Limnol. Oceanogr., 51(4), 2006, 1637–1647

Spatial variability of stable isotopes and fossil pigments in surface sediments of Alaskan coastal lakes: Constraints on quantitative estimates of past salmon abundance

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Abstract

We quantified spatial patterns of stable isotopes of N and C ($\delta^{15}N$, $\delta^{13}C$) and fossil pigment concentrations in the uppermost 10 mm of sediment (~10 yr) from 74 profundal locations and three spawning-stream discharge areas in Lake Nerka, southwest Alaska. Sediment $\delta^{15}N$ (4.3‰ ± 0.7‰) and $\delta^{13}C$ (−26.3‰ ±1.2‰) varied directly ($\delta^{15}N$) or inversely ($\delta^{13}C$) with water column depth, whereas concentrations of most fossil pigments from algae were negatively correlated with depth. Sediment $\delta^{15}N$ and $\delta^{13}C$ were poorly correlated with either fossil pigment abundance or the local densities of spawning salmon. Instead, coastal nursery lakes appeared to integrate marine-derived nutrients rapidly into lakewide nutrient pools, suggesting that while individual cores may be used to reconstruct whole-lake salmon densities, habitat-specific variations of past fish populations cannot be quantified reliably from sedimentary analyses.

During the past several decades, the sustainability of coastal marine fisheries has been subject to considerable study because of dwindling stocks of economically important fishes, particularly in the North Pacific Ocean (Gresh et al. 2000). In this region, salmon are important ecological, economic, and cultural resources; however, wild populations have declined because of human activities that influence the production and survival of salmon at all life stages (Slaney et al. 1996; Willson et al. 1998). Although Pacific salmon species range from California to Alaska, species within the northwest United States (Washington, Oregon, Idaho, California) have experienced the greatest reductions in production during the past 100 years (Gresh et al. 2000), with extirpation from ~40% of their native range (Nehlsen et al. 1991). Similarly, in western Canada, 20% of salmon stocks are at risk or have been extirpated, whereas in contrast only 2% of Alaskan stocks are endangered (Slaney et al. 1996).

Declines in salmon populations have important ecological consequences for freshwater ecosystems that serve as nursery lakes (Willson et al. 1998; Gende et al. 2002; Schindler et al. 2003). In particular, fisheries interceptions may affect the production, biodiversity, and community structure of freshwater, riparian, and terrestrial ecosystems that rely on marine-derived nutrients (MDN) transported by salmon (Cederholm et al. 1999; Helfield and Naiman 2002). For example, anadromous, semelparous salmon accumulate ~95% of their mass in the marine environment and can act as substantial sources of nitrogen (N) and phosphorus (P) to lakes after spawning (Mathisen et al. 1988) because adult fish are numerous, large (2–20 kg), and rich in P (0.36% by mass) and N (3.04% by mass) (Larkin and Slaney 1997). Although smolt emigrations may export up to 20% of MDN contributions from spawning adults (Moore and Schindler 2004), variations in fisheries escapement (i.e., unharvested fish) and associated MDN influx appear to regulate the primary production of nursery lakes (Finney et al. 2000; Schindler et al. 2005). Because salmon feed at an elevated trophic level in the ocean (Beacham 1986), their body tissues are enriched with the ^{15}N isotope (~11‰) in comparison to N from terrestrial (~2‰) and atmospheric (~0‰) sources (Mathisen et al. 1988; Kline et al. 1993). As a result, influxes of MDN in salmon can alter the isotopic composition of dissolved, planktonic, and sedimentary N pools in nursery lakes (Finney et al. 2000, 2002). Unfortunately, although the ability of migratory salmon to alter biogeochemical signatures of lakes is well established (but see Holtham et al. 2004), little is known of how these signatures vary among habitats within a lake.

Analysis of stratigraphic changes in sediment $\delta^{15}N$ has been used recently to reconstruct historical variation in salmon populations (Finney et al. 2000, 2002; Schindler et al. 2005). However, published reconstructions of past salmonid densities have been based on analysis of a centrally located sediment core, despite recognition that profundal sediments are not deposited evenly throughout lake basins (Downing and Rath 1988) and that salmon spawning activities are often distributed heterogeneously within nursery lakes. Similarly, little is known of how sediment proxies of lake response to MDN (e.g., diatom

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Acknowledgments

We thank Wendy Palen and Monika Winder for field assistance, Richard Hughes for assistance with isotope analyses, and Suzanne McGowan for assistance with HPLC analyses.

Funding for this research was provided by an NSF Biological Oceanography Grant to D.E.S. and an NSERC Canada Discovery Grant to P.R.L. Additional funding was provided by the University of Washington Alaska Salmon Program and Fisheries Research Institute, the Canada Research Chair Program, Saskatchewan Learning, and the Canada Foundation for Innovation.

frustules, algal pigments, invertebrate remains) vary among regions within lakes (Anderson 1990). As a result, it remains unknown whether individual cores integrate past escapement densities throughout entire basins or whether MDN from individual spawning habitats alter fossil concentrations in local sedimentary environments. Therefore, with expansion of such paleoecological reconstructions into lakes atypical of previous studies (e.g., stained or rapidly flushing) (Gregory-Eaves et al. 2004; Holtham et al. 2004), and because these retrospective analyses represent the sole method to quantify variation in salmon production and its controls beyond the past century (e.g., Finney et al. 2002), there is an increasing need for detailed spatial analysis to quantify the geographic complexity of MDN deposition to lake sediments and related variation in lake production.

To address these issues, we quantified the spatial variability of paleolimnological indicators of past salmon density ($\delta^{15}N$), algal abundance (fossil pigments), and lake production ($\delta^{13}C$) in 74 surface sediment samples from Lake Nerka, one of the principle sockeye nursery lakes of the Wood River–Tikchik ecosystem of southwest Alaska. In addition, we analyzed surficial lake sediments within 800-m × 300-m grids located across the mouths of significant spawning streams to quantify the extent to which local sources of MDN could be identified from sedimentary deposits. Overall, our analysis revealed that nursery lakes rapidly mix local sources of MDN such that paleoecological reconstructions on the basis of single cores record mainly basinwide patterns of past fish abundance and whole ecosystem responses to MDN inputs.

Methods

Catchment description—The Wood River–Tikchik drainage (59°20′N, 56°40′W) occupies a largely undisturbed region of southwest Alaska (Fig. 1). Surface waters within the catchment flow southward through a chain of five lakes including Kulik, Mikchalk, Beverly, Nerka, and Aleknagik. Catchment topography to the west of the lake is steep and consists of mountainous regions that rise to 800 m above sea level. Terrestrial vegetation is dominated by white spruce (*Picea glauca*), balsam poplar (*Populus balsamifera*), willow (*Salix* spp.), and alder (*Alnus* spp.). The eastern catchment is level and consists mainly of muskeg. At higher elevations, alder is common, whereas lowland vegetation is composed mainly of moist tundra plant communities (Helfield and Naiman 2001).

Lake Nerka is large (201 km^2) and exhibits complex basin morphology with distinct regions including the North Arm, Central Arm, Amakuk Arm, South Arm, and River Bay (Fig. 1). In all cases, the surface water is dilute, unproductive, and stratified between late June and late September (Table 1), with severe phosphorus limitation arising in part because of the high precipitation (51–89 cm yr^{-1}) and rapid hydrologic flushing (~2 yr) (Hartman and Johnson 1984). At least 60 surface streams discharge into Lake Nerka, along with innumerable mountain seepages (Rogers and Rogers 1998*a*).

Commercial catch and escapement of salmon in the Wood River system have been monitored since 1958 by the University of Washington and the Alaska Department of Fish and Game (Hilborn et al. 2003). During the past 45 yr, an average $\sim 1.14 \times 10^6$ adult sockeye salmon (*Oncorhynchus nerka*) have evaded the fishery and return annually to spawn on lake beaches (47%), in tributary creeks (26%), and in rivers between lakes (27%) in the Wood River system, with ~42% returning to Lake Nerka (Schindler et al. 2005). In addition, the Little Togiak Lake River flows into the central portion of Lake Nerka and provides a nursery to $\sim 1.3 \times 10^4$ fish annually, whereas the Agulukpak River flows into the north end of the lake and supports an additional $\sim 1.25 \times 10^5$ sockeye salmon (Fig. 1). Smaller populations of chum (*O. keta*), pink (*O. gorbuscha*), coho (*O. kisutch*), and king salmon (*O. tshawytscha*) are also present within Lake Nerka.

Creek descriptions—Characteristics of lake sediments in the discharge areas of nursery streams were surveyed to determine whether MDN were rapidly integrated within Lake Nerka and to identify the relative contribution of nutrients from each stream to the lake. Consequently sites were selected to represent different regions of the lake, including Fenno Creek in the South Arm, Pick Creek in the central basin, and Hidden Creek in the North Arm (Fig. 1). All creeks exhibit similar physical characteristics, but have different mean salmon abundance for the period 1993–2003 (Table 2). Fenno Creek is the longest of the spawning streams and receives an annual average of 4,880 ± 2,335 adult salmon, whereas Pick Creek supports 5,360 ± 1,322 spawning individuals yr^{-1}. In contrast, Hidden Creek supports only 2,533 ± 1,869 spawning salmon because of poor benthic characteristics (rapid flow, coarse gravel) in the lowest 0.5 km of the creek (Rogers and Rogers 1998*b*).

Sedimentary analyses—In August 2003, 74 sediment cores were collected from Lake Nerka using a Glew gravity corer equipped with a 10-cm-diameter coring tube. The uppermost 10 mm of sediment in each core were isolated using a vertical sediment extrusion device, sections were transferred to black airtight containers, and sediments were stored in coolers containing ice. In all cases, sediments were frozen within 4 h of collection and remained so until analysis at the University of Regina. Comparison of ratios of labile (chlorophyll *a* [Chl *a*]) to stable (pheophytin *a*) pigments in samples collected throughout the summer revealed no substantial degradation or transformation of fossil pigments as a result of the 2-month storage period. Although no sediment chronology was established for these cores, prior analysis of ^{210}Pb inventories in sediment cores from Lake Nerka suggests that this surface sediment interval encompassed ~10 yr of sediment deposition (Schindler et al. 2005). Similar sediment collection protocols were used to obtain surficial samples from nearby Little Togiak Lake (20 cores), Lynx Lake (10 cores), and Hidden Lake (5 cores).

Core locations were predetermined to maximize spatial coverage and avoid discontinuities (e.g., deltaic processes) associated with obvious surface water inflows. Instead,

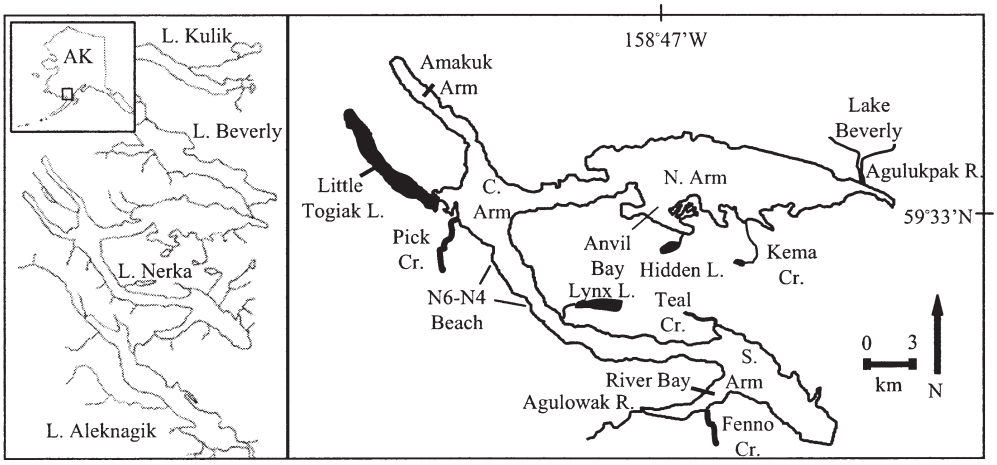


Fig. 1. Spatial position of study lakes (Nerka, Little Togiak, Lynx, Hidden), salmon-spawning creeks (Fenno, Pick, Hidden), and the Wood River–Tikchik drainage system (inset) within Alaska.

sediment characteristics associated with the discharge areas of three spawning streams were quantified within grids across stream outflows to examine patterns of MDN export and deposition. In each creek survey, sediments were sampled at 15 well-spaced stations within an 800-m (along shore) by 300-m (off shore) grid. Cores were collected at each station and the uppermost 10 mm of sediment isolated and stored as detailed above.

Sediment samples for fossil pigment analysis were freeze-dried, homogenized, and weighed (50–150 mg) immediately before chemical analysis by high-performance liquid chromatography (HPLC) following Leavitt and Hodgson (2001). Fossil pigments were extracted using standard procedures, filtered (0.2-μm pore), and dried with N_2 gas under minimal indirect lighting. Carotenoid, chlorophyll, and derivative-compound concentrations were quantified with a Hewlett-Packard 1100 HPLC using Sudan II dye as an internal standard. Sediment pigment concentrations were expressed as nmol g^{-1} dry mass because sediment carbon content was similar among sites (5.4% ± 1.3% C), because we did not quantify the organic matter content of samples (Leavitt and Findlay 1994), and because spatial patterns were similar if pigments were also expressed as nmol g^{-1} total C.

Table 1. Selected physical, chemical, and biological properties of Lake Nerka, Alaska.

	Lake Nerka
Elevation (m)	21
Surface area (km^2)	201
Mean depth (m)	39
Max depth (m)	164
Volume (km^3)	5.2
Distance from sea (km)	63
Water residence time (yr)	2
Photic zone depth (m)*	22
Total P ($\mu g\ L^{-1}$)†	6.5
Total N ($\mu g\ L^{-1}$)	314.0
N : P	50.3
Total sockeye abundance (1,000 of fish)‡	480
Sockeye density (1,000 km^{-2})	2.39

* Mean of south, central, and north basin sampling programs (1996), modified from Rogers and Rogers (1998*a*).

† Average of biweekly sampling through ice-free season (June–September 2002).

‡ Mean of compiled stream and lake counts of total spawning salmon provided by the Alaska Salmon Program and Fisheries Research Institute (1956–2003).

Sedimentary pigments were identified by chromatographic position and spectral characteristics in comparison to authentic standards and isolates from unialgal cultures of known pigment composition (Leavitt and Hodgson 2001). Analysis was restricted to bio-indicator compounds characteristic of siliceous algae and some dinoflagellates (fucoxanthin), mainly diatoms (diatoxanthin), cryptophytes (alloxanthin), chlorophytes and cyanobacteria (lutein–zeaxanthin), and total algae (β-carotene, Chl *a*, pheophytin *a*). Although structural isomers lutein (chlorophytes) and zeaxanthin (cyanobacteria) were not separated on our HPLC system, the contribution of cyanobacteria to the sedimentary pigment composition is assumed to be negligible because of the scarcity of other carotenoids characteristic of cyanobacteria (e.g., echinenone, canthaxanthin, myxoxanthophyll) and low cyanobacterial abundance within modern planktonic and benthic communities.

Sediment samples remained frozen until analysis of stable isotopic ratios of N and C following the methods of Savage et al. (2004). Briefly, subsamples were freeze-dried 48 h before thorough homogenization and weighing of sediments (5 ± 0.05 mg) into tin capsules for combustion. Quantitative determinations of stable N and C isotope ratios and relative N and C contents (% dry mass) were conducted at the University of Regina's Environmental Quality Analysis Laboratory using a ThermoQuest (F-MAT) Delta^{plus} XL isotope ratio mass spectrometer equipped with a ConFlow III dilution inlet system. Stable isotope ratios and elemental composition analyses were conducted on whole dried sediments after acidification tests confirmed that inorganic C was a minor constituent of bulk sediments and were presented in standard δ notation ($\delta^{15}N$,

Table 2. Physical characteristics of selected spawning streams tributary to Lake Nerka. Modified from Rogers and Rogers (1998*b*). Mean abundance of spawning sockeye salmon are presented for the period 1993–2003.

Location	Fenno Creek	Pick Creek	Hidden Creek
	South Nerka	Central Nerka	North Nerka
Length (km)	5.2	4.0	4.2
Mean width (m)	7.6	4.6	4.6
Mean depth (m)	4.3	5.5	3
Velocity (m s^{-1})	0.9	0.7	0.6
Flow (m^3 s^{-1})	3	0.6	0.7
Spawning area (km^2)	0.027	0.017	0.013
Total sockeye abundance	4,880 ± 2,335	5,360 ± 1,322	2,533 ± 1,869

$\delta^{13}C$). Replicate samples varied less than 0.28‰ and 0.1‰ for $\delta^{15}N$ and $\delta^{13}C$ determinations, respectively.

Graphical and statistical analyses—Patterns of spatial variability of sedimentary isotope ratios and pigment concentrations were quantified using Surfer v. 8.0, a high-precision spatial analysis graphics package. Lake Nerka's shoreline was digitized from maps obtained from the Alaskan Department of Fish and Game (1 : 125,000 scale). Global positioning satellite locations taken at the time of sampling were overlaid onto maps and abundance contours plotted for each sedimentary variable. The one-sample Kolmogorov–Smirnov test was used to compare the shape and location of sample distributions to a normal distribution. Relations among variables were examined with Pearson product-moment correlation coefficients without correction for sample size. In all cases, sedimentary pigment concentrations were $\log_{10}(x + 1)$ transformed to normalize data, whereas metrics of isotopic ($\delta^{15}N$, $\delta^{13}C$) and elemental (%) composition were normally distributed and did not require transformation. All statistical analyses were performed using SYSTAT v. 10.

Results

Spatial analysis of Lake Nerka sediments—Analysis of $\delta^{15}N$ and $\delta^{13}C$ in surficial sediments of Lake Nerka revealed only minor variation in N (mean ± SD; 4.3‰ ± 0.7‰) and C isotope ratios (−26.3‰ ± 1.2‰) (Fig. 2). Analysis of geographic patterns revealed that $\delta^{15}N$ was enriched both in the central North Arm and in the upper reaches of the South Arm, whereas low $\delta^{15}N$ values occurred in the Amakuk Arm, near the outflow of the Agulukpak River, Anvil Bay, and the South Arm (Fig. 2). Similarly, carbon isotope signatures exhibited only modest spatial variation in Lake Nerka, with northern and southern basins exhibiting slightly higher $\delta^{13}C$ values (−25.9‰ ± 1.0‰) than those of central locations (−26.7‰ ± 1.2‰).

Pigment concentrations exhibited greater spatial variability than did isotope ratios (Fig. 3). In particular, concentrations of ubiquitous biomarkers (Chl *a*, pheophytin *a*, β-carotene) were low in the deep central regions of the lake, but exhibited higher values in shallow areas (South Arm), near major rivers inflows (Little Togiak River, Agulukpak River) and in embayments (River Bay, Anvil Bay). Similarly, concentrations of taxonomically diagnostic carotenoids (alloxanthin, fucoxanthin, lutein–zeaxanthin, diatoxanthin) were positively correlated ($p < 0.05$) with β-carotene, our most chemically stable indicator of total algal abundance (Leavitt and Hodgson 2001).

Sediment characteristics varied significantly with water column depth, although the sign of the relation varied between N and C (Fig. 4). For example, $\delta^{15}N$ and C : N ratios increased significantly with water column depth ($r = 0.27$, $p < 0.02$; $r = 0.39$, $p < 0.001$, respectively), whereas $\delta^{13}C$ values declined with water column depth ($r = -0.33$, $p < 0.001$). Similarly, concentrations of pigments indicating total algal abundance decreased with depth ($r = -0.34$ to -0.68, $p < 0.005$), as did concentrations of all taxon-specific carotenoids except alloxanthin from cryptophytes (Fig. 4).

Sediment biogeochemistry near spawning streams—Analyses of three spawning stream discharge areas suggested that marine-derived N was transported to deepwater depositional areas in Lake Nerka and only occasionally remained in an identifiable sedimentary plume near the creek mouth (Fig. 5). For example, sediment $\delta^{15}N$ values ranged 1.9–4.0‰ but were elevated only near the outflow of Fenno Creek and remained high throughout the discharge area of that creek alone. As in the overall lake survey, $\delta^{13}C$ enrichment declined as a function of depth in the Fenno Creek grid ($r = -0.69$, $p < 0.005$), unlike $\delta^{15}N$ signatures ($r = 0.07$, $p = 0.81$). In contrast to Fenno Creek, analysis of sediment $\delta^{15}N$ within the Pick Creek grid revealed little evidence of MDN deposition, although $\delta^{15}N$ and water column depth were correlated ($r = 0.76$, $p < 0.001$). Instead, $\delta^{13}C$ values apparently retained evidence of stream inflow, with depleted values evident near the creek mouth and higher values at deep regions of the grid although weak ($r = -0.39$, $p = 0.15$). Finally, N signatures were positively correlated with water column depth near the Hidden Creek outflow ($r = 0.87$, $p < 0.0001$), whereas those of $\delta^{13}C$ declined with depth ($r = -0.79$, $p < 0.0005$). In addition, $\delta^{13}C$ values apparently distinguished the stream discharge zone (−28‰) from other shallow water deposits (−24‰), although there was little evidence of marine-derived N inputs.

Spatial patterns of ubiquitous pigment concentrations (not shown) varied substantially among creek sites and did not show a consistent pattern of deposition related to lake

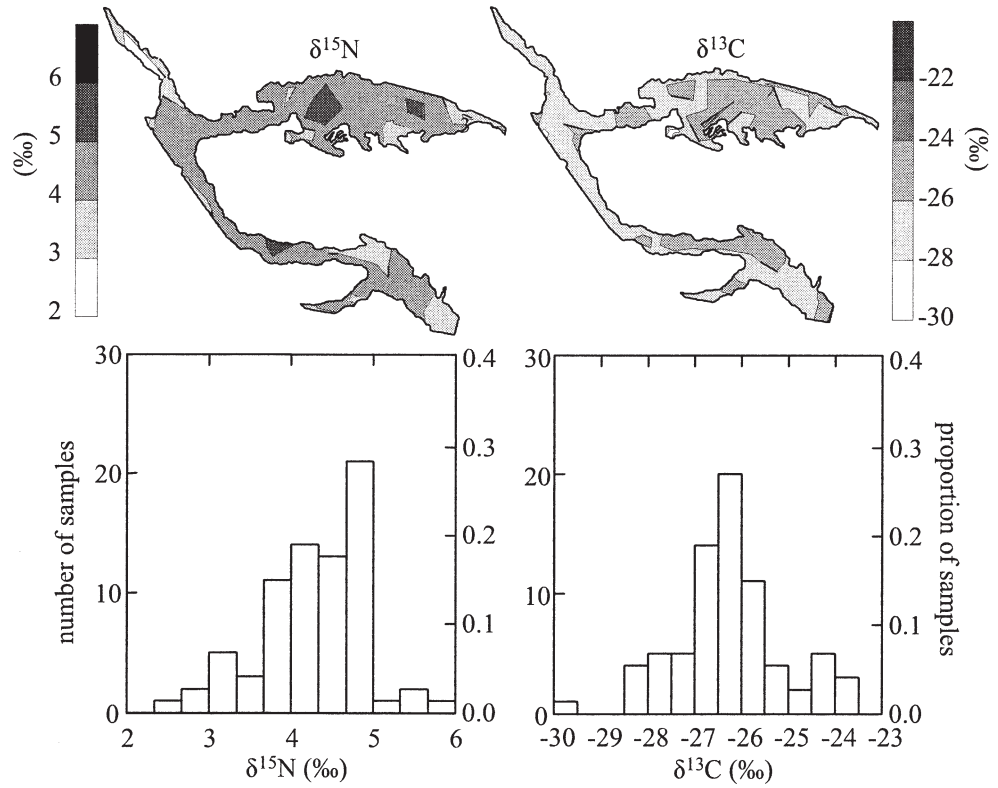


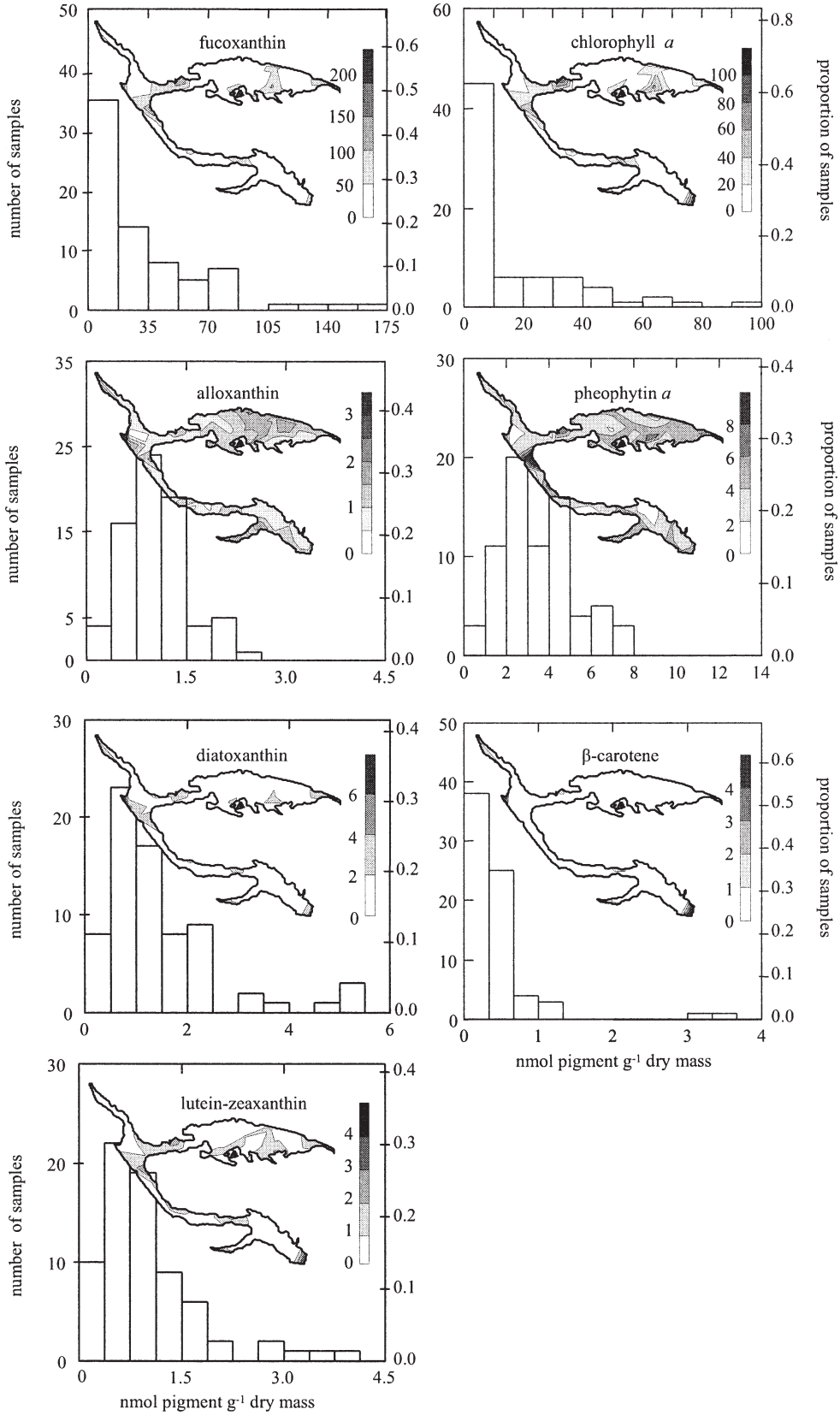
Fig. 2. Spatial patterns of sedimentary $\delta^{15}N$ (‰) and $\delta^{13}C$ (‰) within Lake Nerka on the basis of analysis of surface sediments (10-mm depth) from 74 cores. Frequency histograms for isotope ratios are presented below each map.

depth or position relative to the creek mouth. For example, pigments in sediments near the outflow of Fenno Creek were unrelated to either water column depth or inflow position ($r < 0.1$, $p > 0.30$), whereas concentrations of taxon-specific pigments showed no common pattern near the Pick Creek deposition area. Instead, at this latter site, concentrations of Chl *a* and β-carotene decreased as a function of water column depth ($r > -0.81$, $p < 0.001$), possibly reflecting the greater depth gradient (14–58 m) relative to Fenno Creek (1–28 m). Finally, sedimentary pigment concentrations decreased strongly with depth of deposition within the Hidden Creek grid ($r > 0.77$, $p < 0.01$) and along a west-to-east gradient.

N isotopes as indicators of salmon escapement—To further evaluate the reliability of $\delta^{15}N$ as a proxy of salmonid escapement (Fig. 6), we expanded our surface sediment spatial analysis to include Little Togiak Lake (20 cores), Lynx Lake (10 cores), and Hidden Lake (five cores), all sites located within the Wood River catchment (Fig. 1). Overall, mean sediment N isotope signatures were positively correlated to estimates of modern sockeye escapement ($r = 0.84$, $p < 0.0001$) when examined in the context of other Alaskan lakes (Finney et al. 2000). However, at any given level of salmon escapement the observed variation of sediment $\delta^{15}N$ values among lakes (~3‰; Fig. 6) was similar to that arising from spatial variation within Lake Nerka (Fig. 2), its nursery creek outflows (Table 3), or in other lakes of the region.

Discussion

Analysis of surface sediments throughout Lake Nerka revealed only modest spatial heterogeneity of stable isotope ($\delta^{15}N$, $\delta^{13}C$) signatures (Fig. 2), but relatively great geographic variance in sediment pigment concentrations (Fig. 3). Overall, deposition of stable isotopes and pigments were correlated to water column depth, although it is likely that different processes governed the flux of individual components to the lake bottom. For example, marine-derived N (as $\delta^{15}N$) appeared to be rapidly integrated into whole-lake N pools (Fig. 5), possibly due to large-scale processes that control organic matter deposition and the mixing of aquatic and terrestrial materials (e.g., water circulation, sediment redistribution). Similarly, C isotopic signatures showed relatively low levels of spatial variability, with heterogeneity possibly arising from localized inputs of terrestrial or stream matter (see following). In contrast, deposition of fossil pigments was strongly and inversely correlated to the depth of water column, likely reflecting both rapid degradation during sedimentation (Cuddington and Leavitt 1999) and the influence of benthic algal production within the littoral zone (Leavitt and Carpenter 1989). Together these patterns suggest that while reconstructions of past MDN fluxes may be insensitive to the precise location of cores within the lake central basin (e.g., Schindler et al. 2005), relations between MDN flux and lake production inferred from algal pigments may be influenced by water column depth.


fucoxanthin
chlorophyll *a*
alloxanthin
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nmol pigment g⁻¹ dry mass

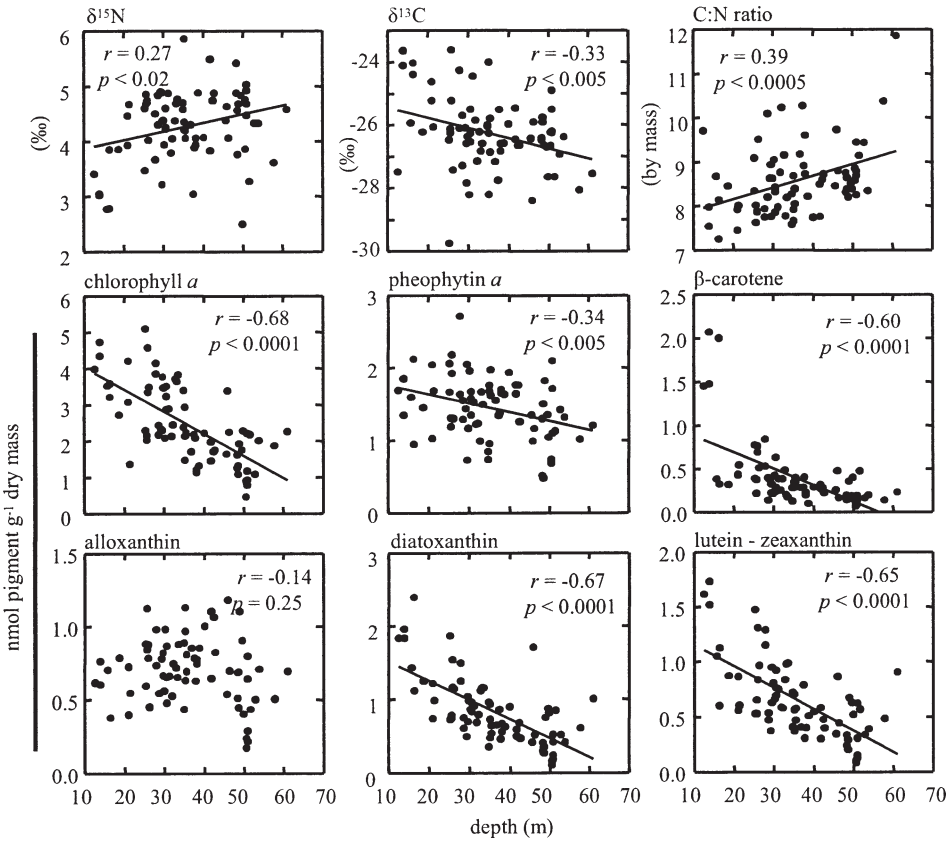

Fig. 4. Relation between sediment geochemistry ($\delta^{15}N$, $\delta^{13}C$, %C, %N), fossil pigments (Chl *a*, pheophytin *a*, β-carotene, alloxanthin, diatoxanthin, lutein–zeaxanthin), and water column depth (m) within Lake Nerka. Pigment concentrations (nmol g^{-1} dry mass) were log (x+1) transformed for regressions. Solid lines indicate significant ($p < 0.05$) correlations. Taxonomic affinity of each pigment as in Fig. 3.

Distribution of marine-derived N—Several mechanisms may have combined to produce low spatial variability in N stable isotopes (Fig. 2) yet a positive correlation between $\delta^{15}N$ and water column depth (Fig. 4). First, relatively uniform spatial distribution of $\delta^{15}N$ could have arisen from rapid and complete mixing of discrete isotopic sources, either as dissolved N or following uptake by phytoplankton (e.g., Hilton et al. 1986). Support for such basinwide mixing arises from comparison of sedimentary isotopic signatures of Lake Nerka with those of nearby lakes. For example, the main basin of Lake Nerka exhibited low spatial variability of $\delta^{15}N$ (4.3‰ ± 1.2‰) but unique isotopic signatures relative to those of Little Togiak (3.2‰ ± 1.3‰), Lynx (0.9‰ ± 1.0‰), and Hidden lakes (2.7‰ ± 1.2‰), all sites of similarly low spatial variance (Table 3). Further, isotopic signatures of the northern Amakuk Arm (2.9‰ ± 0.6‰) were also constant and discrete relative to the main basin of Lake Nerka, likely reflecting the fact that the Amakuk Arm is isolated by a shallow sill (~2-m deep) at the mouth of the embayment. Because the $\delta^{15}N$ signature of each basin arises from a unique mixture of $\delta^{15}N$ from marine (~11‰) and terrestrial sources (~0–2‰) (Helfield and Naiman 2002), each weighted by the mass of N from each source, rapid mixing of dissolved or particulate N should produce uniform spatial signatures of isotopes within individual lakes, yet consistent differences among basins.

Second, sediment redistribution may have played an important role in reducing spatial heterogeneity of sedimentary $\delta^{15}N$ values within Lake Nerka. For example, regression analyses demonstrated that deposition of ^{15}N increased significantly with water column depth in Nerka

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Fig. 3. Spatial patterns of fossil pigment concentrations (insets; nmol g^{-1} dry mass) within surface sediments of Lake Nerka (n = 74 cores), as well as frequency histograms for concentrations of fossil pigments from siliceous algae and dinoflagellates (fucoxanthin), cryptophytes (alloxanthin), mainly diatoms (diatoxanthin), chlorophytes and cyanobacteria (lutein–zeaxanthin), and total algae (Chl *a*, pheophytin *a*, β-carotene).

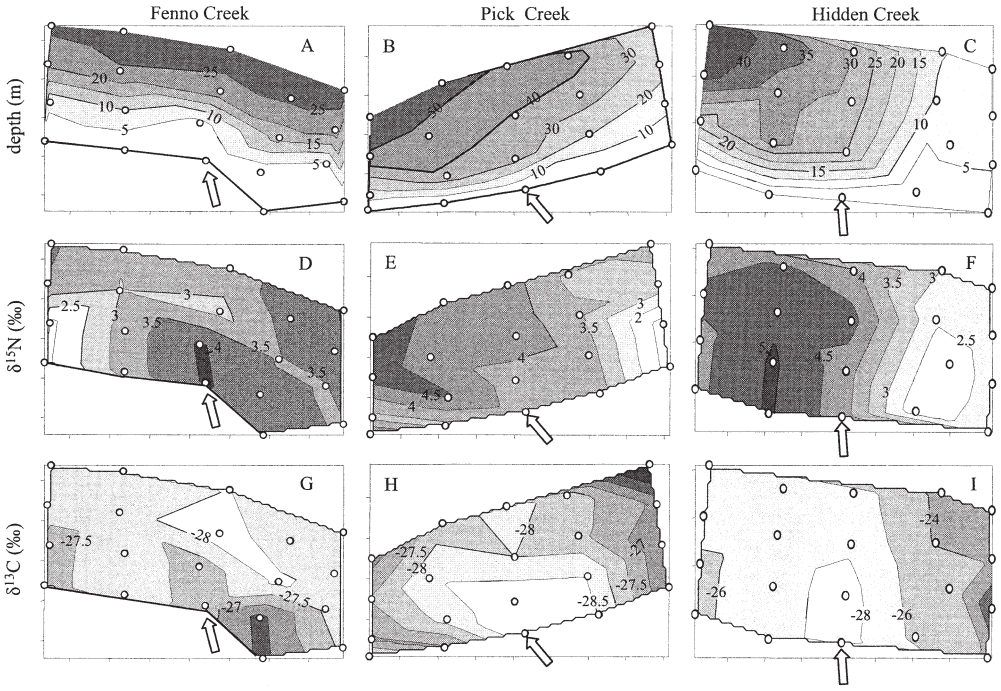

Fig. 5. Contour plots of water column depth (m; A–C), $\delta^{15}N$ signatures (‰; D–F), and $\delta^{13}C$ content (‰; G–I) of surface sediments (10-mm depth) at near-shore locations adjacent to salmon-spawning steams. Cores were collected within 800-m × 300-m grids for Fenno, Hidden, and Pick creeks. Arrows indicate location and direction of stream entry into Lake Nerka.

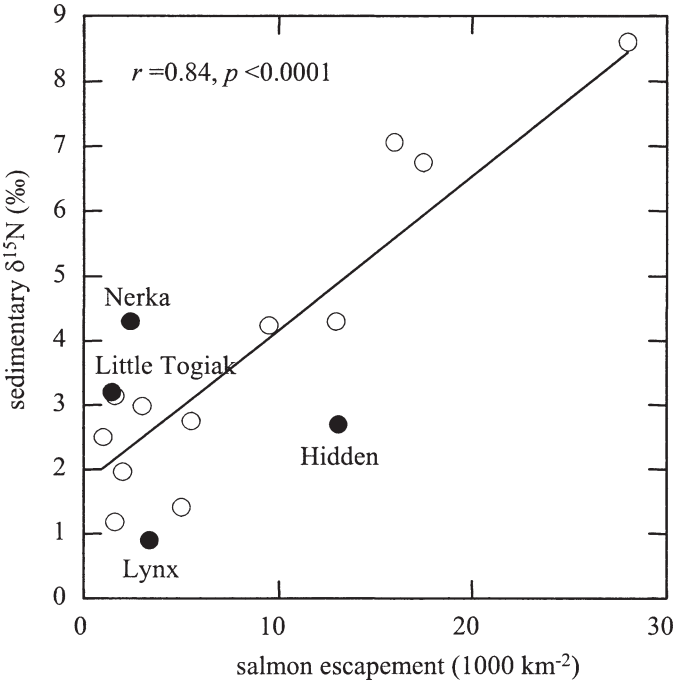

Fig. 6. Relation between sedimentary $\delta^{15}N$ (‰) and returning salmon densities (escapement km^{-2}) during the past 10 yr in Nerka, Little Togiak, Lynx, and Hidden lakes (solid symbols) and in other salmon nursery lakes in Alaska (open symbols; data from Finney et al. 2000). Spawning salmon densities estimated from a combination of weir estimates of escapement (Nerka), aerial density estimates (Little Togiak, Lynx, Hidden), and lakeside beach surveys (Hidden).

Lake (Fig. 4) and two inflow stream deltas. Due to the great fetch of each site, surface waves entering the littoral zone probably create sufficient energy and turbulence to resuspend particulate matter, including salmon remains, for translocation to offshore sites (Smith 1979). Similarly, the relatively steep littoral zone substrate (10–16% grade; Fig. 5) may have facilitated sediment redistribution toward deeper locations. Previous studies have shown that permanent accumulation of sediments is reduced in regions with slopes >4% and <14% and is minimal if grades exceed 14% (Håkanson 1977). In addition, selective deposition of coarse material within creek alluvial deltas (e.g., plant matter, fish remains) and continued transport of fine particulates to offshore locations (e.g., periphyton, algal detritus, colloidal dissolved organic matter) may have helped homogenize MDN within the lake. In particular, the nest-building activities of mating salmon are known to increase export of fine sediment, periphyton, and particulate organic matter from stream spawning areas (Moore et al. 2004), possibly improving MDN transport to offshore regions.

Finally, correlations between sediment $\delta^{15}N$ and water column depth may have arisen because of spatial gradients of nutrients from littoral to pelagic habitats. For example, N_2 fixation by prokaryotes associated with *Alnus* spp. is thought to be the principal source of N within these terrestrial ecosystems (Engstrom et al. 2000) and should have a $\delta^{15}N$ signature near 0‰ (Hu et al. 2001). Uptake of this depleted N by phytobenthos should be most intense in well-lit waters near shore and should decline with depth because of light limitation. Consistent with this hypothesis,

Table 3. Mean and standard deviation (SD) of sedimentary biogeochemical variables observed in basinwide spatial surveys of Lakes Nerka, Little Togiak, Lynx, and Hidden, and grid surveys of salmon spawning streams tributary to Lake Nerka, including Hidden, Pick, Fenno creeks.

	Basinwide surveys							
	Lake Nerka (n=74)		Little Togiak (n=20)		Lynx Lake (n=10)		Hidden Lake (n=5)	
	mean	SD	mean	SD	mean	SD	mean	SD
$\delta^{15}N$ (‰)	4.3	0.7	3.2	1.3	0.9	1.0	2.7	1.2
%N	0.6	0.2	0.9	0.6	2.0	0.3	2.0	0.1
$\delta^{13}C$ (‰)	−26.3	1.2	−29.5	2.5	−34.4	0.6	−34.8	1.3
%C	5.4	1.3	6.8	4.6	14.1	2.1	15.3	1.1
C : N, by mass	8.6	0.8	8.1	0.7	7.0	0.2	7.5	0.6

	Creek surveys					
	Hidden Creek (n=15)		Pick Creek (n=15)		Fenno Creek (n=15)	
	mean	SD	mean	SD	mean	SD
$\delta^{15}N$ (‰)	3.8	1.0	3.9	0.8	3.4	0.6
%N	0.7	0.2	0.7	0.1	0.7	0.2
$\delta^{13}C$ (‰)	−25.6	2.3	−27.6	1.0	−27.7	0.5
%C	6.2	1.0	7.0	1.1	8.6	2.4
C : N, by mass	8.9	1.0	9.5	0.9	11.4	0.6

sedimentary C : N ratios were characteristic of algae (8.6 ± 0.8, by mass) rather than terrestrial plants (20–100; Meyer and Lallier-Verges 1999) and pigment concentrations generally declined with water column depth (Fig. 4). However, because direct estimates of benthic production were not available, and because the $\delta^{15}N$ of algae can vary also as a function of absolute N concentration, the chemical species of N, and algal species composition (e.g., Hodell and Schelske 1998), further research will be required to evaluate how terrestrially derived N and benthic production may influence spatial gradients of N isotope composition.

C isotopes as a proxy of freshwater production—Variability of sedimentary $\delta^{13}C$ values has been used to infer changes in past primary production of lakes (e.g., Gu et al. 1996), although little is known of the intrinsic spatial variability of C isotopes, nor of the influence of terrestrial or lotic sources of C on sedimentary isotope values. In Lake Nerka, sediment $\delta^{13}C$ values were positively correlated with total algal abundance estimated as fossil concentrations of chemically stable β-carotene ($r = 0.34$, $p < 0.005$). In such soft-water sites, enriched $\delta^{13}C$ values are thought to indicate elevated algal production because the degree of discrimination against the heavier ^{13}C isotope is reduced as demand for CO_2 increases but dissolved inorganic carbon (DIC) pools decline. Further, as DIC concentrations decrease, invasion of atmospheric CO_2 can increase, leading to an enrichment of water column CO_2 pools with atmospheric ^{13}C and increases in algal $\delta^{13}C$ (Schindler et al. 1997). However, although the positive correlation of $\delta^{13}C$ and total algal abundance is consistent with the use of C isotopes as a geochemical index of lake production, the low proportion of isotopic variance explained by direct estimates of algal abundance (11.5%) suggests that sedimentary $\delta^{13}C$ signatures may be influenced by more complex mechanisms than simple deposition of phytoplankton alone. In particular, the role of benthic algae should be evaluated carefully, as these organisms often exhibit more enriched $\delta^{13}C$ signatures than do phytoplankton because of CO_2 limitation within benthic boundary layers (Hecky and Hesslein 1995).

The presence of distinctive plumes of $\delta^{13}C$ in depositional areas adjacent to two stream discharge locations suggest that C inputs to sediments may arise in part from terrestrial or stream sources. For example, physical mixing of stream substrates by nest-building salmon increases loss of algal periphyton and fine terrestrial detritus from streams (Moore et al. 2004). Preliminary isotopic analyses demonstrate that this resuspended material exhibits highly depleted $\delta^{13}C$ signatures in both Pick (−31.1 ± 2.2‰) and Hidden creeks (−26.2 ± 1.4‰) (Moore and Brock unpubl. data), similar to the sedimentary values recorded at the mouths of the respective creeks (Fig. 5). Although these observations suggest that lotic systems may act as important conduits of C into littoral regions, there was no correlation between the presence of a $\delta^{13}C$ plume and the abundance of spawning salmon (Table 2). Consequently, further research is required to evaluate the exact mechanism by which terrestrial carbon subsidies to lakes may influence the isotopic signature of aquatic habitats (Schindler and Scheuerell 2002).

Spatial distribution of sedimentary pigments—Sedimentary pigments have been used to examine diverse ecosystem processes that alter algal production and community structure (Leavitt 1993; Leavitt and Hodgson 2001). The validity of such biochemical proxies requires clear un-

derstanding of the processes that regulate the relation between algal production and pigment deposition in sediments. Fortunately, pigment biogeochemistry has been well documented using whole-lake mass balances, ecosystem manipulations, microcosm experiments, theoretical modeling, and empirical calibration of fossils with long-term plankton records (reviewed in Cuddington and Leavitt 1999). In many cases, fossil pigment concentrations are well correlated with past changes in algal abundance (e.g., Leavitt and Findlay 1994). However, despite convincing evidence that historical changes in past algal communities can be reconstructed from individual sediment cores, little is known of how spatial variability of deposition processes may affect sedimentary pigment concentrations across entire lake basins (Leavitt and Carpenter 1989).

In Lake Nerka, fossil pigment concentrations decreased strongly with water column depth for all pigments except alloxanthin from cryptophytes (Fig. 5). These observations are consistent with both theoretical predictions (Cuddington and Leavitt 1999) and results from whole-lake mass balances that demonstrate alloxanthin is over-represented in deepwater sediments because of preferential deposition via zooplankton fecal material (Leavitt and Carpenter 1990). In both types of studies, fossil pigment concentrations are inversely correlated with the residence time of sinking algae in oxygenated waters prior to burial in sediments. Further, pigment deposition rates are inversely correlated with water column depth, the depth of oxygenated waters, and the initial starting position of algal cells within the water column, but are directly correlated with cell sinking rates. Therefore, despite substantial decomposition during sinking, fossil pigment concentrations are correlated with algal production over a wide range of lake conditions, so long as basic lake morphometry (e.g., depth, degree of stratification) does not vary greatly through time (Cuddington and Leavitt 1999; Leavitt and Hodgson 2001). Under these conditions, fossil pigments from individual cores can be used to reconstruct changes in past algal abundance, although as shown in the present study, these fossils are less suitable for comparisons of algal production among lakes or within complex lake basins (see also Vinebrooke et al. 1998).

Finally, negative correlations between pigment concentrations and water column depth may reflect diminishing contributions of benthic algal production to the sedimentary pigment pool (Leavitt and Carpenter 1989). The euphotic zone of Lake Nerka is ~22 m deep during most of the ice-free season, hence the large depth gradients seen here (Fig. 5) would be expected to encompass a wide range of phytobenthic production. Similar transects of surficial sediments in other dimictic lakes reveal that concentrations of pigments from benthic algae (e.g., diatoxanthin from diatoms) usually decline sharply at the base of the photic zone (Leavitt and Carpenter 1989). Unfortunately, because diatoms are the main component of both planktonic and benthic algal assemblages in Lake Nerka (Brock unpubl. data), it is difficult to identify the unique contribution of benthic algae to the fossil pigment assemblages from an analysis of carotenoids alone. Instead, future studies could combine fossil pigment analyses with identification of algal remains (e.g., diatom frustules, nonsiliceous fossils) to quantify the importance of phytobenthos to the sedimentary pigment assemblage.

In conclusion, our analyses showed that although $\delta^{15}N$ signatures were correlated with salmon escapement at the scale of entire lake basins (Fig. 6), sediments did not archive habitat-specific records of local salmon densities. For example, analysis of spatial patterns revealed that sediments exhibited comparatively uniform $\delta^{15}N$ and $\delta^{13}C$ signatures (Fig. 2), even though unique N isotope values were recorded in individual, physically isolated basins (Fig. 6). Further, analysis of sediment grids near nursery stream discharge areas did not capture the fine-scale variation in isotopes signatures arising from local spawning populations even though discrete plumes of $\delta^{13}C$ were apparently present (Fig. 5). Instead, lake sediments appeared to record overall salmon density regardless of precise position within the lake. However, because spatial variability of fossil pigments was substantial and strongly related to water column depth, it was difficult to compare MDN effects on algae among habitats within a lake. Fortunately, because lake depth at a given central site is unlikely to vary substantially during the typical period of salmon population reconstruction (e.g., Finney et al. 2000), fossil pigments should remain a useful metric of lake response to past changes in MDN flux when reconstructions are based on individual cores (e.g., Schindler et al. 2005).

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Received: 6 August 2005
Amended: 8 February 2006
Accepted: 13 March 2006