Centennial-scale fluctuations and regional complexity characterize Pacific salmon population dynamics over the past five centuries

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Observational data from the past century have highlighted the importance of interdecadal modes of variability in fish population dynamics, but how these patterns of variation fit into a broader temporal and spatial context remains largely unknown. We analyzed a time series of stable nitrogen isotopes from the sediments of 20 sockeye salmon nursery lakes across western Alaska to characterize temporal and spatial patterns in salmon abundance over the past ∼500 y. Although some stocks varied on interdecadal time scales (30- to 80-y cycles), centennial-scale variation, undetectable in modern-day catch records and survey data, has dominated salmon population dynamics over the past 500 y. Before 1900, variation in abundance was clearly not synchronous among stocks, and the only temporal signal common to this region was the onset of commercial fishing in the late 1800s. Thus, historical changes in climate did not synchronize stock dynamics over centennial time scales, emphasizing that ecosystem complexity can produce a diversity of ecological responses to regional climate forcing. Our results show that marine fish populations may alternate between naturally driven periods of high and low abundance over time scales of decades to centuries and suggest that management models that assume time-invariant productivity or carrying capacity parameters may be poor representations of the biological reality in these systems.

fisheries | nitrogen stable isotopes | *Oncorhynchus nerka* | paleolimnology

Large fluctuations in abundance are a hallmark of fish stocks (1, 2); fish abundance can fluctuate substantially over interannual to centennial time scales (3–5). Recent short-term variation in stock abundance can be characterized by fisheries catch records and scientific survey data, but to characterize long-term low-frequency variability requires novel ecological approaches (6). Knowing how fish stocks have varied over long time scales can provide an important context for recently observed shifts in abundance, provide insight into the potential effects of climate change, and inform management frameworks (7). In this study, we describe and analyze a time series of nitrogen (N) stable isotopes in sediments from 20 lakes as a proxy for the abundance of anadromous sockeye salmon, *Oncorhynchus nerka*, to quantify how salmon stocks have varied in abundance during the past ∼500 y. This analysis provides a comprehensive synthesis of the natural patterns of variability in salmon abundance before the onset of commercial fishing and encompasses a study region that currently produces over 70% of global sockeye salmon catches (8).

Low-frequency variation in fish abundance is often attributed to climatic forcing (2, 9) or harvesting (10 ,11). At a broad scale, persistent multidecadal shifts in North Pacific salmon production throughout the 20th century have been linked to the Pacific Decadal Oscillation (PDO), with total salmon production in Alaska high when the PDO is in a warm phase and vice versa for cold phases (12). At finer spatial and temporal scales, however, salmon populations have varied in their responses to climatic variation, exhibiting asynchronous dynamics even within close proximity, presumably due to differences in habitats, life histories, and other local drivers of population dynamics (13, 14). Although the mechanisms that produce this response diversity remain elusive, these spatial differences in productivity patterns, which have been observed in interannual to interdecadal time scales, can stabilize fisheries and ecosystem processes by reducing the variation in aggregate salmon returns over time (13, 15). Whether low-frequency modes of climate variation have synchronized salmon production at time scales longer than provided by direct fishery observations is unknown.

Sediments store information about past ecosystem characteristics, including the abundance of fish (3, 16, 17). In the case of sockeye salmon, the ratio of stable N isotopes ($^{15}N/^{14}N$) preserved in lake sediments can be used to quantitatively reconstruct historical abundances. After accumulating most of their body mass at sea, anadromous sockeye salmon return to natal freshwater ecosystems, including lakes and lake tributaries, to reproduce and die. The nitrogen from their carcasses, substantially enriched in the heavier ^{15}N isotope ($\delta^{15}n = 11.3\%$) (18) relative to freshwater or terrestrial N sources, is eventually incorporated into lake sediments (6). Thus, in watersheds where salmon-derived N inputs are high relative to watershed N inputs, historical changes in sedimentary $\delta^{15}N$ can be used to infer past variation in salmon densities. Although this method has been validated widely in Alaskan lakes (6, 7, 19–23), to date there has been no comprehensive synthesis of how salmon densities have varied on decadal to centennial time scales.

In this study, we present a synthesis of recent and past time series of sedimentary stable N isotopes as proxies for past sockeye salmon abundances in 20 sockeye nursery lakes within 16 major watersheds in southwestern Alaska, including the major watersheds of Bristol Bay (Fig. 1 and Table 1). Our objectives were to (*i*) characterize patterns of variability in sockeye salmon abundance over multiple centuries, (*ii*) identify the dominant periodicities associated with these fluctuations, and (*iii*) determine the extent to which stocks have shown synchronous shifts in abundance over the past 500 y.

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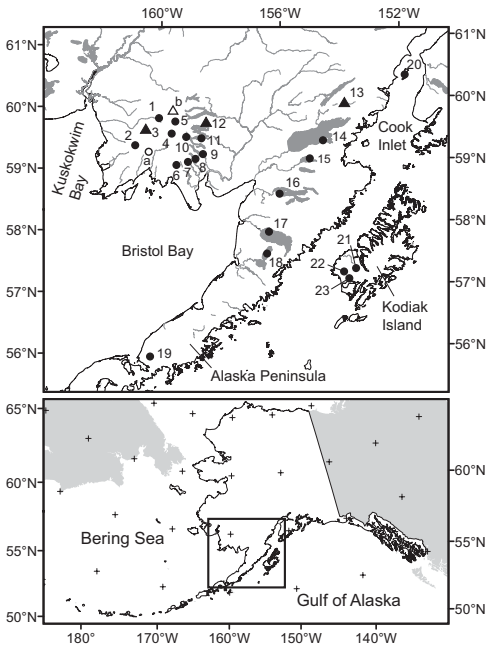

Fig. 1. Locations of lakes in Alaska cored for this study. Numbers correspond to lake numbers in Table 1. Triangles indicate reference lakes, and open symbols indicate lakes excluded from further analysis (*Results*).

Results

Sediment Chronologies for Newly Dated Cores. Sediment deposition dates were estimated from down-core profiles of ^{210}Pb activities (*Methods* and *SI Methods*). In all cases, ^{210}Pb profiles were fit well by simple exponential decay models (R^2 from 0.92 to >0.99) (Table S1 and Fig. S1). This lack of deviations from the exponential model provided strong evidence that mass accumulation rates (ω) were constant over the ^{210}Pb-dated period of the cores (~150 y) and could be used to extrapolate sediment ages beyond this period. Likelihood profile-based confidence intervals for ω were used to estimate uncertainty in extrapolated sediment ages (*SI Methods* and Table S1). Down-core changes in the C:N ratio were negligible in all but two cores, indicating little change in the relative contribution of terrestrial- versus aquatic-derived organic matter to sediment accumulation (23). Cores from High and Gechiak lakes showed substantial discontinuities in C:N ratios around 1850 and 1650, respectively, and were thus excluded from further analyses.

Stable Nitrogen Isotopes in Sediments. In sockeye salmon nursery lakes, the degree of sedimentary enrichment with ^{15}N ranged from a mean δ^{15}N of 3.1% in Goodnews Lake to a mean δ^{15}N of 8.3% in Karluk Lake (Fig. 2 and Fig. S2). In all cases, mean δ^{15}N was higher in sockeye nursery lakes than in nonsalmon reference lakes from the same or nearby drainage basins (mean $\delta^{15}n = 2.1$, 3.1, and 2.7% for Nagugun, Grant, and Tazimina lakes, respectively), suggesting that sedimentary δ^{15}N was responsive to marine-derived N delivered by anadromous sockeye salmon. Nursery lakes also exhibited more variable δ^{15}N profiles than reference lakes (average SDs = 0.76 and 0.36, respectively) (Fig. 2 and Fig. S2), demonstrating that δ^{15}N values varied little in the absence of anadromous fish. The δ^{15}N in reference lakes declined by about 1% in the past century, likely due to deposition of industrial nitrogen oxide emissions (24), but these shifts were subtle compared with the historical variability observed in salmon-bearing lakes (Fig. 2).

Temporal Trends and Periodicities in δ^{15}N. Commercial fisheries in Alaska for sockeye salmon began in the 1880s with the construction of salmon canneries, and by the early 1900s fisheries were fully developed in Bristol Bay, Cook Inlet, and near Kodiak Island, with catches comparable to the present day (25). Fisheries intercept salmon-derived N and thus cause the isotopic signal in sediments

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Table 1. Lakes included in this study

Lake no.	Lake name	Region	Drainage	Latitude (°N)	Longitude (°W)
1	Kagati	Kuskokwim Bay	Kanektok	59.87	160.06
2	Goodnews	Kuskokwim Bay	Goodnews	59.5	160.53
3	Nagugun (R)	Bristol Bay	Togiak	59.68	160.38
a	Gechiak*	Bristol Bay	Togiak	59.39	160.37
b	High (R)*	Bristol Bay	Togiak	59.94	159.5
4	Togiak	Bristol Bay	Togiak	59.62	159.62
5	Upper Togiak	Bristol Bay	Togiak	59.83	159.48
6	Ualik	Bristol Bay	Igushik	59.09	159.44
7	Amanka	Bristol Bay	Igushik	59.1	159.19
8	Nunavaugaluk	Bristol Bay	Nunavaugaluk	59.19	158.9
9	Aleknagik	Bristol Bay	Wood	59.33	158.8
10	Little Togiak	Bristol Bay	Wood	59.57	159.13
11	Nerka	Bristol Bay	Wood	59.56	158.83
12	Grant (R)	Bristol Bay	Wood	59.81	158.52
13	Tazimina (R)	Bristol Bay	Kvichak	60.05	154.16
14	Iliamna	Bristol Bay	Kvichak	59.48	154.8
15	Kukaklek	Bristol Bay	Alagnak	59.18	155.36
16	Naknek	Bristol Bay	Naknek	58.7	156.31
17	Becharof	Bristol Bay	Egegik	57.99	156.56
18	Lower Ugashik	Bristol Bay	Ugashik	57.67	156.69
19	Bear	Alaska Peninsula	Bear	56.02	160.25
20	Packers Creek	Cook Inlet	Packers Creek	60.47	151.92
21	Karluk	Kodiak	Karluk	57.38	154.05
22	Red	Kodiak	Ayakulik	57.25	154.29
23	Akalura	Kodiak	Akulara	57.19	154.22

Reference lakes (without salmon) are indicated by "(R)."
*Exluded from further analyses due to C:N discontinuity.

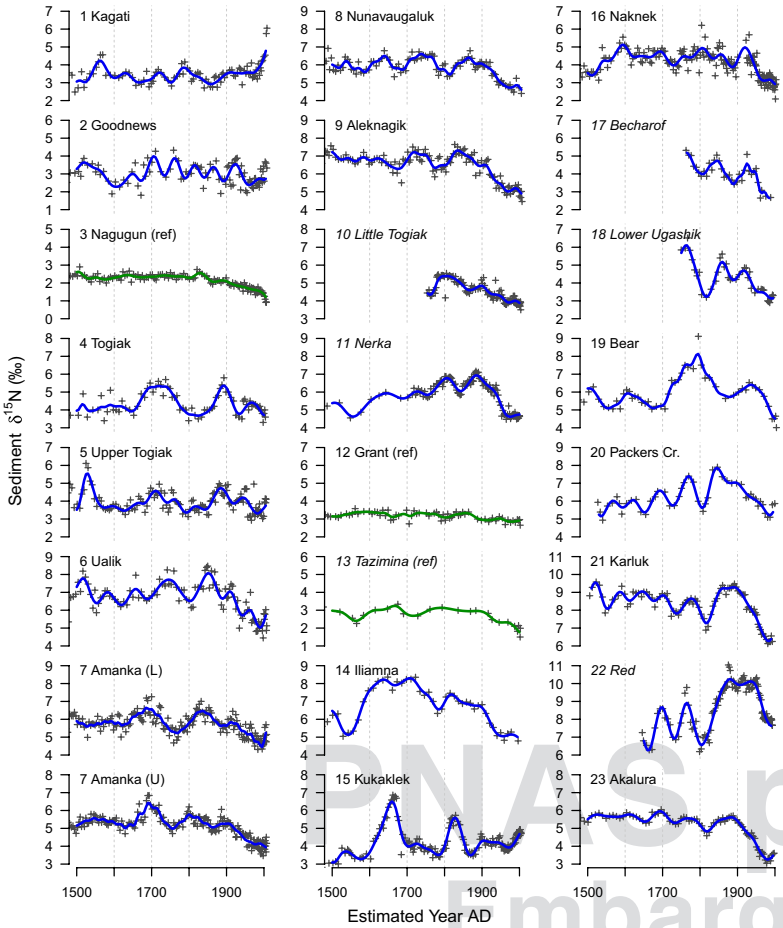

Fig. 2. Measured δ^{15}N values (+) and eigenvector-filtered time series of δ^{15}N reconstructed from the first four principal components for each core (lines) (*Methods*). Raw δ^{15}N values (+) were first interpolated to a 5-y time interval before filtering. Note that the *y* axis scale is consistent, but the range differs. Reference lakes are indicated by "ref" and shown in green; italics indicate lakes not included in the wavelet analysis due to either the length or the sampling frequency of the core.

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to become decoupled from total salmon production (7, 22). To study natural patterns of variation in salmon abundance, we therefore focus on sedimentary N deposited before ∼1900.

Eigenvector filtering (EVF) (26) over the period 1530–1900 decomposed each time series into a combination of slowly varying time trends and higher-frequency periodic or quasi-periodic components. Filtered time series reconstructed from the first four components (i.e., those that explained the highest proportion of the variance) showed that low-frequency modes dominated the historical variation in most time series (Fig. 2). This was confirmed by wavelet analysis, which found high power associated with low frequencies (periodicities >80 y) in most cores (Fig. 3 and Fig. S3). Although some lakes exhibited slowly developing trends through time (e.g., Nerka, Iliamna), other basins were characterized by oscillations at periods from ∼120 (Amanka, Nunavaugaluk, Aleknagik) to ∼200 y (Togiak, Upper Togiak, Kukaklek, Bear). Evidence for variation at 80- to 100-y time scales was found in Kagati, Ualik, Packers Creek, Karluk and Akalura lakes (Fig. 3 and Fig. S3). Q:15

Higher-frequency "interdecadal" modes of variation (<80 y) were evident in fewer stocks (Figs. 2 and 3; Fig. S3). The salmon lakes with the strongest evidence for variation at interdecadal time scales were Goodnews and Naknek, with some evidence for interdecadal patterns in Kagati, Packers Creek, and Karluk (Fig. 3). The two reference lakes (Grant and Nagugun) also showed evidence for periodic variation, but had relatively more power at high frequencies than salmon lakes. Although six lakes were excluded from the wavelet analysis due to low sampling resolution or insufficiently long time series, the eigenvector-filtered time series in Fig. 2 showed that low-frequency patterns were common to all sockeye salmon lakes. Taken together, these patterns demonstrate that although interdecadal variation in stock abundance was present in some salmon-bearing lakes, the predominant mode of historical variation was exhibited at the scale of centuries. Importantly, simulations demonstrated that these results were robust to sediment dating errors and interpolation (*SI Methods* and Fig. 3).

Spatial Complexity in Salmon Production Trends. To characterize common temporal patterns in salmon production across lakes, we performed Principal Component Analysis (PCA) on the interpolated δ^{15}N time series for the periods 1530–1900 and 1530–1990 (n = 16 cores) (*Methods*). A PCA for the period 1530–1900 (i.e., not including the period of commercial fishing) resulted in no significant PCs, indicating a distinct lack of common dynamics among lakes before 1900 (Fig. 4, *Top Left*). Simulations indicated Q:16 that it was highly unlikely that this result was due to dating errors alone (*SI Methods*). Distributions of δ^{15}N anomalies showed that, before commercial fishing, at any given time some lakes had higher-than-average δ^{15}N whereas others had lower-than-average δ^{15}N (Fig. 4, *Bottom*). This pattern held even for the period 1860–1900, when confidence in sediment chronologies is highest, further indicating a lack of a common signal in salmon production among lakes.

The PCA of the period 1530–1990 produced one significant PC, accounting for 35% of the total variance in δ^{15}N observed among lakes (Fig. 4, *Top Right*). The dominant feature of this PC was a sharp drop in δ^{15}N beginning around 1900, corresponding to the development of commercial fishing on most of these stocks (25). Minor peaks were detected in 1700 and 1850 (Fig. 4, *Middle*). Kagati Lake had an opposite loading on PC1 from the rest of the lakes, and Bear, Kukaklek, Togiak, and Upper Togiak lakes were only weakly correlated with PC1 (r < 0.3) (Fig. S4).

Discussion

This study is a comprehensive synthesis of historical δ^{15}N vari- Q:17 ation in sockeye salmon nursery lakes and provides a broad

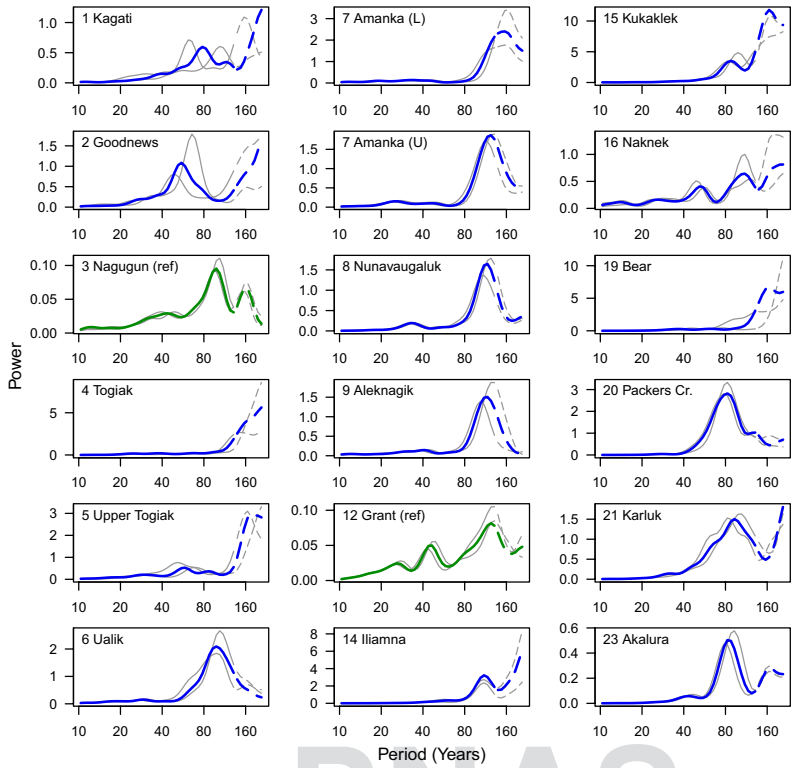

Fig. 3. Global wavelet power spectra of $\delta^{15}N$ time series (1530–1900) for 16 cores from salmon lakes (blue lines) and 2 cores from reference lakes (green lines). Power spectra calculated on the basis of 5th and 95th percentile dates are shown in gray. Dashed lines indicate where edge effects may influence the decomposition.

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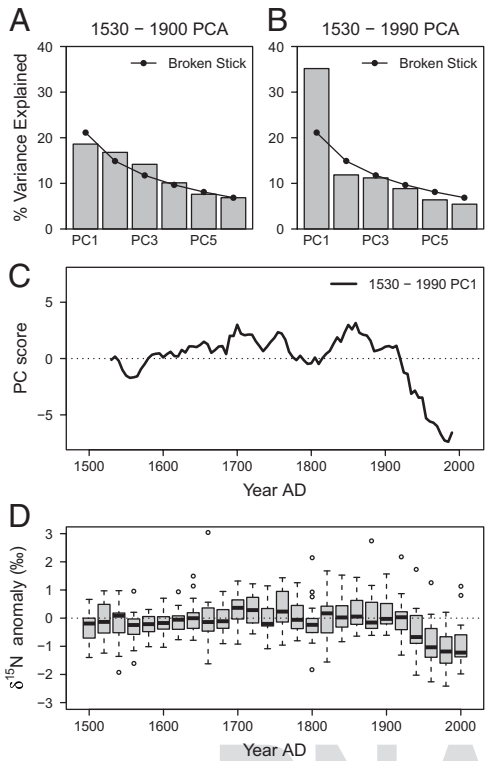
perspective on patterns of variation in salmon abundance over multicentury time scales. Although previous studies using these methods have provided perspectives for individual lake systems (7, 21, 22), or for small groups of lakes in limited geographic regions (6, 19), this study examines historical patterns of inferred salmon densities in watersheds across southwestern Alaska, an area of global importance for salmon fisheries (8). The picture that emerges from this synthesis is that low-frequency fluctuations in abundance are a fundamental characteristic of natural (unexploited) salmon populations and that these fluctuations are not necessarily synchronous across southwestern Alaska.

Low-Frequency Variation in $\delta^{15}N$ Before Commercial Fisheries. Before 1900, the dominant feature in cores from nursery lakes was the presence of large fluctuations in $\delta^{15}N$, indicating prolonged periods of higher-than-average and lower-than-average salmon abundance lasting for decades to centuries. Although interdecadal variability in salmon abundance is well documented in 20th-century catch records (12), centennial-scale variability falls outside the scope of most modern-day fisheries data. However, the dominant mode of variability in most lakes was on centennial time scales, including cycles in abundance lasting up to 200 y. Such a historical perspective on natural population variability can provide an important context for current patterns of production. For example, anomalously high returns of adult salmon to Kukaklek Lake in the past decade, unprecedented since record keeping began in 1956, appear to have been part of a natural cycle in sockeye productivity for that lake (7).

In the absence of harvesting, climate is often considered to be the main driver of large shifts in fish abundance (2). Indeed, interdecadal variability in northern Pacific sockeye salmon production during the past century has been tied to marine ecosystem shifts linked to the PDO (12, 27). However, the extent to which the PDO has driven changes in historical (pre-1900) salmon abundance is unknown. Reconstructions of the PDO based on tree rings and coral records suggest that the strength and periodicity of the PDO has varied over the past 400 y (28, 29) and that the commonly referenced 50- to 70-y mode of variability was only intermittently detectable before ~1800 (30). Instead, periodicities of 20–30 y may have been the predominant characteristic of the PDO before the past century (28), suggesting in turn that the 80- to 90-y oscillations observed in some lake sediments (e.g., Packers Creek, Karluk, Akalura), which extend back to at least 1600, were not due to oscillations in the PDO as it is currently characterized. However, other unidentified climate-driven changes in marine or freshwater ecosystems could have played a role.

Climate is not the only possible driver of low-frequency variation in salmon abundance. For example, age-structured populations may exhibit low-frequency oscillations over time scales much longer than the life span of the organism due to cohort interactions (31). Localized food-web interactions and disease dynamics may also lead to shifts in abundance over long time scales. Bottom–up changes in the primary and secondary productivity of lakes could influence rearing capacity for juveniles and thus the abundance of returning adults (6, 32, 33). Such changes in lake productivity could be caused by changes in nutrient inputs from surrounding watersheds or from salmon themselves. The importance of this "marine-derived nutrients" mechanism has been found to differ across systems (6, 22, 32). Alternatively, top–down effects via a slow build-up of predator populations in lakes or estuaries used in smolt migrations could cause a subsequent increase in sockeye salmon mortality at juvenile life stages. Thus, although there are many possibilities, the mechanistic basis for these low-frequency oscillations is unknown and is likely to vary by stock and over time. Furthermore, climate variation is likely to interact with these ecological mechanisms to create nonlinear dynamics that may play out uniquely in different ecosystems.

Decadal- and centennial-scale production regimes observed in these Alaskan salmon lakes were not regionally coherent. A visual assessment of the patterns of variation across the 20 salmon stocks suggests fundamentally different temporal patterns in abundance (Fig. 2), which is supported by the different relative contributions of interdecadal versus centennial-scale variability among lakes (Fig. 3), as well as the lack of a common temporal signal among lakes before 1900 as indicated by PCA (Fig. 4, *Upper*). Based on our estimates of sediment deposition dates, the ~200-y cycles in Togiak and Upper Togiak lakes were coherent with one another, but out of phase with those in Bear and



Q:23 **Fig. 4.** Results from principal components analyses of interpolated $\delta^{15}N$ time series from sockeye salmon nursery lakes, along with $\delta^{15}N$ anomaly distributions. The percentage of variance explained by principal components 1–6 from PCAs over the periods (*A*) 1530–1900 and (*B*) 1530–1990 is shown. According to a broken-stick test, no PCs were significant in the data at the *Top Left*, and one PC was significant in the data at the *Top Right*. (*C*) The first PC from the period 1530–1990. (*D*) Distributions of $\delta^{15}N$ anomalies across all cores from sockeye salmon nursery lakes ($n = 21$) show that, at any point in the past, lakes exhibited both higher-than-average and lower-than-average $\delta^{15}N$ values. Anomalies were calculated relative to the pre-1900 mean $\delta^{15}N$ values for each core, based on 5-y interpolated $\delta^{15}N$ values and Q:24 plotted at 20-y intervals.

Kukaklek lakes. Many lakes exhibited lower-than-average $\delta^{15}N$ around 1800, consistent with previous findings (6), but this pattern was not universal (Fig. 4), and, during all periods of the past 500 y, both higher-than-average and lower-than-average $\delta^{15}N$ values were found in salmon nursery lakes (Fig. 4, *Bottom*). Thus, despite substantial changes in climate conditions in this region over the past five centuries (30), regional scale forcing did not synchronize stock dynamics, emphasizing the response diversity that can emerge from interactions among features of watersheds (or analogous marine domains), local ecosystem characteristics, and climate variation. Furthermore, such a lack of a coherent pattern of variation in historical salmon abundance suggests that a portfolio effect, i.e., a reduction in regional variation in salmon returns over time, which has been previously described for sockeye salmon ecosystems on interannual to decadal time scales (15), plays out over centennial time scales as well.

Interpreting 20th-Century Changes in Sedimentary $\delta^{15}N$. The single most coherent pattern observed in salmon-bearing lakes during the past 500 y was the nearly ubiquitous decrease in $\delta^{15}N$ beginning around 1900. Although some of this decrease may reflect changes in the atmospheric N pool due to human activities (24), commercial fisheries, which developed between 1882 and 1910 in most regions of southwest Alaska (25), have reduced the amount of salmon-derived N reaching freshwaters. Across Bristol Bay, an average of 60% of the total sockeye run has been harvested each year since detailed record keeping began in 1956 (34), resulting in a proportional decrease in the influx of salmon-derived N to natal lakes in this region relative to a no-fishing scenario (22). However, a comparison of the magnitude of this recent decline in sedimentary $\delta^{15}N$ with previous fluctuations (Figs. 2 and 4, *Bottom*) indicates that natural processes are capable of reducing salmon densities to a similar extent as commercial fisheries. Interestingly, these same fluctuations also highlight that salmon stocks have the capacity to rebuild naturally following prolonged periods with low densities, suggesting a strong resilience of salmon to natural and anthropogenic depletion processes. Indeed, total salmon production (catches plus escapements) has been relatively high in recent years for most sockeye salmon stocks in southwestern Alaska (13, 34–36), despite a century of intense harvesting.

In some lakes, values of $\delta^{15}N$ have shown a stable or increasing trend in the past century despite commercial fishing. Two of these lakes, Kagati and Goodnews, are nursery grounds for sockeye salmon that are harvested in Kuskokwim Bay, where commercial fisheries did not intensify until the 1970s (25), substantially later than other regions of southwestern Alaska. Current exploitation rates for these stocks are unknown due to large uncertainties in escapement estimates and allocation of catches to specific rivers and lakes; however, our data suggest that harvest rates are relatively low and that productivity has increased in these stocks during the past few decades. Kukaklek Lake, mentioned previously, has experienced high returns in recent years likely related to a ~200-y natural cycle in sockeye productivity not detectable in most other lakes in this study. Thus, the lake-specific patterns in $\delta^{15}N$ during the past century reflect natural variation in productivity among stocks combined with differences in fishing pressure.

Conclusions. Sockeye salmon dynamics in different ecosystems are likely shaped by a combination of climate effects filtered through nonlinear ecological processes that may differ among watersheds and among oceanic domains used by specific stocks. Regardless of the underlying mechanism(s), this study indicates that sockeye salmon abundances do not vary from decade to decade around a stationary mean. Although interdecadal variability in Pacific salmon production has been well established (12, 27), we show that this is often layered on top of lower frequency trends and oscillations, a perspective that would not be possible without multicentury records of salmon abundance across multiple systems. The current study places the interdecadal variation observed in fishery catches from the past century within a deeper temporal context and suggests that salmon stocks may remain in persistent high- or low-productivity regimes for not just decades, but for centuries.

Our results show that managers and society should be prepared for persistent and potentially abrupt changes in salmon production, even apart from fisheries impacts. Current management practices for Alaskan salmon use escapement goals that are set based on observed stock productivity levels from the past half-century (34). However, management models that assume time-invariant parameters (e.g., for carrying capacity or intrinsic productivity) are unrealistic representations of the biology in these systems, and a more realistic approach would allow for changes in the underlying model parameters through time (e.g., 37). As it is unlikely that we will ever gain a detailed enough mechanistic understanding of what drives variation in salmon production for every exploited stock to be able to anticipate abrupt changes, we would be wise to invest in management strategies that are robust to large, unpredictable shifts in productivity (38–40). Our results also suggest that future shifts in productivity are unlikely to be synchronous across all stocks, and a risk-averse approach to fisheries would allow fishers the flexibility to shift effort between watersheds and regions to integrate across spatial variability in salmon returns, as is currently the case in Bristol Bay (15, 41). Although there has been a recent call to attention that "stationarity is dead" when managing water resources (42), our data re-emphasize this point with respect to marine fish productivity as it plays out in spatially

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complex ways over interdecadal, centennial, and perhaps even longer (e.g., 19) unresolved time scales.

Methods

Sediment Collection, Chronologies, and Stable N Isotopic Analyses. Sediment cores were collected from 21 sockeye salmon nursery lakes and four reference lakes (i.e., lakes without anadromous salmon) in southwestern Alaska, distributed across 16 watersheds draining into Bristol Bay, the Eastern Bering Sea, or the Gulf of Alaska (Fig. 1, Table 1, *SI Methods*). Data from some of these cores have been previously published (6, 7, 19, 21, 22, 24), and more information can be found therein. All new sediment cores were taken by floatplane or boat with a Glew gravity corer (6.5 cm diameter) (43) from 2000 to 2008. Cores were extruded into 0.2- to 0.5-cm sections in the field and frozen at −10 °C in the dark. Within 6 mo, core samples were thawed, freeze-dried to constant mass, and analyzed for ^{210}Pb and δ^{15}N.

We used ^{210}Pb-dating techniques to estimate mass accumulation rates (ω) and ages of sediments. To characterize uncertainty in estimated ages, we calculated confidence intervals for ω using likelihood profiles. Further analyses that assessed the importance of dating errors used these core-specific likelihood profiles for ω to calculate alternative chronologies (details in *SI Methods*).

The stable N isotopic composition of sediments was determined by continuous flow isotope ratio mass spectrometry coupled to an automated elemental analyzer inlet device at the University of Regina, University of Washington, and University of Alaska–Fairbanks. Stable N isotopes are expressed in percentage of units: $\delta^{15}n = (R_{sample}/R_{standard} - 1) * 1{,}000$, where R_{sample} is the ratio of ^{15}N/^{14}N in the sample and $R_{standard}$ is the isotopic ratio of N_2 in air. Analytical precision for δ^{15}N measured by continuous flow is typically <0.2%, well below the intra- and interlake variation in δ^{15}N.

Numerical Methods. Time series of δ^{15}N were first linearly interpolated to a common 5-y time step (the average sampling interval across all cores for the past 500 y). To determine the dominant mode(s) of variation shared across nursery lakes, a PCA (44) was performed on the standardized time series of interpolated δ^{15}N data for 16 cores. Reference lakes were excluded, as well as cores that did not extend back to 1530. Only one of the two Amanka cores (lower basin) was included (*SI Methods*). The number of significant principal components to retain was determined using the broken-stick method (44), whereby components are sequentially retained as long as their associated variance exceeds the corresponding broken-stick value. A simulation was used to assess the possible influence of dating errors on PCA results (*SI Methods*).

To investigate time trends and patterns of variation in δ^{15}N within the cores, we used EVF (5, 26) and wavelet analysis (45). EVF was used to smooth the time series to emphasize the dominant trends and periodicities. This method is closely related to PCA, except it is applied to a matrix consisting of versions of a single time series lagged from 0 to m steps. An autocovariance matrix is calculated, and the dominant eigenvectors represent the dominant quasi-periodic modes in the original time series (26). The time series is thus decomposed into m PCs, and a filtered time series can be reconstructed by projecting a subset of the PCs back on to the original data. We used $m = 18$ (90 y), which is greater than the lag at which the autocorrelation decreases to zero in all cores. Filtered time series were reconstructed with the first four PCs, which by definition were those explaining the most variance. To characterize the dominant frequencies, we used wavelet analysis on the interpolated time series. This method decomposes a time series in both the time and frequency domains and is well-suited for nonstationary data (45). The Morlet wavelet was used, which has high resolution in the frequency domain. The global wavelet power spectrum gives the average of the continuous wavelet power spectrum over time and is analogous to a classical Fourier spectrum. Very low frequencies (periods >120 y) were poorly resolved due to edge effects, and quantitative assessments of power in these frequencies should be interpreted with care.

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Supporting Information

Rogers et al. 10.1073/pnas.1212858110

SI Methods

Detailed Site Description. Cores were collected from a total of 25 lakes distributed across southwestern Alaska (Table 1 and Fig. 1). Two cores were taken from Amanka Lake, one each from the upper basin and lower basin, which are separated by a shallow sill (1). Cores from Gechiak and High lakes were excluded from further analyses due to downcore discontinuities in C:N ratios, thus leaving 24 cores from 23 lakes for further study. All except for the three reference lakes provide spawning and nursery areas for anadromous sockeye salmon. The three reference lakes (Grant, Tazimina, and Nagugun) are inaccessible to anadromous fish due to natural physical migration barriers. Nagugun appears to be marginally accessible to migrating fish, but no salmon have been observed there, so we considered it a reference lake for this study.

The study areas are largely pristine apart from commercial fisheries; there are no dams, major watershed developments, or hatcheries. Sockeye salmon have been harvested for subsistence purposes for centuries, but human population densities have been low (fewer than 40,000 estimated in all of Alaska from 1800 to 1880) (2), and the amount of salmon intercepted by humans and removed from watersheds likely constituted a small fraction of salmon run sizes, which range from tens of thousands to tens of millions of fish, depending on the stock (3).

Chronologies. For newly dated cores (Table S1), we used ^{210}Pb-dating techniques to estimate mass accumulation rates and ages of sediments. The activity of ^{210}Pb was determined for at least 15 samples in each core using α-spectrometric analysis by Flett Research. An exponential model was fit to the ^{210}Pb activities and cumulative downcore dry sediment mass to determine mass accumulation rates (modified from refs. 4 and 5), assuming a constant accumulation rate. We simultaneously estimated the level of supported ^{210}Pb in the sediments (P_{sup}), as well as the intercept of unsupported ^{210}Pb (α) and the mass accumulation rate (ω) (in $\mathrm{g{\cdot}cm^{-2}{\cdot}yr^{-1}}$) based on known decay rates of ^{210}Pb (decay constant $\lambda = 0.0311\ \mathrm{y}^{-1}$):

$$P_i = \alpha e^{-\lambda m_i/\omega} + P_{\mathrm{sup}}, \qquad (1)$$

where P_i is the measured ^{210}Pb activity and m_i the cumulative down-core dry mass associated with sample i. For some of the cores, the ^{210}Pb profile was flat for the most recent samples or peaked subsurface. This can occur due to mixing of the relatively unconsolidated sediments at the surface. In these cases, we excluded the surface samples when fitting the model if it improved the R^2 of the model fit. Dating models for all cores were fit using generalized nonlinear least squares with the *nlme* package (6) in R (7), with the variance of the errors modeled as a power function of the fitted activities.

Activities of ^{210}Pb can be used to date sediments back to ∼1860. Below this horizon, the point estimate of ω was used to extrapolate sediment ages backward in time based on the cumulative down-core sample mass. This assumes a constant mass accumulation rate through time, a reasonable assumption given the excellent fits of ^{210}Pb activity versus cumulative sample mass in the surface sediments of these lakes (*Results* and Fig. S1). We visually assessed whether there were changes in the C:N ratio through the core that can be indicative of changes in watershed processes or major sedimentation events that could affect this assumption. Two lakes (High and Gechiak, both in the Togiak National Wildlife Refuge) showed substantial discontinuities in C:N ratios around 1850 and 1650, respectively, and were thus excluded from further analysis.

Cores from Karluk, Red, Akalura, Becharof, Ugashik, and Packers lakes were published previously (8–10), and the dating methodology differed for these lakes. Namely, chronologies were determined using a combination of a constant rate of supply model based on ^{210}Pb activities (4), ^{14}C dates, and the presence of volcanic tephra. The same procedure was used to date the Iliamna and Naknek cores.

Quantifying Uncertainty in Sediment Deposition Dates. Uncertainty in sediment deposition dates can be assessed by using, for example, the 90% confidence intervalss of ω to calculate the chronologies for each core. It should be noted that these error estimates only incorporated model uncertainty, and not uncertainty associated with potential changes in sedimentation rates before ∼1860, and thus are an underestimate of the true uncertainty in sediment ages.

Confidence intervals for the mass accumulation rates (ω) were obtained using likelihood profiles to reflect model estimation uncertainty (11). We also generated confidence intervals using a parametric bootstrap approach (11), whereby we generated bootstrapped ^{210}Pb data using the measurement error for each sample and then refit the exponential model to these bootstrapped data to estimate the mass accumulation rate. We repeated this 1,000 times and used the 5th and 95th percentiles as confidence limits for ω. For all cores, the bootstrapped 90% confidence intervals for ω were narrower than the 90% confidence intervals calculated based on likelihood profiles, and so we present only the profile-based confidence intervals as a more conservative estimate of the error associated with the estimation of ω based on ^{210}Pb (Table S1).

Chronologies based on multiple markers were assumed to have less error than those based on ^{210}Pb alone. For the cores with preexisting chronologies (listed above), dating errors were thus assigned at a level corresponding to the 25th percentile of errors observed among the ^{210}Pb-dated cores.

Simulation of Dating Errors in Principal Component Analysis. Because errors in the estimates of sediment deposition dates can affect the temporal coherence of fluctuations, and thus the detection of common trends using principal component analysis (PCA), we used a simulation analysis to assess how dating errors may affect our results. In particular, we asked how likely is it to find no significant PCs, given that the true patterns in δ^{15}N are synchronous across lakes? We simulated 16 cores with identical patterns in δ^{15}N characteristic of a typical core (Nunavaugaluk Lake), but with sampling intervals and dating errors matching the true cores. For each core, we then drew a random value of ω from a distribution defined by the likelihood profile of ω for that core and re-estimated the sediment deposition dates based on that mass accumulation rate. Cores were then interpolated to a common 5-y interval, a PCA was performed on the period 1530–1900, and the number of significant PCs was determined using the broken-stick method. This procedure was repeated 1,000 times to generate a distribution of expected significant PCs, given errors in the estimated sediment deposition dates. At least one significant PC was found in all simulations, and at least two significant PCs were found in 98% of the simulations.

Simulation of Dating Errors in Wavelet Analysis. To test the robustness of our global wavelet spectra to dating errors, we repeated the analysis for each core using instead the 5th and 95th percentiles of ω

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to calculate sediment ages. These power spectra are shown in gray in Fig. 4.

Detecting High- Versus Low-Frequency Variation. High-frequency variation in the cores may be masked by sediment mixing, the sampling interval, and interpolation. To test whether the relative ability to detect variation at interdecadal versus centennial time scales was affected by these processes, we simulated 400-y time series with known periodicities at 10 y, either 20, 30, 40, or 50 y, 80 y, 120 y, and 200 y (i.e., five periodicities per simulated time series). Random error was added, and time series were smoothed with a 10-y running mean (to mimic sediment mixing and the sampling process) and then interpolated on a 5-y interval. We then estimated the global wavelet power spectrum and compared this to the spectrum of the original (unsmoothed, uninterpolated) time series. This test showed a slight decrease in the power associated with periods of 20–30 y, but no change in the power associated with periods of 40 y or greater. The 10-y periodicity could not be detected, as this was the minimum scale of the wavelet analysis. Variation on time scales of 40 y or greater should thus be well detected, whereas power at 20- to 40-y time scales may be underestimated.

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10. Gregory-Eaves I, Finney BP, Douglas MSV, Smol JP (2004) Inferring sockeye salmon (*Oncorhynchus nerka*) population dynamics and water quality changes in a stained nursery lake over the past ~500 years. *Can J Fish Aquat Sci* 61(7):1235–1246.
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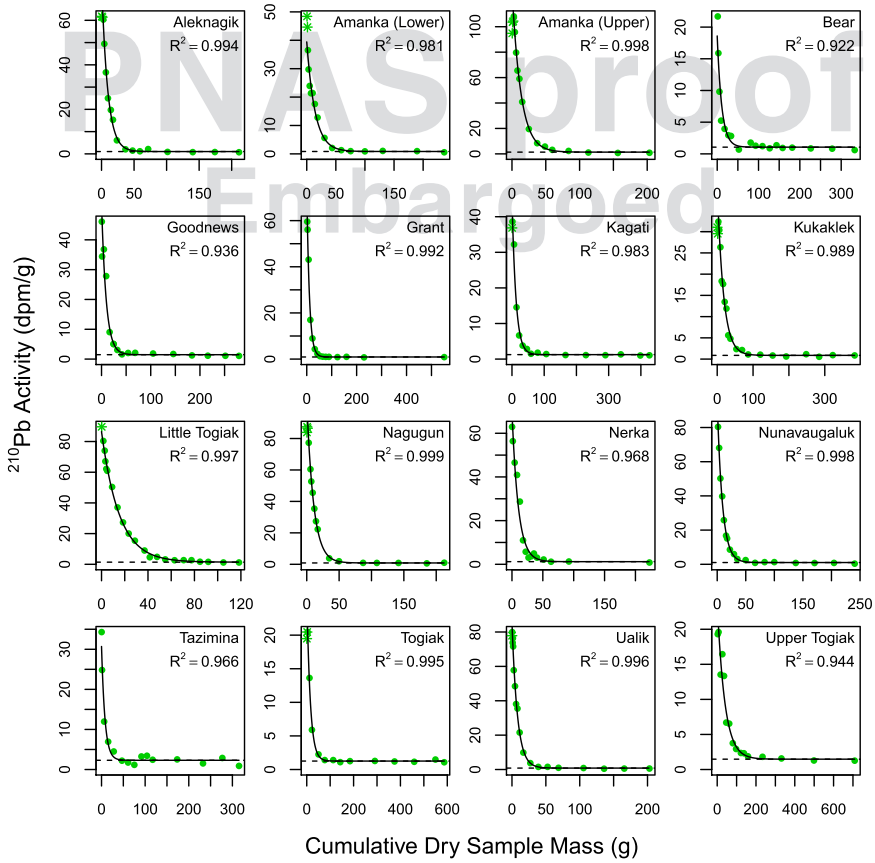

Fig. S1. Fits of an exponential decay model (Eq. **1**) to total ^{210}Pb activities and cumulative down-core sample mass. Surface data points indicated by stars were excluded from the model fit based on an improvement in model R^2. Dashed lines indicate the estimated level of supported ^{210}Pb (P_{sup}) for each core.

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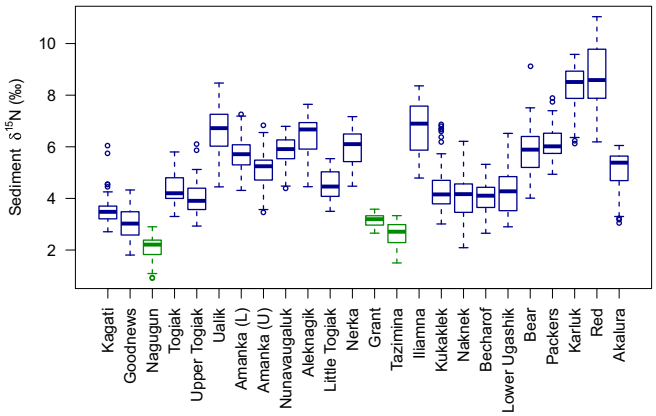

Fig. S2. Distributions of $\delta^{15}N$ measured in sediments estimated to have been deposited from 1500 to present. Reference lakes are shown in green.

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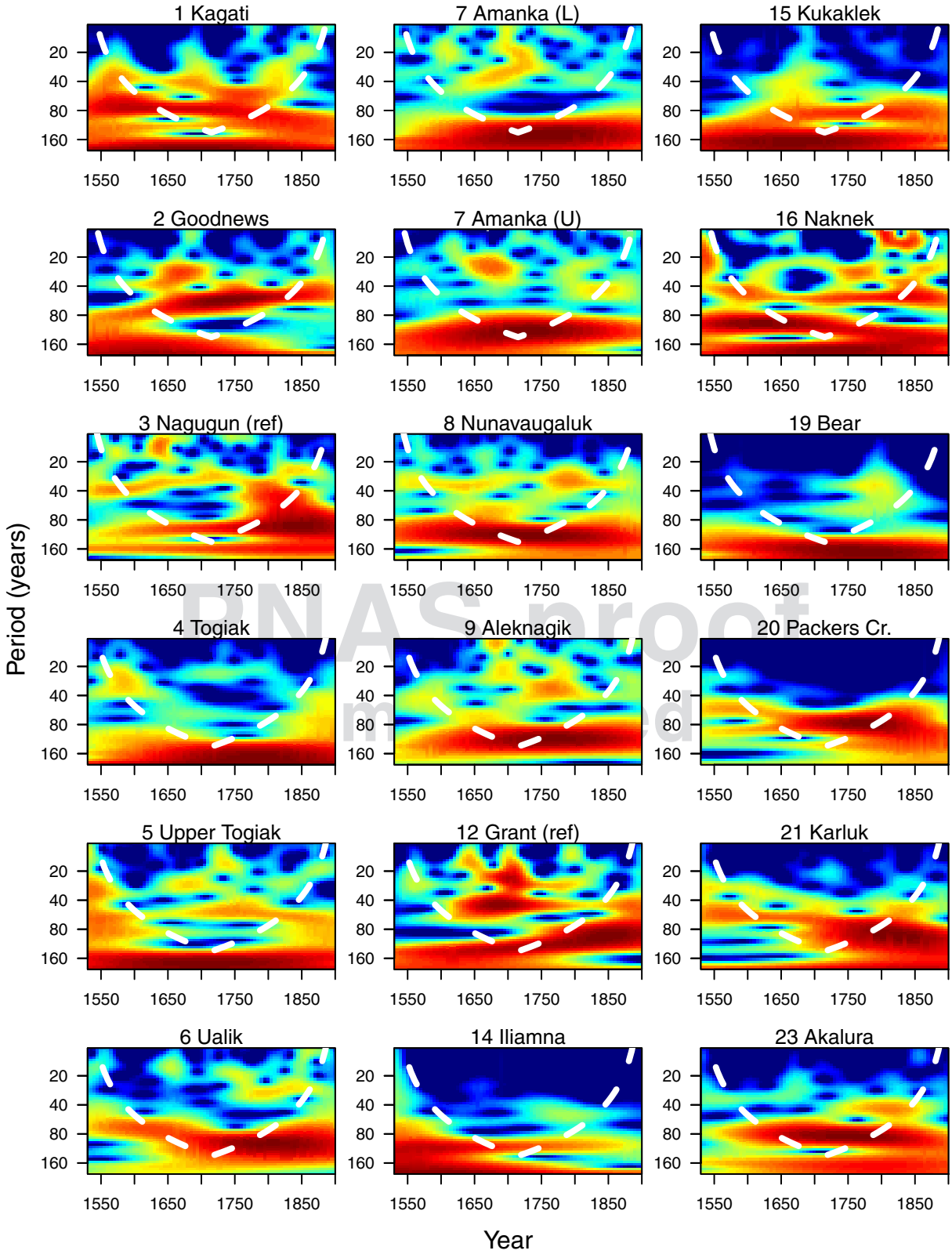

Fig. S3. Wavelet power spectra of 5-y interpolated sedimentary $\delta^{15}N$ time series. Color indicates power, ranging from dark blue (low power) to dark red (high power). Areas outside the white dashed lines indicate where edge effects may influence the decomposition.

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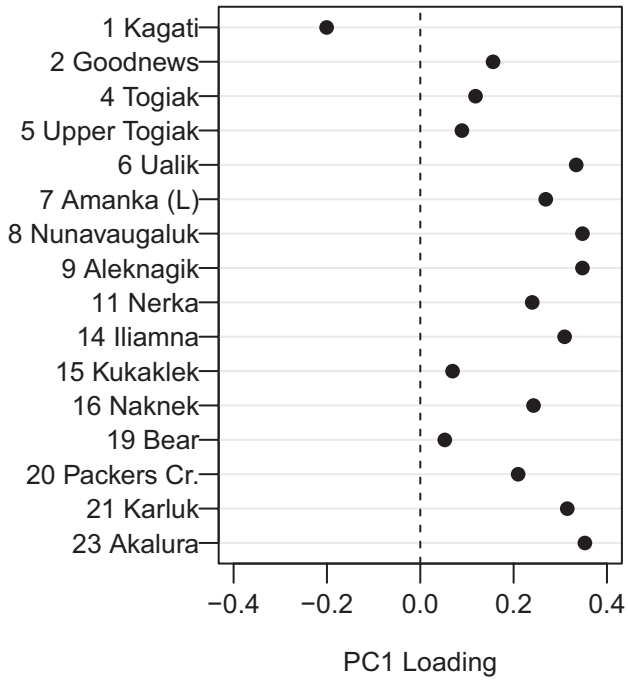

Fig. S4. Lake-specific loadings on PC1 for the PCA of $\delta^{15}N$ time series from 1530 to 1990.

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Table S1. Exponential dating model fits based on ^{210}Pb activity in the core

Lake	Year cored	Bottom date	α (dpm·g^{-1})	P_{sup} (dpm·g^{-1})	ω (90% CI) (g·cm^{-2}·yr^{-1})	*n*	R^2
Aleknagik	2007	1219	77.03	1.04	0.0088 (0.0080, 0.0097)	15 (2)	0.99
Amanka (Lower)	2007	1438	38.57	0.84	0.0133 (0.0120, 0.0148)	15 (2)	0.98
Amanka (Upper)	2007	1466	128.39	1.37	0.0123 (0.0115, 0.0132)	14 (3)	1.00
Bear	2004	956	17.53	1.06	0.0105 (0.0083, 0.0149)	18 (0)	0.92
Goodnews	2008	1060	50.63	1.47	0.0089 (0.0073, 0.0102)	17 (0)	0.94
Grant	2002	305	74.53	0.91	0.0098 (0.0093, 0.0103)	15 (0)	0.99
Kagati	2008	889	43.88	1.25	0.0115 (0.0102, 0.0145)	15 (1)	0.98
Kukaklek	2004	1299	40.39	0.87	0.0161 (0.0148, 0.0180)	19 (2)	0.99
Little Togiak	2003	1754	84.98	1.40	0.0143 (0.0136, 0.0150)	21 (1)	1.00
Nagugun	2006	1353	102.96	0.86	0.0099 (0.0096, 0.0103)	14 (3)	1.00
Nerka	2000	1303	68.66	1.21	0.0096 (0.0085, 0.0127)	15 (0)	0.97
Nunavaugaluk	2007	1151	94.17	1.03	0.0086 (0.0082, 0.0091)	18 (0)	1.00
Tazimina	2003	745	28.39	2.30	0.0074 (0.0050, 0.0106)	15 (0)	0.97
Togiak	2005	720	25.39	1.26	0.0138 (0.0122, 0.0160)	13 (2)	1.00
Ualik	2007	1147	84.58	0.83	0.0075 (0.0071, 0.0080)	18 (1)	1.00
Upper Togiak	2006	1408	22.43	1.48	0.0364 (0.0311, 0.0419)	16 (0)	0.94

The "bottom date" shown is the estimated date of the oldest layer in the core that was analyzed for $\delta^{15}N$. The estimated model parameters are the intercept (α), the estimated activity of supported ^{210}Pb in the core (P_{sup}), and the mass accumulation rate (ω). Confidence intervals are based on likelihood profiles. Also shown are the numbers of ^{210}Pb samples (*n*) used to fit the model, and, in parentheses, the number omitted from the surface layer of each core due to disequilibria. The sum of these two is the total number of ^{210}Pb samples analyzed for each core. CI, confidence interval.

Q:2

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