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Abstract

We studied a series of recently formed lakes along a deglaciation chronosequence in Glacier Bay National Park to examine changes in water chemistry, primary production, and biotic composition that accompany the early ontogeny of north-temperate lakes. Successional trends in these freshwater ecosystems have been explored with a two-tiered approach that includes (1) the comparison of limnological conditions among lakes of known age and in different stages of primary catchment succession, and (2) the inference of water-chemistry trends in individual sites based on fossil diatom stratigraphy. This paper emphasizes the reconstruction of limnological trends from fossil diatom assemblages. The modern distribution of diatoms in relation to water-chemistry gradients within 32 lakes of varied age is used to derive a transfer function for the reconstruction of chemical trends from fossil assemblages in sediment cores. The modern data suggest that pH and TN (total nitrogen) exert significant and independent controls on diatom distributions, and thus trends in these variables are reconstructed for Bartlett Lake, as an example of our approach. Core reconstruction corroborates patterns in pH suggested by the modern chronosequence and shows a gradual decline in lakewater pH after about 100 years. The Bartlett Lake core also follows the chronosequence pattern in TN concentration, with an initial increase followed by a decline after ca. 100 years. Reconstructions from other sites, however, suggest that trends in total nitrogen concentration are variable, and thus that localized patterns of plant colonization and soil development may result in regional variability in lakewater nitrogen concentration over time.

KEY WORDS: Chronosequence, diatoms, paleolimnology, succession, lake chemistry.

The description and evaluation of patterns and controls of long-term limnological change over time has been a major theme in limnology since the work of Pearsall in the English Lake District in the 1920s (Pearsall 1932). Because direct observation of lake development over long temporal scales (decades, centuries, millennia) is usually impossible, limnologists rely on fossil records from lake sediments to infer patterns of limnological development and derive hypotheses about the factors controlling direction and rate. A variety of chemical and biological fossils have been utilized in these paleolimnological investigations of lake ontogeny, but one of the most widely used and sensitive groups of fossil indicators are diatoms, an abundant and ecologically diverse algal group sensitive to changes in lake chemistry and morphometry.

The Glacier Bay region offers an unusual opportunity to study patterns of early limnological development in boreal regions by comparing lakes within landscapes of differing ages and inferring patterns of limnological change from this chronosequence of sites. In essence successional patterns for lakes can be described with a space for time substitution in the same way that terrestrial succession has been described through the classic work of plant ecologists including Cooper (Cooper 1923), Lawrence (Lawrence 1958), and their colleagues.

We use a suite of regional lakes and lake catchments to evaluate several hypotheses advanced in the literature about patterns of limnological change in boreal regions. Our work includes an evaluation of chemical and biological trends in a chronosequence of 32 lakes (Engstrom and Fritz 1990), as well as the inference of temporal trends in individual sites based on diatom analysis of sediment cores. This paper includes both an examination of successional patterns in diatoms in the chronosequence and the reconstruction of water-chemistry change in one of these sites from the stratigraphy of fossil diatoms. These water-chemistry reconstructions are based on transfer functions derived from the relationships between diatoms and water-chemistry gradients in the modern lakes.

Site selection

Diatom and water-chemistry gradients were analyzed in 32 glacially formed lakes within Glacier Bay National Park. The lakes range in age from ca. 10 to 12,000 years and are in primary catchments in low-elevation forelands along the Bay and Outer Coast. Approximately two-thirds of the lakes are along the lower and east arms of Glacier Bay proper (10-220 yrs), 5 are in the Lituya Bay area (350-400 yrs), 4 south of Lituya Bay along the Outer Coast (400-2700 yrs), and 3 are outside the Neoglacial ice limit on Pleasant Island (>10,000 yrs) (Figure 1). The lakes vary in water chemistry and size, although most are relatively small (<8 ha.). Chemical and morphometric characteristics of the sites are summarized by Engstrom and Fritz (1990).

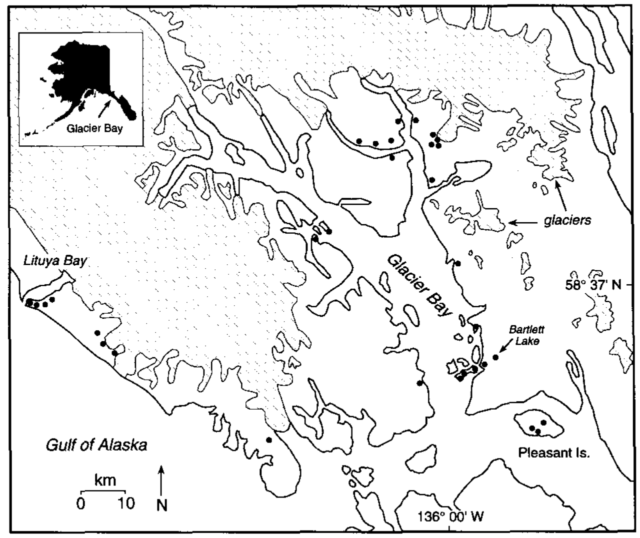

Fig. 1. Map of Glacier Bay, showing the location of the lake sites.

Methods

Field sampling and analytical methods

Each lake in the chronosequence was sampled for chemical analysis in July 1988, May 1989, and September 1990. pH and conductivity were measured in the field, and water samples were filtered for chlorophyll analysis. Color and alkalinity were measured within 12 hours of sample collection. Water was filtered and frozen for subsequent analysis of dissolved organic carbon (DOC), dissolved Si, and anions, and additional unfiltered water samples were transported to the laboratory for nutrient analysis and measurement of major cations.

The diatom analyses presented here are based on surface-sediment samples (the uppermost 1 cm from sediment cores) that represent a temporal integration of several years of sediment accumulation and a spatial integration of both littoral and open-water habitats. Sediment cores were collected from the deepwater 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, and samples were stored in polypropylene jars at 4° C until subsampled. Cores from sites older than 150 years were dated by ^{210}Pb analysis, using the constant rate of supply model (c.r.s.) to calculate age (Eakins and Morrison 1978).

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 of the subsample with distilled water to remove oxidation by-products. Prepared sediment was dried onto coverslips, and coverslips were mounted on slides with Naphrax. Diatoms were counted on an Olympus BH-2 microscope at a magnification of 1000x using an oil immersion objective (N.A.=1.4). A minimum of 500 individuals was counted in the surface samples and 400 in core samples.

Statistical analyses

The relationship between diatom distribution and environmental variables was determined using detrended canonical correspondence analysis (DCCA), an ordination technique that compares lakes based on their diatom assemblages and constrains each of the axes to be linear combinations of measured environmental variables. This technique is described in greater detail by ter Braak (1987). A number of variables are highly correlated (e.g. Ca, alkalinity), and thus only select variables were included in the analyses presented here.

Results and Discussion

The distribution of many diatom taxa is related to lake age (Figure 2). *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 ca. 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, Navicula radiosa* v. *tenella*, but not in older sites, whereas taxa such as *Fragilaria virescens* v. *exigua, Cymbella gaeumannii,* 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.

An ordination of the diatom and water-chemistry data with DCCA suggests the major environmental gradients correlated with diatom distribution (Figure 3). The first axis is related to major-ion chemistry, including pH, calcium concentration, total silica concentration, and other correlated factors, such as alkalinity, conductivity, and water color. The second axis is related primarily to nutrient (total nitrogen TN, total phosphorus TP) and chlorophyll-a concentrations. Axis 1 and 2 account for 12.5% of the total variance in the diatom data. A low percentage of explained variance is common in complex multi-species assemblages, such as are characteristic of diatom communities in many freshwater lakes. The two principal gradients in the diatom/water-chemistry data are clearly correlated with lake age. The youngest lakes cluster in the upper left of the ordination plot (high pH, low TN), those ca. 100-300 years in the lower left of the ordination (high pH, high TN), and the older sites >300 years are arrayed along the right side of the first axis (lower pH, intermediate TN).

These data can be used to derive transfer functions for the reconstruction of water chemistry from diatom assemblages and subsequently to infer past trends in water chemistry from diatom assemblages in sediment cores. Further details on transfer function development and core reconstruction are in ter Braak (1990). Statistical analysis of the Glacier Bay diatom data using forward selection suggests that pH and TN concentrations exert significant and independent influences on diatom distributions, and thus we have reconstructed pH and TN concentrations from stratigraphic diatom data in cores.

The diatom stratigraphy of a sediment core from Bartlett Lake (Figure 4) is used as an example of the reconstruction of temporal trends in pH and TN. The core shows clear changes in the diatom assemblage over time, with *Gyrosigma spencerii, Achnanthes minutissima, Fragilaria pinnata*, and *Nitzschia fonticola* dominant in the basal sediments, deposited in the early years after lake formation. Subsequently these taxa are replaced by increasing percentages of *Fragilaria construens* v. *venter, Navicula seminuloides, N. leptostriata, Stauroneis anceps* v. *gracilis,* and *Eunotia naeglii*. Application of the transfer function to these data suggests a gradual decline in lakewater pH from ca 7.6 at the time of lake formation to 6.5 in the modern day. TN reconstruction suggests an increase in TN concentration in the early years following lake formation followed by a decline after about 100 years.

The modern water-chemistry data from the chronosequence of lakes (Engstrom and Fritz 1990) suggest that lakes begin to decline in pH 100-300 years after formation. Core reconstructions from 10 lakes ranging in age from 100 to 2000 years, including Bartlett Lake, show pH declines in lakes >100 years in age (Fritz, unpublished data). Thus, the cores verify that pH trends as inferred from the spatially arrayed modern chronosequence reflect temporal pH trends in individual sites. However, the initial starting conditions and the magnitude and rate of pH change varies among lakes, which suggests that local factors, particularly lake hydrology (Almendinger 1990), play an important role as well. TN reconstructions from these 10 lakes show more variation in pattern than is present for pH (Fritz, unpublished

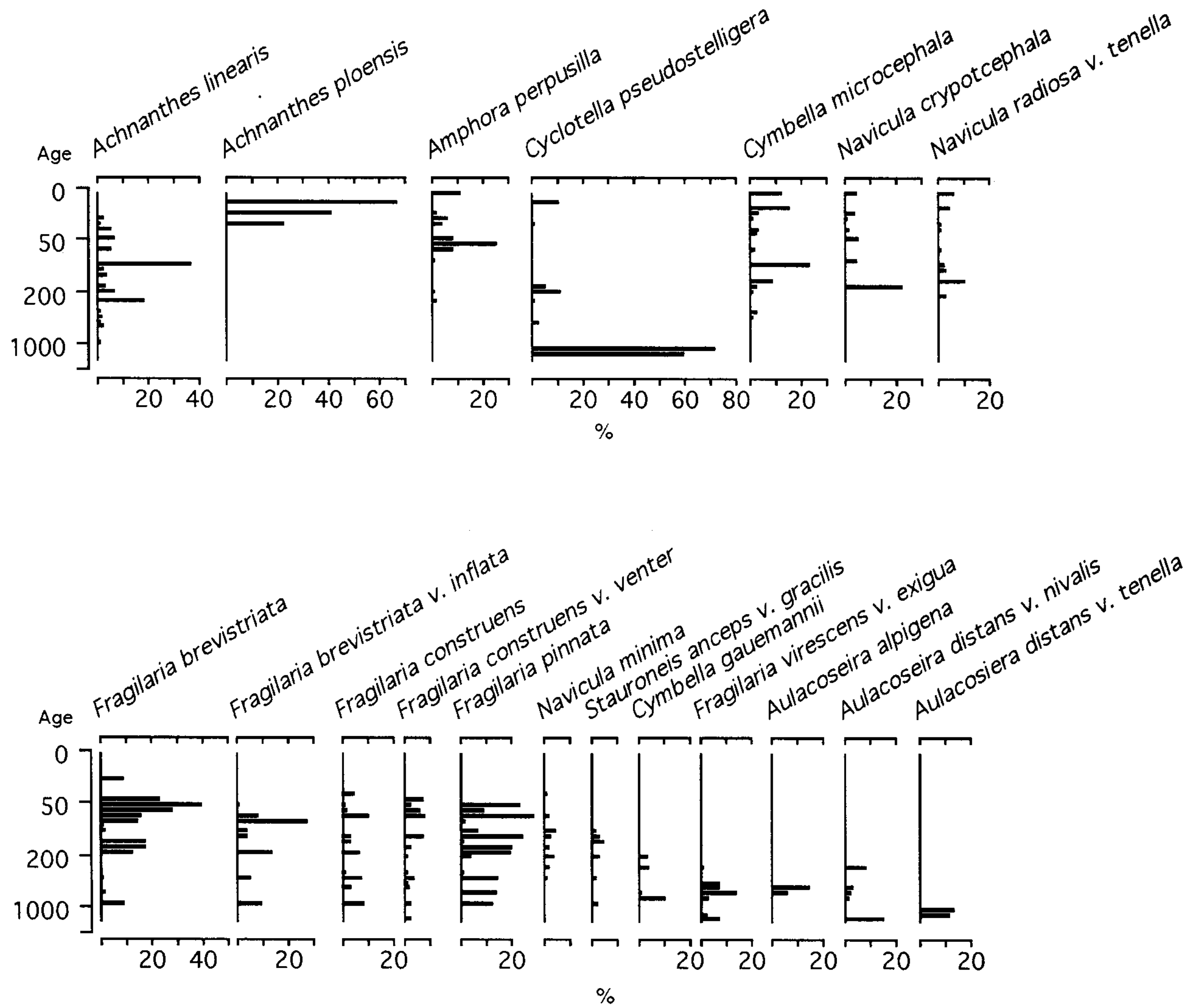

Fig. 2. Plot of the relative abundance (%) of selected diatom species along an age gradient. Lakes are arrayed on the vertical axis in order of increasing age (in years).

data). Most of the lakes in the east arm of Glacier Bay show generalized patterns similar to that of Bartlett Lake, with an early increase in TN concentration followed by a subsequent decline. Lake cores from the Outer Coast, however, show different patterns thus suggesting different environmental controls. The variability in pattern probably reflects the variability in plant succession and subsequent soil development described in recent studies on plant succession (Chapin *et al.* 1994).

The modern analyses of water-chemistry trends in the lakes of the Glacier Bay chronosequence and the diatom-inferred water-chemistry patterns suggest that both broad-scale regional processes and local variability play significant roles in determining lakewater chemistry. The dominant regional pattern is one of a gradual decline in lakewater pH through time, beginning one to several hundred years after lake formation. This decline in pH is probably primarily a result of the development of indurated soil horizons (Ugolini and Mann 1979) and the subsequent shift from a lake system dominated by calcareous groundwater flow to one receiving primarily surface runoff and flow through peaty soils. A depletion of base cations from catchment soils by leaching may also contribute to gradual loss of alkalinity. In terms of nutrient concentrations, the

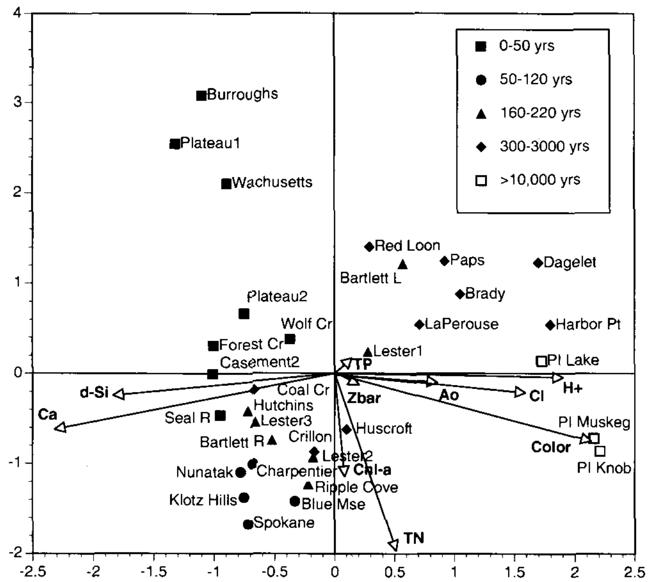

Fig. 3. DCCA ordination of the diatom assemblages in Glacier Bay lakes in relationship to selected environmental gradients. The arrows show the direction of maximum variation of the measured environmental variables (dissolved silica, d-Si; mean depth, Zbar; lake surface area, Ao; hydrogen ion concentration H+; other symbols as mentioned in text). Sites plotting close together have similar diatom composition, while those at distance from one another are more dissimilar.

chronosequence data suggest that lakewater nutrient trends, specifically those in total nitrogen, follow patterns in soil nitrogen as suggested by Crocker and Major (1955) with a gradual increase in concentration, followed by a subsequent decline. Core reconstructions, however, suggest variability in temporal changes in lake nitrogen, possibly reflecting variability within the region in plant succession and soil development. Clearly subsequent research should involve coupled studies of the chemical and hydrologic linkages between aquatic and terrestrial systems, thus providing a mechanistic understanding of the processes that drive the observed patterns of limnological change.

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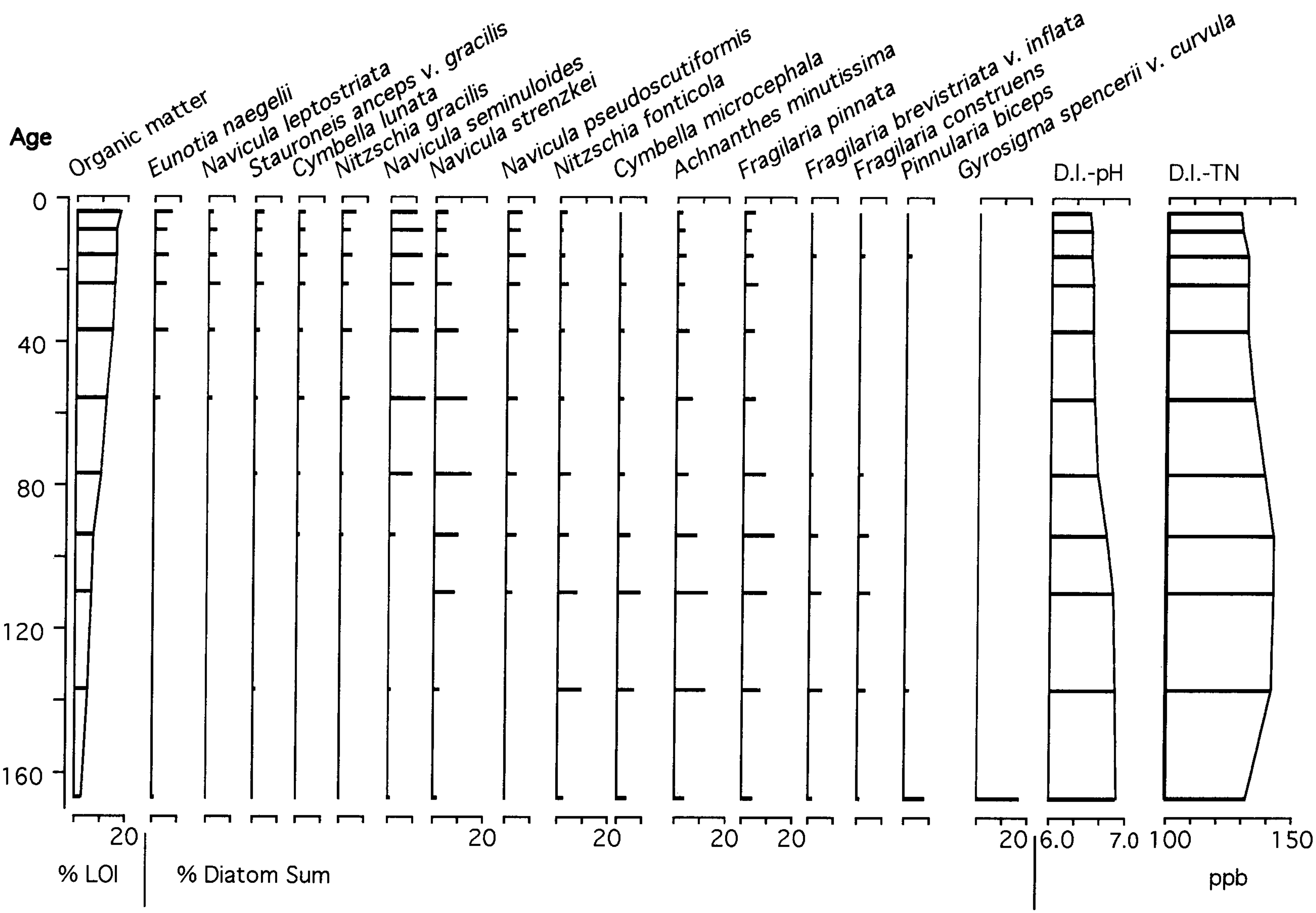

Fig. 4. Stratigraphy of the dominant diatoms in the Bartlett Lake core (% relative abundance) and diatom inferred (D.I.) values for pH and TN, as reconstructed from diatom assemblages. Sediment age is determined by ^{210}Pb dating.

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