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Contribution of Log Mat Periphyton to Benthic Productivity at Spirit Lake, Mount St. Helens National Volcanic Monument, WA, USA

Abstract

Spirit Lake, in southwest Washington, USA, was changed as a result of the 1980 eruption of Mount St. Helens. The lake morphology was altered by debris flows and the water was sterilized of most living organisms. Trees felled by the lateral blast and subsequently washed into the lake comprise a floating log mat which now covers 20% of the lake's surface area, providing a novel substrate for benthic productivity. By investigating the succession in this volcanic landscape's rapidly recovering aquatic ecosystem, our research specifically addressed the following questions related to the role of the floating log mat and associated benthic periphyton on sedimentary inputs of organic material: (1) Do patterns of log mat occupancy and related deposition of benthic periphyton correlate to spatial variation in organic sedimentary inputs? (2) Has benthic productivity changed over the lake's 40-year history since the initial establishment of the log mat? To address our questions, we analyzed biological and geochemical data derived from sampling the floating logs, sediment traps in the water column, a set of shallow sediment samples, and two sediment cores in areas of differing log mat occupancy. We used carbon and nitrogen elemental concentrations and stable isotope values of sediment organics to estimate the relative contributions of organic source materials (phytoplankton, macrophytes, periphyton) and diatom assemblages to infer information about changes through time. We found that spatial trends in sources of sediment organics corresponded to patterns of floating log mat occupancy, with higher contributions of periphyton-derived biomass in areas with more frequent log presence. These results provide insight into the dynamic role of log mat-derived productivity in the ongoing recovery and evolution of the Spirit Lake ecosystem. Our findings also underscore the importance of understanding and managing coarse woody debris in oligotrophic lakes as a substrate for benthic primary productivity that supports the whole lake ecosystem.

Keywords: diatom assemblage, carbon stable isotopes, coarse woody debris, lake ecosystem, sediment organics

Introduction

Spirit Lake is located northeast of Loowit/Mount St. Helens (Figure 1a) and prior to the 1980 eruption the lake was well-oxygenated and nutrient-poor, sustaining healthy populations of zooplankton and phytoplankton (Larson 1993, Dahm et al. 2005). The lake was physically and biogeochemically altered by the eruption. A landslide of hot volcanic debris sterilized the lake of most living organisms

and changed lake morphology, resulting in a 30% increase in lake volume and a 108% increase in surface area (Gawel et al. 2018). The pre-eruption lake basin was 5.3 km² with a mean depth of 37 m, while the post-eruption lake's surface area is approximately 11 km², with a mean depth of 23 m (Larson 1993, Figure 1a). At present, Spirit Lake is temperate, oligotrophic, and dimictic (Gawel et al. 2018).

Limnological research in the 40 years since the eruption has largely focused on the recovery of the open water ecosystem, with an emphasis on changes in primary productivity and lake chemistry (Larson 1993, Dahm et al. 2005, Larson et al. 2006,

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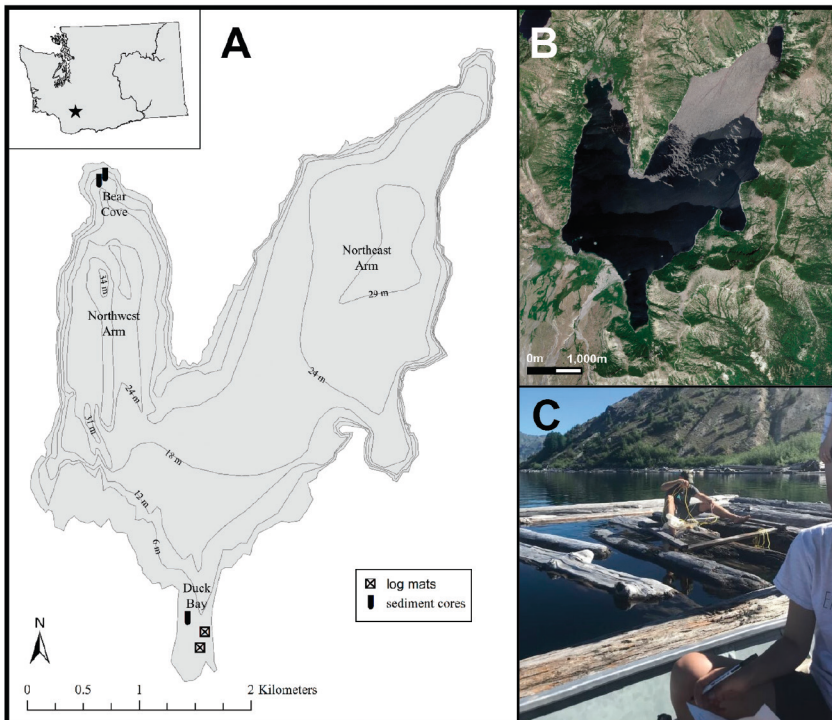


Figure 1. (A) General location and bathymetric map of Spirit Lake. Core locations are marked with a dagger and constructed log mats are marked with a boxed X. (B) Satellite image (Map data: Google ©2021, Image Landsat, Copernicus) showing floating log mat coverage of Spirit Lake. (C) Photo of log mat constructed for sampling.

Gawel et al. 2018). Despite the abundance of volcanic volatiles, Spirit Lake remained nitrogen-limited, likely as a result of the nitrogen depletion of source material, including ash and vegetation deposited in the lake basin. Nitrogen-fixing blue-green algae were present in the lake several years post-eruption, in addition to heterotrophs and detritivores that derived energy from decomposing organics and oxidizing particulate organic carbon (Larson 1993).

As lake levels stabilized and dissolved oxygen levels increased, the period between 1983 and 1986 represented a “biological renaissance” for the Spirit Lake ecosystem. During this period, nearly 138 species of phytoplankton were recorded in the lake’s annual sampling—65% of which were diatoms (Larson 1993). In the early 1990s, beds of submerged aquatic macrophytes developed and became locally extensive in Duck Bay

and along the lake’s south shore (Dahm et al. 2005). Presently, Spirit Lake supports a diverse community of zooplankton, phytoplankton, periphyton, and aquatic plants. Although fish were not able to re-establish in the lake naturally, rainbow trout (*Oncorhynchus mykiss*) were introduced in 1993 through unsanctioned stocking (Lucas and Weinheimer 2005).

Although post-eruption monitoring has established the timeline of recovery for Spirit Lake’s open water environ-

ment, benthic habitats were not well sampled over the same time period. Of particular interest to us was the knowledge gap regarding the extensive floating log mat and its potential influence on primary productivity and sediment deposition. Trees felled during the eruption were washed into Spirit Lake, forming a floating log mat that initially covered 40%—now 20%—of the lake’s surface area (Larson 1993, Gawel et al. 2018). The floating log mat is mobile and propelled by prevailing winds; analysis of time lapse photos taken in 2014 showed that logs were tightly packed in the northern arms of the lake most often, with some seasonal variation (Figure 1b). Logs were often present in high numbers in the Northwest Arm (NW Arm) in the late summer to early fall. Regardless of season, the log mat spent comparatively little time in Duck Bay (Gawel et al. 2018).

Spirit Lake's floating logs are covered below the waterline in a variable thickness of biofilm, which includes a periphyton community primarily composed of diatoms, green algae, and cyanobacteria, as well as wood fibers and smaller amounts of other organic material including invertebrates, insect and amphibian eggs, insect larva, and extracellular material. Our research was specifically focused on the periphyton fraction of the biofilm as a source of benthic primary productivity for the lake.

The role of coarse woody debris (CWD, also referred to in the literature as coarse woody habitat) in riverine ecosystems is well understood (Thompson et al. 2017, Keddy 2023) but has been less studied in lakes (Vadeboncoeur et al. 2008, Czarnecka 2016). Coarse woody debris can persist in lakes for centuries and provide a wide range of benefits to lake ecosystems, including habitat heterogeneity and structure, and disturbance regulation (Guyette and Cole 1999, Helmus and Sass 2008, Czarnecka 2016, Pearce et al. 2022). It is important to understand the biogeochemical and ecological role of CWD in lake ecosystems as human activities such as shoreline deforestation during lakeshore development and removal of CWD for recreation and timber harvest result in a loss of the benthic habitat it provides (reviews in: Schindler and Scheuerell 2002, Francis and Schindler 2006, Czarnecka 2016).

Coarse woody debris often occurs in the littoral zones of alpine lakes, providing a substrate for benthic productivity, yet in Spirit Lake the abundant CWD is not restricted to the littoral zone. Since most of the CWD in Spirit Lake exists as a floating log mat, this typically shoreline-based benthic habitat is extensive and mobile throughout the lake. Although CWD typically hosts a small fraction of total lake productivity, particularly in large lakes (Vadeboncoeur et al. 2008), Spirit Lake's floating log mat provides a substantial amount of substrate for benthic primary productivity across nearly a fifth of the lake's total surface area (Gawel et al. 2018). The rapid and massive pulse of CWD into Spirit Lake during the 1980 eruption, and the persistence of the resulting log mat, provides a unique opportunity to study the role of CWD in

linking benthic and pelagic habitats after a major disturbance event (Schindler and Scheuerell 2002).

A nutrient budget developed for Spirit Lake highlighted the potential role of log mat periphyton as an important nutrient input (Gawel et al. 2018). Benthic productivity to lake ecosystems is often underestimated (Vadeboncoeur et al. 2002, Vander Zanden and Vadeboncoeur 2020) and may be more important in a lake with abundant CWD surface area available for periphyton growth. We investigated the role of the floating log mat in the Spirit Lake ecosystem by asking: (1) Do patterns of log mat occupancy and related deposition of benthic periphyton correlate to spatial variation in organic sedimentary inputs? (2) Has benthic productivity changed over the lake's 40-year history since the initial establishment of the log mat?

Methods

Floating Log Mat Surface Area Estimates

We used Google Earth satellite imagery (taken in July 2017) to estimate the three-dimensional wetted surface area of floating log mat wood available for periphyton production (Smokorowski et al. 2006). We randomly chose ten 100-m² sections of log mat from the aerial image (0.045% of the total log mat area), and within each section we measured the length (*l*) and mid-length diameter (*d*) of every log. If the dimensions of a log extended past the edges of the image section, we scaled the measurements accordingly to only include the portion of the log inside the section. Since the image includes logs and the water matrix between logs, we accounted for the portions of the image occupied by the water matrix. We used the radius (*d*/2), length (*l*), and surface area of a semi-cylinder $[(2\pi rl) + (2\pi r^2) \times 0.5]$, assuming the logs were half submerged, to estimate the total wetted surface area of all logs within each image section. We then averaged the total surface area across the ten image sections to obtain an estimate per 100 m² of floating log mat. We extrapolated the average surface area per 100 m² of log mat to a published two-dimensional estimate of log mat coverage for the entire lake (approximately 2.2 km²; Gawel et al. 2018) to obtain a full lake

surface area value. All data organization was done in Microsoft Excel, and average values were calculated as means, with variation around the means reported as standard deviation.

Sampling Summary

Samples were collected during the summer seasons of 2010, 2011, 2017, and 2018 from a fixed log mat constructed for the purpose of sampling periphyton and log wood, from sediment traps suspended beneath the fixed log mats and in open water locations, using plankton nets in open water locations, and via dredging and coring lake bottom sediments. Dredged surface sediment samples were collected from throughout the lake, and sediment cores were taken from two locations with similar depth and bathymetry in the NW Arm and Duck Bay. The locations available for sediment sampling were limited by log mat interference, the thickness of woody debris on the lake bottom, and the logistical challenge of transporting sediment cores from the lake without road access (Figure 1a).

Ecosystem sampling was concentrated in shallow bays on the south end of the lake nearest the trail approach to support safe and regular access. Duck Bay is a shallow bay with approximately a 7 m depth located at the south end of the lake. Here, we constructed two 25-m² experimental floating log mats for repeated sampling. Existing floating logs were collected from Duck Bay and the shoreline. Four of the longest logs were secured together to form a square outer frame for the mat by chaining together eyebolts drilled into the top of the ends of each log. Smaller logs were enclosed inside the square but not attached; they remained free-floating within the frame. The log frame was anchored by one corner such that it remained in the same location to facilitate repeat sampling but was able to move and reorient with the wind (Figure 1c).

Ecosystem Sample Collection

Macrophytes and Phytoplankton—Macrophyte foliage samples ($n = 12$) were collected in 2017 using a plant rake in approximately 1 m water depth. Samples included the most common taxa at three locations in Duck Bay and the NW Arm:

Eurasian watermilfoil (*Myriophyllum spicatum*), charophyte algae (*Charophyta* sp.), and *Potamogeton* sp. Phytoplankton samples ($n = 2$) were collected in 2017 by vertical tow from a depth of 5 m in open water using an 80 μ m mesh plankton net (30.5 cm diameter). Samples were then preserved in 1% Lugols solution in 250 mL Nalgene bottles (Gawel et al. 2018).

Log Mat Periphyton and Wood—Periphyton samples ($n = 9$) were collected in 2017 by suspending Wildco periphyton samplers (containing glass slides) and ceramic tiles directly under the constructed log mats using a weighted rope. Tiles and glass slides were left for two to six weeks to allow for sufficient periphyton biomass accumulation, and then retrieved and scraped into a sampling container using a razor blade. Floating log wood samples ($n = 3$) were collected in 2010 from free-floating Douglas-fir (*Pseudotsuga menziesii*) logs using an oscillating saw. The outer 5 mm of each sample was discarded, and then wood samples were taken from a depth of 5 to 10 mm below the log surface to look at wood characteristics separate from surface wood that is colonized by biofilm periphyton.

Suspended Sediment Traps and Surface Sediment—Sinking particulate matter samples ($n = 5$) were collected in 2017 from sediment traps constructed from 61-cm long, 10-cm diameter black acrylonitrile butadiene styrene (ABS) pipe with a conical funnel glued to the bottom fitted with a removable 125 mL acid-washed Nalgene bottle. Sediment traps were suspended 2 m above the lake bottom attached to nylon line anchored to the bottom and buoyed by near-surface floats (Gawel et al. 2018). Lake bottom surface sediment samples (composite of top 0–3 cm) were collected in the summers of 2010, 2011, and 2018 from 36 locations throughout Spirit Lake using a hand-hauled petite ponar dredge (Wildco, Yulee, FL). The relatively low sedimentation rate in Spirit Lake (approximately 0.25 cm·yr⁻¹) and the low temporal resolution provided by the dredging method mean that surface sediments collected from the three years of sampling represent time-averaged and overlapping windows of sediment accumulation.

A 10 mL subsample of dredge sediment was retained for analyses after removal of any vegetative or wood fragments. All samples were transported on ice and refrigerated until analysis.

Sediment Cores

Two sediment cores were collected in 2018 using a Wildco K-B gravity corer. Sediment cores (17 cm length each) were collected from Duck Bay and the NW Arm at sites in 6 m water depth (Figure 1a). The length of both cores was constrained by eruption derived debris, including large pieces of pumice and wood that plugged the bottom of the coring device, indicating a complete retrieval of the post-eruption sedimentation from the lake. The sediment cores were transported on ice and kept in refrigerated storage. Cores were split vertically and subsampled at 0.5–2.0 cm intervals for biogeochemical analyses and 1 cm intervals for diatom analyses.

Because of the short time horizon of the sediment cores, dating of the materials using ^{210}Pb or other isotopic methods was not possible. When both cores were retrieved, large pieces of pumice and woody debris were lodged in the coring tube, through which we could core no further. We used this base of the core as a presumed date of approximately 1980; other possible temporal markers are discussed in the results.

Sediment Core Diatom Assemblages—Sediment subsamples were processed using standard preparation techniques to clean samples of carbonate and organic material (Renberg 1990). Slides were examined with a 100x oil immersion microscope. Each slide was counted until either 10 transects of the slide had been completed, or 300 diatoms per slide were identified using standard diatom reference materials (e.g., Krammer and Lange-Bertalot 1986–1991, Spaulding et al. 2021) with taxonomic reference to published limnological studies from Spirit Lake (Larson 1993). Hill's N_2 index was used to calculate the effective diversity (Hill 1973).

Elemental and Isotopic Analyses

Macrophyte, periphyton, wood, and sediment (suspended, surface, and core) samples were dried

at 50 °C to a constant weight and homogenized with a mortar and pestle. Subsamples of 1–5 mg (approximately 30 mg for sediments) were weighed into tin capsules. Phytoplankton and suspended sediment samples were vacuum filtered (5 μm polycarbonate). Samples were dried and 0.5 mg filtrate was gently scraped from the filter and weighed into tin capsules.

Samples were analyzed for weight percent of carbon and nitrogen (%C and %N) and carbon stable isotope ($\delta^{13}\text{C}$) values at the Washington State University Laboratory for Biotechnology and Bioanalysis (WSU LBB2), the University of Washington Seattle IsoLab (UW ISOLAB), and the Central Washington University Murdock Research Laboratory (CWU MRL) using an elemental analyzer coupled to an isotope ratio mass spectrometer. $\delta^{13}\text{C}$ values are reported relative to the PeeDee Belemnite standard and in parts per thousand (‰). All biogeochemical data are reported in Supplemental Table S1 (available online only).

Results

Floating Log Mat Wetted Surface Area Estimate

The floating log mat occupies approximately 20%, or 2.2 km², of the 11 km² lake surface area when at high packing density (Gawel et al. 2018). The average (\pm standard deviation) log mat wetted surface area for the 100-m² image sections was 97.5 \pm 16.3 m² (range 72.5–122.5 m²), translating to a whole-lake estimate of 2.15 \pm 0.36 km² of available log mat substrate for periphyton in Spirit Lake.

Elemental and Isotopic Values of Organic Sources to Sediment

The two sources directly contributing carbon and nitrogen to pelagic lake areas, log mat periphyton and phytoplankton, had $\delta^{13}\text{C}$ values and C:N ratios that were used together to infer general patterns of organic material inputs. The log wood itself did not have measurable nitrogen content, and thus a C:N ratio for log wood is not reported (Table 1). Sinking particulate matter captured in the sediment

traps beneath the experimental log mat had %C, C:N, and $\delta^{13}\text{C}$ values that were similar to the log mat periphyton values (Table 1). The log wood itself did not appear to contribute substantially to the sediment traps.

Biogeochemical Patterns in Surface Sediments

The %C values in surface sediments were used to interpret differences in the quantity of organic material incorporated across sediment sampling locations. Surface sediment %C values were highest (> 3.0) in the samples collected from shallow reaches of Duck Bay and the NW Arm which were occupied by macrophyte beds (Figure 2a). The rest of the samples were collected from sites without observable macrophytes, either because the lakebed depth was below the photic zone, or because log coverage precluded consistent light penetration to the lakebed. The weight percent C:N ratios were calculated for the samples with values for both elements, and the C:N and $\delta^{13}\text{C}$ values (Figure 2b and 2c, Table 1) were used to examine spatial differences in organic source contributions to surface sediments. While the organic sources had discreet C:N ratios, their $\delta^{13}\text{C}$ distributions were overlapping and surface sediment $\delta^{13}\text{C}$ values were interpreted conservatively and in tandem with C:N ratios. Generally, surface sediments from areas of the lake with high log mat occupancy, such as the NW Arm and NE Arm, had C:N and $\delta^{13}\text{C}$ values similar to log mat periphyton. Duck Bay and the area immediately north had variable C:N and $\delta^{13}\text{C}$ values, including values that were most consistent with phytoplankton.

Sediment Cores

Biogeochemistry—The %C values decreased with core depth at both sites, although the %C values in the top approximately 10 cm were consistently higher in the NW Arm than Duck Bay (Figure 3a), which was in agreement with the spatial difference in the dredge sample results. The NW Arm sediment core $\delta^{13}\text{C}$ record was relatively invariant with depth and ranged from -25.1 to -27.9‰ (Figure 3b). In contrast, the Duck Bay core $\delta^{13}\text{C}$ record was bimodal; from 0 to 7 cm depth the core $\delta^{13}\text{C}$ values were on average 6‰ lower than in samples from 10 to 17 cm depth (-33.4 vs. -27.2‰ , respectively; Figure 3b). %N values were low in both cores, and C:N ratios were consistently higher in the NW Arm core than the Duck Bay core (Figure 3c).

Diatom Assemblages—Cleaned sediments in the Duck Bay and NW Arm cores were composed exclusively of siliciclastic sediment and amorphous volcanic glass below 10 cm core depth. In Duck Bay, the 9–10 cm interval contained numerous broken diatom frustules and some complete frustules, however, only 54 frustules were identifiable in a standard slide preparation after 10 slide transects. Interval 8–9 cm had more complete frustules, with 100 identifiable in a standard slide preparation. Between 8–10 cm, species were predominantly large *Navicula*, *Nitzschia* and *Pinnularia* species; plankton tows in 1980–1982 found no evidence of living diatoms but noted a few remnants of non-living frustules of similar species (Larson 1993, Larson et al. 2006).

Table 1. Means (and standard deviations) for potential organic sources to lake sediments, with sample size (n) given after sample type. All samples were collected in 2017, except for log wood in 2010. Weight %N values from log wood were below detection.

Sample type (n)	Sample location	%C	C:N	$\delta^{13}\text{C}$ (‰)
Log mat periphyton (9)	Glass and ceramic slides suspended beneath tethered logs	12.1 (2.1)	9.4 (1.6)	-28.4 (1.8)
Phytoplankton (2)	Open water plankton tow	25.3	5.1	-31.9
Macrophyte (12)	Shoreline rake samples in Duck Bay	35.4 (5.0)	18.6 (3.3)	-21.2 (5.9)
Log wood (3)	Floating logs	46.0 (2.4)	NA	-24.2 (1.1)
Suspended sediment trap (5)	Sediment traps suspended from experimental log mat	13.5 (5.1)	8.3 (0.9)	-30.8 (2.6)

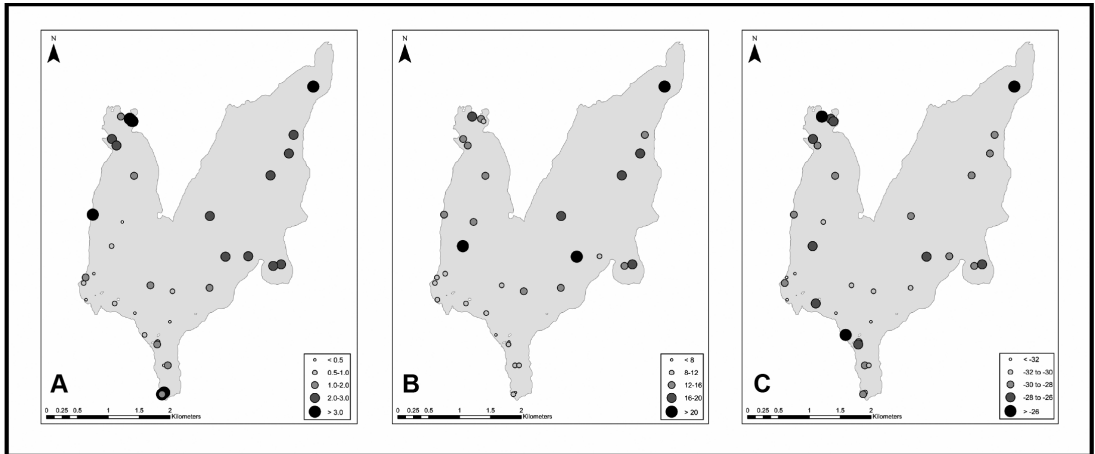


Figure 2. Distribution of surface sediment organic elemental and isotopic values. (A) %C, (B) C:N, (C) $\delta^{13}\text{C}$ (‰).

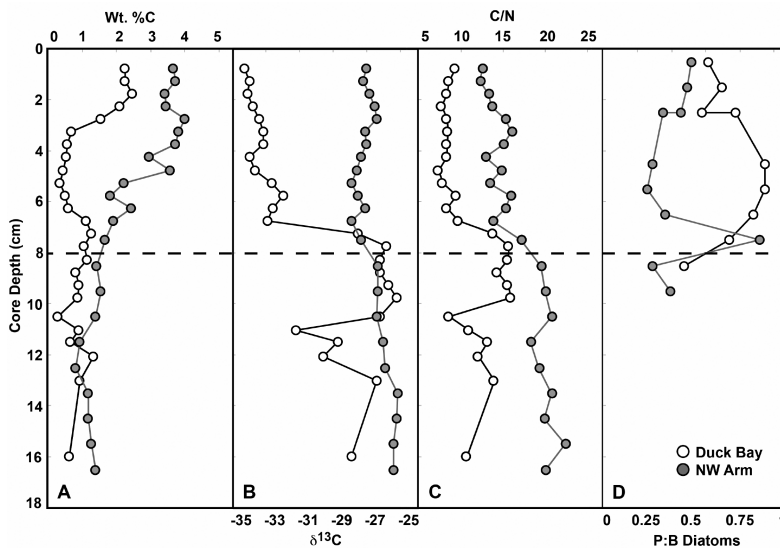


Figure 3. Biogeochemical and diatom records from the Duck Bay and NW Arm sediment cores. (A) %C, (B) $\delta^{13}\text{C}$ (‰), (C) C:N, (D) ratio of pelagic to benthic taxa (P:B) in diatom assemblages. The dashed line indicates an approximate age of 1983 in both cores.

Sediments from the NW Arm were similar, with no whole diatom valves present below 9 cm depth. Beginning at the 7–8 cm interval in both cores, diatom frustules were found in much greater abundance and diversity (Figures 4a and 4b). Species composition at this time also more closely resembled the contemporaneous monitoring

in 1983, with *Asterionella formosa* and *Diatoma tenuis* (identified at the time as *Diatoma tenue* v. *elongatum*; Larson et al. 2006) found in abundance; the 7–8 cm interval in Duck Bay and 8–9 cm section in the NW Arm therefore are inferred to represent approximately 1983.

Duck Bay Diatoms—In the Duck Bay core, 120 total diatom species and varieties were identified. Overall richness and diversity of the assemblage was lower from 9 to 5 cm, then increased to the present (Figure 4a).

From approximately 8 cm depth, where presumed autochthonous diatoms begin to appear, until 5 cm depth, the Duck Bay planktonic diatom community was comprised primarily of *A. formosa* and a number of small *Stephanodiscus* species, mainly *Stephanodiscus minutulus*, along with *D. tenuis*, and several benthic attached species, predominantly from the

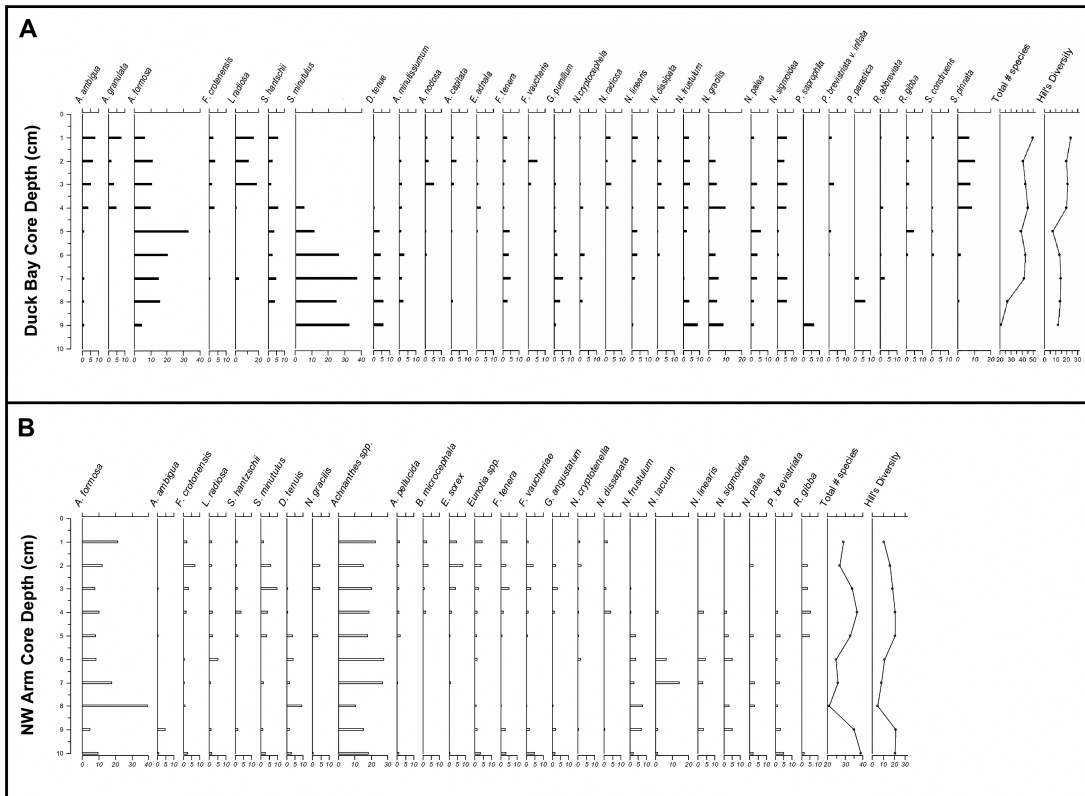


Figure 4. Diatom assemblage changes in the (A) Duck Bay and (B) NW Arm sediment cores. Species or species complexes occurring in > 5 intervals or at greater than 5% in two or more intervals are shown as relative abundances on the x-axis; planktonic and tychoplanktonic species are listed first, moving to benthic species at the right of the panels. Total number of species encountered and Hill's diversity are also provided. Full species names and relative abundance data are in Supplemental Table S2 (available online only).

Gomphonema and *Nitzschia* genera. Over time, the relative abundance of *A. formosa* waned while *Aulacoseira* species became the more abundant open-water taxa starting at approximately 4 cm depth. The benthic diatom community was varied, with *Nitzschia*, *Gomphonema*, and small fragilarioid taxa, including tychoplanktonic *Staurosira* and *Staurosirella*, being relatively common and becoming more diverse through time (Figure 4a). The ratio of planktonic to benthic species (P:B, Figure 3d) showed a dominance of planktonic species in most of the Duck Bay core, with a shift to an even relative abundance in the top 3–4 samples.

NW Arm Diatoms—114 total diatom species and varieties were recorded in the NW Arm core. Overall species richness and diversity was lower than in the Duck Bay core (Figures 4a and 4b) and

did not show the same increasing species diversity toward the top of the core as seen in Duck Bay. The NW Arm core followed broadly similar patterns to Duck Bay, with *A. formosa* comprising a large portion of the initial plankton recovery post-eruption; however, unlike Duck Bay, after that initial bloom, benthic taxa were relatively more abundant than plankton (Figure 3d). Small *Achnanthes* species were relatively abundant throughout the core. *Nitzschia* species, and to a lesser extent species in *Navicula* and *Pinnularia* genera, were common toward the base of the core. At interval 5–6 cm, small *Stephanodiscus* species and *Lindavia radiosa* (identified at the time as *Cyclotella comta* v. *radiosa*; Larson et al. 2006) became more common before declining again toward the top of the core. Around the same

interval, roughly 5–6 cm, the benthic assemblage became more diverse, with a decline in the more common *Nitzschia* species as a more diverse assemblage including *Epithemia* and *Eunotia* species and *Rhopalodia gibba* became more common (Figure 4b).

Discussion

The Relationship Between Log Mat Occupancy and Spatial Distribution of Sedimentary Inputs of Organic Material

To test for spatial variation in sedimentary inputs of organic material related to log mat occupancy we relied upon elemental and isotopic analyses of potential organic sources and surface sediments. We found predictable differences in the biogeochemical values of the three main primary producers in Spirit Lake. The relatively high %C values of aquatic macrophytes compared to phytoplankton and periphyton likely reflect the contribution of carbon-rich structural materials, such as cellulose, to macrophyte biomass. The C:N ratios of the three organic sources at Spirit Lake were similar to the general ranges reported by Finlay and Kendall (2007) for other lacustrine systems; phytoplankton was lowest (range = 5–8), and periphyton was at the lower end of the range given for periphyton and macrophytes (range = 10–30). Differences among Spirit Lake primary producer $\delta^{13}\text{C}$ values reflected a complex set of interacting factors, including physiological differences which influence the isotopic fractionations that occur during photosynthesis, and variation in the $\delta^{13}\text{C}$ values and concentrations of dissolved inorganic carbon (DIC) sources. Variation in the $\delta^{13}\text{C}$ values of DIC can be due to physical factors such as mixing and the formation of boundary layers, as well as biological factors such as rates of photosynthesis and respiration by aquatic autotrophs. Finlay and Kendall (2007) reported a general range of $\delta^{13}\text{C}$ values for freshwater primary producers of -30 to -20‰. The average $\delta^{13}\text{C}$ values (with standard deviation) of the Spirit Lake primary producers fall within this range, and also meet the expectation that $\delta^{13}\text{C}$ values among autotrophs will increase in order from planktonic (free living phytoplankton), to periphytic

(benthic periphyton), to lentic (shallow embayment macrophytes) (Finlay and Kendall 2007).

In deep oligotrophic lakes, spatial variation in sedimentation rate and organic carbon storage can be related to a number of factors, including distance from riverine inputs and water column productivity (Zhang et al. 2023) and the extent of different habitats in the lake as controlled by water depth, clarity, and availability of various substrates (Hofmann et al. 2020). Typically, attached periphyton is limited to regions of the lake where sediment, CWD, rock, or macrophytes provide substrate within the photic zone. Macrophyte growth is spatially restricted and therefore likely to influence the isotopic signature of the sediments predominantly in the shallowest portions of shoreline embayments (Madsen et al. 2001, Gawel et al. 2018).

We used the %C, C:N, and $\delta^{13}\text{C}$ values of the primary producers in Spirit Lake to make inferences about the relative contributions of these sedimentary organic sources to surface sediments. Specifically, we identified the influence of floating log mat occupancy (controlled by prevailing winds) on the spatial variability of periphyton-derived organic material supplied to pelagic sediments. We directly compared the periphyton biogeochemical values to those of the suspended sediment in the water column under the log mat to confirm that periphyton was the main source of organic material derived from the log mat. The absence of debris from log wood in the sediment traps may be because over the 40 years the log mat has existed, the log surface has been weathered and abraded to the extent that the wood that remains is resistant.

Higher log mat occupancy allows for higher organic loading in what would otherwise be open water areas in the NW and NE Arms as evidenced by higher surface sediment %C values compared to the sediment on the southern side of the lake (Figure 2a). The elevated sediment %C values found in the shallowest nearshore areas of the lake (including Duck Bay) likely reflect the input of macrophyte-derived biomass. Surface sediment C:N and $\delta^{13}\text{C}$ (Figure 2b and 2c) values suggest a higher relative input of phytoplankton-derived

biomass in the open water of Duck Bay and the southern areas of the lake and a higher relative input of periphyton-derived biomass in the NW and NE Arms.

Surface sediments provide a spatially integrated record of the Spirit Lake ecosystem, and yield insight into how and where energy and nutrients are cycling through the ecosystem. The wetted surface of the log mat on average provides $> 2 \text{ km}^2$ of benthic habitat for periphyton growth. Maps of surface sediment %C, C:N, and $\delta^{13}\text{C}$ values illustrate the connection between periphyton productivity and high organic input and storage, and the role of the log mat in regulating the distribution of periphyton-derived energy and nutrients throughout the lake. Future research is needed to understand the dynamics of the food web supported by log mat periphyton in Spirit Lake and how this unique benthic food web interacts with the pelagic food webs in different areas of the lake.

Sediment Core Records and Benthic Productivity Over 40 Years

Core retrieval was limited by pumice and wood which was encountered at approximately the same depth in both collected cores and in several additional trial cores. From the base of both cores, to approximately 10 cm depth in the NW Arm and 9 cm depth in Duck Bay, the sediment had low organic content ($< 1.5 \text{ \%C}$) and slide samples prepared for diatom analysis were composed entirely of siliciclastic sediments, presumably from rapid deposition of volcanoclastic material following the eruption. Above these depths, diatom fragments began to appear; however, initially frustules were low in abundance relative to volcanic glass and from heavily silicified diatom taxa consistent with being derived from re-worked older sediment entering the lake. We related this period of sedimentation with plankton tows taken in 1982 which found non-living frustules of several similar diatom taxa, but no living cells; this was a time of high bacterial productivity in the lake (Larson 1993).

Beginning around 8 cm depth in both cores, diatom frustules became orders of magnitude more abundant and were initially dominated by

Asterionella formosa, *Diatoma tenue* and *Achnanthes* species in the NW Arm and *A. formosa*, *D. tenue* and *Stephanodiscus* species in Duck Bay. This was consistent with observations from contemporaneous plankton tows, which noted *A. formosa* as the predominant taxon and abundant *D. tenue* (identified at the time as *D. elongatum* v. *tenuis*) in samples collected in 1983 (Larson et al. 2006). We use these markers to approximate 1983, the beginning of the lake's post-eruption recovery phase, at approximately 8 cm in the sediment core records. Although the lack of independent dating markers hindered dating certainty, the preponderance of evidence suggested that below this depth sediments were from rapid post-eruption deposition and re-working rather than autochthonous sedimentation.

Although difficult to discern the exact timing of later changes in the sediment cores without isotopic dating, there are a few lines of reasoning to roughly link observations in the core to known lake events; Larson et al. (2006) reported a number of notable changes in the planktonic species composition in samples during the 1989 season that we tentatively tied to our core diatom records. Specifically, they noted the stable return of cyanobacteria to the water column, alongside a higher count of *Epithemia sorex*, a diatom that can have a symbiotic relationship with cyanobacteria. We observed a small increase in *E. sorex* in the NW Arm core beginning at approximately 4 cm. The 1989 plankton tows (Larson et al. 2006) also noted a change in dominance from *A. formosa* to *Lindavia radiosa* (identified at the time as *Cyclotella comta*). This same species shift was apparent at approximately 4–5 cm in Duck Bay where *A. formosa* declined in relative abundance and *L. radiosa*, as well as several *Aulacoseira* species, became more common. Although imprecise, we reasoned that the intervals between approximately 4–5 cm correlated with changes noted in plankton tows during the late 1980s to early 1990s. Overall sedimentation rates were reasonable with this interpretation; if 1983 was marked at 8 cm it would indicate a sedimentation rate of roughly 0.25 cm per year.

Comparison of the two core diatom records shows higher relative abundance of planktonic diatom taxa in Duck Bay than the NW Arm. The Duck Bay C:N and $\delta^{13}\text{C}$ records were also consistent with phytoplankton as the main sedimentary organic source, while core values appeared closer to periphyton in the NW Arm. Our findings are consistent with the lower presence of the log mat and its substrate for benthic taxa in Duck Bay. The locations where sediment cores were collected were deep enough that sediment resuspension in those locations should be relatively minor (see as a comparison results for Lake Tahoe, Reardon et al. 2014). While it is possible that some sediment from nearby shallow nearshore areas could be transported to these locations and deposited, it is very unlikely that the sandy sediments found here would be transported the length of Spirit Lake, a distance of 3.2 km, and therefore the two sampling locations should be independent of each other.

Overall diatom species richness and diversity were slightly higher in Duck Bay compared to the NW Arm; diversity increased with time, with the main increase occurring between 4 to 5 cm when a number of new planktonic species become relatively abundant, as well as *S. pinnata* which is commonly associated with epiphytic substrate. We inferred that this increase in diatom diversity roughly correlated to the time period when macrophyte beds were observed to increase in Duck Bay and fish were introduced to the lake. The impact of CWD on fish habitat and food webs is well documented (Sass et al. 2022) and while the direct influence of fish introductions on primary producer communities may be better understood in eutrophic settings (Jeppesen et al. 1997, Hu et al. 2017), influences of fish introductions have been documented in many lake contexts (Larson et al. 2002, Strock et al. 2013, Sienkiewicz and Gasirowski 2016).

The NW Arm was generally slightly lower in species richness and more stable in overall diversity, although there was turnover in the dominance and relative abundance of particular benthic species over time. This may be due to a more static environment dominated by the presence of the log mat for most of the year. The NW

Arm, after the initial pulse of *A. formosa* as the lake was re-oxygenated and began to recover, recorded a relatively steady ratio of planktonic to benthic diatoms, although it also recorded a subtle assemblage shift around 4 cm with the appearance of *Epithemia*, *Rhopalodia*, and *Amphipleura* taxa, among others that had not been present in lower intervals. This assemblage shift may also be related to ongoing ecological re-structuring in the lake, although the relationship between ecological re-structuring and fish or macrophytes is less clear.

Although Duck Bay has a more dynamic set of habitats compared to the NW Arm, evidence suggests that the NW Arm may be more productive. From the inferred start of autochthonous organic productivity around 8 cm depth, the invariant $\delta^{13}\text{C}$ and C:N values in the NW Arm suggested a stable source of log mat periphyton. While periphyton abundance in the shoreline photic zone would vary as water level fluctuated, the floating log mat remained a dominant and comparatively stable platform for productivity. Based on %C data, the NW Arm is accumulating more organic sedimentary material than Duck Bay; as the two cores appear to have similar rates of sediment accumulation, autochthonous productivity in the NW Arm is keeping pace with higher inputs of inorganic material in Duck Bay where riverine inputs from the pumice plain are relatively higher. Together these observations provide evidence that, once colonized post-eruption, the logs have been a stable and highly productive habitat over time. This finding is consistent with surface sediment data and helps underscore the interpretation that this pattern in sedimentation has been consistent over the four-decade post-eruption history of the lake.

Importance of CWD for Benthic Productivity

The role of CWD in deep, oligotrophic lake ecosystems has been less studied compared to river systems; lakes described as having high productivity from periphyton are typically shallow with high light penetration to a large surface area. There is, however, a large range in the relative importance of periphyton to a lake's overall productivity, based on lake morphometry, clarity, and available habitat (Vadeboncoeur and

Steinman 2002). Spirit Lake's Duck Bay and NW Arm represent two different environments; Duck Bay is shallow, with low presence of woody substrate and with macrophyte beds only in the later part of the 40-year post-eruption period, while the NW Arm is approximately 30 m deep with low light penetration but high log mat substrate availability. Macrophytes were a spatially-restricted organic source in Spirit Lake and found mainly at water depths of 2–8 m; in water less than 2 m deep, plant growth was limited by the scouring action of wind-driven logs, and the photic zone did not reach more than 8 m water depth (Gawel et al. 2018).

Connectivity between benthic and pelagic food webs in lakes regulates the flow of energy and nutrients between habitats (reviews in: Schindler and Scheuerell 2002, Reynolds 2008). For example, a study of a deep oligotrophic lake in the Pacific Northwest showed how disturbance to nearshore habitats, which altered littoral benthic productivity, influenced the entire lake food web (Hampton et al. 2011). Although more research into the role of CWD-hosted benthic food webs in lakes is needed, we do know that CWD can provide habitat for benthic productivity in lacustrine ecosystems across broad temporal and spatial scales, as CWD can persist in lakes for hundreds of years (Czarnecka 2016) and can be distributed throughout littoral and pelagic areas (Gawel et al. 2018). We also observed that benthic productivity on the Spirit Lake log mat can support a diverse array of consumers at multiple trophic levels: habitat for emergent terrestrial insects, substrate for amphibians and aquatic invertebrates to feed and lay eggs, and perches for birds and mammals.

Plankton sampling in post-eruption surveys varied in location, timing, and frequency, and thus provided snapshots of seasonal primary productivity. Sediment cores add to these records with an integrated longer-term documentation of typical diatom community composition over time. The survey sampling throughout the 1980s and 1990s did not explicitly sample periphyton or benthic habitats and focused only on plankton tows from open water. Therefore, the sediment cores also add new information about the relative importance of

diatoms in those habitats to the primary producer community in the lake and their importance to total biomass in the lake over time. Benthic productivity is often under-studied in lake ecosystems and provides a significant organic contribution to Spirit Lake where the lake bottom, macrophytes, and the floating log mat all provide a substrate for primary productivity.

Conclusions

Spirit Lake's recent volcanic history allowed us to examine the dynamics of lake recovery and evolution after a major disturbance event. The extensive floating log mat provided an opportunity to understand the role of CWD at a larger scale than is typical for an alpine, oligotrophic lake. We examined the contribution of benthic productivity, specifically the role of log mat periphyton, to lake organic inputs and sedimentation patterns. Over the course of the past 40 years, floating log-mat-derived periphyton has been an identifiable source of sedimentary organic material in Spirit Lake. Biogeochemical and benthic diatom records showed higher accumulation of log mat organics in areas with higher log mat occupancy, despite a lower relative abundance of phytoplankton and low to absent submerged macrophyte communities, underscoring the importance of understanding and managing CWD in oligotrophic lake ecosystems as a substrate for primary productivity.

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