}$ (Nadelhoffer and Fry 1994). Because terrestrially derived N is isotopically depleted relative to sockeye salmon, we interpret the low $\delta^{15}\text{N}$ of Fraser Lake sediments to reflect a large terrestrial contribution to sediment OM.

The main compositional change in diatom assemblages over about the past 265 yr is in the mid- to late 1800s (Fig. 3). Having established that Fraser Lake is not responding to changes in MDN, the observed change in diatom assemblages can be attributed to either human disturbance within the catchment, through forestry and agricultural activities, or regional warming following the Little Ice Age (Wilson and Luckman 2003). The increased presence of meso- to eutrophic species (i.e., *F. capucina*, *S. parvus/minusculus*) suggests an increased nutrient load. Elevated sediment C:N values in diatom zone 2 are consistent with sustained terrestrial inputs (Kaushal and Binford 1999). A second compositional change in the 1980s, highlighted by further increase in *S. minutulus/parvus*, seems to track further anthropogenic enrichment of Fraser Lake. However, none of these changes can be reliably tied to the lake's salmon history, unlike the diatom signatures observed in Alaskan counterparts (Finney et al. 2000).

Paleolimnology and sockeye salmon—To investigate the first-order controls on the likelihood of success using paleolimnology to infer historical salmon abundances, we analyzed known key variables in site selection (sockeye escapement, spawner density, catchment area, catchment:lake ratio) and subsequent analytical results (mean $\delta^{15}\text{N}$ and C:N) for a number of salmon nursery lakes on a latitudinal gradient from Kodiak Island, Alaska, to southern coastal BC (Fig. 5). PCA loadings of the collated parameters reveal that variability among the sites on the primary axis is strongly influenced by C:N, $\delta^{15}\text{N}$, and sockeye escapement (Fig. 5A). The first axis explains 50% of variability within the data set. Catchment area and catchment:lake ratio are associated with the second PCA axis (29%). The PCA biplot shows Alaskan lakes to be most closely associated with sockeye escapement, spawner density, and sediment $\delta^{15}\text{N}$ (Fig. 5B). Coastal and interior lakes from BC are more influenced by catchment area and catchment:lake ratio. Coastal BC lakes are inversely correlated to salmon escapement and strongly loaded by sediment C:N (Fig. 5B), further attesting to the high

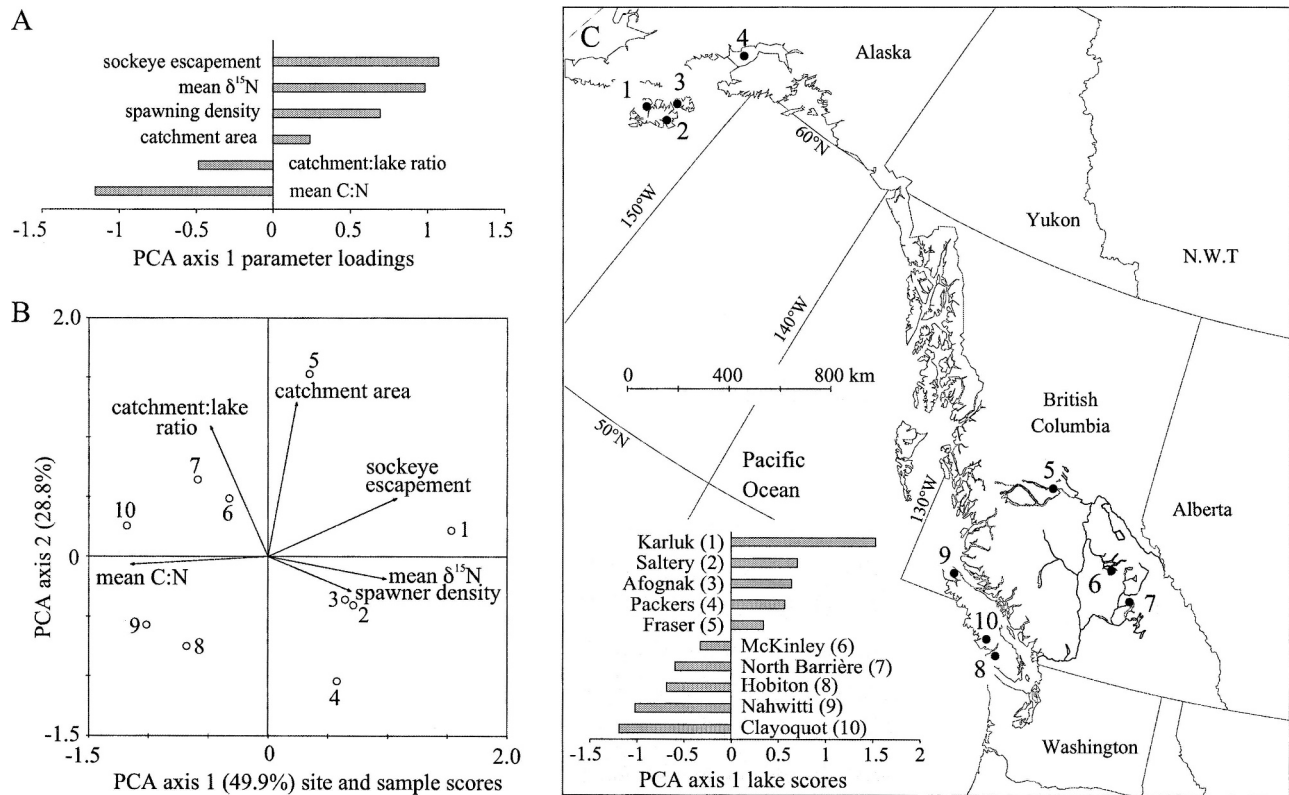


Fig. 5. PCA ordination results using catchment characteristics and paleosalmon proxies from 10 sockeye salmon nursery lakes. (A) Parameter loadings on the primary PCA axis. (B) PCA biplot of lake parameters (arrows) and sample locations (numbered open dots) for the first two PCA axes. Proximity of samples to a given variable implies strong loading by that parameter. (C) Locations of the analyzed lakes and their loadings on axis 1, showing the progression from the BC coast, to the BC interior, and finally to coastal Alaska. Sources: N. Barrière, McKinley, Clayoquot, and Nahwitti Lakes (Hobbs, unpubl. data); Packers Lake (Gregory-Eaves et al. 2004); Hobiton, Afognack, and Saltery Lakes (Holtham et al. 2004); and Karluk Lake (Finney et al. 2000).

allochthonous inputs they receive. The PCA analysis reveals that C:N and $\delta^{15}\text{N}$ load strongly in opposite directions on axis 1. BC coastal lakes, in a general sense, are “high C:N–low $\delta^{15}\text{N}$,” whereas Karluk Lake might be considered a representative “low C:N–high $\delta^{15}\text{N}$ ” site. Although this provides only a general set of guidelines based on currently available data, this direction of sediment C:N and $\delta^{15}\text{N}$ variability is supported by additional results from coastal BC (Brahney et al. 2006). Catchment:lake ratio, as used here, is a proxy for water residence time. BC lakes, especially from the interior, are most strongly influenced by this parameter, which dominates PCA axis 2 (Fig. 5B). Shorter residence times imply faster flushing of any MDN accrued in the ecosystem, which may represent another fundamental difference between the BC and Alaskan lakes considered in this analysis. The responsiveness of lakes to MDN appears to vary geographically over a primary gradient of latitude (Fig. 5C). Sediments from lakes situated in southern Alaska may thus archive a clearer response to past variability of MDN, relative to lakes from interior and coastal BC. In BC, the signals investigated appear either highly muted or completely absent. These lakes are more heavily subsidized by catchment-derived organic matter, whether of natural or anthropogenic provenance.

Studies from southern Alaska have demonstrated the reliability of paleolimnology to infer historical populations of sockeye salmon. Inherent to this success is the positive feedback between MDN and juvenile salmon in the nursery lake. A sediment record from Fraser Lake, BC, failed to track the well-documented shifts in sockeye escapement over about the past 60 yr. The proportion of this lake’s annual nutrient supply contributed by sockeye appears to be small, compared to lakes that successfully record MDN variability in their sediments. Catchment-derived nutrients appear to dominate the sediment geochemical records from lakes within the interior and coastal regions of BC in addition to shaping their diatom records. These findings corroborate the observation that juvenile salmon need not be completely reliant on MDN subsidies (Schindler et al. 2005). This assessment in no way dismisses the acknowledged importance of MDN in these ecosystems but rather places caveats on how reliably they stand to be preserved in sedimentary archives.

References

APPELBY, P. G., AND F. OLDFIELD. 1978. The calculation of lead-210 dates assuming a constant rate of supply of unsupported ^{210}Pb to the sediment. *Catena* 5: 1–8.

- BATTARBEE, R. W., V. J. JONES, R. J. FLOWER, N. G. CAMERON, H. BENNION, L. CARVALHO, AND S. JUGGINS. 2001. Diatoms, p. 155–202. *In* J. P. Smol, H. J. B. Birks and W. M. Last [eds.], Tracking environmental change using lake sediments. V. 3. Terrestrial, algal, and siliceous indicators. Kluwer Academic.
- BIRKS, H. H., R. W. BATTARBEE, AND H. J. B. BIRKS. 2000. The development of the aquatic ecosystem at Kråkenes Lake, western Norway, during the late-glacial and early-Holocene—a synthesis. *J. Paleolimnol.* **23**: 91–114.
- BRAHNEY, J., D. G. BOS, M. G. PELLATT, T. W. D. EDWARDS, AND R. ROUTLEDGE. 2006. The influence of nitrogen limitation on $\delta^{15}\text{N}$ and carbon:nitrogen ratios in sediments from sockeye salmon nursery lakes in British Columbia, Canada. *Limnol. Oceanogr.* **51**: 2333–2340.
- CARMICHAEL, N. B. 1985. Fraser Lake water quality assessment. Ministry of Environment, Province of British Columbia.
- CHRISTIE, C. E., AND J. P. SMOL. 1993. Diatom assemblages as indicators of trophic status in southeastern Ontario lakes. *J. Phycol.* **29**: 575–586.
- CUMMING, B. F. 2001. Assessment of changes in total phosphorus in Fraser Lake, B.C.: A paleolimnological assessment. BC Ministry of Environment, Lands, and Parks.
- , S. E. WILSON, R. I. HALL, AND J. P. SMOL. 1995. Diatoms from British Columbia (Canada) and their relationship to salinity, nutrients and other limnological variables. *Bibliotheca Diatomologica*. V. 31. J. Cramer.
- FALLU, M. A., N. ALLAIRE, AND R. PIENITZ. 2000. Freshwater diatoms from northern Québec and Labrador (Canada): Species-environment relationships in lakes of boreal forest, forest-tundra and tundra regions. *Bibliotheca Diatomologica*. V. 45. J. Cramer.
- FINNEY, B. P., I. GREGORY-EAVES, J. SWEETMAN, M. S. V. DOUGLAS, AND J. P. SMOL. 2000. Impacts of climate change and fishing on Pacific salmon abundance over the past 300 years. *Science* **290**: 795–799.
- GLEW, J. R., J. P. SMOL, AND W. M. LAST. 2001. Sediment core collection and extrusion, p. 73–106. *In* W. M. Last and J. P. Smol [eds.], Tracking environmental change using lake sediments. V. 1. Basin analysis, coring, and chronological techniques. Kluwer Academic.
- GREGORY-EAVES, I., B. P. FINNEY, M. S. V. DOUGLAS, AND J. P. SMOL. 2004. Inferring sockeye salmon (*Oncorhynchus nerka*) population dynamics and water-quality changes in a stained nursery lake over the past ~500 years. *Can. J. Fish. Aquat. Sci.* **61**: 1235–1246.
- GROOT, C., AND L. MARGOLIS. 1991. Pacific Salmon Life Histories. UBC Press.
- HAMILTON, S. K., S. J. SIPPEL, AND S. E. BUNN. 2005. Separation of algae from detritus for stable isotope or ecological stoichiometry studies using density fractionation in colloidal silica. *Limnol. Oceanogr. Methods* **3**: 149–257.
- HEIRI, O., A. F. LOTTER, AND G. LEMCKE. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. *J. Paleolimnol.* **25**: 101–110.
- HELFIELD, J. M., AND R. J. NAIMAN. 2006. Keystone interactions: Salmon and bear in riparian forests of Alaska. *Ecosystems* **9**: 167–180.
- HILL, M. O., AND H. G. GAUCH. 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* **42**: 47–58.
- HODELL, D. A., AND C. L. SCHELSKE. 1998. Production, sedimentation and isotopic composition of organic matter in Lake Ontario. *Limnol. Oceanogr.* **43**: 200–214.
- HOLTHAM, A. J., I. GREGORY-EAVES, M. PELLATT, D. T. SELBIE, L. STEWART, B. P. FINNEY, AND J. P. SMOL. 2004. The influence of flushing rates, terrestrial input and low salmon escapement densities on paleolimnological reconstructions of sockeye salmon (*Oncorhynchus nerka*) nutrient dynamics in Alaska and British Columbia. *J. Paleolimnol.* **32**: 255–271.
- KAUSHAL, S., AND M. W. BINFORD. 1999. Sediment C:N ratios and sources in a central Massachusetts lake. *J. Paleolimnol.* **22**: 439–442.
- KOENINGS, J. P., AND R. D. BURKETT. 1987. An aquatic rubic's cube: Restoration of the Karluk Lake sockeye salmon (*Oncorhynchus nerka*), p. 419–434. *In* H. D. Smith, L. Margolis and C. C. Wood [eds.], Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Can. Spec. Publ. Fish. Aquat. Sci.* 96.
- KRAMMER, K., AND H. LANGE-BERTALOT. 1986–1991. Bacillariophyceae. *In* H. Ettl, J. Gerlof, H. Heynig and D. Mollenhauer [eds.], Süßwasserflora von Mitteleuropa 2/1–4. Gustav Fischer Verlag.
- MACKO, S. A., AND N. E. OSTROM. 1994. Pollution studies using stable isotopes, p. 45–62. *In* K. Lajtha and R. H. Michener [eds.], Stable isotope studies in ecology and environmental science. Oxford Blackwell.
- NADELHOFFER, K. J., AND B. FRY. 1994. Nitrogen isotope studies in forest ecosystems, p. 22–44. *In* K. Lajtha and R. H. Michener [eds.], Stable isotope studies in ecology and environmental science. Oxford Blackwell.
- NAIMAN, R. J., R. E. BILBY, D. E. SCHINDLER, AND J. M. HELFIELD. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*. **5**: 399–417.
- PETERSON, B. J., AND B. FRY. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**: 293–320.
- REAVIE, E. D., R. I. HALL, AND J. P. SMOL. 1995. An expanded weighted-averaging model for phosphorus concentrations from diatom assemblages in eutrophic British Columbia (Canada) lakes. *J. Paleolimnol.* **14**: 49–67.
- REIMCHEN, T. E., D. MATHEWSON, M. D. HOCKING, AND J. MORAN. 2002. Isotopic evidence for enrichment of salmon-derived nutrients in vegetation, soil, and insects in riparian zones in coastal British Columbia. *Am. Fish. Soc. Symp.* **34**: 59–69.
- ROUND, F. E., R. M. CRAWFORD, AND D. G. MANN. 1990. The diatoms: Biology and morphology of the genera. Cambridge University Press.
- SCHINDLER, D. E., P. R. LEAVITT, C. S. BROCK, S. P. JOHNSON, AND P. D. QUAY. 2005. Marine-derived nutrients, commercial fisheries, and production of salmon and lake algae in Alaska. *Ecology* **86**: 3225–3231.
- SHORTREED, K. S., K. F. MORTON, K. MALANGE, AND J. M. B. HUME. 2001. Factors limiting juvenile sockeye production for selected BC nursery lakes. Canadian Science Advisory Secretariat Research Document 2001/098. Department of Fisheries and Oceans Canada.
- STEVENSON, R. J. 1995. Community dynamics and differential species performance of benthic diatoms along a nitrate gradient, p. 29–46. *In* J. P. Kociolek and M. J. Sullivan [eds.], A century of diatom research in North America. Koeltz Scientific Books.
- TERANES, J. L., AND S. M. BERNASCONI. 2000. The record of nitrate utilization and productivity limitation provided by $\delta^{15}\text{N}$ values in lake organic matter—a study of sediment trap and core sediments from Baldeggersee, Switzerland. *Limnol. Oceanogr.* **45**: 801–813.

- THOMPSON, W. F. 1945. Effect of the obstruction at Hell's Gate on the sockeye salmon of the Fraser River. *Int. Pac. Salmon Fish. Comm. Bull.* 1.
- WILSON, R. J. S., AND B. H. LUCKMAN. 2003. Dendroclimatic reconstruction of maximum summer temperatures from upper treeline sites in Interior British Columbia, Canada. *The Holocene* **13**: 851–861.
- WOLFE, A. P., R. D. VINEBROOKE, N. MICHELUTTI, B. RIVARD, AND B. DAS. 2006. Detecting chlorophyll *a* in lake sediments using reflectance spectroscopy: A simple calibration exercise for paleolimnological applications. *J. Paleolimnol.* **36**: 91–10.

Received: 5 October 2006

Accepted: 24 April 2007

Amended: 23 May 2007