

Coupling Between Primary Terrestrial Succession and the Trophic Development of Lakes at Glacier Bay

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Abstract. We use sediment cores from lakes in Glacier Bay National Park to examine the relationship between successional changes in catchment vegetation and trends in water-column nitrogen (a limiting nutrient) and lake primary production. Terrestrial succession at Glacier Bay follows several different pathways, with older sites in the lower bay being colonized directly by spruce (*Picea*) and by-passing a prolonged alder (*Alnus*) stage that characterizes younger upper-bay sites. Sediment cores from three sites spanning this successional gradient demonstrate that the variability in trophic development among lakes is a consequence of the establishment and duration of N-fixing alder in the lake catchment.

Introduction

The natural eutrophication of lakes is a widely held concept in limnology, arising from the earliest efforts to classify lakes and place them in an evolutionary sequence. Recent studies of newly formed lakes at Glacier Bay, Alaska, only partially support this idea, and suggest more variable trends in lake trophic development (Engstrom and others, 2000; Fritz and others, 2004). This variability is thought to relate to successional trends in catchment vegetation, which have been shown to differ between sites in upper and lower Glacier Bay. Rather than a single successional pathway going from early colonizers to alder (*Alnus crispa* v. *sinuata*) to spruce (*Picea sitchensis*), terrestrial succession actually follows several pathways depending on seed availability and the life-history traits of the dominant species (Chapin and others, 1994). Thus, older sites in the lower bay were colonized directly by spruce and effectively by-passed the prolonged alder stage that characterizes younger upper-bay sites.

The purpose of this study is to explore the consequences of these contrasting pathways in terrestrial succession on lake trophic development—in particular, nitrogen levels and primary productivity. Because lake sediments record both vegetation (through pollen) and lake chemistry (though diatoms), it should be possible to test the idea that the local presence of N-fixing alder influences lake ontogeny at Glacier Bay. The study lakes are particularly well-suited to this task, as most are small (1–5 ha surface area), have a strong local-pollen signature, and are nitrogen limited, so fossil diatom assemblages provide a robust indicator of historical lake-water N. Moreover, the accumulation rate of diatoms in the sediments provides a direct measure of whole-lake primary productivity. Diatoms are well preserved in most sediments

(unlike carbon), and sediments integrate year-round diatom production from all habitats, including benthic, which is not captured in any manner by conventional measurement of water-column productivity.

Study Sites

Our original study of lakes in Glacier Bay National Park included 32 sites ranging in age from 10 years to >10,000 years (Engstrom and others, 2000). Three lakes from this original set are the focus of the current study: Bartlett Lake, adjacent to the terminal neoglacial moraine, Lester Island (Lester-1 in the original chronosequence), also in the lower bay, but in the Beardslee Islands and far from the terminal moraine, and Blue Mouse Cove at the lower end of the west arm of the Glacier Bay fjord (fig. 1). The first two sites, Bartlett Lake and Lester Island occupy land surfaces deglaciated about 200 years ago and are today vegetated by closed spruce/hemlock (*Tsuga heterophylla*) forest. The third site at Blue Mouse Cove is about 110 years old, and has a catchment cloaked in dense alder thickets with scattered spruce and cottonwood (*Populus balsamifera*) poking through the alder canopy. The lakes range from 4.0 to 8.0 m maximum depth, and except for Bartlett Lake (62 ha) are small (1.7–3.5 ha).

Methods

A single sediment core was collected from the deepwater zone of each lake with a piston corer operated from the lake surface by rigid drive rods. Cores were sectioned in the field at 0.5–1.0 cm intervals and later analyzed for diatoms and pollen and dated by ²¹⁰Pb. Subsamples for diatom analysis were oxidized in HNO₃/K₂Cr₂O₇, spiked with a calibrated microsphere solution, dried onto coverslips, and mounted with Naphrax. A minimum of 400 individual diatoms were counted at 1000x under oil immersion. Standard laboratory procedures were used to prepare subsamples for pollen analysis, and a sum of 200–250 pollen and spores were counted. Lead-210 was measured by ²¹⁰Po-distillation and alpha-spectrometry methods, and dates were determined according to the c.r.s.

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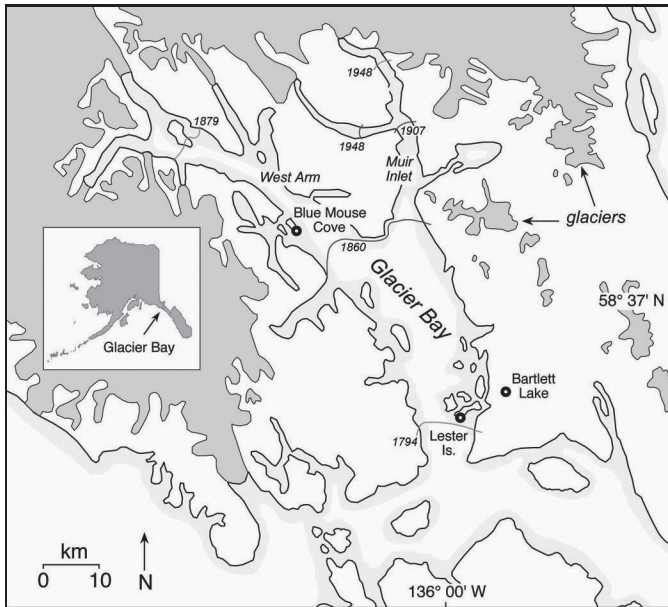


Figure 1. Glacier Bay National Park and Preserve and the three lake sites discussed in the text. Neoglacial ice margins are marked by dated isochrons.

(constant rate of supply) model (Appleby, 2001). Total-nitrogen (TN) trends were reconstructed from fossil diatom assemblages by using a weighted averaging (WA) transfer function (Fritz and others, 2004).

Results

Pollen data reveal distinct differences in vegetational development among the study sites which are explicable in terms of the different pathways that primary succession follows in the upper and lower parts of Glacier Bay (Chapin and others, 1994; Fastie, 1995). Core trajectories projected onto a biplot of the two major pollen types, *Alnus* (alder) and *Picea* (spruce), show increasing percentages of alder during the early histories of the three sites (fig. 2A). This trend is quickly reversed at Bartlett Lake by increasing percentages of spruce pollen, and similarly so, but with a greater delay, at Lester Island. The Bartlett Lake trajectory differs from Lester Island by higher spruce (>40 percent at present) and lower alder (generally <50 percent) overall. Blue Mouse Cove shows steadily increasing alder throughout the entire sequence, with percentages equal to that found in surface-sediment samples at other sites in Muir Inlet (all less than 80 years old).

The core trajectory for Bartlett Lake describes local vegetational succession dominated at the outset by spruce—a consequence of the site's proximity to spruce seed sources on the Glacier Bay terminal moraine—with only a minor and transient alder component. Blue Mouse Cove shows alder dominance throughout its history on account of the rapid migration of alder onto the glacial forelands of the upper bay. The Lester Island site, although located in the lower bay, is

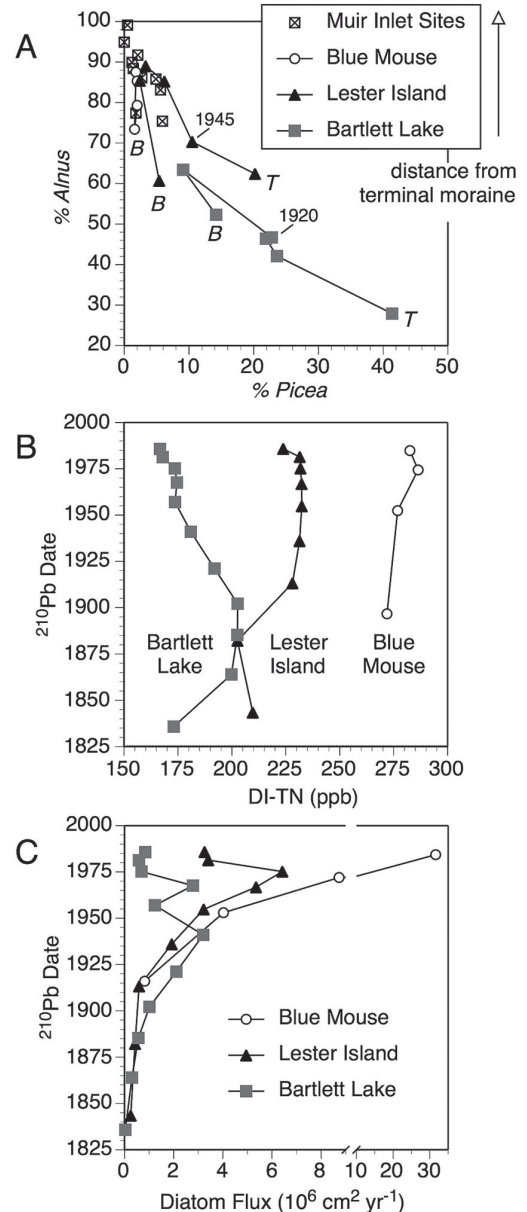


Figure 2. Sediment proxies representing (A) catchment vegetation, (B) lake-water total-nitrogen, and (C) whole-lake primary production for the three study lakes. Vegetational trends (A) are represented by changing percentages of the two major pollen types, *Picea* (spruce) and *Alnus* (alder); for each lake, "T" denotes the core top (modern) and "B" the base of the core. TN trends (B) are reconstructed from fossil diatom assemblages using a weighted averaging (WA) transfer function as described in Fritz and others (2004). Primary production (C) is represented by the accumulation rate of diatoms in each of the three cores.

more distant from the terminal moraine and thus shows an intermediate pattern with the early development of a healthy alder component and its subsequent replacement by an advancing spruce forest.

Diatom-based reconstructions of nitrogen concentrations in the three lakes follow trends that are consistent with the contrasting patterns of vegetational succession shown by pollen analysis (fig. 2B). In Bartlett Lake, diatom-inferred TN concentrations increased early in the lake's history, peaked between 1850 and 1900, and then decreased gradually to the present. TN concentrations show a similar (though slightly delayed) increase at Lester Island, with elevated concentrations persisting to near modern times. Blue Mouse Cove exhibits steady or slightly increasing TN concentrations throughout its shorter record. Diatom-inferred TN is consistently higher at Blue Mouse Cove than at Lester Island, which in turn is higher than at Bartlett lake. These trends are explicable in terms of the successional importance of N-fixing alder in the lakes' catchments.

Diatom accumulation rates, which reflect whole-lake biological productivity, are lowest during early lake development and increase steadily for the first 100 years or so following deglaciation (fig. 2C). Values peak for Bartlett Lake about 1940 and decrease irregularly thereafter, while at Lester Island the peak is delayed until about 1975 and also is somewhat higher. Blue Mouse Cove, by contrast, shows an exponential increase in diatom accumulation to a present-day maximum. The increase and decrease in diatom flux at Bartlett Lake and Lester Island correspond fairly closely with the trends in diatom-inferred TN, although the decrease appears to lag slightly that for TN. At Blue Mouse Cove, the monotonic rise in diatom accumulation matches the steady increase in lake-water TN.

Discussion

The diatom and pollen profiles from these three contrasting sites demonstrate an internally consistent linkage between local vegetational succession and the biogeochemical development of the receiving lakes. The multi-successional pathways of terrestrial succession at Glacier Bay, as described by Fastie (1995), are confirmed by pollen trends that demonstrate temporal and spatial differences in the local appearance and dominance of N-fixing alder thickets. Alder abundance is then correlated with the changing concentrations of lake-water TN, which in turn is manifest in differential patterns of diatom productivity in the lakes.

In all cases, there is an initial rise in lake productivity that is consistent with some of the earliest hypotheses regarding lake ontogeny (e.g., Pearsall, 1921; Deevey, 1942). For the period of record contained in these young lakes, this rise is dependent on sustained inputs of nitrogen from catchment vegetation. The successional development to spruce forests at the two lower-bay sites is accompanied by a gradual loss of N from the water column and a reduction in diatom production. Classic studies of post-glacial soil development at Glacier Bay have shown how soil-N concentrations increase with the

initial succession to alder, and then decrease as spruce forests appear and N becomes sequestered in living and dead biomass (Crocker and Major, 1955; Bormann and Sidle, 1990). The diatom-inferred TN trajectories would suggest that soil-N concentrations are tightly linked via runoff to those in lake-water. The near-absence of alder in the early history of the Bartlett Lake catchment is thus manifest in overall lower N concentrations in the lake, however, the abundant alder at Blue Mouse Cove leads to high and sustained lake-water N.

The importance of local differences in hydrology, geology, and terrestrial succession in controlling lake development has been emphasized in our previous discussions of the Glacier Bay chronosequence (Engstrom and others, 2000; Fritz and others, 2004). What we demonstrate here is just how tight the biogeochemical coupling is between terrestrial succession and lake development. These results imply that autogenic succession in lakes—especially small lakes, as those studied here—is largely a deterministic consequence of primary succession in the terrestrial catchment.

Management Implications

Lake systems exhibit natural variability in water chemistry and trophic condition that is closely tied to changes in their terrestrial catchments. In Glacier Bay, vegetation and soils continue to evolve in a dynamic response to deglaciation that occurred decades or even centuries ago. Understanding this landscape evolution and the linkages between terrestrial and aquatic environments is crucial to discerning impacts of human origin in any program for long-term environmental monitoring.

Acknowledgments

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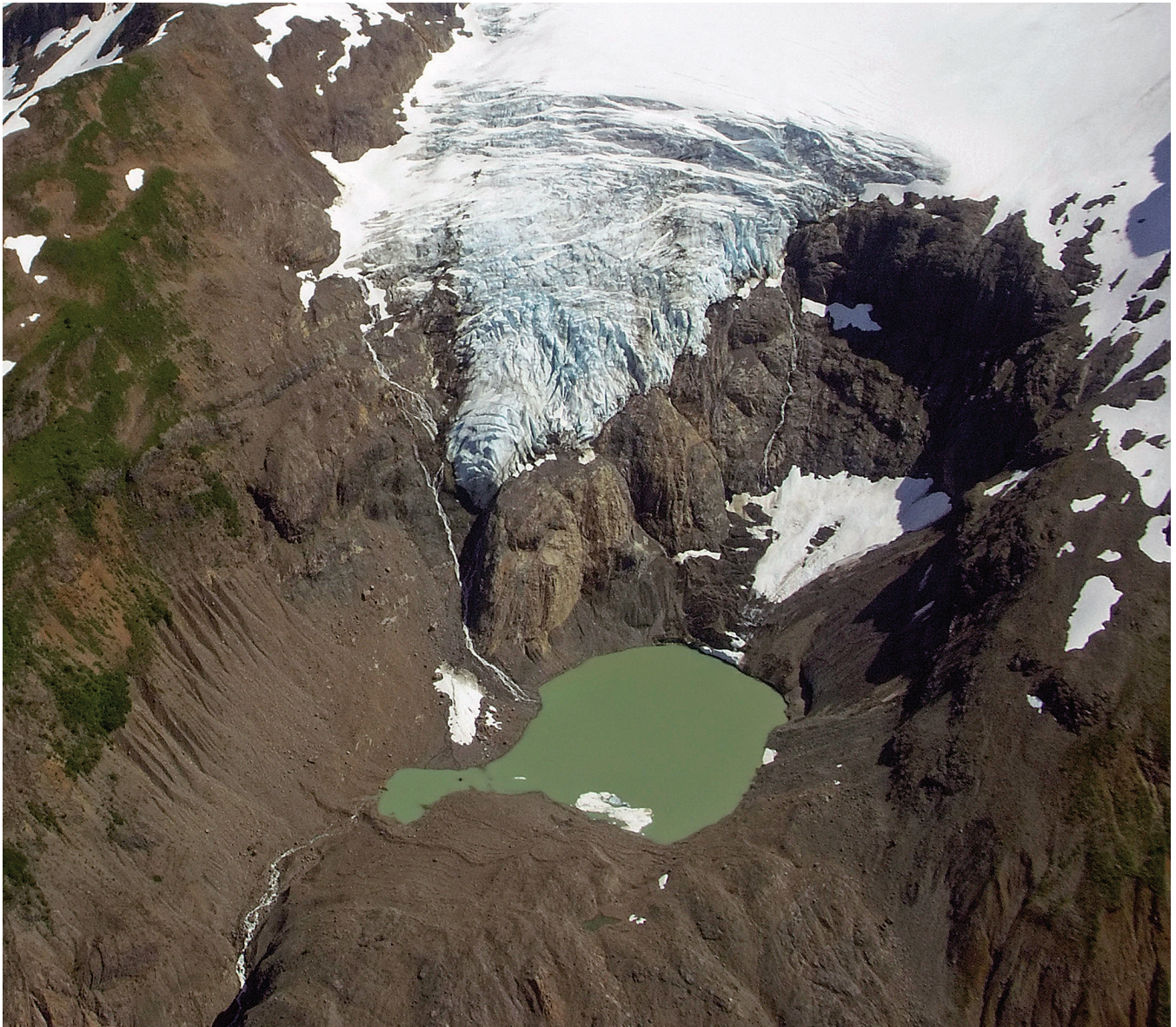
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An unnamed cirque lake in the Fairweather Mountains. (Photograph taken by Bill Eichenlaub, National Park Service.)