ENVIRONMENTAL STUDIES

Deglaciation of the Pacific coastal corridor directly preceded the human colonization of the Americas

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The route and timing of early human migration to the Americas have been a contentious topic for decades. Recent paleogenetic analyses suggest that the initial colonization from Beringia took place as early as 16 thousand years (ka) ago via a deglaciated corridor along the North Pacific coast. However, the feasibility of such a migration depends on the extent of the western Cordilleran Ice Sheet (CIS) and the available resources along the hypothesized coastal route during this timeframe. We date the culmination of maximum CIS conditions in southeastern Alaska, a potential bottleneck region for human migration, to ~20 to 17 ka ago with cosmogenic ¹⁰Be exposure dating and ¹⁴C dating of bones from an ice-overrun cave. We also show that productive marine and terrestrial ecosystems were established almost immediately following deglaciation. We conclude that CIS retreat ensured that an open and ecologically viable pathway through southeastern Alaska was available after 17 ka ago, which may have been traversed by early humans as they colonized the Americas.

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INTRODUCTION

Despite decades of research, the debate surrounding the timing and route of the initial human colonization of the Americas continues (1, 2). Early hypotheses about human dispersal into the Americas from Beringia, the land mass that joined Northeast Asia and northwestern North America during the Late Pleistocene, relied heavily on the discovery of Clovis points in the interior plains of North America, and the resulting "Clovis First" paradigm (3) dominated archeological thinking for most of the 20th century. This hypothesis hinges on the presence of a corridor of unglaciated terrain in west-central Canada separating the Laurentide Ice Sheet and Cordilleran Ice Sheet (CIS) throughout the Late Pleistocene (the so-called ice-free corridor) (Fig. 1) (4). It is now widely recognized that these ice sheets coalesced during the Last Glacial Maximum [LGM; 26 to 19 thousand years (ka) ago] (5) and well into the deglacial period (6). Recently, research in the ice-free corridor has determined that while the corridor became physically open sometime between 15.6 and 14.8 ka ago (6), the region was not biologically viable (that is, able to support human life) until 13.0 ka ago (7) or perhaps even 12.6 ka ago (8). Furthermore, the increasing antiquity of known American archeological settlements (9-11), including Clovis sites (12), as well as mounting evidence from genetic studies (13-15), has pushed back the timing of the initial migration into the Americas to 16 ka ago (16). It is therefore unlikely that this first pulse of human migration took place through the ice-free corridor, and attention has accordingly shifted to the Pacific coast as an alternative, viable entry route to the Americas (Fig. 1) (17, 18).

The feasibility of a coastal migration depends on two environmental factors: (i) the biological productivity and availability of food resources along the coastal route during the colonization event(s) and (ii) the presence or absence of significant physical barriers to migration. The movement of sea-faring peoples (19) from Asia to the Americas may have been facilitated by highly productive coastal kelp forests (20), but it remains unclear whether a continuous "kelp highway" existed during the latest Pleistocene (2). Perhaps of greater importance, along the

northeastern Pacific coast, marine margins of the CIS could have posed a major physical challenge to migration. The presence of small mountain glaciers independent of the CIS may have also impeded coastal travel. However, if ice did not extend to the continental shelf



Fig. 1. North American Ice Sheet extents and potential colonization pathways. Extent of the Cordilleran and Laurentide ice sheets at 19 ka ago (white) and 15.5 ka ago. Areas of exposed continental shelf at 19 ka ago are shown in brown (6). Yellow stars indicate locations of offshore marine data discussed in the main text.

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break, lower sea levels during the latest Pleistocene (21) may have exposed portions of the now-submerged continental shelf, potentially providing habitable terrain for early human migration along the outermost coast. The viability of the coastal route is therefore intimately tied to CIS and mountain glacier extent during the latest Pleistocene. Offshore marine data have been used to infer that marine-terminating CIS margins in southern Alaska and western British Columbia (Fig. 1) were in retreat by 17 ka ago (22–26), but few chronological controls exist for the >500 km of the southeastern Alaskan coastline that separates these two regions and the timing of mountain glacier retreat has not yet been investigated. Because of a lack of direct constraints on southeastern Alaska's glacial history, assessing the feasibility of coastal migration to the Americas has proven challenging.

Early syntheses of CIS extent in southeastern Alaska depicted a continuous LGM ice margin extending to the edge of continental shelf (6), and sedimentological data from offshore marine records have been used to infer regional CIS retreat sometime after 19 ka ago (27). Recent studies of southeastern Alaska's palynology (28) and biology (29) suggest that some locations, including several of the region's westernmost islands and portions of the now-submerged continental shelf, remained ice-free during the LGM. On the basis of regional geomorphology and bathymetry, Carrara et al. (30) mapped coastal areas that may have escaped glaciation during the LGM, assuming a uniform regional sea level lowering of 125 m (Fig. 2). We note here that this value for the LGM sea level lowstand is a minimum estimate; the westernmost zone of southeastern Alaska may have experienced sea levels ~140 to 165 m lower than today (21). Furthermore, the weight of the CIS produced a crustal forebulge beyond its western margin that ranged in height from 63 to 30 m during the latest Pleistocene (31). If they existed, continuously ice-free areas may have facilitated human migration through southeastern Alaska by serving as refugia for plant and animal populations (32), which could provide sustenance, resources, and shelter from relatively harsh conditions along the North Pacific coast. In addition, the occurrence of ice-free terrain along the outer coast may have hastened the development of viable ecosystems elsewhere in the region following the retreat of the CIS (33). While the presence of LGM refugia in southeastern Alaska is often invoked to support the coastal migration hypothesis (22), to date, there remains no direct evidence for their existence. Here, we test the refugia hypothesis and assess the viability of a bottleneck region of the coastal migration route by reconstructing the timing of latest Pleistocene glaciation in southeastern Alaska.

RESULTS

The unique geology of southeastern Alaska allows us to construct our CIS chronology using two proxies: cosmogenic 10 Be exposuredated rock surfaces at previously mapped refugial sites (30) and previously published 14 C-dated mammal and bird bones found in caves on nearby islands (29). Ten new 10 Be ages from bedrock and perched boulders from hypothesized refugia at Dall, Suemez, and Warren islands (Fig. 2) (30) provide evidence for CIS extent during the LGM. If these sites were indeed refugia, the 10 Be ages would predate the LGM, which occurred sometime before 19 ka ago in the region (27). However, the 10 Be ages (reported at 1 SD external uncertainty throughout; table S1) range from 15.8 ± 0.7 to 24.8 ± 1.0 ka ago (n = 10) and average 17.0 ± 0.7 ka ago (n = 9; average uncertainty reported as 1 SD of the population). This average value excludes one older outlier from a bedrock surface at Warren Island (15SEAK-12; 24.8 ± 1.0 ka ago)

that is >3 SD older than the remaining 10 Be ages. Field observations of ice-molded bedrock and glacial striations oriented in the direction of regional ice flow also suggest cover by an ice sheet, rather than local ice (see Materials and Methods). Therefore, these hypothesized refugia were not continuously exposed but rather covered by the CIS during the LGM and became ice-free at ~17 ka ago. On Baker Island, 10 Be ages from perched boulders in an alpine valley range from 15.3 \pm 0.6 to 15.7 \pm 0.7 ka ago and average 15.5 \pm 0.2 ka ago (n = 3; fig. S3). The perched boulder ages indicate that Baker Island was not an ice-free refugium during the LGM and that mountain glaciers persisted there until 15.5 ka ago, ~1500 years later than regional CIS deglaciation.

To further refine the glacial history of southeastern Alaska, we calibrated 177 previously published fossilized mammal and bird bone ¹⁴C ages (29) from 15 caves in the Alexander Archipelago (see the Supplementary Materials). Most of these fossils (n = 108) were excavated from Shuká Káa (formerly known as On Your Knees Cave), which lies about 30 km upflow from Warren Island on the northern tip of Prince of Wales Island (Fig. 2) and served as a carnivore den before the LGM and during the postglacial period (29). Calibrated ¹⁴C ages (Fig. 2 and table S3) reveal an exceptional record of nearly continuous fossil preservation from >45 ka ago to the present (Fig. 3 and fig. S4). While fossils were deposited almost throughout the LGM, the scarcity of ages between ~20 and ~15 ka ago is conspicuous, and no fossils date to a 2600-year window from 19.8 to 17.2 thousand calibrated years before 1950 (cal ka BP). Immediately surrounding this hiatus are ringed seal (Phoca hispida) bones that have been modified by mammalian carnivores (29), indicating an availability of marine environments to these predators.

DISCUSSION

The lack of fossilized cave bones dating between 19.8 and 17.2 cal ka BP implies one of two scenarios: cover of Shuká Káa's entrance by the CIS or nondeposition of fossils in the cave unrelated to CIS extent. In the 45-ka period that animals made regular use of Shuká Káa, the period from 19.8 to 17.2 cal ka BP is the longest interval in the record with no dated bones (Fig. 3). Moreover, our ¹⁰Be ages suggest that retreat of the CIS from Dall, Suemez, and Warren islands occurred at 17.0 \pm 0.7 ka ago. When these outermost islands were glaciated, the entrance to Shuká Káa, at only 125 m above sea level (asl), would have also been covered by ice. We note that Shuká Káa is a slightly up flowline (~30 km), and thus may have been covered sooner, and uncovered later than our study sites farther west. Regardless, given the close correspondence in timing of the 10Be ages and the end of the ¹⁴C hiatus, we interpret the gap in fossilized cave bone ages from 19.8 to 17.2 cal ka BP to reflect ice cover over Shuká Káa. Together, our ¹⁴C and ¹⁰Be chronologies suggest that the maximum extent of the CIS in southeastern Alaska occurred between ~20 and 17 ka ago.

In contrast to the latest reconstructions of CIS extent (29), our results demonstrate that currently emergent outer islands of southeastern Alaska were not refugia throughout the latest Pleistocene. However, these islands became ice-free at 17 ka ago, early enough to accommodate human coastal migration at 16 ka ago (13). Although local glaciers lingered until ~15.5 ka ago, these small ice masses should not have impeded migration through the region, especially if areas of the continental shelf remained ice-free. On the other hand, outlet glaciers residing in the deep fjords between our sampling sites could have posed a challenge to human travel. Because our ¹⁰Be ages on Dall,

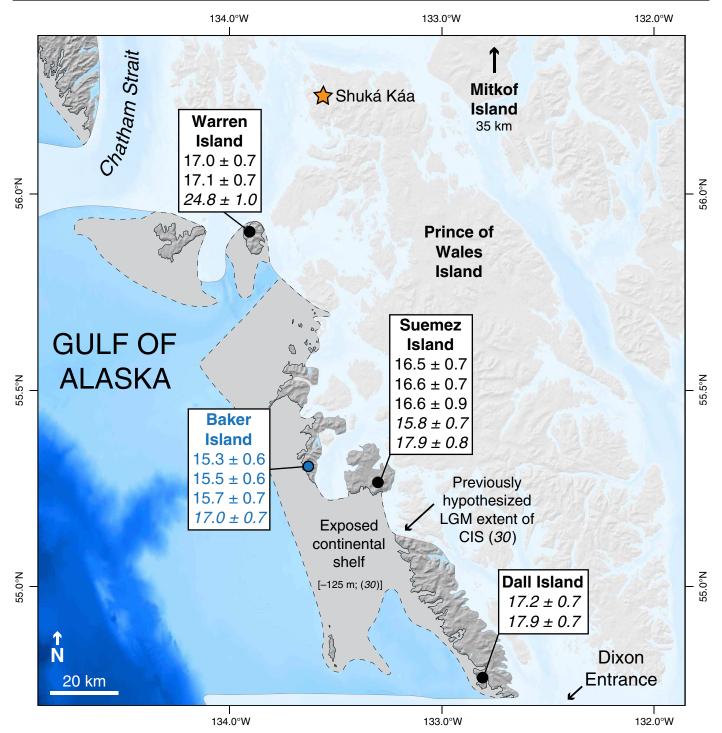


Fig. 2. New ¹⁰Be ages from southeastern Alaska. Study region showing previously hypothesized CIS extent (white) and regions of potentially exposed continental shelf (solid gray; determined by subtracting 125 m from modern sea level) during the LGM (30). Sampling sites for ¹⁰Be dating were selected within areas hypothesized by Carrara *et al.* (30) to have been ice-free during the LGM. Boulder (normal text) and bedrock (italicized text) ¹⁰Be ages (thousand years; 1 SD external uncertainty) constrain CIS (black) and local deglaciation (blue) and demonstrate that sampling sites were not ice-free refugia. The location of Shuká Káa cave on Prince of Wales Island is marked with an orange star.

Suemez, and Warren islands are from ridges between fjords, our data alone cannot eliminate the possibility that low-gradient outlet glaciers extended beyond these islands for some amount of time after the CIS thinned below our sampling locations. However, minimum-limiting

ages from marine sediments suggest that ice had largely disappeared from the major fjords in and around southeastern Alaska by 16 ka ago (26, 28, 34, 35). If outlet glaciers occupied the fjords adjacent to our sampling sites after 17 ka ago, they likely did not persist there for long

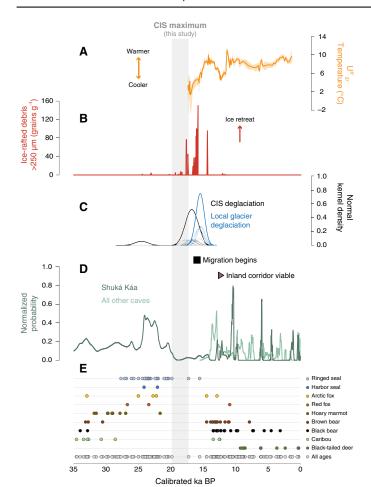


Fig. 3. Climate records and key chronologies along the Pacific coast. (A) Alkenone-derived sea surface temperature reconstruction from the Gulf of Alaska (36). (B) Icerafted debris from core MD0299, collected near Vancouver Island (23). (C) Composite diagram of individual ¹⁰Be ages from southeastern Alaska (gray and light blue lines; this study), summed ¹⁰Be ages for CIS deglaciation (black lines; this study), and local deglaciation (blue lines; this study). (D) Timing of the first pulse of human migration to the Americas [black square; (13)], the ecological opening of the inland corridor [purple triangle; (8)], and ¹⁴C ages from Shuká Káa (dark green lines; this study) and other caves in southeastern Alaska (light green lines; this study). (E) Timeline of selected cave fauna from southeastern Alaska [(29); this study]. Dots represent the means of the total range of each calibrated ¹⁴C age (this study). Vertical gray bar denotes the timing of maximum CIS extent in southeastern Alaska determined from the cave fauna ¹⁴C ages and ¹⁰Be ages reported in this study.

and therefore would not have hindered human travel through southeastern Alaska by 16 ka ago.

But was this portion of southeastern Alaska ecologically viable for human migration by 16 ka ago? On Mitkof Island (Fig. 2), which was covered by the CIS during the LGM, open pine forests developed fewer than 1000 years after isostatically depressed lowlands emerged from marine waters (28), indicating a short lag between landscape exposure and regional revegetation. Furthermore, a carnivore-modified ringed seal bone in Shuká Káa that dates to 17.2 ± 1.3 cal ka BP suggests that robust terrestrial and marine ecosystems were established soon after deglaciation. Because modern ringed seals inhabit areas with seasonal sea ice, the occurrence of ringed seal bones in Shuká Káa indicates that southeastern Alaska had at least seasonal sea ice after CIS deglaciation.

No additional ringed seals appear after 15.5 ± 0.4 cal ka BP, perhaps related to increasing sea surface temperatures (36) and declining sea ice concentrations. Rising ocean temperatures in the North Pacific between ~17 and 14 ka ago may have further increased the favorability of coastal regions by allowing productive kelp forests to expand (20), and a study of postglacial vegetation on nearby Haida Gwaii suggests that the region supported abundant plant resources that could have been used by humans migrating south along the coast (35).

Records from several other locales along the hypothesized coastal migration route suggest that a deglaciated Pacific coastal corridor may have developed by 16 ka ago. On the southern side of Dixon Entrance (Fig. 2), near Haida Gwaii, the maximum extent of the CIS and local glaciers occurred between ~19 and 17 ka ago (26, 37). Farther north, in the western Gulf of Alaska, radiocarbon-dated lake sediments record deglaciation just before 17 ka ago (22). Paleotemperature proxies in marine sediment cores show warming in the northeastern Pacific Ocean beginning as late as 17 ka ago and persisting until 14 ka ago (Fig. 3) (36, 38). This warming is coincident with increases in icerafted debris in marine sediment cores off southern Alaska and British Columbia (Fig. 3) (24, 39), indicating calving and retreat of two major marine-terminating CIS margins. Our new ¹⁰Be ages from southeastern Alaska's outer coast corroborate these inferences from elsewhere along the Pacific coast, suggesting that a coastal migration route into the Americas may have been available by 16 ka ago. However, additional direct chronologies of CIS expansion and retreat are needed at the regional to subcontinental scale to assess the extent and interconnectedness of deglaciated terrain during the latest Pleistocene.

The multiproxy data set presented here provides constraints on the maximum latest Pleistocene extent of the CIS in a bottleneck region of the Pacific coastal corridor, and our results highlight the importance of generating direct records of ice margin change along the hypothesized coastal migration route. We demonstrate that currently exposed land surfaces on Dall, Suemez, and Warren islands were glaciated between ~20 and 17 ka ago and therefore did not serve as refugia during the LGM. However, deglaciation of these islands after 17 ka ago ensured that an open, productive corridor through the southern Alexander Archipelago was available for human coastal migration. This corridor may have been connected to other recently deglaciated landscapes elsewhere along the northeastern Pacific coast. Although evaluating hypotheses about the peopling of the Americas ultimately requires archeological evidence of human occupation along potential migration routes, our results support the hypothesis that the Pacific coastal corridor was a viable pathway for the initial colonization.

MATERIALS AND METHODS

Regional setting

Located in coastal southeastern Alaska, the Alexander Archipelago is composed of more than 1100 islands, including 7 of the largest 10 in the United States (Fig. 2). Several of these islands host peaks that exceed 1000 meters in elevation and support local snowfields and glaciers. The peaks are surrounded by low foothills and a broad, shallow continental shelf. Wide, deep glacial troughs separate many of the islands. The climate of southeastern Alaska is characterized by cool summers and mild winters, with heavy precipitation for much of the year.

The bedrock geology of southeastern Alaska consists of a complex assemblage of sedimentary, igneous, and metamorphic rocks that range in age from Precambrian to Jurassic (40). The outer islands of

southeastern Alaska, where we focused our ¹⁰Be sampling, host felsic (that is, quartz-rich) Paleozoic and Mesozoic plutons. Southeastern Alaska is also home to vast karst regions, which form extensive, fossil-rich cave systems.

During the LGM, outlet glaciers on the marine margin of the CIS flowed through fjords, carving troughs up to 650 m in depth (26). These outlet glaciers merged with local glaciers in peripheral islands of southeastern Alaska and Haida Gwaii, flowing westward and covering large portions of the continental shelf (6). Radiocarbondated marine sediments showed that the CIS reached its maximum extent in southeastern Alaska sometime after 25 ka ago (26, 34). Deglaciation of the continental shelf began sometime after 19 ka ago in British Columbia (27), and CIS retreat in southeastern Alaska may have also begun around that time. Minimum-limiting ages from marine sediments suggest that marine-terminating CIS margins had retreated to near their modern positions by 16 ka ago (26, 28, 34, 35). Cosmogenic ¹⁰Be ages from interior British Columbia and model simulations suggest substantial loss of land-based ice between ~14.5 and 14 ka ago (41), and widespread glacier readvances occurred during the Younger Dryas cold interval (41) and the Holocene (42).

¹⁰Be sample collection

On the basis of analyses of air photographs, examination of bathymetric data, and identification of glacial features, Carrara et al. (30) identified eight areas of southeastern Alaska that may have been ice-free refugia during the LGM, including currently exposed islands and portions of the continental shelf (Fig. 2, main text). Although the Carrara et al. (30) map has been adopted by other glacier reconstruction compilations (43), its accuracy has not been assessed by directly dating surfaces in the hypothesized refugia. To test whether these areas did remain icefree during the LGM, we ¹⁰Be-dated five perched boulders and five bedrock samples from three proposed refugia: Dall Island, Suemez Island, and Warren Island (Fig. 2 and fig. S2). Boulders on Suemez and Warren islands were perched on or near glacially scoured bedrock surfaces. These surfaces exhibited erosional features (for example, rôche moutonnées, striations, and chatter marks) that were oriented in the direction of regional ice flow (340° at Suemez Island). Bedrock on Dall Island was subangular and did not have any obvious signs of glacial erosion in the field. To constrain the timing of deglaciation of local valley glaciers in the peripheral islands, we dated three perched boulders and one bedrock surface within a cirque on Baker Island.

All ¹⁰Be samples were collected from the upper several centimeters of rock surfaces using a rock saw, hammer, and chisel. We sampled the flat upper surfaces of boulders, avoiding the edges. A clinometer was used to measure topographic shielding, and a handheld Global Positioning System receiver with an approximate vertical uncertainty of 5 m was used to record the sample coordinates and elevations. Sample elevations ranged from 181 to 590 m asl.

Quartz isolation and accelerator mass spectrometry

Samples underwent physical and chemical preparation at the University at Buffalo Cosmogenic Isotope Laboratory using well-established protocols (44, 45). Samples were processed in batches of 12 (including one process blank) and spiked with ~199 to 228 μg of $^9 Be$ prepared from phenakite mineral (GFZ German Research Centre for Geosciences "Phenakite" standard; $^9 Be$ concentration of 372.5 \pm 3.5 ppm; table S1). Accelerator mass spectrometry (AMS) for all samples was completed at the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory. Sample ratios were measured with respect to the

07KNSTD3110 standard, which has an assumed 10 Be/ 9 Be ratio of 2.85×10^{-12} (46). Sample ratios were corrected using batch-specific blank values, which ranged from 1.11×10^{-15} to 2.46×10^{-15} (n = 4). AMS analytical uncertainty ranged from 1.1 to 3.7%, with an average of 2.1%.

¹⁰Be exposure age calculations and assumptions

All ¹⁰Be exposure ages (fig. S2 and table S1) were calculated with the online CRONUS-Earth exposure age calculator version 3 (http://hess.ess.washington.edu/math/index_dev.html) (47) using the regionally calibrated Baffin Bay/Arctic ¹⁰Be production rate (48) and the Lal/Stone time-varying scaling scheme (49, 50). This production rate is used to calculate exposure ages in British Columbia (51) and is similar to independently-derived ¹⁰Be production rates from other regions (52, 53). Ages calculated using alternative production rates and scaling schemes are reported in table S2.

Crustal uplift or subsidence alters the thickness of the atmosphere above a rock surface, resulting in a time-varying ¹⁰Be production rate. To account for this effect, sample elevations can be corrected with a time-averaged uplift value calculated using well-constrained regional emergence curves. However, no chronological constraints on relative sea level exist for southeastern Alaska in the early deglacial period (21). Thus, although the outer islands of southeastern Alaska likely experienced elevation changes during the latest Pleistocene and Holocene, we reported ¹⁰Be exposure ages without elevation corrections.

We made no corrections for snow shielding or erosion. Samples were collected from windswept topographic highs, and we found no correlation between boulder height and 10 Be age, suggesting that the boulders did not experience significant snow cover. Modern (1949-2016) snowfall measurements for weather stations in coastal communities indicated very little accumulated snowfall during the winter months—on average, less than 5 cm across the region (https://wrcc. dri.edu/summary/Climsmak.html). Our sampling sites may have received more snowfall than the coastal weather stations referenced above. It is also likely that our high elevation sampling sites at Dall and Suemez islands experienced more significant snowfall than the lower elevation sites at Baker and Warren islands. However, because of a lack of snowfall data for these areas, we did not attempt to correct our ¹⁰Be ages for any potential snow shielding. We observed pristine glacially scoured surfaces on Suemez Island, suggesting minimal surface erosion since deglaciation. We therefore assumed erosion to be negligible for our exposure age calculations.

Another factor that may influence our 10 Be chronology is muongenerated (muogenic) 10 Be production at depth. Briner *et al.* (*54*) found that erratic boulders in a similar ice sheet distal setting yielded exposure ages that were ~10% too old due to inherited muogenic 10 Be. Our study area lies along the peripheral margins of the CIS, so it is possible that our boulder ages are similarly influenced by minor amounts of inherited muogenic 10 Be. However, the agreement between the timing of deglaciation derived from 10 Be dating (17.0 \pm 0.7 ka ago) and the first postglacial appearance of fossils in Shuká Káa (17.2 \pm 1.3 cal ka BP) suggested that our boulder ages may not be significantly affected by inherited muogenic 10 Be.

We note here that there is some uncertainty concerning the impact of persistently high modern concentrations of atmospheric water vapor on in situ ¹⁰Be production in southeastern Alaska. Because water vapor has a lower density than air, local in situ ¹⁰Be production rates have the potential to be systematically underestimated, resulting in younger "true" exposure ages than are reported here. Yet, paleoclimatic

reconstructions (55, 56) for the early Holocene suggested that the North Pacific coast was warmer and drier relative to modern conditions. Without precise, quantitative estimates of atmospheric water vapor concentrations through time, we believed that attempting to correct our ages for this uncertainty was premature. Conducting a local ¹⁰Be production rate calibration study (48) could help address this issue and would also improve the accuracy and precision of future ¹⁰Be dating studies in the region.

¹⁴C calibration

We calibrated 177 previously published fossilized mammal and bird bone ¹⁴C ages from 15 different caves in the Alexander Archipelago (figs. S1 and S4). See review by Heaton and Grady (29) for further details on bone collection, identification, cave locations and taphonomies, and ¹⁴C dating methodology. We note here that the bone collagen used for ¹⁴C dating was not treated using ultrafiltration methods (57), and the collagen may have therefore been contaminated by humic and fulvic acids. These compounds are abundant in southeastern Alaskan soils (58) and can bind with degrading bone collagen fragments (59), resulting in ¹⁴C age determinations that are erroneously young (60). In the future, redating a subsample of the overall bone collection using modern ultrafiltration methods to remove potential humic and fulvic acid contaminants (57, 59) will be a priority. These ages were originally reported in ¹⁴C years due to (i) a lack of control on the local marine reservoir correction and (ii) uncertainties regarding the percentage of marine carbon in the bones. Since the ¹⁴C ages from the Alexander Archipelago were published, the marine reservoir effect was better constrained for southeastern Alaska during the Pleistocene and Holocene (61, 62), and our understanding of carbon isotope fractionation in bone collagen relative to diet was also improved (63). Taking advantage of these new developments, we calibrated the fossil ¹⁴C ages to constrain the timing of maximum CIS extent in southeastern Alaska.

Ages were calibrated using CALIB version 7.0.4 by correcting for the marine reservoir effect and the varying amounts of marine carbon in the bones, which is influenced by the organism's diet (64). We applied a marine reservoir correction of 732 years ($\Delta R = 332$) for Pleistocene samples (61) and 600 years ($\Delta R = 200$ years) for Holocene samples (62). These marine reservoir corrections were originally reported without error estimates. To account for the uncertainty associated with marine reservoir correction calculations, we calibrated our ages using ΔR uncertainties of 130 years for Holocene samples and 60 years for Pleistocene samples, which were selected on the basis of the uncertainties of the ¹⁴C ages that were used to calculate the marine reservoir age in the above studies. The estimated percentage of marine carbon was determined using a simple mixing model of the cave bone δ^{13} C values (fig. S5 and table S3) (29). For bone δ^{13} C values lower than −18 per mil (‰), we assumed a 0% contribution of marine carbon (that is, the organism's diet was completely terrestrial). For δ^{13} C values between -18 and -15‰, we assumed a 50% contribution of marine carbon. For δ^{13} C values higher than -15%, we assumed a 100% contribution of marine carbon. Cutoffs for each diet type were empirically determined by examining the modern diets of each species and choosing a dividing line between the diet types where most species within a given type ate a similar diet to their modern counterparts. Under this scheme, certain individuals in the cave fossil record appeared to have atypical diets (for example, a black bear consuming a 100% marine diet). However, on the whole, this system enabled us to quickly estimate the percentage of marine carbon in each sample (table S3).

Calibrated ¹⁴C ages are reported in table S3 as the mean value of the entire calibrated age range at 2 SD, and the uncertainty for each age is represented as one-half of the entire calibrated age range. For some samples, particularly in later parts of the record where the ¹⁴C calibration curve was highly variable, calibration resulted in multiple solutions for a single ¹⁴C age. In this case, we also reported the calibrated age as the mean value of the entire range of possible ages, which resulted in relatively large uncertainties for these calibrated ages.

To assess the sensitivity of our calibration to the applied marine reservoir corrections and the calculated marine carbon percentage outlined above, we calibrated the ¹⁴C ages under several schemes (fig. S6). First, we calibrated the ¹⁴C ages with no additional reservoir correction (that is, using the CALIB default of R = 400 years; $\Delta R =$ 0 years) but with variations in marine carbon percentage derived from our δ^{13} C mixing model (fig. S6A). Next, we calibrated the 14 C ages with the additional reservoir correction ($\Delta R = 332$ years for Pleistocene samples; $\Delta R = 200$ years for Holocene samples) but no variations in marine carbon percentage (fig. S6B). In this scenario, cave bones with δ^{13} C values higher than -18% were assumed to have a 100% contribution of marine carbon, and cave bones with δ^{13} C values lower than -18‰ were assumed to have a 0% contribution of marine carbon. We then calibrated the ¹⁴C ages with no additional corrections (fig. S6C). In this case, $\Delta R = 0$ years for all marine samples. In addition, as in the previous calibration, no variations in marine carbon percentage were applied; cave bones were assumed to have either 100 or 0% contribution of marine carbon. Finally, we completed the same three exercises using a total marine reservoir correction of 1110 ± 107 years (65), resulting in a hiatus from 19.37 ± 0.60 to 17.01 ± 1.12 cal ka BP.

Overall, these alterations produced minor changes in the calibrated age distribution, but the gap in fossilized cave bone ages from approximately 20 to 17 ka ago appeared in each scenario (fig. S6). Although the precise timing of the hiatus shifted by a few hundred years depending on the calibration scheme and the marine reservoir correction applied, its persistence suggested that it was a robust feature in the record and not merely an artifact of our ¹⁴C calibration. We argued then that the hiatus in fossilized cave bone ages from ~20 to 17 ka ago reflected CIS cover of northern Prince of Wales Island. We also observed a general trend toward marine-based diets before and shortly after the hiatus in fossil deposition (fig. S7), suggesting that the presence of the CIS in the region altered resource availability.

Sample AA-36661, the P. hispida bone that constrains the younger end of the hiatus to 17.15 ± 1.23 cal ka BP, warrants further discussion. We acknowledged that the 95% confidence interval for the calibrated age of this sample was relatively large. This was due to the calibration process itself. For the portion of the ¹⁴C calibration curve around 14.5 ¹⁴C ka BP, the ratio between ¹⁴C years and calendar years is less than 1:1, resulting in an increased calibrated age uncertainty relative to that of the uncalibrated age. The assignment of a "mixed" diet to this organism also plays a role in determining its age in calendar years. If we ignored the δ^{13} C value for AA-36661 and instead calibrated the age assuming a 100% marine diet (which is a reasonable assumption for a ringed seal), we calculated a slightly younger age of 16.62 \pm 1.29 cal ka BP (fig. S6). Overall, the calibrated age of this particular sample was given some weight in that we argued that the coherency between our ¹⁰Be and ¹⁴C data sets suggested that the hiatus in fossilized cave bone ages likely reflected CIS cover of northern Prince of Wales Island (see Discussion). However, we did not derive the timing of regional CIS retreat from this fossil; we instead constrained CIS retreat with our ¹⁰Be ages because they were direct indicators of deglaciation. If we

were to use only the fossilized cave bone ¹⁴C ages to estimate the timing of CIS retreat, the inference of a mixed diet for sample AA-36661 and the large uncertainty of its calibrated age would be of greater concern.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/4/5/eaar5040/DC1

- fig. S1. Map of southeastern Alaska with labeled islands.
- fig. S2. Representative boulder and bedrock samples collected for ¹⁰Be dating.
- fig. S3. Normal kernel density estimates of ¹⁰Be ages.
- fig. S4. Fossilized mammal bone ¹⁴C ages from caves in southeastern Alaska.
- fig. S5. Box-and-whisker plot of fossilized cave bone $\delta^{13}\text{C}$ values from Prince of Wales Island.
- fig. S6. Sensitivity testing of the fossilized cave bone ¹⁴C age calibration.
- fig. S7. Fossilized cave bone δ^{13} C values and marine carbon percentages through time. table S1. 10 Be sample information.
- table S2. $^{10}\mbox{Be}$ ages calculated with alternative production rates and scaling schemes.
- table S3. Fossilized cave bone sample information used for ¹⁴C calibration. Reference (*66*)

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Acknowledgments: We thank A. D. Schweinsberg and C. Sbarra for the assistance with sample preparation and S. Zimmerman for the ¹⁰Be measurements at Lawrence Livermore National Laboratory's Center for Accelerator Mass Spectrometry, We thank L. Corbett and three anonymous reviewers for providing thoughtful comments that improved the manuscript. Funding: J.P.B. and C.L. acknowledge support from the University at Buffalo Innovative Micro-Programs Accelerating Collaboration in Themes Program, C.L. also acknowledges funding from the NSF (Division of Environmental Biology award #1556565). T.H.H. acknowledges support from the National Geographic Society and the National Speleological Society. Additional support was provided by the U.S. Forest Service and a Geological Society of America Graduate Student Research Grant to A.J.L. Author contributions: A.J.L. and J.P.B. designed the overall study and conducted the exposure dating and radiocarbon calibration. J.F.B. assisted with the field sampling and interpretation, C.L. and T.H.H. provided the radiocarbon data and fossil identifications and helped interpret the cave bone data set. A.J.L. wrote the first draft of the manuscript, and all authors contributed to interpretations and revisions. Competing interests: The authors declare that they have no competing interests. Data and materials availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 15 November 2017 Accepted 18 April 2018 Published 30 May 2018 10.1126/sciadv.aar5040

Citation: A. J. Lesnek, J. P. Briner, C. Lindqvist, J. F. Baichtal, T. H. Heaton, Deglaciation of the Pacific coastal corridor directly preceded the human colonization of the Americas. Sci. Adv. 4, eaar5040 (2018).



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Sci Adv 4 (5), eaar5040. DOI: 10.1126/sciadv.aar5040

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