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Patterns of early lake evolution in boreal landscapes: A comparison of stratigraphic inferences with a modern chronosequence in Glacier Bay, Alaska

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Abstract

The chronosequence approach, which infers temporal patterns of environmental change from a spatial array of modern sites, has been a major tool for studying successional processes. A model of early lake ontogeny in boreal landscapes, developed from a chronosequence of lakes in Alaska, suggests that long-term soil development and related hydrological change produce a loss of alkalinity and base cations, a decrease in pH, an increase in DOC and a transient increase followed by a decrease in lakewater nitrogen concentrations over time. We compare this model of lake ontogeny with patterns of change reconstructed from diatom assemblages in 10 sediment cores from the same region. Lakewater pH declined in the majority of lakes, but the pattern, rate and magnitude of decline varied considerably among sites, apparently related to local differences in hydrologic setting. Inferred trends in nitrogen concentration over time are not spatially uniform and appear to vary because of local differences in vegetation history. Thus, patterns of early lake ontogeny may be spatially heterogeneous over timescales of many hundreds of years, even within relatively small geographic areas.

Keywords: Lake, paleolimnology, diatoms, succession, boreal, chronosequence, stratigraphy, Alaska

Introduction

Long-term ecological change can be studied via several approaches, including direct observation, inferences from paleoecological data and comparisons derived from a chronosequence of contemporary sites; each has inherent strengths and weaknesses. Observational data that span periods much longer than 100 years are extremely limited both in number and spatial coverage and cannot address patterns that take longer to develop. Moreover, in contemporary observational data, it is difficult to disentangle the anthropogenic influence from patterns that would occur in the absence of significant human modification of the landscape (Renberg *et al.*, 1994). The chronosequence approach can be used where sites of differing age exist within a relatively uniform environmental setting (Cooper, 1923; Chapin *et al.*, 1994; Chadwick *et al.*, 1999). Here, the fundamental assumption is that a spatially arrayed set of sites of increasing age replicate temporal patterns

exhibited by a single location during its history. Such an assumption may not be wholly valid, however, either because modern environments do not adequately capture the range of environments present in the past, because extrinsic factors have not been adequately controlled within the chronosequence, or because stochastic processes play a major role in temporal trajectories. The most commonly used approach for understanding landscape evolution is reconstruction based on paleoecological data, which in the best circumstances can be used to describe patterns over thousands of years and at high temporal resolution. However, paleoecological inferences are dependent upon a well-developed knowledge of the processes that affect the proxy record. Many early post-glacial diatom assemblages, for example, are dominated by benthic *Fragilaria* species. However, because of the paucity of modern analogues, it is unclear whether this assemblage is a product of low nutrient concentrations or high light penetration or both (Haworth, 1976; Wright, 1980).

Hypotheses regarding factors that control the direction and rate of lake evolution over scales of decades to millennia have been generated primarily from stratigraphic data, because relatively few recently formed glacial lakes exist to serve as modern analogues. Pioneering paleolimnological studies from glacially formed lakes in temperate regions emphasized temporal changes in lake nutrient concentrations and associated changes in productivity and hypothesized that over time lakes become enriched (Deevey, 1942). Subsequent studies in boreal regions suggested that, in areas of base-poor soils, lakes become progressively more acidic as a result of the leaching of base cations from catchment soils (Round, 1961; Pennington *et al.*, 1972; Whitehead *et al.*, 1989; Ford, 1990), with a concomitant increase in water color associated with the buildup of soil organic matter (Hansen and Engstrom, 1996; Pienitz *et al.*, 1999). In most of these studies, a relatively small number of lakes has been analyzed, such that the degree of spatial heterogeneity in patterns and rates of change has not been assessed.

A few relatively accessible regions of active glacier advance and retreat have enabled researchers to study the early stages of aquatic development through observation of modern systems (Bradbury and Whiteside, 1980; Matthews, 1992). One such region is Glacier Bay National Park in southeast Alaska, where a chronosequence of recently formed lakes was used to characterize long-term limnological development using a space for time substitution (Engstrom *et al.*, 2000). In this paper, we compare the inferences regarding boreal lake ontogeny derived from the chronosequence approach with detailed reconstructions of limnological trends based on sediment cores from individual lakes. The limnological histories are reconstructed from cores based on transfer functions developed from the relationship between modern diatom assemblages and water-chemistry variables. We use the comparison to evaluate whether the cores follow the trajectory predicted by the chronosequence, to evaluate the degree of spatial heterogeneity in pattern and rate of change, and to suggest some of the limnological controls on early diatom succession in late-glacial and postglacial stratigraphic sequences. We also present a detailed description of the diatom distribution in the modern chronosequence, which is used as a foundation for quantitative reconstruction of water-chemistry trends from stratigraphic data.

Environmental setting

Glacier Bay National Park and Preserve is located in southeastern Alaska, about 60 km northwest of Juneau. It was set aside as a National Monument in 1925, primarily for scientific observation of glacial and ecological processes. At the core of the park is the Glacier Bay fjord, presently over 100 km long and 20 km wide, with numerous arms and tributaries (Figure 1). Glacier Bay is flanked by the Chilkat Mountains to the east and the Fairweather Mountains to the west, with the highest peaks reaching over 4600 m in elevation. The bedrock geology of the region is varied (Brew *et al.*, 1978), although surficial deposits are generally comprised of calcareous drift, predominantly outwash overlain by a thin veneer of till. Glacial ice, which filled the Glacier Bay fjord during the Neoglacial period, began a catastrophic retreat about 220 years ago, exposing land surfaces for biotic colonization and primary succession. Deglaciation began earlier to the west, along Lituya Bay and the Outer Coast. Along the Glacier Bay fjord itself the position of the ice at various points in time (Figure 1) is known from reports of early explorers and scientists, including Vancouver in 1794 and John Muir in the late nineteenth century. In the two centuries since

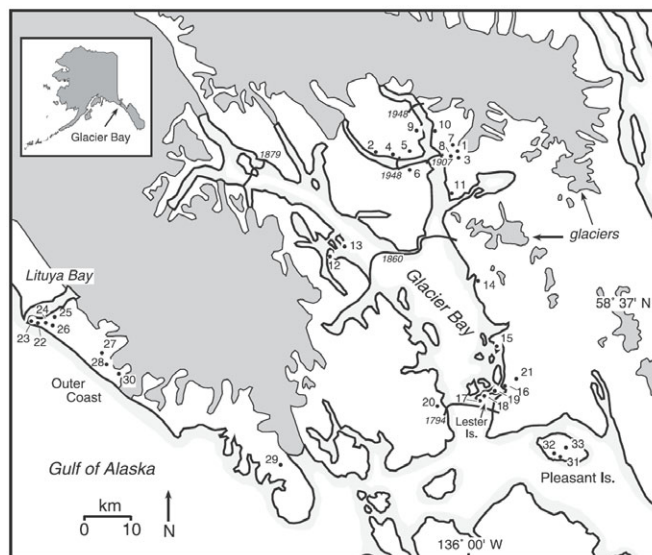


Figure 1 Map of Glacier Bay National Park and Preserve showing the lake sites discussed in the text. Lake numbers correspond to names in Table 1. Neoglacial ice margins are marked by dated isochrons.

Vancouver first observed the terminal position of the ice margin, the ice has receded over 100 km, and today nearly all of the tide-water glaciers are grounded. Glacier Bay National Park has been the site of classic studies of both glacial geology (Wright, 1887; Reid, 1896) and ecological processes (Cooper, 1923; Crocker and Major, 1955; Lawrence, 1958).

In the classic view of primary terrestrial succession at Glacier Bay, the recently deglaciated land surfaces are initially colonized by scattered mosses, lichens, mountain avens (*Dryas drummondii*), fireweed (*Epilobium latifolium*), dwarf willows (*Salix* sp.), and cottonwood (*Populus balsamifera* v. *trichocarpa*), and dense colonies of *Dryas* soon spread across the landscape. Within 20–40 years of deglaciation, shrub thickets of alder (*Alnus crispa* v. *sinuata*), as well as willow and cottonwood, develop, which in turn are replaced by an overstorey of spruce (*Picea sitchensis*) and cottonwood. Closure of the spruce forest canopy occurs after about 75–100 years and is accompanied by the appearance of western and mountain hemlock (*Tsuga heterophylla* and *T. mertensiana*), with a dense groundcover of pleurocarpous mosses. Muskegs have expanded to varied degrees on older surfaces along the Outer Coast and Lituya Bay, with open mires interspersed with stunted woodlands of western and mountain hemlock, lodgepole pine (*Pinus contorta*) and Alaskan yellow cedar (*Chamaecyparis nootkatensis*).

The Glacier Bay region has a maritime climate, with small annual temperature variations, frequent cloud cover, and heavy precipitation. Lowland areas have mean annual temperatures near 5°C, with summer and winter extremes no greater than 24°C and –23°C, respectively. Precipitation is poorly documented but ranges from about 150 to 300 cm yr⁻¹ near sea level to an estimated 600 cm yr⁻¹ at high elevations in the Fairweather range (Loewe, 1966).

We studied 33 lakes formed by glacial retreat (Figure 1), which range in age from 10 years to >10,000 years. The lakes are in lowland areas at the foothills of the mountains, at elevations <200 m. They are small (3–16 ha), of moderate depth (3–18 m), and are in small primary catchments receiving no drainage from other lakes. Eleven of the lakes are <100 years in age, 10 range from 100 to 250 years, nine range from c. 350 to 1,200 years, and three lie outside the Neoglacial ice limit and were formed about 13,000 years ago.

Methods

Field sampling

Each lake in the chronosequence was sampled for water chemistry in July 1988, May 1989, and September 1990. Supplemental data are available for 17 of the lakes from collections in three previous years. Samples were taken from the pelagic region with a Kemmerer water bottle at a depth of 1 m. pH and conductivity were measured in the field, and water was filtered for chlorophyll analysis. Samples were filtered and frozen for subsequent analysis of DOC, dissolved Si, and major anions, and additional unfiltered water samples were transported to the laboratory for analysis of total phosphorus (TP), total nitrogen (TN), and major cations. Samples for nitrogen analysis were acidified.

Sediment cores were collected from the deep-water zone of each lake with a piston corer mounted on rigid drive rods. Cores were sectioned in the field at 0.5–1.0 cm intervals. Samples were stored in polypropylene jars and kept refrigerated until subsampled. The uppermost core interval was used as a diatom surface-sediment sample to represent temporal integration of several years of sediment accumulation and spatial integration of both littoral and open-water habitats. We were unable to recover a sediment core or surface sample from one lake, Casement 1.

Water chemistry

Color and alkalinity were measured within 12 hours of sample collection with a Hach color comparator and by Gran titration, respectively. Cations were analyzed by direct-current plasma-atomic-emission spectrometry (DCP-AES), anions by ion chromatography, and pigments (chlorophyll- α and fucoxanthin) by HPLC. TP and TN were measured by colorimetric methods following, respectively, acid and alkaline persulphate digestion.

Diatom analysis and sediment dating

Diatom assemblages were analyzed from all surface samples and stratigraphically from sediment cores for 10 lakes of varied age: two lakes that are approximately 100 years in age (Spokane Cove, Blue Mouse), four lakes about 200 years in age (Lester 1, Lester 2, Lester 3, Bartlett L), two lakes in the Lituya Bay area about 350 years in age (Paps, Harbor Point) and two lakes c. 1,000 years in age on the Outer Coast (Dagelet, Brady). Subsamples of sediment were prepared for diatom analysis by oxidizing organic matter in hot nitric acid and potassium dichromate for 15 minutes, followed by repeated rinsing with distilled water to remove oxidation by-products. Prepared sediment was dried onto cover-slips, and cover-slips were mounted on slides with Naphrax. Diatoms were counted on an Olympus BH-2 microscope at a magnification of $\times 1000$ with an oil immersion objective (N.A. = 1.4). A minimum of 500 individuals was counted in the surface samples and 400 in core samples. Cores were analyzed for ^{210}Pb by ^{210}Po distillation and alpha spectrometry methods, and dates were calculated according to the c.r.s. (constant rate of supply) model (Appleby and Oldfield, 1978). Basal sediments from older sites on the Outer Coast were also dated by ^{14}C .

Data analysis

The chronosequence lakes contained a total of 390 diatom taxa. For statistical analysis and transfer-function development, we excluded rare taxa and used only taxa present in two or more lakes and with a relative abundance of at least 0.5% in any chro-

nosequence or fossil sample. This resulted in a final data set of 223 diatom taxa. Water-chemistry data are mean values. Many of the chemical variables were positively skewed and were either $\log_{10}(x)$ (K, Na, Ca, Mg, Fe, Al, Cl, SO_4 , chlorophyll- α), $\log_{10}(x + 1)$ (color), $\log_{10}(x + 32)$ (alkalinity), or square-root (conductivity, dissolved silica, TN, TP, and fucoxanthin) transformed prior to statistical analyses.

Principal components analysis (PCA) (Jolliffe, 1986) and cluster analysis (single linkage method) (Everitt and Dunn, 1991) of a correlation matrix of the transformed chemical data were used to determine the major patterns of chemical variation in the chronosequence and to define groups of highly correlated variables reflecting underlying environmental gradients.

The relationship between diatom distribution and water chemistry was explored using canonical correspondence analysis (CCA) and detrended CCA (ter Braak, 1986). Data sets, such as that developed for the chronosequence lakes, often contain redundancy in chemical information. We therefore used forward selection and associated Monte Carlo permutation tests (999 unrestricted permutations; $p \leq 0.05$) to select a subset of variables from each group of correlated variables that account for significant and independent fractions of variation in the diatom data. Probability levels in the forward selection were adjusted using the Bonferroni inequality (p/m , where m is the number of variables tested; Manly, 1991). The strength and relative independence of the different environmental gradients were assessed using a series of partial CCAs to partition the total variation in the diatom data into components representing (i) the unique contribution of individual gradients, (ii) the contribution of interaction between pairs of variables and (iii) unexplained variance (Borcard *et al.*, 1992). This approach gives quantitative information on the relative importance of the different environmental gradients as factors explaining the variation in diatom abundances (cf. Okland and Odd, 1994). All ordinations and cluster analyses were performed using the programs CANOCO (version 4.0; ter Braak and Smilauer, 1998) and MINITAB (Ryan and Joiner, 2000), respectively.

Diatom-based transfer functions or inference models were developed using the method of weighted averaging (WA) with inverse deshrinking (ter Braak and VanDam, 1989; Birks *et al.*, 1990). The performance of the transfer functions is reported in terms of the root mean square of the error (RMSE) (observed-inferred), the squared correlation coefficient (r^2) between observed and inferred values, and the jackknife RMSE, or RMSE of prediction (RMSEP; ter Braak *et al.*, 1993). The first two statistics give a measure of the "apparent" error, while the latter is a more reliable indicator of the true predictive ability of the transfer function, because it is less biased by sample resubstitution (Dixon, 1993). As a further indication of the reliability of our environmental reconstructions, we also calculated the dissimilarity between each fossil sample and its closest floristic analogue in the chronosequence lakes. We then used squared chord distance (d^2) as a measure of dissimilarity (Overpeck *et al.*, 1985) and define a good analogue as a fossil sample having a d^2 less than the critical value defined by the fifth percentile of the distribution of the 992 distances among all modern samples (Bartlein and Whitlock, 1993). We consider reconstructions for fossil samples with good analogues in the chronosequence to be more reliable. Weighted averaging (WA) and analogue calculations were performed using the programs CALIBRATE (Juggins and ter Braak, 1992) and MAT (Juggins, unpublished), respectively.

Table 1 Environmental data for lakes described in text (site numbers are linked to the locations shown in Figure 1)

No.	Site	Age (years)	pH	Colour (Pt-Co)	DOC (mg L ⁻¹)	Cond. (µS cm ⁻¹)	Ca (mg L ⁻¹)	Mg (mg L ⁻¹)	Na (mg L ⁻¹)	K (mg L ⁻¹)	Alk (µeq L ⁻¹)	Cl (mg L ⁻¹)	SO ₄ (mg L ⁻¹)	d-Si (mg L ⁻¹)	total-N (ppb)	total-P (ppb)	chl. <i>a</i> (ppb)
1	Casement 1	10	8.18	0	1.02	157	28.16	1.81	1.27	1.64	1.17	0.49	20.13	1.30	55	5.5	0.04
2	Plateau 2	10	7.93	0	1.29	57	9.70	0.52	0.46	0.45	0.51	0.33	1.09	0.58	114	9.3	1.18
3	Casement 2	20	8.35	1	1.83	199	34.69	3.03	2.64	1.55	1.77	0.44	12.37	2.76	161	3.1	0.23
4	Plateau-1	20	8.14	0	1.01	199	36.49	1.51	1.91	0.72	1.46	0.49	22.56	1.89	199	8.6	0.24
5	Burroughs	25	8.11	0	1.33	204	37.07	1.37	1.88	0.53	1.19	0.44	36.00	2.21	111	4.9	0.23
6	Wachusett	30	8.23	0	0.91	161	22.77	2.40	4.54	1.06	1.08	0.71	19.78	0.96	168	5.2	0.18
7	Seal River	30	8.11	0	2.02	262	49.01	2.60	0.84	1.54	2.44	0.42	9.77	1.98	264	3.2	0.32
8	Forest Creek	35	8.24	2	1.73	255	52.56	4.14	2.93	1.60	2.73	0.52	14.98	2.97	146	4.1	0.25
9	Wolf Creek	45	7.89	8	2.21	61	10.68	0.43	0.48	0.67	0.53	0.70	16.75	0.30	209	9.2	0.38
10	Nunatak	50	8.17	2	1.57	199	36.16	2.13	1.48	1.01	1.55	0.70	5.87	2.43	336	5.2	0.28
11	Klotz Hills	80	8.05	6	3.62	243	44.09	2.26	3.47	1.30	2.41	1.68	13.7	2.28	271	6.0	0.39
12	Charpentier	100	8.04	8	2.47	136	24.17	1.94	1.56	0.40	1.34	0.88	1.37	1.16	213	5.7	0.47
13	Blue Mouse	110	7.47	36	5.42	75	12.40	1.08	1.30	0.87	0.63	1.21	1.63	0.64	338	8.1	0.41
14	Spokane Cove	120	8.06	4	2.10	251	40.84	6.48	1.59	0.98	2.26	0.91	13.83	1.70	284	3.7	0.21
15	Hutchins Bay	160	8.29	5	2.78	134	20.70	3.14	1.17	1.38	1.19	1.37	5.14	1.03	216	4.9	0.53
16	Bartlett River	180	8.15	4	3.24	87	15.10	1.35	1.01	0.84	0.82	1.52	1.96	0.18	260	9.5	0.34
17	Lester 1	180	6.27	38	5.12	21	1.31	0.36	1.67	0.50	0.03	3.25	0.64	0.03	295	9.9	0.30
18	Lester 2	180	7.70	25	4.88	75	11.74	1.08	1.70	0.88	0.61	2.77	1.14	0.14	266	10.5	1.05
19	Lester 3	180	7.91	8	3.24	238	41.81	3.02	1.85	2.66	2.25	2.61	2.58	1.90	222	7.5	0.63
20	Ripple Cove	190	7.97	2	1.69	145	25.12	0.96	1.80	0.37	1.03	2.87	12.46	1.46	235	3.8	0.67
21	Bartlett	220	6.19	2	2.11	8	0.56	0.13	0.67	0.13	0.01	1.45	0.34	0.02	122	7.9	0.28
22	Paps	350	6.55	80	7.97	52	1.96	1.30	5.59	0.53	0.07	9.81	2.52	0.23	147	5.1	0.12
23	Harbor Point	350	5.62	93	8.69	63	0.92	1.47	7.75	0.43	-0.02	14.39	2.17	0.08	270	9.0	0.45
24	Red Loon	350	7.14	15	2.65	55	3.92	1.70	3.58	0.66	0.26	4.94	2.55	1.35	220	2.6	-
25	Coal Creek	350	7.83	13	2.08	213	29.86	4.84	6.12	0.95	1.69	3.76	14.84	2.54	138	5.9	0.49
26	Huscroft	400	7.27	28	3.72	66	7.14	1.39	3.38	0.98	0.61	5.29	3.73	1.80	215	5.5	0.35
27	Crillon	400	7.19	25	5.08	70	9.71	1.02	2.44	0.55	0.53	3.64	1.77	1.37	167	3.8	0.07
28	Dagelet	1100	6.18	33	2.87	21	0.47	0.68	2.04	0.13	0.02	3.57	0.58	0.05	167	3.9	0.08
29	Brady	1200	6.34	33	2.32	15	0.85	0.30	1.25	0.25	0.03	1.51	0.85	0.11	154	5.3	0.11
30	LaPerouse	2700	6.96	55	4.52	55	5.53	1.17	4.11	0.15	0.40	3.24	1.08	1.73	138	10.2	0.30
31	Pleasant 1	12 000	6.18	81	10.66	27	1.85	0.74	2.85	0.22	0.06	4.02	0.75	0.18	263	4.1	0.70
32	Pleasant Muskeg	13 000	4.74	143	13.71	19	0.76	0.28	1.30	0.09	-0.03	1.78	0.25	0.12	396	7.7	1.23
33	Pleasant 3	13 000	5.40	170	12.14	18	1.62	0.33	1.56	0.12	0.01	1.78	0.30	0.13	273	6.3	1.21

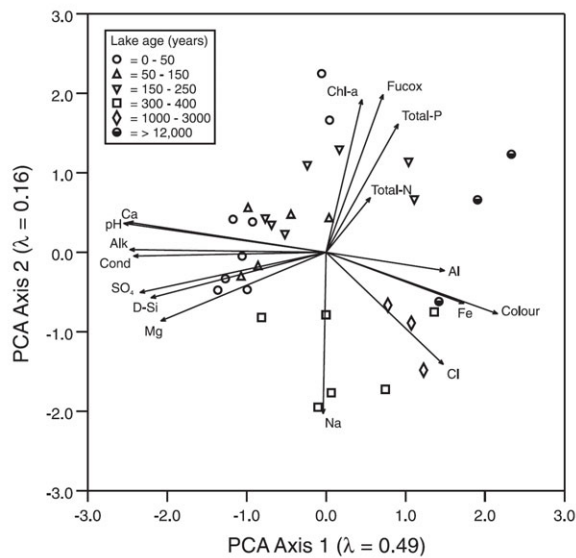


Figure 2 Principal components analysis correlation biplot of the chemical data for the chronosequence lakes.

Results

Water chemistry

A summary of major water-chemistry variables is presented in Table 1. General patterns in the water-chemistry data from the modern lakes are shown in a principal components analysis (PCA) correlation biplot (Figure 2). The major gradient in the water-chemistry data is related to pH and alkalinity and separates lakes with high pH, alkalinity, conductivity, and concentrations of Ca, Mg, SO₄, and dissolved-Si from more dilute sites. The dilute sites are also colored with organic acids and show high concentrations of Fe and Al. The second axis is a nutrient gradient and separates lakes with high TP, TN, chlorophyll-*a* (chl-*a*), and fucoxanthin from those with lower concentrations. The second axis also reflects the influence of sea spray and separates the sites on the Outer Coast, with high concentrations of Na and Cl, from lakes along the Glacier Bay fjord, which are in more protected locations.

Some of these patterns in water chemistry (Figure 2) are clearly related to lake age. The more dilute lakes (with low pH and alka-

linity and higher concentrations of organic acids, Al, and Fe) are primarily those >250 years in age, on the Outer Coast, and Pleasant Island. Only two younger lakes (c. 200 yr) have relatively low pH (Bartlett Lake, Lester 1) and are distinct from lakes of similar age. Highest concentrations of DOC (color) occur in the older lakes on the Outer Coast and on Pleasant Island, where peatlands occupy parts of the lake catchments. Nutrient and pigment concentrations are not as strongly related to lake age, but some trends are apparent. With the exception of lakes on Pleasant Island, total nitrogen concentrations (TN) are highest after 50 years and lowest in sites 300–3,000 years in age (Engstrom *et al.*, 2000). The Pleasant Island sites (>12,000 years in age) have very high TN concentrations. Chl-*a* concentrations are extremely low in all the lakes (< 3 µg L⁻¹) but to some extent parallel trends in TN. Total phosphorus (TP) concentrations are less than 10 µg L⁻¹ and show no clear trends with lake age (Engstrom *et al.*, 2000).

Diatom/water-chemistry relationships

The distribution of many diatom taxa is related to lake age (Figure 3). *Achnanthes ploensis* is present only in lakes less than 50 years in age, and *Amphora perpusilla* is abundant in many lakes less than 120 years but is rare in older sites. The benthic *Fragilaria* spp. are not present in the youngest lakes but appear in abundance after c. 50 years. A number of taxa occur in many of the sites in the lower and east arms of Glacier Bay, including *Cymbella microcephala*, *Navicula cryptocephala*, and *Navicula radiosa* v. *tenella*, but not in older sites, whereas taxa such as *Fragilaria virescens* v. *exigua*, *Cymbella gauemanii*, and acidophilous *Aulacoseira* spp. are present only in the older lakes of the Outer Coast area and on Pleasant Island. *Achnanthes minutissima* is one of the few taxa that shows no age-related trends, and the *Cyclotella stelligera*/glomerata/pseudostelligera group appears in lakes of varied age, although they are abundant only in the oldest lakes with high TN.

Results from the PCA and cluster analysis (not shown) reveal groupings of chemical variables that represent four underlying environmental gradients. These are gradients of (1) catchment weathering and hydrology (pH, alkalinity, conductivity, Ca, Mg, SO₄, and Si), (2) sea-spray (Na and Cl), (3) development of organic soils and subsequent paludification (color, DOC, Al, and Fe), and (4) trophic status (TP, TN, chl-*a*, and fucoxanthin). CCA of the diatom data, with forward selection and considering each of the four gradients

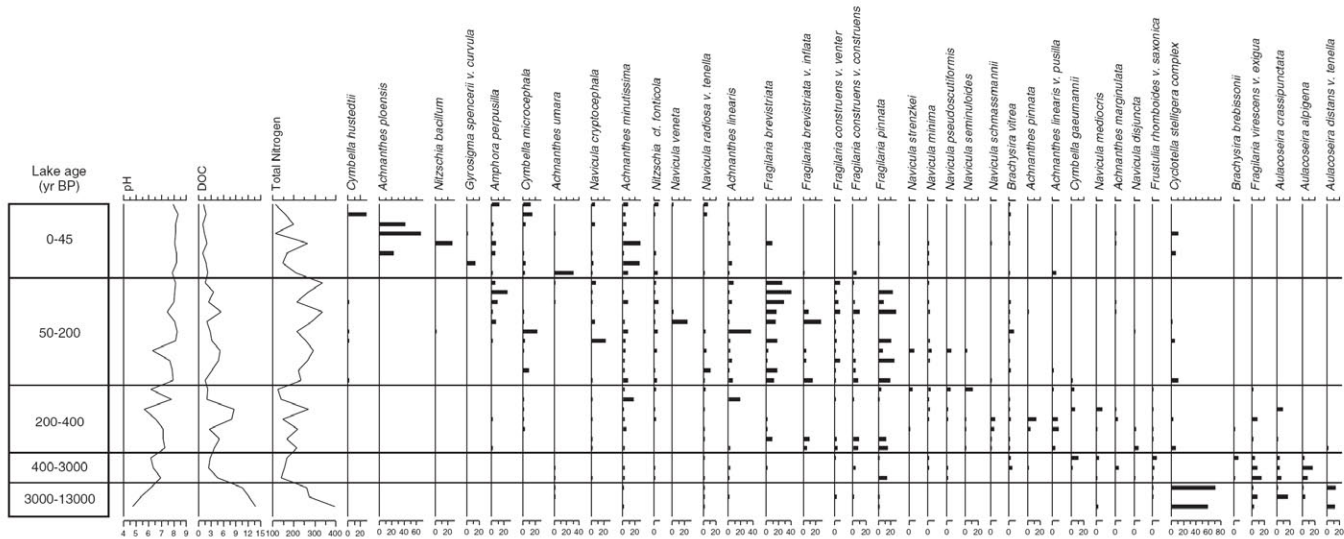


Figure 3 Most abundant diatom taxa in the modern surface samples. Lakes are arrayed in order of increasing lake age.

separately, indicated that these gradients could be adequately represented, in a statistical sense, by just one (trophic status) or two (weathering, organic soils and sea-spray) chemical variables.

An initial CCA using a reduced set of seven chemical variables (pH, color, TN, Na, Cl, SO₄, Al) showed a strong arch on the second axis. We therefore used DCCA, with detrending by second-order polynomial to explore the relationships between floristic composition and environmental gradients (ter Braak, 1986). The sample-environment biplot for axes 1 and 2 is shown in Figure 4. Both axes are statistically significant (999 permutations: $p < 0.05$) and together account for 14.4% of the variance in the diatom data. The first axis ($\lambda = 0.63$) is strongly related to variables reflecting gradients in catchment weathering (pH and SO₄), hydrology, and the development of organic soils (color, Al). The second axis ($\lambda = 0.37$) is related to trophic status and is most strongly correlated with TN concentration. Axis 3 (not shown; $\lambda = 0.22$) is related to variables reflecting the influence of sea-spray (Na, Cl). The ordination also indicates that diatom assemblages in lakes of similar age are similar in species composition. The youngest lakes (< 50 years) cluster in the top left of the diagram (high pH, low TN), the lakes of intermediate age (50–250 years) fall in the lower left (high pH, medium to high TN), and the older lakes fall on the right side of the first axis (lower pH, mid-range TN).

The seven chemical variables account for 30.8% of the total variation in the diatom data (Figure 5a). In Figure 5b this total explained variance is partitioned into components representing the unique contributions of the four environmental gradients, interactions between pairs of gradients, and other interactions among gradients. The total explained variance is made up of unique contributions of 7.1, 6.3, 5.7, and 4.4% for variables representing catchment weathering, development of organic soils, sea-spray and trophic status respectively.

Interactions or shared variances between pairs of gradients account for only 3.5% of the total explained variance. This is a result of conditional effects between variables representing organic soils and (i) catchment weathering (2.6%)—older, more dilute sites generally have a greater development of organic soils; or (ii) sea-spray

(0.9%)—most of the older sites are nearer the coast. The remaining variation (3.8%) is due to the joint effect of variables representing all three gradients (weathering, organic soils and sea-spray): interactions between trophic status, represented by TN, and other gradients are negligible and account far less than 0.1% of the total explained variance.

Water-chemistry reconstruction

The results of the variance partitioning (Figure 5) indicate that the four environmental gradients represent largely independent directions of variation in the modern diatom data from the chronosequence lakes. On this basis, we developed diatom-based transfer functions for pH and TN reconstruction using weighted averaging (WA). We chose these two variables, because trophic status and pH have been the focus of most discussions of lake ontogeny. In this data set, we reconstruct TN rather than TP, because TN explains more of the variance in the data. TN accounts for 4.5% of the variance (uniquely 4.4%) in the diatom data. This is highly significant ($p = 0.03$, Monte Carlo permutation test, 999 permutations). TP only accounts for a total of 3.0% of the variance, and this is not significant ($p = 0.62$).

Table 2 summarizes the performance of the pH and TN transfer functions. As expected from the results of the variance partitioning, the relationship between diatom-inferred and measured pH is the strongest of the two, with a squared correlation of 0.93 and RMSE of 0.26 (Figure 6a). This performance is comparable to that of other diatom-pH transfer functions (e.g., Birks *et al.*, 1990; Dixit *et al.*, 1993). The transfer function for square root TN is also strong ($r^2 = 0.71$, RMSE = 1.29, Figure 6b) and is again comparable to other WA transfer functions constructed for TP (Hall and Smol, 1992; Anderson *et al.*, 1993; Fritz *et al.*, 1993; Bennion *et al.*, 1996) or TN (Christie and Smol, 1993). The RMSEP will always be higher than the apparent RMSE, and for large training sets (>100 lakes) increases in prediction error of 15–50% are common. For the

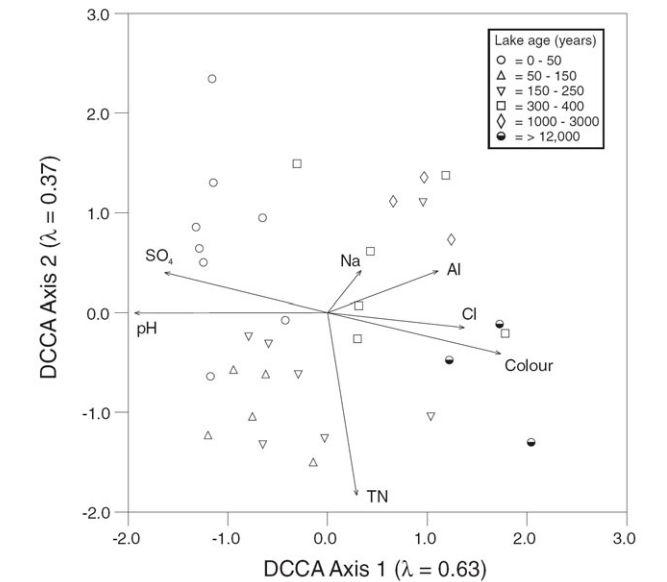


Figure 4 Detrended canonical correspondence analysis biplot of diatom-water chemistry relationships showing forward-selected chemical variables and site (lake) scores. The arrows show the direction of maximum variation of the measured environmental variables.

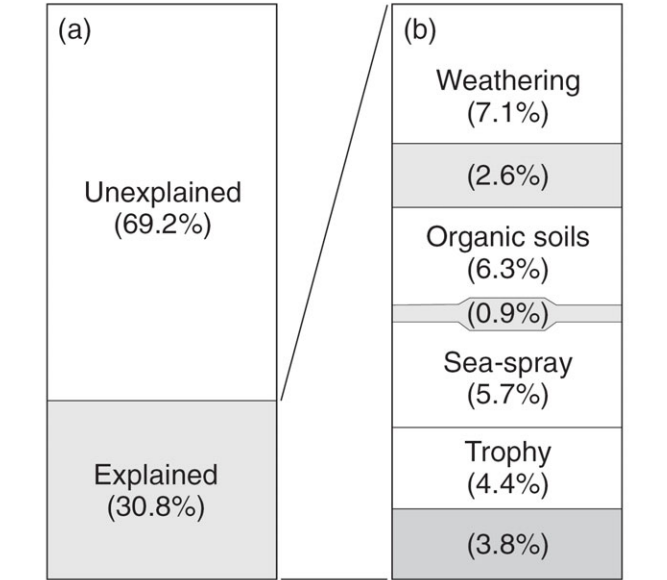


Figure 5 Results of partial CCAs, which partition the total variance in the diatom data into (a) explained and unexplained portions and (b) components representing the unique contributions of variables representing gradients of catchment weathering/hydrology, development of organic soils, sea-spray, and trophic status (open), interactions or conditional effects between pairs of gradients (light shaded), and other interactions (dark shaded).

Table 2 Statistics summarizing the performance of the transfer functions for pH and total nitrogen (TN) derived from weighted averaging regression, with inverse deshrinking (see text for further description).

	R ²	Bootstrap R ²	RMSE	RMSEP
pH	0.93	0.80	0.26	0.44
TN	0.71	0.24	1.29	2.39

chronosequence training set, the RMSEP is considerably higher than the apparent RMSE for both pH and TN (69% and 85% higher, respectively). Such large inflation of the prediction error under cross-validation is in part a reflection of the small size of the training-set; as training-set size increases the RMSEP approaches the RMSE (Martens and Naes, 1989). Although the RMSEP are relatively large, especially for TN, these transfer functions may still provide insights into chemical changes in the Glacier Bay lakes and broad-scale successional trends.

Diatom stratigraphy

A total of 388 taxa is present in the 10 cores, of which 210 are represented in the surface-sample data set. Most of the taxa absent from the surface-sample counts are < 1% relative abundance in the cores (n = 135). The only taxa abundant (> 5%) in cores but absent from modern counts are *Achnanthes kriegeri* (up to 8% in Brady), *Eunotia sudetica* (to 7% in Dagelet), *Pinnularia mesolepta* (to 5% in Dagelet) and *Navicula cf. globosa* (to 19% in Harbor Point).

Figure 7 shows the diatom stratigraphies of individual sites and illustrates the diverse patterns of change in diatom species assemblages among neighboring lakes in similar environmental settings. However, some similarities of pattern exist among the sites along the Glacier Bay fjord and among the older sites along the Outer Coast. The basal assemblages of lakes near the Glacier Bay fjord are dominated by a suite of taxa, including *Gyrosigma spencerii* v. *curvula*, *Amphora perpusilla*, *A. ovalis* v. *affinis*, *Achnanthes minutissima*, *A. biasoletiana*, *Navicula veneta*, *N. radiosa* v. *tenella*, and benthic *Fragilaria* spp. Subsequent patterns of change vary,

but in most sites *Fragilaria* spp. increase in relative abundance. Other taxa that increase in relative abundance in the later histories of the lakes include *Navicula pupula*, several small *Navicula* spp. (*N. strenzekei*, *N. minima*, *N. seminuloides*) and acidophilous species, such as *Achnanthes marginulata*, *Cymbella gaeumannii*, *Stauroneis anceps* v. *gracilis*, and *Eunotia naegeli*.

The stratigraphy of sites along the Outer Coast differs from those in Glacier Bay proper. Basal assemblages include a greater diversity of taxa, such as *Cymbella gaeumannii*, *Nitzschia perminuta*, *Amphora perpusilla*, *Achnanthes minutissima*, *Navicula pupula*, *Fragilaria virescens* v. *exigua*, acidophilous *Aulacoseira* spp., and *Cyclotella pseudostelligera*. Subsequent species assemblages are varied and include *Navicula mediocris*, *N. soehrensii*, *Frustulia rhomboides* and v. *saxomica*, acidophilous *Aulacoseira* spp., as well as other taxa in the genera *Achnanthes*, *Navicula*, *Cymbella*, and *Brachysira*. In these lakes, the *Fragilaria* characteristic of the lakes near the Glacier Bay fjord are rare (*F. brevistriata*, *F. construens*, *F. pinnata*) and the only common benthic *Fragilaria* spp. are *F. virescens* v. *exigua*, *F. oldenburgiana*, and *F. lata*.

The efficacy of the surface samples for environmental reconstruction was assessed by calculating the squared chord distances (d^2) between each core and surface sediment sample (data not shown). In all cases, except Blue Mouse Cove and Brady, the basal sample or samples have a minimum d^2 greater than the critical value of 0.74 and do not have good analogues in the calibration data set. All other samples are described well by the variation in the modern surface samples.

Reconstruction of pH and TN histories of individual lakes

The pattern of change in lakewater chemistry of individual lakes was inferred from stratigraphic diatom assemblages using the transfer functions derived for pH and TN (Figure 8). Seven of the lakes show pH declines since the time of formation, but the pH decline is greater than the RMSEP of the transfer function for only two sites, Harbor Point and Bartlett Lake (Figure 8b). However, given the uniformity of the pattern, we argue that the trends

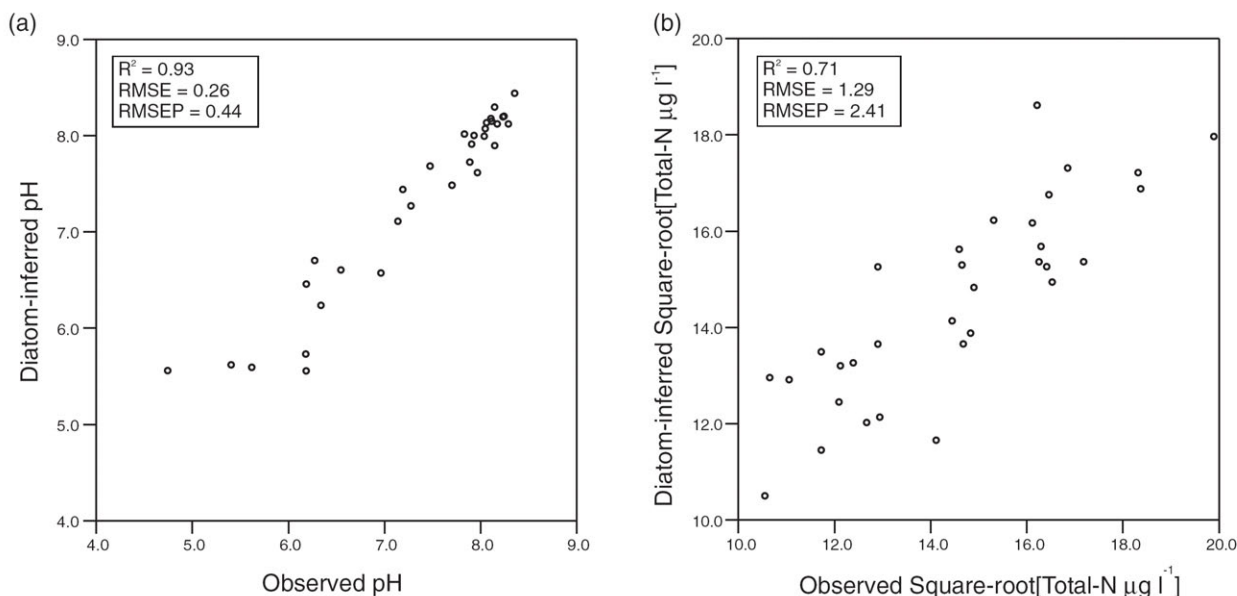


Figure 6 Observed versus diatom-inferred (a) pH; and (b) TN.

are representative of real patterns of change. Three of the youngest lakes do not exhibit net declines in pH (Blue Mouse, Spokane, Lester 3). Among lakes of similar age, the magnitude and pattern of pH change differs. For example, of the sites on Lester Island, all of which are on the same substrate and of the same age, the magnitude of pH change ranges from no net change in Lester 3 to approximately 1.0 pH unit in Lester 1 and 0.7 in Lester 2. The greatest pH change is reconstructed for the 200-year-old Bartlett Lake, where a pH change of 1.1 units exceeds that in even the older Outer Coast lakes.

Patterns and net change in reconstructed TN concentrations over time are quite variable (Figure 8b). Bartlett, Brady, and Dagelet, for example, show little net change in TN, although the reconstructions do suggest transient change in nitrogen concentrations. Blue Mouse Cove, Spokane Cove, Lester 1, Lester 2, and Harbor Point show net increases in TN over time, whereas Lester 3 and Paps show net declines.

Patterns of lake development

The pattern of limnological development through time for each of the lake cores is summarized by projecting the core assemblages onto axes 1 and 2 of the DCCA biplot of modern samples (Figure 9). Although the pattern of limnological change is very different among lakes, some similarities are apparent. The majority of lakes show change over time from left to right along axis 1, although the timing of movement along axis 1, the actual pattern of change, and the net magnitude of change varies among lakes. The sites along the Outer Coast region cluster together in the upper right of the figure, whereas the sites along Glacier Bay proper, with the exception of Bartlett Lake, cluster in the lower left of the plot. Bartlett Lake plots intermediate between the two. The separation of the lakes into two groups along the first axis suggests that the initial conditions of the Outer Coast sites along the first-axis gradient differed from the other lakes. Patterns of change along the second axis vary more than those along the first axis. The sites along Glacier Bay, however, show some similarity of pattern, with an early downward movement along the second axis, followed in most cases by subsequent upward movement. The sites on the Outer Coast show either no net changes on axis 2 or an upward trend.

Discussion

The Glacier Bay chronosequence presents a model for early lake development in boreal regions on calcareous terrain with a maritime climate. Comparison of lakewater chemistry among the 33 lakes of the modern chronosequence suggests two major ontogenetic trends correlated with early lake development in Glacier Bay and regions under similar environmental controls (Engstrom *et al.*, 2000). The primary trend is a loss of pH, alkalinity, and base cations over time and a correlated increase in apparent color and DOC. The data suggest that lakes maintain high and relatively constant pH, alkalinity, and conductivity for the first several hundred years after formation, followed by a rapid decline. This trend has been postulated in the paleolimnological literature and attributed to the leaching of base cations from catchment soils (Round, 1901; Pennington *et al.*, 1972; Whitehead *et al.*, 1989; Ford, 1990). The chronosequence data suggest a corollary increase in water color after about 100 years, as a consequence of paludification of catchment soils (Ugolini and Mann, 1979) and increased inputs of organic acids, a trend also postulated in the literature.

The second major trend suggested by the chronosequence is an early increase in TN concentration, paralleling the development of alder thickets (Cooper, 1923) and the consequent increase in soil nitrogen from nitrogen fixation by rhizobacterium associated with alder (Crocker and Major, 1955), followed by a subsequent decline. These trends are paralleled by changes in chlorophyll-*a* concentration. However, there is considerable scatter in the nitrogen data, and thus this trend is less conclusively defined than patterns of pH change over time. The tracking of lakewater TN by chlorophyll-*a* suggests that algal production may be controlled by nitrogen availability. One particularly interesting feature of the chronosequence diatom assemblage data is the increased abundance of benthic *Fragilaria* species after ~50 years, paralleling the increase in lake TN concentrations. This suggests a relationship between the two variables.

The diatom stratigraphies of 10 lakes in the chronosequence, which range in age from 100 to 1,200 years, show considerable variability in diatom species assemblages among lakes and in patterns of change over time. Comparison of core assemblages with modern analogues using squared chord distance indicates that the modern data set adequately describes the assemblages found in cores, with the exception of basal core assemblages in eight lakes, where dissimilarity exceeds the critical value derived from the matrix of dissimilarities among modern samples. The lack of good analogues for the basal assemblages probably reflects the nature of the modern calibration data set, which did not include proglacial lakes or lakes currently receiving glacial meltwater, environments dominated by benthic taxa capable of tolerating high turbidity, such as *Gyrosigma spenserii* v. *curvula*.

Despite the variability in diatom species composition and patterns of change among cored lakes, statistical analysis of these data suggests that changes in diatom assemblages are reflecting some common trends in limnological development. pH reconstruction from stratigraphic diatom assemblages suggests that most lakes undergo a decline in pH (and correlated variables) sometime after 100 years in age. However, the timing and rate of decline differ considerably among lakes and are apparently regulated by more local factors, particularly groundwater hydrology (Engstrom *et al.*, 2000).

The modern chronosequence predicts that TN concentrations in lake water should increase in the initial years following lake formation, peak at c. 100 years, and subsequently decline in sites up to about 2,000 years in age. This pattern parallels the pattern of change in soil TN concentrations as reported in the chronosequence of Crocker and Major (1955). TN reconstructions from diatom assemblages in cores, however, suggest that this is not a universal ontogenetic trend in lakes (Figure 8b). Core trajectories indicate that most sites along Glacier Bay itself (Lester 1, Lester 2, Lester 3, Bartlett L, Blue Mouse, Spokane Cove) show an increase in TN concentrations over time, whereas the lakes along the Outer Coast (Brady, Dagelet, Harbor Point, Paps) show either a decline in TN or no net change. The difference in pattern between sites along Glacier Bay and the sites along the Outer Coast may relate to differences in vegetation history and soil development. Early ecological studies in the Glacier Bay region (Cooper, 1923; Lawrence, 1958) proposed a single successional pathway leading from *Dryas* and other herbaceous species to alder thickets, to mixed shrub/woodland, to closed spruce-hemlock forest. However, more recent research (Chapin *et al.*, 1994; Fastie, 1995) indicates that the dense alder thickets presently characteristic of 50–150-year-old surfaces in the upper reaches of the Glacier Bay may not have been char-

acteristic of young successional landscapes throughout the region, and that sites close to seed sources of spruce may have “by-passed” the alder thicket stage. Even within relatively small areas

of the lower reaches of Glacier Bay, tree reconstructions (Fastie, 1995) suggest that, although alder was widespread, it was not present at all sites. Therefore, just as there are multiple pathways of

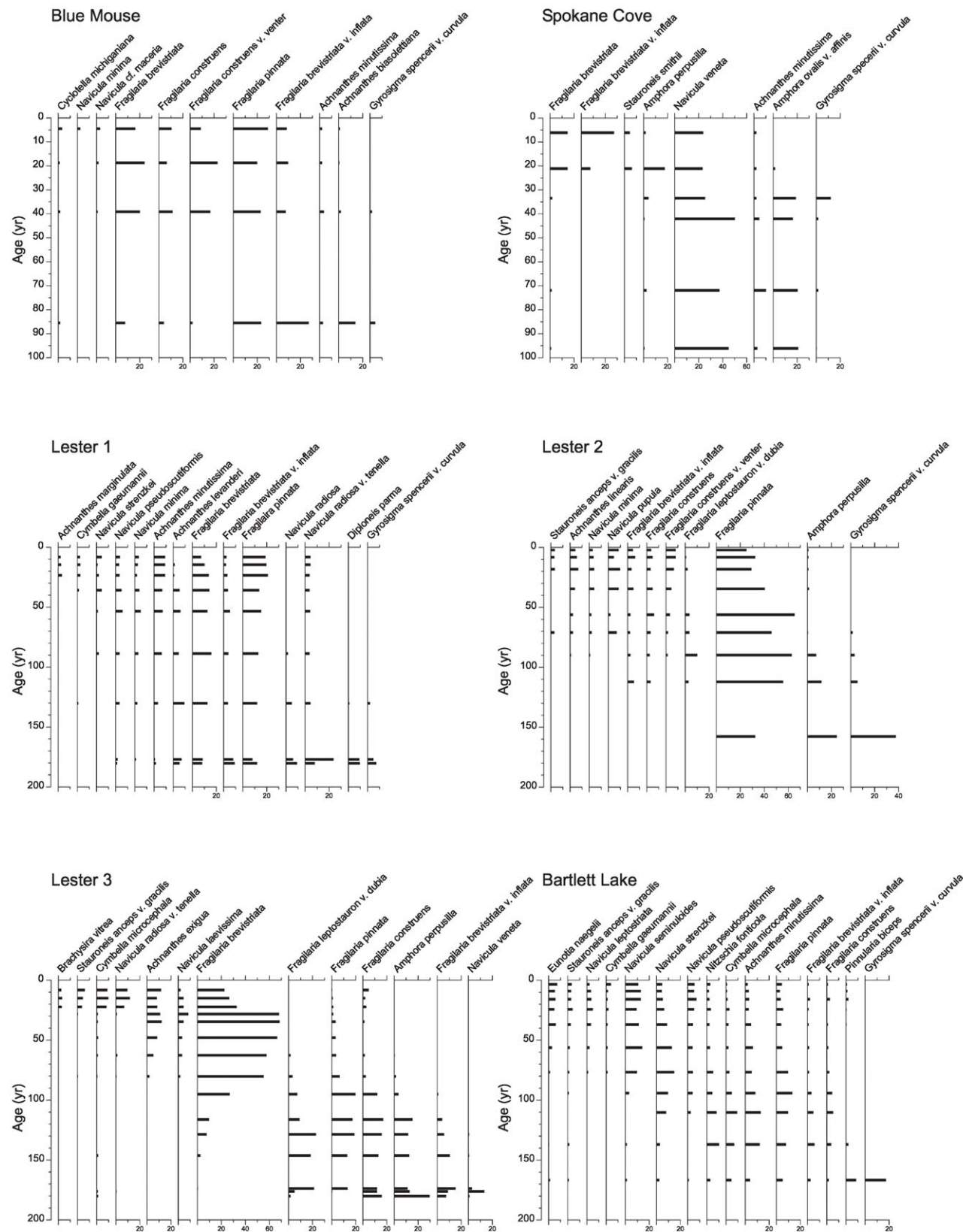


Figure 7 Diatom relative abundance (%) versus lake age for the 10 lakes analyzed stratigraphically.

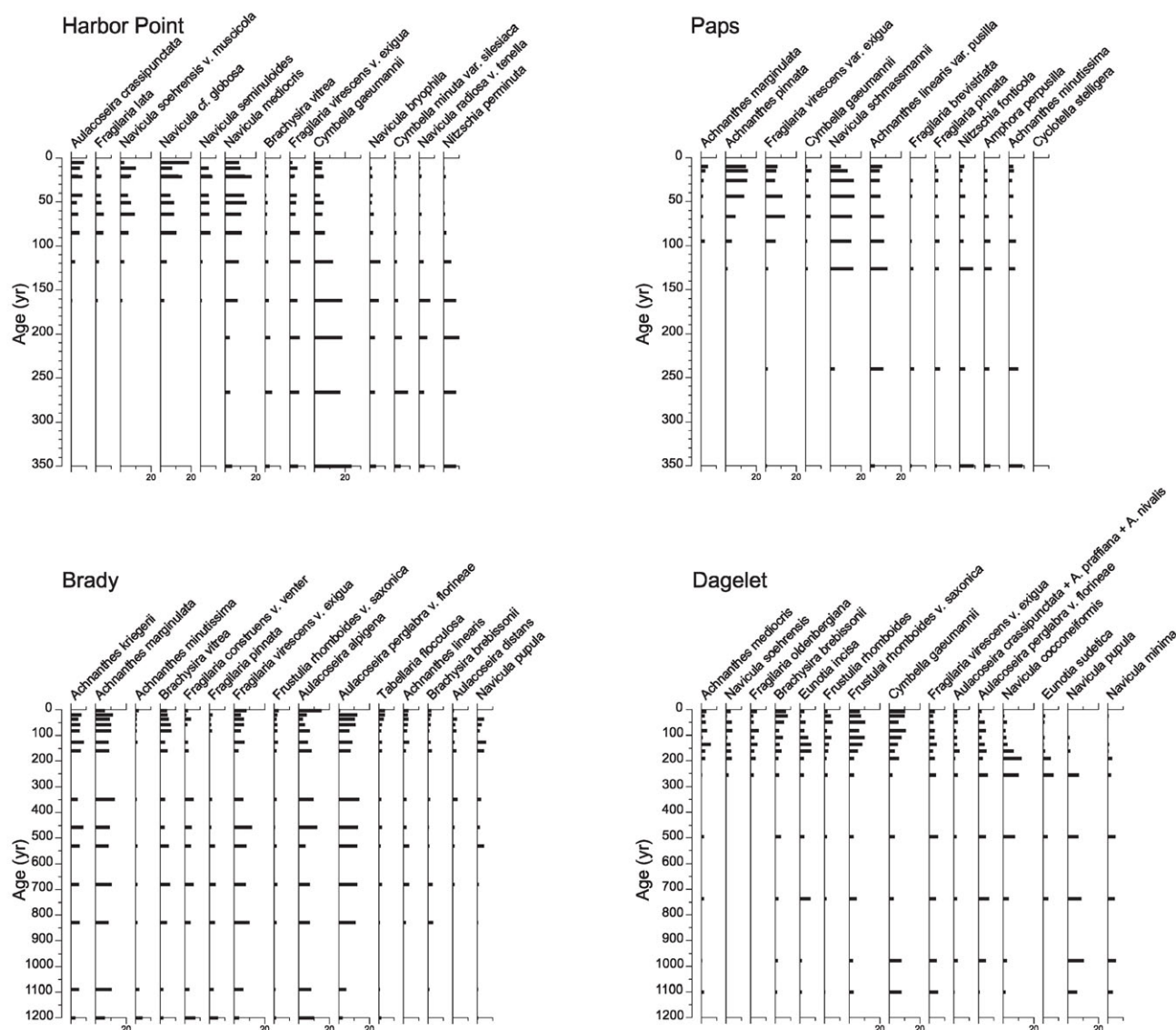


Figure 7 (continued)

vegetation change over time, temporal patterns of change in lake-water nutrient concentration may not follow universal trends across broad geographic regions but instead may reflect localized patterns of vegetation and soil development over relatively small spatial scales. Thus, lake catchments without alder and the associated nitrogen fixation in soils have a different trajectory than sites where alder has been a major component of the vegetation.

The importance of localized factors in controlling lake ontogeny is emphasized by the split between core samples from the Outer Coast and those from the lakes surrounding Glacier Bay proper along the first two axes of the ordination (Figure 9). The clustering of Outer Coast sites in the upper right of the diagram and of Glacier Bay sites in the lower left suggests that localized factors differed between the two regions at the time of lake formation and thus controlled initial limnological starting points, as well as subsequent trajectories.

Thus, comparison of trends inferred from the spatially arrayed chronosequence of lakes with the trajectories inferred from diatom assemblages in cores suggests spatial heterogeneity in pattern of change and that trends inferred from the chronosequence re-

flect temporal patterns for some variables but not others. Both the chronosequence and the core data suggest that lakes in boreal landscapes undergo a pH decline and an increase in color with time, beginning 100 to 300 years after lake formation. However, the initial starting point, the details of the pattern of change and the rate of change vary among lakes and are controlled in large part by local factors, particularly those related to lake hydrology. The core data, however, indicate that trends in nutrient concentrations (TN) and algal biomass inferred from the chronosequence are not replicated among all the cored lakes and thus are not under broad regional control. This spatial variability suggests that localized factors related to vegetation history and soil development exert the primary control on nutrient concentrations within a region of broadly similar geology. It is possible that over longer time periods of several millennia patterns of nutrient change will show broader regional convergence, but such is not the case during early limnological development at scales of less than 1,000 years. Thus, even at a small geographic scale, lakes do not follow a universal developmental pathway. This spatial variability is captured most clearly by analysis of multiple stratigraphic sequences.

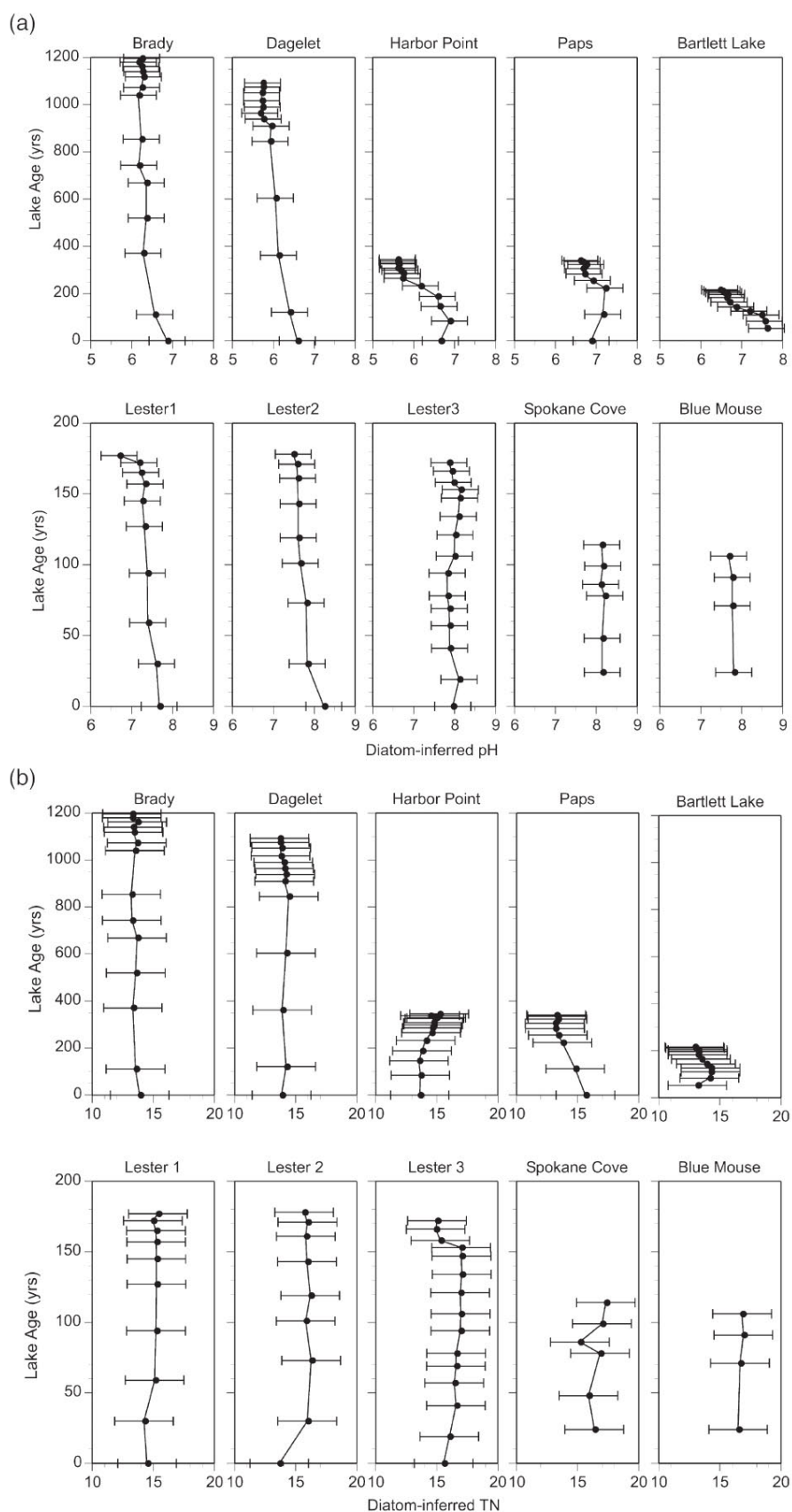


Figure 8 Temporal trends in diatom-inferred (a) pH and (b) TN versus lake age (years since lake formation) for the 10 lakes, based on the application of transfer functions to the stratigraphies presented in Figure 7. Error bars are the RMSEP generated from weighted averaging regression (see text). Differences between two values greater than the RMSEP are significantly different statistically (see Table 2). Note that the TN reconstructions are a square-root transformation of the TN concentrations (ppb) (see text).

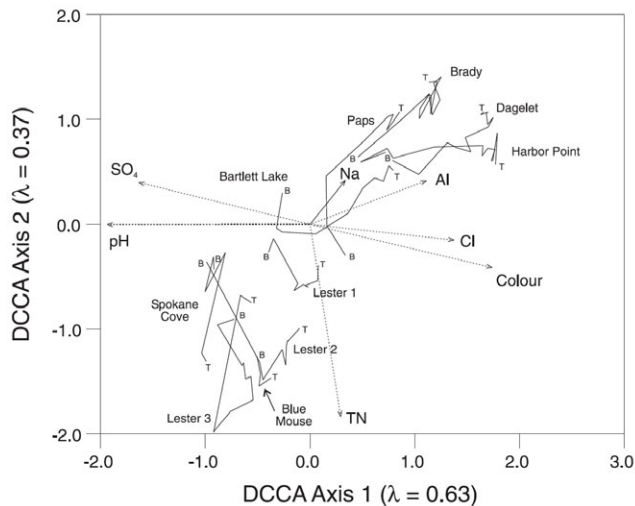


Figure 9 Detrended canonical correspondence analysis biplot showing forward-selected chemical variables and timetracks of the core diatom assemblages. Core assemblages were projected onto the biplot by adding them to the analysis as “passive” samples (ter Braak, 1988). For each lake, “T” denotes the core top (modern) and “B” the base of the core.

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