

The influence of nitrogen limitation on $\delta^{15}\text{N}$ and carbon : nitrogen ratios in sediments from sockeye salmon nursery lakes in British Columbia, Canada

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Abstract

Carbon (C) and nitrogen (N) elemental and nitrogen isotopic ratios were determined for bulk organic matter in surface sediments of 11 sockeye salmon (*Onchorynchus nerka*) nursery lakes in British Columbia, Canada. Chitinous exoskeletons of *Bosmina* spp. were also picked from the sediments and analyzed for $\delta^{15}\text{N}$. The correlation between salmon escapement (spawner abundance) and bulk organic $\delta^{15}\text{N}$ confirms the importance of marine-derived nitrogen to the study lakes. The relation between sediment $\delta^{15}\text{N}$ and escapement, however, suggests that simple mixing models may significantly underestimate spawner abundance in nitrogen-limited lakes. In addition, the use of sediment and chitin $\delta^{15}\text{N}$ and C:N data to characterize lake-specific differences demonstrates that sediment isotope signatures are dependent on attendant nitrogen deficiency. The sediment C:N ratio, on its own, provides a sensitive measure of nutrient status in these lakes. This finding provides an alternate additional interpretation of C:N ratios that may be more appropriate in large lakes where terrestrial contributions to the central basin are insignificant.

Pacific salmon (*Onchorynchus* sp.) are both anadromous and semelparous. Juvenile salmon leave freshwater systems in 0–4 yr as smolts and migrate to the sea (anadromy). At sexual maturity, they return to their natal stream to spawn and die (semelparity). Spawning salmon provide a source of nutrients for local predators and fertilize local aquatic ecosystems (for example, Kline et al. 1993). Over-fishing, habitat loss, and poor marine survival have contributed to the decline of salmon returns to British Columbia, Canada, streams during the last century (Gresh et al. 2000). As

a result, many coastal ecosystems likely have suffered deficits of 50–80% of historical nitrogen and phosphorus loads in the recent past (Gresh et al. 2000).

Juvenile sockeye salmon (*Onchorynchus nerka*) may be particularly sensitive to nutrient deficits in lacustrine environments. Sockeye smolts spend 1–4 yr in freshwater nursery lakes feeding on pelagic zooplankton before migrating to the sea. Coastal British Columbia lakes are typically oligotrophic, thus nutrient transfer by spawning salmon may be critical for maintaining adequate productivity to support rearing smolts (Anchord et al. 2003). Observed positive relations between smolt size and survival during both the winter and early marine phases suggest nutrient status plays an important role in maintaining stock size (Hyatt et al. 2004).

A strong positive correlation between spawner abundance and lake productivity has been demonstrated at several locations (for example, Johnston et al. 2004); however, the response of individual aquatic ecosystems to spawning numbers will differ depending on local conditions. Marine-derived nutrients are released through a variety of pathways, and the ultimate fate of nutrients

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will differ from site to site. Factors such as nutrient loading from sources other than salmon, high flushing rates, and stream characteristics will influence the relative contribution of nutrients per spawner to downstream lake systems (review in Naiman et al. 2002). Coastal British Columbia lakes tend to be deficient in both phosphorus and nitrogen, and nitrogen is commonly the limiting nutrient (Stockner and Shortreed 1978, 1979). Although reasons for these nutrient deficiencies are currently unclear, high rainfall and rapid flushing may facilitate loss of dissolved nitrogen in some lakes. A more thorough understanding of spawner-induced productivity in specific lake systems is vital for improving stock management strategies.

Using surface sediment proxies, we examine the relation between sockeye salmon escapement and nutrient limitation in 11 British Columbia nursery lakes. The study is based on a comparison of nitrogen isotope data, carbon/nitrogen (C:N) ratios, and escapement (5-yr average) records. Results provide new understanding of the relations between past salmon returns and changes in ecosystem structure and nutrient availability. This new insight can be used to set targets for escapement based on past salmon abundance to improve the sustainability of sockeye fisheries. Our results also shed light on the interpretation of sedimentary organic matter C:N ratios as paleoenvironmental indicators, which will aid in the interpretation of paleolimnological reconstructions of sockeye salmon escapement in nitrogen-deficient lakes.

Background

Nitrogen isotope ratios—Nitrogen isotopes can be used to trace the fate of marine-derived nitrogen through terrestrial and freshwater food webs (Kline et al. 1993). Empirical relations between salmon nutrient loading and sediment $\delta^{15}\text{N}$ have been used to track historical variations in salmon spawner abundance in Alaskan lakes (Finney et al. 2000; Finney et al. 2002). This approach capitalizes on the life history of Pacific salmon, which accumulate >95% of adult biomass in the marine environment, feeding on relatively ^{15}N -rich food sources. Salmon biomass has an average $\delta^{15}\text{N}$ value of approximately +12‰ relative to the atmospheric standard (Kline et al. 1993), whereas non-marine nitrogen sources have isotopic compositions closer to the atmospheric value (0‰).

Nitrogen isotopes are also systematically fractionated by processes occurring within the lake basin itself. Algae normally discriminate strongly against the heavier isotope, producing organic matter depleted in ^{15}N relative to the dissolved inorganic nitrogen (DIN) pool. As DIN is consumed, Rayleigh effects eventually lead to progressive ^{15}N enrichment in residual DIN, which is transferred, in turn, to newly growing algae. If nitrogen becomes critically limiting, however, algal ^{15}N discrimination diminishes and algal $\delta^{15}\text{N}$ approaches that of the bulk DIN pool (Teranes and Bernasconi 2000). Thus, algal $\delta^{15}\text{N}$ tracks lake-water DIN $\delta^{15}\text{N}$ when nitrogen is in ample supply, but should exhibit more complex behavior when the nitrogen supply is limited.

Transfer of the nitrogen isotope signature from the source DIN to sediment organic matter involves two levels of fractionation: isotope discrimination between the DIN source and algae, which may decrease when nitrogen is limited, and the isotopic fractionation between the algal food source and the zooplankton grazer. The latter fractionation occurs through heterotrophic transfers of nitrogen, resulting in an increase in the whole-body $\delta^{15}\text{N}$ of organisms at higher trophic levels (DeNiro and Epstein 1980). This effect is attributed to metabolic processes that partition nitrogen isotopes between various amino acids and excreted by-products (McClelland and Montoya 2002). Because of its weaker bonding, ^{14}N is preferentially removed in de-amination reactions, forming ammonium-based liquid excretions. The resulting isotopic offset between zooplankton and algae is also sensitive to nitrogen limitation. Metabolic reactions may continue at a higher rate than nitrogen is supplied, resulting in further loss of excreted ^{14}N and, therefore, enrichment of ^{15}N in whole-body tissues. Increasing fractionation as nitrogen becomes limiting can be described in terms of the algal C:N ratio: $\delta^{15}\text{N}_{\text{zooplankton}} - \delta^{15}\text{N}_{\text{algae}} = 0.21(\text{C:N} - 0.0002)$ (Adams and Sterner 2000).

In contrast to liquid excretions, zooplankton fecal matter is generally enriched in ^{15}N with respect to the food source (Altabet and Small 1990). Sediment organic matter typically is a composite of dead algal material and zooplankton fecal matter, thus the $\delta^{15}\text{N}$ of bulk sedimentary organic matter should be slightly higher than that of live algae in the epilimnion. Sediment $\delta^{15}\text{N}$ is likely to vary in tandem with changes in the $\delta^{15}\text{N}$ of the DIN pool when nitrogen is abundant (Finney et al. 2000), whereas nitrogen-limited systems will show a progressive reduction in the offset between sediment $\delta^{15}\text{N}$ and DIN $\delta^{15}\text{N}$.

In summary, when nitrogen is limited, we should expect a nonlinear relation between sedimentary $\delta^{15}\text{N}$ and escapement because of variations in the isotopic offset from DIN to algae at low nitrogen levels. We would also expect the nitrogen isotopic composition of zooplankton to reflect the source algal $\delta^{15}\text{N}$ and the metabolic influence of nitrogen deficiency.

C:N elemental ratios—Algal C:N ratios are also influenced by nitrogen availability; the ratios increase as nitrogen becomes limiting (Healy and Hendzel 1979). Based on lake seston studies, Hecky et al. (1993) suggested that atomic C:N values of 8.3–14.6 in phytoplankton indicate moderate nitrogen deficiency and values >14.6 indicate extreme nitrogen deficiency. This interpretation has been confirmed in laboratory culture experiments; Adams and Sterner (2000), for example, produced algal C:N ratios as high as 25 by limiting DIN availability. Admixture of terrestrial organic matter is commonly invoked to explain elevated C:N ratios (>15) in lake sediments cores (Meyer and Teranes 2001) and consequently has also been used to explain low sedimentary ^{15}N values in salmon-bearing lakes (Holtham et al. 2004). However, C:N ratios as high as 25 in lacustrine sediments have been ascribed to nitrogen limitation after visual

inspection confirmed a dominant algal component (Talbot and Lærdal 2000).

In contrast to algae, zooplankton biomass has a relatively constant, species-specific C:N ratio (Urabe 1993). Thus, the elemental composition of the algal food source will influence the elemental composition of zooplankton egestion products. In situations where nitrogen is limited, zooplankton will preferentially conserve more nitrogen in their biomass while excreting more carbon, resulting in zooplankton fecal matter that has relatively high C:N ratios (Urabe 1993). Carbon-rich fecal pellets sink rapidly to the lake floor and are enclosed in a membranous tissue that inhibits rapid decomposition (Ferrante and Parker 1977). In contrast, nitrogen bound in zooplankton tissue may be recycled through incorporation into predator biomass and through excretions of nitrate and ammonia. Ungrazed, dead zooplankton tissue may also be recycled through bacterial degradation as it settles through the water column. Thus, carbon-rich material may be preferentially transferred to the lake bottom while nitrogen is efficiently maintained in the active food web.

Selective degradation of labile N-rich compounds will also increase the C:N ratio of organic matter preserved within the sediments. C:N ratios for non-nitrogen-limited algae can be increased from 5–6 to as high as 12.1 in sediments through partial degradation (Wetzel 2001). The extent of degradation will differ with sedimentation rate, the oxidation state at the sediment–water interface, and other factors, but nevertheless, sediment C:N ratios are commonly slightly higher than their seston counterparts.

Methods

Surface sediment samples were collected from the deepest regions of 11 British Columbia salmon nursery lakes (Fig. 1) in the summer of 2002 and analyzed for bulk organic carbon and nitrogen isotopic and elemental concentrations. Surface samples were dried at 80°C for 24 h before analyses with a Finnigan Delta Plus mass spectrometer at the University of Alaska.

Chitinous carapaces of *Bosmina* spp. were hand-picked from surface sediment samples treated with 10% potassium hydroxide solution, sieved, and washed with deionized water. Approximately 800–1,200 specimens were required to obtain measurable weights. The carapaces were analyzed on a Finigan MAT 252 continuous flow–isotope ratio mass spectrometer at the University of Victoria. Isotope ratios are expressed as δ values relative to the atmospheric standard, such that $\delta^{15}\text{N}_{\text{sample}} = (\text{R}_{\text{sample}}/\text{R}_{\text{air}} - 1)10\text{‰}$, where R is the $^{15}\text{N}:^{14}\text{N}$ ratio. Analytical uncertainties are $\pm 0.2\text{‰}$.

The 11 nursery lakes span a broad geographic area across British Columbia. Most are deep, but they have a variety of morphometric characteristics (Table 1). Escapement for each lake was calculated as a 5-yr average for the years 1998–2002 (where data are available).

In addition to direct measurement of chitin and sediment $\delta^{15}\text{N}$ values, algal $\delta^{15}\text{N}$ values were estimated for each lake, assuming (1) a fixed isotopic offset between chitin and muscle tissue of 4.2‰ (Montoya 1994) and (2) variable offset between zooplankton and algae, calculated as

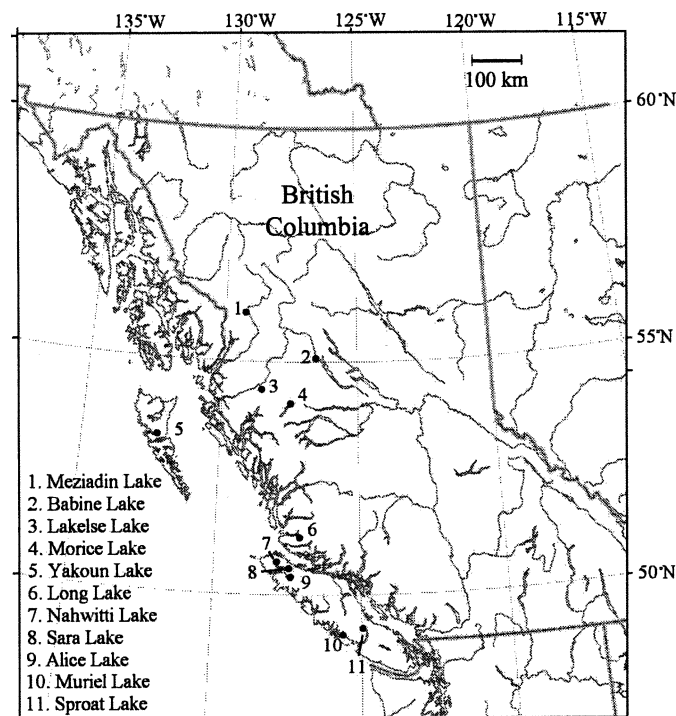


Fig. 1. Location map of 11 sockeye nursery lakes in British Columbia, Canada.

a function of sediment C:N ratio using the aforementioned equation of Adams and Sterner (2000).

Results

Elemental and isotopic results and transformations are presented in Table 1. Sediment $\delta^{15}\text{N}$ shows a positive logarithmic relation to 5-yr average escapement per lake surface area ($r^2 = 0.46$; $p = 0.0325$) (Fig. 2). A strong negative relation exists between escapement and sediment C:N ratios ($r^2 = 0.63$; $p = 0.0064$) (Fig. 3). Raw chitin $\delta^{15}\text{N}$ shows no correlation with escapement or sediment $\delta^{15}\text{N}$, however, chitin-inferred algal $\delta^{15}\text{N}$ is similar to sediment $\delta^{15}\text{N}$ and correlates logarithmically with escapement ($r^2 = 0.75$; $p = 0.0014$) (Fig. 4) and linearly with sediment $\delta^{15}\text{N}$ ($r^2 = 0.74$; $p = 0.0007$). A particularly strong relation exists between sediment C:N and the sediment–chitin $\Delta^{15}\text{N}$ difference ($r^2 = 0.83$; $p < 0.0001$) (Fig. 5).

In addition, no identifiable terrestrial remains were observed during the sieving process. Nor were any discovered during the intensive microscopic searches for cladoceran remains.

Discussion

The correlation between escapement and sediment $\delta^{15}\text{N}$ demonstrates a clear relation between marine-derived nutrients and the sediment record. However, a logarithmic rather than linear relation between escapement and sediment $\delta^{15}\text{N}$ suggests that varying fractionation influences sediment nitrogen-isotope labeling (Fig. 2). This

Table 1. Morphometric and sediment characteristics and sockeye salmon escapement of the 11 nursery lakes.

Lake	Lake area (km ²)	Volume (m ²)	Max depth (m)	Catchment area (km ²)	Flushing rate (years)	Sockeye salmon escapement*	δ ¹⁵ N	Atomic C:N	Chitin δ ¹⁵ N	Chitin-inferred algal δ ¹⁵ N†	Sediment-chitin δ ¹⁵ N	DIN:DP
Meziadin	39.6	1.78×10 ⁹	120	676.37	1.4	188,770	3.419	9.168	0.387	2.662	3.032	17-18
Babine	471.7	2.74×10 ¹⁰	186	6,420.10	8	1,165,214	3.972	11.802	1.111	2.833	2.861	N/A
Sproat	42.0	2.84×10 ⁹	195	351.65	4.4	457,255	3.192	14.501	2.197	3.352	0.995	4-18‡
Morice	93.8	9.38×10 ⁹	236	1,843.81	2.6	55,900	1.501	15.537	-0.395	0.543	1.896	5.7-5.9
Alice	10.9	3.37×10 ⁸	71	472.99	0.4	4,858	1.883	15.763	-0.299	0.591	2.182	N/A
Sara	0.5	5.80×10 ⁶	35	7.97	0.4	N/A	2.978	16.612	1.166	1.878	1.812	N/A
Lakelse	13.7	1.16×10 ⁵	32	394.7	0.2	8,869	2.400	16.619	1.161	1.871	1.239	N/A
Long	21.3	1.63×10 ⁹	170	391.75	2.5	36,738	2.310	18.803	1.32	1.571	0.990	5-49‡
Yakoun	8.2	2.85×10 ⁸	91	76.53	3	29,093	1.307	23.170	2.303	1.637	-0.996	8.7
Nahwitti	2.5	6.10×10 ⁷	49	50.88	0.3	3,200	1.858	25.295	1.491	0.379	0.367	N/A
Muriel	1.6	3.57×10 ⁷	45	9.56	1.1	260	0.153	27.128	1.431	-0.066	-1.278	N/A

* Five-year average escapement.

† Chitin-inferred algal δ¹⁵N calculated using the variable fractionation determined by Adams and Sterner (2000).

‡ Range of values from seasonal sampling.

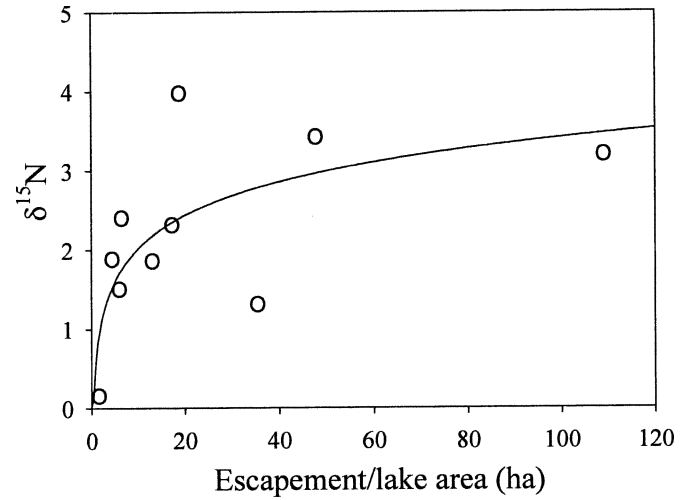


Fig. 2. Bulk sediment δ¹⁵N and 5-yr average escapement per hectare for 10 British Columbia lakes ($r^2 = 0.46$).

relation indicates that bulk sediment δ¹⁵N does not reflect the average DIN input (marine-derived spawner plus terrestrial), but rather the intensity of nutrient utilization. That is, the available nitrogen pool is used to a greater extent at lower escapements, and the organic matter δ¹⁵N reflects the source DIN. At higher escapements, nitrogen is less limiting and isotope fractionation is greater. The logarithmic relation also suggests that simple mixing models using bulk sediment δ¹⁵N will underestimate escapement at higher marine-derived nitrogen loads because ¹⁴N is used in greater proportions.

Nitrogen limitation in British Columbia coastal lakes can be determined using dissolved nitrogen : phosphorus (N:P) ratios. The optimal N:P ratio for algal growth, as indicated by the Redfield ratio, is 16:1 (Redfield et al. 1963); N:P ratios <16 should indicate a general nitrogen

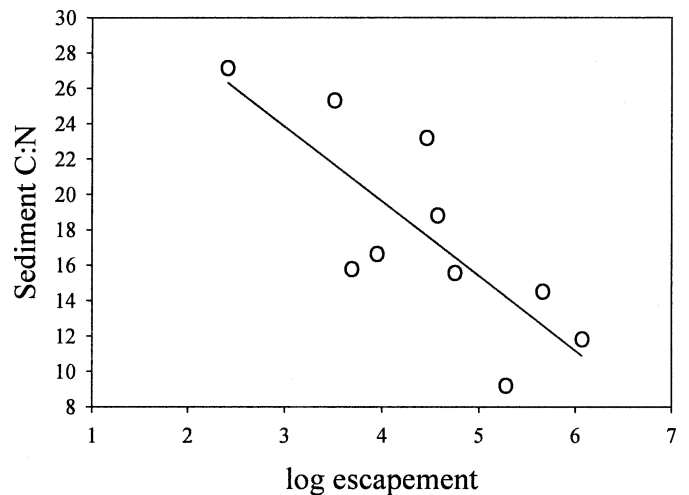


Fig. 3. C:N ratios in surface sediment organic matter and log 5-yr average escapement for 10 British Columbia lakes ($r^2 = 0.63$).

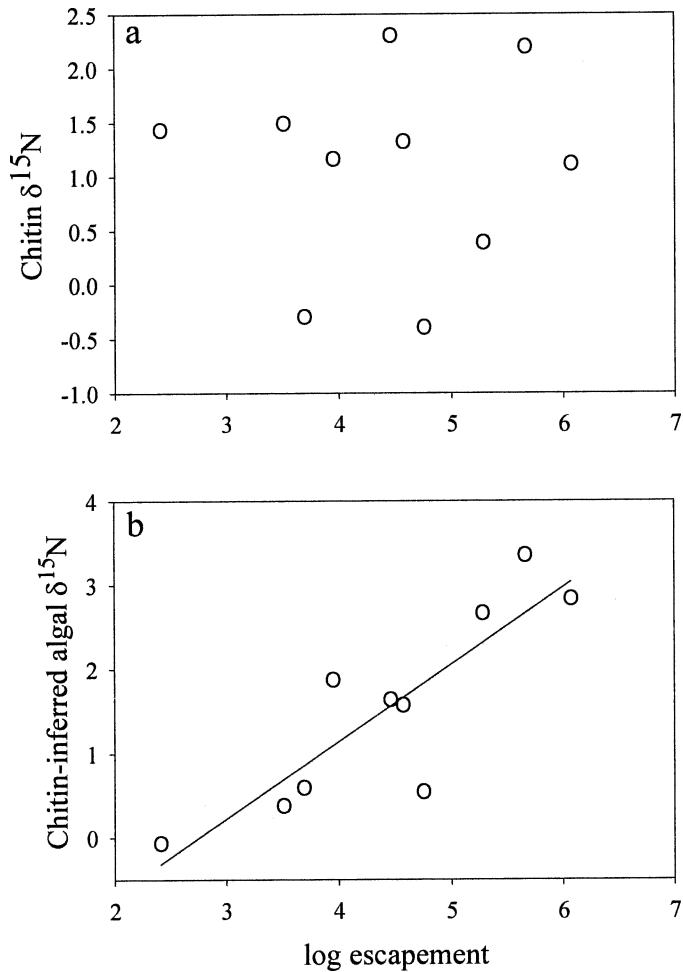


Fig. 4. (a) Raw chitin and (b) chitin-inferred algal $\delta^{15}\text{N}$ versus the log of escapement. (A) $r^2 = 0$. (B) $r^2 = 0.74$.

deficiency for most algal species. The baseline nutrient status of several of the study lakes was analyzed under the British Columbia Lake Enrichment Program (Stockner and Shortreed 1978, 1979; Costella et al. 1983). Measurements

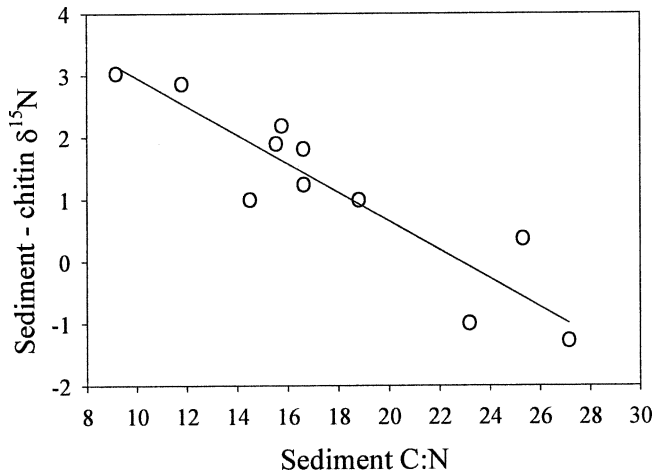


Fig. 5. Sediment-chitin $\delta^{15}\text{N}$ offset and the C:N ratio of sediment ($r^2 = 0.83$).

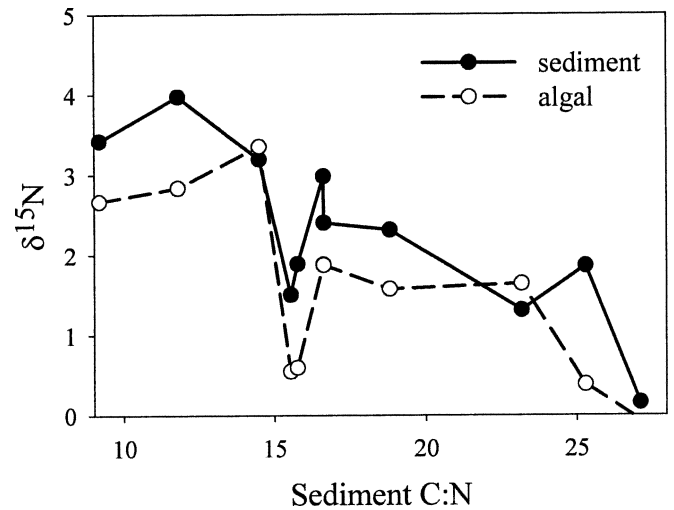


Fig. 6. The relation between algal and sediment $\delta^{15}\text{N}$ and C:N ratios of corresponding sediments. The relation between sediment and chitin-inferred algae has an r^2 of 0.74. Algal $\delta^{15}\text{N}$ values are chitin-adjusted for C:N.

of nitrate, ammonium, and phosphate revealed that Meziadan Lake is borderline nitrogen-limited, with a N:P ratio of 17–18. Morice Lake, Sproat Lake, and Yakoun Lake are severely nitrogen-limited with N:P ratios of 5.7–5.9, 4–18, and 8.7, respectively (Stockner and Shortreed 1978, 1979; Costella et al. 1983). Only point-sampling data are available for some of the study lakes, which may not be representative of the entire growing season; however, values for Sproat Lake represent seasonal sampling data. Seasonal nutrient measurements also taken in Long Lake revealed a progressive trend toward increasing nitrogen limitation throughout the summer: N:P ratios dropped from 49 in May to approximately 5 in August (Costella et al. 1983). These values are consistent with our inferred gradient of nitrogen limitation for the study lakes, based on C:N ratios. Dissolved phosphorous data are not available for the remaining study lakes; however, nitrate levels were below the detection limit for most of the sampling season in Muriel Lake (Nidle et al. 1984). Stockner and Shortreed (1979) noted that despite low N:P ratios in many of these lakes, no nitrogen-fixing algae were present. Suttle and Harrison (1988) attributed the lack of nitrogen-fixing algae in the lakes to their inability to compete for the low levels of available phosphorus.

Nitrogen limitation at lower escapements is consistent with the observed relation between sedimentary C:N ratios and the log of escapement (Fig. 3). Evidence for varying nitrogen limitation with salmon escapement is also provided by the patterns evident in Figs. 4, 5, and 6. Raw chitin $\delta^{15}\text{N}$ values show no correlation between escapement or sediment $\delta^{15}\text{N}$, suggesting another control on zooplankton $\delta^{15}\text{N}$. Chitin-inferred algal $\delta^{15}\text{N}$ values, however, are strongly correlated to both log escapement ($r^2 = 0.74$; Fig. 4b) and sediment $\delta^{15}\text{N}$ ($r^2 = 0.74$). The latter two relations suggest nitrogen limitation is indeed a control on C:N ratios and, moreover, that sediment organic matter is

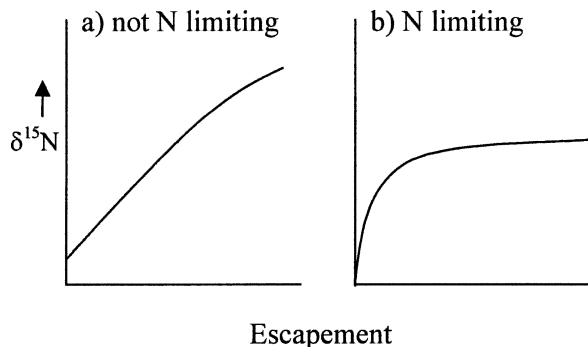


Fig. 7. (a) Sediment $\delta^{15}\text{N}$ response to increased escapement in a lake system that is not nitrogen-limiting. (b) Sediment $\delta^{15}\text{N}$ response to increased escapement in a lake system that is nitrogen-limiting.

dominantly aquatic in nature. The good agreement between measured sediment $\delta^{15}\text{N}$ and chitin-inferred algal $\delta^{15}\text{N}$ values (Fig. 6) further suggests that the fixed chitin-muscle tissue fractionation for zooplankton of 4.2‰ derived by Montoya (1994) may be generally applicable (Fig. 6). Finally, the strong inverse relation between measured sediment-chitin $\delta^{15}\text{N}$ offset and the sediment C:N ratio ($r^2 = 0.83$; Fig. 5) is a compelling indication that the broad spectrum of nitrogen-limiting conditions in these salmon nursery lakes is governed by salmon escapement.

The relation between sediment and chitin-inferred algal $\delta^{15}\text{N}$ and C:N ratios (Fig. 6) demonstrates how lake systems differ in response to escapement-based attendant nutrient status. This relation could be teased apart to investigate lake-specific differences that might be probed in subsequent investigations. For example, the low $\delta^{15}\text{N}$ sediment and chitin-inferred algae in Morice and Alice lakes suggest a higher natural loading of isotopically light-dissolved inorganic nitrogen. The catchment-to-lake area ratios are relatively large for both lakes, consistent with a higher natural loading rate. Conversely, raw chitin $\delta^{15}\text{N}$ values for Muriel and Yakoun lakes are relatively high and larger than their sediment counterparts (Table 1). In the absence of sufficient nitrogen in the food source, a progressive increase in whole body ^{15}N may occur as metabolic processes continue to eliminate ^{14}N . Both Muriel and Yakoun lakes have relatively low catchment-to-surface area ratios and high flushing rates, which may exaggerate the effects of nitrogen limitation.

Our findings have important implications for the use of sediment $\delta^{15}\text{N}$ as a tool for assessing historical salmon escapement from nursery lakes in British Columbia. These British Columbia study lakes clearly behave differently from the Alaskan lakes investigated by Finney et al. (2000). As demonstrated, C:N ratios are useful in interpreting sedimentary $\delta^{15}\text{N}$ and determining the importance of salmon escapement for the available nitrogen pool of individual lakes. This concept is best illustrated through a conceptual model of nitrogen isotope fractionation at low- and high-background nitrogen loading (Fig. 7). In situations where nitrogen is in sufficient supply, sediment

$\delta^{15}\text{N}$ will respond to salmon loading in an essentially linear fashion (Fig. 7a). The increase in $\delta^{15}\text{N}$ is a direct result of the proportional increase in ^{15}N in the available nitrogen pool. That is, isotope discrimination of ^{15}N is the same for both low- and high-fish densities. In these situations, because nitrogen is not limiting, C:N ratios should remain relatively low. However, in lakes where nitrogen is the dominant limiting nutrient, $\delta^{15}\text{N}$ variability will reflect decreased ^{15}N discrimination at low escapements, but will be proportionally damped at high escapements because of preferential use of ^{14}N . This response should manifest itself in a $\delta^{15}\text{N}$ curve that rises rapidly in response to increased escapement and then flattens as nitrogen becomes less limiting (Fig. 7b), consistent with observed British Columbia data (Fig. 2). As nitrogen is indeed limiting in many British Columbia lakes, C:N ratios in sediments will be relatively high. Our results confirm the need for caution in interpreting high sediment C:N ratios as indicative of terrestrial organic matter input into lakes.

The use of sedimentary C:N ratios as a reference for nitrogen limitation may require further clarification. Terrestrial organic matter is efficiently recycled in stream and littoral habitats and will not contribute significantly to profundal regions of large, deep lakes (Wetzel 2001). Tenzer et al. (1997) demonstrated that terrestrial material comprises a minor component of the sedimentary organic matter in samples collected more than a few hundred meters from the shores of Pyramid Lake, Nevada. Despite these specifics, C:N ratios have commonly been used in paleolimnological studies to determine relative contributions of terrestrial organic matter in lake sediments, regardless of lake size and morphology. This interpretation is based on the premise that land plants, having a greater concentration of carbon-rich structural compounds, have C:N ratios >20 ; whereas protein-rich algal material has C:N values of 4–10 (Meyers 1994). The interpretation generally assumes that there are only two possible sources of organic matter in lake sediments, terrestrial plant material and algae, and that the elemental and isotopic compositions of neither source material is modified by in-lake processes. However, sediment can contain large amounts of organic matter composed of other pelagic organic sources, such as zooplankton fecal material and disarticulated body parts. Failure to account for these components can lead to inaccurate conclusions. To illustrate, analyses of suspended organic matter in Lake Michigan indicated that a significant proportion of organic matter reaching the lake floor comprises zooplankton fecal material and carapaces (Evans et al. 1998). Yet, the high C:N ratios of the organic matter in Lake Michigan (8.7–22.5; average = 16.8; Meyers and Eadie 1993) suggest high terrestrial contributions if conventional interpretations are applied.

In lakes where the size and depth will preclude abundant terrestrial organic contributions, bulk organic matter should be composed mainly of algal remains and zooplankton fecal material. In these cases, the C:N ratio should reflect the level of nitrogen limitation experienced by these pelagic organisms. The relation between sediment C:N ratios and the sediment-chitin $\delta^{15}\text{N}$ offset in British

Columbia lakes also exists at C:N ratios that are lower than those expected with terrestrial influence (Fig. 5) and therefore are not reflective of variations in terrestrial organic contributions. However, we are not suggesting that terrestrial organic matter has no influence on C:N ratios in large lakes, but rather that any contribution is insignificant in comparison to the flux of organic matter from the epilimnion.

The relation between C:N ratios in sediment organic matter and sockeye salmon escapement can be used as a proxy for nitrogen limitation, although several uncertainties remain. Full nitrogen budgets of the 11 British Columbia lakes and quantification of the species-specific cladoceran chitin offset are required to fully account for the observed isotopic variations. The potential for influence by terrestrial material remains in some systems, although this influence is likely to be caused by extreme events and should leave a discrete signature in the sediment profile (Meyers and Teranes 2001). Sieving of sediment before analyses should eliminate the possibility of contamination by terrestrial macrofossils.

The isotope data from these British Columbia lakes suggest nitrogen limitation at low to moderate escapements through algal and zooplankton trophic levels. The data support the notion that coastal lakes are salmon-supported and adequate escapement needs to be maintained to avoid severe nitrogen limitation. The data also support an alternate and additional interpretation of sedimentary C:N ratios and illustrate that $\delta^{15}\text{N}$ will underestimate escapement at high spawner densities in these systems. Information derived from these proxies may be useful in setting appropriate lake-specific sockeye escapement goals and determining the magnitude of loss of historical nutrient subsidies to many Pacific-coast lacustrine ecosystems.

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