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Peatland formation, succession and carbon accumulation at a mid-elevation poor fen in Pacific Canada

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Abstract

We reconstructed peatland formation, succession and long-term rates of carbon (C) accumulation at a mid-elevation poor fen on Vancouver Island in coastal British Columbia, Canada. Multi-proxy paleoecological analyses including bulk chemistry, peat composition, macrofossils, pollen, and non-pollen palynomorphs show terrestrialization starting from a small oligotrophic lake 14,000 cal BP. Peat accumulation began by 11,600 cal BP with the transition to an emergent *Nuphar*-dominated shallow-water marsh. Terrestrialization in the center of the peatland was more or less complete by 10,400 cal BP with the development of a *Sphagnum*-dominated poor fen that continues to the present. Outward expansion by paludification appears to have brought the peatland close to its modern lateral extent by 10,000 cal BP, suggesting that terrestrialization and paludification played important concurrent roles in the early development of this poor fen. Mean long-term rates of C accumulation (13 g $C/m^2/yr$) are lower than at most Northern Hemisphere peatlands including nearby lowland bogs. Maximum rates of 43 g $C/m^2/yr$ occurred in the early Holocene during accumulation of *Nuphar* peat and the transition to *Sphagnum* peat, and coincided with high summer temperatures and increased seasonality, which promote growing season productivity and reduce winter decomposition. Early Holocene increases in C accumulation rates occurred at two nearby lowland bogs during similar wetland stages. Collectively, these studies demonstrate that climate and autogenic succession including changes in relative water table depth and plant functional groups interacted to drive Holocene peatland dynamics and C accumulation rates in the maritime setting of coastal British Columbia.

Keywords: peatlands; poor fen; terrestrialization; paludification; carbon accumulation; *Nuphar* peat; non-pollen palynomorphs; coastal British Columbia

Introduction

Peatland ecosystems are wetlands characterized by primary production that exceeds organic matter decay, resulting in substantial accumulations of partially-decomposed, carbon-rich organic matter i.e., peat (Weider and Vitt, 2006; Rydin and Jeglum, 2013). In these ecosystems, waterlogged, acidic conditions, low decomposability of plant material, especially *Sphagnum* moss, and limited microbial activity promote peat accumulation and therefore carbon storage on long ecological timescales. A number of factors including topography, hydrological conditions, species composition and disturbance interact to drive the development and dynamics of peatlands including peatland carbon accumulation (Kuhry, 1997; Belyea and Baird, 2006; Limpens et al., 2008; Shiller et al., 2014). Climatic conditions play an overarching role, through both direct and indirect effects of temperature, photosynthetically active radiation, effective moisture, seasonality and growing season length (Jones and Yu, 2010; Fenner and Freeman, 2011; Charman et al., 2013; Gallego-Sala et al., 2018). On long timescales, peatlands are important CO_2 sinks and CH_4 sources that have had a net cooling effect on macroscale climate over the Holocene (Frolking and Roulet, 2007; Ciais et al., 2013).

Peatlands form through three main developmental pathways (Wieder and Vitt, 2006; Rydin and Jeglum, 2013). Primary peat formation occurs when peat accumulates directly on newly-exposed wet mineral ground following, for example, a decrease in relative sea level or ice retreat. Peatland formation through paludification occurs when increases in the local water table inundate mineral soils that have either been long exposed or already support terrestrial plant communities, allowing peat-forming plants such as *Sphagnum* mosses to invade. Paludification can occur at the margins of established peatlands as well as on forested uplands through build-up of organic matter and waterlogging that suppresses soil respiration. Terrestrialization occurs when a water body is gradually converted to peatland via infilling with organic material and/or floating mats that expand out over the basin. Typically, peat accumulates in and/or on the margins of shallow water, eventually filling the basin and leading to the development of a fen or bog. Based on a compilation of almost 700 peatland records, Ruppel et al. (2013) suggest that these three processes are more or less equally responsible for peatland formation in North America and northern Europe.

Wetlands including peatlands are common landscape features along the north Pacific coast of North America (National Wetlands Working Group, 1988). In coastal British Columbia (BC), Canada, mild year-round temperatures and abundant precipitation promote peat formation. Peatlands in the region occur on both gentle and steep terrain (Vitt et al., 1990; Golinski, 2004; Asada and Warner, 2005), and bogs are generally more common than fens (Maynard, 1989; MacKenzie and Moran, 2004). A number of peat-based paleoecological studies have been conducted in coastal BC (e.g., Hansen, 1950; Hebda, 1983; Banner et al., 1983; Brown and Hebda, 2002; Huntley et al., 2013); however, most have focussed on inferring Holocene changes in forest composition and climate. Only a few peer-reviewed studies have explicitly addressed changes in peatland ecosystems and carbon accumulation in this maritime setting. Banner et al. (1983) and Turunen and Turunen (2003) conducted paleoecological studies in a bog woodland and at a blanket/slope bog, respectively, both of which formed through paludification in lowland settings on BC's north coast. To the south, on Vancouver Island, Lacourse and Davies (2015) and Lacourse et al. (2019) conducted multi-proxy studies including reconstruction of carbon accumulation rates at two lowland bogs that formed through terrestrialization.

Here, we focus on the developmental history of Anderson Fen, a mid-elevation poor fen on Vancouver Island in coastal BC, a region where there are no previous studies focussed on past peatland dynamics of fens. The main objectives of the study are to i) determine the developmental history of Anderson Fen including the timing and nature of peatland initiation, ii) estimate long-term rates of C accumulation, and iii) shed light on the interacting roles of climate and autogenic factors in driving peatland dynamics and long-term C accumulation in this maritime setting. We use multi-proxy analyses including peat composition, bulk chemistry, macrofossils, pollen and non-pollen palynomorphs to infer the fen's formation, successional stages, and associated changes in plant communities, and hydrological and edaphic conditions over the last 14,000 years. Carbon and nitrogen analyses are used to estimate long-term rates of C and N accumulation. We evaluate the multi-proxy record and C accumulation rates from Anderson Fen in relation to paleoclimatic records from the region and place the results in a broader context through comparison to other peatland records including two nearby lowland bogs. Our research suggests that both terrestrialization and paludification played important roles in early peatland development at Anderson Fen. In addition, C and N accumulation rates were highest in Vancouver Island peatlands including Anderson Fen, in the early Holocene, when climatic conditions and autogenic factors acted together to promote rapid peat accumulation.

Materials and methods

Anderson Fen (49º 44.1’ N, 125º 11.6’ W; 554 m asl) is a mid-elevation poor fen located 15 km northwest of Courtenay on central Vancouver Island, BC (Figure 1a). The fen sits in the Leeward Island Mountain Ecosection at a higher elevation to the west of the Nanaimo Lowlands. The region is characterized by a maritime climate of cool summers, mild winters and a relatively narrow annual temperature range. Mean annual temperature is 6.9 ºC and the mean temperature of the warmest (August) and coldest (December) months are 15.1 ºC and –0.2 ºC, respectively

(Wang et al., 2016). Mean annual precipitation is 2270 mm/yr, with most precipitation falling as rain between October and March. Snow accounts for <15% of annual precipitation, but covers the fen for up to three months in winter. The fen is surrounded by *Tsuga heterophylla*-dominated forest that also includes conifers such as *Tsuga mertensiana* and *Chamaecyparis nootkatensis* that are more common at higher elevations.

Anderson Fen (informal name) is approximately 1 km long and 100 m wide at its widest point with a surface area of 5.5 ha. The fen is part of the Courtenay River watershed. A small amount of surface flow connects the fen to Anderson Lake (14 ha) and other wetlands to the northwest. In August 2016, the water table was 20 cm below the surface at the central coring location (Figure 1b), although pockets of standing water were present in some areas. Mean pH and temperature-corrected conductivity of the standing water were 4.6 and 146 μS, respectively. Golinksi (2004) provides a detailed account of modern plant communities at Anderson Fen. Plant cover is characterized by an almost complete bryophyte layer of *Sphagnum* mosses including *Sphagnum angustifolium*, *S. papillosum*, *S. fuscum* and *S. pacificum* with an open layer of sedges that includes *Eriophorum angustifolium* and *Carex* spp. (Figure 1c). Creeping and low ericaceous shrubs (*Vaccinium oxycoccos*, *Kalmia microphylla* var. *occidentalis*) are also common. Other taxa in lower abundance include *Rubus chamaemorus*, *Drosera anglica*, *Rhododendron groenlandicum* and *Vaccinium uliginosum*. *Menyanthes trifoliata*, *Scheuchzeria palustris* and *Nuphar polysepala* occur in scattered wet areas, often in standing water and in association with *Rhynchospora alba* sedges. *Spiraea douglasii* and *Lysichiton americanus* occur on the margin of the fen.

Peat cores were collected from three locations in Anderson Fen (Figure 1b) in August 2016, using a side-filling Russian sampler with a 50 cm-long and 5 cm-diameter semi-cylindrical chamber. Coring locations were 15–20 m apart, from the centre of the fen towards its edge. At each location, coring was conducted from two adjacent boreholes with 10 cm of overlap for each 50 cm section. The uppermost 50 cm of peat at location C, closest to the fen edge, could not be collected because of an abundance of large woody roots. We analyzed the core from the centre of the fen (Core A, 4.7 m in length) in detail using a multi-proxy approach described below. Nine AMS radiocarbon ages were obtained on plant macrofossils or bulk peat/organic lake sediment from Core A (Table 1). Cores B (3.8 m) and C (2.9 m) were collected to provide insight into the nature and timing of lateral peatland expansion. We conducted loss-on-ignition (LOI) on these two supplemental cores and obtained AMS radiocarbon ages on the basal peat. All ages were calibrated to calendar years before present (cal BP) using the IntCal13 data set (Reimer et al., 2013). An age-depth model was built for Core A on calendar age probability distributions and an age of −66 cal BP for the top of the core, using 10,000 iterations of a smooth spline in the 'clam' package (Blaauw, 2010) in R.

LOI was conducted on 1–3 cm^3 samples along the length of each core following Heiri et al. (2001). Samples were dried at 105 ºC for 20 h and ignited at 550 ºC for 4 h. Carbon and nitrogen analyses were conducted at 88 depths in Core A corresponding to a temporal resolution of ~150 cal yr. For C and N analyses, 1–3 cm^3 samples were dried for 48 h at 50 ºC and ground to a fine powder with a steel ball mill. Tin capsules were packed with 3–5 mg of homogenized peat and analyzed on an Elementar Americas vario MICRO cube elemental analyzer with acetanilide as the calibration standard. Replicate analyses were conducted on 15% of samples. Carbon and nitrogen accumulation rates (CAR and NAR, respectively) were calculated using ash-free bulk density from LOI analyses, measured %C and %N, and accumulation rates based on the age-depth model.

We used a quadrat technique similar to Barber et al. (1994) to characterize peat composition. The >150 µm fraction of 1–2 cm^3 samples was placed in gridded petri dishes and all remains in 15 randomly selected 1×1 cm quadrats were differentiated into four major components i.e., herbaceous stems/leaves, moss stems/leaves, ligneous remains and unidentifiable organic matter (UOM). These data are presented as percentages of the total count in each sample. Macrofossils such as fungal sclerotia, seeds and *Nuphar* sclereids (idioblasts) were also identified in the same 15 quadrats.

Pollen and non-pollen palynomorphs (NPP) such as testate amoebae, fungal spores, and various plant and algal remains were identified in 1–2 cm^3 samples at a mean sampling resolution of 120 cal yr. Sample preparation involved minimal chemical treatment i.e., warm 10% KOH for 8 min, acetolysis for 2.5 min and mounting in 2000 cs silicone oil. One *Lycopodium* tablet of 18,584 ± 829 spores (Batch 177745) was added to each sample in order to estimate palynomorph concentrations. Identification of NPPs was based on van Geel (1978), Pals et al. (1980), van Geel et al. (1989), Kuhry (1997), Charman et al. (2000) and Payne et al. (2012). Cluster analysis on the 18 most abundant NPP types was used to identify zones of similar NPP assemblages. The data were square root transformed and then clustered using incremental sum-of-squares. Pollen assemblages in the Anderson Fen core are dominated by conifer pollen from regional forests. Our focus here is on local pollen types relevant to the developmental history of the fen. At least 400 pollen and spores, not including *Sphagnum*, were identified in each sample except those in the basal inorganic sediments where a minimum sum of 100 was used due to low palynomorph concentrations. Pollen percentages are based on all pollen and spores, except those from *Sphagnum* and obligate aquatic plants, which are based on the main sum in addition to the sum of each group.

Results

Chronology, Stratigraphy and Macrofossils

The age-depth model for Core A (Figure 2), from the center of the fen, yields accumulation rates that are surprisingly steady along much of the core's length; the model resembles those more typical of slowly-accumulating lake sediments with few changes in rates. Accumulation rates generally vary between 0.02-0.03 cm/yr with mean deposition times of 37 yr/cm. However, modelled rates are an order of magnitude higher in the uppermost 45 cm and between 320 and 365 cm, where there is a plateau in the age model (Figure 2). The model predicts an age of 13,305 cal BP (12,890–13,430 cal BP) for the base of the organic lake sediments (454 cm) and an age of 11,630 cal BP (11,490–11,880 cal BP) for the beginning of peat accumulation at 411 cm (Figure 3).

The basal portion of Core A is composed of clay (470–454 cm) with minor amounts of sand. Rounded gravel occurs at the very bottom of the core. These inorganic sediments are overlain by organic lake sediment (454–411 cm) composed primarily of unidentifiable organic matter (40–90%) with occasional sand grains and an abundance of chironomid head capsules (Figure 3). *Potamogeton* and *Nuphar polysepala* seeds, *Isoëtes* megaspores and daphnid ephippia also occur in these lake sediments, as do *Sphagnum* stems/leaves although these account for less than 2%. The lake sediment grades into limnic-telmatic peat (411–335 cm) that is dominated by herbaceous remains, which are mostly fragments of *Nuphar polysepala* stems covered in sclereids. Disassociated *Nuphar* sclereids and *Nuphar* seeds are also abundant (Figure 3). *Sphagnum* stems/leaves account for up to 12% of the peat composition between 365 and 348 cm, but are otherwise more or less absent in the *Nuphar*-dominated section of the core. Eight *Vaccinium* seeds were encountered at 352 cm, but do not occur elsewhere in the core. *Nuphar* peat is followed by an abrupt transition to well-preserved *Sphagnum* peat (335–286 cm) composed of 60–80% *Sphagnum* stems/leaves and up to 30% ligneous remains. Seeds from *Dulichium arundinaceum* sedges and *Menyanthes trifoliata*, a semi-aquatic herb, are also present in this *Sphagnum* peat (Figure 3). Mixed peat composed of herbaceous (mostly Cyperaceae), woody and *Sphagnum* remains in varying proportions occurs between 286 and 162 cm. Fungal sclerotia and *Drosera anglica* seeds occur occasionally in this mixed peat. The uppermost peat (162–0 cm) consists primarily of *Sphagnum* stems/leaves; however, herbaceous and woody components account for up to ~50% of some samples between 140 and 76 cm. *Sphagnum* opercula and fungal sclerotia are generally more abundant in the uppermost *Sphagnum* peat than elsewhere in the core.

Loss-on-ignition and C and N analyses

Organic matter content in Core A from Anderson Fen correlates with changes in overall stratigraphy with 3–6% LOI in the inorganic sediments at the base and 20–50% LOI in the overlying organic lake sediments (Figure 4). LOI increases abruptly to 84% at the beginning of *Nuphar* peat accumulation (411 cm, ~11,600 cal BP) and is 93–100% in the overlying *Sphagnum* and mixed peat. In Cores B and C, basal inorganic sediments have LOI values of 3–5% (Figure 5). In Core B, peat accumulation begins at 339 cm (~11,200 cal BP; Table 1) when LOI increases abruptly to 86%. In Core C, peat begins at 264 cm (~10,000 cal BP) with 91% LOI. In both cases, basal inorganic sediments are directly overlain by peat containing abundant *Sphagnum* stems/leaves as well as *Nuphar* remains, *Menyanthes* seeds and fungal sclerotia, without an intervening organic lake sediment unit as in Core A. This suggests terrestrialization in the center of the basin and expansion outwards through paludification. Over the course of the Holocene, ~35% less peat (1.5 m) accumulated on the fen margin than in the center. In all three cores, mean ash-free bulk density is 0.09 g/cm^3 and downcore variations in density are similar with values between 0.04 and 0.13 g/cm^3 (Figure 5).

Changes in the C and N contents of Core A also correspond with changes in stratigraphy (Figure 4). The lake sediments have relatively low C and N contents (18% C and 1.1% N, on average) with C:N values of ~20. C and N increase to 47% and 2–3%, respectively, in the *Nuphar* peat, which is characterized by C:N values that increase from 20 to 35. The overlying terrestrial peat has a mean C content of 50.4% and N fluctuates between 0.5 and 2.3%.

Accordingly, C:N values show considerable variation: C:N is about 70 in the early Holocene *Sphagnum* peat, about 40 in the mid-Holocene mixed peat, and 30–100 in peat that accumulated in the late Holocene, with the highest values occurring in *Sphagnum*-dominated samples (Figure 4). Fluctuations in C:N generally match variation in the proportion of *Sphagnum* remains and there is a moderate positive correlation (r=0.65, p<0.0001) between %C and ash-free bulk density.

Over the length of Core A, rates of C accumulation generally range between 10 and 15 g C/m^2/yr (Figure 4) with a time-weighted mean rate of 12.8 g C/m^2/yr in the peat portion of the core. Rates are substantially higher near the surface (up to 120 g C/m^2/yr), although these high apparent rates are primarily an artifact of undecomposed plant matter that has yet to be transferred to the catotelm (Loisel and Yu, 2013). Rates are also high in the early Holocene during accumulation of *Nuphar* peat and the transition to *Sphagnum* peat. The time-weighted mean rate between 10,800 and 10,200 cal BP is 42.6 g C/m^2/yr. Simple estimates of long-term C rates for Cores B and C, using ash-free bulk density (Figure 5), the mean %C content of peat in Core A (50.4%) and basal peat ages, are 13.4 and 11.5 g C/m^2/yr, which are more or less equivalent to the time-weighted mean rate in the central coring location. However, these rates for Cores B and C may well be overestimates, as they do not account for downcore changes in C content and peat accumulation rates. When this simple approach is applied to Core A, the long-term C accumulation rate is 16.6 g C/m^2/yr i.e., 30% faster than the rate based on direct %C measurements and a robust geochronology that permits weighting rates by downcore variation in deposition times.

Rates of N accumulation in Core A are low over the entire record (Figure 4) with a time-weighted mean rate of only 0.4 g N/m^2/yr, which is typical of peatlands. N accumulation increased by an order of magnitude in the early Holocene, reaching a maximum apparent rate of 3.7 g N/m^2/yr during accumulation of *Nuphar* peat, just before the transition to *Sphagnum* peat.

Non-pollen palynomorphs (NPP) and other microfossils

We identified over 50 different NPP types in Core A, but focus here only on the most abundant types with clear indicator value. Cluster analysis of NPP concentrations identified three main assemblage zones (Figure 6). Diatom frustules and Nymphaeaceae leaf hair basal cells are the most abundant NPPs in zone 1 (13,300–11,250 cal BP), which corresponds with accumulation of organic lake sediment towards the base of the core. As these lake sediments transition into *Nuphar* peat, diatom concentrations decrease, Nymphaeaceae cells increase, and fungal spores begin to appear. At the boundary to zone 2a (11,250–8900 cal BP), which corresponds with the transition to *Sphagnum* peat, there is an abrupt change from microfossils indicative of a freshwater environment to those that suggest a terrestrialized setting (Figure 6). A number of protists (e.g., *Assulina muscorum*, *Archerella flavum*, *Heleopera*) appear for the first time and various fungal remains (e.g., Microthyriaceae fruiting bodies, *Entophlyctis* sporangia, *Gaeumannomyces* hyphopodia) also increase. NPPs are generally less abundant in zone 2b (~8900–2000 cal BP); however, there are sporadic occurrences of various protists and *Entophlyctis* sporangia and *Gaeumannomyces* hyphopodia are more or less continuously present. Zone 3 (2000 cal BP to the present) is marked by increases in Type 19 fungal ascospores. Protist concentrations including most notably *A. muscorum*, *Hyalosphenia papilio*, *Hyalosphenia elegans*, *Trigonopyxis arcula* type and *Arcella vulgaris* increase over the last 600 cal yr (Figure 6) in the uppermost 72 cm of peat that is composed almost exclusively of *Sphagnum* stems and leaves (Figure 3). In general, protists are more abundant in sections of the core composed of *Sphagnum* peat with low decomposition i.e., near the surface (0–72 cm) and between 284 and 330 cm (~9500–10,400 cal BP), than elsewhere in the core.

Pollen and spores from wetland plants

Changes in pollen assemblages in Core A (Figure 7) generally follow the overall stratigraphy and changes in peat composition. Pollen assemblages between 14,000 and 11,500 cal BP, in the basal clays and lake sediment, include Cyperaceae and aquatic plants such as *Potamogeton* and *Typha*. *Isoëtes* microspores are particularly abundant at the transition between inorganic and organic lake sediment. *Nuphar polysepala* reached a maximum of 4% between ~11,400 and 10,500 cal BP (Figure 7), during accumulation of *Nuphar* peat when *Nuphar* sclereids and seeds are also abundant (Figure 3). Low levels of *Potamogeton*, Cyperaceae, *Spiraea* type and Ericaceae pollen are also present during this interval. The transition to *Sphagnum*-dominated peat ~10,400 cal BP is marked by large increases in *Sphagnum* spores and Ericaceae pollen (Figure 7). A number of other wetland taxa including Cyperaceae, *M. trifoliata*, *Sanguisorba*, *Lysichiton americanus* and *Rubus chamaemorus* are also present during this transition. *Sphagnum* spores are present throughout the rest of the record, but there are large fluctuations in their relative abundance up to a maximum of nearly 80% in the uppermost *Sphagnum* peat. Ericaceae pollen is similarly present, but is most abundant at the transition to *Sphagnum* peat at 10,500 cal BP and about 9500–6800 cal BP (Figure 7), when ligneous remains account for a substantial proportion of the peat composition (Figure 3). *Spiraea* type pollen is also abundant during this interval. Single occurrences of *D. anglica* type pollen were found at ~7000 and 5500 cal BP (Figure 7), coincident with *D. anglica* seeds (Figure 3).

Discussion

Developmental history from an oligotrophic lake to a poor fen over the last 14,000 years

During the last glaciation, much of Vancouver Island was covered by the Juan de Fuca lobe of the Cordilleran Ice Sheet (Clague and James, 2002). Deglaciation began by 17,000 cal BP and appears to have progressed rapidly (Blaise et al., 1990; Cosma et al., 2008), with some mid-elevation areas on Vancouver Island ice-free as early as 16,000 cal BP (Alley and Chatwin, 1979). Clay-rich sediments were deposited in the Anderson Fen basin starting about 14,000 cal BP, suggesting ice-free conditions at the site by this time. Pollen and spores from Cyperaceae, *Potamogeton*, *Typha* and *Isoëtes* (Figure 7) indicate these taxa were among the first plants to colonize the basin and its margins. Colonies of nitrogen-fixing *Gloeotrichia* cyanobacteria suggest that conditions in the basin were initially oligotrophic, as would be expected following deglaciation (van Geel et al., 1989). Organic lake sediments with ~15% C and 1% N began to accumulate in the centre of the basin by 13,300 cal BP (Figure 4). The absence of organic lake sediments in Cores B and C suggests that the paleo-lake was smaller in spatial extent than the modern fen i.e., that the lake did not extend to these coring locations away from the center of the basin. The presence of an inflowing stream can be inferred from occasional sand grains (Figure 3), although various *Nuphar* remains (Figures 3, 6 and 7) starting about 13,100 cal BP suggest lentic conditions within the basin itself. Over the next thousand years, the organic matter content of the lake sediment gradually increased (Figure 4), becoming increasingly composed of stems and leaves of herbaceous plants, as opposed to unidentifiable organic material (Figure 3), and reflecting increased productivity in and around the small lake.

By 11,600 cal BP, peat began to accumulate in the center of the Anderson Fen basin in a shallow-water, marsh-like environment. A similar transition from lake sediment to peat also occurred at 11,600 cal BP at Grant's Bog (Figure 8) in the lowlands 7.5 km east of Anderson

Fen. These transitions from open lake environments to peat-accumulating marshy wetlands were likely aided by the reduction in precipitation that occurred at this time (Figure 8), which would have led to lowered lake levels (e.g., Brown et al., 2006; Shuman and Serravezza, 2017). This suggests that changes in regional climate played a facilitating role in peatland initiation.

Peat that accumulated at Anderson Fen between 11,600 and 10,500 cal BP consists almost exclusively of herbaceous remains (Figure 3), much of which derives from *Nuphar polysepala*, an aquatic perennial with thick, fleshy stems and rhizomes. C and N increased to 40–50% and 2–3%, respectively, during this interval (Figure 4). The C:N ratio (20–35) is similar to limnic peat reported from boreal sites (e.g., Treat et al., 2016); it is higher than most lake sediment but lower than most *Sphagnum* or ligneous peat (Meyers and Teranes, 2001; Loisel et al., 2014). *Nuphar polysepala* remains including stems, seeds, pollen, sclereids and leaf hair basal cells (Figures 3, 6 and 7) are substantially more abundant than in the underlying organic lake sediments. High concentrations of *Nuphar* sclereids suggest these plants were growing with erect aerial leaves, as sclereids provide structural support for petioles and are more abundant in emergent leaves than floating lily pads (Etnier and Villani, 2007). Analogous modern communities with dense *Nuphar* beds, often with erect aerial leaves, occur in topographic depressions, bog hollows and lake margins throughout coastal BC today (Golinski 2004; MacKenzie and Moran, 2004). Similar early Holocene *Nuphar*-dominated wetland stages characterized by substantial peat accumulation have been recognized elsewhere in the region (Hebda, 1983; Lacourse and Davies, 2005; Lacourse et al., 2019).

Other plants that occurred in and around this *Nuphar*-dominated marshy wetland include *Potamogeton*, *Typha*, *Sphagnum*, various herbs (Cyperaceae, *Menyanthes trifoliata*, *Sanguisorba*) and shrubs (*Spiraea*, Ericaceae). Peat began to accumulate away from the center of the basin by 11,200 cal BP i.e., the age of basal peat in Core B (Figure 5). This basal peat consists of abundant *Sphagnum* stems/leaves as well as *Nuphar* and *Menyanthes* remains, and directly overlies inorganic sediments. This suggests outward expansion by paludification concurrent with terrestrialization in the center of the basin. *Lysichiton americanus* pollen and *Vaccinium* seeds indicate these taxa were present by at least 10,600 cal BP. There is an isolated peak of Cyperaceae pollen to 27% at 10,500 cal BP (Figure 7) that coincides with seeds of *Dulichium arundinaceum* (Figure 3), a sedge that occurs in wetlands in many areas including coastal BC.

There was an abrupt transition to a *Sphagnum*-dominated peatland just before ~10,400 cal BP, evidenced by substantial increases in *Sphagnum* stems/leaves and spores (Figures 3, 7 and 8). Peat accumulation was relatively rapid during the transition from *Nuphar* peat to *Sphagnum* peat; 80 cm of peat accumulated in Core A between ~10,700 and 9900 cal BP. Expansion via paludification appears to have brought the peatland close to its modern lateral extent by ~10,000 cal BP i.e., the age of basal peat in Core C (Figure 5). Ligneous remains and Ericaceae pollen, including both *Rhododendrom* and *Vaccinium* types, also increased abruptly with accumulation of *Sphagnum* peat, indicating that woody shrubs were also growing on the peatland surface at this time. Pollen and/or seeds from various other plants (e.g., Cyperaceae, *M. trifoliata*, *D. arundinaceum*, *Sanguisorba*) indicate they continued to be present as well. Various standing water indicators (e.g., chironomid head capsules, *Nuphar* remains, *Potamogeton* pollen) more or less disappear with the transition to *Sphagnum* peat and were replaced by microfossils that suggest an increasingly terrestrialized environment (Figure 6). Increases in fungal remains including sporangia from saprotrophic *E. lobata* reflect lowering of the water table and increasingly oxic conditions (Wieder and Vitt, 2006). Protists including *Assulina muscorum*, *Archerella flavum* and *Heleopera* also increased abruptly (Figure 6). These taxa are typical of *Sphagnum*-dominated bogs and poor fens (e.g., Lamentowicz and Mitchell, 2005; Payne et al., 2006; Lamentowicz et al., 2011).

The abrupt changes in plant macrofossils and various microfossils that occurred with the transition to *Sphagnum* peat are matched by substantial changes in physico-chemical properties of the peat: N decreased to ~0.8% and C:N increased to 50–85 (Figure 4). Peat C:N values reflect both initial C:N and the degree of decomposition, and have proven useful in discriminating between different wetland types in a variety of settings including boreal (Wang et al., 2015), shoreline (Pendea and Chmura, 2012) and permafrost (Treat et al., 2016) peatlands. The high C:N values at Anderson Fen between 10,400 and 9600 cal BP are typical of well-preserved peat in *Sphagnum*-dominated wetlands. During this interval, peat composition (Figure 3), microfossil assemblages (Figures 6 and 7), and nitrogen content and C:N (Figure 4) are notably similar to those over the last 3800 cal yr. Thus, the various lines of evidence suggest development of a wetland analogous to the modern environment i.e., a *Sphagnum*-dominated poor fen with a lower water table relative to the preceding *Nuphar*-dominated marsh. Autogenic succession likely drove the transition to a poor fen; however, lowering of the water table, changes in plant functional groups, and development of the peatland may have also been facilitated by macroscale changes in climate. Summers were relatively warm and dry in the early Holocene and seasonal differences in insolation were maximized (Figure 8; Heusser et al., 1985; Berger and Loutre, 1991; Kienast and McKay, 2001; Walker and Pellatt, 2003).

Peat accumulated at a slow, but fairly steady rate of 0.02–0.03 cm/yr between ~9800 and 1000 cal BP (Figure 2); however, peat composition varied substantially over this interval (Figures 3 and 8), reflecting temporal variability in plant communities and edaphic conditions. Between 9600 and 3800 cal BP, peat composed of herbaceous (mostly Cyperaceae), woody and *Sphagnum* remains in varying proportions accumulated in the center of Anderson Fen. *Sphagnum* spores and Ericaceae pollen (*Rhododendron* and *Vaccinium* types) are abundant, and isolated occurrences of pollen and seeds from other taxa (e.g., *Typha*, *Nuphar*, *Menyanthes*, *Lysichiton*) point to their continued presence. Seeds and pollen of carnivorous *Drosera anglica* first appear in the record at 7000 cal BP, indicative of nutrient poor conditions that continue to the present. Nitrogen content of the mixed peat is 1.7%, on average, and C:N values generally range between 25 and 40, both of which are typical of poor fens (e.g., Wang et al., 2015; Treat et al., 2016). Changes in peat composition, bulk chemistry and microfossil assemblages suggest fluctuating hydrological conditions during the mid-Holocene. Increases in herbaceous remains (mostly Cyperaceae) occurred 9500–9000 and 6000–4000 cal BP. During these intervals, a variety of wet and/or standing-water indicators (chironomid head capsules, daphnid ephippia, *Archerella flavum* tests, *Nuphar* pollen and sclereids) are present, suggesting wet surface conditions, at least at the coring location. A rising water table may have been driven in part by shifting climate, which became cooler, wetter and less seasonal through the mid-Holocene (Figure 8; Heusser et al., 1985; Berger and Loutre, 1991; Kienast and McKay, 2001; Walker and Pellatt, 2003). However, climate alone cannot explain the relative variability and fluctuations in peat composition, particularly those that might suggest shifts to drier conditions. For example, increases in ligneous remains, pollen from ericaceous shrubs, and fungal sclerotia between 9000 and 7200 cal BP likely reflect drier surface conditions (Väliranta et al., 2007) at the coring location. Autogenic processes associated with peat accumulation and succession likely played important roles in driving changes in peat composition and plant communities through the Holocene (e.g., Tuittila et al., 2007; Shiller et al., 2014).

Spiraea pollen is relatively abundant 9500–7000 cal BP (Figure 7) and is likely derived from *Spiraea douglasii*, a species characteristic of poor fens and other wetlands in BC that are seasonally inundated (Golinski 2004, MacKenzie and Moran, 2004). Few protists were recovered from the mixed peat between 9400 and 6000 cal BP (Figure 6). This could be related to our sample preparation for pollen and non-pollen palynomorphs (Payne et al., 2012); however, samples from elsewhere in the core contain abundant xenosome protists including *Heleopera* and *Trigonopyxis arcula*, which can be destroyed during acetylation (Hendon and Charman, 1997). The low protist concentrations might also be related to preservation conditions e.g., seasonal water table drawdown might have promoted decomposition of protist tests. Lamentowicz et al. (2008) suggest that low protist concentrations during the early Holocene at a peatland in northern Poland may be associated with abrupt, seasonal water level changes. It is possible that this also explains the interval of low protist concentrations at Anderson Fen, as the abundance of *Spiraea* may reflect seasonally fluctuating water levels.

The uppermost 162 cm of the core from the center of Anderson Fen, which corresponds to the last ~3800 cal yr, is composed primarily of well-preserved *Sphagnum* peat (Figure 3) with abundant *Sphagnum* spores (Figure 7) and fungal microfossils (Figure 6). Various plants including sedges and ericaceous shrubs are also present. Fluctuations in %N over the last 3800 years match changes in the relative abundance of *Sphagnum* macro-remains, with higher C:N and therefore presumably lower decomposition when *Sphagnum* remains account for more of the peat composition than herbaceous and woody remains (Figures 3 and 4). Between 1300–700 cal BP, increases in ligneous and fungal remains including sclerotia likely reflect drier surface conditions, at least at the coring location. There is little macroscopic charcoal in the Anderson Fen record, suggesting that fire did not play an important role in driving peatland dynamics at this mid-elevation site. The largest peak in charcoal occurs at 1000 cal BP concurrent with an increase in fungal sclerotia (Figure 3). However, without a visible ash layer in the core, it is likely that fire occurred in nearby forests and not within the peatland itself.

Over the last ~600 cal yr (0–72 cm), various testate amoebae including *Assulina* spp., *Arcella* spp., *Hyalosphenia* spp. and *Trigonopyxis arcula* increase (Figure 6). *Archerella flavum* and *Hyalosphenia papilio*, two species that are associated with nutrient poor conditions (e.g., Lamentowicz and Mitchell, 2005; Lamentowicz et al., 2011), are most abundant. The different moisture preferences of taxa in the uppermost peat (Charman et al., 2000; Payne et al., 2006;

Amesbury et al., 2018) might suggest variability in surface wetness with standing water in some areas and drier surface conditions in others, as is the case now at Anderson Fen. The diversity of protists may simply reflect their occupation of different microhabitats near the surface. It is noteworthy that total protist concentrations increase substantially in the upper 72 cm of peat and that species richness is at its highest with a number of taxa such as *Trigonopyxis arcula*, *Arcella vulgaris* and *Hyalosphenia elegans* appearing for the first time in the record (Figure 6). Similar patterns of high protist concentrations and species richness have also been observed in the uppermost peat from *Sphagnum*-dominated bogs on Vancouver Island (Lacourse and Davies, 2015; Lacourse et al., 2019). There are a number of possible explanations for these patterns. It is possible that the apparent increase in richness reflects real increases in the number of different species over the last millennium. Other studies have linked recent increases in testate amoeba diversity to changes in land cover, lowering of water tables and regional warming (e.g., Oris et al., 2013; van Bellen et al., 2018). Alternatively, it may be a matter of differential preservation, such that some taxa are not preserved down-core due to increased decomposition. Indeed, ash-free bulk density is relatively low (0.05–0.08 g/cm^3) in the uppermost peat at Anderson Fen (Figure 4). Finally, it is also possible that the apparent increases in protist concentrations and richness in our uppermost samples are artefacts of sample preparation, although taxa that are sensitive to acetylation (Hendon and Charman, 1997) are present in the uppermost peat and elsewhere in the core (Figure 6). Comparing testate amoeba assemblages from our palynomorph slides to those isolated via simple wet-sieving could elucidate sample preparation effects.

Holocene carbon accumulation at Vancouver Island peatlands

C accumulation rates at Anderson Fen are generally low. In the peat portion of the record, the long-term mean rate is only 12.8 g C/m^2/yr. Long-term rates are slightly higher at two nearby lowland bogs. At Grant's Bog (80 m asl), located 7.5 km east of Anderson Fen (Figure 1a), the mean CAR is 19.5 g C/m^2/yr over the last 11,600 cal BP (Lacourse et al., 2019). At Port McNeill Bog (93 m asl), located 160 km northwest of Anderson Fen, the mean CAR is 16.1 g C/m^2/yr over the last 10,400 cal BP (Lacourse and Davies, 2015). These differences in CAR are subtle but may be linked in part to the role that climate plays in driving productivity and therefore net peat accumulation. Mild year-round temperatures in coastal BC lead to long growing seasons and high primary productivity, but this is offset by high decomposition over much of the year (Asada and Warner, 2005). Winters at Anderson Fen (554 m asl) are 2–4 ºC colder than at the two lowland sites, with temperatures hovering around 0 ºC for two to four months (Wang et al., 2016; Environment Canada, 2019). Accordingly, one might expect decomposition to be lower at Anderson Fen with slowdown if not cessation during winter, but this does not appear to have led to higher peat accumulation overall. Higher long-term C accumulation rates at the two lowland bogs may be related in part to higher primary productivity in a slightly warmer climate, despite year-round decomposition acting as a counter-balance. Differences in peatland type, plant communities and peat composition are likely more important in explaining the slightly higher CAR at the two low elevation sites, which have been ombrotrophic bogs since the early Holocene. Anderson Fen has been a poor fen characterized by *Sphagnum* moss and Cyperaceae communities for much of the Holocene, with only 4 m of peat accumulation since 11,600 cal BP. In contrast, Grant's Bog has accumulated 70% more peat (i.e., 7 m) over the same period and has been an ombrotrophic bog since ~8700 cal BP. Port McNeill Bog has been an ombrotrophic bog since 8000 cal BP with abundant ericaceous shrubs after 5000 cal BP. These shrubs contribute plant matter with relatively high C content and lignin that is recalcitrant to decomposition, increasing peat bulk density and ultimately C accumulation.

C accumulation at each of the three Vancouver Island peatlands increased during the early Holocene, which was characterized by higher summer temperatures, lower precipitation and amplification of the seasonal cycle of insolation, relative to the present (Figure 8; Heusser et al., 1985; Berger and Loutre, 1991; Kienast and McKay, 2001; Walker and Pellatt, 2003). Maximum CAR coincide with the timing of the Holocene thermal maximum in most northern peatlands (Yu et al., 2009; Loisel et al., 2014), suggesting that increased growing season temperatures played an important role in driving C accumulation by enhancing plant productivity, as is the case with peatland initiation more generally (Morris et al., 2018). Lower winter temperatures during the early Holocene would have further promoted C sequestration by reducing winter respiration rates and decomposition (Asada and Warner, 2005; Jones and Yu, 2010). Precipitation decreased at the beginning of the Holocene and remained relatively low until ~7500 cal BP (Figure 8), but there was still sufficient moisture to support peat accumulation. The reduction in precipitation at the beginning of the early Holocene may have indirectly aided C accumulation by facilitating terrestrialization via a reduction in lake level. At Anderson Fen, peat accumulation began at 11,600 cal BP when precipitation decreased, and there was a four-fold increase in C accumulation soon after, with mean rates reaching 51 g C/m^2/yr between ~11,000 and 10,500 cal BP, as summer temperatures and seasonality increased (Figure 8). Similar early Holocene increases in C accumulation occurred at the two lowland bogs. At nearby Grant's Bog, peat accumulation began at the same time as at Anderson Fen i.e., 11,600 cal BP (Lacourse et al., 2019). C accumulation rates increased after 10,000 cal BP, reaching a mean rate of ~50 g C/m^2/yr between 9000 and 8500 cal BP. The record from Port McNeill Bog, located further north on Vancouver Island (Figure 1a), extends back to only 10,400 cal BP (Lacourse and Davies, 2015). However, mean C rates at that time were similarly high i.e., 40–50 g C/m^2/yr.

At each Vancouver Island peatland, relatively high CAR occurred during the early Holocene period of higher summer temperatures and greater seasonality; however, local-scale changes in plant communities and hydrological conditions appear to have played an equally if not more important role in driving temporal changes in C accumulation. At all three sites, high rates of C accumulation occurred immediately before and during the transition to a *Sphagnum*-dominated peatland (Figure 8). At Anderson Fen and Port McNeill Bog, high accumulation rates occurred in the earliest Holocene (~10,500 cal BP) when both sites were marsh-like wetlands with abundant *Nuphar* and relatively low C:N ratios. This is in line with Treat et al. (2016), who report higher CAR in limnic peat than in ligneous and *Sphagnum* peat. At Grant's Bog, accumulation rates began to increase when *Nuphar* was abundant, but the highest accumulation rates occurred somewhat later (~9000 cal BP) during a sedge-dominated poor fen stage, when a high water table and wet surface conditions would have lowered overall decay and also facilitated high rates of C accumulation. Collectively, these records suggest that changes in local wetland conditions, peat-forming plant communities and climate interacted to drive Holocene fluctuations in C accumulation rates in Vancouver Island peatlands.

In general, long-term CAR are lower in our Vancouver Island peatlands (13–20 g C/m^2/yr) and elsewhere along the northeast Pacific coast (9–19 g C/m^2/yr; Turunen and Turunen, 2003; Jones and Yu, 2010; Nichols et al., 2014) compared to other Northern Hemisphere peatlands. Similar long-term rates have been documented at maritime sites further afield e.g., in eastern Canada and in northern Scotland (Magnan and Garneau, 2014; Loisel et al., 2014; Ratcliffe et al., 2018). Based on a compilation of 127 sites, Loisel et al. (2014) estimated a mean long-term rate of 23 g C/m^2/yr for northern peatlands. Some continental peatlands such as rich and poor fens in Alberta (Yu et al., 2014), fens and bogs in western Siberia (Borren et al., 2004), and sedge-dominated peatlands on the Tibetan Plateau (Zhao et al., 2014) reach mean long-term rates in excess of 30 g C/m^2/yr. Higher seasonality and more sunshine hours in continental settings promote greater CAR by reducing respiration and decomposition during the dormant season and fostering productivity in the growing season (Yu et al., 2014). Differences in hydrology and precipitation regimes also appear important, particularly in terms of the timing of moisture stress. Although annual precipitation at our Vancouver Island peatlands is relatively high (~1600-2300 mm/yr), these sites are exposed to moisture stress during the growing season, which constrains primary production at a critical time. The inverse occurs at peatlands on the Tibetan Plateau, where monsoons bring abundant precipitation during summer (Zhao et al., 2014). At the fens in continental Alberta, surface and groundwater inputs help to limit moisture stress (Yu et al., 2014).

Nitrogen accumulation is typically low in peatlands, particularly those that are *Sphagnum*-dominated. Loisel et al. (2014) estimated a mean long-term NAR of 0.5 g N/m^2/yr for northern peatlands. N accumulation rates at Anderson Fen are 0.39 g N/m^2/yr, on average, which is more or less equivalent to the rates observed at the two lowland bogs: at Grant's Bog and Port McNeill Bog, mean rates are 0.56 g N/m^2/yr and 0.41 g N/m^2/yr, respectively (Lacourse and Davies, 2015; Lacourse et al., 2019). As with C accumulation, there was a four-fold increase in N accumulation during the earliest Holocene at Anderson Fen with mean rates reaching 2.0 g N/m^2/yr between 11,000 and 10,500 cal BP. Nitrogen content was at its maximum of 2-3% between 11,500 and 10,500 cal BP during *Nuphar* peat accumulation. N-rich *Nuphar* stems and leaves are likely the principal source of this increased nitrogen (Longhi et al., 2008). Similar early Holocene increases in NAR occurred at the two lowland bogs as well as in many northern peatlands (Loisel et al., 2014).

Conclusion

Multi-proxy analyses on cores from Anderson Fen show that a small oligotrophic lake was present by ~14,000 cal BP. Organic lake sediments began to accumulate in the centre of the basin by 13,300 cal BP and by 11,600 cal BP, accumulation of *Nuphar* peat suggests the transition to an emergent *Nuphar*-dominated shallow-water marsh. Terrestrialization in the center of the wetland ultimately resulted in the development of a *Sphagnum*-dominated poor fen by 10,400 cal BP. Concurrent with terrestrialization in the center of the basin, outward expansion by paludification appears to have brought the peatland close to its modern lateral extent by ~10,000 cal BP. Thus, in the case of Anderson Fen, both terrestrialization and paludification were important in early peatland development. Autogenic succession likely drove the transition to a poor fen; however, lowering of the water table, changes in dominant plant communities, and ultimately development of the peatland would have also been facilitated by macroscale changes in climate. Multi-proxy analyses on multiple cores from throughout Anderson Fen would further clarify the relative importance of autogenic and allogenic drivers, and help discriminate between changes that occurred across the whole peatland from those that were limited in spatial extent. Additional cores would also further clarify the extent to which terrestrialization and paludification acted concurrently during peatland development.

Long-term rates of C accumulation at Anderson Fen are low compared to most Northern Hemisphere peatlands. Lower rates at Anderson Fen are likely related to differences in climate as well as autogenic factors such as plant functional groups. As in many Northern Hemisphere peatlands, maximum CAR at Anderson Fen occurred during the early Holocene, coinciding with high summer temperatures and increased seasonality, which promote growing season productivity and reduce winter decomposition. The early Holocene increase in CAR occurred during accumulation of *Nuphar* peat in marsh-like conditions and the transition to a *Sphagnum*-dominated poor fen. Early Holocene increases in rates of C accumulation also occurred at two nearby lowland sites during similar wetland stages, highlighting the importance of both climate and autogenic factors in driving C storage on long timescales. Additional peatland studies at middle and high elevations on Vancouver Island, to compare to the previous lowland studies and the mid-elevation record from Anderson Fen, should help to further elucidate the interacting effects of climate, topography, hydrological conditions, and plant communities on peatland dynamics and C accumulation in maritime settings along the North Pacific coast.

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Figure captions

Figure 1. A: Map of central Vancouver Island in coastal British Columbia, Canada showing location of Anderson Fen (red star), Port McNeill Bog (1) and Grant's Bog (2). B: Aerial view of center of Anderson Fen (554 m asl) in June 2016 showing the three coring locations. B: Landscape view of Anderson Fen in July 2016 looking northwest to Mt. Washington (1580 m asl), which is located 7.5 km from the fen.

Figure 2. Age-depth model for Core A from Anderson Fen. Grey bands are 95% confidence intervals based on 10,000 iterations of a smooth spline model.

Figure 3. Stratigraphy, peat component percentages, and macrofossils from Anderson Fen (Core A). Triangles along the y-axis mark the position of ^{14}C ages (Table 1). UOM=unidentifiable organic matter; (s)=seeds.

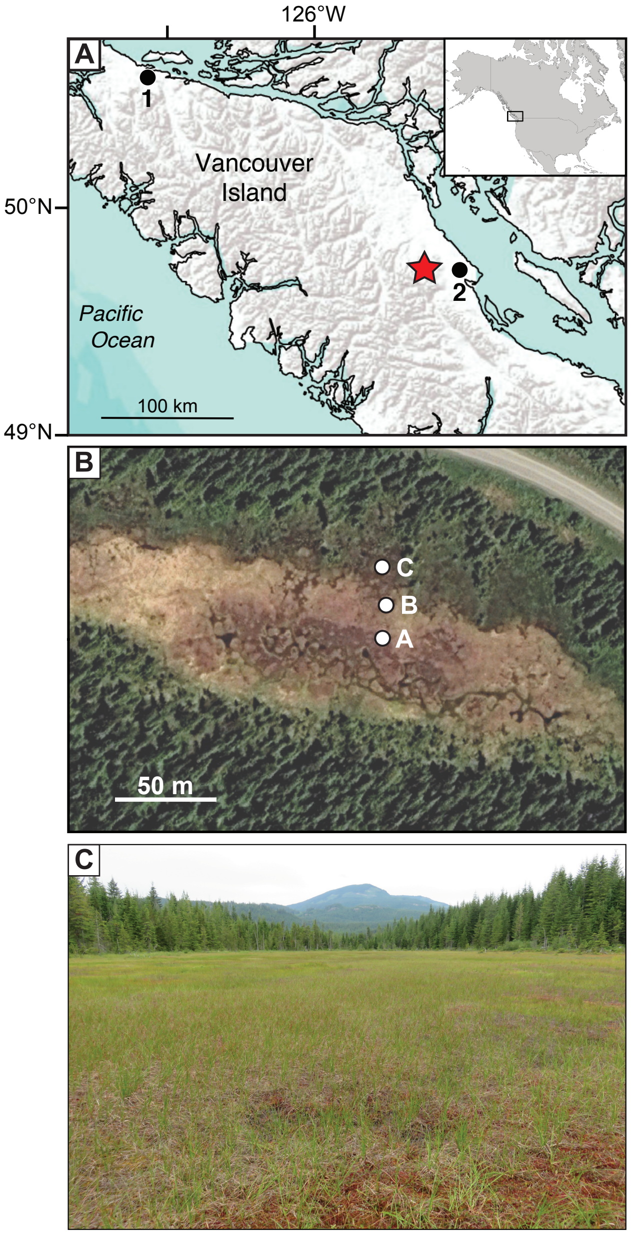
Figure 4. Physico-chemical records from Anderson Fen (Core A). Carbon and nitrogen accumulation rates are shown as apparent rates (dashed line) and mean rates in 500 cal yr bins (solid line). See Fig. 3 for stratigraphy legend. LOI=Loss-on-ignition; AFBD=Ash-free bulk density.

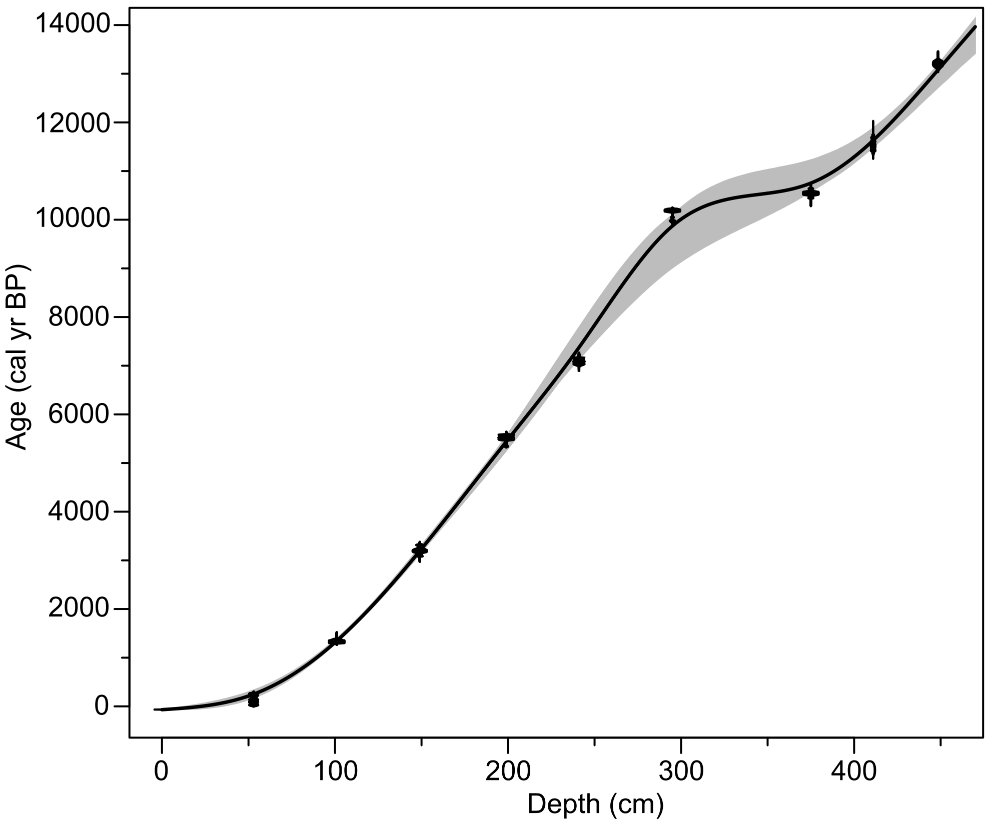
Figure 5. Loss-on-ignition (LOI) and ash-free bulk density (AFBD) for all three cores from Anderson Fen with the timing of initial peat accumulation in thousands of calendar years before present (ka). In Cores B and C, basal inorganic sediments are directly overlain by peat with abundant *Sphagnum* remains, without intervening organic lake sediments as in Core A.

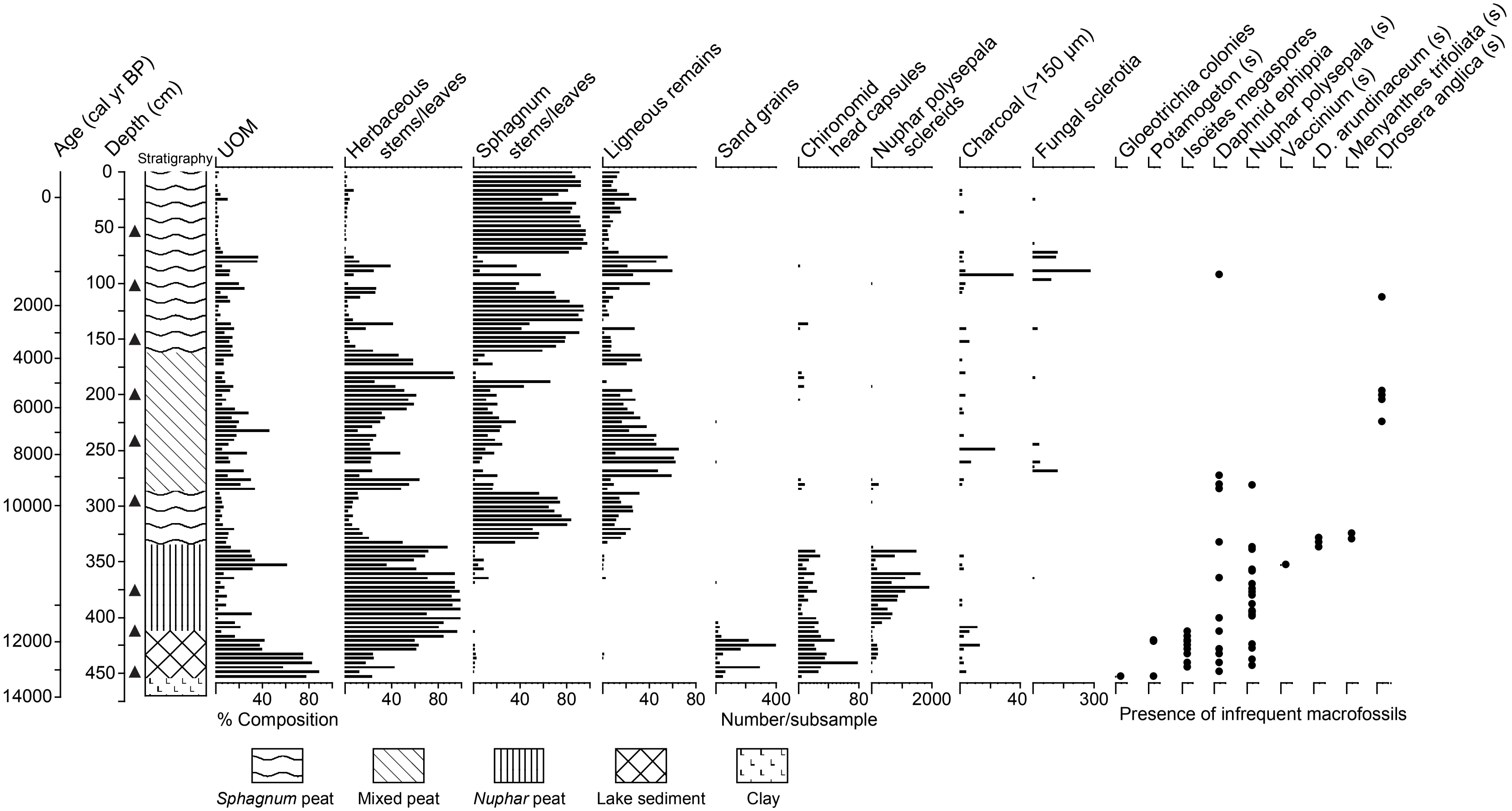
Figure 6. Concentrations of the most abundant non-pollen palynomorphs from Anderson Fen (Core A). Note changes in scale on x-axes. Numbers in brackets refer to NPP types (van Geel, 1978; Pals et al., 1980). See Fig. 3 for stratigraphy legend.

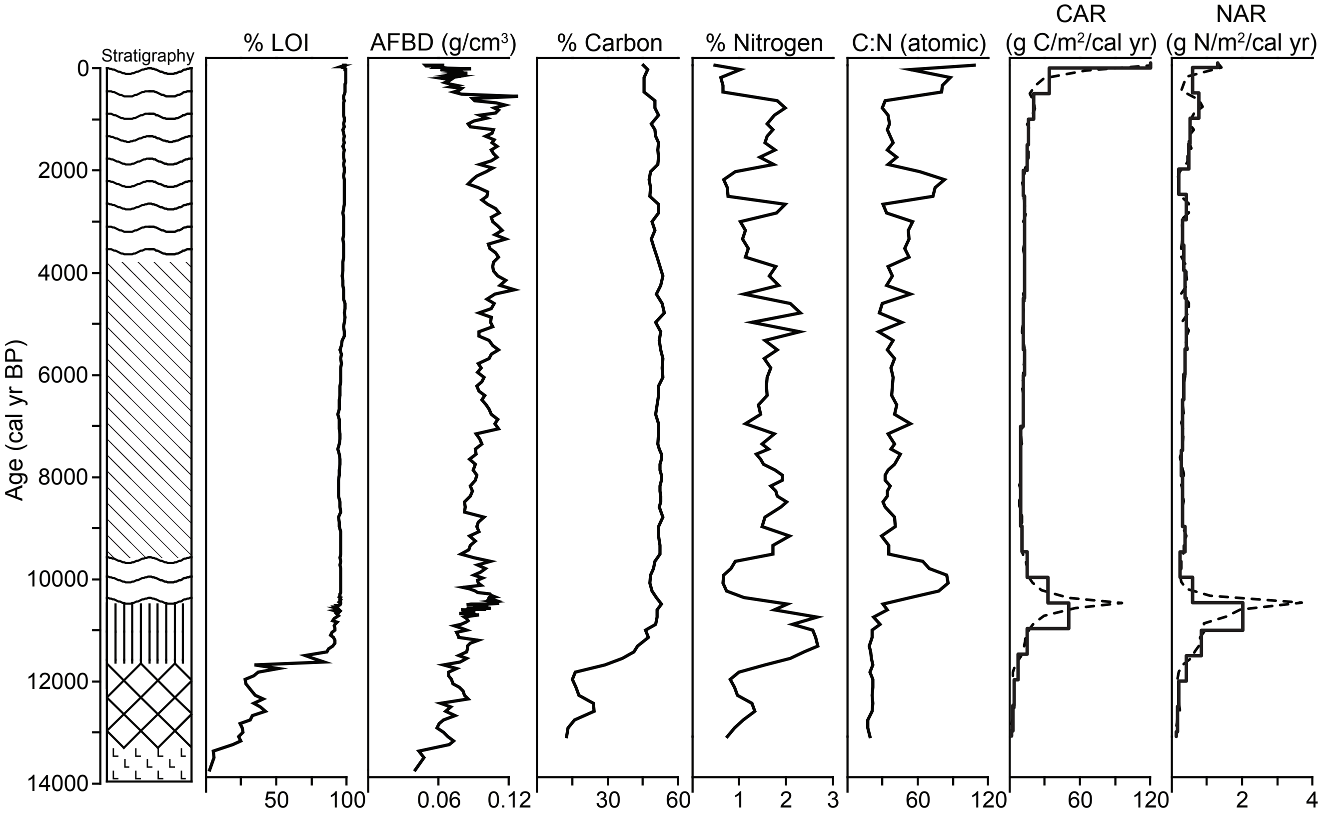
Figure 7. Pollen and spore percentages from Anderson Fen (Core A) showing wetland taxa only. Infrequent taxa are shown with 10× exaggeration (grey silhouettes) and the presence of rare pollen types is shown as circles. See Fig. 3 for stratigraphy legend.

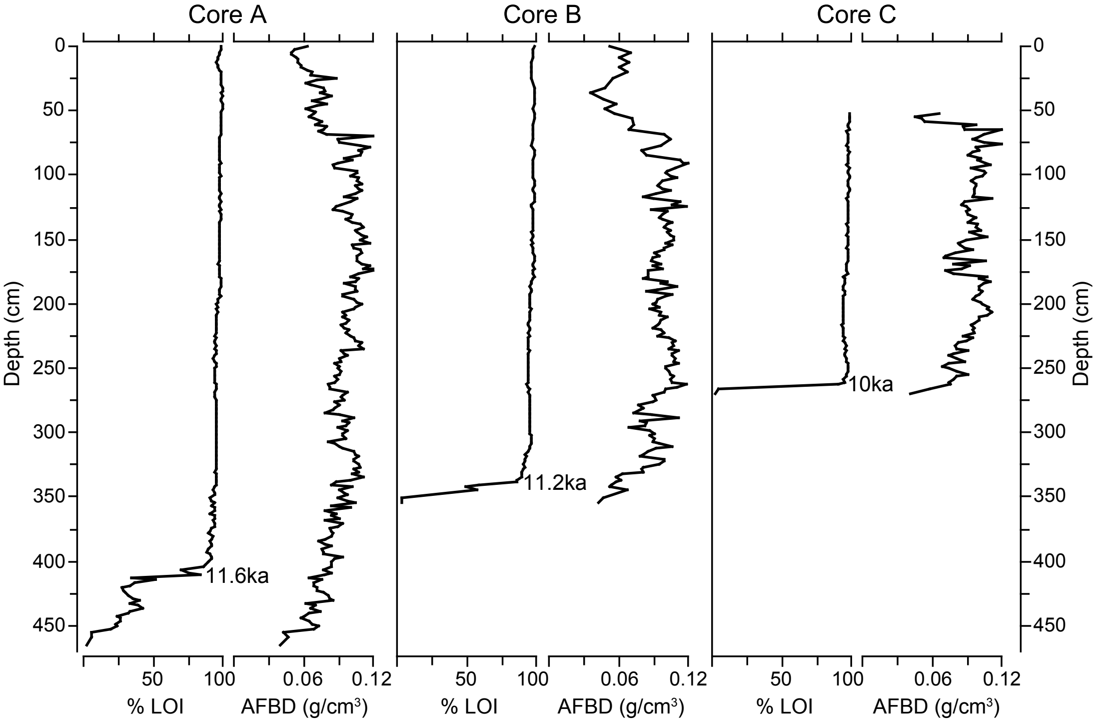
Figure 8. January and July insolation anomaly at 50ºN (Berger and Loutre, 1991), alkenone-inferred sea surface temperatures (SST) 60 km west of Vancouver Island (Kienast and McKay 2001), pollen-inferred mean annual precipitation (MAP) from Grant's Bog based on Brown et al. (2006) transfer function, and carbon accumulation rates (CAR) at three Vancouver Island peatlands: Anderson Fen (this study), Grant's Bog (Lacourse et al., 2019) and Port McNeill Bog (Lacourse and Davies, 2015). Peat components are plotted in the following order: unidentifiable organic matter (dark grey), herbaceous (white), ligneous (light grey), *Sphagnum* (black) and *Drepanocladus* (hatched). *Nuphar polysepala* sclereids are shown as one proxy for marsh-like wetlands at each site. Horizontal orange band marks the early Holocene period of maximum seasonal difference in insolation.

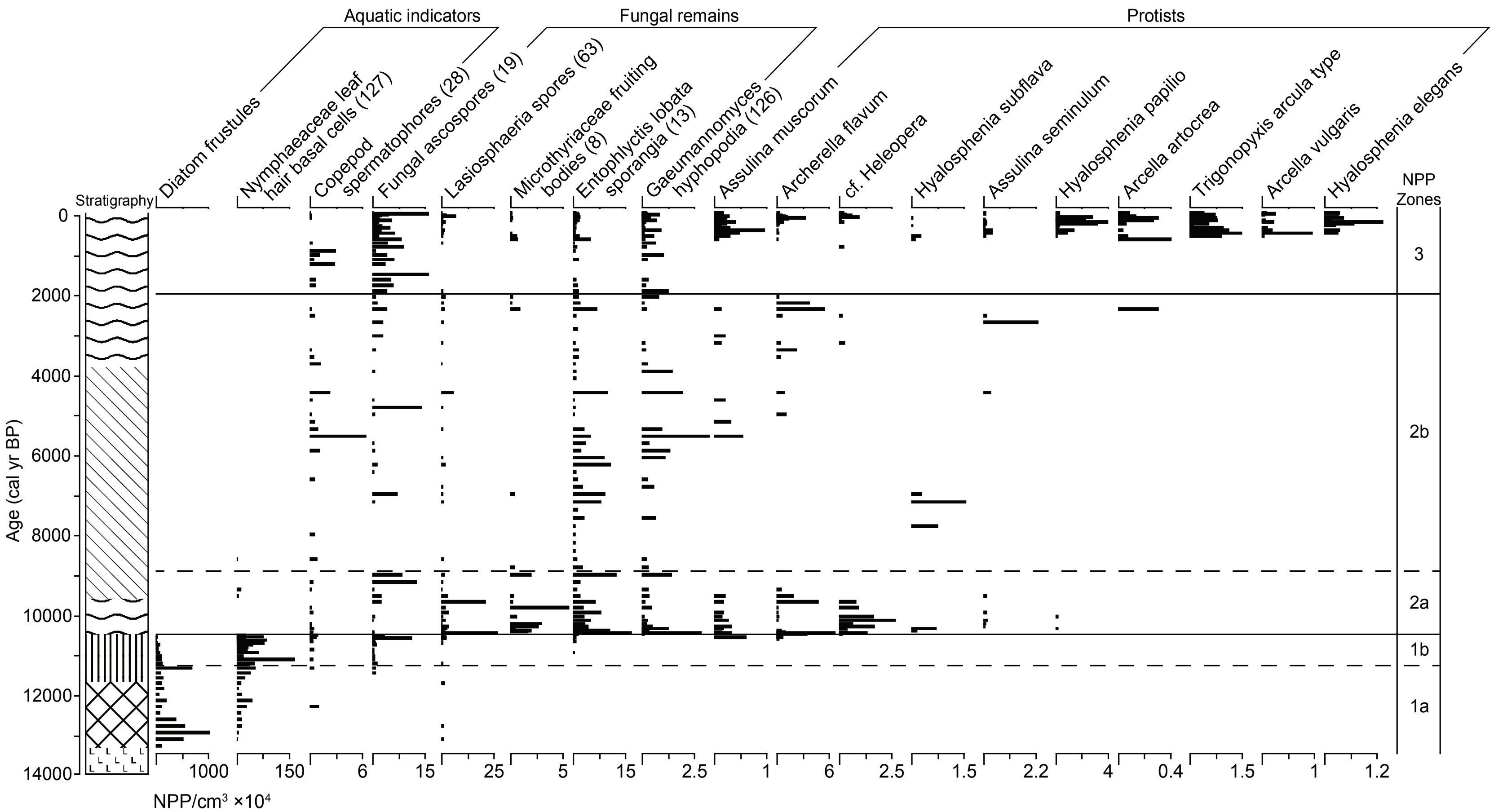

126°W
A
1
Vancouver Island
50°N
2
Pacific Ocean
100 km
49°N
B
C
B
A
50 m
C

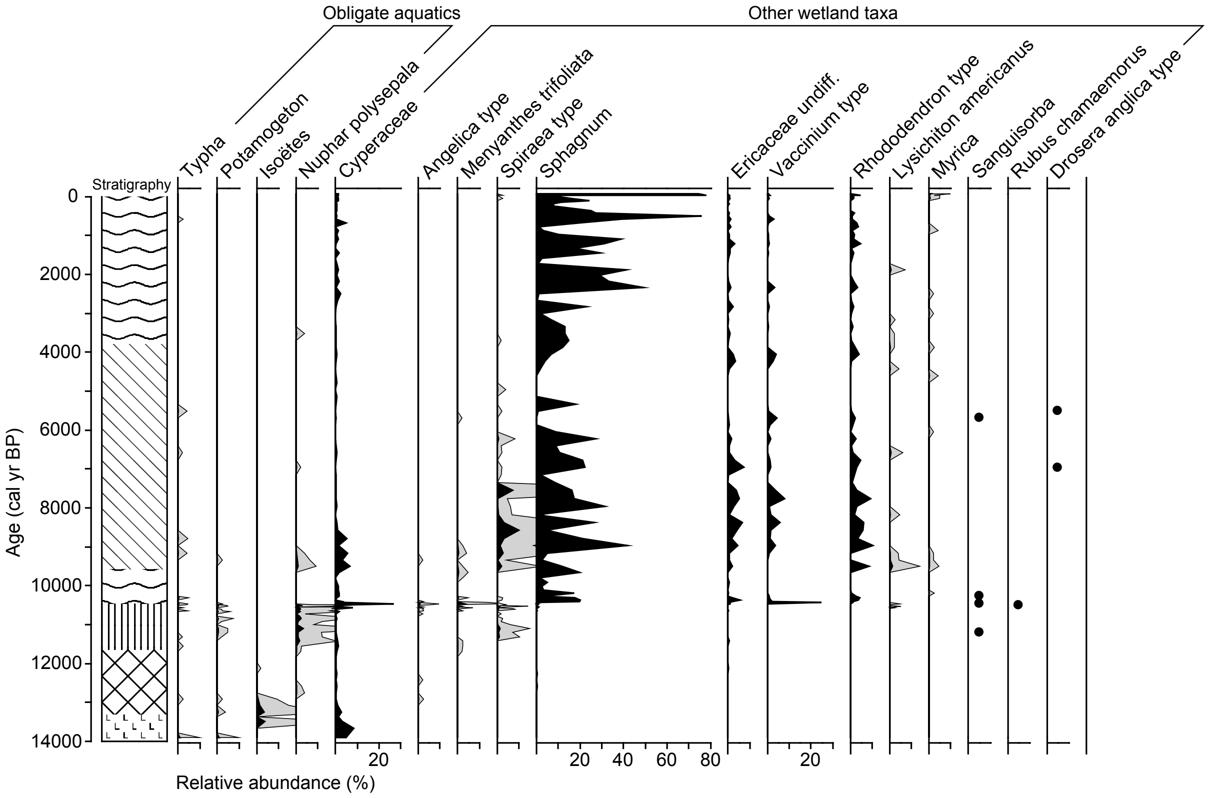

14000
12000
10000
8000
6000
4000
2000
0
Age (cal yr BP)
0
100
200
300
400
Depth (cm)


Age (cal yr BP)
Depth (cm)
Stratigraphy
UOM
Herbaceous stems/leaves
Sphagnum stems/leaves
Ligneous remains
Sand grains
Chironomid head capsules
Nuphar polysepala sclereids
Charcoal (>150 µm)
Fungal sclerotia
Gloeotrichia colonies
Potamogeton (s)
Isoëtes megaspores
Daphnid ephippia
Nuphar polysepala (s)
Vaccinium (s)
D. arundinaceum (s)
Menyanthes trifoliata (s)
Drosera anglica (s)
0
2000
4000
6000
8000
10000
12000
14000
0
50
100
150
200
250
300
350
400
450
40
80
% Composition
400
80
2000
40
300
Number/subsample
Presence of infrequent macrofossils
Sphagnum peat
Mixed peat
Nuphar peat
Lake sediment
Clay


Stratigraphy
% LOI
AFBD (g/cm^3)
% Carbon
% Nitrogen
C:N (atomic)
CAR
(g C/m^2/cal yr)
NAR
(g N/m^2/cal yr)
Age (cal yr BP)
0
2000
4000
6000
8000
10000
12000
14000
50
100
0.06
0.12
30
60
1
2
3
60
120
60
120
2
4


Core A
Core B
Core C
Depth (cm)
0
50
100
150
200
250
300
350
400
450
11.6ka
11.2ka
10ka
50
100
0.06
0.12
% LOI
AFBD (g/cm³)


Aquatic indicators
Fungal remains
Protists
Stratigraphy
Diatom frustules
Nymphaeaceae leaf hair basal cells (127)
Copepod spermatophores (28)
Fungal ascospores (19)
Lasiosphaeria spores (63)
Microthyriaceae fruiting bodies (8)
Entophlyctis lobata sporangia (13)
Gaeumannomyces hyphopodia (126)
Assulina muscorum
Archerella flavum
cf. Heleopera
Hyalosphenia subflava
Assulina seminulum
Hyalosphenia papilio
Arcella artocrea
Trigonopyxis arcula type
Arcella vulgaris
Hyalosphenia elegans
NPP Zones
3
2b
2a
1b
1a
Age (cal yr BP)
0
2000
4000
6000
8000
10000
12000
14000
1000
150
6
15
25
5
15
2.5
1
6
2.5
1.5
2.2
4
0.4
1.5
1
1.2
NPP/cm³ ×10⁴


Obligate aquatics
Other wetland taxa
Stratigraphy
Typha
Potamogeton
Isoëtes
Nuphar polysepala
Cyperaceae
Angelica type
Menyanthes trifoliata
Spiraea type
Sphagnum
Ericaceae undiff.
Vaccinium type
Rhododendron type
Lysichiton americanus
Myrica
Sanguisorba
Rubus chamaemorus
Drosera anglica type
Age (cal yr BP)
0
2000
4000
6000
8000
10000
12000
14000
20
20
40
60
80
20
Relative abundance (%)

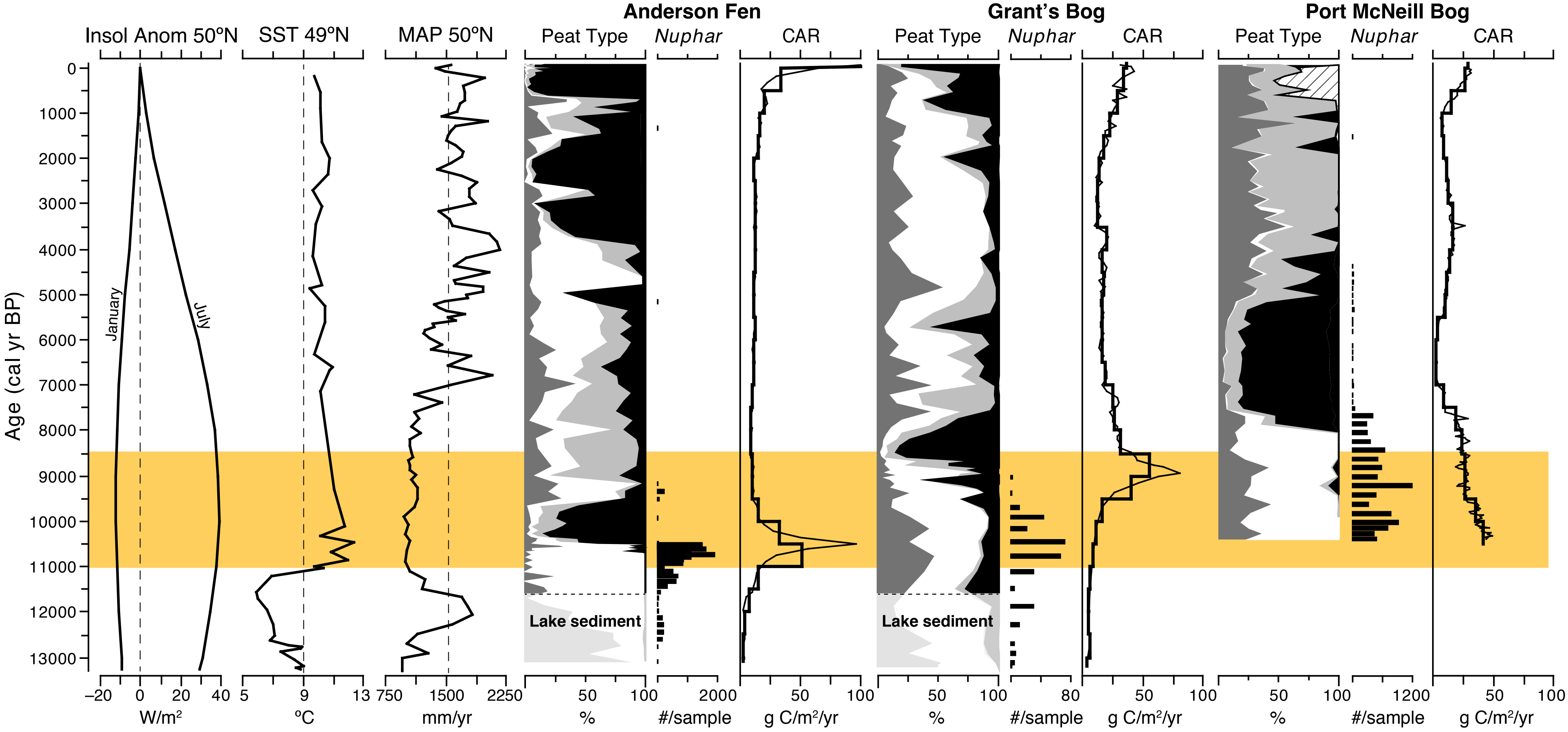

Anderson Fen
Grant's Bog
Port McNeill Bog
Insol Anom 50ºN
SST 49ºN
MAP 50ºN
Peat Type
Nuphar
CAR
Peat Type
Nuphar
CAR
Peat Type
Nuphar
CAR
Age (cal yr BP)
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
January
July
Lake sediment
Lake sediment
–20
0
20
40
W/m²
5
9
13
ºC
750
1500
2250
mm/yr
50
100
%
2000
#/sample
50
100
g C/m²/yr
50
100
%
80
#/sample
50
100
g C/m²/yr
50
100
%
1200
#/sample
50
100
g C/m²/yr

Table 1. AMS radiocarbon and calibrated ages from Anderson Fen on Vancouver Island, British Columbia.

Core	Depth (cm)	Material	$\delta^{13}C$ (‰)	Radiocarbon Age (^{14}C yr BP ± 1σ)	Calendar Age (cal BP) [a]	Lab Code
A	53–54	*Sphagnum*	–25.4	130 ± 30	130 (10–280)	Beta-466163
A	101–102	Woody plant fragments, *Sphagnum*	–27.8	1440 ± 30	1330 (1300–1380)	Beta-472225
A	149–150	*Sphagnum*, woody plant fragments	–25.6	3010 ± 30	3200 (3080–3330)	Beta-466164
A	199–200	Herbaceous plant fragments, *Sphagnum*	–25.3	4770 ± 30	5520 (5330–5590)	Beta-472226
A	241–242	Woody and herbaceous plant fragments, *Sphagnum*	–28.1	6190 ± 30	7080 (6990–7180)	Beta-475649
A	295–295.5	*Sphagnum*, woody plant fragments	–24.8	8980 ± 30	10,190 (9940–10,230)	Beta-463066
A	375–376	Herbaceous plant fragments	–25.0	9330 ± 30	10,540 (10,430–10,650)	Beta-472227
A	411–412	Limnic peat/organic lake sediment (60% LOI)	–28.2	10,040 ± 40	11,540 (11,340–11,760)	Beta-505925
A	448.5–449	Unidentifiable plant fragments	–24.8	11,360 ± 50	13,200 (13,100–13,300)	Beta-463067
B	337–338	Basal peat	–27.6	9780 ± 30	11,210 (11,180–11,240)	Beta-515800
C	261–261.5	Basal peat	–27.9	8850 ± 30	9990 (9770–10,150)	Beta-515799

[a] Median and 2σ age ranges rounded to nearest 10 yr