Late Pleistocene palaeoenvironments and a possible glacial refugium on northern Vancouver Island, Canada: Evidence for the viability of early human settlement on the northwest coast of North America

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ARTICLE INFO

ABSTRACT

Multi-proxy palaeoecological analyses of lake cores from two sites on northern Vancouver Island reveal previously undocumented non-arboreal environments in the region during the late Pleistocene. Radiocarbon, pollen, sedimentary ancient DNA (sedaDNA), diatom, and grain size analyses indicate that Topknot Lake on the west coast of northern Vancouver Island was not glaciated in the last 18,500 years, extending into the hypothesized regional glacial maximum. A cold herb-shrub coastal tundra existed at the site from ca. 17,500−16,000 cal BP with species including willows (*Salix*), grasses (Poaceae), sedges (Cyperaceae), heathers (Ericaceae), and sagebrush (*Artemisia*). SedaDNA analysis also supports the presence of rare non-arboreal taxa at Topknot Lake during this interval including Jacob's-ladder (*Polemonium*), bistort (*Bistorta*), and wild berries (*Rubus*). After ca. 16,000 cal BP and through the terminal Pleistocene, pine (*Pinus*), alder (*Alnus*), and ferns formed open forests under cool and dry conditions. At Little Woss Lake in the mountains of north-central Vancouver Island, fir (*Abies*) stands dominated from ca. 14,200−14,100 cal BP, then were replaced by open pine woodland with alder and ferns from ca. 14,100 −12,000 cal BP. SedaDNA corroborates these plant taxa as well as indicating grizzly bear (*Ursus arctos horribilis*) and Chinook salmon (*Oncorhynchus tshawytscha*) in and around the basin by ca. 14,100 cal BP. Mixed conifer forests of pine, western hemlock (*Tsuga heterophylla*), and alder spread into the island's interior ca. 12,000−11,100 cal BP during the Pleistocene-Holocene transition. The records from these two lakes demonstrate the diachronous development of postglacial ecosystems on northern Vancouver Island. Furthermore, these data provide key evidence for environments that could have supported human populations on the northwest coast of North America for several millennia during the terminal Pleistocene.

1. Introduction

The advance and retreat of glaciers has been a fundamental driver in shaping the landscapes and biota of northwestern North America for over two million years. Therefore, understanding the chronology and extent of these glaciations as well as their effects on local ecologies is of great interest to Quaternary scientists. Despite wide-ranging studies across what is now British Columbia (BC) and Alaska focusing on the most recent glacial episode (the Fraser Glaciation, equivalent to the late Wisconsin), gaps remain in understanding the ecological and geological dynamics of many areas during this interval. In particular, the late Pleistocene glaciation and palaeoecology of northern Vancouver Island, Canada, is relatively unknown (see Howes, 1981, 1983; Hebda, 1983; Hebda and Haggarty, 1997; Lacourse et al., 2003; Lacourse, 2005). Here, we seek to fill this gap in knowledge by describing sedimentary records
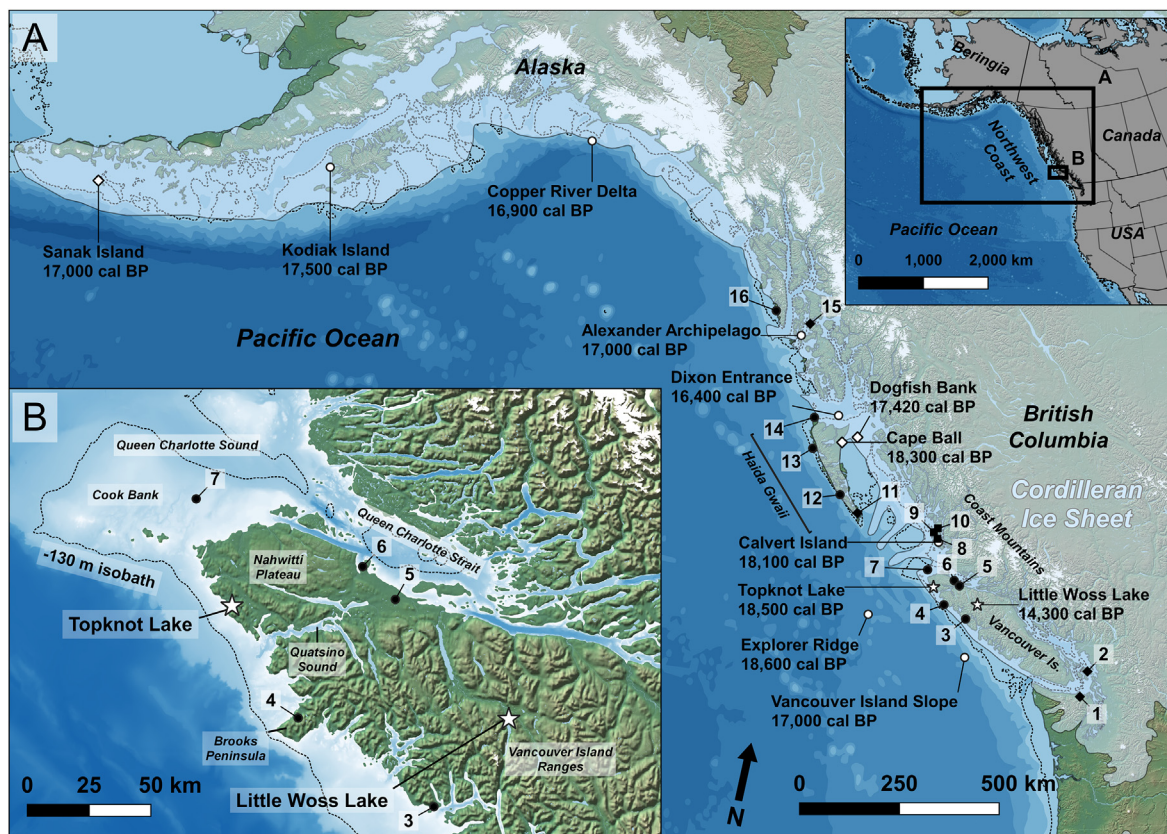
Fig. 1. (A) Maximum glacial cover ca. 20,000−17,500 cal BP (in light blue, after Dyke, 2004, Lesnek et al., 2020; Shaw et al., 2020) and the commencement of deglacial processes for selected sites on the northwest coast of North America. Key sites are labeled with white circles (glacial extent), black circles (palaeoecological record), black squares (archaeological record), white diamonds (both deglacial and palaeoecological record), black diamonds (both palaeoecological and archaeological record), or white stars (sites from this study). Labeled sites: Sanak Island (Misarti et al., 2012); Kodiak Island (Mann and Peteet, 1994); Copper River Delta (Davies et al., 2011); Alexander Archipelago (Lesnek et al., 2018, 2020); Dixon Entrance (Barrie and Conway, 1999); Dogfish Bank (Lacourse et al., 2005); Cape Ball (Warner et al., 1982; Warner, 1984); Calvert Island (Darvill et al., 2018); Topknot Lake (this study); Explorer Ridge (Blaise et al., 1990); Little Woss Lake (this study); Vancouver Island Slope (Cosma et al., 2008). Numbered sites: 1: Manis Mastodon (Waters et al., 2011); 2: Ayer Pond (Kenady et al., 2011); 3: Port Eliza Cave (Al-Suwaidi et al., 2006); 4: Brooks Peninsula (Hebda, 1997); 5: Misty Lake (Lacourse, 2005); 6: Bear Cove Bog (Hebda, 1983) 7: Cook Bank (Lacourse et al., 2003); 8: Meay Channel 1 (McLaren et al., 2018); 9: Triquet Island (Gauvreau and McLaren, 2017; Gauvreau et al., in prep); 10: Kildidt Narrows (McLaren et al., 2015); 11: Kilgii Gwaay (Mathewes et al., 2019; Fedje et al., 2021); 12: West Side Pond (Lacourse et al., 2005); 13: Hippa Island (Lacourse et al., 2012); 14: Langara Island (Heusser, 1995); 15: Shuká Káa (Lesnek et al., 2018); 16: Hummingbird Lake (Ager, 2019). **(B)** Detail of Study Area, including locations of Topknot Lake and Little Woss Lake on northern Vancouver Island. All maps include a −130 m isobath to indicate the global eustatic sea level lowstand during the LGM (Clark et al., 2009). Map data: Natural Earth, Viewfinder DEM, NOAA ETOPO1, GeoBC. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

from two lakes on northern Vancouver Island using pollen, sedimentary ancient DNA (sedaDNA), diatom, grain size, and radiocarbon analyses. Together, these palaeoenvironmental proxies indicate the presence of ice-free environments during the interval of greatest regional glaciation, creating ecological conditions which may have supported human settlement immediately following—and possibly during—the global glacial maximum.

1.1. Glacial history

During the Pleistocene epoch (2,580,000 to 11,700 years ago), colder climatic conditions caused the landscape of coastal BC to be carved and ground away by glaciers emerging from the high mainland Coast Mountains, coalescing into a complex known as the Cordilleran Ice Sheet (CIS) (Clague, 1989a). These glaciers flowed from the fjords and across the narrow coastal channels and straits, in some places joining with local icefields on Vancouver Island and Haida Gwaii (Howes, 1981, 1983; Clague, 1989b). The most recent major glacial period in BC, the Fraser Glaciation, generally corresponds with global MIS 2 (ca. 29,000−14,000 cal BP, Clague and Ward, 2011). The coldest period of this glaciation (ca. 26,000−19,000 cal BP) is known as the Last Glacial Maximum

(LGM) (Clark et al., 2009). This interval was characterized by widespread advance of the southwestern margin of the CIS, estimated to be hundreds or even thousands of metres thick at its greatest development in different locations (Armstrong et al., 1965; Clague and Ward, 2011). However, the timing of the most extensive glacial cover by the CIS during the Fraser Glaciation varied across the northwest coast of North America, ranging anywhere from ca. 27,000 to 17,000 cal BP in response to regional geomorphic and climatic processes (Clague et al., 1980; Hicock et al., 1982; Clague, 1983; Barnosky et al., 1987; Thompson et al., 1993; Hebda and Whitlock, 1997; Clague and James, 2002; Hendy and Cosma, 2008; Seguinot et al., 2016; Shaw et al., 2020). Moreover, current evidence suggests that the increase in ice cover during the Fraser Glaciation was not time-transgressive between regions (i.e., glaciation proceeding north to south); but was instead linked with factors such as local topography and proximity to ice source areas, broadly proceeding from interior mountain ranges to the coast (e.g., Barrie and Conway, 1999; Lesnek et al., 2020; Shaw et al., 2020, Fig. 1).

In addition to the diachronous nature of Pacific coastal glaciation, the maximum extent of ice cover during and after the LGM was also regionally specific (Hicock et al., 1982; Luternauer et al.,

1989a; Barrie et al., 2005; Al-Suwaidi et al., 2006; Reger et al., 2007; Cosma et al., 2008; Dallimore et al., 2008; Addison et al., 2012; Briner et al., 2017; Mathewes and Clague, 2017; Darvill et al., 2018; Shaw et al., 2020; Lesnek et al., 2020). During the Vashon Stade (ca. 19,000–17,000 cal BP), the CIS extended to the continental shelf margin in some places with local mountain glaciers contributing to a patchwork of on- and off-shore ice at the edge of the sheet (Hicock and Armstrong, 1985; Clague, 1989b; Barrie and Conway, 1999; Lesnek et al., 2020; Shaw et al., 2020). However, some outer coastal environments and low-lying plains exposed by isostatic rebound and crustal forebulge effects (see Clague, 1983) may have served as refugia for numerous plant and animal species during and immediately following the LGM (Heusser, 1989; Hebda et al., 1997; Soltis et al., 1997; Lacourse et al., 2003; Gapare and Aitken, 2005; Gapare et al., 2005; Reimchen and Byun, 2005; Godbout et al., 2008; Shafer et al., 2010; Mathewes and Clague, 2017). After ca. 15,000 cal BP, rapid deglaciation was underway across the coast (Clague, 1989a; Hebda and Whitlock, 1997).

1.2. Palaeoecology

Plants and animals on the northwest coast of North America were displaced by the ebb and flow of ice and cold climates during the Fraser Glaciation. Sometimes these organisms persisted in peripheral coastal refugia (e.g., Hebda et al., 1997; Mathewes and Clague, 2017) and sometimes they were extirpated from their pre-LGM ranges. Palaeoecological records from coastal BC and Alaska are barren between ca. 20,000 and 17,500 cal BP (Al-Suwaidi et al., 2006; Lesnek et al., 2018), though cold-adapted mammals such as ringed seals and arctic fox may have survived during the glacial maximum (Wigen, 2005; Al-Suwaidi et al., 2006; Carrara et al., 2007). Phylogeographic studies also indicate the possible persistence of other varied taxa including salmon, rodents, land birds, and several types of trees, herbs, and shrubs through the peak of the Fraser Glaciation in cryptic coastal refugia (Kondzela et al., 1994; Byun et al., 1997; Soltis et al., 1997; Conroy and Cook, 2000; Smith et al., 2001; Fleming and Cook, 2002; Burg et al., 2005; Walser et al., 2005; Beacham et al., 2006; Godbout et al., 2008; COSEWIC, 2013; Pruett et al., 2013; see Shafer et al., 2010 for a summary to that year). However, direct palaeoecological evidence for refugial biota in coastal BC and Alaska has not yet been demonstrated for this interval, and alternative biogeographical hypotheses are possible for some of these organisms (e.g., Demboski et al., 1999; Peacock et al., 2007).

Postglacial revegetation of coastal landscapes depended on factors such as deglacial history, relative sea level change, the presence of nearby refugia, and the varied dispersal rates of different flora and fauna from those refugia. Early plant and animal communities emerged between ca. 17,500–14,000 cal BP as environmental conditions ameliorated in different regions of the coast. Palaeoenvironmental records from the early portion of this interval reveal a brief period of cold and dry herb/shrub tundra dominated by *Salix* (willow), Poaceae (grass), Cyperaceae (sedge), and ericaceous taxa such as *Empetrum nigrum* (crowberry) in Haida Gwaii and parts of southeast Alaska (Barrie et al., 1993; Hansen and Engstrom, 1996; Heusser, 1995; Lacourse and Mathewes, 2005; Lacourse et al., 2005; Mathewes et al., 2019). As the climate warmed and the ice retreated, *Pinus* (pine) parkland emerged and prevailed ca. 15,000–14,000 cal BP from southeast Alaska to southern Vancouver Island (e.g., Hebda, 1983; Brown and Hebda, 2002; Lacourse, 2005; Lacourse and Mathewes, 2005; Brown et al., 2008; Galloway et al., 2008; Ager et al., 2010; Eamer, 2015; Leopold et al., 2016; Ager, 2019). Alongside these pioneering communities, data from caves in southeast Alaska (Heaton and Grady, 2003), Haida Gwaii (Ramsey et al., 2004; Wigen, 2005; Fedje

et al., 2011), and northern Vancouver Island (Nagorsen and Keddie, 2000; Al-Suwaidi et al., 2006; Steffen and McLaren, 2008; Steffen and Fulton, 2018) indicate the presence of varied mammals, birds, and fish during the terminal Pleistocene. Following the dominance of *Pinus* parkland, mixed conifer forests of *Picea* (spruce), *Abies* (fir), and *Tsuga mertensiana* (mountain hemlock) emerged during the latter part of the Bølling-Allerød interstadial and persisted through the Younger Dryas ca. 14,000–11,700 cal BP (Mathewes, 1993; Brown et al., 2008). By the end of the Younger Dryas (ca. 11,700 cal BP; Rasmussen et al., 2014) and through the early Holocene, closed conifer forests and diverse animal taxa were present across coastal BC and Alaska (e.g., Brown and Hebda, 2002; Hebda et al., 2005; Lacourse, 2005; Lacourse and Mathewes, 2005; Wigen, 2005; Cannon and Yang, 2006; Fedje et al., 2011; Fargo, 2013; Eamer, 2015; McLaren et al., 2015; Ager, 2019).

1.3. Late Pleistocene archaeology

The peopling of the Americas was a complex, long-term process involving movements across vast distances as early Indigenous peoples adapted to dynamic geographies and ecologies. However, the nature and timing of this process during the late Pleistocene remains poorly known and is tied to factors including glacial extent and ecological conditions in northern and northwestern North America. Previous archaeological consensus was that the first humans in the Americas, known as the Clovis people, were terrestrial megafauna hunters who arrived through an ice-free corridor between the retreating Cordilleran and Laurentide ice sheets by ca. 13,000 cal BP (Waters et al., 2020). However, wide acceptance of cultural deposits dating to >14,000 cal BP at Monte Verde in Chile (Dillehay, 1997; Meltzer et al., 1997) and elsewhere (e.g., Davis et al., 2019; Shillito et al., 2020; see Waters, 2019 for a review to that year) has led researchers to question whether the postglacial chronology of the interior ice-free route can explain evidence for early humans south of the ice limits (Heintzman et al., 2016; Pedersen et al., 2016; Moreno-Mayar et al., 2018a, 2018b; Froese et al., 2019; though see Potter et al., 2017; Potter et al., 2018). Recent research showing evidence for human settlement in Mexico (Ardelean et al., 2020), the southwestern United States (Bennett et al., 2021), and elsewhere (see Becerra-Valdivia and Higham, 2020) during or prior to the LGM further demonstrates the need to re-evaluate the environmental context for human movement into and within the Americas.

Returning to theories that early humans traversed from Beringia along the northwest coast of North America (Heusser, 1960; Fladmark, 1979), researchers have begun to consider a coastal route for the early peopling of the Americas with new archaeological, geological, and palaeoecological data (e.g., Braje et al., 2019; Davis and Madsen, 2020). Collectively, these data suggest two main conclusions:

1. Humans were living on the northwest coast of North America during the late Pleistocene; and
2. Environmental conditions (e.g., sea level, climate, and flora and fauna) were variable in different regions through time, but some parts of the coast may have experienced minimal or no ice cover through the global LGM.

However, the archaeological signature of early peoples on the postglacial landscape of the northwest coast of North America is difficult to detect because marine transgression during the Holocene has submerged many previously terrestrial archaeological sites (Josenhans et al., 1997; Fedje and Christensen, 1999; Fedje and Josenhans, 2000; Mackie et al. 2011, 2018; Monteleone et al., 2012; McLaren et al., 2020). Furthermore, inland sites are difficult to

detect in thick rainforest environments which are resistant to erosion and exposure (Carlson and Baichtal, 2015; Fedje et al., 2018). Most early archaeological sites on the coast are known from areas where relative sea level during the late Pleistocene was either comparable to or higher than today (Ackerman, 1996; Fedje et al. 2011, 2018; McLaren et al., 2011, 2014, 2015, 2018, 2019; Shugar et al., 2014; Letham et al., 2016; Gauvreau and McLaren, 2017; Gauvreau et al., in prep).

The earliest reported evidence of human occupation of coastal BC comes from Triquet Island, dating to ca. 14,450−13,500 cal BP (Gauvreau and McLaren, 2017; Gauvreau et al., in prep). The evidence at Triquet Island together with remains from other nearby sites such as Kildidt Narrows (McLaren et al., 2015) and Meay Channel I (McLaren et al., 2018) demonstrate human presence on this part of the coast by at least ca. 14,000−13,000 cal BP. Archaeological sites in Haida Gwaii and southeast Alaska are similarly old (ca. 13,100 to 10,000 cal BP; Fedje et al., 2011; Mackie et al., 2011; Dixon, 2013; Mathewes et al., 2019; Fedje et al., 2021), as are human-modified remains of megafauna to the south in Washington state at Ayer Pond and the Manis Mastodon site (ca. 13,900−13,750 cal BP; Kenady et al., 2011; Waters et al., 2011). Collectively, these sites demonstrate relatively early human occupation in the region. However, none yet are as old as sites farther south in the Americas (e.g., Braje et al., 2019; Waters, 2019; Becerra-Valdivia and Higham, 2020). Understanding the complex local and regional processes of deglaciation, relative sea level change, and ecological succession across the northwest coast of North America is key to searching for sites coeval with the early archaeological record elsewhere on the continents.

2. Setting and study sites

Today, northern Vancouver Island and the adjacent mainland are blanketed by coastal temperate rainforest fringed with rocky shorelines and rugged archipelagoes. The high, glaciated peaks of the Coast Mountains to the east and open Pacific Ocean to the west create a narrow littoral band which supports highly diverse and productive coastal ecosystems. The climate is characterized by cool summers and mild winters with abundant precipitation and fog (Green and Klinka, 1994). Lower elevations in the region are dominated by variants of the Coastal Western Hemlock (CWH) biogeoclimatic ecosystem classification (BEC). The CWH is characterized by rainforest consisting of *Tsuga heterophylla* (western hemlock), *Thuja plicata* (western redcedar), *Abies amabilis* (amabilis fir), *Picea sitchensis* (Sitka spruce), and *Xanthocyparis nootkatensis* (yellow-cedar) with an understory dominated by *Gaultheria shallon* (salal) (Green and Klinka, 1994).

Two sites on northern Vancouver Island, Topknot Lake and Little Woss Lake, were investigated in this study (Fig. 1; Fig. 2). Topknot Lake was selected because of its location on the outer
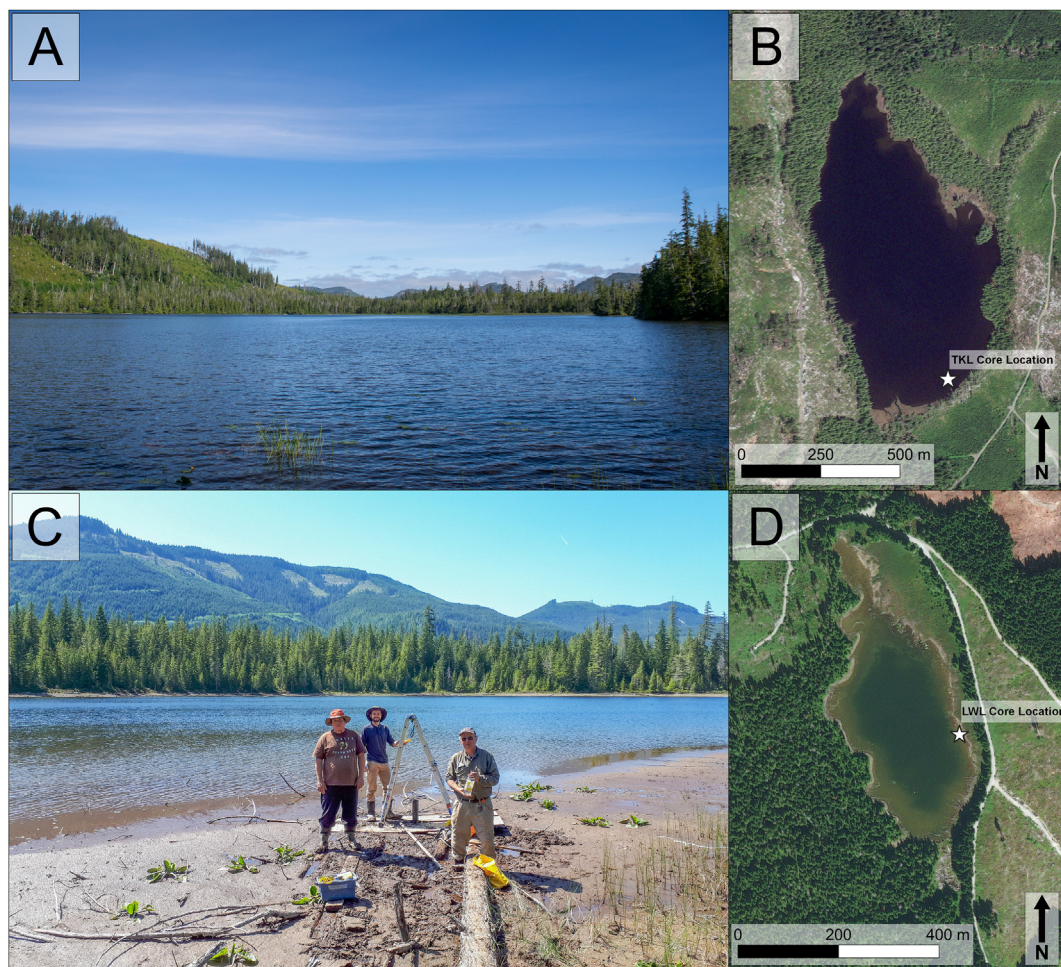
Fig. 2. Context and location of study sites at Topknot Lake and Little Woss Lake on northern Vancouver Island. **(A)** View of Topknot Lake, looking northwest from eastern shoreline. Photo: C. Hebda. **(B)** Satellite imagery of Topknot Lake including core collection location. **(C)** View of Little Woss Lake, looking west from eastern shoreline. From left to right: D. Wall, C. Hebda, R. Hebda. Photo: D. McLaren. **(D)** Satellite imagery of Little Woss Lake including core collection location. Map data: Microsoft Corporation, Maxar Technologies.

coast—distant from sources of ice during the Fraser Glaciation—as well as its elevation above the theoretical late Pleistocene/early Holocene relative sea level highstand (Howes, 1983). Little Woss Lake was chosen because of its location in the rain shadow of the Vancouver Island Ranges and its proximity to the Woss River, a salmon-bearing river with high potential for late Pleistocene archaeological sites.

2.1. Topknot Lake

Topknot Lake (50.5619° N, 128.1876° W, 13 m above modern sea level [asl], Fig. 2a and b) is located within Quatsino First Nation territory on the outer west coast of northern Vancouver Island, BC, Canada. The lake is less than 2 km from the Pacific Ocean near the mouth of Quatsino Sound on the Nahwitti Plateau. The lake has an area of 38.5 ha with a small catchment. Runoff flows into Topknot Lake from low hills to the east, west, and south and collects in a marginal wetland at the lake's southern end. The basin drains northward into the Macjack River, which flows a short distance west into the Pacific Ocean. Topknot Lake falls within the Southern Very Wet Hypermaritime subzone of the Coastal Western Hemlock BEC zone (CWHvh1; BC Forest Analysis and Inventory Branch, 2018), which is cool and wet year-round with little snowfall. Vegetation in this subzone is characterized by *T. heterophylla*, *T. plicata*, and *A. amabilis*, with lesser amounts of *X. nootkatensis* and *T. mertensiana*. The understory is composed of diverse shrubs and herbs including *G. shallon*, *Blechnum spicant* (deer fern), *Vaccinium parvifolium* (red huckleberry), *V. alaskaense* (Alaskan blueberry), *Menziesia ferruginea* (false azalea), *Cornus canadensis* (bunchberry), and *Linnaea borealis* (twinflower), among other species (Green and Klinka, 1994).

2.2. Little Woss Lake

Little Woss Lake (50.1807° N, 126.6104° W, 153 m asl, Fig. 2c and d) is located within 'Namgis First Nation territory on north-central Vancouver Island, BC, Canada. The lake is nestled in a valley bottom within the northern Vancouver Island Ranges at the north end of Woss Lake. Both Woss Lake and Little Woss Lake are part of a valley watershed that feeds north-northwest into the Nimpkish River Valley and Nimpkish Lake beyond. Little Woss Lake has an area of 10 ha and drains south into Woss Lake, with a catchment that includes slopes to the east which rise to 550 m asl. Little Woss Lake falls within the Western Very Dry Maritime subzone of the Coastal Western Hemlock BEC zone (CWHxm2; BC Forest Analysis and Inventory Branch, 2018), which is warm and dry in the summer with mild, moist winters and little snowfall. Vegetation in this subzone is characterized by *Pseudotsuga menziesii* (Douglas-fir), *T. heterophylla*, and *T. plicata*. The understory is composed of *G. shallon*, *Mahonia nervosa* (dull Oregon-grape), *V. parviflorum*, *Achlys triphylla* (vanilla-leaf), *Polystichum munitum* (sword fern), and *L. borealis*, among other species (Green and Klinka, 1994).

3. Materials and methods

3.1. Coring

Sediments from Topknot Lake and Little Woss Lake were collected using a combination of a Livingstone corer (Livingstone, 1955; Wright, 1967) and a modified version of the Reasoner percussion coring method (Reasoner, 1986, 1993). Livingstone core sections were collected in 90 cm to 1 m drives using a 5-cm diameter stainless steel core barrel and were extruded in the field. Reasoner-method cores were collected continuously using 3.5-m sections of 7.5-cm diameter solid-core ABS tubing and cut

into manageable lengths in the field. All cores were stored at 4 °C at the Pacific Forestry Centre, Natural Resources Canada, in Victoria, BC, before being subsampled for analysis using sedaDNA, pollen and spores (henceforth 'pollen'), diatoms, radiocarbon dating, and laser granulometry.

3.2. SedaDNA

Recent research has demonstrated that analysis of sedaDNA can corroborate and expand upon other palaeoecological evidence such as that provided by pollen, macrofossils, and diatoms (e.g., Jørgensen et al., 2012; Pedersen et al., 2013; Pedersen et al., 2016). In this study, we used sedaDNA as a complementary proxy to these established methods. Sampling for sedaDNA analysis was performed at Hakai Institute lab facilities in Victoria, where samples were collected throughout the cores from both study sites. Sampling focused on the lower sections of the cores, with variable resolution from 2 to 15 cm dependent on the presence of sediment transitions and obtaining representative core coverage. In total, 74 samples were collected (Topknot Lake, 52 samples; Little Woss Lake, 22 samples). DNA sample handling and preparation followed protocols described by Pedersen et al. (2016). DNA extractions and library preparations were performed in dedicated ancient DNA laboratories belonging to the Lundbeck Foundation GeoGenetics Centre at the University of Copenhagen, Denmark, using protocols for sedaDNA established by Pedersen et al. (2016). Of the samples collected, 14 underwent extraction (Topknot Lake, 9 samples; Little Woss Lake, 5 samples). DNA concentrations (ng of DNA per g of sample) were quantified using a Qubit 2.0 fluorometer according to the manufacturer's instructions to identify appropriate samples for library preparation and downstream sequencing. Extracts were then converted to Illumina libraries following Meyer and Kirscher (2010). The libraries were amplified using AmpliTaq Gold PCR enzyme and purified with Agencourt AMPure XP microbeads prior to sequencing. Following PCR amplification and library evaluation with an Agilent 2100 Bioanalyzer, three samples (Topknot Lake, 1 sample; Little Woss Lake, 2 samples) were selected for sequencing on an Illumina HiSeq 2500 platform, resulting in a total of 42,686,131 reads.

Bioinformatic analysis of the sedaDNA reads was performed using a modified version of 'Holi,' the pipeline described by Pedersen et al. (2016). After trimming the adaptor sequences and parsing reads of 30 bp or longer, a total of 40,860,871 reads remained. PCR duplicates were removed along with reads with poly-A/T tails ≥ 4, and the result was filtered for low-complexity sequences (DUST = 4). The remaining total of 13,173,653 trimmed and cleaned sequences were compared against international genomic databases including the NCBI Nucleotide database (downloaded August 16, 2019) and RefSeq full genomes (version 92) using BowTie2 (end-to-end alignments, using sensitive settings and -k 5000) and were taxonomically classified using an in-house naïve least common ancestor (LCA) algorithm. The results presented here include taxon identifications with an edit distance of 0 nucleobases—sequences with 100% similarity to the reference genome. Due to low read counts, ancient DNA damage patterns were unable to be estimated for these samples. All Viridiplantae and Metazoan sedaDNA identifications including contaminants are presented in the Supplementary Material (Table S1).

3.3. Pollen and diatoms

Sampling for pollen and diatoms was carried out in laboratory facilities at the Pacific Forestry Centre in Victoria. Sampling resolution was variable and depended on the presence of sediment transitions and obtaining representative core coverage. Pollen

samples (Topknot Lake, 17 samples; Little Woss Lake, 14 samples) consisting of 1 cm^3 of sediment were prepared using standard methods (Faegri and Iversen, 1989; Moore et al., 1995). Samples were spiked with an exotic marker to calculate pollen flux (20848 $\pm$ 1546 *Lycopodium* spores/tablet; Dept. Quaternary Geology, University of Lund, batch no. 1031). Several of the basal pollen samples from both study sites required screening with 10 μm Nitex mesh and/or treatment with technical grade hydrofluoric acid (HF) at the University of Victoria School of Earth and Ocean Sciences micropalaeoecology laboratory to remove excess silica.

Where possible, pollen was counted to 300 grains per sample; however, individual counts vary from as high as 409 grains to as few as 30 grains in the deepest, most minerogenic sediments of Topknot Lake. Pollen identifications relied on references including Kapp (1969), Moore et al. (1995), Demske et al. (2013), Martin and Harvey (2017), an unpublished key by Hebda et al. (2002) and a modern pollen reference collection at the Pacific Forestry Centre. Raw counts for each site were subjected to stratigraphically constrained cluster analysis in the computer program Tilia (Grimm, 1990) using CONISS (Grimm, 1987) to establish pollen zones based on Edwards and Cavalli-Sforza's chord distance, which places higher weight on rare taxa. Up-weighting rare taxa is useful for late Pleistocene records because infrequent herbaceous taxa can help characterize ecological conditions and succession in non-forested environments with little vegetation cover (Grimm, 1987). All pollen sample counts are presented in the Supplementary Material (Table S2).

Diatom samples consisting of 1 cm^3 of sediment were collected from the cores, with 0.25−0.5 cm^3 subsamples of these prepared using standard methods (Battarbee, 1986; Fedje et al., 2018). Diatom counts were tallied based on the presence or absence of diagnostic algal taxa. Observed assemblages were characterized as either fresh, fresh-brackish/alkaline, brackish, or marine, generalized from the halobian classes described by Hustedt (1953). Diatom identifications relied on references including Witkowski et al. (2000), Pienitz et al. (2003), and Spaulding et al. (2021). Water salinity affiliation was used to evaluate potential sea level transgressions and/or changes in nutrient availability in each basin (see Fedje et al., 2018). Diatom counts for the basal samples from each core and taxa lists for all samples are presented in the Supplementary Material (Table S3).

Botanical nomenclature for vascular and non-vascular plants follows e-Flora BC (Klinkenberg, 2021a), zoological nomenclature follows e-Fauna BC (Klinkenberg, 2021b), and diatom nomenclature follows AlgaeBase (Guiry and Guiry, 2021).

3.4. Radiocarbon

Macrofossils including fragments of leaves, stems, needles, arthropods, and other remains were collected opportunistically for dating from both cores. Chronological coverage includes most of the analyzed core sections except for the basal inorganic sediments of Topknot Lake. Macrofossils were identified to genus level where possible, relying on references including Lévesque et al. (1988). Material dated from Topknot Lake includes monocot leaf and stem fragments (cf. Cyperaceae), *Sphagnum* fragments, arthropod remains, and *Nuphar* seed and leaf fragments. Material dated from Little Woss Lake includes woody twig fragments, a *Nuphar* flower, and a *Pinus* needle. Reservoir effects on these samples are considered negligible due to a lack of carbonate bedrock in the direct catchment of either lake, a lack of carbonate encrustation on Characeae oospores observed in the lower sediments of Topknot Lake (Fig. 4b), as well as the concordance of dates from *Nuphar* with other dated materials in both lakes. Where larger organic material was unavailable, bulk samples of sediment were screened using a

125 μm sieve and picked for fragmentary remains. Macrofossils were sent for AMS radiocarbon dating at the A.E. Lalonde AMS Laboratory at the University of Ottawa and the W.M. Keck Carbon Cycle AMS Facility at the University of California, Irvine. Radiocarbon results are presented in Table 1. Calibrated age ranges at 2σ are derived from CALIB 8.20 (Stuiver et al., 2020) using the IntCal20 northern hemisphere calibration curve (Reimer et al., 2020).

Age-depth models (Fig. 3) were developed for the lower deposits at both lakes using the Bacon software package 2.5.5 (Blaauw and Christen, 2011) for R x64 4.0.5 (R Core Team, 2021) with the IntCal20 calibration curve (Reimer et al., 2020). A boundary was introduced in the age-depth model for Topknot Lake at 591 cm (i.e., at the sediment transition between TKL Unit 5 and TKL Unit 6) to accommodate the differential accumulation rates apparent in the upper and lower sections of the record. Additionally, a duplicate and concordant radiocarbon sample at 799 cm (UOC-8917) was removed from the model input to prevent the generation of spuriously old dates. The basal date from Topknot Lake (UCIAMS-229009) at 995 cm depth has a large error ($\pm$750 cal years). Nevertheless, it has been included in the age-depth modeling as it is stratigraphically consistent with the other dates and receives a proportionally smaller weight in the output generated by Bacon due to its higher uncertainty. Furthermore, the date helps constrain the extrapolation of basal core ages. When discussed in the text, dates derived from the age-depth models are rounded to the nearest 10 years.

3.5. Grain size

Grain size analysis was performed at the Pacific Forestry Centre on 10 samples from the lower sediments of Topknot Lake to better understand the source of the sediments and their deposition in the basin. To determine particle size, sediment subsamples were deflocculated in a 5% sodium hexametaphosphate ([NaPO$_3$]$_6$) solution to separate particles and then treated with hydrogen peroxide (H$_2$O$_2$) to remove organic material. Sediment particle size distributions were then obtained using laser diffraction with a Beckman Coulter LS 13 320 Laser Particle Size Analyzer, yielding a distribution curve of particle sizes ranging from 17 nm to 2 mm. In addition to the samples themselves, replication and control samples were also measured. Reported clay, silt and sand fractions correspond to 0.04−2 μm, 2−50 μm, and 50−2000 μm size ranges, respectively. Size distribution within each fraction was also measured. Full grain size measurement data are available in the Supplementary Material (Table S4).

4. Results

4.1. Chronology

Thirteen radiocarbon dates were obtained from the Topknot Lake core, and six dates were obtained from the Little Woss Lake core. The samples from Topknot Lake range in depth from 509 to 995 cm below the sediment-water interface with median calibrated ages ranging from 9807 to 19,259 cal BP. The samples from Little Woss Lake range in depth from 286 to 527 cm below the sediment-water interface with median calibrated ages ranging from 10,700 to 14,306 cal BP. See Table 1 for details on the radiocarbon samples from each site, including depths, uncalibrated ages, and calibrated age ranges. See Fig. 3 for age-depth models derived from the radiocarbon dates obtained for each site.

Table 1
Radiocarbon ages from Topknot Lake and Little Woss Lake including associated pollen zones, sample collection depth, type of material dated, lab #, conventional ^{14}C ages, calibrated age ranges, and median calibrated age for each sample.

| Site	Pollen Zone	Depth (cm)	Material	Lab #	Radiocarbon age (^{14}C BP)	Calibrated age range (cal BP) ±2σ	Median calibrated age (cal BP)
Topknot Lake	–	509	matted dicot leaves	UOC-7369	8792 ± 31	9636–9631 (0.2%) 9917–9666 (94.0%) 9956–9939 (0.9%) 10,006–9997 (0.4%) 10,115–10,068 (4.5%)	9807
Topknot Lake	–	526	*Nuphar* leaf	UOC-8914	11252 ± 31	13,181–13,095 (97.1%) 13,228–13,214 (2.9%)	13,141
Topknot Lake	TKL-3	538	*Nuphar* seed and leaf	UOC-8915	11565 ± 37	13,501–13,330 (100%)	13,429
Topknot Lake	TKL-3	553	cf. Cyperaceae leaf fragment	UOC-8916	12890 ± 45	15,585–15,250 (100%)	15,409
Topknot Lake	TKL-3	591	matted dicot leaves	UOC-7368	13049 ± 39	15,791–15,475 (100%)	15,642
Topknot Lake	TKL-2b	622	cf. Cyperaceae leaf fragment	UOC-7367	13232 ± 47	16,049–15,720 (100%)	15,887
Topknot Lake	TKL-2b	701	cf. Cyperaceae leaf fragment	UOC-7366	14033 ± 43	17,316–16,964 (100%)	17,067
Topknot Lake	TKL-2b	799	cf. Cyperaceae leaf and stem fragment	UOC-8917	14536 ± 43	17,946–17,463 (100%)	17,748
Topknot Lake	TKL-2b	799	cf. Cyperaceae leaf and stem fragment	UOC-7365	14611 ± 40	18,156–17,728 (100%)	17,913
Topknot Lake	TKL-2b	837.5	cf. Cyperaceae leaf fragment	UOC-7364	13350 ± 49	16,242–15,871 (100%)	16,065
Topknot Lake	TKL-2b	865	cf. Cyperaceae leaf	UOC-8918	14154 ± 66	17,378–17,053 (100%)	17,210
Topknot Lake	TKL-2a	920	cf. Cyperaceae leaf fragments and arthropod chitin	UOC-8920	14109 ± 61	17,355–17,027 (100%)	17,183
Topknot Lake	TKL-1	995	*Sphagnum* stem fragments	UCIAMS-229009	15880 ± 750	21,002–17,378 (100%)	19,259
Little Woss Lake	LWL-3b	286	matted dicot leaves	UOC-7374	9464 ± 36	10,782–10,579 (91.5%) 10,999–10,971 (5.6%) 11,061–11,039 (2.9%)	10,700
Little Woss Lake	LWL-3a	336.5	woody twig fragment	UOC-7373	9995 ± 31	11,622–11,275 (97.5%) 11,688–11,671 (2.5%)	11,465
Little Woss Lake	LWL-2	401.5	*Nuphar* flower	UOC-7375	10356 ± 33	11,981–11,978 (0.2%) 12,209–11,995 (48.5%) 12,279–12,216 (13.0%) 12,334–12,290 (8.9%) 12,469–12,342 (29.5%)	12,223
Little Woss Lake	LWL-2	499.5	woody twig fragment	UOC-7372	11637 ± 38	13,526–13,413 (67.3%) 13,593–13,540 (32.7%)	13,498
Little Woss Lake	LWL-2	513.5	woody twig fragment	UOC-7371	12034 ± 38	14,030–13,802 (100%)	13,915
Little Woss Lake	LWL-1	527	*Pinus* needle	UOC-7370	12332 ± 35	14,500–14,119 (79.2%) 14,814–14,702 (20.8%)	14,306

4.2. Topknot Lake

4.2.1. Stratigraphy

Sediment from Topknot Lake was collected from the surface to a depth of 1125 cm below the sediment-water interface, though only material from 475 to 1125 cm was examined. Stratigraphy at Topknot Lake consists of fine laminated clayey silts at the base overlain by massive fine silts grading to diatomaceous silts, then diatomaceous gyttja with embedded plant material. Six stratigraphic units were identified, as follows:

(1) **TKL Unit 1, >1125 cm (>18,500 cal BP)**: Basal inorganic laminated clayey silts at 1125 cm depth. Sediments beneath 1125 cm depth were not collected but could be recovered with extended coring equipment.

(2) **TKL Unit 2, 1125–1057 cm (ca. 18,500–18,130 cal BP)**: Inorganic laminated light grey fine silts, clay increasing with depth. Each couplet consists of a sharp contact at the base with coarse dark grey sandy silts, becoming progressively finer upward into light grey silts. The thickness of each couplet varies from 1 mm to 9 mm or more, and the coarse and fine laminae within each couplet also vary in thickness. This unit contains little organic material and could not be radiocarbon dated. Scanning electron microscopy (SEM) reveals that the matrix consists largely of angular silt and clay particles (Fig. 4i).

(3) **TKL Unit 3, 1057–845 cm (ca. 18,130–17,070 cal BP)**: Largely inorganic massive medium grey fine silts with laminated fine

light grey sandy silts and clays between 1030 and 1020 cm. Little organic material is present in the lower section of the unit, though dispersed fragments of arthropod chitin, *Sphagnum*, and aquatic plants were recovered. The deepest successful radiocarbon date was on *Sphagnum* stem fragments collected at 995 cm (UCIAMS-229009). From 920 to 905 cm, leaves and stems (cf. Cyperaceae), arthropod chitin, aquatic plants, *Daphnia* (water flea) resting eggs, and Characeae (stonewort) reproductive oospores were observed (see Fig. 4a and b) and were dated at 920 cm (UOC-8920). SEM imagery of a sample of fine silts at 870 cm indicates that the upper component of this unit is partially composed of diatom remains (~15%), but no diatoms were visible in SEM imagery of samples from 920 cm or below (see Fig. 4h and i). A leaf macrofossil (cf. Cyperaceae) was dated at 865 cm (UOC-8918).

(4) **TKL Unit 4, 845–755 cm (ca. 17,070–16,680 cal BP)**: Somewhat organic light brownish-grey diatomaceous silts. SEM images reveal abundant diatoms at 836 cm (up to ~40% of the matrix) and at 797 cm (up to ~75% of the matrix) (see Fig. 4c). Leaves and stems (cf. Cyperaceae) in this unit yielded three radiocarbon dates from 837.5 cm (UOC-7364) and 799 cm (two separate samples, UOC-7365 and UOC-8917, see Fig. 4d).

(5) **TKL Unit 5, 755–591 cm (ca. 16,680–15,880 cal BP)**: Moderately organic and silty medium brownish-grey diatomaceous gyttja. SEM images reveal abundant diatoms at 701 cm (up to ~75% or more of the matrix) (see Fig. 4e). Leaf
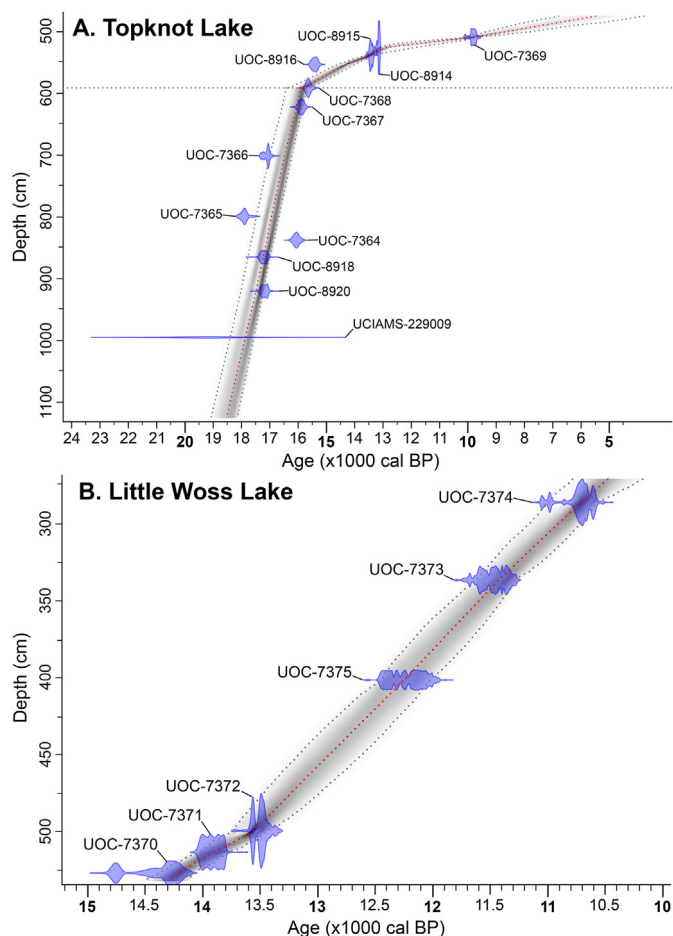
Fig. 3. Age-depth models for Topknot Lake (**A**) and Little Woss Lake (**B**) based on radiocarbon results, generated using Bacon package 2.5.5 for R x64 4.0.5. Dark grey sections indicate a higher likelihood of the sediment being associated with that age at a particular depth. The results of individual assays are depicted in blue. The model in (**A**) has been extrapolated to the base of the core. Note the change in sedimentation in Topknot Lake at ~591 cm, where the record beneath this depth saw rapid accumulation of sediment between ca. 18,500–16,000 cal BP. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

fragments (dicots and cf. Cyperaceae) occur scattered throughout the unit, yielding three radiocarbon dates from 701 cm (UOC-7366), 622 cm (UOC-7367), and 591 cm (UOC-7368).

(6) **TKL Unit 6, 591–475 cm (ca. 15,880–5550 cal BP)**: Matted brown fibrous organic lenses interbedded with dark brownish-grey diatomaceous gyttja. The fibrous lenses consist of mats of dicot leaves, cf. Cyperaceae, *Nuphar*, and other organic debris up to 6 cm thick. Four radiocarbon samples were dated from this component at 553 cm (cf. Cyperaceae leaf fragment, UOC-8916), 538 cm (*Nuphar* seed and leaf, UOC-8915), 526 cm (*Nuphar* leaf, UOC-8914), and 509 cm (matted dicot leaves and fibrous organics, UOC-7369). Sediment above 475 cm consists of medium brown gyttja and was not analyzed.

4.2.2. Pollen, diatoms, sedaDNA, and grain size

Fifteen pollen samples from Topknot Lake were divided into three major pollen zones, TKL-1 to TKL-3 from bottom to top. One of these zones, TKL-2, was further divided into two subzones, TKL-2a and TKL-2b. Samples analyzed from the sediments below 1060 cm

contained little pollen (<30 grains per sample) and were omitted from the results. Counts presented from pollen zone TKL-1 are higher but are still comparatively low (30–174 grains per sample). Pollen percentages are presented in the text as the mean value for each zone unless otherwise noted. Percentages and pollen accumulation rate (PAR) for each sample are depicted on Fig. 5. Other proxies, including diatoms, sedaDNA, and laser granulometry are presented alongside the pollen data in the text for ease of comparison.

4.2.2.1. TKL-1: 1060-935 cm; 18,150–17,480 cal BP. The earliest pollen zone at Topknot Lake, TKL-1, consists of arboreal pollen (AP) (60%) with a notable component of non-arboreal pollen (NAP) from herb and shrub taxa (26%) and pteridophytes (14%). Conifers are the largest constituent of AP in this zone, including a mixed assemblage of *Picea* (12%), *Abies* (12%), *Tsuga mertensiana* (variable between 6% and 27%; more numerous in the lower portion and less common higher in the zone), *Pinus* (10%), and *T. heterophylla* (5%). The abundance of other arboreal and shrub taxa varies in TKL-1, including *Alnus* (0%–13%), *Salix* (0%–3%) and ericaceous shrubs (0%–5%). The herbaceous component of TKL-1 is characterized by Poaceae (10%) along with Cyperaceae (4%) and lesser amounts of other herbs including *Artemisia* (2%), Ranunculaceae (2%), Rosaceae (1.3%), Asteraceae (1.0%), and Apiaceae (0.4%). Pteridophyte contribution to this zone is notable and includes polypodiaceous fern spores (10%) and *Lycopodium* (2%, not to be confused with the exotic *Lycopodium* spike) with <1% of *Cryptogramma* spores. The PAR is extremely low, ranging from ~50 to 400 grains cm^{-2} cal yr^{-1}. Additionally, carbonized and highly degraded pollen grains were noted in several samples from TKL-1. These grains may represent material redeposited by aeolian or alluvial processes during deglaciation (e.g., Zhang et al., 2017) and are not included in the pollen counts. SEM images coupled with pollen and diatom counts from the lower sediments of Topknot Lake show little evidence of organic material in zone TKL-1 and the lower portion of TKL-2 (Fig. 4h and i). A diatom sample examined from 1115 cm did not yield any identifiable specimens. However, a sample at 1005 cm yielded an unidentifiable diatom fragment along with one example of *Aulacoseira canadensis*, a pre-Pleistocene species—further suggestive of redeposition in this zone.

Grain size analysis was performed on eight samples representing pollen zone TKL-1 and the barren basal sediments underlying it to determine the source of the sediment. All samples were composed mostly of silt (2–50 μm) with minor fractions of clay (0.04–2 μm) and sand (>50 μm) (Fig. 6). In the pollen-poor laminated deposits (TKL Unit 1 and TKL Unit 2), one couplet sampled from the basal sediments of the core (1111–1112 cm, combined coarse and fine laminae) was dominated by silt (68%) with a notable contribution of clay (32%) and almost no sand (<1%). Slightly higher in the same deposits (1071–1073 cm), silts comprised 81% of the fine laminae and 80% of the coarse laminae of the couplets that were sampled. The difference in the coarse and fine laminae of these couplets was derived from the contribution of clay and sand to the sediment (fine: 17% clay, 2% sand; coarse: 11% clay, 9% sand). Massive sediments corresponding with pollen zone TKL-1 between 940 and 1031 cm contained an average of 16% clay (range 13–20%), 82% silt (range 77–84%), and 2% sand (range 1–3%). Most of these silts consist of medium-sized grains (15–31 μm) or smaller. See the Supplementary Material (Table S4) for full grain size measurement data.

4.2.2.2. TKL-2: 935-614 cm; 17,480–15,980 cal BP

4.2.2.2.1. Subzone 2a: 935-875 cm; subzone 2b: 875-614 cm. In the second oldest zone, TKL-2, arboreal pollen declines markedly (20%) and herb and shrub taxa predominate (73%), with few
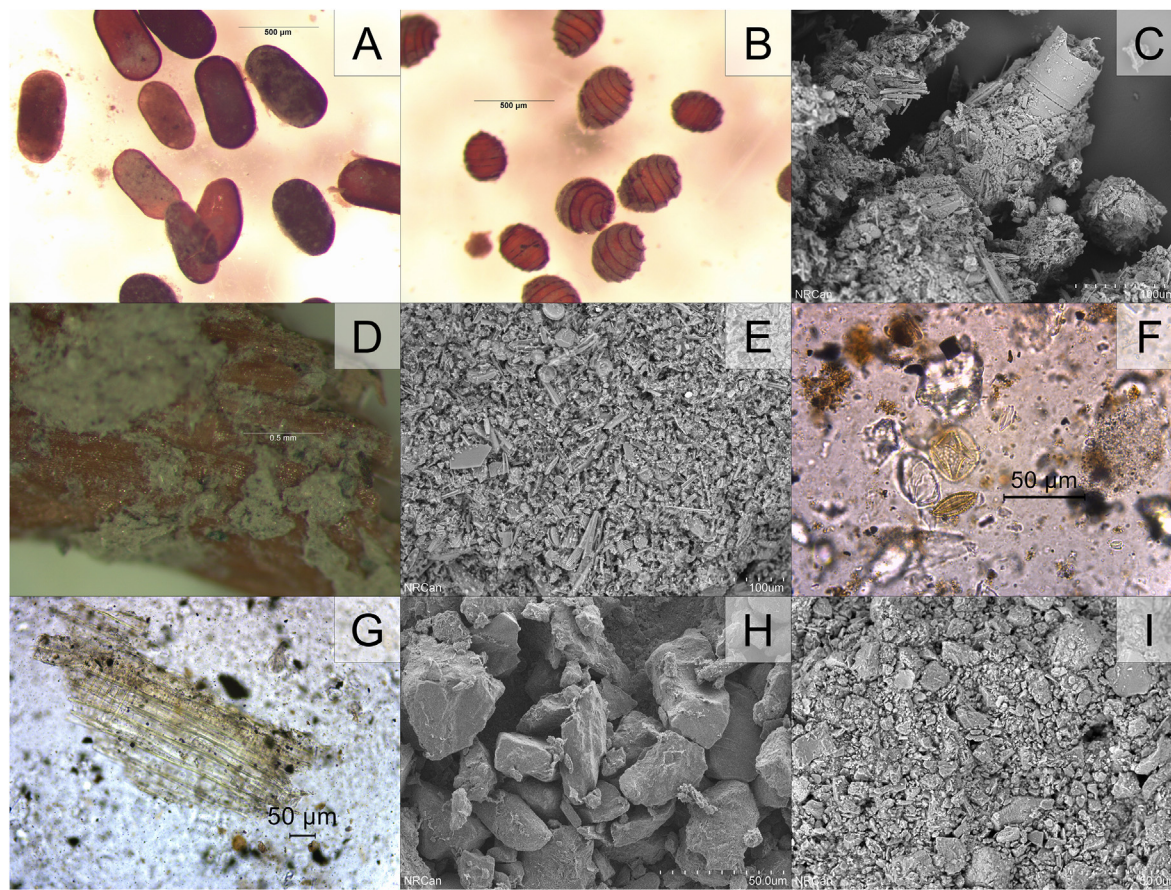
Fig. 4. Macro- and microfossil remains and sediment clasts from Topknot Lake. Varying scales—see each image. **(A)** *Daphnia* eggs at 910 cm. **(B)** Characeae reproductive oospores at 910 cm. Note that these are free of encrusted carbonate deposits, indicating low or no carbonate content in the lake water. **(C)** Diatomaceous component of sediment at 836 cm in silts **(D)** Monocot leaf fragment (cf. Cyperaceae). collected for radiocarbon dating at 799 cm. **(E)** Diatomaceous sediments at 701 cm in gyttja. **(F)** Multiple co-occurring *Salix* pollen morphotypes at 910 cm, immediately to the left of the scale bar. **(G)** Radial section of conifer wood preserved on pollen slide at 935 cm. **(H)** Inorganic sediments at 920 cm in fine silts. **(I)** Inorganic sediments near base of core at 1118 cm in laminated fine silts.

pteridophytes (4%) or aquatics (0.4%) present. The comparatively low arboreal contribution to this zone consists mostly of *Pinus* (9%), with other conifers (*Abies* 1.8%; *Tsuga mertensiana* 1.3%; *Picea* 0.7%; *T. heterophylla* 0.5%) and *Alnus* (0.9%) nearly absent. *Salix* pollen dominates the earliest part of the zone (TKL-2a, up to 35%), whereas herbs, especially Poaceae and Cyperaceae, are exceptionally abundant in the longer, later part of the zone (TKL-2b). The *Salix* grains observed in this zone belong to numerous morphotypes (Fig. 4f). Other shrubs including multiple Ericaceae pollen types (4%) were also present. Diverse herbaceous pollen types constitute a higher proportion of the assemblage than in zone TKL-1. Cyperaceae (22%) and Poaceae (18%) form the bulk of the herb component throughout both subzones, but many other taxa are also present including Asteraceae (4%), *Sanguisorba* (3%), *Artemisia* (2%), Rosaceae (2%), Caryophyllaceae (1.3%), and <1% of *Polemonium*, Fabaceae, Ranunculaceae, Apiaceae, *Heracleum*, *Thalictrum*, Brassicaceae, Saxifragaceae, Onagraceae, Polygonaceae, Liliaceae, and others. Pteridophytes observed include polypodiaceous fern spores (2.5%) with <1% spores of *Equisetum*, *Cryptogramma*, and other taxa. Aquatic vascular plants are rare and include <1% of *Typha*, *Isoëtes*, and *Triglochin*. Pollen accumulation begins low in TKL-2, with pollen influx in subzone TKL-2a at ~450 to 550 grains cm^{-2} cal yr^{-1}. This is nevertheless an order of magnitude greater than the lowest accumulation rates in TKL-1, driven by a notable increase in *Salix* pollen. PAR rises in subzone TKL-2b, ranging from ~1900 grains cm^{-2} cal yr^{-1} at the base of the zone to a peak of

~5150 grains cm^{-2} cal yr^{-1} before slowly decreasing to ~3200 grains cm^{-2} cal yr^{-1} at the top of the zone. Higher influx values in subzone TKL-2b are driven by increased herbaceous pollen, especially Cyperaceae and Poaceae. Despite a higher NAP signal, a fragment of conifer wood in radial section (~500 μm length) was observed on a pollen side from 935 cm (Fig. 4g) and is inferred to be derived from *in situ Picea* or *Tsuga* in the lake catchment at ca. 17,480 cal BP.

Diatom assemblages examined at 910 cm and 875 cm are characterized by fresh-brackish taxa that generally favour alkaline freshwater environments (910 cm: 45% brackish, 40% fresh-brackish, 13% freshwater; 875 cm: 67% fresh-brackish, 33% freshwater). Taxa identified include freshwater diatoms such as *Cocconeis placentula*, *Eunotia lapponica*, and *Gyrosigma acuminatum* as well as fresh-brackish diatoms such as *Amphora libyca*, *Epithemia adnata*, *E. sorex*, and *Fragilariforma virescens*. A significant assemblage of brackish/alkaline *Campylodiscus hibernicus* was also noted at 910 cm. Higher in the core, three diatom assemblages examined at 837 cm, 799 cm, and 700 cm all demonstrate fresh-brackish/ alkaline assemblages. Taxa noted in these samples include *Cocconeis placentula*, *Stephanodiscus oregonicus*, *Fragilaria*-types, *Pseudostaurosira brevistriata*, *Cymbella muelleri*, *Epithemia adnata* and *E. sorex*, and others. Sediment examined at 910 cm also contained an assemblage of *Daphnia* resting eggs (see Hiruta and Tochinai, 2014) as well as Characeae oospore reproductive bodies (Fig. 4a and b) which were not observed in any other samples. A sample of
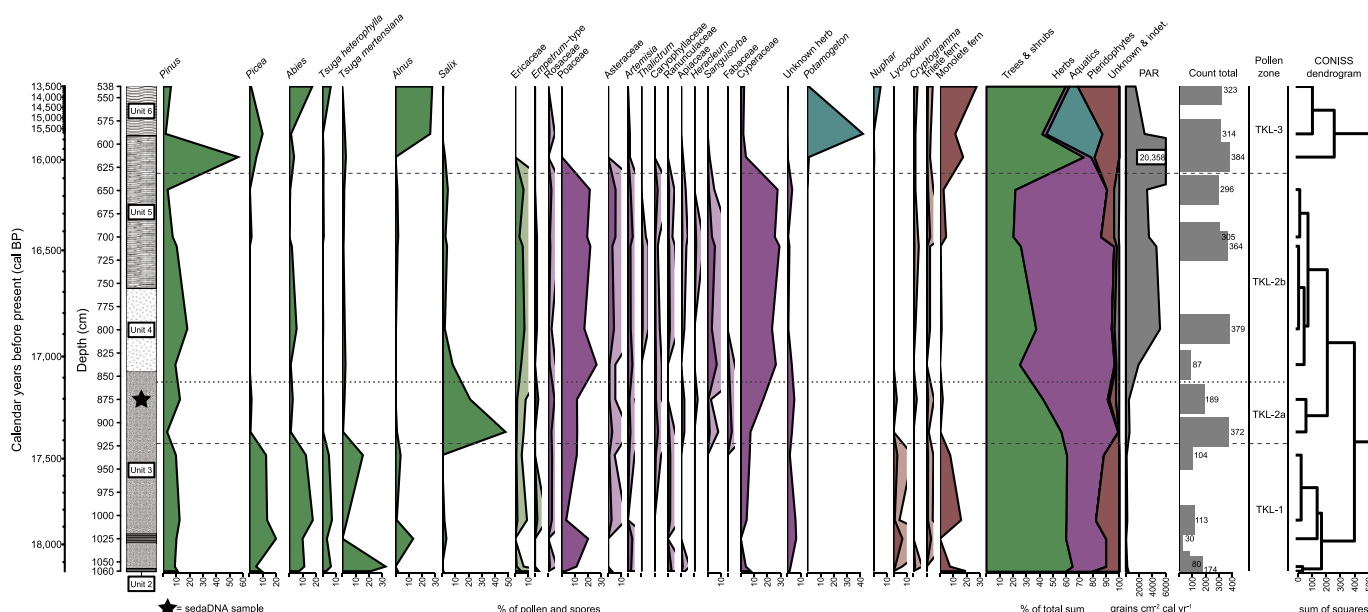
Fig. 5. Percentages of selected pollen and spore taxa from Topknot Lake plotted by depth/age in years cal BP. Core stratigraphy is shown by sedimentary unit to the left of the main panels. The location of the sample analyzed for sedaDNA is marked on the stratigraphy with a yellow star. A 5x exaggeration has been applied to selected less frequent taxa to demonstrate variability through time, particularly for herbaceous types. Pollen accumulation rate (PAR) is plotted to the right of the main panels, demonstrating low influx during pollen zones TKL-1 and TKL-2a. The PAR value for the sample at 614 cm has been truncated with its value appended as it is much higher than any other sample. The total pollen count for each sample is depicted to the right of PAR along with the dendrogram and pollen zones resulting from CONISS analysis (Grimm, 1987). Full count data Topknot Lake are available in Supplementary Table S2a. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
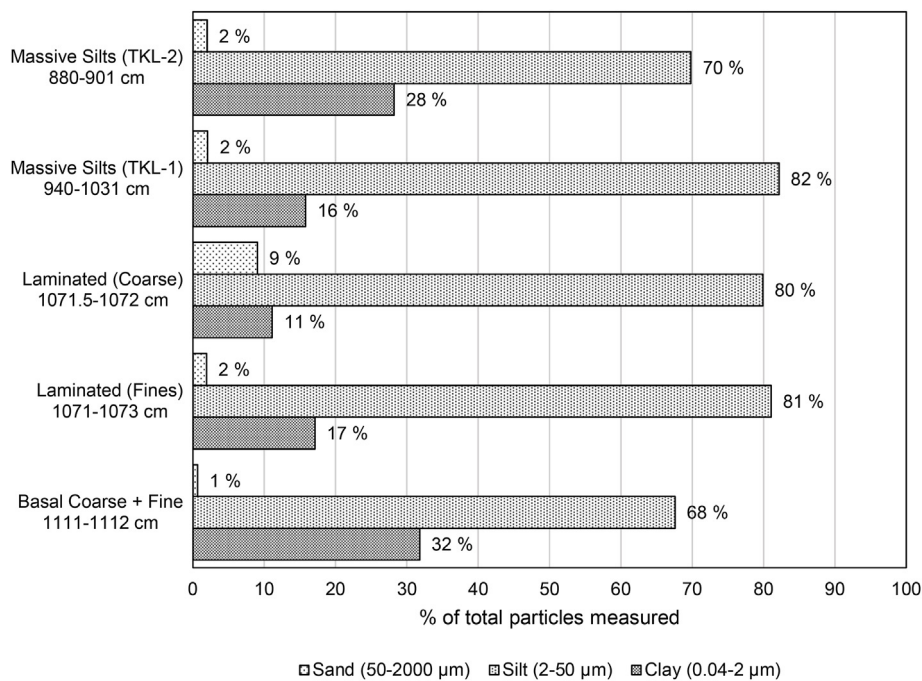
Fig. 6. Percentages of recorded laser diffraction grain size measurements for samples from the minerogenic lower sediments of Topknot Lake. Grain size is divided into three size bins for each sample: sand (50–2000 μm), silt 2–50 μm, and clay (0.04–2 μm).

sedaDNA at 875 cm bridges the transition between TKL-2a and TKL-2b. Genomic reads identified in this sample include several herbaceous species as well as conifers including *Abies*, *Picea*, Pinaceae (pine family—possibly *Pinus*, *Picea*, or *Abies*), *Populus trichocarpa* (black cottonwood), *Salix*, *Polemonium boreale* (northern Jacob's-ladder), *Bistorta*, Asteraceae, and *Rubus*. A single possible non-contaminant Metazoan read aligned with this sample,

Dendroctonus ponderosae (mountain pine beetle).

Grain size analysis was performed on two samples collected from pollen zone TKL-2 in massive fine deposits (TKL Unit 3) to determine the source of the sediment. Both samples were mostly composed of silt (average 70%, range 67–72%) with smaller fractions of clay (28%, range 27–30%) and sand (2%, range 1–3%) (Fig. 6).

4.2.2.3. TKL-3: 614-538 cm; 15,980–13,460 cal BP. Woody taxa dominated by *Pinus* and *Alnus* become more abundant in TKL-3, replacing the herb component of zones TKL-2a and -2b. Aquatic vascular plants and pteridophytes are also more common than in the older part of the record. AP rises to a mean of 57% of the total pollen in TKL-3 and is characterized by the early dominance of *Pinus* pollen (57%, then dropping to 4%) and a rise in *Alnus* (from 0% to 27%) and a modest increase in conifer pollen including *Abies* (7%), *Picea* (5%), *Tsuga heterophylla* (2%), and *T. mertensiana* (1.5%). Conversely, herb and shrub taxa drop to only 5% of the total pollen in TKL-3 and are represented largely by Cyperaceae (3%) with infrequent incidence of *Salix* (1.1%) and <1% of Poaceae, Rosaceae, *Artemisia*, Liliaceae, Apiaceae, and *Sanguisorba*. Pteridophyte spore abundance increases notably (21%), largely represented by polypodiaceous fern spores (20%). Aquatic vascular plants, mostly *Nuphar* and *Potamogeton*, increase mainly due to a spike in the middle of this zone (up to 42%) driven by the overwhelming presence of *Potamogeton* pollen at 589 cm. The pollen accumulation rate at the base of TKL-3 (~20,350 grains cm^{-2} cal yr^{-1}) is dramatically higher than any of the other samples from Topknot Lake, coincident with a spike in *Pinus* pollen and a notable increase in fern spores. Influx declines again in the upper portion of this zone, ranging from ~1450 to 2850 grains cm^{-2} cal yr^{-1}.

Two diatom assemblages from 589 cm to 558 cm show fresh-brackish/alkaline taxa including *Epithemia adnata*, *E. sorex*, *Gomphonema*, *Cocconeis*, *Rhopalodia gibba*, and *Fragilaria*-types. Four diatom assemblages between 548 and 510 cm all contain freshwater taxa including *Tabellaria flocculosa*, *Pinnularia*, *Stauroneis*, *Cymbella*, *Aulacoseira*, *Fragilaria*-types, *Gomphonema*, and *Cyclotella*.

4.3. Little Woss Lake

4.3.1. Stratigraphy

Sediment from Little Woss Lake was collected from the surface of a lake marginal wetland to a depth of 532 cm. Stratigraphy at Little Woss Lake consists of basal grey fine silty gyttja overlain by highly organic dark brown gyttja with embedded plant material. Four stratigraphic units were identified, as follows:

- **LWL Unit 1, >532 cm (>14,300 cal BP):** Pebbles and pea gravels that were not retained in the core tube except for a few basal clasts embedded at the base of the overlying silty gyttja. These gravels were not further analyzed.
- **LWL Unit 2, 532–520.5 cm (ca. 14,300–14,075 cal BP):** Light brownish-grey fine silty gyttja with a limited organic component. One *Pinus* needle was dated at 527 cm (UOC-7370). This unit includes all of pollen zone LWL-1 and the basal portion of LWL-2.
- **LWL Unit 3, 520.5–505 cm (ca. 14,075–13,690 cal BP):** Moderately organic fine silty gyttja grading to fibrous gyttja above. LWL Unit 3 has a medium-brown organic component and is progressively finer and siltier with depth. One twig fragment (UOC-7371) was dated at 513.5 cm. This unit includes the lower portion of pollen zone LWL-2.
- **LWL Unit 4, 505–271 cm (ca. 13,690–10,470 cal BP):** Highly organic dark brown fibrous gyttja with leafy organic lenses throughout. These sediments represent most of the late Pleistocene and early Holocene sequence at the site. Four macrofossil samples were dated at 499.5 cm (twig fragment, UOC-7372), 401.5 cm (*Nuphar* flower, UOC-7375), 336.5 cm (twig fragment, UOC-7373), and 286 cm (matted dicot leaves, UOC-7374). This unit includes the middle and upper portions of pollen zone LWL-2 and the entirety of zones LWL-3a and LWL-3b. Sediment above 271 cm was not analyzed.

4.3.2. Pollen, diatoms, and sedaDNA

Fourteen pollen samples from the lower segment of the Little Woss Lake core were divided into three major pollen zones, LWL-1 to LWL-3 from bottom to top. The third zone, LWL-3, is further split into two subzones, LWL-3a and LWL-3b. Arboreal pollen dominates all three zones with varying composition, and non-arboreal pollen is infrequent. Pollen percentages in the text are presented as the mean value for each zone unless otherwise noted. Percentages and PAR for each sample are depicted on Fig. 7. Other proxies, including diatoms and sedaDNA, are presented alongside the pollen data for ease of comparison.

4.3.2.1. LWL-1: 525.5–522 cm; 14,180–14,100 cal BP. The basal pollen zone, LWL-1, consists of a mixed conifer assemblage (96% arboreal pollen) dominated by *Abies* (35%) and *Pinus* (33%) with notable *Alnus* (24%) and few pteridophytes (2.4%), herbs (1.4%), and aquatic vascular plants (0.5%). Identified non-arboreal taxa include Cyperaceae (1.3%) and <1% of *Salix* and Ericaceae; aquatic taxa include <1% of *Nuphar* and *Typha*. Pteridophytes include polypodiaceous ferns (1.5%) and <1% of *Cryptogramma* and *Equisetum*. Pollen accumulation rates in zone LWL-1 are moderate when compared to other zones, ranging from ~7350 to 7750 grains cm^{-2} cal yr^{-1}. A diatom assemblage at 525.5 cm consists largely of freshwater (53%) or fresh/brackish taxa (42%) including freshwater *Cocconeis placentula* and *Rhopalodia gibba*, fresh-brackish *Pseudostaurosira* and *Staurosirella*, and several species of *Navicula*. A sample of sedaDNA from 522 cm corroborates the presence of numerous plant and animal taxa by ca. 14,100 cal BP. Plant taxa detected in this DNA sample include *Pinus contorta*, *Populus trichocarpa*, *Nuphar*, *Potamogeton*, Cyperaceae, and Poaceae. Animal sequences in the sample include *Oncorhynchus tshawytscha* (Chinook salmon), *Ursus arctos horribilis* (grizzly bear), *Ixodes pacificus* (Pacific black-legged tick) and possibly *Dendroctonus ponderosae* (mountain pine beetle).

4.3.2.2. LWL-2: 522-388 cm; 14,100–12,080 cal BP. Pollen from LWL-2 consists largely of woody taxa (92%) dominated by *Pinus* (45%) and *Alnus* (30%) with notably reduced incidence of *Abies* (6%) compared with LWL-1 and accompanied by the appearance of *Tsuga mertensiana* (5%), *T. heterophylla* (3%), and low values of *Picea* (2%) and *Populus* (0.5%). This zone also contains elevated and varied NAP values including herbaceous, aquatic, and fern taxa. The incidence of herbaceous taxa varies through this section (0%–8%), with modestly abundant pteridophytes (5%) and low levels of aquatic vascular plants (1.1%). Herb and shrub taxa in this zone include low levels of Cyperaceae (1.5%) and <1% of *Salix* and Poaceae; aquatics include <1% of *Nuphar* and *Potamogeton*. Pteridophytes include polypodiaceous ferns (3.5%) and <1% of *Pteridium*, *Cryptogramma*, and *Equisetum*. PAR values in LWL-2 begin relatively low (~3550 grains cm^{-2} cal yr^{-1}) but show an upward trend driven by increasing *Alnus* and *Pinus* pollen toward the top of the zone, to a maximum of ~16,700 grains cm^{-2} cal yr^{-1}.

Two diatom assemblages in the lower portion of this zone at 513.5 cm and 505 cm consist of largely freshwater (42%) or fresh/brackish taxa (54%) including freshwater *Pinnularia brebissonii*, *Gomphonema*, *Tabellaria fenestrata*, fresh-brackish *Pseudostaurosira*, *Staurosirella*, and *Nitzschia semirobusta*, and several species of *Navicula*.

4.3.2.3. LWL-3: 388–287.5 cm; 12,080–10,720 cal BP

4.3.2.3.1. Subzone 3a: 388-313 cm; subzone 3b: 313–287.5 cm. The pollen assemblage from zone LWL-3 is dominated by trees and shrubs (95%), particularly *Pinus* (36%), *Alnus* (27%), and *Tsuga heterophylla* (16%) with little NAP (1.3% herbaceous pollen; 0.6% aquatics; 3% pteridophytes). *Populus* pollen (1%) is present but infrequent. Subzone LWL-3a exhibits a moderate incidence of *Pinus*
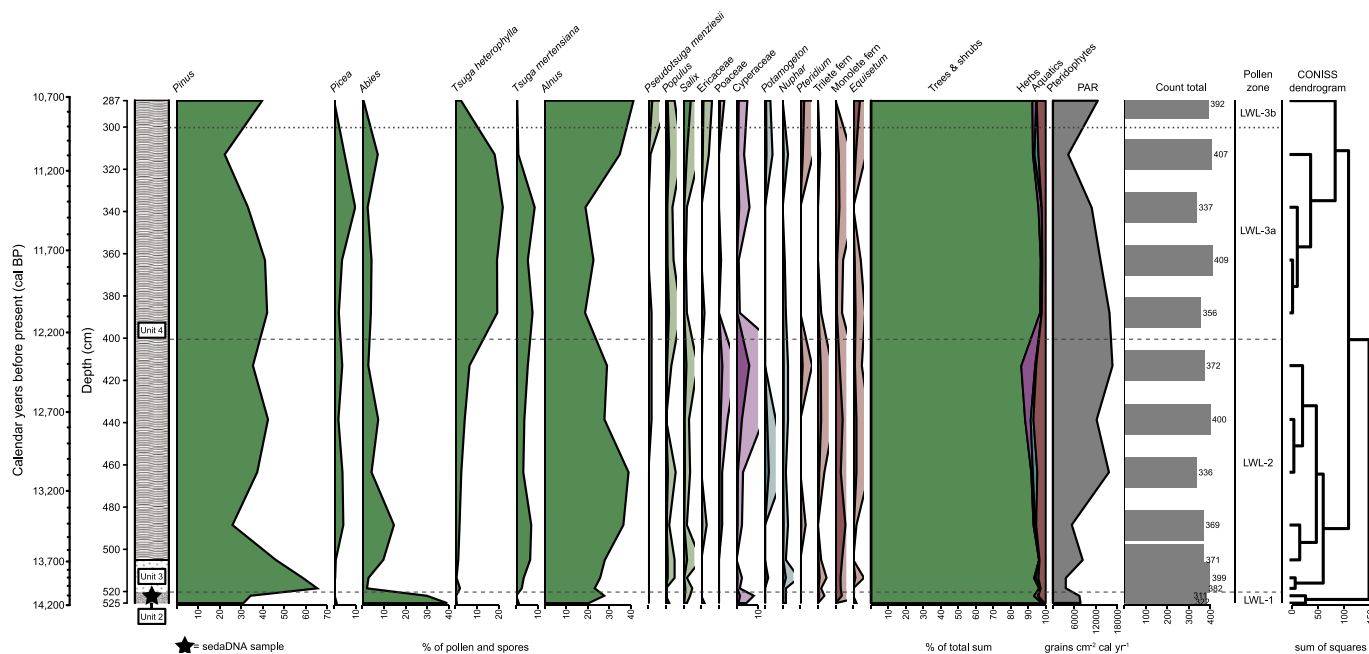
Fig. 7. Percentages of selected pollen and spore taxa from Little Woss Lake plotted by depth/age in years cal BP. Core stratigraphy is shown by sedimentary unit to the left of the main panels. The location of the sample analyzed for sedaDNA is marked on the stratigraphy with a yellow star. A 5x exaggeration has been applied to selected less frequent taxa to demonstrate variability through time. Pollen accumulation rate (PAR) is plotted to the right of the main panels. The total pollen count for each sample is depicted to the right of PAR along with the dendrogram and pollen zones resulting from CONISS analysis (Grimm, 1987). Full count data for Little Woss Lake are available in Supplementary Table S2b. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

pollen (35%) along with an increase in *T. heterophylla* (20%) and a decrease in *Alnus* (24%) when compared with LWL-2. Mixed conifer species persist at low levels through LWL-3a with *T. mertensiana* (6%) *Picea* (5%), and *Abies* (4%) present. Non-arboreal taxa are infrequent in the subzone with <1% of Cyperaceae, *Salix*, Rosaceae, Ericaceae, *Nuphar*, *Equisetum*, and fern spores. Subzone LWL-3b differs from LWL-3a with modest increases in *Pinus* (40%) and *Alnus* (41%) and decreases in *T. heterophylla* (3%) and *T. mertensiana* (0.5%). *Pseudotsuga* pollen (1.8%) also appears for the first time. Overall, NAP remains infrequent in LWL-3b, though with somewhat higher values than in LWL-3a for herbs (2%) and pteridophytes (5%) and low incidence of aquatic vascular plants (0.5%). Non-arboreal taxa present include *Salix* (3%), Ericaceae (1.0%), Cyperaceae (1.0%), and <1% of Poaceae and *Lysichiton*. Pteridophytes include *Equisetum* (3%) and *Pteridium* (1.8%); aquatics in this zone are limited to <1% of *Potamogeton* pollen. PAR values begin high in subzone LWL-3a at ~15,800 grains cm^{-2} cal yr^{-1} before decreasing to a low of ~4250 grains cm^{-2} cal yr^{-1} due to declining *Pinus* pollen influx. PAR then rises again in subzone LWL-3b to ~12,500 grains cm^{-2} cal yr^{-1}, driven largely by the increasing accumulation of *Alnus* and *Pinus* pollen.

5. Interpretation and discussion

This investigation provides new insight on the chronology and extent of late Pleistocene coastal glaciation in BC, helping to characterize ecological succession during a previously unrecognized postglacial interval on Vancouver Island and allowing better understanding of the timing and conditions for the settlement of early peoples along the northwest coast of North America.

5.1. Glacial chronology and coastal refugia

Between ca. 19,000–17,000 cal BP in coastal BC, lobes of the CIS originating from mainland fjords probably occupied Queen

Charlotte Strait and advanced into Queen Charlotte Sound while flowing across the Nahwitti Plateau (Fig. 1; Howes, 1983; Clague and James, 2002). The ice is believed to have covered most, but not all, of northern Vancouver Island (see Hebda et al., 1997). Outer coastal areas would have been covered by glaciers last and exposed first, leading to only brief periods of ice cover. The antiquity of the sedimentary record from Topknot Lake corroborates this, inferring that deglaciation began north of Quatsino Sound on the outer west coast of northern Vancouver Island no later than ca. 18,500 cal BP, ca. 2000–3000 years earlier than on the eastern side of the island at sites like Bear Cove Bog (Hebda, 1983) and ca. 3000–4000 years earlier than sites closer to sources of glacial ice such as Little Woss Lake. The deglacial chronology of Topknot Lake is instead comparable with, but slightly earlier than other outer coastal areas on the central coast of BC (~18,100 cal BP; Darvill et al., 2018) and in southeast Alaska (~17,000 cal BP; Lesnek et al., 2020).

Grain size analysis reveals that both the massive sediments and underlying laminations in the basal record from Topknot Lake are composed mainly of silt-sized particles. In the basal laminated sediments, both fine and coarse laminae contain nearly the same dominant silt component (81% in the fine deposits, 80% in the coarse deposits), with some variation in the clay and sand components (more clay in the fine laminae; nearly equal clay and sand in the coarse laminae). This consistency indicates that the sediments were derived from a primarily silt-based source, most likely loess, which is generally composed of ~60–90% silts and often occurs in massive deposits (Muhs, 2013). Aeolian loess would certainly have been produced from frost shatter and glacial grinding by Cordilleran ice (Muhs and Bettis, 2003) and may have been blown from continental glacial sources and washed into the basin. The periodicity of these laminations was not specifically investigated using biological or lake chemistry proxies (e.g., Hausmann et al., 2002; Lotter and Anderson, 2012). However, the physical characteristics of the sediment are typical of annual varved lake deposits, where each couplet is composed of a coarser dark

basal layer which fines upward into a lighter upper layer (Zolitschka, 2013). Therefore, the laminations may be the result of annual deposition from lake surface ice melt and seasonal slope-wash of recently deposited loess in the nearby catchment. Laminations like these have also been shown to be derived from glaciomarine or glaciolacustrine sediments deposited as couplets during periodic melt cycles (Evans, 2013; Ó Cofaigh, 2013). A glaciomarine source is unlikely but cannot be ruled out: freshwater diatoms extend to 910 cm (ca. 17,350 cal BP) in massive silts, but no diagnostic diatoms were recovered from the laminated sediments beneath, so the basal salinity conditions are unknown. However, if the laminations were glaciomarine in origin, at least some marine diatoms would be expected in the basal sediments as a result of nearshore mixing. Ice-distal glaciolacustrine deposition is also possible, as annual couplets can result from summer ice ablation (coarse) and winter settling (fine) from a direct glacial source (Palmer et al., 2008; Zolitschka, 2013). However, Topknot Lake is situated on a saddle ridge between the Macjack River to the north and Topknot Bay to the southwest, making it unlikely to have been part of a larger glaciolacustrine basin where such distal deposition of fine sediment could occur (Evans, 2013).

The massive sediments above the laminations (TKL Unit 3) are also mostly composed of silts (82%), and may represent loess deposition under slightly warmer, less seasonally affected conditions. Distance-decay functions for loess transport vary regionally; therefore, comparing the distribution of grain size fractions in the laminated and massive sediments at Topknot Lake with data from elsewhere (e.g., Smith, 1942; Ruhe, 1983; Muhs et al., 2004) to determine the specific distance of the basin from glacial ice is not reliable. However, most of the loess in these sediments is composed of well-sorted medium-sized or smaller silt particles (<31 μm) and the deposits are relatively thin (~2 m of massive silts, ~80 cm of laminations), both of which indicate increased distance from the source of aeolian sediment (Porter, 2001; Muhs, 2013). The character of these basal silty sediments suggests that not only was Topknot Lake free of ice early, but that glacial ice may have been several kilometres away from the basin by ca. 18,000–17,000 cal BP.

As Cordilleran ice retreated east across Vancouver Island, decaying ice masses exposed the area now occupied by Bear Cove Bog by ca. 15,610 cal BP (Hebda, 1983) and Misty Lake by ca. 14,900 cal BP (Lacourse, 2005). Nestled in the Vancouver Island Ranges, Little Woss Lake was deglaciated after these coastal sites. This later emergence may be explained by Little Woss Lake's proximity to icefields in the nearby Haihte Range and other areas on north-central Vancouver Island where late-stage valley glaciers may have persisted following retreat of the major ice masses. The disappearance of Cordilleran ice from these and other sites across coastal BC is largely coincident with the arrival of a warmer and drier climate during the Bølling-Allerød interstadial (ca. 14,700–12,900 cal BP; Hebda, 1995).

In summary, based on radiocarbon dating, stratigraphy, and sedimentology, the outer coast of northern Vancouver Island near Topknot Lake was ice-free several millennia before other parts of the island (including Little Woss Lake) and earlier than most of coastal BC and Alaska. This ice-free interval occurred while glaciers widely covered other parts of the island and the adjacent mainland. Whether or not there was a local or regional glacial refugium around Topknot Lake such as that on Brooks Peninsula (Hebda et al., 1997) or on Haida Gwaii (Mathewes and Clague, 2017) remains to be confirmed.

5.2. Late Pleistocene environments of northern Vancouver Island

5.2.1. Non-arboreal: Topknot Lake

The sedimentary record from Topknot Lake is unique in the region, providing an environmental and climatic record coincident with the Vashon Stade of the Fraser Glaciation known from Vancouver Island and elsewhere on the coast (Hicock and Armstrong, 1985). Laminated silts at the base of the core are inferred to be as old as ca. 18,500 cal BP, and inorganic fine silts with a modeled age of ca. 18,150 cal BP provide the earliest record of vegetation in the lake (zone TKL-1). Though characterized by low pollen counts, the pollen assemblage in TKL-1 indicates a mix of conifers including *Picea*, *Abies*, *Tsuga mertensiana*, and *Pinus*. As *Pinus* is a prolific producer of pollen which can be carried long distances (MacDonald and Cwynar, 1985; Cwynar and MacDonald, 1987; Hebda and Allen, 1993; Rousseau et al., 2008; Szczepanek et al., 2017), comparatively low values of *Pinus* in TKL-1 suggest that most of the pollen was not derived from nearby trees. However, a fragment of conifer wood found at 935 cm (Fig. 4g) suggests that at least a portion of the arboreal pollen signal in TKL-1 was local rather than the result of reworking or long-distance transport. The remainder of the assemblage (~40%) consists of non-arboreal shrubs, herbs (mainly Poaceae) and ferns, which collectively suggest an open environment or parkland with patches of conifers amidst grasses and forbs, possibly with wetlands near the lake itself. Similar mixed conifer and non-arboreal assemblages are known from pre-Fraser Glaciation deposits on southeast Vancouver Island and the lower mainland of BC where they are interpreted to represent subalpine parkland in a climate ~5 °C cooler than today (Hicock et al., 1982; Miskelly, 2012; Hebda et al., 2016). On Haida Gwaii, other sites have also been described with early non-arboreal assemblages accompanied by low pollen counts and influx (Lacourse et al., 2005; Mathewes et al., 2019), probably the result of sparse vegetation and/or high sedimentation. Both factors may have affected the accumulation of pollen at Topknot Lake in zones TKL-1 and TKL-2. The fact that TKL-1 is contained within massive, well-sorted silts with some carbonized and degraded palynomorphs further indicates a possible aeolian (loess) origin of the sediments. Therefore, some of the degraded pollen observed in this zone may not be contemporaneous with TKL-1 and may instead be derived from reworked older sediments or from the weathering of pre-Pleistocene sedimentary rocks which have subsequently been entrained and redeposited by glacial ice (e.g., Zhang et al., 2017).

Zone TKL-2 (ca. 17,480–15,980 cal BP) demonstrates a distinctive, diverse, and dominant non-arboreal assemblage. Notably, pollen counts and influx are much greater than in zone TKL-1, particularly in the upper portion of the zone. This increased PAR may be the result of lessened deposition of loess as ice retreated further combined with an increasingly vegetated landscape undergoing less erosion and a reduced sediment supply. Conifer pollen is nearly absent except for low levels of *Pinus*, most of which can likely be ascribed to long-distance aeolian transport as observed in TKL-1 (MacDonald and Cwynar, 1985; Hebda and Allen, 1993). Abundant *Salix* pollen at the base of the zone may be derived from a band of wetland shrubs at the lake margin or from dry-adapted prostrate species like *Salix arctica* (arctic willow) on nearby slopes. Multiple species must have been present, because numerous *Salix* pollen morphotypes were observed in these samples (Fig. 4f). Abundant *Salix* pollen has been observed in coeval deposits (ca. 16,890 cal BP) at West Side Pond in Haida Gwaii, where it was interpreted to represent increased plant cover as a result of climatic amelioration and increased soil development (Lacourse et al., 2005).

The varied and abundant non-arboreal pollen assemblage of TKL-2 reveals an open landscape at ca. 17,500 cal BP at Topknot Lake. Poaceae and especially Cyperaceae pollen were common; however, there were also varied forbs including Asteraceae (asters), Rosaceae (rose family), Caryophyllaceae (pink family), Ranunculaceae (buttercup), *Sanguisorba* (burnet), *Polemonium* (Jacob's-

ladder), *Heracleum* (cow-parsnip), Liliaceae (lilies), *Pedicularis* (louseworts), Fabaceae (lupines and vetches), Caprifoliaceae (valerian), *Thalictrum* (meadowrue), Saxifragaceae (saxifrages), *Epilobium angustifolium* (fireweed) and other Onagraceae (evening primrose family), and Polygonaceae (buckwheat family). Numerous shrubs and subshrubs also occurred such as *Shepherdia* (soapberry) as well as Ericaceae (heathers, several morphotypes), *Empetrum nigrum*, and possibly *Cornus* (bunchberry/dwarf dogwood). Such diverse non-arboreal assemblages are not commonly recorded following deglaciation on the coast (Hebda, 1995; Hebda and Whitlock, 1997). However, comparable assemblages of herbs and low, shrubby vegetation have been documented on Vancouver Island at Port Eliza Cave during slightly older cold and dry glacial climates (ca. 21,000−19,000 cal BP; Al-Suwaidi et al., 2006) and widely during the global LGM on southern Vancouver Island (Miskelly, 2012) and the Fraser Lowland (Hebda et al., 2016).

Similar herb-shrub assemblages have also been described elsewhere on the Pacific coast of North America at sites that may have remained unglaciated during local glacial maxima or were deglaciated early, including parts of Haida Gwaii and Vancouver Island (Warner et al., 1982; Warner, 1984; Heusser, 1989; Barrie et al., 1993; Brown and Hebda, 2003; Lacourse et al. 2003, 2005; Mathewes and Clague, 2017), the islands off southern Alaska (Misarti et al., 2012), and on the western slopes of the Olympic Mountains in Washington state (Heusser, 1983). Furthermore, these tundra-like coastal assemblages can be compared with late Pleistocene glacial assemblages in Beringia which are characterized by the presence of Poaceae, Cyperaceae, *Salix*, *Artemisia*, and other non-arboreal taxa (Colinvaux, 1964, 1996; Rampton, 1971; Ager, 1975; West, 1981; Anderson and Brubaker, 1996; Savvinova et al., 1996).

Few aquatic species were observed in the early part of the record from Topknot Lake (TKL-1 and TKL-2), only appearing in pollen assemblages after ca. 16,000 cal BP. This may be a result of oligotrophic lake conditions and higher sediment accumulation in the basin prior to ca. 16,000 cal BP as demonstrated by the presence of basal inorganic silts (see Fig. 4h and i) followed by indications of increased nutrient input and the build-up of diatoms and other algae in the sediment (see Fig. 4a and b). Diatom assemblages analyzed throughout this zone between 910 and 700 cm (ca. 17,350−16,430 cal BP) indicate largely freshwater taxa in the lake with a few fresh-brackish/alkaline types. The mixing of fresh-brackish and freshwater taxa in the absence of typical brackish-marine transitional indicators (such as *Paralia sulcata*) suggests alkaline freshwater conditions without any marine influence (Zong, 1997; McQuoid and Hobson, 1998). The abundance of both *Daphnia* resting eggs and Characeae oospores in the diatomaceous gyttja at the base of TKL-2 is indicative of significant nutrient deposition in the lake and further suggests alkaline conditions in the basin. However, the lack of carbonate encrustations on the Characeae specimens (see Fig. 4b) indicates that the water chemistry at that time was low in carbonate. Similar assemblages of *Daphnia* and Characeae have been documented at low-latitude arctic lakes in Greenland (Fredskild, 1983) as well as lakes on Haida Gwaii during both the advance phase of the Fraser Glaciation (Mathewes and Clague, 2017) and in the early postglacial (Warner et al., 1982; Warner, 1984). Comparing the fossil evidence from Topknot Lake with these assemblages indicates that the basin was cold and eutrophic at ca. 17,350 cal BP.

The sedaDNA sample from Topknot Lake at 875 cm (ca. 17,200 cal BP) provides a key perspective on this interval, though the interpretation is based upon few successful taxa IDs. The results indicate the local occurrence of non-arboreal taxa such as *Salix*, *Polemonium*, *Bistorta*, and asterids in the lake catchment, corroborating the pollen assemblages. Despite the low proportions of arboreal pollen in this zone, the sedaDNA evidence suggests that *Abies*, *Picea*, and notably *Populus trichocarpa* were present near the lake. The identification of *Populus* demonstrates that sedaDNA can reveal the occurrence of taxa which are often undetected or underrepresented in pollen assemblages (e.g., Mott, 1978; see also Liu et al., 2020 for a discussion of the ability of sedaDNA to accurately represent local vegetation at a site). These results identify late-glacial populations of several taxa near Topknot Lake which could then have spread onto the deglaciating landscape to the east over the next several thousand years.

Collectively, the data from zone TKL-1 and TKL-2 provide a glimpse of the environments on northern Vancouver Island during the maximum extent of the Fraser Glaciation across much of the coast. Though mostly tundra-like, the landscape was populated with diverse taxa and was apparently productive, including some conifers in the catchment of Topknot Lake. These varied environmental indicators reveal that the climate was cold and dry by ca. 17,500 cal BP, possibly as a result of regional cooling associated with the presence of Cordilleran ice combined with changes in north Pacific atmospheric circulation and a southward displacement of the jet stream (Hebda and Whitlock, 1997).

After ca. 15,980 cal BP (zone TKL-3), the record at Topknot Lake indicates a resurgence of woody species, especially *Pinus* and *Alnus*. Shrubs and shade-intolerant herbaceous species nearly disappeared, with only a small component of *Salix*, Poaceae, and forbs in woodland openings while ferns increased in abundance. This assemblage is comparable to and roughly coeval with the *Pinus*-dominated basal zone at Bear Cove Bog on the eastern side of Vancouver Island (Hebda, 1983). Other sites from Alaska to southern Vancouver Island including Little Woss Lake demonstrate similar *Pinus* woodland environments, but generally not until after ca. 15,000 cal BP (Cwynar, 1990; Hansen and Engstrom, 1996; Hebda, 1997; Brown and Hebda, 2002; Lacourse et al. 2003, 2005; Hebda et al., 2005; Lacourse, 2005; Lacourse and Mathewes, 2005; Galloway et al., 2008; McLaren, 2008; Brown et al., 2008; Ager, 2019). Though still cool and dry, this assemblage likely represents a warming trend beginning after ca. 16,000 and continuing through the global Bølling-Allerød interstadial between ca. 14,700−12,900 cal BP (Hebda, 1995).

In addition to providing a local palaeoenvironmental record, an examination of broader regional palynostratigraphy provides insight into the length and chronology of the sequence from Topknot Lake. Hebda et al. (2016) demonstrate that major vegetation changes in the region during the late Pleistocene correlate closely with subcontinental and hemispheric climatic changes. Therefore, the occurrence of a relatively wooded assemblage at Topknot Lake (TKL-1) before a large open herbaceous pollen zone (TKL-2) may have chronological implications despite the lack of radiocarbon dates from the deepest deposits at the site. Hicock et al. (1982) and Lian et al. (2001) describe a subalpine forested to semi-open landscape in the lower mainland of BC and Washington state occurring during a time known as the Port Moody Interstade (ca. 22,500−22,200 cal BP) prior to the Fraser Glaciation maximum (ca. 19,000−17,000 cal BP). Considering the radiocarbon dates, stratigraphic position, and palynological assemblages, zone TKL-1 may correlate with a semi-open landscape during the same timeframe. On a palynostratigraphic basis, this would imply that Topknot Lake and the surrounding area may have escaped the advance of ice during the Fraser Glaciation. However, this association also implies the existence of a disconformity at ca. 925 cm representing the interval from ca. 22,000−17,500 cal BP, which is possible but is not obvious from the continuous silty stratigraphy at that depth. If TKL-1 is coeval with the Port Moody Interstade, it is still possible that the site was covered by an earlier out-of-phase advance of Cordilleran ice during the global LGM (correlated with the Coquitlam

Stade ca. 26,000−22,500 cal BP), but this advance appears to be restricted to parts of the lower mainland of BC (Ward and Thomson, 2004; Hebda et al., 2016) and there is no known evidence for it on Vancouver Island (Miskelly, 2012). Overall, an interpretation of unglaciated Port Moody Interstade-age environments at Topknot Lake remains tentative due to low pollen counts and the potential for redeposition of pollen in the basal sediments. Further work at the site and others in the surrounding area is needed to confirm the presence of a full-glacial refugium.

5.2.2. Pine zone and early Holocene: Little Woss Lake

In contrast with the early non-arboreal record at Topknot Lake, the oldest pollen zones at Little Woss Lake (LWL-1 and LWL-2, ca. 14,180−12,080 cal BP) are coeval with the upper sediments from TKL-3 and are broadly comparable to late Pleistocene records across the northwest coast of North America which are interpreted to represent dry and cool *Pinus* woodlands (Hebda, 1983; Hebda and Whitlock, 1997; Brown and Hebda, 2002; Lacourse, 2005; Eamer, 2015; Ager, 2019). However, at Little Woss Lake, the basal zone (LWL-1) includes abundant *Abies* pollen as well as *Pinus* and *Alnus* with few non-arboreal taxa. The early predominance of *Abies* rather than *Pinus* is unique and may be explained by the physiography of the area around Woss Lake and the Nimpkish River Valley. The north-south orientation of Nimpkish Lake and Woss Lake may have created a funnel for cold and dry winds blowing from the main Cordilleran ice mass (Hebda and Whitlock, 1997). Even today, Little Woss Lake experiences a drier interior-like climate (BEC zone CWHxm2) when compared with the typical wet, cool coastal environment. This valley climate is characterized today by the presence of *Pseudotsuga menziesii*, a species whose modern range on Vancouver Island is usually limited to drier, warmer areas to the south (Pojar and MacKinnon, 2004). Under these interior-like conditions, *Abies*-type pollen in the late Pleistocene assemblage in Little Woss Lake may be derived from dry-adapted *A. lasiocarpa* (subalpine fir) rather than *A. amabilis*. This brief *Abies* zone at Little Woss Lake could represent a late Pleistocene interior-coastal assemblage rarely documented in BC (see Heinrichs et al., 2002). However, the zone is represented by only two samples at the base of the core, so interpretation of this assemblage is tentative. Additional studies focusing on interior lakes on Vancouver Island may reveal similar cold- and dry-adapted postglacial wooded ecosystems.

At the boundary between LWL-1 and LWL-2 (ca. 14,100 cal BP), sedaDNA analysis identified taxa in and around the lake that were not detected by pollen. In addition to expected woodland taxa such as *Pinus contorta*, the sedaDNA results indicate the occurrence of Poaceae as well as lake-marginal species including *Populus* and aquatics such as *Nuphar*, *Potamogeton*, and Cyperaceae. Furthermore, sedaDNA results suggest the presence of animals in and around the lake during this time including *Oncorhynchus tshawytscha* and *Ursus arctos horribilis*, both of which are indicators of a well-developed ecosystem and high biodiversity (Hyatt et al., 2000; COSEWIC, 2012).

In zone LWL-2 after ca. 14,100 cal BP, *Abies* pollen values drop precipitously. Non-arboreal taxa including Poaceae, Cyperaceae, Asteraceae, Rosaceae, and *Artemisia* as well as several fern taxa are present. The occurrence of ferns and NAP in this assemblage suggest that the climate at Little Woss Lake remained moderately dry between ca. 14,100 and 12,080 cal BP, though the presence of *Tsuga mertensiana* indicates at least somewhat increased moisture compared with LWL-1 (Hebda, 1995; Brown et al., 2008).

Conifers persisted through the cooler and moister climates of the terminal Pleistocene and into the early Holocene (subzone LWL-3a, ca. 12,080−11,080 cal BP), and shade-tolerant *T. heterophylla* became more abundant. Similar coeval mixed conifer assemblages occur at other sites on northern Vancouver Island, including at Bear Cove Bog (Hebda, 1983) and Misty Lake (Lacourse, 2005). This cool and moist climate appears to have prevailed at the site into the early Holocene. Mathewes (1993) notes that increases in moisture-dependent taxa, especially *T. mertensiana*, are characteristic of the Younger Dryas (12,900−11,700 cal BP) on the northwest coast of North America. However, Mathewes (1993) also notes that Younger Dryas assemblages are generally accompanied by thinning forests and increases in non-arboreal pollen, conditions which were not observed in the record at Little Woss Lake. Instead, herb and shrub taxa that depend on gaps in the canopy were less common—though not entirely absent—in the record through this interval. In the uppermost subzone (LWL-3b) after ca. 11,080 cal BP, *Pseudotsuga* appeared for the first time and *T. mertensiana* disappeared from the record. The shift toward warm- and dry-adapted species like *Pseudotsuga* is typically associated with climatic warming during the early Holocene (Hebda, 1983; Hebda and Whitlock, 1997) but may also be the result of variable migration rates into the region following deglaciation.

5.3. Implications for late Pleistocene human settlement on the northwest coast of North America

Northern Vancouver Island during the local glacial maximum has previously been characterized as a barrier of ice and otherwise harsh environmental conditions which hindered the movement of early peoples arriving in the region (e.g., Mathews, 1979; Clague and James, 2002). However, geological and palaeoecological studies have now established widespread glacial retreat along various parts of coastal BC and Alaska by at least ca. 17,000 cal BP (Mann and Peteet, 1994; Misarti et al., 2012; Briner et al., 2017; Darvill et al., 2018; Lesnek et al., 2020; Shaw et al., 2020). As additional environmental and archaeological data become available, such as the recent publication of footprints from White Sands National Park in New Mexico suggested to date to ca. 23,000−21,000 cal BP (Bennett et al., 2021; see also Becerra-Valdivia and Higham, 2020), the importance of chronologically extensive late Pleistocene records from northwestern North America becomes more evident. At the time these footprints are said to have been made, previous studies suggest that both the ice-free corridor and the interior of BC were occupied by ice sheets (Dyke, 2004; Heintzman et al., 2016), while parts of the northwest coast of North America remained uncovered by ice until ca. 19,500 cal BP (Wigen, 2005; Al-Suwaidi et al., 2006; Miskelly, 2012) or were refugia (e.g., Hebda et al., 1997; Mathewes and Clague, 2017). The deposits at Topknot Lake demonstrate ice-free conditions on part of the northwest coast of North America which are inferred to date to at least ca. 18,500 cal BP, and which may tentatively extend into the Port Moody Interstade (ca. 22,500−22,200 cal BP) based on undated palynostratigraphic associations. Taken together with previous research, these data suggest that the interval of glacial cover on parts of the outer coast of Vancouver Island was brief, if it existed at all. Therefore, the coastal environment would likely have been available to early peoples for longer intervals both during and immediately following the LGM than the interior ice-free corridor. Future investigations at these and other sites may produce new environmental records from the coast extending further into the glacial maximum.

The data also help to address the oft-raised issue of limited food and resources for humans in paraglacial or other biotically depauperate environments. Several studies (e.g., Mackie et al., 2011; Bjerck and Zangrando, 2013; Breivik, 2014; Fletcher, 2015; Bjerck et al., 2016; Breivik et al., 2016; Bjerck, 2017) discuss these concerns and propose human use of various types of resources (e.g.,

pinnipeds for food; *Salix* or other shrubs for tools) and technologies (e.g., flexible skin boats) in postglacial non-arboreal environments. Along the northwest coast of North America at sites like Topknot Lake and Little Woss Lake, palaeoecological records derived from pollen, macrofossils, sedaDNA, and other proxies now demonstrate the presence of both arboreal and non-arboreal environments which in some places are inferred to extend to at least ca. 18,000 cal BP and which could yield appropriate resources for these technologies. Though dispersed across the northwest coast, these terrestrial environments offered largely coeval tundra or subalpine parkland-like conditions for people who may have been making their way along the Pacific Rim from Beringia during the late Pleistocene. Such conditions are demonstrated by early postglacial non-arboreal pollen records and evidence for cold-adapted animals from sites in southern Alaska (Misarti et al., 2012), southeast Alaska (Heaton and Grady, 2003; Ager, 2019), and Haida Gwaii (Warner et al., 1982; Heusser, 1995; Lacourse and Mathewes, 2005; Lacourse et al. 2005, 2012; Wigen, 2005) between ca. 18,000 and 15,000 cal BP. Additionally, early deglaciation and lower relative sea level (up to 135 m below modern) during and following the LGM would have exposed low-lying coastal plains and islands along parts of the outer coast of BC and Alaska during the same interval, further expanding the landscape available for human settlement (Luternauer et al., 1989b; Lacourse et al., 2003; Hetherington et al., 2004; Carrara et al., 2007; Darvill et al., 2018; Shaw et al., 2020; though see Lesnek et al., 2020).

Overall, the glacial and ecological histories of the wider northeast Pacific Rim emphasize broad environmental continuity for early people settling along the northwest coast of North America. During and immediately after the LGM, tundra-like environments are inferred to have existed from Beringia to Vancouver Island, followed by pine woodlands and other arboreal ecosystems developing in refugia and on recently deglaciated landscapes. Alongside previous research, the new palaeoecological records from Topknot Lake and Little Woss Lake strengthen the growing evidence for resources including trees, shrubs, berries, medicines, and numerous animal species along the northwest coast of North America during the terminal Pleistocene, with some areas extending into the glacial maximum.

6. Conclusions

The palaeoecological records from Topknot Lake and Little Woss Lake demonstrate that the outer west coast of northern Vancouver Island had a different environmental history than many other sites in coastal BC and Alaska during the Fraser Glaciation. The area around Topknot Lake is inferred to have been free of glacial ice since at least 18,500 cal BP. Between ca. 18,000 and 16,000 cal BP, parkland and herb-shrub vegetation at Topknot Lake resembled late-glacial and refugial environments in Haida Gwaii and pre-Fraser Glaciation maximum records on Vancouver Island and the Fraser Lowland. After 16,000 cal BP and into the Bølling-Allerød interstadial, the ecosystems on the outer west coast begin to resemble the pine woodlands from elsewhere in the region. Further inland, the area around Little Woss Lake supported a unique *Abies* forest after 14,200 cal BP, then developed into a *Pinus*-dominated ecosystem after 14,100 cal BP. The differing glacial and ecological histories of Topknot Lake and Little Woss Lake demonstrate that parts of the outer coast of northern Vancouver Island and the adjacent coastal plains were either unglaciated when the Cordilleran Ice Sheet reached its maximum extent or had well-established biotic communities during a time when other parts of the coast were covered by ice. When combined with previous research, the results presented here raise doubts about the perception of the coast as a barrier blocking the movement of

humans along the northwest coast of North America during the interval of maximum ice cover. Furthermore, our observations weaken the argument that the plants and animals in these environments were not sufficiently abundant or diverse to sustain people. Rather, late Pleistocene conditions along parts of the northwest coast of North America resembled those with which early peoples were familiar in Beringia for thousands of years.

This study demonstrates the importance of continued, widespread multi-disciplinary research on late Pleistocene palaeoenvironments in western North America. The successful use of sedaDNA in this study illustrates that new analytical methods can reveal substantial complementary information about the ecological history of the Pacific coast, especially concerning the interval relevant to early human settlement during and after the LGM. The records from Topknot Lake and Little Woss Lake are only two of many that will continue to shed light on the geological, ecological, and archaeological histories of this region. Future archaeological and palaeoecological research will benefit greatly from a deeper understanding of the late Pleistocene glacial dynamics of Canada's west coast.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2022.107388.

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