QUATERNARY RESEARCH **49,** 86–95 (1998)
ARTICLE NO. QR971936

Ostracode Geochemical Record of Holocene Climatic Change and Implications for Vegetational Response in the Northwestern Alaska Range

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Received January 29, 1997

Trace-element analysis of the calcareous shells of ostracodes in a sediment core from Farewell Lake provides the first limnogeochemical record for climatic reconstructions in Alaska. When compared with pollen data from the same site, this record offers new insights into climatic controls over vegetation dynamics during the Holocene. The low Mg/Ca ratios and high Sr/Ca ratios suggest that a relatively cold dry climate prevailed in this region between 11,000 and 9000 yr B.P. (uncalibrated ^{14}C ages are used throughout the paper). This result contrasts with previous interpretations of a thermal maximum at this time, corresponding to the widespread establishment of *Populus* woodland/forest. The trace-element record suggests, instead, that the warmest period of the early Holocene at Farewell Lake was between 8500 and 8000 yr B.P. during the decline of *Populus.* Marked decreases in Sr/Ca and Mg/Ca suggest a major increase in effective moisture around 6500 yr B.P., which coincided with the establishment of *Picea* boreal forests in the Farewell Lake region. This climatic change was probably widespread throughout much of Alaska and adjacent Canada and might have induced the rapid spread of *Alnus* and the shift from *Picea glauca* to *P. mariana* dominance across that region. Our geochemical record also suggests that the late-Holocene climate history was more complex than previously thought on the basis of palynological studies. According to this record, growing-season temperatures increased 6000–4500 yr B.P., decreased 4500–1500 yr B.P., and increased with fluctuations afterward. After 6000 yr B.P. stratigraphic changes in pollen percentages of *Picea* appear to be positively related with those of Mg/Ca. This relationship implies that once the threshold of effective moisture was crossed for the establishment of *Picea* forests temperature was the primary control of *Picea* population density.

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INTRODUCTION

The effects of climatic change on the boreal forest have been the subject of many recent investigations because of the concern about the sensitivity of the northern high-latitude climate to increased atmospheric CO_2 and the potential complex feedbacks of ecosystem changes in these regions to the global climate (e.g., Bonan *et al.,* 1990, 1992; Foley *et al.,* 1994). One important means for improving our understanding of the possible responses of boreal forests to climatic forcing is to decipher climatic and ecological records archived in lake sediments (e.g., MacDonald *et al.,* 1993). In Alaska, pollen data from lake sediments have greatly enhanced our knowledge of the regional vegetation history during the late Quaternary (Anderson and Brubaker, 1994; Edwards and Barker, 1994). Comparisons of these pollen data and AGCM (atmospheric general circulation model) simulations have served as a major approach to interpreting the climatic cause of these vegetation changes (e.g., Barnosky *et al.,* 1987). Although these comparisons have substantially improved our understanding of the complex relationships between climate and ecosystems (COHMAP, 1988; Anderson and Brubaker, 1994), this approach suffers from major differences in the spatial and temporal scales of existing simulations and pollen data (Anderson and Brubaker, 1994).

In order to assess the effects of climatic forcing on past vegetation changes, it is necessary to acquire proxy climatic records independent of pollen data but with comparable spatial and temporal resolutions. Geochemical studies of calcareous lake sediments offer an effective tool for acquiring such climatic records. Recent studies, for example, have applied trace-element analysis of the calcitic carapaces of ostracodes preserved in lake sediments to reconstruct paleoclimate in various regions (Chivas *et al.,* 1985, 1986, 1993; Curtis and

0033-5894/98 $25.00

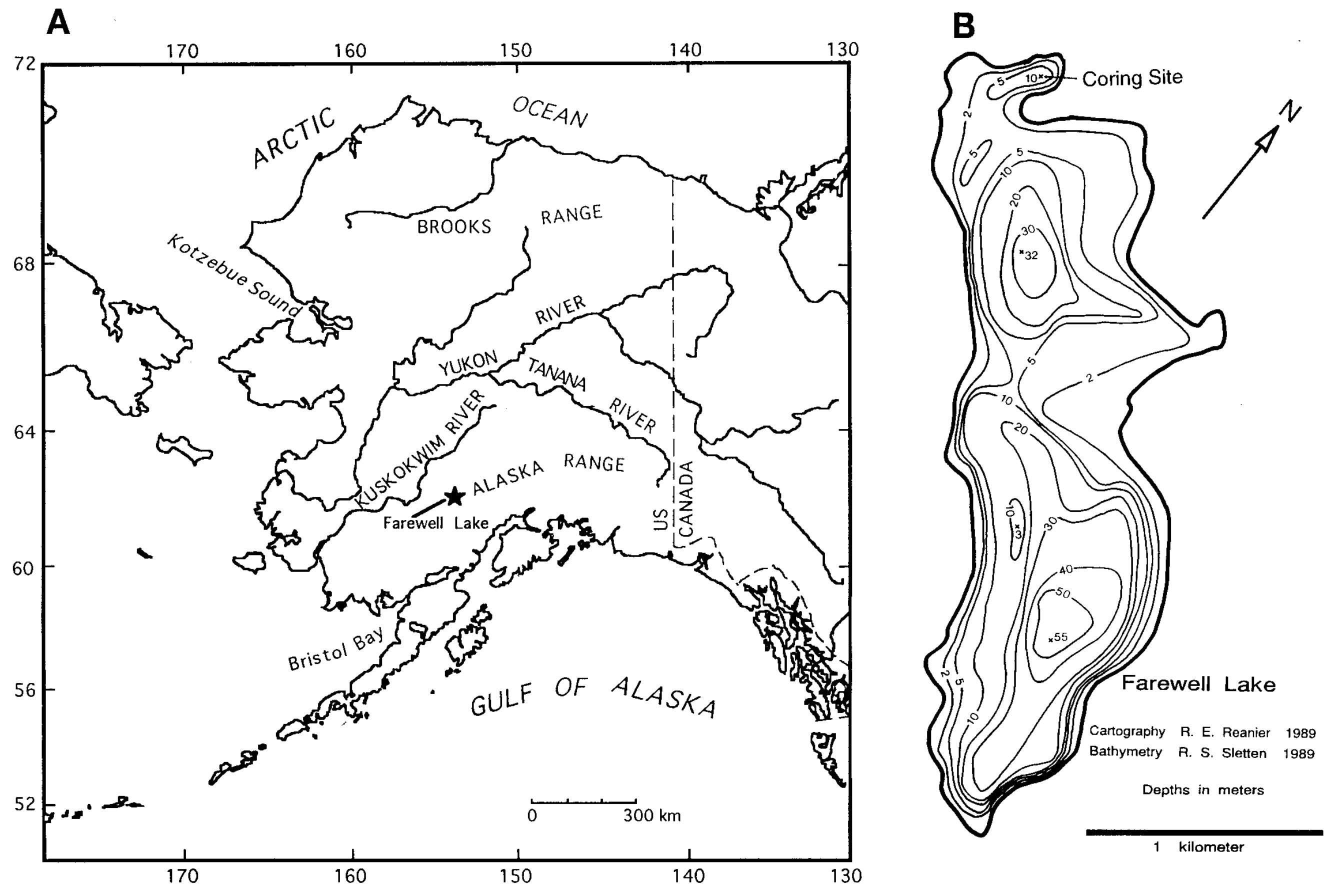

FIG. 1. (a) Map of Alaska showing location of Farewell Lake. (b) Bathymetry of Farewell Lake and coring location.

Hodell, 1993; Xia *et al.,* 1997b). These studies demonstrate that the chemistry of ostracode shells reflects paleo-water chemistry and is related to changes in temperature and effective moisture. In particular, the Mg/Ca ratio of ostracode shells increases with both water temperature and salinity (a negative function of effective moisture) in a hydrologically closed basin, whereas Sr/Ca ratio increases with salinity but is independent of temperature. When both ratios are measured, it is possible to separate signals of temperature and effective moisture.

We report here the results of trace-element analyses of ostracodes in sediment cores from Farewell Lake (62°33′N, 153°38′W, Fig. 1). To the extent that variations in trace-element composition are determined by changes in lake-water salinity and temperature that may be caused by regional fluctuations in effective moisture and atmospheric temperature, we use the data to infer the Holocene climatic history of the Farewell Lake region. The climatic trends are then compared with vegetation reconstructions from fossil pollen at the same site (Hu *et al.,* 1996) to evaluate the potential climatic causes of vegetation changes near Farewell Lake. These geochemical and fossil data together offer new information on the regional climatic change and vegetation response during the Holocene.

STUDY SITE

Farewell Lake is located in the northwestern foothills of the Alaska Range (Fig. 1) at an elevation of 320 m above sea level. The lake is within the limits of Late Wisconsin glacial expansion from the Alaska Range and lies on a large, gently north-sloping piedmont covered with moraines and glacial outwash. Bedrock in the area is primarily Paleozoic limestone with slate, phyllite, and chert (Fernald, 1960). Modern climate of the region is characterized by large seasonal variations in temperature and relatively dry conditions. The mean annual temperature is −3.5°C, mean January temperature −16.7°C, and mean July temperature 12.7°C. The lake lies within the rain shadow of the Alaska Range. The mean annual precipitation is 41.3 cm, of which over half falls during the summer months from June to September. Modern vegetation is typical of closed boreal forests in Alaska (Van Cleve *et al.,* 1986; Viereck *et al.,* 1992), with *Picea mariana* muskegs on poorly drained lowlands and

TABLE 1
Water Chemistry of Farewell Lake, June 1989 (in ppm, Except for pH)

pH	8.2
TOC	5.8
Ca	34.1
Mg	15.7
Na	3.26
K	1.52
Si	3.38
Ba	0.16
Cl	0.872
SO_4	5.35
NO_3	0.018
PO_4	0.238

mixed conifer-deciduous forests of *P. glauca*, *Betula papyrifera*, and *Populus tremuloides* on well-drained upland sites.

At present the lake lacks major surficial inflow–outflow systems and has a surface area of ca. 4 km^2 and a maximum water depth of 55 m. The lake water in August, 1989, was highly supersaturated with calcite (Table 1). The primary productivity is through charaphytes and planktonic algae. Sediments from the lake contain authigenic carbonate materials, including charaphyte-stem encrustations and calcitic shells of ostracodes.

MATERIALS AND METHODS

Two overlapping sediment cores were recovered from the deepest locality (water depth 10 m) of a subbasin near the northern end of the lake (Fig. 1) with a modified Livingstone corer (Wright *et al.*, 1984). The cores are well-correlated with magnetic-susceptibility profiles. One core was initially analyzed for pollen, plant macrofossils, magnetic susceptibility, and bulk-sediment elemental geochemistry to reconstruct vegetation and soil development during the last 11,000 years (Hu *et al.*, 1996). The ostracode samples for this study are primarily from this core, with a few samples from the second core for stratigraphic intervals where ostracode concentrations are low.

After samples were taken for other analyses, the sediment core was cut into 5-cm continuous sections, each of which was washed through 1.18-mm (U.S.A. standard testing sieve No. 16) and 0.425-mm (U.S.A. standard testing sieve No. 40) mesh sieves. The sieving was initially done to concentrate plant macrofossils (Hu *et al.*, 1996), but the residue contained ostracode valves suitable for trace-element studies. The residue was filtered through a Buchner funnel fitted with a coarse paper filter and was air-dried. Ostracode valves were picked with a fine brush under a dissecting microscope with 20× magnification.

The ostracode valves used for trace-element analysis were identified according to Delorme (1970). No single species was present in adequate abundance throughout the entire core. The partitioning of Sr and Mg is taxon-specific between host water and authigenic calcite, but it is thought to be the same for ostracode species within the same genus (Chivas *et al.*, 1985, 1986; Engstrom and Nelson, 1991). We used the shells of benthic ostracode *Candona* for trace-element analysis at most levels. Where *Candona* was absent, *Limnocythere* was used, and the Mg/Ca and Sr/Ca values of *Limnocythere* were then corrected by the difference of chemical composition between these two genera at stratigraphic levels where they coexisted. At each level, 3 to 12 valves of adult ostracodes of a given species were used for trace-element analyses.

Prior to geochemical analyses, ostracode valves were cleaned in 5% H_2O_2 at 80°C for 10 min, washed in triply distilled H_2O, and dried on a polycarbonate membrane filter in a laminar-flow hood. The valves were then reacted at 80°C for 30 min with 104% phosphoric acid made from ultra-pure P_2O_5 and triply-distilled H_2O (Xia *et al.*, 1997a). The acid solution was diluted 40 times with 0.5 M ultra-pure HCl and analyzed with a Perkin Elmer/Sciex Elan 5000 inductively coupled plasma mass spectrometer (ICP–MS) for Mg, Sr, and Ca. The mean precision of the analysis was about 2%.

CLIMATIC RECONSTRUCTION

Background for Climatic Interpretations of Ostracode Trace-Element Geochemistry

The trace-element chemistry of lake water is a sensitive monitor of climate in arid and semi-arid regions. If the water concentration of Ca is held constant by the inorganic precipitation of calcite, a decrease in salinity (i.e., an increase in effective moisture) should result in decreased Mg/Ca and Sr/Ca ratios, because Mg and Sr concentrations are undersaturated with respect to the minerals commonly precipitated within lakes (Chivas *et al.*, 1985, 1986; Engstrom and Nelson, 1991). These changes in water chemistry are recorded in the calcitic shells of ostracodes, as ostracodes incorporate trace elements into their shells in proportion to the concentrations of these elements in the host water. The quantitative relationship between the ratios of Sr/Ca and Mg/Ca in ostracodes and those in water is determined by their partition coefficients (K_d). The K_d of Sr/Ca is independent of water temperature and is a positive function of the Sr/Ca ratio of the host water, whereas the K_d of Mg/Ca is a positive function of both water temperature and the Mg/Ca ratio of the host water lakes (Chivas *et al.*, 1986; Engstrom and Nelson, 1991). Thus Sr/Ca can be used to reconstruct effective moisture, and Mg/Ca can be used to reconstruct effective moisture as well as temperature. Engstrom and Nelson (1991) determined that the K_d of *Candona rawsoni* is 0.406 for Sr/Ca and $9.68 \times 10^{-5} \times T(°C)$ for Mg/Ca. These K_d values suggest that $(Sr/Ca)_{ostracode}$ is much more sensitive to changes in water chemistry (and thus effective moisture) than $(Mg/Ca)_{ostracode}$ at a given temperature of lake water. However, these K_d values may not be useful for the quantitative climatic interpretation of the Farewell Lake data, as they were determined on the basis of calibration data from saline lakes much more concentrated than Farewell Lake.

Recent studies (Haskell *et al.*, 1996; Xia *et al.*, 1997b) showed that the reconstruction of water chemistry and climate from ostracode trace-element composition can be complicated by the types of inorganic carbonate minerals precipitated from the water because the K_d's for Mg and Sr vary for different carbonate minerals. For example, high Mg/Ca ratios in lake water favor the formation of aragonite over calcite. Since aragonite incorporates more Sr than calcite, the onset of aragonite precipitation during high-salinity events resulting from decreased effective moisture would cause Sr/Ca in the water to decrease rather than increase as expected. In addition, an upper limit appears to exist for the amount of Mg that can be incorporated into ostracode shells. These factors, however, are likely to be unimportant for Farewell Lake, as its water has low Mg concentration and very low Mg/Ca molar ratio of 0.76 today (Table 1). X-ray diffraction analyses of six samples along the Farewell Lake core also indicate that aragonite precipitation did not occur in a detectable amount and that the mineral composition was relatively constant throughout the lake history.

Climatic Change in the Farewell Lake Region

Both Sr/Ca and Mg/Ca ratios of ostracodes in the Farewell Lake sediments show distinct stratigraphic changes (Fig. 2). We interpret these trace-element profiles in terms of effective moisture and temperature in the Farewell Lake region on the basis of the background provided above. Because we used the composite of a number of ostracode valves for trace-element analysis in each sample, we assume that the trace-element ratios reflect average climatic conditions during the growing season. Our climatic interpretations are subject to the possible flaws in the assumptions about the climatic controls of ostracode trace-element composition and must be tested with additional paleoclimatic studies in the Farewell Lake region. The chronology is based on the linear interpolation of five AMS ^{14}C dates of plant macrofossils and a conventional ^{14}C date of the basal bulk sediments (Fig. 3). We assume that the basal bulk-sediment ^{14}C date is reliable because the sample is characterized by low carbonate concentration and abundant terrestrial organic remains including large charred particles and small twigs (Hu *et al.*, 1996).

Sr/Ca molar ratio. Between ca. 11,000 and 7000 yr B.P., Sr/Ca is relatively high, with an average of $\sim 1.9 \times 10^{-3}$. The ratio exhibits large fluctuations without major overall trends during this period. These large fluctuations probably reflected the small hydrochemical buffering capacity of the shallow, small coring subbasin that was probably separated from the two larger subbasins of Farewell Lake during the early Holocene (Fig. 1; Hu *et al.*, 1996). Sr/Ca decreases sharply to $\sim 1.2 \times 10^{-3}$ between 7000 and 6000 yr B.P. and remains low afterward. Between 1000 yr B.P. and present, Sr/Ca shows an increasing trend with fluctuations. However, our sampling resolution and chronological control are inadequate for detailed interpretations of stratigraphic changes in the last 1000 years.

These stratigraphic patterns suggest that the Farewell Lake region was substantially drier between 11,000 and 7000 yr B.P. than after 6000 yr B.P. In addition, effective moisture probably fluctuated greatly prior to 6000 yr B.P. but was relatively constant afterward. Effective moisture increased markedly between 7000 and 6000 yr B.P. and probably fluctuated with a general increase after 1000 yr B.P.

Mg/Ca molar ratio. Between 11,000 and 8500 yr B.P., Mg/Ca shows a general increase with some fluctuations. At the end of this period, the ratio increases sharply to reach peak values between ca. 8500 and 8000 yr B.P. Mg/Ca then decreases to a minimum of $\sim 0.9 \times 10^{-3}$ at 6000 yr B.P., followed by a gradual increase to a late-Holocene maximum of $\sim 5.0 \times 10^{-3}$ around 4500 yr B.P. After 4500 yr B.P., Mg/Ca decreases gradually to a low value of $\sim 3.0 \times 10^{-3}$ at 1500 yr B.P. Mg/Ca then fluctuates with generally higher values than at 1500 yr B.P.

Changes in the Mg/Ca ratio during periods of constant Sr/Ca ratios can be interpreted as changes in the growing-season temperature, because the K_d of Mg/Ca reflects both growing-season temperature and effective moisture, whereas the K_d of Sr/Ca is independent of temperature. The increase in Mg/Ca 11,000–8500 yr B.P. suggests increasing temperature during this period. The peak values of Mg/Ca 8500–8000 yr B.P. suggest that around this time the regional temperature reached a maximum for the period 11,000–7000 yr B.P., during which Sr/Ca ratios show no stratigraphic trends. Temperature then decreased until ca. 6000 yr B.P. The low Mg/Ca values 7000–6000 yr B.P. might have resulted in part from the increase in effective moisture, as indicated by the decrease of Sr/Ca. However, changes in Mg/Ca due to variations in effective moisture are likely to be much smaller than those in Sr/Ca, since the K_d for Mg/Ca is much smaller at a given temperature (Engstrom and Nelson, 1991). During the period of high effective moisture (6000–0 yr B.P.), the region probably experienced warming between 6000 and 4500 yr B.P. and became cooler between 4500 and 1500 yr B.P. Growing-season temperatures probably increased in general with fluctuations in the past 1500 yr.

Comparisons with Other Proxy Records of Climate

The Farewell Lake core is the only sediment record investigated in sufficient detail to infer the Holocene climate of

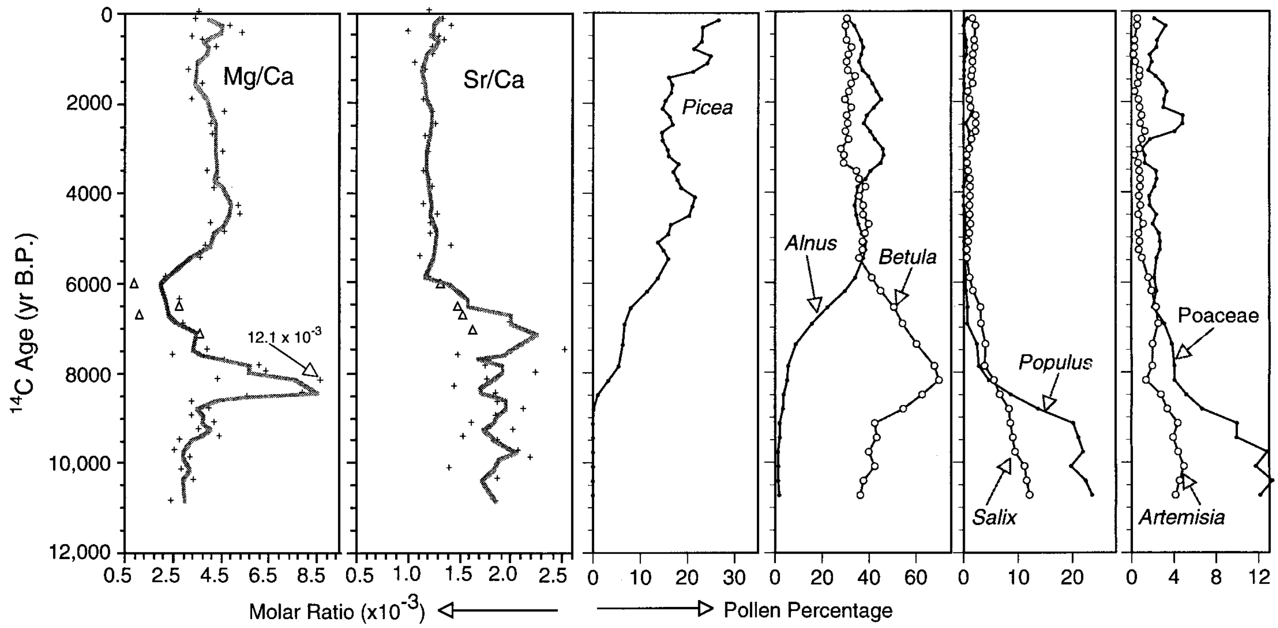

FIG. 2. Mg/Ca and Sr/Ca molar ratios in comparison with percentages of key pollen types, Farewell Lake. All lines are three-point moving averages. Crosses and triangles are original data points for the valves of ostracode *Candona* and *Limnocythere*, respectively.

the northwestern Alaska Range. Thus, we compare the trace-element results with other proxy paleoclimatic records only from this site (Hu *et al.*, 1996). In particular, aquatic biota including mollusks supplemented by pollen and macrofossils of aquatic plants have been used to infer changes in lake productivity and lake levels, which are suitable for comparisons with our reconstructions of effective moisture. These fossils suggest that lake levels were substantially lower during the early Holocene than during the late Holocene. For example, mollusks were most abundant between 11,000 and 7500 yr B.P., and most taxa disappeared from the coring site until 1500 yr B.P. In addition, several species indicative of fluctuating shallow-water environments, including *Fossaria modecella, Gyraulus parvus, G. circumstriatus,* and *G. crista*, were present prior to 8500 yr B.P. These results are generally consistent with our trace-element data suggesting that effective moisture was low with large fluctuations during the early Holocene. The marked increase in effective moisture 7000–6000 yr B.P. as inferred from the sharp decrease in Sr/Ca probably caused the lake level to rise above the sill that separated the coring subbasin from the two larger subbasins of Farewell Lake (Fig. 1; Hu *et al.*, 1996). At 8500 yr B.P. when shallow-water species disappeared, however, the Sr/Ca ratio does not show major directional changes that would suggest increasing effective moisture. This inconsistency between the biological and geochemical data may reflect differences in the controlling factors. For example, the typical habitats of these mollusk species are aquatic macrophytes (Clarke, 1979). The disappearance of these mollusks may result from the decrease of such habitats due to decreased nutrient status of the lake. A decrease in nutrient flux from the watershed might have

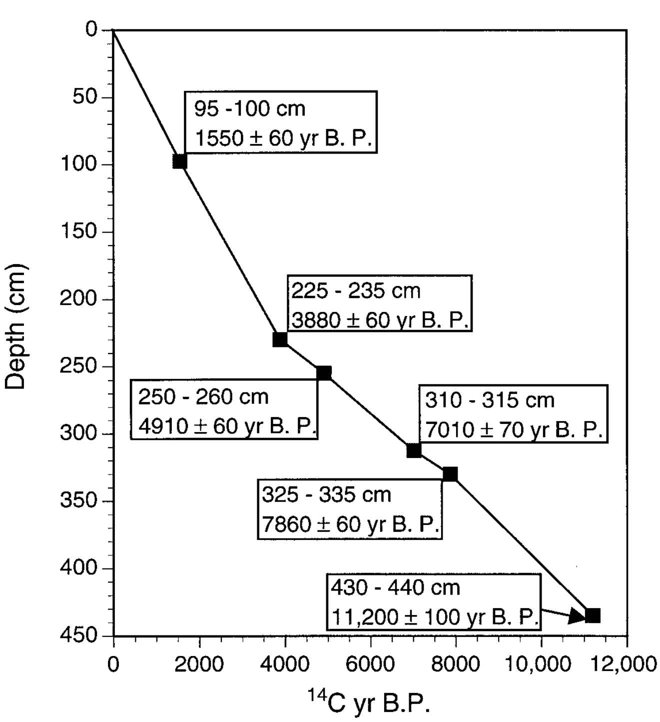

FIG. 3. Radiocarbon chronology, Farewell Lake. See explanation in text and Hu *et al.* (1996).

occurred at this time as a result of soil stabilization, as suggested by major decreases in detrital mineral content and magnetic susceptibility (Hu *et al.*, 1996). Alternatively, it is possible that these mollusks were present only during periods of extreme drought. Such extreme events are not detectable in our geochemical records, since the ostracode individuals used for our trace-element analysis at each level were obtained from a 5-cm interval of the sediment core representing 160 years on average and thus the trace-element data most likely represent averaged climatic conditions.

ASSESSING ECOSYSTEM RESPONSE TO CLIMATIC CHANGE

The ostracode trace-element data from this study provide the first limno-geochemical record for paleoclimatic reconstructions in Alaska. When compared with vegetation history based on the pollen data from the same core (Hu *et al.*, 1996), this record allows us to assess vegetational response to climatic change in the Farewell Lake region. In assessing temperature effects on vegetation, we assume that the lake-water temperature as inferred from our trace-element data reflects the atmospheric temperature, considering that our coring site has likely been relatively shallow throughout the Holocene (Hu *et al.*, 1996). Here we focus on three questions regarding vegetational response to climatic forcing at this site and speculate about the regional implications. The Farewell Lake results must be verified at other sites to determine whether the trace-element composition recorded regional changes in past climate that caused vegetation changes across broader areas of eastern Beringia.

Was the Populus-Dominated Vegetation a Response to a Thermal Maximum during the Early Holocene?

In eastern Beringia, the regional vegetation between 11,000 and 9000 yr B.P. was typically characterized by the dominance of *Populus* (cf. *P. balsamifera*), as evidenced by the common presence of a peak in *Populus* pollen at many sites (Anderson *et al.*, 1988; Anderson and Brubaker, 1994). This vegetation was thought to represent a biotic response to the postglacial maximum summer warmth resulting from an insolation maximum (Ritchie *et al.*, 1983; Ritchie, 1987). However, by calibrating ^{14}C ages to calendar years for the *Populus* subzone at a number of sites in eastern Beringia, Bartlein *et al.* (1995) found that the *Populus* peaks occurred prior to the insolation maximum during the early Holocene, thus arguing against the summer insolation maximum as a potential climatic cause of the *Populus* peaks. These authors concluded that the ultimate climatic controls for the occurrence of the *Populus* subzone were probably increased summer temperatures at the end of the last glacial due to the contemporaneous decrease in ice volume and increase in summer insolation. Summer temperatures likely continued to increase at the end of the *Populus* subzone as a result of the second step in hemispheric deglaciation associated with the near-maximum insolation values.

Our pollen and geochemical records from Farewell Lake provide proxy evidence supporting the conclusions of Bartlein *et al.* (1995). The pollen diagram from Farewell Lake (Hu *et al.*, 1996) indicates that prominent *Populus* populations were present between 11,000 and 9000 yr B.P. However, a comparison of this pollen diagram with the ostracode trace-element data from the same core suggests that a thermal maximum did not exist during the *Populus* period (Fig. 2). The low Mg/Ca ratios and high Sr/Ca ratios suggest that climatic conditions were relatively cold and dry between 11,000 and 9000 yr B.P. compared to the subsequent period. The growing-season temperatures increased gradually during the *Populus* period, and the warmest interval of the early Holocene was probably between 8500 and 8000 yr B.P., during which *Populus* declined.

Instead of a direct response to increased summer temperatures, the early-Holocene dominance of *Populus* likely in part represented an opportunistic response of this early successional taxon to the unstable soil environments at the end of the last glaciation. This proposition is supported by high sediment inorganic content at several sites (Cwynar, 1982; Hu *et al.*, 1993, 1996) and high magnetic susceptibility at Farewell Lake (Hu *et al.*, 1996), suggesting that soil erosion and/or eolian activity were relatively intense during the *Populus* period. At all these sites, the detrital mineral content of the sediments decreased greatly during the *Populus* period. These data imply that landscape stabilization might have induced the decline of *Populus* (Hu *et al.*, 1993). The instability of the landscape during the *Populus* period might have also resulted in high nutrient influx into lake basins. This process, along with lower lake levels, probably contributed to the apparently higher aquatic productivity during the *Populus* period, as suggested by the abundance of mollusk remains at Farewell Lake (Hu *et al.*, 1996) and at several other sites in Alaska (Ager, 1975; Edwards and Brubaker, 1987).

Although our data suggest that the *Populus* subzone should not necessarily be viewed as evidence for a thermal maximum in the Farewell Lake region, we do not argue against the existence of an interval of early-Holocene warmth in eastern Beringia. In far northwestern Canada, evidence of summer warmth during this period includes the range extensions of *Picea*, *Myrica*, and *Typha* farther north than at present (Ritchie *et al.*, 1983). Although such evidence is equivocal from Alaska, other evidence exists for an early-Holocene warm interval. For example, on the North Slope of the Brooks Range, exposures containing *Populus* wood beyond its present range and assemblages of ostracodes and beetles with warm affinities suggest that summer temperatures were 2°C higher than at present during the early Holocene (Carter *et al.,* 1984). Additionally, *Betula papyrifera* extended farther north than at present in the Seward Peninsula between 10,200 to 7270 yr B.P., with a cluster of dates between 9500 and 8500 yr B.P. (McCulloch and Hopkins, 1966; Hopkins *et al.,* 1981). These range expansions probably post-dated the *Populus* pollen peaks, as suggested by comparing the timing of macrofossil records with that of *Populus* peaks within the same subregions where both records are present (Anderson, 1985). This observation is consistent with the geochemical data from Farewell Lake suggesting that the maximum growing-season temperature during the early Holocene occurred immediately after rather than during the *Populus* subzone. Independent proxy records of paleoclimate and pollen records from the same sites are necessary to further understand the temperature history of the early Holocene in relation to *Populus* and other biotic records, given the potential inaccuracy of ^{14}C dating and the asynchrony of *Populus* peaks in different areas of eastern Beringia (Anderson *et al.,* 1988).

What Factors Controlled Picea Dynamics during the Middle Holocene?

Although the history of *Picea* is relatively well documented in Alaska and adjacent Canada, the causes remain poorly understood for the Holocene *Picea* dynamics. Previous studies have speculated about the role of climate, successional changes, and soil development for the spreading and subsequent population fluctuations of *Picea* (Ritchie, 1985; Hu *et al.,* 1993, 1996; Anderson and Brubaker, 1994). The importance of these controlling factors can be evaluated in light of the climatic reconstructions from our geochemical records.

At Farewell Lake, pollen and plant macrofossils suggest that *P. glauca* arrived in the watershed ca. 8000 yr B.P. (Hu *et al.,* 1996) when the regional climate was characterized by relatively warm, dry conditions. Temperature probably decreased between 8000 and 7000 yr B.P., but its effect on vegetation is unclear. *Picea* forests expanded to cover larger areas of the region near Farewell Lake between 7000 and 6000 yr B.P., as suggested by the doubling of *Picea* pollen percentages to reach values similar to those of the later period. This vegetation change coincided with a marked increase in effective moisture, suggesting that increased effective moisture was responsible for the establishment of *Picea* forests ca. 6000 yr B.P. and that prior to this time, the growth of *Picea* populations was limited by inadequate effective moisture. Evidence for the importance of effective moisture for *Picea* forest development has also been provided by other lake-sediment records (Abbott, 1996; Bigelow, 1997), dendrochronological studies (Garfinkel and Brubaker, 1983), and forest simulations (Bonan *et al.,* 1990). Specifically, lake-level and pollen studies at Birch Lake in the Tanana Valley near Fairbanks show that a major increase in *Picea* pollen percentages ca. 8500 yr B.P. corresponded to a rapid rise of the lake level to reach the overflow stage (Abbott, 1996; Bigelow, 1997). Statistical comparisons between tree-ring width sequences and climatic records indicate that precipitation during certain months was strongly correlated with *P. glauca* tree growth in interior Alaska (Garfinkel and Brubaker, 1980). Forest simulations conclude that the effects of future climatic warming on boreal forests in interior Alaska may not be so much a direct response to increased air temperature as it may be a response to the increased potential evapotranspiration demands accompanying climatic warming (Bonan *et al.,* 1990). These studies together underscore the need for investigating the history of effective moisture in order to understand the causes of long-term vegetation dynamics in Alaska.

The history of effective moisture likely varies within eastern Beringia, given the spatial complexity of the regional climate (Mock *et al.,* 1997). However, an increase in effective moisture 7000–6000 yr B.P. might have been a widespread change throughout much of the region. Consistent with our inference of a marked increase in effective moisture, pollen data from the region suggest vegetation changes resulting from the expansion of mesic habitats around this time. In particular, *Alnus* spread rapidly throughout much of Alaska (Anderson and Brubaker, 1994), including the Farewell Lake region (Hu *et al.,* 1996), and the Yukon (Cwynar and Spear, 1995) between 7000 and 6000 yr B.P. As Cwynar and Spear (1995) concluded, such a rapid and widespread expansion of *Alnus* likely resulted from a large-scale increase in moisture availability. Hu *et al.* (1995) speculated that the establishment of extensive *Alnus* shrub thickets resulted from an increase in winter snow cover, on the basis of the general correspondence between patterns of modern *Alnus* pollen percentages (Anderson *et al.,* 1991) and precipitation, particularly mean annual snowfall in Alaska (Viereck and Little, 1975).

A widespread increase in effective moisture 7000–6000 yr B.P. would plausibly explain the mid-Holocene shift in the dominance of *Picea* species in areas of Alaska east of Farewell Lake and in the Yukon. In these areas, an important vegetation event during the middle Holocene is the decline of *P. glauca,* followed by the expansion of *P. mariana* to become the dominant *Picea* species ca. 6500 yr B.P. Two leading hypotheses have been invoked to interpret the cause of this dominance shift: autogenic soil paludification and a climatically induced increase in soil moisture (Ritchie, 1987). The former involves the slow decomposition of coniferous litterfall, resulting in the accumulation of a thick layer of organic matter that insulated mineral soil from summer heat penetration. These soil processes in turn led to a rise of the permafrost table and soil waterlogging under stable climatic conditions. Such soil conditions would have favored *P. mariana* over *P. glauca.* This interpretation is supported by successional studies of the boreal forests in interior Alaska (Van Cleve *et al.*, 1986). However, given the climatic interpretations of the mid-Holocene *Alnus* expansion in eastern Beringia and our geochemical record from Farewell Lake, it is likely that the ultimate cause for the shift from *P. glauca* to *P. mariana* dominance was an increase in effective moisture rather than autogenic soil paludification, although soil changes might have acted as an immediate control.

At Farewell Lake, however, the shift from *P. glauca* to *P. mariana* dominance was not as distinct an event as it was at the sites farther east. Furthermore, such a vegetation change did not occur until 4000 yr B.P., when the development of waterlogged soils also occurred (Hu *et al.*, 1996). This suggests that soil exerted a direct effect on the vegetation, but soil and vegetation might have behaved independently of increased effective moisture 7000–6000 yr B.P. and/or that ecosystem changes might have lagged behind this climatic change by >2000 years at Farewell Lake. Such a hypothesis on vegetation-soil-climate interactions should be evaluated with additional detailed records of ecosystem and climatic changes from the region.

Have the Alaskan Vegetation and Climate Been Relatively Stable since the Middle Holocene?

Paleoecological studies in Alaska have concentrated on the north-central part of the state (Anderson and Brubaker, 1994; Edwards and Barker, 1994). Pollen records from this region commonly display relatively constant assemblages similar to those of surface sediments after ca. 6000 yr B.P., suggesting the establishment of the modern boreal forests at this time and the relative stability of vegetation afterward. These data have led to the inference that the regional climate has not varied greatly in the past 6000 years. In contrast, our geochemical data (Mg/Ca ratios) suggest temperature fluctuations in the Farewell Lake region since 6000 yr B.P. Pollen spectra from the same core also fluctuated during this period. In addition, *Picea* (*P. glauca* + *P. mariana*) pollen percentages appear to covary broadly with Mg/Ca ratios. Both *Picea* pollen percentages and Mg/Ca ratios increased between 6000 and 4500 yr B.P., decreased between 4500 and 1500 yr B.P., and generally increased afterward. These covariations imply that after 6000 yr B.P. the population size of *Picea* might have been primarily determined by growing-season temperature.

In conjunction with the inferred relationship between *Picea* and effective moisture during the previous period, these data suggest that once the threshold of effective moisture was crossed, temperature probably became the dominant climatic control over *Picea* near Farewell Lake. Such climatic effects on vegetation might have also occurred in far western Alaska. For example, in the northern Bristol Bay region, *Picea* arrived ca. 4000 yr B.P. (Hu *et al.*, 1995), and in northwestern Alaska, *Picea* became established ca. 5000 yr B.P. (Anderson, 1985, 1988). These vegetation changes coincided with the warm interval around 4500 yr B.P. as recorded by the Mg/Ca ratios at Farewell Lake, suggesting that the westward movement of treelines might have occurred during this warm interval. Because of the proximity to the Bering Sea, western Alaska was likely wetter and cooler during the growing season than the interior, with effective moisture levels above the threshold for tree invasion throughout much of the Holocene. It is conceivable, therefore, that the late-Holocene invasion of *Picea* onto tundra in this region was primarily a response to increases in the regional temperature, rather than effective moisture.

Recent studies have demonstrated the climatic complexity (O'Brien *et al.*, 1996; Wolfe *et al.*, 1996) of the northern high latitudes and the sensitivity of *Picea* treelines to climatic changes (MacDonald *et al.*, 1993) during the middle and late Holocene. Climatic variations during this period have also been evidenced by the fluctuations of mountain glaciers throughout Alaska, especially after 4000 yr B.P. (Calkin, 1984; Wiles *et al.*, 1994). Our proxy records from Farewell Lake concur with these recent results and provide new evidence for climatic and ecological variations after the middle Holocene in Alaska. The palynological stability in north-central Alaska likely reflects the fact that sites in this region were mostly located within or near the areas where extensive closed boreal forests became established by 6000 yr B.P., in addition to the lack of detailed pollen analysis for this period. Improving our understanding of the late-Holocene climatic changes and assessing their ecological consequences should be a focus of future paleoecological efforts in Alaska. To this end it is necessary to acquire detailed pollen records from sensitive areas such as western Alaska where an extensive forest–tundra ecotone existed during the late Holocene and to investigate nonpalynological proxies of lake sediments throughout Alaska.

ACKNOWLEDGMENTS

This research was supported by the NSF Research Training Group on Paleorecords of Global Change at the University of Minnesota through a postdoctoral fellowship to FSH. Field work was funded by NSF Grant OPP-8922491, and laboratory analyses by NSF Grants ATM-9619583 and BIR-9014277 and NOAA Grant USDOC/NA 36GP0302. We thank Rick Knurr and Reed McEwan for laboratory assistance and Mary Edwards, Paul Glaser, Brian Haskell, and Herb Wright for comments. This paper is Limnological Research Center Contribution 503 and PALE Contribution 99.

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