Quaternary Research 78 (2012) 572–582

Contents lists available at SciVerse ScienceDirect

Quaternary Research

journal homepage: www.elsevier.com/locate/yqres

A 14,000 year vegetation history of a hypermaritime island on the outer Pacific coast of Canada based on fossil pollen, spores and conifer stomata

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ARTICLE INFO

Article history:
Received 15 March 2012
Available online 23 September 2012

Keywords:
Pollen
Conifer stomata
Lake sediments
Temperate rainforest
Species arrival
Population expansion
Paleoecology
Haida Gwaii
British Columbia

ABSTRACT

Pollen and conifer stomata analyses of lake sediments from Hippa Island on the north coast of British Columbia were used to reconstruct the vegetation history of this small hypermaritime island. Between 14,000 and 13,230 cal yr BP, the island supported diverse herb–shrub communities dominated by Cyperaceae, *Artemisia* and *Salix*. *Pinus contorta* and *Picea sitchensis* stomata indicate that these conifers were present among the herb–shrub communities, likely as scattered individuals. Transition to open *P. contorta* woodland by 13,000 cal yr BP was followed by increases in *Alnus viridis*, *Alnus rubra* and *P. sitchensis*. After 12,000 cal yr BP, *Pinus*-dominated communities were replaced by dense *P. sitchensis* and *Tsuga heterophylla* forest with *Lysichiton americanus* and fern understory. *Thuja plicata* stomata indicate that this species was present by 8700 cal yr BP, but the pollen record suggests that its populations did not expand to dominate regional rainforests, along with *Tsuga* and *Picea*, until after 6600 cal yr BP. Conifer stomata indicate that species may be locally present for hundreds to thousands of years before pollen exceed thresholds routinely used to infer local species arrival. When combined, pollen and conifer stomata can provide a more accurate record of paleovegetation than either when used alone.

Introduction

Haida Gwaii is an archipelago, formerly named the Queen Charlotte Islands, composed of about 150 islands, 80 km offshore of the Pacific coast of mainland British Columbia (Fig. 1). The proximity to the Pacific Ocean moderates the climate of these islands, producing a unique hypermaritime environment: cool summers, abundant fog and drizzle, and very mild, wet winters with little to no snowfall near sea level (Banner et al., 2005). Low evapotranspiration and high precipitation result in wet soils and a mosaic of temperate coniferous rainforest communities that vary in productivity and bog-forest wetlands. Given that the dominant tree species in these coastal rainforests have lifespans that exceed several hundred years, paleoecological records are necessary to understand long-term plant community dynamics in this hypermaritime setting.

The remote, outer Pacific coast of Haida Gwaii has been the subject of few well-dated paleoecological reconstructions that span the full postglacial period. A number of studies have been conducted on the archipelago (Fig. 1); however, many of these used low pollen counts and did not differentiate *Alnus viridis* and *Alnus rubra* pollen, and others lack counts of Cupressaceae pollen and/or radiocarbon dating. In addition, some of these studies are based on sediment records with non-uniform sedimentation and unconformities or from ephemeral sites on the presently submerged continental shelf. This paper presents pollen and conifer stomata analyses of radiocarbon-dated lake sediment spanning the last 14,000 cal yr from a small lake on Hippa Island, at the western edge of the archipelago (Fig. 1). The purpose of the study was to reconstruct postglacial vegetation dynamics of this hypermaritime island, including development of temperate rainforest that occupies much of the coast today. The site was initially studied by Walker and Mathewes (1988), who produced one of the first postglacial chironomid stratigraphies in the Pacific Northwest from the same lake sediment core used in this study on postglacial vegetation dynamics.

Coastal British Columbia is an ideal setting for fossil pollen and spore analysis because of the high taxonomic resolution that can be achieved in fossil identifications i.e., pollen of many dominant taxa can be identified to species level. Cupressaceae is an important exception as *Thuja plicata*, *Chamaecyparis nootkatensis* (syn. *Callitropsis nootkatensis* — Little, 2006) and *Juniperus communis* produce morphologically indistinguishable pollen. Here, pollen analysis is coupled with conifer stomata analysis to determine which of the three possible members of the Cupressaceae family were locally present on Hippa Island. An abundance of conifer stomata in the lake sediments from Hippa Island provided a means to directly compare paleovegetation records derived

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http://dx.doi.org/10.1016/j.yqres.2012.08.008

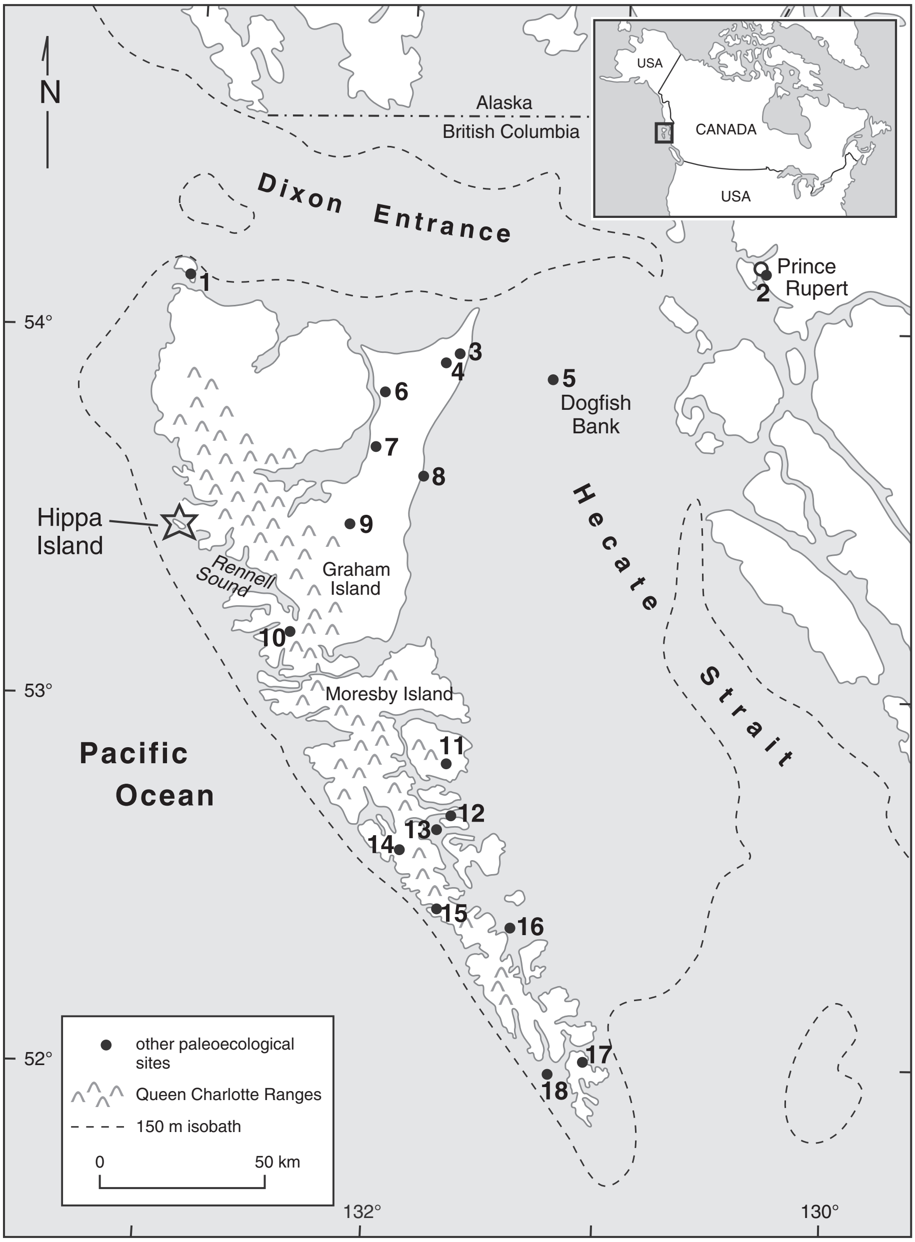

Figure 1. Location of Hippa Island and other paleoecological sites in the Haida Gwaii archipelago (Queen Charlotte Islands), British Columbia, Canada: (1) Langara Island (Heusser, 1995); (2) Hayes Mountain Bog (Banner et al., 1983) and Diana Lake Bog (Turunen and Turunen, 2003); (3) Argonaut Hill Bog (Quickfall, 1987); (4) Serendity Bog Lake (Warner, 1984); (5) Dogfish Bank (Lacourse et al., 2005); (6) Drizzle Pit Bog (Quickfall, 1987); (7) Boulton Lake (Warner, 1984); (8) Cape Ball (Mathewes and Clague, 1982; Warner, 1984; Warner et al., 1984); (9) Pilot Mill (Warner et al., 1984); (10) Shangri-La Bog (Pellatt and Mathewes, 1997); (11) Louise Pond (Pellatt and Mathewes, 1994); (12) Logan Inlet (Lacourse, 2004; Lacourse and Mathewes, 2005); (13) Richardson Island (Lacourse, 2004); (14) SC-1 Pond (Pellatt and Mathewes, 1997); (15) West Side Pond (Fedje, 1993; Lacourse et al., 2005); (16) Juan Perez Sound (Lacourse et al., 2003); (17) Kunghit Island bog (Quickfall, 1987); and, (18) SGang Gwaay (Hebda et al., 2005; Lacourse et al., 2007). Heusser's (1955) sites that lack radiocarbon dating and counts of Cupressaceae pollen are not shown.

from these two lines of evidence. Conifer stomata deposition and preservation in lake sediments are similar to plant macrofossils (MacDonald, 2001): their dispersal range is limited and thus their presence in lake sediments can be used to confirm the local presence of conifers over the postglacial period.

Environmental history and setting

The Haida Gwaii archipelago is located on Canada's north Pacific coast, on the western edge of the continental shelf, immediately south of the Alaskan Panhandle (Fig. 1). Late Quaternary glaciation of these outer islands was short in duration and limited in extent (Clague et al., 1982; Blaise et al., 1990; Barrie and Conway, 1999). The Queen Charlotte Ranges (Fig. 1), which run along the west side of the archipelago with peaks greater than 1100 m asl, supported their own small ice cap up to 500 m thick (Clague et al., 1982; Clague, 1983). Ice from the Queen Charlotte Ranges coalesced with lobes of mainland ice in northern Hecate Strait and Dixon Entrance (Barrie and Conway, 1999) during the last glacial maximum, which occurred sometime after 25,000 cal yr BP (21,000 ^{14}C yr BP) (Blaise et al., 1990). The mainland subsided under the weight of the ~2-km-thick Cordilleran Ice Sheet, forming a glacio-isostatic forebulge to the west as a result of the lateral transfer of mantle material away from the center of ice loading (Clague et al., 1982; Hetherington et al., 2004). This forebulge uplifted Haida Gwaii and other coastal areas, and resulted in the lowering of relative sea level by as much as 150 m below present and exposure of large portions of the continental shelf (Josenhans et al., 1997; Hetherington et al., 2004). Graham Island was deglaciated by 18,000 cal yr BP (ca. 15,000 ^{14}C yr BP) (Mathewes et al., 1985), and ice had retreated to mainland British Columbia by 17,300 cal yr BP (14,300 ^{14}C yr BP) (Lacourse et al., 2005). Maximum sea-level lowering occurred sometime after 15,600 cal yr BP (13,000 ^{14}C yr BP) (Barrie and Conway, 1999), and portions of the now-submerged continental shelf immediately south of Hippa Island at Rennell Sound (Fig. 1) were subaerially exposed and ice-free between at least 14,500 and 13,000 cal yr BP (Hetherington et al., 2004). At present, no studies have been conducted to determine if the subaerially exposed shelf adjacent to Hippa Island supported vegetation, as was the case at Dogfish Bank (Fig. 1, site 5) in Hecate Strait (Lacourse et al., 2005), at Juan Perez Sound (Fig. 1, site 16) in southern Haida Gwaii (Lacourse et al., 2003), and to the south at Cook Bank near northern Vancouver Island (Lacourse et al., 2003). Eustatic sea-level rise and disintegration of the glacio-isostatic forebulge allowed relative sea level to reach modern levels about 10,500 cal yr BP (9400 ^{14}C yr BP) (Fedje and Josenhans, 2000).

Hippa Island is located within the Vladimir J. Krajina Ecological Reserve, on the windward side of the Queen Charlotte Ranges, approximately 700 m offshore of Graham Island (Fig. 1). The island is small (~5 km^2) and reaches a maximum elevation of just over 450 m asl. Hippa Lake (53°31.9′N, 132°58.4′W; 230 m asl) is the only lake on Hippa Island and has no inflowing streams. The lake is shallow (1.1 m) with a surface area of 3.2 ha.

Under the prevailing influence of the Pacific Ocean, the climate on the west coast of Haida Gwaii is characterized as hypermaritime: cool temperatures and abundant rainfall and fog year-round. According to ClimateBC (Wang et al., 2006), mean annual temperature (MAT) at Hippa Island is 7.1°C and mean annual precipitation (MAP) is 2140 mm/yr. These values, which are modeled from regional climate data using latitude, longitude and elevation, compare well with climate normals from the Langara Island climate station (MAT = 7.7°C, MAP = 1957 mm/yr; Environment Canada, 2012), which is located in a similar setting (Fig. 1, site 1), 75 km north of Hippa Island.

Forests on the west coast of Haida Gwaii are part of the very wet hypermaritime variant of the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar, 1991), which is located at low to middle elevations along the coast of British Columbia. Forests on Hippa Island are dominated by mature *Tsuga heterophylla* (western hemlock), *Picea sitchensis* (sitka spruce), and *T. plicata* (western redcedar). *Pinus contorta* var. *contorta* (lodgepole pine) and *C. nootkatensis* (yellow cypress) are present in low relative abundance. *Tsuga mertensiana* (mountain hemlock) and *C. nootkatensis* are abundant in higher elevation forests on adjacent Graham Island. All species of *Abies* (fir) are absent from Haida Gwaii, having not re-colonized the archipelago after the last glaciation. Mosses and various ferns dominate the understory at Hippa Island, as they do elsewhere along much of British Columbia's coast.

Materials and methods

Walker and Mathewes (1988) collected a 3.55-m-long sediment core from a *Nuphar lutea* bed in 1.1 m of water from the center of Hippa Lake, using a 5-cm-diameter Livingstone piston corer from an inflatable raft. The water-sediment interface was recovered using a Brown piston sampler. Walker and Mathewes (1988) identified fossil chironomid head capsules at 13 levels in the Hippa Lake core; however paleotemperatures were not inferred from these assemblages. Radiocarbon ages (^{14}C yr BP) were obtained on five organic-rich sediment samples (Table 1) and then calibrated to calendar years using the mode of the probability distribution determined by CALIB 6.0 (Stuiver and Reimer, 1993; Reimer et al., 2009). Because the sediment core was collected in 1983, the top of the sediment core (0 cm) was given an age of −33 cal yr BP. A chronology based on these six calendar age estimates was constructed using a four-term polynomial curve fitted with weighted least-squares regression (Fig. 2).

Sediment subsamples (1 cm^3) at 2–5 cm intervals along the length of the sediment core were prepared for pollen and conifer stomata analyses following standard methods including acetolysis and were mounted in silicone oil (Fægri and Iversen, 1989; Bennett and Willis, 2001). To calculate pollen and spore concentrations (grains/cm^3), known quantities of *Eucalyptus* pollen (Batch #903722: 16,180 ± 1460 grains) were added to each subsample. Pollen and spore identifications were made according to published dichotomous keys and a modern pollen and spore reference collection at the University of Victoria. Botanical nomenclature follows the Flora of North America Editorial Committee (1993 +). All *Picea* pollen were identified as *P. sitchensis* based on pollen morphology and modern phytogeography, although it is possible that some *Picea* pollen is derived from hybrids of *P. sitchensis* and *Picea glauca* (Warner and Chmielewski, 1987). *Alnus viridis* and *A. rubra* types were differentiated following May and Lacourse (2012). Apiaceae pollen was identified according to Hebda (1985). A minimum sum of 500 pollen grains, excluding pollen from obligate aquatic plants and *Sphagnum* spores, was identified for each subsample except the four basal samples, which had low pollen concentrations and therefore lower pollen sums (i.e., 160–361 pollen and spores). Percentages were calculated using the sum of all terrestrial pollen and pteridophyte spores.

The pollen percentage data were zoned using optimal splitting by sum-of-squares (Bennett, 1996), though in this case constrained cluster analysis i.e., CONISS (Grimm, 1987) returned identical results. Principal components analysis (PCA) was carried out on a covariance matrix after square-root transformation of the dataset. For zonation and PCA, the dataset was limited to pollen types that accounted for at least 1% of the sum at some point within the pollen record, and then recalculated for analysis to proportions of the sum of pollen types included. This reduced the dataset to 95.6% of the original data. Broken-stick models were used to test the statistical significance of both the numerical zonation and the eigenvalues of each PCA axis (Jackson, 1993). *Sphagnum* and aquatic taxa (i.e., *Isoëtes echinospora*, *Nuphar*, and *Potamogeton*) were excluded from all numerical analyses.

Conifer stomata were enumerated and identified using Hansen (1995) and a modern conifer stomata reference collection. The main morphological features used in identification were stomata size and shape, the relative length of upper and lower woody lamellae, and the presence of subsidiary cells. Individual stomata that were incompletely preserved or obscured by organic detritus, but that met the main criteria for identification to species were given the designation cf. Unidentifiable or unknown stomata were designated accordingly. In cases where epidermal tissue was intact, each stoma was counted separately. Stomata concentrations were calculated based on counts of the added *Eucalyptus* pollen.

Results

Sediment stratigraphy and chronology

The basal portion of the Hippa Lake sediment core (347–355 cm) consists of gray clay with occasional gravel (Fig. 3) and less than 5%

Table 1
Radiocarbon ages on organic sediment from Hippa Lake, Haida Gwaii (Queen Charlotte Islands), British Columbia.

Depth (cm)	Lab no.	Radiocarbon age[a] (^{14}C yr BP ± 1σ)	Calendar age[b] (cal yr BP)
80–85	BETA-16579	4860 ± 140	5595 (5460–5740)
170–175	BETA-16580	6760 ± 130	7595 (7490–7720)
260–265	BETA-16581	7020 ± 250	7904 (7610–8050)
320–325	GSC-3773	9780 ± 110	11,209 (11,070–11,330)
340–347	GSC-3760	11,100 ± 220	13,021 (12,740–13,170)

[a] Previously published in Walker and Mathewes (1988).

[b] Mode of the probability distribution and 1σ age range, rounded to the nearest 10 yr, from CALIB 6.0 (Stuiver and Reimer, 1993; Reimer et al., 2009).

organic matter, as determined by loss-on-ignition analyses (Walker and Mathewes, 1988). Between 320 and 347 cm, the sediment is gyttja, light tan in color, with almost 20% organic matter. The remainder of the sediment core is composed of brown coarse detritus gyttja with 20–30% organic matter. *Pediastrum* algal colonies are present throughout the entire sediment core, indicating the continuous presence of freshwater.

The age-depth model for the Hippa Lake sediment core predicted an age of 14,020 ± 225 cal yr BP for the base of the core (Fig. 2). The transition from basal clay to organic sediments at 320 cm dates to approximately 11,040 cal yr BP. Radiocarbon ages obtained at 170 and 260 cm (Table 1) suggest that 90 cm of sediment may have been deposited in only 310 cal yr i.e., 0.29 cm/cal yr. This rate of sediment accumulation is an order of magnitude faster than elsewhere within the sediment core, raising the possibility that one of the two ^{14}C ages bracketing this interval is a poor estimate of the true age of the sediment and/or that sedimentation was indeed more rapid during the early Holocene. Note, however, that the age difference between these two levels is 1030 cal yr in the age-depth model (Fig. 2) and this slower rate of sedimentation (0.087 cm/cal yr) is comparable to other sites on the north Pacific coast (e.g., Lacourse, 2005; Galloway et al., 2009). Due to variation in modeled sedimentation rates, pollen accumulation rates (grains/cm^2/cal yr) are not presented.

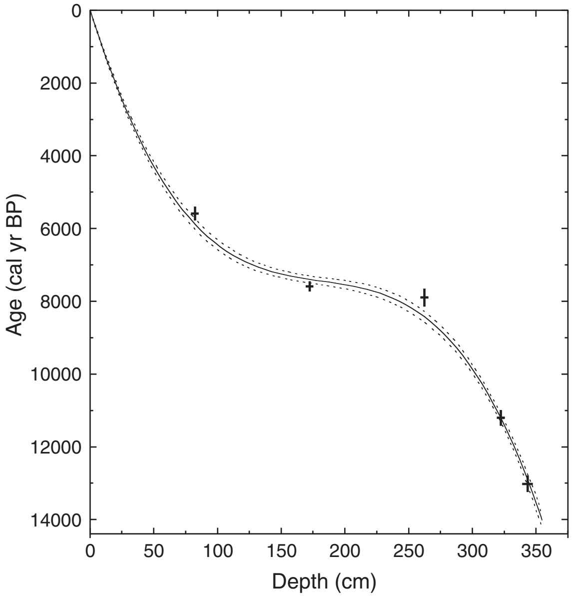

Figure 2. Four-term polynomial age-depth model and 95% confidence intervals obtained via simulation ($n = 100$) for the Hippa Lake sediment core. Crosses mark the stratigraphic position of the five radiocarbon-dated sediment samples (Table 1), with the vertical arms indicating the age measurement standard deviation and horizontal arms indicating the thickness of the dated sample.

Pollen and spore analysis

A total of 61 pollen and spore taxa were identified in the Hippa Lake sediment core, with 28 and 21 of these identified to genus and species, respectively; however, only summary results of the dominant taxa are presented (Fig. 3). Numerical zonation of the pollen and spore data returned four statistically significant pollen assemblage zones (Fig. 3). The pollen record from Hippa Lake begins at 14,020 cal yr BP with a diverse herb–shrub assemblage (HL-1: 14,020–13,230 cal yr BP) dominated by Cyperaceae, *Artemisia*, and *Salix* with Poaceae and other Asteraceae also common. Herbaceous taxa account for up to 84% of the total pollen sum and include *Ranunculus*, *Stellaria*, *Campanula*, Chenopodiaceae, *Polemonium pulcherrimum* and *Pinguicula*. In addition, several members of the Apiaceae are present: *Angelica*, *Ligusticum*, *Heracleum*, *Conioselinum*, *Oenanthe* and *Osmorhiza*. Fern and fern allies, including *Polypodium*, *Athyrium filix-femina*, *Cryptogramma*, *Lycopodium annotinum* and *Botrychium*, account for about 10% of the pollen sum. Total conifer pollen, including *P. contorta*, *P. sitchensis* and *T. heterophylla*, does not exceed 8% in the basal sediments (Fig. 3).

By 13,140 cal yr BP, *P. contorta* pollen becomes abundant (HL-2: 13,230–11,040 cal yr BP), soon reaching a maximum of 35% for the period of record (Fig. 3). This change in the pollen assemblage corresponds with the sedimentological change from clay to organic gyttja at 347 cm in the sediment core (Fig. 3). Increases in *A. viridis*, *A. rubra* and *P. sitchensis* pollen follow, with trees and shrubs accounting for 50% of the pollen sum by 12,800 cal yr BP. *Isoëtes echinospora* spores are consistently present from 12,800 cal yr BP onwards. Fern spores increase to their maximum, in both frequency and concentration, at about 12,000 cal yr BP. By 11,500 cal yr BP, *Picea sitchensis* is the dominant conifer in the pollen record. *Tsuga heterophylla* and *Lysichiton americanus* pollen increase by 10,900 cal yr BP at the boundary to Zone HL-3a (11,040–5120 cal yr BP) and the sedimentological change at 320 cm (Fig. 3). *Picea sitchensis*, *T. heterophylla*, *Alnus* spp., *L. americanus* and Polypodiaceae ferns dominate the early Holocene record (Fig. 3). After 8000 cal yr BP, *Coptis* pollen is consistently present, but below 1.5%. After decreasing in the early Holocene, *P. contorta* pollen increases in frequency and in concentration between 7500 and 3000 cal yr BP. The first occurrence of Cupressaceae pollen occurs at 8100 cal yr BP, but Cupressaceae pollen remain below 2% until after 7000 cal yr BP. Cupressaceae is abundant after 5000 cal yr BP (HL-3b: 5120–0 cal yr BP), when it begins to dominate the pollen record, along with *T. heterophylla* and *P. sitchensis*. Late Holocene sediments are characterized, on average, by 65% conifer pollen and 10% herb pollen, with the remainder consisting mostly of *Alnus* spp. and ferns.

Principal components analysis of pollen and spore data

Principal component axes 1 and 2 account for 46.6% and 27.6% of the total variation, respectively, and were the only statistically significant axes according to a broken-stick model. PC axis 1 separates Cyperaceae, *Artemisia* and other pollen types abundant during the late Pleistocene portion of the record from *T. heterophylla*, *L. americanus* and other taxa that dominate much of the Holocene, which have high negative and positive loadings, respectively (Fig. 4A). Species loadings on axis 1 correspond closely to the order of arrival for the major taxa. PC axis 2 separates Polypodiaceae spores and *Alnus* spp. pollen, which are common during the transition into the Holocene, from Cupressaceae pollen, which dominates the late Holocene portion of the record (Fig. 4A). The ordination of pollen samples (Fig. 4B) and the numerical zonation of the pollen dataset (Fig. 3) reveal similar subdivisions, highlighting the similarity of the pollen assemblages within each of the four zones as well as differences between zones. The clustering of Holocene samples and spread of late Pleistocene samples reflect differences in the rates of compositional change in plant communities at these times: late Pleistocene communities have higher rates of change and less compositional similarity than Holocene communities.

Conifer stomata analysis

Conifer stomata are abundant throughout much of the Hippa Lake sediment core, at concentrations (Fig. 5) that far exceed those found in most other fossil stomata studies (e.g., MacDonald, 2001; Pisaric et al., 2003; Froyd, 2005). Conifer stomata reach a maximum of 65 stomata per pollen count, with most samples averaging about 20 stomata per pollen count; however, incomplete preservation prevented identification in many instances. Stomata of four species were identified: *P. contorta*, *P. sitchensis*, *T. heterophylla* and *T. plicata* (Fig. 5). *Pinus* and *Picea* stomata are rare in basal sediments (up to 50 stomata/cm^3), but their presence nonetheless suggests that these conifers were present on Hippa Island by ~14,000 and 13,800 cal yr

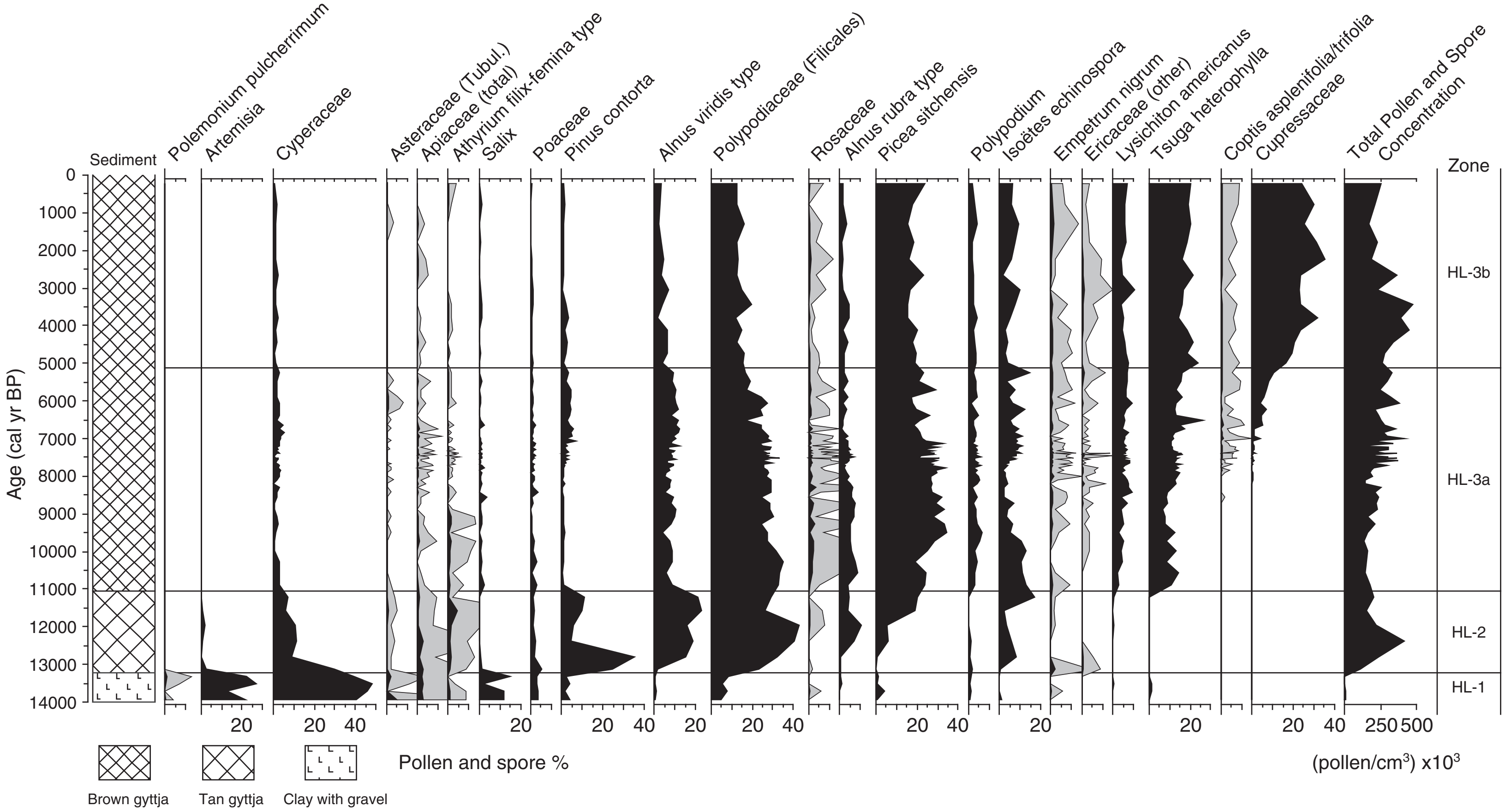

Figure 3. Sediment stratigraphy and selected pollen and spore frequencies from Hippa Lake, British Columbia over the last 14,000 cal yr BP. Apiaceae total includes *Angelica* type, *Conioselinum* type, *Heracleum*, *Ligusticum*, *Oenanthe*, and *Osmorhiza*. Gray curves are 10× exaggeration of percentages for selected taxa. Taxon order is based on weighted averages of the pollen percentages. *Isoëtes echinospora* is excluded from the main pollen sum.

BP, respectively. Stomata from all conifers are absent in sediments between about 13,150 and 11,500 cal yr BP (Zone HL-2). Stomata concentrations increase starting 11,210 cal yr BP, reaching a maximum (>30,000 stomata/cm^3) at 8300 cal yr BP, before decreasing to an average of ~3300 stomata/cm^3 in Zone HL-3b i.e., between 5120 cal yr BP and the present (Fig. 5). Most stomata belong to *P. sitchensis*, with lower abundances of *T. heterophylla*, *P. contorta* and Cupressaceae. Stomata from *T. heterophylla* first appear at 10,875 cal yr BP and are then more or less consistently present to the top of the sediment core. Cupressaceae stomata are present starting 8700 cal yr BP and then occur sporadically until the present. About 25% of all Cupressaceae stomata were identified as *T. plicata*; the remainder could not be identified beyond the family level. No Cupressaceae stomata were identified as *C. nootkatensis* or *J. communis*, although the former is locally present on the island today.

Discussion

Late Pleistocene plant communities on Hippa Island

The pollen, spore and conifer stomata evidence from Hippa Lake reveals substantial changes in vegetation communities over the last 14,000 cal yr. Like other sites of similar age along the north Pacific coast (Lacourse and Mathewes, 2005), the Hippa Lake record begins with a diverse herb and shrub community dominated by Cyperaceae, Poaceae and *Artemisia*. The paleoenvironmental inferences that can be drawn from these assemblages are constrained by the fact that much of the important herb pollen such as Cyperaceae and Poaceae can only be identified to the family level. However, a diverse array of other herbs (e.g., *Angelica*, *Heracleum*, *Ligusticum*, *Stellaria*, *P. pulcherrimum*, *Ranunculus*, *Campanula* and *Pinguicula*) and pteridophytes (e.g., *Polypodium*, *A. filix-femina*, *Cryptogramma* and *L. annotinum*) were also present between 14,000 and 13,500 cal yr BP. *Salix* was the most important shrub component, although willows are now absent from Haida Gwaii at low elevations (Calder and Taylor, 1968). Ericaceous dwarf shrubs such as *Empetrum nigrum* were also present, and the presence of *E. nigrum* at ~14,000 cal yr BP (11,990 ± 50 ^{14}C yr BP, CAMS-61255) is confirmed by radiocarbon-dated seeds of this species from a small lake on Richardson Island (Fig. 1, site 13) in southern Haida Gwaii (Lacourse, 2004). Given the diversity of taxa, a mosaic of habitats of differing moisture levels likely existed in this early post-glacial environment. The presence of taxa such as Apiaceae, *Stellaria* and *Ranunculus* suggests that wet herbaceous meadows were present in the vicinity of Hippa Lake. Low organic content in basal sediments and low total pollen and spore concentrations (~2600 grains/cm^3) indicate that the vegetation was open, if not discontinuous. Pollen and macrofossil evidence from other sites on Haida Gwaii (Warner, 1984; Heusser, 1995; Lacourse and Mathewes, 2005; Lacourse et al., 2005) and in southeastern Alaska (Hansen and Engstrom, 1996) indicates that diverse herb–shrub communities were widespread along the coast, starting as early as 18,000 cal yr BP with herbaceous and wetland communities at Cape Ball (Fig. 1, site 8) on eastern Graham Island (Warner et al., 1982; Mathewes et al., 1985).

Small amounts of conifer pollen (3.5–7.6%; 60–320 pollen/cm^3) occur in 14,000–13,200 cal yr BP sediments at Hippa Lake, as is the case in many late Pleistocene herb–shrub dominated assemblages (e.g., Warner, 1984; Peteet, 1991; Heusser, 1995; Lacourse et al., 2005). In the absence of stomata or macrofossil evidence, trace amounts of conifer pollen (e.g., <5% per species) are usually interpreted as the product of long-distance transport and/or reworking. At Hippa Lake, however, conifer pollen in these early herb–shrub assemblages are accompanied by *P. contorta* and *P. sitchensis* stomata (up to 50 stomata/cm^3), which suggests that these two conifers were present, likely as scattered individuals, among the herb–shrub communities. *Tsuga heterophylla* contributes less than 1.5% to the pollen sum in two samples near the base of the pollen record (Fig. 3). Since stomata of this species were not encountered in these samples, we interpret this trace amount of *T. heterophylla* pollen to reflect regional to long-distance transport from the south.

The presence of scattered *P. contorta* on Hippa Island starting 14,000 cal yr BP, as inferred from stomata during an interval when *Pinus* pollen account for only 2–4% of the total sum, is not altogether surprising when considered in a regional context. Small amounts of *P. contorta* pollen (6%) have also been found with *Pinus* stomata at 15,600 cal yr BP at West Side Pond (Fig. 1, site 15) in southern Haida Gwaii (Lacourse et al., 2005). The local presence of *Pinus* at ~14,140 cal yr BP at that site is also confirmed by a radiocarbon-dated *Pinus* needle (12,190 ± 140 ^{14}C yr BP, CAMS-2525; Lacourse et al., 2005). In Juan Perez Sound (Fig. 1, site 16), abundant *P. contorta* pollen, needles and cones, as well as an in situ *Pinus* stump dated to 14,160 cal yr BP (12,240 ± 50 ^{14}C yr BP, CAMS-59768), indicate that this conifer was locally present on the exposed continental shelf at that time (Fedje and Josenhans, 2000; Lacourse et al., 2003). The local presence of *P. contorta* is also documented on Pleasant Island in southeastern Alaska based on *Pinus* stomata at about 13,750 cal yr BP (Hansen and Engstrom, 1996). These results indicate that *P. contorta* was present at a number of locations on the north Pacific coast prior to marked increases in *Pinus* pollen.

As with *P. contorta*, the presence of *P. sitchensis* in herb–shrub communities on Hippa Island is confirmed by stomata at 13,800 cal yr BP (Fig. 5), despite *Picea* pollen percentages of only 4% (Fig. 4). Macrofossil evidence indicates that *P. sitchensis* was present to the south at West Side Pond (Fig. 1, site 15) by about 13,400 cal yr BP (Lacourse et al., 2005). The local presence of *Picea* is also demonstrated by radiocarbon-dated *Picea* wood (11,300 ± 110 ^{14}C yr BP, GSC-2879) at Cape Ball (Fig. 1, site 8) by about 13,200 cal yr BP (Mathewes and Clague, 1982). Pollen data from Logan Inlet (Fig. 1, site 12), a submerged paleolake on the continental shelf that provides a good regional pollen record of late Pleistocene forests, indicate that *P. sitchensis* was dominant by 13,000 cal yr BP (Josenhans et al., 1997; Lacourse, 2004; Lacourse and Mathewes, 2005). Thus, on Hippa Island, fossil stomata provide robust evidence for the local presence of two conifers between 14,000 and 13,300 cal yr BP, when pollen percentages of these species are significantly lower than thresholds of 5–10% that are used throughout the literature to infer species arrival. Indeed, there is a growing body of stomata and macrofossil evidence (e.g. Peteet, 1986, 1991; Brubaker et al., 2005; Froyd, 2005; Lacourse et al., 2005; Stolze et al., 2007) that indicates that in some instances conifers were locally present, albeit likely in very low abundance, for hundreds to thousands of years before expansion of their populations is reflected in pollen analysis of the same sediments. Accordingly, interpretation of pollen data should proceed cautiously when used without supporting stomata or macrofossil evidence, as fossil pollen may fail to accurately record local species presence.

Fossil chironomid analyses of the Hippa Lake sediment core suggest a cool late Pleistocene climate, as indicated by the presence of taxa typical of cold and/or arctic-alpine environments (Walker and Mathewes, 1988). The Hippa Lake chironomid record shows that *Corynocera* cf. *ambigua* rapidly colonized the lake beginning 14,000 cal yr BP, despite their inability to fly, a finding which could be explained by nearby refugia (Walker and Mathewes, 1988). Continuously ice-free refugia spanning the last glacial period have not been located on Haida Gwaii, but possible refugia have been identified at a number of sites along the north Pacific coast (Heusser, 1989; Hebda and Haggarty, 1997; Lacourse et al., 2003, 2005; Carrara et al., 2007), including a potentially large refugium in now submerged areas of Hecate Strait (Fig. 1) (Hetherington et al., 2004). Coastal refugia may have supported small populations of *P. contorta* and *P. sitchensis*, explaining their seemingly early arrival at Hippa Island and other sites along the north Pacific coast. Fazekas and Yeh (2006) provide genetic evidence that suggests *P. contorta* found refuge somewhere along the north Pacific coast during the last glaciation, as opposed to migrating north following retreat of the Cordilleran Ice Sheet. Low-elevation, hypermaritime sites such as Hippa Island may well have supported small isolated refugial

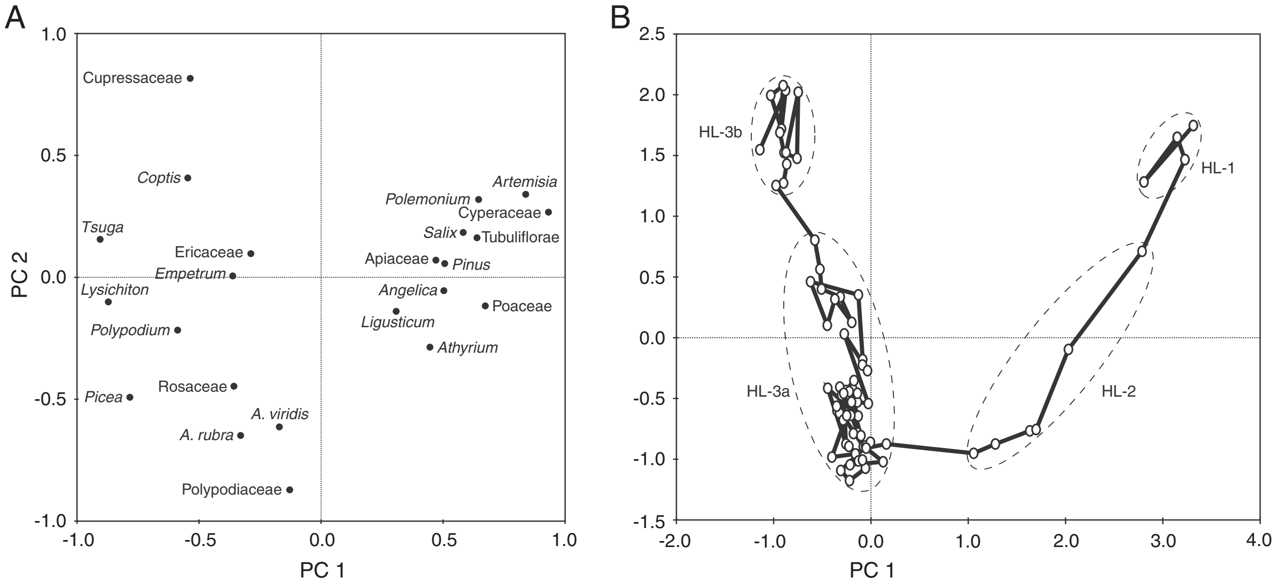

Figure 4. Principal component plot of (A) species loadings for important pollen and spore taxa from Hippa Lake, British Columbia and (B) sample scores in stratigraphic order, plotted on first and second principal axes, which account for 46.6 and 27.6% of the total variation, respectively. In panel A, Apiaceae includes *Heracleum*, *Conioselinum*, *Oenanthe*, *Osmorhiza* and undifferentiated Apiaceae pollen, and Ericaceae includes *Arctostaphylos* and undifferentiated Ericaceae pollen. Pollen assemblage zones derived from numerical zonation are shown in panel B. Note changes in scale.

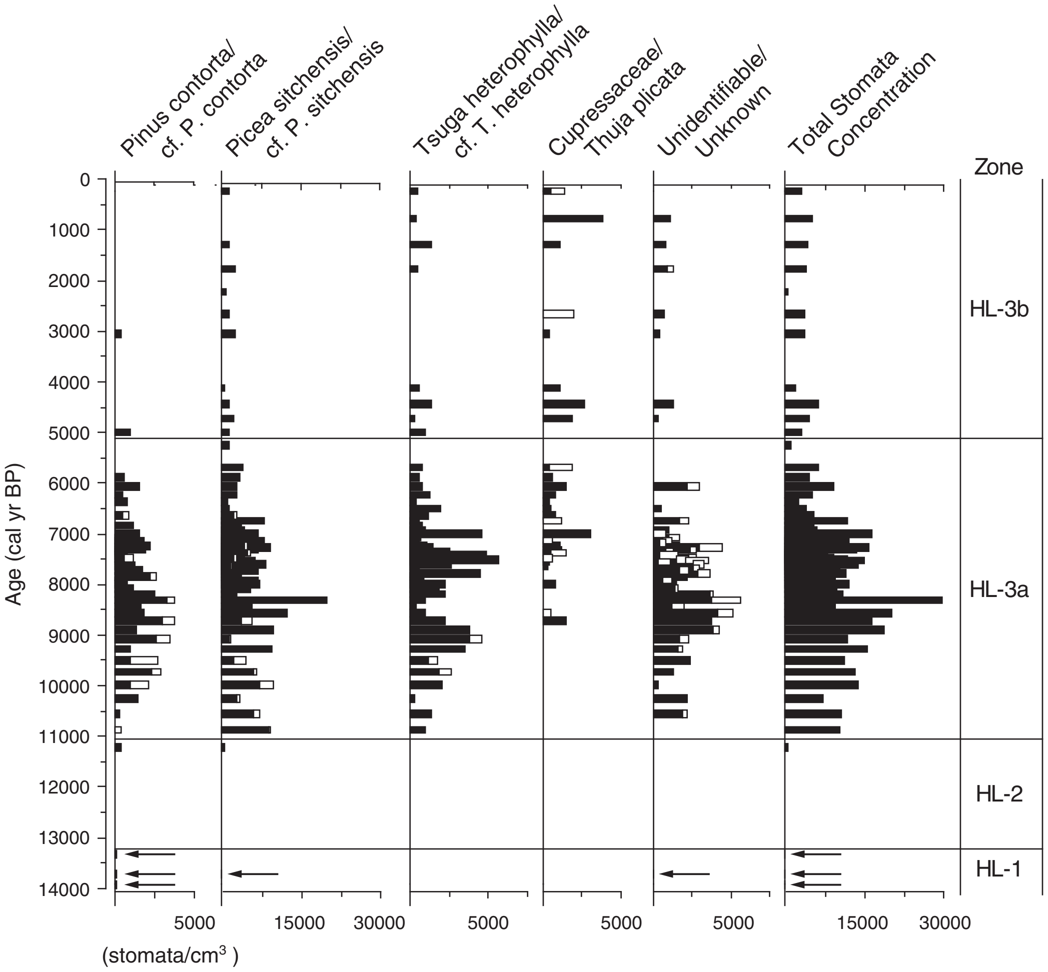

Figure 5. Conifer stomata concentrations (stomata/cm^3) from Hippa Lake, British Columbia over the last 14,000 cal yr BP. Hollow bars denote identifications given the designation cf. In the case of Cupressaceae, hollow bars denote stomata identified as *Thuja plicata*. Arrows mark the stratigraphic position of low stomata concentrations not discernible due to the scale of the x-axes. Note changes in scale. Numerical zonation of the pollen percentage data is superimposed.

populations, but because the Hippa Lake record begins at only 14,000 cal yr BP, identifying the location and nature of late Quaternary ice-free refugia on Haida Gwaii , if indeed they were present, requires further research.

Cyperaceae-dominated communities initially remain abundant amid expansion of *P. contorta* populations on Hippa Island around 13,250 cal yr BP (Fig. 3). The understory of these open *Pinus* communities was dominated by ferns with increasing amounts of *A. viridis* beginning about 13,000 cal yr BP, but the presence of *A. filix-femina* spores throughout late Pleistocene sediments suggests some damp, shaded habitats. Increases in the aquatic *I. echinospora*, which likely grew mostly around the margins of Hippa Lake, coincide with the transition from herb-dominated to *P. contorta*-*A. viridis* communities. This transition in the plant communities would have been facilitated by increased temperatures as well as increased precipitation after 14,000 cal yr BP that are suggested by climate models (Bartlein et al., 1998). This vegetation change is also reflected in the sediment stratigraphy itself i.e., as woody vegetation became abundant on the landscape, clay sedimentation was replaced by the accumulation of organic gyttja at 13,250 cal yr BP (Fig. 3). Despite the presence of *Pinus* and *Picea* stomata in the herb-dominated basal sediments, conifer stomata are absent in Hippa Lake sediments between ~13,150 and 11,500 cal yr BP (Fig. 5). Because conifer stomata have limited dispersal, fossil stomata serve as robust indicators of local species presence, but their absence in the fossil record does not indicate local absence on the landscape (MacDonald, 2001). Pollen preservation is as high during this interval as elsewhere in the sediment core, thus the absence of conifer stomata more likely reflects the stochastic nature of needle and stomata dispersal and deposition, as opposed to poor preservation. Given the abundance of Cyperaceae pollen before 11,000 cal yr BP, it is possible that dense sedge communities in the littoral zone inhibited the delivery of conifer needles to the center of Hippa Lake where the sediment core was collected.

The expansion of *A. rubra* and *P. sitchensis* shortly after 12,500 cal yr BP and the continued presence of *P. contorta* and *A. viridis* and abundance of ferns indicate that mixed forest communities occupied Hippa Island in the latest Pleistocene. The expansion of *P. sitchensis* populations on Hippa Island was likely facilitated by the earlier abundance of *Alnus* spp., which would have increased soil nitrogen and organic matter (Chapin et al., 1994). Expansion of *P. sitchensis* appears to occur about 500 cal yr later than at Logan Inlet (Fig. 1, site 12) and West Side Pond (Fig. 1, site 15) on southern Haida Gwaii, but more or less coincident with its arrival in southeastern Alaska 12,500–12,000 cal yr BP (Mann, 1983). Since fossil stomata indicate clearly that *P. sitchensis* was present on Hippa Island by 13,800 cal yr BP, the expansion of *Picea* populations after 12,500 cal yr BP, as suggested by pollen assemblages, is likely not a migrational lag due to limited seed dispersal or physiographic barriers, but rather a reflection of less favorable conditions, such as limited soil development within the island's rocky, exposed headlands.

Other sites along the northeastern Pacific coast suggest reversion to cooler climate during the Younger Dryas chronozone ~12,900–11,700 cal yr BP (Steffensen et al., 2008). Increases in *T. mertensiana* pollen at sites in south-coastal British Columbia (Mathewes, 1993; Mathewes et al., 1993; Lacourse, 2005) as well as reversion from *Pinus* communities to herb-dominated vegetation on Haida Gwaii (Mathewes et al., 1993) and in southeastern Alaska (Engstrom et al., 1990; Hansen and Engstrom, 1996) indicate that Younger Dryas cooling most pronounced around the North Atlantic Ocean is also recorded on the north Pacific coast. Most bivalve species disappeared from Hecate Strait (Fig. 1) during the Younger Dryas chronozone, leaving only coldwater species (Hetherington and Reid, 2003), and increases in cold-water benthic foraminifera suggest a decrease of 2–3°C in summer temperature off the coast of British Columbia (Mathewes et al., 1993). This cooling is corroborated by increases in benthic diatom species indicative of cool water on the central coast of British Columbia (Galloway et al., 2007) and by decreases in saturated alkenones in marine sediments further south, off the west coast of Vancouver Island (Kienast and McKay, 2001). Mathewes (1993) suggests that the Younger Dryas signal is stronger in marine and coastal sediments in western North America, compared with inland sites, which in general is similar to Younger Dryas-age vegetation change around the North Atlantic. However, this pattern appears to be true in only a very general sense. It is difficult to draw definitive conclusions regarding Younger Dryas cooling at Hippa Island, as there are only three pollen samples that span this interval. In general, there is only subtle evidence of Younger Dryas cooling from the Hippa Lake pollen record: decreases in *P. contorta* pollen and increases in *A. viridis* and herb pollen and Polypodiaceae fern spores are reminiscent of, but less pronounced than, Younger Dryas vegetation change in southeastern Alaska (Engstrom et al., 1990; Hansen and Engstrom, 1996). Furthermore, increases in pollen from taxa typical of mesothermal forests (e.g., *A. rubra* and *P. sitchensis*) suggest that temperatures were not exceptionally cool during this time. In fact, total pollen and spore concentrations in Hippa Lake sediments are higher during the Younger Dryas chronozone than during the previous 1000 cal yr (Fig. 3). At West Side Pond (Fig. 1, site 15), another hypermaritime site exposed to the open Pacific Ocean, there is no evidence of Younger Dryas cooling and total pollen accumulation rates increase during this time at that site (Lacourse et al., 2005), similar to the record from Hippa Lake. Cooling at these hypermaritime sites may not be well recorded in their fossil pollen records if the sites were not ecotonal and only minor changes in plant community composition occurred. It is also possible that cooling was less pronounced in these open ocean settings due to the moderating influence of the Pacific Ocean and/or that cooling did not exceed thresholds of the mostly mesic taxa that dominate the pollen records from these hypermaritime sites.

Holocene forests on Hippa Island

The open herb, shrub and *P. contorta* communities of the late Pleistocene were followed by a series of increasingly closed forest communities in the Holocene. A notable change in vegetation occurs at the transition to the early Holocene with *P. contorta*, *A. viridis* and Cyperaceae giving way to *P. sitchensis* and *T. heterophylla* (Fig. 3). The *Picea–Tsuga* forest included *A. rubra* trees and *A. viridis* shrubs and understory vegetation comprised largely of ferns including *Polypodium* as well as *L. americanus*. The succession to *Picea–Tsuga* forest can be explained by the greater shade tolerance and overall slower life history strategies of these conifers relative to *P. contorta* (Lacourse, 2009) as well as early Holocene warming. The succession to dense mixed forest at the transition to the Holocene is reflected in Hippa Lake sediments via a change from tan gyttja to coarse brown gyttja (Fig. 3) and increased organic matter accumulation (Walker and Mathewes, 1988).

Both pollen and stomata indicate that *T. heterophylla* was established on Hippa Island shortly after 11,000 cal yr BP. The expansion of *T. heterophylla* may have been delayed relative to Cape Ball (Fig. 1, site 8), where there is pollen and macrofossil evidence of its presence around 12,000 cal yr BP and *T. heterophylla* wood dated to 10,500 cal yr BP (9300 ± 80 ^{14}C yr BP, GSC-3477; Warner, 1984; Mathewes et al., 1985). The arrival of *T. heterophylla* at Hippa Island is more or less coincident with West Side Pond (Fedje, 1993; Lacourse et al., 2005), where exposed, hypermaritime conditions are more similar to Hippa Island. In general, postglacial colonization of the north Pacific coast by *T. heterophylla* appears to have been a diachronous event, occurring first in the south and then gradually north along the coast (Ager et al., 2010).

Picea–Tsuga forest was more or less stable in composition between 11,000 and 6000 cal yr BP, with the important addition around 8000 cal yr BP of *Coptis*, a member of the Ranunculaceae. Community dominance by *P. sitchensis*, *T. heterophylla* and ferns and the abundance of *A. rubra*, *L. americanus* and *Coptis* demonstrate that mesic to wet habitats were widespread on Hippa Island throughout much of the Holocene. *Pinus* stomata indicate that this conifer continued to be an important component of the island's vegetation during the early Holocene, despite pollen percentages of only 0.5–4%. The increase in *P. contorta* pollen between 7500 and 3000 cal yr BP, in both frequency and concentration, likely reflects expansion of open scrub forest associated with increased paludification. Indeed, bog–forest complexes were widespread on the north Pacific coast by 8000 cal yr BP (Banner et al., 1983; Warner, 1984; Hansen and Engstrom, 1996; Pellatt and Mathewes, 1997; Turunen and Turunen, 2003; Lacourse and Mathewes, 2005; Ager et al., 2010), due to increasingly cool, wet climate (Heusser et al., 1985). The establishment of mixed *P. sitchensis*–*T. heterophylla*–*A. rubra* forest, with an understory of *A. viridis*, *L. americanus*, *Coptis* and pteridophytes, is common in the early Holocene at most lowland sites on Haida Gwaii (Warner, 1984; Heusser, 1995; Lacourse and Mathewes, 2005; Lacourse et al., 2005) and elsewhere on the north Pacific coast (Banner et al., 1983; Hansen and Engstrom, 1996; Turunen and Turunen, 2003; Lacourse, 2005; Ager et al., 2010).

Early Holocene warming is documented in paleoecological records throughout most of the Northern Hemisphere, including pollen and plant macrofossil records from Shangri-La Bog, Louise Pond and SC-1 Pond (Fig. 1, sites 10, 11, and 14), three sub-alpine sites on Haida Gwaii where tree line increased between ~11,000 and 7500 cal yr BP (Pellatt and Mathewes, 1994, 1997). At Hippa Lake, increases in *P. sitchensis*, *T. heterophylla* and *L. americanus*, i.e. species typical of wet, mesothermal-temperate climate, provide some evidence of early Holocene warming, but also indicate that available moisture was sufficient to support these species. Total pollen and spore concentrations are lowest during the early Holocene (Fig. 3), which may be the result of a warmer and somewhat drier climate in which reduced humidity could have had a limiting effect. In addition, conifer stomata concentrations (Fig. 5) are highest during the early Holocene and this may reflect an increase in needles being deposited into the lake as a result of increased moisture stress and needle drop. Overall, the composition of early Holocene forests on Hippa Island is similar to mid- and late Holocene forests, with the exception of expanding Cupressaceae (*T. plicata*) populations, suggesting that these mesic plant communities were able to buffer early Holocene warming and/or that climate change in this open coastal lowland setting was less pronounced than elsewhere in the Northern Hemisphere, including nearby higher elevations. Similarly, chironomid fauna in Hippa Lake sediments did not change markedly through the Holocene (Walker and Mathewes, 1988); however, this is explained, at least in part, by the lack of profundal chironomid fauna, which are more sensitive to changes in climate than the littoral fauna common to Hippa Lake.

As with *P. contorta* and *P. sitchensis*, Cupressaceae stomata appear in the Hippa Lake record prior to increases in Cupressaceae pollen. Cupressaceae stomata first appear at ~8700 cal yr BP, with the first stomata confidently identified as *T. plicata* at 8570 cal yr BP (Fig. 5). Cupressaceae does not appear in the pollen record until shortly after at 8100 cal yr BP (Fig. 3) and then remains below 5% until after 6700 cal yr BP. In general, the Hippa Lake pollen data correspond well with increases in Cupressaceae pollen across Haida Gwaii beginning about 7000 cal yr BP (Warner, 1984; Fedje, 1993; Pellatt and Mathewes, 1994, 1997; Lacourse and Mathewes, 2005), but based on the stomata evidence from Hippa Lake, *T. plicata* was present well before these increases in Cupressaceae pollen. The first *T. plicata* stomata at 8570 cal yr BP may well represent the leading edge of migrating populations of this species. Macrofossil evidence suggests this species may have been present in southwestern British Columbia as early as 11,000 cal yr BP (Mathewes, 1973) and on northwestern Vancouver Island as early as 10,000 cal yr BP (Hebda and Haggarty, 1997). This northward pattern of post-glacial arrival and expansion suggests that *T. plicata* colonized the north Pacific coast in a time-transgressive manner, much like *T. heterophylla*. However, the paleoecological history of this species and other members of the Cupressaceae family is not well understood, because their pollen can be poorly preserved and easily confused with fossil algal cysts. Even when preservation is excellent, it is not possible to differentiate Cupressaceae pollen to the species level. Additional paleoecological research focusing on plant macrofossils and conifer stomata will be needed to decipher the late Quaternary histories of *T. plicata* and *C. nootkatensis*.

Although *T. plicata* stomata confirm that this species was locally present by ~8700 cal yr BP, the pollen record suggests that widespread expansion of its populations did not occur until after 5500 cal yr BP. Pollen concentrations suggest that *T. plicata* reached peak abundance around 3750 cal yr BP. This late Holocene expansion of *T. plicata* appears to be linked to the development of macro-woodworking technology in northwest coast Indigenous cultures (Hebda and Mathewes, 1984) and may have been driven by mid-Holocene increases in summer precipitation, as this species is most productive under long, wet growing seasons (Russell and Krakowski, 2010). Altogether, however, late Holocene forests are similar in composition to those in the early Holocene, with abundant *T. heterophylla* and *P. sitchensis* and an understory composed largely of pteridophytes, *A. viridis*, ericaceous shrubs and herbs such as *L. americanus*, *Coptis* and *Caltha biflora*. The similarity in Holocene forests is also reflected in the principal components ordination (Fig. 4B), which shows that all Holocene samples have low negative loadings on the first principal components axis. The only distinction in Holocene pollen samples is the addition of Cupressaceae (*T. plicata*), which distinguishes early and late Holocene communities on PC 2 (Fig. 4B). It appears that the mesophytic vegetation communities of Hippa Island tolerated Holocene climate fluctuations, resulting in pollen and spore assemblages that are relatively stable through much of the last 11,000 cal yr. In the context of global change, this resiliency warrants further investigation.

Birks and Birks (2000) concluded that pollen analysis alone is insufficient for accurate paleovegetation reconstructions and that palynological studies should be combined with plant macrofossil analyses. Our research underscores the utility of combining pollen with conifer stomata analyses in much the same way. In this study, conifer stomata increased taxonomic resolution in the case of Cupressaceae, allowing us to confirm that *T. plicata* was locally present thousands of years in advance of increases in Cupressaceae pollen. In fact, in three of four conifers, stomata confirmed their local presence hundreds to thousands of years in advance of when the pollen of each of these species increased beyond threshold percentages routinely used to infer local presence. Conifer stomata provided much better minimum estimates of local species arrival times, whereas pollen assemblages provided a continuous record of vegetation change and better records of local to regional population expansion. Furthermore, the difference between the timing of local species arrival provided by the two lines of evidence increased over the course of the Holocene i.e., ~690 cal yr for *P. contorta*, ~1340 cal yr for *P. sitchensis*, and ~2090 cal yr for *T. plicata*. This suggests that the local pollen signal can become increasingly masked by the regional pollen signal as vegetation communities become dominated by species that produce abundant pollen that is widely dispersed. Clearly, the source area for pollen is larger, more complex and temporally variable than that of conifer stomata, highlighting differences in scale in the paleoecological information provided by each. When combined, pollen and conifer stomata provide a more accurate record of vegetation dynamics on long ecological timescales than either can provide in isolation.

Acknowledgments

We thank B. Warner for help in the field, O. Heggen for help with Fig. 1, and K.D. Bennett for making *psimpoll* freely available.

P.J. Bartlein, R. Hebda, M. Pellatt, J. Galloway and an anonymous reviewer provided constructive feedback on earlier versions of this manuscript. Funding was provided by research grants from the Natural Sciences and Engineering Research Council of Canada to T. Lacourse and R.W. Mathewes, and from the Canadian Foundation for Innovation to T. Lacourse.

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