

Diatoms and sockeye salmon (*Oncorhynchus nerka*) population dynamics: Reconstructions of salmon-derived nutrients over the past 2,200 years in two lakes from Kodiak Island, Alaska

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Abstract

The return of hundreds to millions of adult sockeye salmon (*Oncorhynchus nerka*), which have returned from the ocean to their natal nursery lake environment to spawn, can result in significant nutrient loading. By analyzing sedimentary diatom assemblages from nursery lakes, we demonstrated that a salmon-derived nutrient signal could be traced over time and be used to infer past sockeye salmon population dynamics. We conducted a ~2,200 year paleolimnological study of two Alaskan sockeye salmon nursery lakes, Karluk and Frazer lakes. The two lakes are very similar, except that sockeye salmon were only introduced into Frazer Lake in 1951 (first spawners returned in 1956). In both lakes we found a strong correspondence between diatom assemblages and the number of adult salmon spawners recorded in the historical data (~40 and 70 years for Frazer and Karluk lakes, respectively). Given this robust relationship, we then used our analyses of diatoms from Karluk Lake over the past ~2,200 years to gain insight into salmon-derived nutrient loading changes (which are directly related to the number of sockeye salmon spawners). The diatom record from Karluk Lake recorded dramatic species changes on both decadal and century timescales, and was strongly correlated with an independent indicator of sockeye salmon abundances, $\delta^{15}\text{N}$. Together, these data suggest pronounced variability in sockeye salmon abundances at Karluk Lake over the past ~2,200 years. The direct impacts of regional environmental variability were not likely responsible for the patterns apparent in Karluk Lake, as the diatom and $\delta^{15}\text{N}$ profiles from Frazer Lake were relatively stable prior to the introduction of sockeye salmon. Application of total phosphorus transfer functions to the Karluk and Frazer lakes' diatom records revealed that sockeye salmon carcasses substantially increased the trophic status in these lakes, which has important implications for the health of juvenile salmon that rear in nursery lakes. Overall, this paper illustrates the potential use of diatoms in reconstructing past sockeye salmon population dynamics, which in turn can lead to a greater understanding of the mechanisms influencing abundances of sockeye salmon.

Introduction

Inferring past population dynamics of vertebrates is a challenging task for paleolimnologists, as larger organisms tend to leave few fossils in lake sediments. Whereas a few notable exceptions exist (e.g., Hodgson and Johnson (1997), Daniels and Peteet (1998),

Patterson and Smith (2001)), indicators such as stable isotopes and algal and invertebrate sub-fossils can provide additional proxies through which past vertebrate population dynamics may be indirectly inferred (Uutala 1990; Jones and Juggins 1995; Sun et al. 2000). Remains of Pacific salmon, like many of their vertebrate counterparts, are also sparse in lake sedi-

ments, but a new application of paleolimnological methods, described below, has demonstrated that past sockeye salmon population dynamics can be inferred from proxy indicators (Finney et al. 2000, 2002).

The anadromous life history of sockeye salmon (*Oncorhynchus nerka*) lends itself well to a paleolimnological study. Sockeye salmon spend their first one to three years in lakes and the following one to four years in the North Pacific, but complete their lifecycle by returning to their natal nursery freshwater environment to spawn (i.e., typically in or associated with a lake) and then die (Burgner 1991). In some lakes, sockeye salmon are known to return in relatively high densities (i.e., not unusual to reach densities as high as 5,000 to 30,000/km²; Burgner (1991)) and, as a result, the nutrients derived from their post-spawned carcasses can contribute significantly to the total annual nutrient loading (i.e., as much as 70% of the phosphorus loading; Krohkin (1975), Koenings and Burkett (1987a), Kline et al. (1997), Naiman et al. (2002)). Furthermore, as salmon-derived nutrients have a lower C:N:P ratio (i.e., C:N:P ratio of adult pre-spawning sockeye salmon is 29:6:1; Mathisen et al. (1988)) than the Redfield ratio, sockeye salmon represent an ideal nutrient source for primary production in nursery lakes, which tend to be P-limited (reviewed in Naiman et al. (2002)). In lakes where the nutrient loading is strongly tied to the return of sockeye salmon, proxy indicators preserved in nursery lake sediments can be used to infer their population dynamics (Finney et al. 2000). For example, sedimentary $\delta^{15}\text{N}$ was found to be a reliable indicator of sockeye salmon spawner abundances (Finney et al. 2000), which is not surprising as adult salmon are enriched in $\delta^{15}\text{N}$ relative to other aquatic sources of organic matter (Mathisen et al. 1988; Kline et al. 1993).

Finney et al. (2000) also demonstrated that sedimentary diatom assemblages (Class Bacillariophyceae) had potential for indicating past sockeye salmon population dynamics. Nutrient concentrations are key elements in structuring diatom communities, and sedimentary diatom assemblages have long been used to infer past trophic conditions (Hall and Smol 1999). Advances in statistical techniques have made it possible to develop inference models, and over the past decade a large number of quantitative models for reconstructing past nutrient concentrations from sedimentary diatom assemblages have been published (e.g., Bennion et al. (1996), Gregory-Eaves et al. (1999), Reavie and Smol (2001)).

In this paper, we first explore the response of diatoms to sockeye salmon abundances by comparing sedimentary diatom assemblages to historical sockeye salmon records from two lakes on Kodiak Island, Alaska: Karluk and Frazer lakes. We then use sedimentary diatom assemblages from the same two lakes to track past salmon-derived nutrients (SDN) and other sources of environmental variation over the past ~2,200 years. Comparisons are also drawn between the inferences of sockeye salmon population dynamics based on the diatom assemblages and those inferred from $\delta^{15}\text{N}$.

Whereas Karluk Lake is a natural sockeye salmon nursery lake, sockeye salmon were introduced into Frazer Lake in 1951. As a result, we can both study the impact of the recent salmon introduction on the Frazer Lake diatom assemblages and isolate the influence of regional climatic and environmental variability on diatoms by looking at the pre-salmon introduction portion of the record. This portion of the Frazer Lake record provides a baseline when interpreting the Karluk Lake profile, which has been influenced by both regional climatic and environmental variability, and sockeye salmon population dynamics.

Site description

Karluk and Frazer lakes (57°25'N, 154°05'W and 57°15'N, 154°08'W, respectively) are situated in adjacent valleys in the Kodiak National Wildlife Refuge, Kodiak Island, Alaska (Figure 1). The catchments of these moderately large lakes (surface areas are 39.5 and 16.6 km², respectively) are pristine and the lakes' chemistries are dilute and oligotrophic (Table 1). The two lakes are very similar in many respects, but a steep, 10-m high waterfall close to the outlet of Frazer Lake has prevented sockeye salmon from colonizing this system naturally. However, the planting of sockeye salmon eggs from nearby lakes (beginning in 1951) and the construction of fish ladders over the falls (in 1962 and 1979) has allowed for a self-sustaining sockeye salmon population to establish itself at Frazer Lake (Blackett 1979; Kyle et al. 1988).

In the late-1980's and early-1990's, both Karluk and Frazer lakes were fertilized with the goal of boosting primary and secondary productivity, which in turn could lead to stronger sockeye smolt production (Kyle 1994; Schrof et al. 2000). Karluk Lake

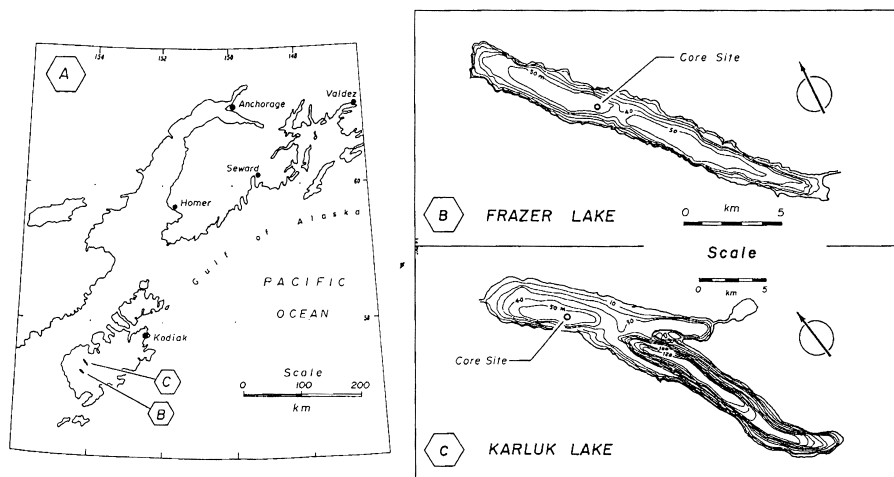


Figure 1. Map of study area. A) Southern Alaska, showing location of Kodiak Island and Frazer (B) and Karluk (C) lakes. Bathymetric map of Frazer (B) and Karluk (C) lakes showing the coring location.

was also stocked with sockeye salmon eyed eggs and fry between 1978 and 1984 (White 1986).

Methods

Sediment core retrieval and analyses

Gravity and percussion cores were collected from each lake at a deep-water location (Figure 1). The gravity and percussion cores were collected from

Karluk Lake in 1995 and 1996, respectively. Both coring methods were also employed at Frazer Lake in 1998. Sediment cores were extruded in 0.5 cm intervals, with the exception of the gravity core from Frazer Lake, which was extruded in 0.25 cm intervals. Core chronologies were developed using ^{210}Pb , ^{137}Cs , and ^{14}C analyses, and volcanic tephra identifications. As the top of percussion cores can be disturbed upon collection, the data from analyses of the gravity and percussion cores of each lake have been spliced together at a tephra layer, that was present in all cores,

Table 1. Average escapement and water chemistry data from Karluk and Frazer lakes from 1980–1996. Water chemistry data represents surface measurements (1 m) that have been seasonally averaged (May–Sept).

	Karluk Lake			Frazer Lake			
	units	Pre-fertilization 1980–1985 [*]	Fertilization 1986–1990 [°]	Post-fertilization 1991–1994 [°]	Pre-fertilization 1985–1987 [*]	Fertilization 1988–1992 [°]	Post fertilization 1993–1996 [°]
Average escapement		397,683	815,794	867,746	217,636	241,993	194,870
Conductivity	($\mu\text{S}/\text{cm}$)	62.6	63.8	68.2	47.4	51.8	53.2
pH		7.3	7.2	7.1	6.9	7.1	6.8
Alkalinity	(mg/L)	23.5	21.9	21.9	13.3	13.4	13.4
Turbidity	(NTU)		0.5	0.8	0.6	0.8	0.8
Color	(Pt units)		5.3	5.7	8.1	6.2	6.1
Iron	($\mu\text{g}/\text{L}$)	11.4	14.6	25.7	14.5	27.5	21.2
Total phosphorus	($\mu\text{g}/\text{L}$)	6.5	8.4	6.7	5.8	5.5	5.4
Total Kjeldahl Nitrogen	($\mu\text{g}/\text{L}$)	88.0	108.3	110.7	90.9	92.9	103.5
Ammonia	($\mu\text{g}/\text{L}$)	7.1	5.8	4.4	7.1	6.2	4.7
Nitrate + nitrite	($\mu\text{g}/\text{L}$)	40.8	78.9	85.2	56.9	49.8	54.0
Reactive silicon	($\mu\text{g}/\text{L}$)	113	115	144	2315	1360	2022
Chlorophyll a	($\mu\text{g}/\text{L}$)	1.3	1.8	1.9	1.0	1.5	1.2
Particulate organic carbon	($\mu\text{g}/\text{L}$)		208	258		184	146

^{*} unpublished data from Alaska Dept. of Fish and Game. [°] data from Shrof et al. 2000. [°] water chemistry data represents only period between 1990 and 1992

to present continuous, long-term records (i.e., this tephra was present at 21 and 20 cm in the Frazer Lake gravity and percussion cores, and present at 28.5 and 25 cm in the Karluk Lake gravity and percussion cores).

Siliceous microfossil slides were prepared by following standard methods (Battarbee et al. 2001). Briefly, sediment sub-samples were first treated with a 10% HCl solution to dissolve any carbonates. After a 24-hour settling period, the supernatant was removed and the slurries were rinsed with deionized water. This step was repeated several times before treating the samples with a strong oxidant (a 50:50 mixture of concentrated sulfuric and nitric acid or 30% hydrogen peroxide) to digest the organic fraction. After 24 hours, sample vials were placed in a heated water bath for approximately two hours. Samples were then allowed to settle over a 24-hour period, after which time the supernatant was aspirated. The remaining slurries were rinsed with deionized water. This step was repeated at least five times. Slurries were then pipetted onto glass coverslips and, once dried, mounted onto glass slides with Naphrax[®] mounting medium (refractive index = 1.74).

At least 400 diatom valves from each sample were identified and enumerated along parallel transects across the coverslips of slides. Primary taxonomic references used to help make identifications included Patrick and Reimer (1966, 1975), Koppen (1975), Foged (1981), Camburn et al. (1984-1986), Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b), Cumming et al. (1995), Reavie and Smol (1998). The taxonomy of problematic species was also discussed at the annual Arctic Antarctic Diatom Workshops (AADW). For example, it was resolved that most North Americans attending AADW would identify the smaller forms of *Cyclotella stelligera* that lack a well-defined star pattern in their central area as *C. pseudo-stelligera*. In contrast, participants of the Mountain Lake Research (MOLAR) working group that attended the AADW identify this taxon as *C. glomerata*. Photomicrographs of all dominant taxa are reproduced in Gregory-Eaves (2002).

Chrysophyte cysts and scales were also enumerated (see Zeeb and Smol (2001)). However, only chrysophyte scales in the Frazer Lake cores were found in substantial abundances. Chrysophyte scales in the Frazer Lake records are expressed as a percentage relative to the number of diatom frustules and chrysophyte scales enumerated.

Sedimentary $\delta^{15}\text{N}$ analyses were conducted on

dried, homogenized and bulk sediment using a Europa Scientific 20/20 or Finnigan Delta Plus. The isotopic analyses are reported in the standard δ notation relative to the international standard, atmospheric N_2 . The analytical uncertainty was better than 0.2 ‰.

Ordination statistics

Multivariate ordinations were performed to identify the main direction of variation (i.e., first eigenvector) in the diatom species data. Regression analyses were then conducted to assess the strength of the relationship between the main direction of variation in each diatom record and historical, $\delta^{15}\text{N}$, or diatom-inferred total phosphorus (TP) data (see below). All ordinations were performed on screened species data (including only taxa that had relative abundances of greater than 2% in at least one sample) using CANOCO v. 4 (ter Braak and Šmilauer 1998). Preliminary detrended correspondence analyses (DCA) were also performed on each record to determine the gradient length of the first axis, which was used to evaluate whether linear (i.e., principal components analysis; PCA) or unimodal (i.e., correspondence analysis; CA) ordination techniques were appropriate; Birks (1995)).

Transfer function application

In order to reconstruct TP concentrations from the Karluk and Frazer lake diatom assemblages, calibration sets from both Alaska (Gregory-Eaves et al. 1999) and British Columbia (B.C.; Bradbury et al. (2002)) were evaluated, as they both had similar species to those found in our cores. The B.C. lake calibration set was first screened to only include dilute lakes (salinities less than 1 g/L), which resulted in a subset of 111 lakes and 178 diatom taxa (Bradbury et al. 2002). For both calibration sets, weighted-averaging models with classical deshrinking were used, as these yielded the highest bootstrapped coefficients of determination (Alaska calibration set $r_{\text{boot}}^2 = 0.53$; B.C. calibration set $r_{\text{boot}}^2 = 0.47$) and lowest residual trends (Gregory-Eaves et al. 1999; Bradbury et al. 2002). WACALIB v. 3.5 (Line et al. 1994) was used to infer down-core TP values.

The ability of the transfer functions to reliably reconstruct past TP values in each lake was evaluated through a fit to TP analysis (Birks et al. 1990). Using CANOCO v. 4 (ter Braak and Šmilauer 1998), a

canonical correspondence analysis (CCA) was conducted on the calibration samples that were constrained to TP alone, and down-core assemblages were run passively. The 75% and 95% confidence limits of the squared residual lengths of the first CCA axis (which is based solely on the calibration samples and TP) were used to screen squared residual lengths of the down-core assemblages for poor and very poor reconstructions of TP.

The strength of the match between the calibration species assemblages and down-core assemblages was assessed using Analog v. 1.6 (Line and Birks unpublished program). We followed similar protocols to those outlined in Laird et al. (1998). Taxa present in the Karluk and Frazer lake records that either had relative abundances of greater than 1% or were represented in the calibration set were included in analog analyses. Intervals that were found to have poor and very poor analogs to the calibration set were those that were outside of the 75% and 95% confidence limits determined from the calibration set.

Results and discussion

Age model development

Gravity cores from both Karluk and Frazer lakes were sufficiently long enough to reach supported levels of ^{210}Pb (Figure 2). Age models for the gravity cores were generated from ^{210}Pb activities using a constant rate of supply model (CRS; Appleby and Oldfield (1978)) and then extended back over the length of the gravity cores by fitting a best fit polynomial through the CRS-generated dates, the ^{137}Cs peak, an established historical tephra layer (Mt. Novarupta, which erupted in 1912) and a tephra dated to AD 1710. An age of 1710 was assigned to this tephra as a result of determining its extrapolated age by fitting the radiosotopic data and 1912 tephra layer from cores of 4 different Kodiak Island lakes (i.e., Karluk, Frazer, Red and Akalura lakes).

The longer percussion cores were dated by using a combination of ^{14}C dates and tephra identifications. In

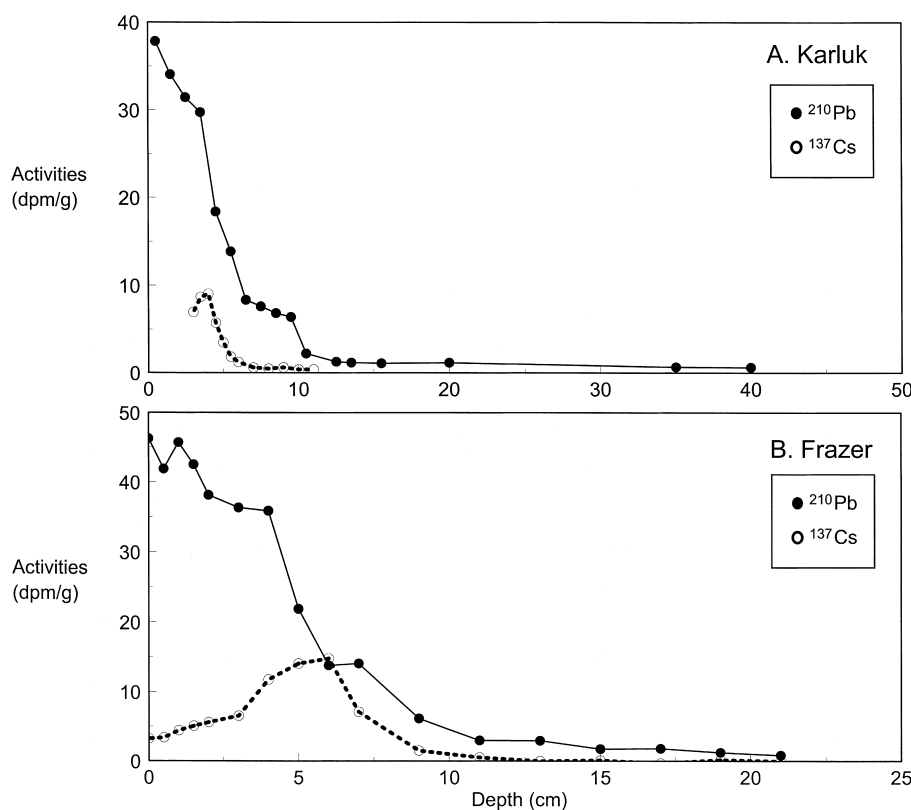


Figure 2. Total ^{210}Pb and ^{137}Cs activities from the Karluk and Frazer gravity cores.

particular, three macrofossil samples from the Karluk core, and one macrofossil sample from the Frazer Lake core were ^{14}C dated (Table 2). The ^{14}C date from the Frazer Lake core was obtained from a prominent tephra layer in the core. This same tephra layer was also identified in the Karluk Lake percussion core, and thus the Frazer Lake ^{14}C date was used in the development of an age model for the Karluk Lake record. Age models were constructed for each core by fitting a third-order polynomial ($r^2 = 0.99$ for Karluk Lake and $r^2 = 0.99$ for Frazer Lake) through the following sequence of dates: coring date, the 1912 and 1710 ash layers, and calibrated ^{14}C dates.

General floristic description

A moderately high number of taxa (i.e., 379 and 364) were identified in the Karluk and Frazer lake sediments. However, many were quite rare and when the data sets were screened (i.e., eliminated taxa whose relative abundances were never greater than 1%), 76 taxa were remaining in the Karluk Lake record (which represented an average of 94% of an interval's total relative abundance) and 53 taxa were remaining in the Frazer Lake record (which represented an average of 89% of an interval's total relative abundance).

Earlier diatom studies of Karluk Lake (Juday et al. 1932; Hilliard 1959; Manguin 1961; Terrell 1987) have reported many of the same species we recorded in our study. In addition, earlier investigations found that diatoms were a dominant portion of the phytoplankton of Karluk Lake (Juday et al. 1932; Hilliard 1959).

Diatoms as indicators of SDN loading: Comparison of the diatom profiles to historical monitoring data

The diatom assemblages from both Karluk and Frazer

lakes appear to accurately reflect changes in sockeye salmon abundances. For Karluk Lake, there is a record beginning in 1922 of the number of adult sockeye salmon returning to spawn (i.e., escapement record), which allows us to evaluate the response of diatoms to changes in sockeye salmon spawners qualitatively and quantitatively (Figure 3,4). The recent fertilization of Karluk Lake (i.e., 1986–1990) is analyzed and discussed separately below. For Frazer Lake, the escapement time series is much shorter and, in the middle of this time series (1988–1992), the lake was fertilized. Therefore, we have decided to restrict our analyses of Frazer Lake to qualitative comparisons of species changes. Even at a qualitative level, however, distinct differences are evident between the pre- and post-salmon introduction diatom assemblages (Figure 5).

Perhaps the first, most striking qualitative observation, however, that we can draw from the fossil diatom assemblages from Karluk and Frazer lakes is the fact that they have very different diatom communities (Figure 3,5). Given that these lakes are located in very close proximity to each other and are of similar size, these results suggest, that even on a first-order level of analysis, the presence and strength of sockeye salmon returns to lakes have a profound effect on diatom assemblages.

Karluk Lake

Over the course of the historical record, the annual escapement of sockeye salmon to Karluk Lake has varied between 140,000 to 2.5 million (Finney et al. 2000). The highest escapements were noted at the beginning of the record whereas the lowest values were recorded between the mid-1950's to the mid-1980's (Figure 3). During this time, the diatom community showed a striking shift from one dominated by meso- to eutrophic species (e.g., *Stephanodiscus*

Table 2. Radiocarbon data for Karluk and Frazer lakes

CAMS#	Sample depth (cm)	Corrected * depth (cm)	Sample	$\delta^{13}\text{C}$ (‰)	^{14}C age (y BP)	Calendar age (AD)	1 σ calibrated age range (AD)
<i>Karluk Lake</i>							
65456	53.5–54	57–57.5	terrestrial macrofossil	–25	970 +/- 70	1090	1000–1160
65457	64.5–65	68–68.5	terrestrial macrofossil	–25	1310 +/- 90	712	651–779
56401	78	81.5	terrestrial macrofossil	–25	1730 +/- 50	306	242–390
<i>Frazer Lake</i>							
56406	90–90.5	91–91.5	terrestrial macrofossil	–25	2020 +/- 40	–12	–50–47

* Corrected depth refers to the sample depth after adjusting for the slight difference in position of the 1710 ash layer in the gravity and percussion cores. We have plotted the corrected depth in the composite profiles (Figures 6–9).

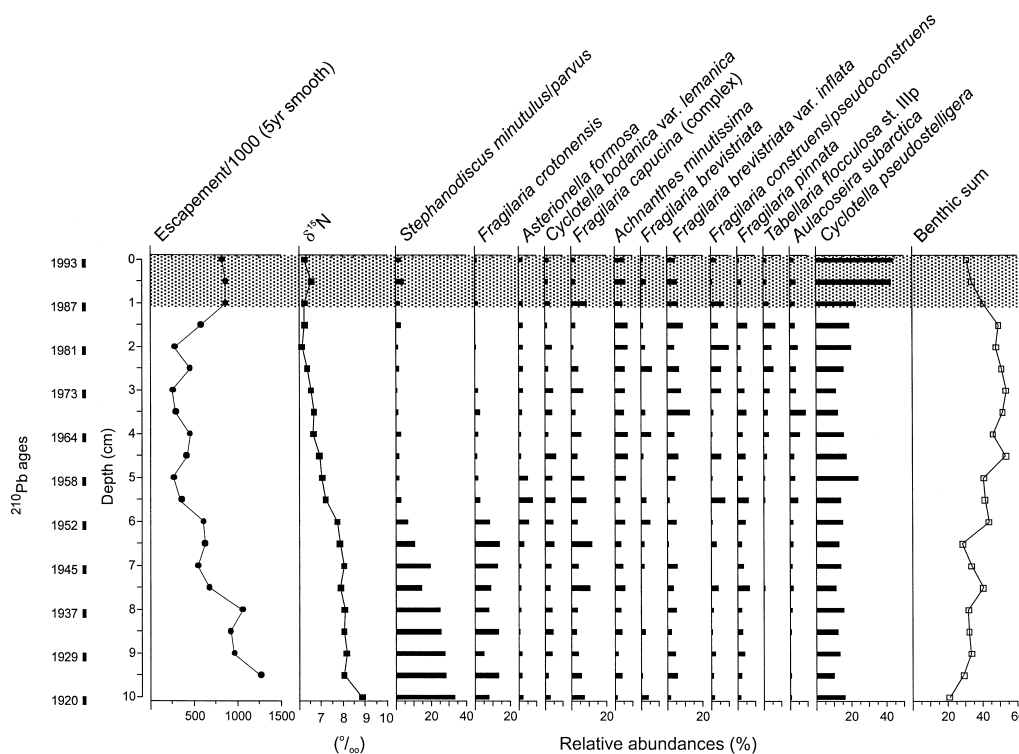


Figure 3. A paleolimnological comparison of the dominant diatom taxa (>5% relative abundances), $\delta^{15}\text{N}$, and total escapement from Karluk Lake. The shaded zone (the top three samples) corresponds to the lake fertilization period.

minutus/parvus and *Fragilaria crotonensis*) to a more nutrient-poor assemblage (e.g., *Fragilaria brevistriata* v. *inflata*, *Tabellaria flocculosa* st. IIIp; Figure 3). In both the B.C. and Alaskan calibration sets, the TP optima for *Stephanodiscus minutulus/parvus* and *Fragilaria crotonensis* range between 14.8 and 21.5 $\mu\text{g/l}$. In contrast, the TP optima for *Fragilaria brevistriata* v. *inflata* and *Tabellaria flocculosa* st. IIIp are substantially lower (i.e., between 9.9–12.3 $\mu\text{g/l}$).

Since the 1980's, escapement to Karluk Lake has increased to over a million fish per year, and therefore SDN loading has correspondingly increased. However, a lake fertilization program was also initiated in the mid-1980's. Due to this confounding factor, we have excluded the top three sediment intervals in our quantitative comparisons of the diatom assemblages and sockeye escapement. The impact of fertilization and the recent increase in escapement is, however, clearly recorded in the diatom data and is discussed in a following section.

Regression analyses between the first PCA axis and escapement measures demonstrate the significance of the abundances of sockeye salmon spawners, as well as the timing of their return. As expected, total

escapement is a strong explanatory variable (Fig. 4a). However, when these data are split into early escapement (i.e., returns before July 15) and late escapement (i.e., returns after July 15), a date that separates two distinct sockeye salmon populations at Karluk Lake (Koenings and Burkett 1987a; Schmidt et al. 1998), early escapees explain the greatest variation in the diatom data (Figures 4b and 4c). These results are not surprising, as diatoms generally bloom in spring and thus may have coincided with the early escapement. In addition, silica concentrations in Karluk Lake are relatively low (Table 1), and may limit diatom production later in the season.

The sum of all benthic taxa was also significantly, but negatively, related to escapement (Figure 4d). A negative relationship between nutrient loading and benthic algal production has also been reported in paleoecological studies of highly eutrophied systems, where extensive phytoplankton growth can lead to shading of benthic habitats (summarized in Hall and Smol (1999)). However, this is not likely the case at Karluk Lake because Secchi measurements taken when escapement was still relatively high suggest that the water was quite transparent (i.e., Secchi depths ranged between 4.5 and 8.6 m; Juday et al. (1932)).

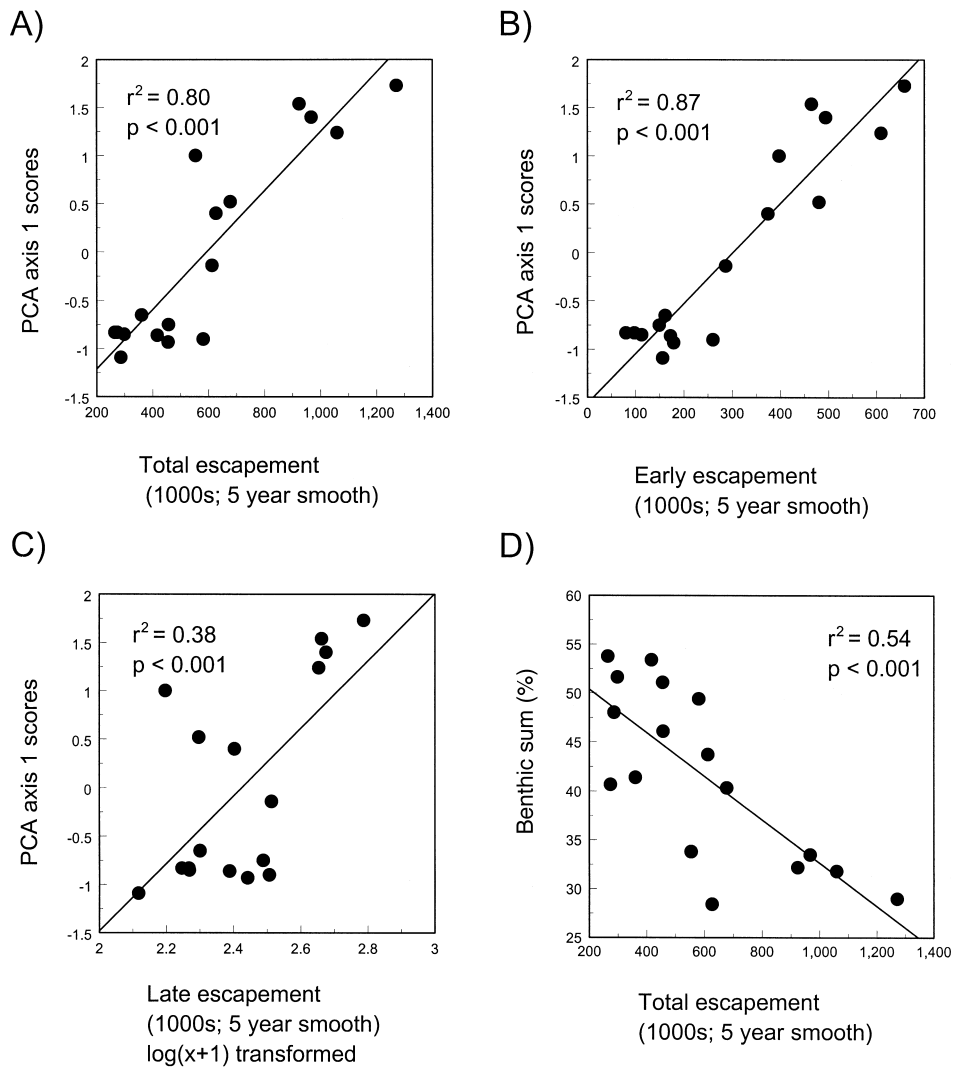


Figure 4. Plots showing the relationship between Karluk Lake escapement measures (A – C; data from Schmidt et al. (1998)) and the main direction of variation in the diatom data (PCA axis 1 sample scores) or benthic diatom relative abundance sum (D). PCA was used to determine main direction of variation because a preliminary DCA analysis revealed that the gradient length of the first ordination axis was 1.5 standard deviation units. Early escapement refers to the number of spawners that returned to Karluk Lake prior to July 15th (B) whereas later escapement refers to the number of spawners that returned to Karluk after to July 15th (C).

We believe that the negative relationship between benthic diatoms and escapement (or positive relationship between planktonic diatoms and escapement) is related to the observation that most salmon carcasses decompose primarily in the littoral environment. We suggest that when spawner numbers are relatively low, periphytic algae are effective at using SDN. In contrast, when salmon returns are plentiful, the SDN are present in such higher concentrations that the benthic community is unable to utilize most of the

nutrients, and thus phytoplankton respond to enhanced nutrient loading.

Frazer Lake

With the introduction of sockeye salmon (first spawners returned in 1956), the Frazer Lake diatom assemblages shifted from dominance of oligotrophic taxa to those indicative of mesotrophic conditions (Figure 5). In particular, *Diatoma tenue* v. *elongatum* and

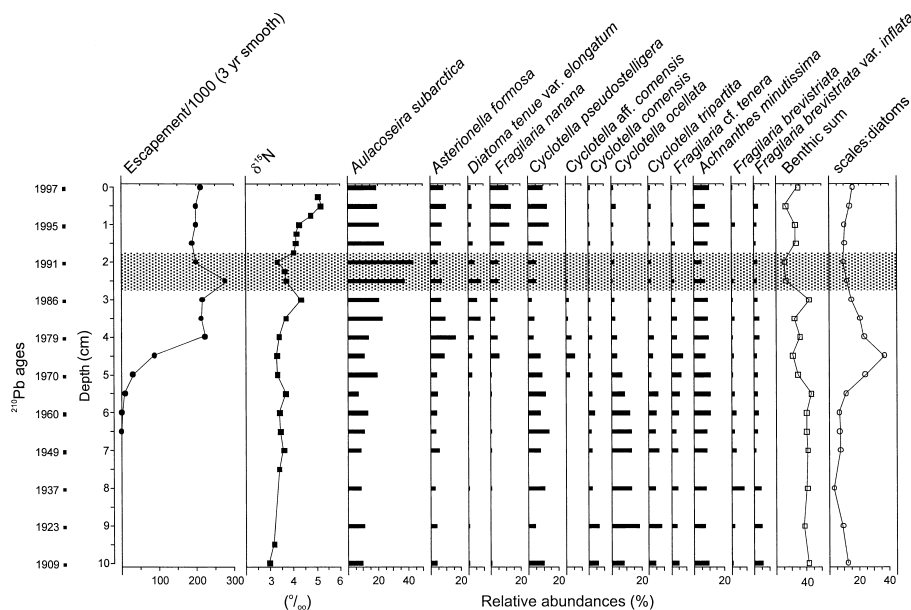


Figure 5. A paleolimnological comparison of dominant diatom taxa (>5% relative abundances), the chrysophyte scale:diatom ratio, $\delta^{15}\text{N}$, and total escapement from Frazer Lake. The shaded zone (from 2.0 to 2.5 cm) corresponds to the lake fertilization period.

Fragilaria nanana, whose TP optima in the B.C. and Alaskan calibration sets range between 13.8 and 19.6 $\mu\text{g}/\text{l}$, greatly increased with the introduction of sockeye salmon. These new dominants replace *Cyclotella ocellata*, *C. comensis*, *C. tripartita* and, *Fragilaria cf. tenera*, which have, on average, lower TP optima in the B.C. and Alaska calibration sets (ranging between 6.5 and 14.8 $\mu\text{g}/\text{l}$). The trend of lower percentages of benthic taxa with increasing SDN loading seen in Karluk Lake is also apparent in Frazer Lake, albeit not as strongly.

Similar to Karluk Lake, the diatom species assemblages of Frazer Lake appear to be sensitive to the abundance of sockeye salmon spawners (Figure 5). For example, the Frazer Lake diatom profile shows only subtle changes (e.g., steady decrease in the relative abundance of *Cyclotella ocellata*) at the start of the introduction of sockeye salmon (between 5.0 and 6.5 cm; 1956 and 1970) when the number of spawners was relatively low. More distinctive changes (e.g., increases in *Asterionella formosa* and *Fragilaria nanana*) are not apparent until the large increases in escapement (greater than 100,000 spawners) occurred in the mid-1970's (i.e., 4.5 cm in the core).

Interestingly, scale-bearing chrysophytes also showed a positive, albeit brief (~10 year) response to

increased salmon abundances (Figure 5). Whereas chrysophytes are generally associated with oligotrophic conditions, a similar short-lived increase in chrysophytes was also observed in Lake 227 of the Experimental Lakes Area (Ontario, Canada) after fertilization (Leavitt et al. 1994). Most of the scales in the high scale:diatom intervals of Frazer Lake were *Mallomonas pseudocoronata* and *M. crassisquama*, which also showed a positive response to fertilization in Lake 227 (Zeeb et al. 1994). Similarly, Fritz et al. (1993) found increased abundances of *Mallomonas pseudocoronata* scales with modest eutrophication in Michigan (U.S.A.) lakes. As chrysophyte scales can easily be enumerated when counting diatoms, we suggest that they should also be enumerated when analyzing diatom assemblages to infer past sockeye salmon dynamics, as they may provide additional information about SDN.

Fertilization of Karluk and Frazer lakes

In the late-1980's and early-1990's, Karluk and Frazer lakes received weekly surface applications of nitrogen-phosphorus mixtures between the months of June and August (Schrof et al. 2000). This program resulted in a substantial increase in the average annual mean phosphorus and nitrogen loading to Frazer Lake

(33 and 20%, respectively), but only modest increases in loading to Karluk Lake (9 and 13%, respectively; Kyle et al. (1997)).

Averaged seasonal water chemistry data for Karluk Lake show an enrichment during the fertilization period (Table 1). However, it is important to note that sockeye salmon escapement to Karluk Lake also doubled during the fertilization period. This increase in sockeye escapement likely contributed to the higher trophic state observed during this time. Enrichment of Frazer Lake during the fertilization period is not as obvious, as seasonal water chemistry data show a decrease in TP but an increase in total Kjeldahl nitrogen and chlorophyll *a* (Table 1). Unfortunately, water chemistry data from Frazer Lake were not available for two of the fertilization years (Table 1). Across all years of fertilization, but constrained to the months of June to August, Kyle (1994) demonstrated that the average TP concentrations at Frazer Lake did increase by 1.3 $\mu\text{g}/\text{l}$ over the mean from the previous three years (6.5 $\mu\text{g}/\text{l}$). Changes in trophic status during this period are likely due to fertilization itself (rather than escapement changes; see Table 1) as the fertilizer loading into this lake was substantial.

Sediments corresponding to the fertilization period at Karluk Lake show a distinct increase in *Cyclotella pseudostelligera* (Figure 3). Whereas this taxon (or *C. glomerata*, which we believe is the same species) has been reported in a wide range of trophic conditions (e.g., Bennion (1994), Anderson et al. (1997), Gregory-Eaves et al. (1999), Reavie and Smol (2001)), it has previously been shown to be responsive to fertilization (Ennis et al. 1983; Yang et al. 1996; Anderson et al. 1997). The rise in *C. pseudostelligera* may also be due, in part, to the large increase in late-run sockeye salmon (the increase in escapement beginning in 1985 is driven mostly by an increase in late-run spawners (i.e., returning after July 15)). Seasonal data suggest that this taxon is most abundant during low silica conditions (Belcher et al. (1966), Kalff et al. (1975), referring to *C. glomerata*). As both the fertilizer and SDN would have increased nutrient levels in mid-summer when silica concentrations are low in Karluk Lake (Table 1 and Alaska Department of Fish and Game, unpublished data), both factors could have favored the production of *Cyclotella pseudostelligera*.

The diatom community of Frazer Lake also showed a striking change during the fertilization period, with a large increase in *Aulacoseira subarctica* (Figure 5). This taxon is generally considered to represent meso-

to eutrophic conditions and has TP optima of 15.6 and 37.3 $\mu\text{g}/\text{l}$ in the Alaskan and B.C. calibration sets, respectively. Interestingly, Kyle (1994) noted from analyses of phytoplankton samples collected during the fertilization period that the flora was dominated by *Aulacoseira* and *Asterionella* spp. The lack of a strong presence of *Asterionella* spp. in the paleolimnological record at this time is likely due to the fact that sediments represent an integration of algal growth over the entire water column and throughout the year, whereas Kyle (1994) data were based on spot sampling from a depth of 1 m between the months of June and August.

The different responses reflected in the Karluk and Frazer lake records during fertilization are likely due to the differences in nutrient loading and in silica concentrations present in each lake. As stated above, Karluk Lake received a modest fertilizer application and a substantial increase in average escapement, whereas Frazer Lake received a relatively large fertilizer application and only a slight increase in average escapement. Karluk Lake also had silica concentrations that were an order of magnitude lower than those in Frazer Lake (Table 1). The dominant taxon in Frazer Lake during the fertilization period, *Aulacoseira subarctica*, is heavily silicified and does not thrive in low silica environments (Lund 1971).

The fertilizer also had an effect on the $\delta^{15}\text{N}$ profiles from both lakes. Frazer Lake shows a distinct decrease in $\delta^{15}\text{N}$ during the fertilization period and the $\delta^{15}\text{N}$ values in Karluk Lake remain low during the fertilization period, despite the large increases in escapement. These trends are the product of the dilution of the salmon $\delta^{15}\text{N}$ signal by the commercial fertilizer, which has a $\delta^{15}\text{N}$ of 0‰.

Diatom-based inferences of changes in SDN loading and other sources of environmental variability over the past ~2,200 years

Given the strong correspondence between historical monitoring records of escapement and the diatom assemblages from Karluk and Frazer lakes, we believe that sedimentary diatom records can be used to track past changes in SDN. Another line of evidence that would support this interpretation is the strong relationship between the sedimentary $\delta^{15}\text{N}$ signature and the primary direction of variation in the Karluk Lake diatom assemblages over the past 2,200 years ($r^2 = 0.79$, $n = 100$, $p < 0.001$; Finney et al. (2002)). Application of the TP transfer functions to

the diatom records of Karluk and Frazer lakes (discussed below) have allowed us to quantitatively reconstruct past nutrient trends, which we believe are derived primarily from sockeye salmon carcasses.

Assessment of our TP reconstructions for Karluk and Frazer lakes

Based on our fit to TP analyses, we found that the B.C. calibration set produced more reliable TP inferences than the Alaskan calibration set for the Karluk Lake record, whereas the Alaskan calibration set produced more reliable TP inferences for the Frazer Lake record. In particular, very poor fits to TP were found over the more eutrophic fossil intervals when the Alaskan calibration set was applied to the Karluk Lake record. This is likely due to the poor representation of *Stephanodiscus minutulus/parvus* in the Alaskan calibration set. Very poor fits to TP were also found over the more eutrophic intervals when the B.C. calibration set was applied to the Frazer Lake record. The dominant taxon in the more nutrient-rich intervals of the Frazer Lake profile, *Aulacoseira subarctica*, was present in greater than 10% relative abundance in only a single B.C. calibration lake, and thus is likely responsible for the very poor fits observed for these intervals. As a result, we present results from the B.C. calibration set for Karluk Lake and from the Alaskan calibration set for Frazer Lake.

The fit to TP and analog assessments from this subset of down-core and calibration set combinations (i.e., the B.C. transfer function applied to the Karluk record and the Alaskan transfer function applied to the Frazer record) demonstrated that most samples have good analogs and should provide reliable TP reconstructions (Figure 6,7). In the Karluk Lake record, the weakest analogs and fits to TP corresponded to intervals where oligotrophic conditions were inferred (Figure 6). This is likely caused by the absence of some oligotrophic species in the B.C. calibration set (e.g., *Cyclotella ocellata* and *C. tripartita*) that are present in the down-core assemblages. In contrast, taxa at the more eutrophic end of the gradient are well represented (e.g., *Stephanodiscus minutulus/parvus* is present in 67 lakes). Overall, only one of the Karluk Lake samples had a very poor analog and none of the Karluk Lake samples had very poor fits to TP. In the Frazer Lake record, none of the down-core assemblages had fits to TP or analog matches that were beyond the 95% confidence intervals of the Alaskan calibration set (Figure 7). In both records, the inferred

TP values were strongly correlated with the main direction of variation (i.e., PCA axis 1 for Frazer, $r^2 = 0.78$, $n = 52$, $p < 0.001$, and CA axis 1 for Karluk, $r^2 = 0.58$, $n = 100$, $p < 0.001$), which further supports the idea that nutrient fluctuations are the main signals in these records. In summary, the B.C. model is appropriate for inferring past TP trends in Karluk Lake, and the Alaskan model is appropriate for inferring past TP trends in Frazer Lake.

Karluk Lake ~2,200 year record

The diatom assemblages from Karluk Lake over the past ~2,200 years show pronounced variability on decadal and century time scales (Figure 8). We identified seven zones of stratigraphic similarity in the diatom record (Figure 8) by conducting a cluster analysis, using the CONISS program associated with TILIA v. 1.09 (Grimm unpublished program) and a square chord dissimilarity index (Grimm 1987).

In Zone 1, most samples are strongly dominated by the meso- to eutrophic indicator *Stephanodiscus minutulus/parvus*, which peaked in relative abundances in this zone (Figure 8). Other mesotrophic indicators included *Asterionella formosa*, *Fragilaria crotonensis*, and *S. medius*. Two samples in this zone (i.e., 107.5 and 109.5 cm), however, reflect a distinct but brief change in conditions, as oligotrophic indicators (e.g., *Cyclotella comensis*, whose TP optimum is less than 10 $\mu\text{g}/\text{l}$ in both B.C. and Alaskan calibration sets) and benthic taxa become more abundant. The inferred TP values closely track the species changes in this zone, as both very high and low TP concentrations are inferred. Sedimentary $\delta^{15}\text{N}$ values are also high on average in this zone, and show a parallel, short-lived decrease. Together, these data suggest that sockeye salmon abundances were, on average, as great or greater in Zone 1 than observed at the inception of the commercial fishery in the Karluk estuary (i.e., ~3 million fish caught annually in the 1880's and 1890's).

The near loss of *Stephanodiscus minutulus/parvus* characterizes Zone 2 (Figure 8). Instead, more oligotrophic diatoms (e.g., *Fragilaria brevistriata* v. *inflata*, *Cyclotella comensis*, *C. ocellata* and *C. tripartita*) are dominant. The almost complete shift in diatom assemblages between Zones 1 and 2 is reflected in a substantial decrease in inferred TP. The $\delta^{15}\text{N}$ profile closely matches the diatom record, showing an abrupt and sustained departure (Figure 8).

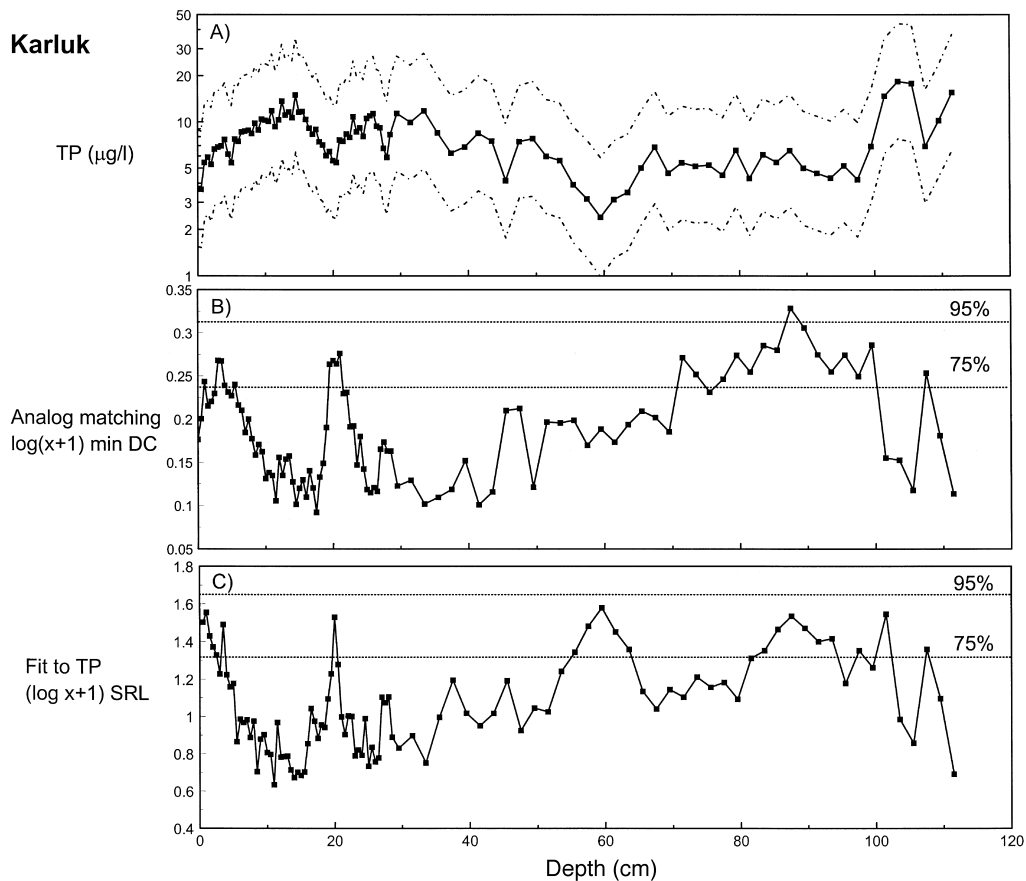


Figure 6. Inferred TP trends and assessment of reconstructed values from the application of the B.C. TP transfer function on the Karluk Lake ~2,200 year diatom record. A) Reconstructed TP concentrations and model error estimates (i.e., \pm estimated standard error of prediction). B) Analog results expressed as minimum dissimilarity coefficients (min DC) with 75% and 95% confidence intervals indicating poor and very poor analogs. C) Fit to TP values expressed as squared residual lengths (SRL) with 75% and 95% confidence intervals indicating poor and very poor fits to TP.

These data suggest that sockeye salmon abundances were reduced to very low numbers during this time.

The assemblage shift in Zone 3 is characterized by a large increase in *Cyclotella pseudostelligera* and subtle rises in *Stephanodiscus minutulus/parvus* and *Asterionella formosa*, suggesting a slight nutrient enrichment over Zone 2 (Figure 8). The rise in $\delta^{15}\text{N}$ values over this interval supports this interpretation. We therefore infer slight increases in the number of sockeye salmon spawners during Zone 3.

The TP reconstruction during Zone 3, however, shows a decrease in nutrients with increasing contributions of *Cyclotella pseudostelligera* (Figure 8). We believe that this is due to the limitations of the calibration model, as high abundances of the *C. stelligera* complex (which includes *C. pseudostelligera*, *C. glomerata* and *C. stelligera*) are poorly

represented in the B.C. calibration set. The fit to TP values also suggest weaker TP inferences in this zone, as increasingly poorer fits are apparent with greater abundances of *C. pseudostelligera* (Figure 6,8).

The return of assemblages dominated by *Stephanodiscus minutulus/parvus* is evident in Zone 4, and coincides with a rise in reconstructed TP values (Figure 8). However, this zone is also punctuated by several short-term decreases in the relative abundances of *Stephanodiscus minutulus/parvus*, which show corresponding increases in oligotrophic (e.g., *C. comensis*, *C. ocellata*, *C. tripartita*) and benthic taxa (e.g., *Fragilaria brevistriata* v. *inflata*). Similar to the marked deviation noted in Zone 1, the $\delta^{15}\text{N}$ and diatom profiles in Zone 4 reflect synchronous changes. Together, these results strongly suggest that sockeye salmon abundances responded to both low

and high frequency forcing factors over the past ~2,200 years.

Interestingly, there is a marked difference in the presence of *Cyclotella pseudostelligera* between Zones 1 and 4, which otherwise have very similar diatom assemblages (Figure 8). This difference may be the product of lower numbers of sockeye salmon spawners in Zone 4 (which might favour *C. pseudostelligera* over *Stephanodiscus minutulus/parvus*), or the result of a shift in the return dates of spawners. Although there is limited information on the seasonal distribution of diatoms, *S. minutulus* has been found to bloom early in the season (Nuhfer et al. 1993; Interlandi et al. 1999), whereas *C. pseudostelligera* may be more abundant in late summer and autumn (Kalff et al. (1975), referred to as *C. glomerata* by these authors).

Another decadal-scale shift to oligotrophic (e.g., *Cyclotella comensis*) and benthic (e.g., *Fragilaria brevistriata* v. *inflata*) taxa characterizes Zone 5. Sedimentary analyses of $\delta^{15}\text{N}$ from five sockeye salmon nursery lakes in Alaska demonstrated that this shift (seen as a decrease in $\delta^{15}\text{N}$, e.g., in Karluk Lake this departure centered is around 20 cm (Figure 8)), and the one preceding it (e.g., centered around 28 cm in Figure 8), were regionally synchronous (Finney et al. 2000). Comparing these data to a climatic reconstruction extending back until the mid-1700's, Finney et al. (2000) demonstrated that the early-1800's decrease in inferred salmon abundances (seen in Zone 5) corresponded to the lowest temperatures on record (inferred from the tree-ring analysis by D'Arrigo et al. (1999)).

The two uppermost zones (Zones 6 and 7) capture the last ~150 years of the record. The earliest zone is dominated by *Stephanodiscus minutulus/parvus*, and is characterized by high $\delta^{15}\text{N}$ values (Figure 8). The commercial fishery at the mouth of the Karluk River began during this time and is at least partly responsible for the decline in sockeye salmon abundances seen over the 20th century (Finney et al. 2000). The TP reconstruction closely tracks the decline in SDN over the past century, but does not show an increase in inferred TP in the recent sediments (i.e., top 3 samples) because of the dominance of *Cyclotella pseudostelligera*.

Frazer Lake ~2,200 year record

In contrast to the Karluk Lake profile, the Frazer Lake diatom and inferred TP records are relatively stable

over the past ~2,200 years, with the exception of a marked change in the recent sediments corresponding to the sockeye salmon introduction period (Figures 7,9). However, only the trends from the inferred TP profile should be interpreted, as large abundances of *Aulacoseira subarctica* (i.e., the dominant taxon in recent Frazer Lake sediments) are not overly well represented in the Alaskan calibration set.

Prior to the introduction of sockeye salmon, Frazer Lake was dominated by *Cyclotella* spp. (*C. comensis*, *C. pseudostelligera*, *C. ocellata*, *C. tripartita*), which reflect oligotrophic conditions (Figures 7 and 9). There is some variation in the relative abundances of dominant taxa, particularly *C. comensis* and *C. pseudostelligera*, but no new dominants appear. This record leads us to conclude that the direct impacts of climatic and other sources of environmental variation have only a limited influence on the diatom assemblages in these large, deep lakes.

Whereas our historical analyses of the diatom records from Karluk and Frazer lakes demonstrated that these algal communities were sensitive to changes in sockeye salmon spawner abundances, our ~2,200 year comparison of diatom profiles from these lakes further reinforces the idea that dramatic variations seen in the Karluk record are due to large shifts in sockeye salmon escapement (and not due to the direct impacts from regional environmental forcing). This conclusion is also supported by the $\delta^{15}\text{N}$ profile from Karluk Lake (Figure 8).

Significance of changes in sockeye salmon abundances at Karluk Lake and its implications on ecosystem dynamics

The dramatic variation in sockeye salmon abundances inferred from both the diatom and $\delta^{15}\text{N}$ records of Karluk Lake provide powerful insights into their natural population dynamics and their impacts on nursery lake environments. A regional comparison of past population dynamics in sockeye salmon and other fish populations over the past ~2,200 years has demonstrated that the low-frequency variation seen in Karluk Lake is not unique (Finney et al. 2002). Paleolimnological analysis from another Kodiak Island sockeye salmon nursery lake, Akalura Lake (57°11'N, 154°12'W), has reproduced the same pattern of lower numbers of sockeye salmon from ca. AD 0 to AD 800 (Finney et al. 2002). Furthermore, Finney et al. (2002) compared these ~2,200 year inferences of Alaskan sockeye salmon to reconstruc-

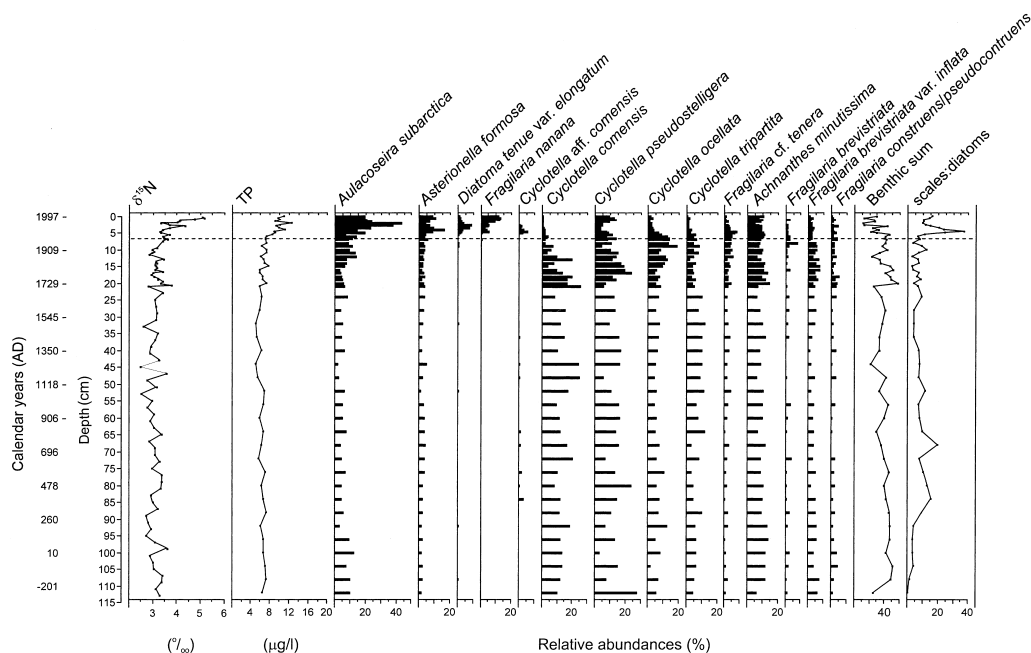


Figure 9. Profiles of the dominant diatom taxa (>5% relative abundances), chrysophyte scale:diatom ratio, inferred TP and $\delta^{15}\text{N}$ from Frazer Lake over the past ~2,200 years. Dashed line indicates when sockeye salmon were introduced into Frazer Lake.

tions of other fish populations further south on the west coast of North America, and revealed that these north and south fish populations varied synchronously, but in opposite directions, over low frequencies. Overall, these broadly synchronous trends suggest that ecological processes within the North Pacific are important in determining fish population dynamics (Finney et al. 2002).

The profound impact that sockeye salmon carcasses have had on lake trophic state can be appreciated by comparing the inferred TP concentrations from diatom analyses to $\delta^{15}\text{N}$, an independent proxy of sockeye salmon abundances (Finney et al. 2000). Over the course of the Karluk Lake record, TP concentrations have fluctuated between ~5 to 18 $\mu\text{g/L}$, and at times trophic state has changed markedly over short periods of time (i.e., within ~30 years).

It has long been believed that nutrients released from the carcasses of Pacific salmon spawners would promote primary and secondary production, which in turn would support the next generation (Juday et al. 1932). However, substantial quantitative data supporting this hypothesis have only recently emerged (e.g., Mathisen et al. (1988), Kline et al. (1993), Bilby et al. (1998), Wipfli et al. (1998)). For Karluk Lake, the nutrient reconstructions we present here, together with data demonstrating that SDN benefit zooplank-

ton production (Finney et al. 2000; Sweetman 2001) and are incorporated into sockeye salmon smolts (Kline et al. 1997; Finney et al. 2000), leave little doubt that SDN are playing a significant role in the development of these juvenile fish (i.e., the carcasses represent a nutrient feedback to the next generation). As increases in smolt size (up to 110 mm) are known to increase ocean survival (e.g., Koenings and Burkett (1987b)), our results suggest that greater SDN loading could enhance sockeye salmon smolt survival in the ocean. However, it is important to recognize that in some nursery lakes, high numbers of sockeye salmon spawners have produced high fry densities, which in turn has led to unfavorable conditions for smolt development (e.g., Kyle et al. (1988), Schmidt et al. (1996)). Relatively high sockeye salmon fry densities can result in intense predation pressure on zooplankton assemblages, which can cause a decrease in the densities or availability of preferred fry forage, and in turn result in smaller smolt sizes (e.g., Kyle et al. (1988), Schmidt et al. (1996)).

Whereas SDN can be important in juvenile sockeye development, our data also suggest, as others have shown, that changes in marine environmental conditions significantly affect adult sockeye salmon production. The presence of shifts in adult sockeye salmon abundances, which are synchronous across

multiple populations (e.g., Mantua et al. (1997), Finney et al. (2000, 2002)) and synchronous with abundance shifts in numerous fish species (including those which are strictly marine; Beamish (1993), Finney et al. (2002)), suggests that ocean conditions may at times largely override any of the benefits that sockeye smolts may have gained from their freshwater rearing environment. Temporal shifts in the relationship between smolt size and percent ocean survival of smolts described by Koenings and Burkett (1987b) support this idea. Not surprisingly, both the freshwater and marine phases of the lifecycle of sockeye salmon can influence the production of adult spawners. Furthermore, the significance of the freshwater nutrient feedback loop may vary among lake systems and is likely dependent on the nursery lake zooplankton community and density of sockeye salmon spawners.

Conclusions

The strong relationships between historical sockeye salmon escapement and sedimentary diatom assemblages from two lakes on Kodiak Island have demonstrated that diatom-based paleolimnological methods can be used to infer past trends in sockeye salmon spawner abundances. Over the historical record, periods of higher sockeye salmon abundances corresponded to greater abundances of meso- to eutrophic diatoms and higher diatom-inferred TP concentrations.

By establishing the significant influence of SDN on sedimentary diatom assemblages spanning the historical record, we then analyzed diatom assemblages which represented the last ~2,200 years of sediment accumulation at Karluk Lake and inferred from these data dramatic decadal and centennial-scale shifts in sockeye salmon abundances. These inferences were also supported by our observations that: 1) an independent proxy of sockeye salmon, $\delta^{15}\text{N}$, showed similar trends; and 2) our nearby control lake showed only subtle variation in $\delta^{15}\text{N}$ and in diatom species assemblages over this time.

Together, this study and the few others that have reconstructed past sockeye salmon abundances (Finney et al. 2000, 2002) highlight a key strength of paleoenvironmental studies: their ability to reveal ecological “surprises” (Gorham et al. 2001). Prior to our work on reconstructing past sockeye salmon abundances from paleolimnological records (this study; Finney et al. (2000, 2002)), data which sug-

gested that decadal-scale climatic variability had a significant influence on Pacific salmon were based on monitoring records for the 20th century (e.g., Beamish (1993), Mantua et al. (1997)) and were confounded by the presence of other factors (e.g., commercial fishing, habitat alteration, hatchery releases). By extending the historical monitoring window with paleolimnological records (this study; Finney et al. (2000, 2002)), we can show that decadal-scale variability in Pacific salmon is not a phenomenon unique to the 20th century and is caused, at least in part, by climatic forcing. Furthermore, the ~2,200 year perspective has revealed a novel mode of variability, one that varies over centuries and has operated in addition to the decadal-scale variability (this study; Finney et al. (2000, 2002)). Clearly, we are just beginning to understand modes of variability in sockeye salmon abundance and their causes. Diatom-based paleolimnology of sockeye nursery lakes may provide key insights into the population dynamics of sockeye salmon, potentially extending records back to the time of lake formation.

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