

# Variable effects of marine-derived nutrients on algal production in salmon nursery lakes of Alaska during the past 300 years

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## Abstract

We measured historical changes in sedimentary  $\delta^{15}\text{N}$  and fossil pigments in four lakes with anadromous semelparous salmon and two reference lakes to quantify the degree to which the flux of marine-derived nutrients (MDNs as N isotopes) regulate algal production (as pigments). During the past 300 yr, production of the predominant algae (diatoms) was positively correlated ( $r = 0.42\text{--}0.93$ ,  $p < 0.02$ ) with sedimentary  $\delta^{15}\text{N}$  in nursery lakes of sockeye salmon (*Oncorhynchus nerka*) but was inversely correlated with sedimentary  $\delta^{15}\text{N}$  ( $r = -0.71$  to  $-0.73$ ,  $p < 0.0001$ ) in reference lakes that lacked migratory fishes. Overall, the pigment– $\delta^{15}\text{N}$  correlation during the 20th century was strongly correlated with both mean densities of spawning sockeye salmon during 1956–2000 ( $r = 0.97$ ,  $p < 0.002$ ) and the fraction of total ecosystem N derived from salmon during 1900–2000 ( $r = 0.98$ ,  $p < 0.001$ ). Together these patterns suggest that the sign of the  $\delta^{15}\text{N}$ –pigment correlation can be used to distinguish among lakes or periods of time in which algal production is regulated mainly by MDN influx (positive correlation) or other factors (negative correlation). Tests of this hypothesis revealed that the degree to which MDNs regulated algal production in nursery lakes varied greatly since 1700, with significant periods of weak control even in lakes with abundant salmon. Further, when considered at the landscape scale, the importance of MDNs to individual lakes varied substantially through time and in space, with little evidence of synchrony among sites or catchments.

Pacific salmon can be an important source of allochthonous nutrients and energy to freshwater coastal ecosystems as a result of their anadromous and semelparous life histories (Gende et al. 2002; Naiman et al. 2002). These fishes accumulate >95% of their biomass in the marine environment then return to natal lakes and streams to spawn and die (Groot and Margolis 1991). Because adult salmon are large (2–20 kg), nutrient rich (0.36% P, 3.0% N), and often numerous (Larkin and Slaney 1997; Gresh et al. 2000), release of their marine-derived nutrients (MDNs) can represent a considerable subsidy to coastal nursery lakes, rivers, or streams. For example, recent estimates

suggest that nitrogen (N) from sockeye salmon (*Oncorhynchus nerka*) can account for over 25% of N influx to Alaskan nursery lakes (Naiman et al. 2002), whereas fish may contribute up to 90% of total phosphorus (P) inputs to coastal freshwater ecosystems (Schmidt et al. 1998; Naiman et al. 2002; Mitchell and Lamberti 2005). However, because the overall importance of nutrients from salmon (as percentage of total nutrient influx) depends on density of spawning fish that have evaded harvest (termed escapement) relative to background loading of N and P from terrestrial and atmospheric sources (Naiman et al. 2002), there is substantial disagreement concerning the effects of nutrients from salmon on primary and secondary production of nursery ecosystems (Wipfli et al. 1998; Scheuerell et al. 2005; Schindler et al. 2005). Improved understanding of the relationships between escapement (MDN flux) and lake production is needed to help prioritize restoration strategies for salmon populations that have dwindled throughout much of western North America during the 20th century (Gresh et al. 2000; Gende et al. 2002; Ruckelshaus et al. 2002).

Nutrients released from spawning salmon should increase the primary production of recipient freshwater ecosystems in which N and P from migratory fish account for a substantial proportion of total nutrient influx (e.g., Wipfli et al. 1998; Schindler et al. 2005). However, although stream-water concentrations of ammonium ( $\text{NH}_4$ ), soluble reactive P, and benthic invertebrates can increase up to 10-fold in the presence of salmon carcasses (Chaloner et al.

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2002, 2004), it is uncertain whether this pattern arises because nutrients sequentially stimulate primary then secondary production (Mitchell and Lamberti 2005), or whether invertebrates feed directly on dead fish (Chaloner et al. 2002; Winder et al. 2005). Similarly, MDNs from beach- and stream-spawning sockeye salmon do not appear to be captured immediately by algae in nursery lakes (Brock et al. 2006), rather they are circulated throughout the lake basin before stimulating primary production (Finney et al. 2000, 2002; Schindler et al. 2005). Unfortunately, for many lakes and rivers, little is known either of the relative magnitudes of marine-derived and allochthonous nutrients or of the mechanisms that regulate the spatial or temporal variability of algal response to nutrient inputs.

The combination of paleoecological analyses and mass balances of stable isotopes can be used to evaluate the relationship between flux of MDNs and algal production in nursery lakes (Schindler et al. 2005). For example, salmon are enriched in  $^{15}\text{N}$  relative to  $^{14}\text{N}$  because they feed at a relatively high trophic position in marine environments, where they accumulate most of their biomass (Welch and Parsons 1993). Therefore, when semelparous anadromous salmon spawn, they release N of an elevated  $\delta^{15}\text{N}$  signature that can label both the freshwater web and lake sediments in proportion to spawner density (Finney et al. 2000; Brock et al. 2006). Further, such sedimentary N isotope ratios can be used to reconstruct past densities of spawning salmon when the relationship between salmon density and sedimentary  $\delta^{15}\text{N}$  can be established (Schindler et al. 2005). Similarly, fossil pigments from algae are commonly preserved in lake sediments in direct proportion to the algal standing stock in the water column (reviewed in Leavitt 1993; Cuddington and Leavitt 1999) and can be used to reconstruct historical changes in both algal abundance and gross community composition (reviewed in Leavitt and Hodgson 2001). Thus, by comparing time series of fossil pigments and  $\delta^{15}\text{N}$ , investigators can quantify the relationship between MDN flux and lake production over century-long timescales (Schindler et al. 2005).

In this paper, we measured temporal changes in sedimentary  $\delta^{15}\text{N}$  and fossil pigment concentrations in four lakes with sockeye salmon and two reference lakes to quantify the degree to which the flux of MDNs regulated algal production during the past 100 to 300 yr. We hypothesized that fossil pigment concentrations would be positively correlated to sedimentary  $\delta^{15}\text{N}$  but that the strength of correlation would be strongest in lakes where salmon accounted for a high proportion of total nutrient input. Our analyses showed that while marine-derived N accounted for <30% of total ecosystem N, variation in past salmon abundance has been an important control of algal production in nursery lakes. Unexpectedly, there was little evidence of spatial or temporal coherence in the importance of MDNs among lakes, even in adjacent sites with substantial densities of spawning salmon.

## Materials and methods

**Site description**—Study lakes are located in the Bristol Bay region of southwest Alaska (Fig. 1). This region

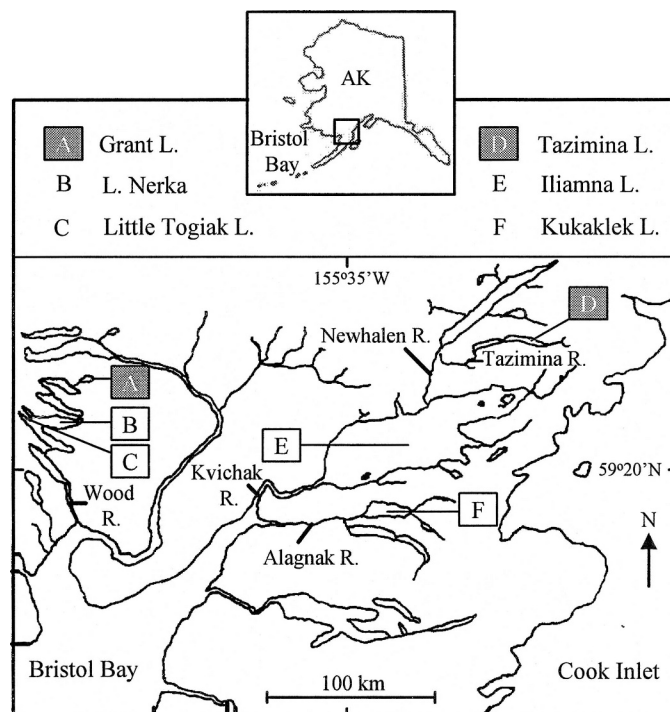


Fig. 1. Location of nursery lakes (Nerka, Little Togiak, Iliamna, Kukaklek) and reference ecosystems (Grant, Tazimina; gray shading) within Wood River, Alagnak, and Kvichak drainage systems of southern Alaska.

supports the largest sockeye salmon fishery in the world, where annual catch is  $\sim 20 \times 10^6$  adults, while  $\sim 8 \times 10^6$  individuals return to natal systems to spawn (Alaska Department of Fish and Game unpubl. data). This region is characterized by maritime climates with greater precipitation (66 cm rain, 220 cm snow) in coastal areas than interior habitats (37 cm rain, 187 cm snow) (Western Regional Climate Center unpubl. data). During recent centuries, vegetation has been typical of mixed coastal tundra and closed boreal forest, with moist lowland areas composed mainly of willow (*Salix* spp.), birch (*Betula nana*), sedge (Cyperaceae), and dwarf shrub (Ericaceae), while forest communities are composed of white spruce (*Picea glauca*) on well-drained slopes and herbaceous or fern taxa in damp forest meadows (Hu et al. 2001b). Green alder (*Alnus crispa*) are also common on hillsides from lakeshore to tree line ( $\sim 300$ – $360$  m above sea level; Helfield and Naiman 2002) and are the main source of N to terrestrial landscapes in coastal Alaskan ecosystems (Engstrom et al. 2000; Hu et al. 2001a).

Salmon nursery lakes studied herein are located within three drainage systems including the Wood (Lake Nerka, Little Togiak Lake), Kvichak (Iliamna Lake), and Alagnak River catchments (Kukaklek Lake). In addition, two reference lakes with natural blockages to salmon migration were selected from the Newhalen–Tazimina River (Tazimina Lake) and Wood River catchments (Grant Lake) to quantify historical changes in past algal abundance and sedimentary N signatures in the absence of salmon. All lakes are characterized by low nutrient content, high

transparency, chronic P limitation, and low algal production (Schindler et al. 2003, 2005 and unpubl. data) but differ in terms of catchment area, proportion of basin with forest, and intensity of thermal stratification during summer (Hartman and Burgner 1972).

Escapement to each nursery lake has been monitored jointly by the Alaska Department of Fish and Game and the University of Washington since the 1950s (Hilborn et al. 2003). Estimates of MDN influx to each nursery lake are based on observed escapements and average nutrient content of semelparous adult salmon ( $\sim 82$  g N,  $\sim 10$  g P) (Larkin and Slaney 1997). Over the coeval monitoring period since 1956, the average annual contribution of nutrients from salmon to these lakes has ranged from 103 to 1,080 kg N km<sup>-2</sup> and from 13 to 132 kg P km<sup>-2</sup>.

*Sediment analyses*—Sediment cores were collected from all sites using a Glew gravity corer equipped with a 7.5-cm diameter coring tube. Multiple cores were collected from diverse locations within each study lake. However, while densities of spawning salmon are known to vary greatly among habitats within individual lakes, recent analyses of 74 cores from Nerka Lake demonstrate that a single core records only basin-wide changes in MDN influx and algal abundance (Brock et al. 2006). Consequently, all subsequent analyses were based on a single core from each lake, collected either from embayments near spawning habitats (large lakes) or from central locations (small lakes). Sediments from all cores were sectioned at 1.7-mm intervals using a vertical extrusion device, transferred to darkened air-tight vials, and frozen to  $-20^{\circ}\text{C}$  until laboratory analysis in less than 8 weeks.

Chronology of individual sediment records was based on vertical profiles of <sup>210</sup>Pb activity in sediments. Briefly, samples for determination of sediment age were freeze-dried (48 h, 0.1 Pa), homogenized, and analyzed for <sup>210</sup>Pb using alpha-spectrometric analysis by Flett Industries. Sediment ages and chronological errors were estimated using the constant rate of supply method based on excess (unsupported) <sup>210</sup>Pb activity (Binford 1990). All calendar dates are presented as year Common Era (CE). Approximate ages of sediments beyond the maximum age estimated by <sup>210</sup>Pb analyses (125–150 yr old) were estimated by extrapolation of mass accumulation rate relationships until ca. 1700 (Binford 1990).

Historical changes in algal abundance and community composition were quantified from analysis of sedimentary carotenoids, chlorophylls, and accessory pigments by high-performance liquid chromatography (HPLC) following the protocols of Leavitt and Hodgson (2001). Briefly, sediments were freeze-dried (48 h, 0.1 Pa), homogenized, and weighed (150–300 mg) prior to extraction of pigments using a mixture of acetone:methanol:water (80:15:5; by vol). Crude extracts were filtered (0.2- $\mu\text{m}$  pore) and dried completely with inert N<sub>2</sub> gas under indirect lighting. Samples were then dissolved in a standard injection solvent mixture containing Sudan II as internal standard and were quantified using an Agilent (Hewlett-Packard) model 1100 HPLC system equipped with a photodiode array detector (Leavitt and Hodgson 2001). Sedimentary pigment con-

centrations were expressed as nmol pigment g<sup>-1</sup> dry mass sediment, an index that is linearly related to algal biomass in the water column (Leavitt and Findlay 1994). Similar historical patterns were obtained for these lakes if pigment abundance was expressed as organic-matter specific concentrations (nmol pigment g<sup>-1</sup> organic matter).

Sedimentary pigments were identified by chromatographic position and spectral characteristics in comparison with authentic standards and isolates from unialgal cultures of known pigment composition (Leavitt and Hodgson 2001). However, because past and present algal communities in these and other regional lakes are composed mainly of diatoms (Schindler et al. 2005; Brock et al. 2006), and because the diatom indicator diatoxanthin was the predominant pigment (mean 40–90%) in all fossil carotenoid assemblages (P. R. Leavitt unpubl. data), only time series of diatoxanthin were used for subsequent statistical analyses. Further, because concentrations of diatoxanthin were significantly correlated (Pearson  $r = 0.266$ – $0.806$ ; mean  $r = 0.639$ , all  $p < 0.05$ ) with those of ubiquitous, chemically stable  $\beta$ -carotene in all lakes, historical changes in diatom abundance are also useful indicators of total algal response to changes in MDN flux. Additional information on pigment biogeochemistry is provided in Leavitt (1993), Cuddington and Leavitt (1999), and Leavitt and Hodgson (2001).

Quantitative determinations of stable N isotope ratio (‰) and relative N content (percentage dry mass) were conducted at the University of Regina's Environmental Quality Analysis Laboratory (EQAL) and the University of Washington's Stable Isotope Laboratory (UWSIL) using a ThermoQuest (F-MAT) Delta<sup>plus</sup> XL isotope ratio mass spectrometer (IRMS; Savage et al. 2004) and a Delta XL IRMS, respectively. Each IRMS unit used an automated Carlo Erba elemental analyzer as an inlet device and was calibrated independently by reference to atmospheric N. All stable isotope ratios are expressed in the conventional  $\delta$  notation ( $\delta^{15}\text{N}$ ) in units of per mil (‰) deviation from atmospheric N. Sample reproducibility was better than 0.25‰ for both instruments.

*Numerical analyses*—Linear regression was used to quantify the relationship between  $\log(x + 1)$ -transformed concentrations of fossil pigments and untransformed (normally distributed) N isotope ratio measurements over either 100- or 300-yr periods. Initially, no correction was made for temporal autocorrelation within time series, both because prior analyses revealed that significant correlations between past algal abundance and fossil  $\delta^{15}\text{N}$  arose mainly from long-term trends rather than interannual variability (Schindler et al. 2005) and because our objective was to quantify historical associations between past flux of MDNs ( $\delta^{15}\text{N}$ ) and algal production (diatoxanthin) at the century timescale. We anticipated that pigment-isotope correlations would be strongest in lakes where MDNs were a substantial proportion of total nutrient influx.

In addition to these long-term regressions, we also quantified pigment-isotope correlations within overlapping consecutive 50-yr intervals throughout fossil time series from each lake to evaluate how the strength of association

between MDNs and algae has changed during the past 300 yr. In this procedure, raw fossil time series of  $\log(x + 1)$ -transformed pigment concentrations and untransformed stable N isotope ratios were first converted to decadal resolution by averaging or linear interpolation, then pigment–isotope correlations were calculated for five-point (50-yr) intervals beginning every decade (i.e.,  $r_{2000-1950}$ ,  $r_{1990-1940}$ ,  $r_{1980-1930}$ ... $r_{1750-1700}$ ). This calculation resulted in a new time series of pigment–isotope correlations that could be compared among lakes to evaluate the degree of temporal synchrony in ecosystem control processes. In this latter case, temporal autocorrelation was removed first by calculating first differences of each correlation time series (Patoine and Leavitt 2006); then lake-pair synchrony was estimated using a Pearson correlation coefficient. High lake-pair correlations suggest that lakes are regulated by similar forcing mechanisms acting in a coherent manner at the regional or landscape scale. Similar synchrony analyses were also conducted using three-, seven-, and nine-point moving intervals, but differed mainly in the degree to which high-frequency signals were expressed, and are not presented further. All statistical analyses were performed using Systat v.10 (Microcomputer Power).

Finally, we used sedimentary  $\delta^{15}\text{N}$  values to estimate the fraction of ecosystem N uniquely derived from marine sources using a two-source mixing model modified from Schindler et al. (2005, 2006). Briefly, this approach first uses observed salmon escapement to estimate terrestrial N influx to each lake, then calculates the importance of MDNs in the overall nutrient budget of the lake during the 20th century. For example, the average background loading of N from allochthonous sources ( $N_{\text{ws}}$ , as  $\text{kg N m}^{-2}$ ) to lakes since 1956 was estimated from

$$N_{\text{ws}} = \frac{N_{\text{sal}}(\delta^{15}\text{N}_{\text{sal}} - \delta^{15}\text{N}_{\text{sed}})}{(\delta^{15}\text{N}_{\text{sed}} - \delta^{15}\text{N}_{\text{ws}})}$$

where  $N_{\text{sal}}$  is the mean annual influx of N based on observed escapement of salmon since 1956 (as  $\text{kg N km}^{-2}$ ),  $\delta^{15}\text{N}_{\text{sal}}$  is the N isotope ratio of adult salmon ( $11.2 \pm 0.45\text{‰}$ ; Schindler et al. 2005),  $\delta^{15}\text{N}_{\text{sed}}$  is the average sedimentary N ratio since 1956, and  $\delta^{15}\text{N}_{\text{ws}}$  is the average N isotope values from reference lakes for Wood River (Grant Lake) and Newhalen–Tazimina catchments (Tazimina Lake). This equation was solved for lake-specific  $N_{\text{ws}}$  values, which were then used to calculate the relative importance of N from marine sources during the 20th century as  $\% \text{MDN} = N_{\text{sal}} [N_{\text{sal}} + N_{\text{ws}}]^{-1} \times 100$ , by assuming that the average background N influx during 1956–2000 is similar to that during 1900–2000. This approach further assumes that the N isotopic signature of allochthonous sources in each catchment ( $\delta^{15}\text{N}_{\text{ws}}$ ) has varied relatively little since ca. 1900, that isotopic signatures of sediments do not exceed that of spawning salmon (e.g., as a result of nitrification or denitrification), and that there is little processing of  $\delta^{15}\text{N}$  following deposition in the sediments (Teranes and Bernasconi 2000). Linear regression was then used to test the hypothesis that the degree of correlation between sedimentary  $\delta^{15}\text{N}$  and fossil pigment signatures during the 20th

century was a linear function of the relative importance of MDNs in the overall nutrient budget of the lake during the same period.

## Results

Total  $^{210}\text{Pb}$  activities declined with cumulative mass of sediment deposited (Fig. 2;  $\text{g cm}^{-2}$ ) and burial depth (not shown) at near-exponential rates for all study sites. In particular,  $^{210}\text{Pb}$  activity exhibited monotonic declines with sediment mass deposited in Little Togiak, Grant, and Tazimina lakes, suggesting that there was very little mixing of surface sediments. In contrast, surface sediments of Kukaklek, Nerka, and Iliamna lakes deviated slightly from the expected log-linear relationship, likely because of minor mixing of surficial sediments or because of recent changes in mass accumulation rates. Regardless of the cause, sedimentary profiles of  $^{210}\text{Pb}$  were sufficiently well resolved at all sites to allow depth–age relationships (Fig. 2; solid line) to be used to approximate sediment ages between  $\sim 1700$  and  $\sim 1875$ .

Past diatom abundance (as  $\log[x + 1]$  diatoxanthin) was strongly correlated with sedimentary  $\delta^{15}\text{N}$  in all study lakes for the period ca. 1700–2000 (Fig. 3). However, while past algal abundance was positively correlated to sedimentary  $\delta^{15}\text{N}$  in nursery lakes Nerka ( $r = 0.93$ ,  $p < 0.0001$ ), Iliamna ( $r = 0.89$ ,  $p < 0.0001$ ), Little Togiak ( $r = 0.82$ ,  $p < 0.0001$ ), and Kukaklek ( $r = 0.42$ ,  $p < 0.02$ ), algal production and  $\delta^{15}\text{N}$  were inversely correlated in Grant ( $r = -0.71$ ,  $p < 0.0001$ ) and Tazimina lakes ( $r = -0.73$ ,  $p < 0.0001$ ), sites that lack anadromous fishes. Overall, the range of  $\delta^{15}\text{N}$  values observed in each core was similar ( $\sim 1.5\text{‰}$ ), with the exception of Grant Lake ( $\sim 0.6\text{‰}$ ).

The strength of fossil pigment–isotope correlations was linearly related to salmon population density and the importance of N from salmon in whole-lake N budgets during the 20th century (Fig. 4). For example, Pearson correlation coefficients during 1900–2000 were strongly and positively correlated to both average density of sockeye salmon during 1956–2000 ( $r = 0.97$ ,  $p < 0.002$ ; not shown) and the fraction of total N derived from marine sources since 1900 ( $r = 0.98$ ,  $p < 0.001$ ; Fig. 4), as estimated from isotope mixing models. As in the past 300 yr (Fig. 3), all nursery lakes exhibited significant positive correlations ( $r = 0.16$ – $0.82$ ), whereas reference lakes showed significant negative relationships ( $r = -0.21$  to  $-0.46$ ).

The strength of correlations between fossil diatoxanthin and  $\delta^{15}\text{N}$  varied substantially during the past 300 yr for both nursery and reference lakes (Fig. 5). For example, although past algal abundance was positively correlated with sedimentary  $\delta^{15}\text{N}$  signatures during the past 100 (Fig. 4) and 300 yr (Fig. 3a), fossil diatoxanthin concentrations were negatively correlated with  $\delta^{15}\text{N}$  within Nerka Lake sediments during ca. 1700–1725 and ca. 1800–1860 (Fig. 5a), suggesting that the relative importance of MDNs declined during these intervals. Although periods of negative correlation were recorded also for Iliamna (Fig. 5b), Little Togiak (Fig. 5c), and Kukaklek lakes (Fig. 5d), the timing of these periods differed among sites. Similarly, the degree to which algal and N isotope

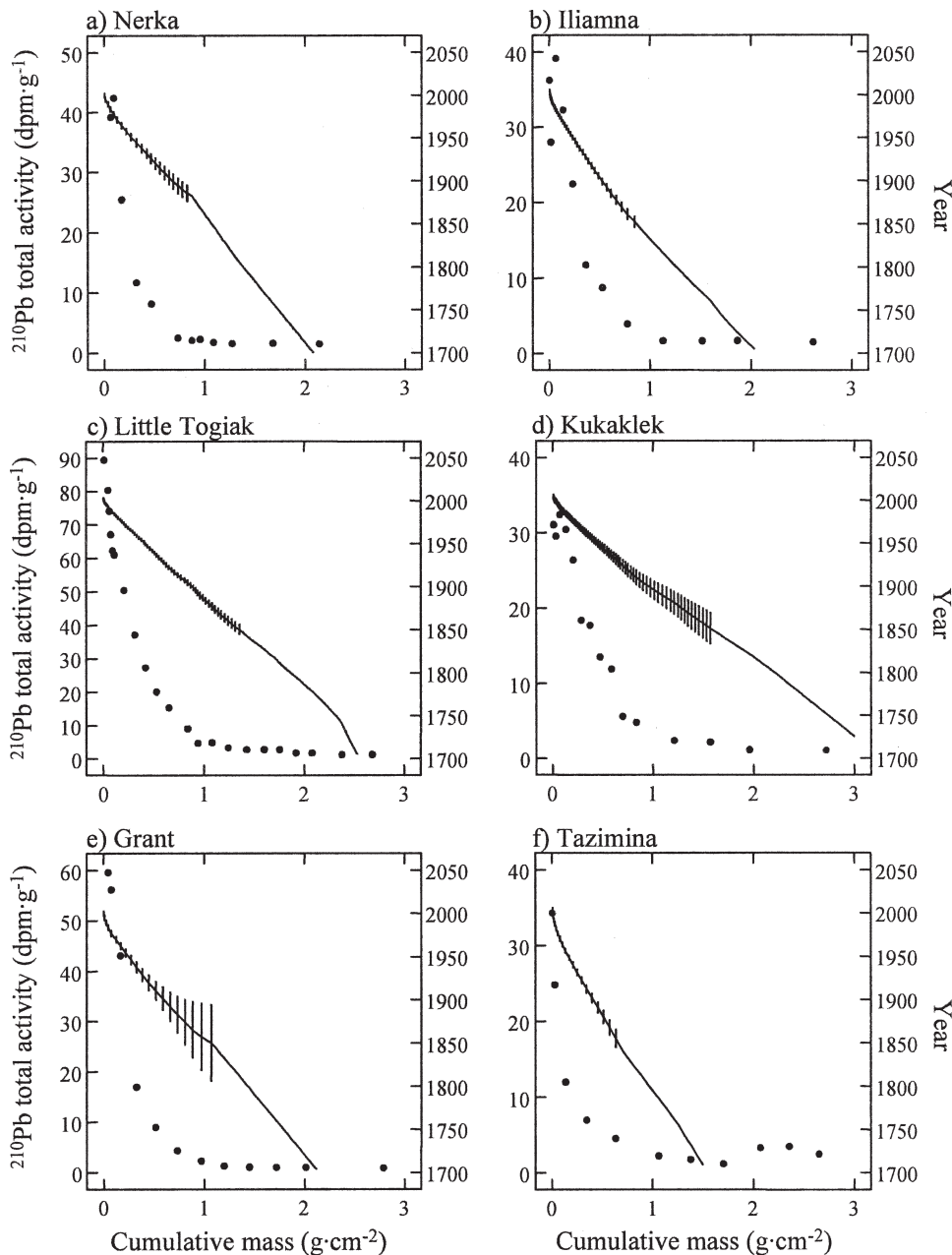


Fig. 2. Total activity of <sup>210</sup>Pb (dpm g<sup>-1</sup> dry mass; left axis, closed symbols) and estimated year of deposition ( $\pm$ dating error; right axis, continuous line) as a function of cumulative dry mass accumulation (g cm<sup>-2</sup>) in sediment cores from (a) Nerka, (b) Iliamna, (c) Little Togiak, (d) Kukaklek, (e) Grant, and (f) Tazimina lakes, southern Alaska.

signatures were inversely correlated varied substantially through time in both reference lakes, with Grant Lake exhibiting brief, albeit nonsignificant ( $p > 0.05$ ), periods of positive correlation (Fig. 5e). Coherence was also poor for both nursery and reference lakes during the 20th century, demonstrating that lack of synchrony did not arise from errors in sediment chronology (Fig. 2).

Nursery and reference lakes exhibited little evidence of temporal coherence for 300-yr time series of either  $\delta^{15}\text{N}$  or pigment- $\delta^{15}\text{N}$  correlations once the effects of temporal

autocorrelation were removed by first differences (Fig. 6). For example, while Grant and Little Togiak lakes exhibited significant negative correlations for  $\delta^{15}\text{N}$  during 1700–2000, no other pairing of reference–nursery lakes was statistically significant ( $p > 0.05$ , dashed lines in Fig. 6), nor were changes in isotope signals synchronous among any nursery lakes. Similarly, historical changes in pigment–isotope correlations were coherent only in Tazimina and Kukaklek lakes. Together, these patterns suggest that historical changes in inferred salmon abundance ( $\delta^{15}\text{N}$  in

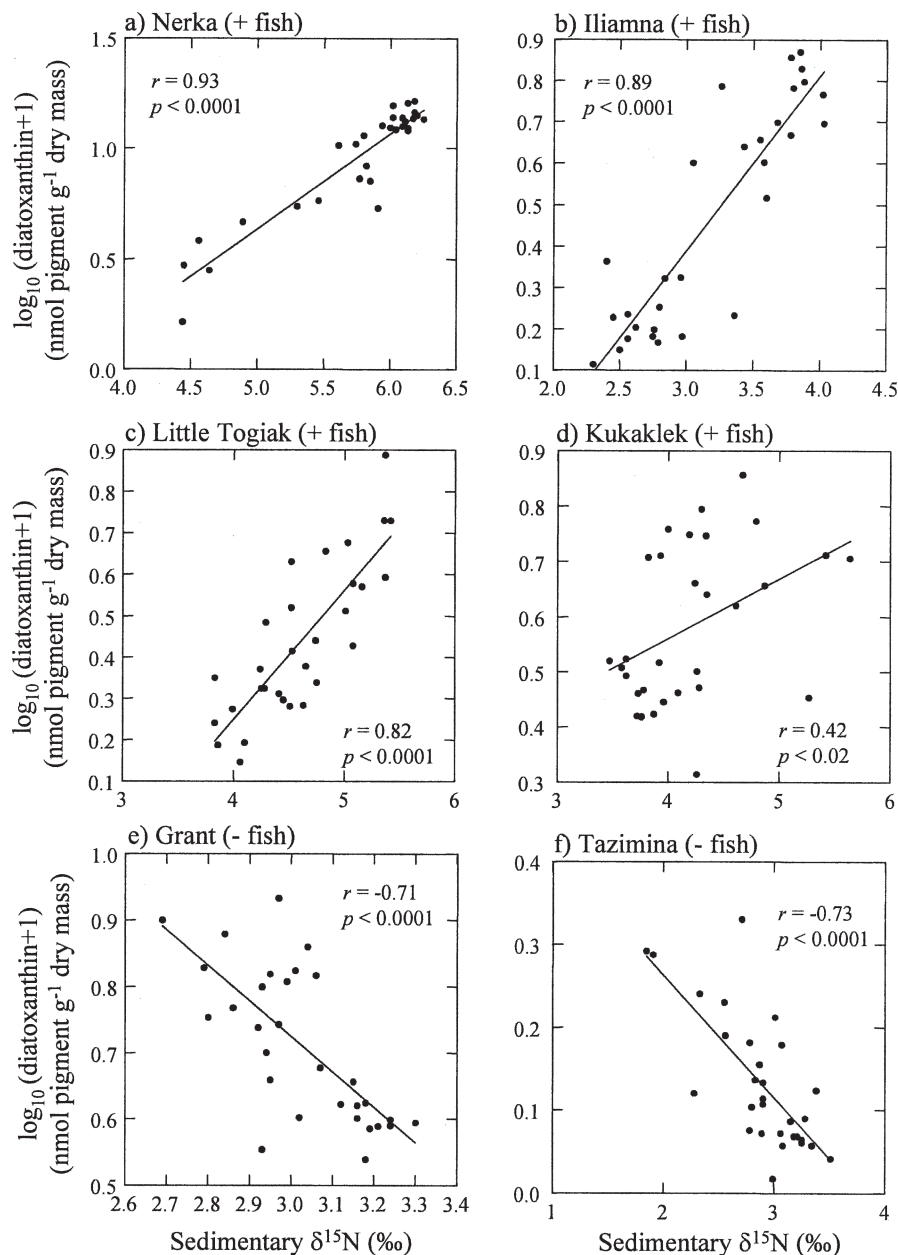


Fig. 3. Relationship between past algal abundance (as fossil diatoxanthin;  $\text{nmol pigment g}^{-1}$  dry sediment) and sedimentary  $\delta^{15}\text{N}$  (‰) during the past 300 yr at salmon nursery lakes (Nerka, Little Togiak, Iliamna, Kukaklek), and reference ecosystems (Grant and Tazimina).

nursery lakes) and the importance of MDNs in ecosystem nutrition (diatoxanthin– $\delta^{15}\text{N}$  correlations) were asynchronous at both catchment and regional levels.

## Discussion

Paleoecological analysis of six coastal lakes in Bristol Bay, Alaska, revealed that algal abundance during the past 300 yr was linearly correlated with sedimentary  $\delta^{15}\text{N}$  at all sites, but that sign of the correlation was positive in lakes with spawning sockeye salmon and negative in reference systems (Fig. 3). Further, the strength of pigment–isotope correlations since 1900 was a linear function of both

salmon escapement and the importance of N from salmon to whole-lake N budgets during the 20th century (Fig. 4). These findings are consistent with studies in these and other regional nursery lakes that show that sedimentary  $\delta^{15}\text{N}$  is strongly correlated to the density of spawning salmon (Finney et al. 2000; Brock et al. 2006). However, unlike prior studies, our analysis also revealed that the importance of MDNs to individual lakes varied substantially through time and space (Fig. 5), with little evidence of synchrony among lakes or catchments (Fig. 6).

*Controls of lake production*—Previous mass-balance studies demonstrate that adult salmon have transported

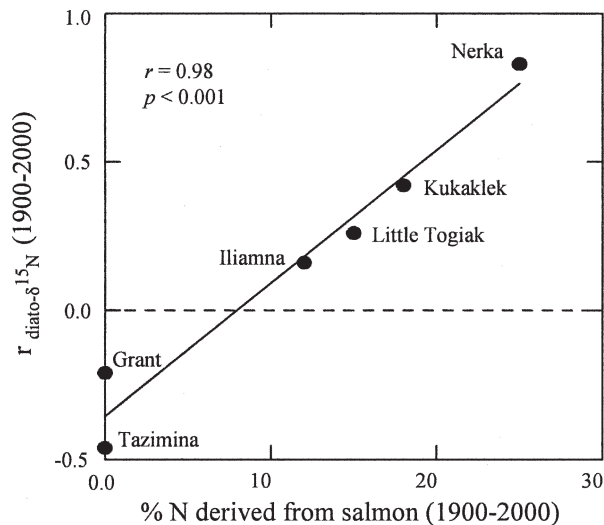


Fig. 4. Relationship between diatoxanthin- $\delta^{15}\text{N}$  correlations ( $r$ ) during 1900–2000 and the proportion of ecosystem N derived from marine sources in lakes of southwest Alaska since 1900. The unreplicated linear regressions is significant at  $p < 0.001$ . Diatoxanthin concentrations were  $\log(x + 1)$ -transformed before  $r$  was estimated.

$\sim 49,000$  kg of P and  $\sim 395,000$  kg of N per year to the Kvichak system in Bristol Bay, a quantity that would be expected to increase primary production of these oligotrophic lakes (Moore and Schindler 2004). Consistent with this view, algal production was positively correlated to measured salmon escapement in Bristol Bay nursery lakes during the past 100 yr and to inferred salmon abundance since  $\sim 1700$  (Fig. 3). This result also confirms analyses of fossil diatoms in other Alaskan nursery lakes, which demonstrate that historical changes in algal species composition are strongly correlated to variations in sedimentary  $\delta^{15}\text{N}$  during the past 300–2,000 yr (Finney et al. 2000, 2002; Gregory-Eaves et al. 2003), despite recent observations that MDNs are not immediately available to primary producers (e.g., Mitchell and Lamberti 2005; Brock et al. 2006).

Effects of MDNs on lake production were unexpectedly strong given the low proportion of ecosystem N supplied by salmon (Fig. 4). Independent analysis of the importance of MDNs to 12 Alaskan nursery lakes by Naiman et al. (2002) also found that N from sockeye salmon accounted for an average of  $\sim 25 \pm 19.0\%$  of total N inputs. In contrast, anadromous salmon can provide up to 90% of P influx to some regional nursery lakes (Schmidt et al. 1998; Finney et al. 2000), a pattern that suggests that lakes may be responding to P from salmon rather than marine-derived N. Consistent with this hypothesis, bottle bioassays from our study lakes reveal chronic algal limitation by P as a result of elevated water-column ratios of N:P at all sites ( $>50:1$ ) (Schindler et al. 2005 and unpubl. data). Because adult salmon are rich in P, because their N:P ratio is relatively constant ( $\sim 8:1$ ; Larkin and Slaney 1997), and because P supply in coastal Alaskan lakes is controlled by local geology rather than development of terrestrial vegetation (Engstrom et al. 2000), we infer that sedimen-

tary  $\delta^{15}\text{N}$  signatures are useful proxies for fluxes of both N and P from marine sources, at least in these Alaskan coastal ecosystems.

In contrast to nursery lakes, past algal production was inversely correlated to stable N isotope ratios in sediments of reference lakes both during the last 100 (Fig. 4) and 300 yr (Fig. 3e,f). Such negative correlations could arise if N supply limits algal production in lakes without salmon and if increased inputs of allochthonous N were also associated with low  $\delta^{15}\text{N}$  signatures (e.g.,  $\text{N}_2$  fixed by alder from atmospheric sources; Engstrom et al. 2000). However, while N limitation of algae is common early in the evolution of coastal Alaskan lakes (Engstrom et al. 2000), our modern study lakes are usually characterized by P limitation (see above). Furthermore, unpublished isotopic analysis of local soils and terrestrial vegetation (fern) reveals that the mean ( $\pm \text{SD}$ ,  $n = 28$ )  $\delta^{15}\text{N}$  of N associated with  $\text{N}_2$ -fixing alder ( $\delta^{15}\text{N}_{\text{soil}} = 1.78 \pm 1.16\text{‰}$ ,  $\delta^{15}\text{N}_{\text{fern}} = 3.22 \pm 1.22\text{‰}$ ) is greater than that of N associated with non- $\text{N}_2$ -fixing spruce ( $\delta^{15}\text{N}_{\text{soil}} = 1.23 \pm 0.74\text{‰}$ ,  $\delta^{15}\text{N}_{\text{fern}} = 0.72 \pm 1.59\text{‰}$ ), a pattern that is inconsistent with observed negative correlations between sedimentary  $\delta^{15}\text{N}$  and fossil pigment abundance in reference lakes (Fig. 3e,f).

Alternately, negative correlations between past diatom abundance and sedimentary  $\delta^{15}\text{N}$  signatures may reflect hydrologic control of allochthonous nutrient inputs to coastal lakes, as suggested by Gregory-Eaves et al. (1999) and Hobbie et al. (2003). We speculate that N fixed by actinomycte symbionts of *Alnus* (e.g., *Frankia* spp.) may remain in soils for more prolonged periods under dry conditions and should be subject to more intense microbial processing (e.g., nitrification, denitrification) or  $\text{NH}_3$  volatilization. Such processes enrich the  $^{15}\text{N}$  content of soils and vegetation but reduce N flux to lakes in the absence of runoff. In contrast, with greater precipitation, fixed N is exported more rapidly to lakes but with a lower  $\delta^{15}\text{N}$  signal owing to shorter residence time in the soils and reduced isotopic enrichment. Because elevated runoff should also increase export of P to lakes, negative correlations between fossil pigments and N isotope ratios may arise even under circumstances where P supply limits algal growth. Unfortunately, the additional research required to verify this hypothesis is beyond the scope of the present study.

*Coherence of regulatory mechanisms*—Our analysis revealed little evidence of temporal coherence in regulatory mechanisms among nursery or reference lakes (Fig. 6), despite the fact that all sites have experienced common climatic warming since ca. 1700 (Hu et al. 2001b). For example, past densities of sockeye salmon within Nerka Lake have averaged from 6 to  $8 \times 10^4$  spawners  $\text{km}^{-2}$  since ca. 1700 (Schindler et al. 2005), yet pigment–isotope correlations suggest that other allochthonous inputs of nutrients controlled algal production during ca. 1700–1725 and ca. 1800–1850 (Fig. 5a). Given that Little Togiak Lake is separated from Lake Nerka by  $<0.5$  km of permanent river (Little Togiak River), we had expected similar patterns of historical variation in the importance of marine-derived and allochthonous nutrients among the

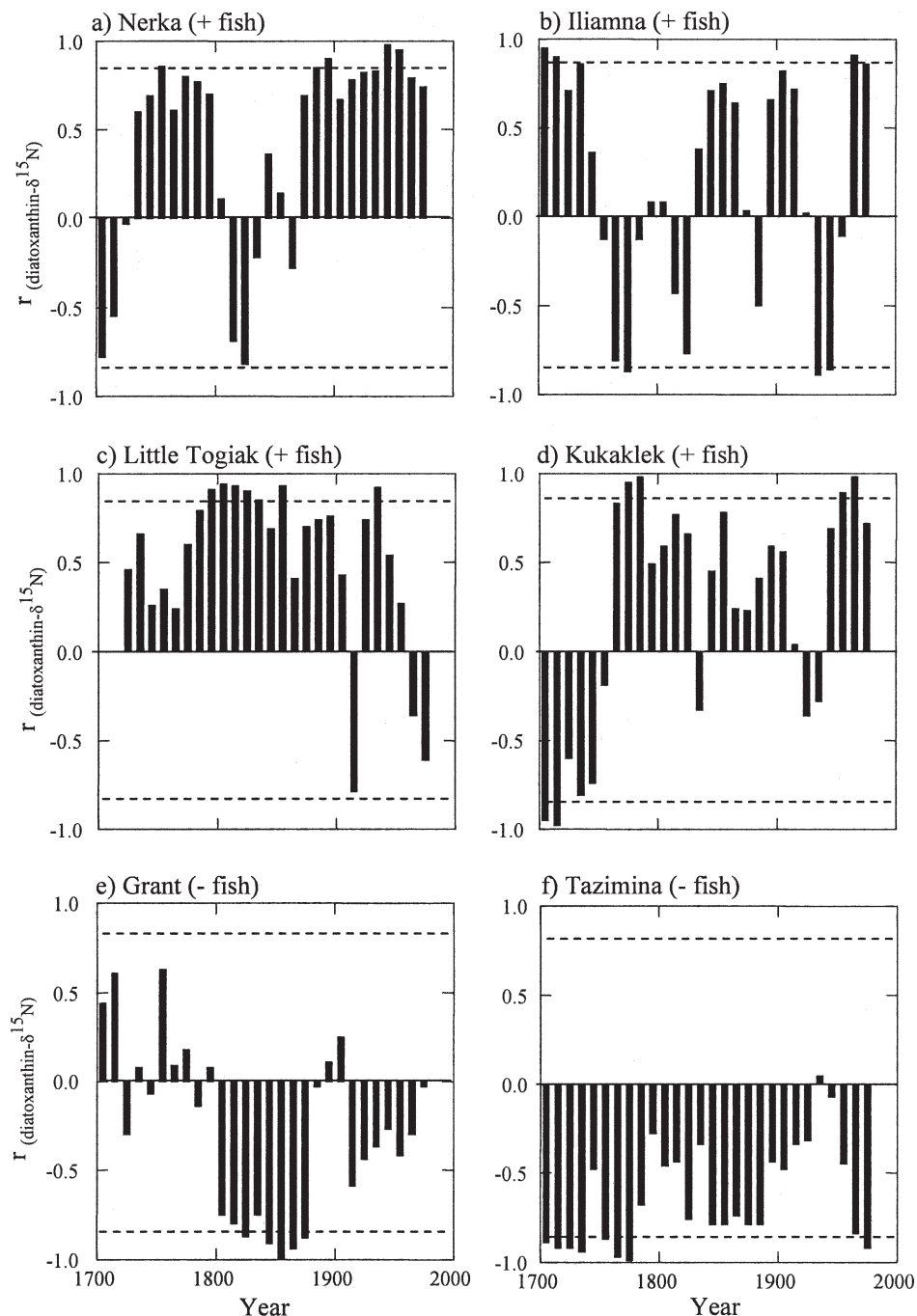


Fig. 5. Time series of Pearson correlation coefficients ( $r$ ) for diatoxanthin and  $\delta^{15}\text{N}$  measured for overlapping consecutive 50-yr (five-point) intervals during the period 1700–2000. All time series were converted to decadal resolution before pigment–isotope correlations were estimated for (a) Nerka, (b) Iliamna, (c) Little Togiak, (d) Kukaklek, (e) Grant, and (f) Tazimina Lakes. Values greater than dashed line are statistically significant at  $p < 0.05$ . Diatoxanthin as in Fig. 4.

two lakes. Instead, analysis of pigment–isotope correlations suggests that MDNs regulated production of Little Togiak Lake during 1800–1850, whereas other factors influenced diatom abundance since ca. 1960 (Fig. 5c). Such high variability among sites is consistent with both conceptual and empirical studies that show that lake response to

climatic forcing, especially precipitation, is strongly dependent on lake position within the hydrologic landscape (Webster et al. 2000), as well as the degree to which catchment characteristics regulate export of dissolved substances to aquatic ecosystems (e.g., “catchment filter” of Blenckner 2005).

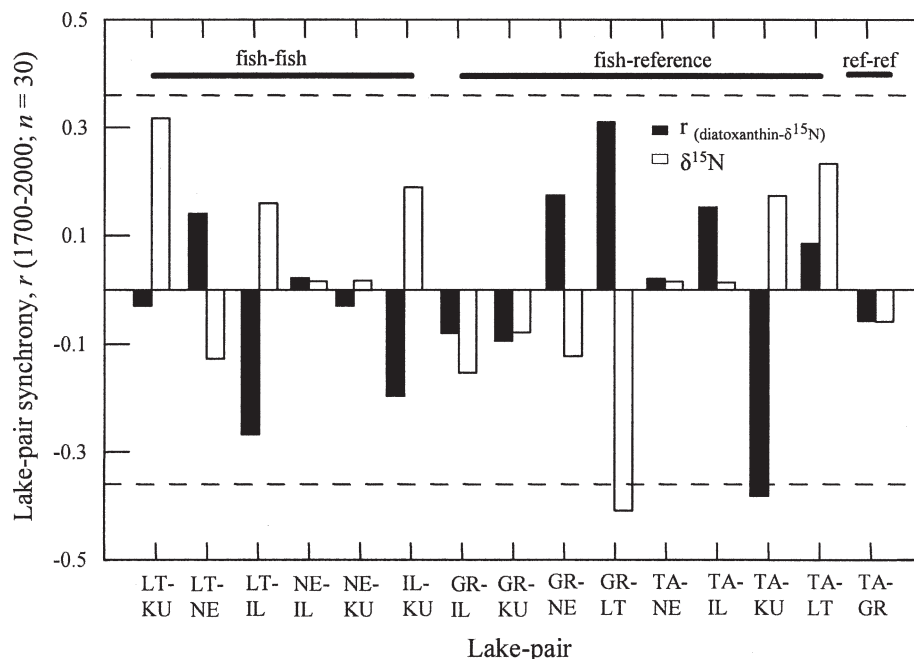


Fig. 6. Lake-pair synchrony ( $r$ ) of time series of  $\delta^{15}\text{N}$ –diatoxanthin correlation coefficients (black histograms) and untransformed  $\delta^{15}\text{N}$  (open histograms) following removal of temporal autocorrelation for using first-difference procedures. Time series are derived for both nursery (Nerka = NE, Little Togiak = LT, Iliamna = IL, Kukaklek = KU) and reference lakes (Grant = GR, Tazimina = TA). Values beyond upper and lower dashed lines were significant at  $p < 0.05$ . Diatoxanthin as in Fig. 4.

**Management implications**—Several aspects of the present study may be useful to managers of aquatic resources in Bristol Bay. First, although marine-nutrient subsidies appeared to regulate primary production within nursery lakes over the scale of decades (Fig. 5) to centuries (Figs. 3, 4), responses of algae to N and P supplements from salmon are much less predictable on annual timescales (e.g., Mitchell and Lamberti 2005; Brock et al. 2006). In streams, disturbance of the benthic environment by spawning salmon may restrict algal growth (Mitchell and Lamberti 2005) and can facilitate MDN export to coastal lakes and estuaries (Chaloner et al. 2004). However, such nutrients are also attenuated slowly by algae in nursery lakes, possibly reflecting either rapid mixing throughout the basin (Brock et al. 2006) or that N and P associated with organic matter must be mineralized before nutrients become available to primary producers (but *see* discussion of Mitchell and Lamberti 2005). Although further work is required to resolve the mechanisms that influence immediate nutrient availability to algae, these studies do suggest that short-term analyses may be of limited value in identifying the relationship between nutrient influx and primary production of nursery lakes.

The relatively low proportion of total ecosystem N derived from fisheries escapement (Fig. 4) is consistent with findings of Schindler et al. (2005) that continued exploitation of salmon stocks will not immediately impoverish the fertility of nursery lakes. Previously, we showed that total production of sockeye salmon in Nerka Lake has remained

at levels characteristic of the 19th century, even following nearly a century of commercial exploitation of salmon stocks. Given that N (and likely P) from marine sources is more important in Nerka Lake than in any of our other nursery lakes (Fig. 4), it seems likely that continued fishing will not degrade production of our other sites in the near future.

Finally, we recommend that similar analysis of sedimentary pigments and isotopes be conducted in diverse nursery lakes to identify possible continental-scale variability in the importance of MDNs as an ecosystem subsidy. To date, few studies south of Alaska have revealed significant correlations between sedimentary  $\delta^{15}\text{N}$  and population density of anadromous, semelparous fishes. Such poor correlations could arise either because of elevated background loading of N, rapid hydrologic flushing (Holtham et al. 2004), or because climate effects on lakes differ among districts (e.g., Californian Current vs. Alaskan Gyre) (Blenckner 2005). We believe that expansion of the analyses presented here will help distinguish among these possibilities and improve our understanding of the factors that regulate primary production of coastal lakes.

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