

# LICHENOMETRIC DATING OF LITTLE ICE AGE GLACIER MORAINES USING EXPLICIT DEMOGRAPHIC MODELS OF LICHEN COLONIZATION, GROWTH, AND SURVIVAL

MICHAEL G. LOSO<sup>1</sup>, DANIEL F. DOAK<sup>2</sup> and ROBERT S. ANDERSON<sup>3</sup>

<sup>1</sup>Department of Environmental Science, Alaska Pacific University, Anchorage, Alaska, USA

<sup>2</sup>Environmental Studies Program, University of Colorado, Boulder, Colorado, USA

<sup>3</sup>Department of Geological Sciences and INSTAAR, University of Colorado, Boulder, Colorado, USA

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**ABSTRACT.** Contemporary variants of the lichenometric dating technique depend upon statistical correlations between surface age and maximum lichen sizes, rather than an understanding of lichen biology. To date three terminal moraines of an Alaskan glacier, we used a new lichenometric technique in which surfaces are dated by comparing lichen population distributions with the predictions of ecological demography models with explicit rules for the biological processes that govern lichen populations: colonization, growth, and survival. These rules were inferred from size–frequency distributions of lichens on calibration surfaces, but could be taken directly from biological studies. Working with two lichen taxa, we used multinomial-based likelihood functions to compare model predictions with measured lichen populations, using only the thalli in the largest 25% of the size distribution. Joint likelihoods that combine the results of both species estimated moraine ages of AD 1938, 1917, and 1816. Ages predicted by *Rhizocarpon* alone were older than those of *P. pubescens*. Predicted ages are geologically plausible, and reveal glacier terminus retreat after a Little Ice Age maximum advance around AD 1816, with accelerated retreat starting in the early to mid twentieth century. Importantly, our technique permits calculation of prediction and model uncertainty. We attribute large confidence intervals for some dates to the use of the biologically variable *Rhizocarpon* subgenus, small sample sizes, and high inferred lichen mortality. We also suggest the need for improvement in demographic models. A primary advantage of our technique is that a process-based approach to lichenometry will allow direct incorporation of ongoing advances in lichen biology.

**Key words:** lichenometry, lichen biology, *Pseudophebe pubescens*, *Rhizocarpon* subgenus, Alaska

## Introduction

Lichenometry is a surface-dating technique in which measurements of lichen diameters are

employed to date landforms (Noller and Locke 2000), some of which are undatable by any other means. Of particular importance for glaciologists and climate scientists, lichenometry is used to date Late Holocene fluctuations in glacier terminus position that are too recent for accurate radiocarbon dating (Matthews 1994). Driven in part by intense contemporary interest in climate variability, much effort has been invested to improve the accuracy and precision of lichenometric dates.

Based on the assumption that the largest lichen was the first to colonize a given surface, early lichenometrists advocated measurement of a single “largest lichen” from each surface to minimize the unknown time lag between landform creation and lichen colonization (Beschel 1961). Many investigators remain focused upon the use of the largest thalli as their metric, but now use non-parametric statistics to analyze measurements of hundreds or even thousands of largest lichens from small sampling units (Matthews 1974; Innes 1985; McCarroll 1994; Bull and Brandon 1998; Jomelli *et al.* 2007; Orwin *et al.* 2008). Other investigators have broadened their sampling to include full lichen populations, typically using the shape of the resulting size–frequency distributions as the statistical basis for dating landforms (Benedict 1967; Caseldine and Baker 1998; Bradwell 2004). Details of these approaches vary, but there is a clear trend towards larger sample sizes that facilitate calculation of confidence intervals.

Other research has focused on better understanding the lichens themselves. The slow-growing crustose lichens used most often in lichenometry are difficult to study ecologically, but lichenometrists are nonetheless paying more attention to the biological processes that underlie lichenometric dating (Armstrong 2011). The greatest emphasis

has understandably been placed on lichen growth rates, focusing especially on direct observation and measurement of thallus growth (Armstrong and Bradwell 2010). Nonetheless, Trenbith and Matthews (2010) recently noted that most lichenometric studies have paid little attention to such progress, and instead continue to base their dates on calibration curves derived empirically from measurements of largest lichens on independently dated surfaces.

Many lichenometrists persist in interpreting these calibration curves as simple time integrals of growth rate, but they are not. Lichenometric calibration curves commonly show largest-lichen sizes increasing rapidly with age on young surfaces, and increasing more slowly on older surfaces (e.g. Denton and Karlén 1973; Innes 1985; Bull and Brandon 1998; Wiles *et al.* 2010). The common inference that this indicates rapid “great growth” of young lichen thalli, followed by a period of slower-growing senescence, is supported by neither direct observations of lichen growth (e.g. Proctor 1977; Clark *et al.* 2000; Clayden *et al.* 2004; Bradwell and Armstrong 2007; Trenbith and Matthews 2010; Roof and Werner 2011) nor by theory (Childress and Keller 1980; Hill 1981) that suggests young thalli should grow slowly with radial growth rates increasing asymptotically with thallus size. Although the true nature of crustose lichen growth is surely both variable and complex (Armstrong 2011), it is clear that the sizes of the largest lichens in a population, and especially the probabilities of finding them, are functions not only of the pattern and variability of individual growth rates, but also of colonization and survival rates (Clayden *et al.* 2004; Loso and Doak 2005). The well known contradiction between directly measured growth rates and those inferred from calibration curves reflects the persistent need for a lichenometric dating technique that builds upon, rather than contradicts, our growing understanding of the biological processes that govern lichen population dynamics.

Here, we introduce a lichenometric technique that relates lichen sizes to surface ages through explicitly quantified biological processes. We have previously shown how maximum-likelihood techniques can be used in conjunction with lichen size distributions to quantify demographic rates (colonization, growth, and survival) of two lichen types commonly used for lichenometry (Loso and Doak 2005). In this paper, we apply the derived rates to the calculation of surface ages for *Little Ice Age*

(LIA) terminal moraines of a small Alaskan glacier. The resulting dates are presented with confidence intervals that reflect both sampling uncertainty and model uncertainty, allowing us to assess the confidence of our age estimates. In addition to presenting the basic protocols of this new methodology, we also examine our methods and results to suggest improvements to this first application of the technique. We present our approach in three parts:

- (1) Data collection: describes how and where we collected measurements of lichens on a variety of independently dated surfaces (“calibration surfaces”) and undated surfaces (“dating surfaces”).
- (2) Model calibration: presents our measured *size–frequency distributions* (SFDs) and lichen densities from both the calibration and dating surfaces, and then briefly reviews the demographic models that were previously fit to the calibration surface data.
- (3) Dating surfaces of unknown age: describes in detail the methods for deriving surface ages and confidence intervals from our demographic models, and then presents the results of those analyses.

## Data collection

In the summers of 2002 and 2003, we measured lichens growing between 900 and 1000 m elevation around Chisma Glacier and proglacial Iceberg Lake (both are informal names) in the eastern Chugach Mountains of Alaska (Fig. 1). Mean annual air temperature at Tana Knob, a nearby weather station, is  $-2^{\circ}\text{C}$ , with an average daily high of  $12^{\circ}\text{C}$  in July and an average daily low of  $-16^{\circ}\text{C}$  in January (Western Regional Climate Center, <http://www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?akatan>, 20-Jun-13). Calibration surfaces included four concentric rings around glacier-dammed Iceberg Lake, each bounded by conspicuous strandlines that demonstrate a history of episodic shoreline retreat in response to post-LIA shrinkage of the glacier dam. Dates of these shoreline regression events were previously established by varve counting of the sediments in the lake basin (Loso *et al.* 2004). Population size distributions from these well dated surfaces, which range in age from 45 to 177 years, allowed us to fit demographic models of lichen population development (Loso and Doak 2005).

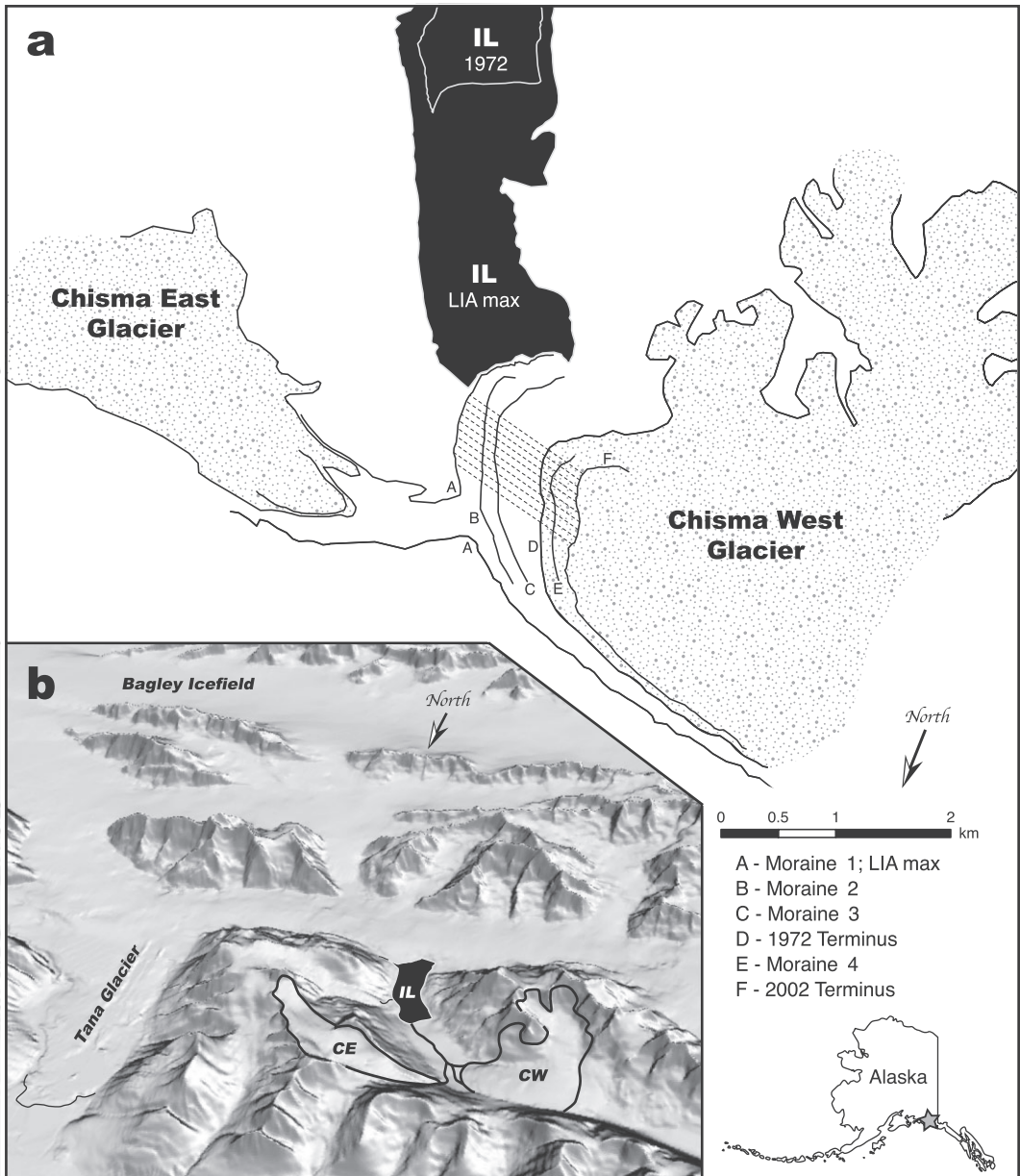


Fig. 1. Study area and location (star on inset map of Alaska). Chisma Glaciers and associated terminus positions (a) are shown in oblique aerial view for landscape context in inset (b). Note that, for clarity, north is to the lower left and the lake is black on both maps. The oldest and most extensive glacier advance, shown by terminus position A ('moraine 1'), demonstrates that the Chisma West ('CW') and Chisma East ('CE') Glaciers were connected at the height of the Little Ice Age, and terminated at a strandline that marks the LIA-maximum highstand of Iceberg Lake (IL). Subsequent glacier retreat history is marked by terminus positions B–F. Positions E and F are inboard of the mapped glacier boundaries because these outlines and the smaller shoreline of Iceberg Lake are from AD 1972 aerial photos. The larger, LIA maximum shoreline is from Loso *et al.* (2004). Unbounded portions of the glacier outlines are ice divides where contiguous ice flows in a different direction. Glacier terminus retreat was measured along 10 transects shown by parallel dotted lines in (a).

Dating surfaces included four conspicuous moraine loops identified and mapped around the retreating terminus of Chisma Glacier (Fig. 1). These moraine loops, along with two terminus positions whose occupation dates were obtained from published topographic maps (position D) and field mapping (position F), collectively provided six snapshots of LIA retreat of the Chisma Glacier margin. Terminus positions D and F are not associated with clearly distinguishable terminal moraines. The objective of this case study is to provide abandonment ages for the other four terminus positions, moraines 1–4, using our new lichenometric technique.

At all sites, we measured lichens of two types, the *Rhizocarpon* subgenus and *Pseudophebe pubescens*. The *Rhizocarpon* subgenus (*Rhizocarpon* Ram. em. Th. Fr. subgenus *Rhizocarpon*; Benedict 1988) includes several species of closely related, yellow-green, slow growing, long-lived, and widely distributed crustose saxicolous lichens that are broadly used for lichenometric dating. We used all individuals within the subgenus (hereafter *Rhizocarpon*) because we were unable to definitively identify species, especially of the smallest thalli, in the field; it is possible that our study aggregated data from two or more species. *Pseudophebe pubescens* (L.) Choisy is a black, fast-growing, shorter-lived and widely distributed prostrate fruticose saxicolous lichen. We used the more rounded branches of *P. pubescens* to distinguish it from *Pseudophebe miniscula*, a related species that is rare at our study site but has been used for lichenometry (under the synonym *Alectoria*) elsewhere (Miller 1973; Davis 1985; Haworth and Calkin 1986). We added *P. pubescens* to the study for two reasons. First, it grows around three times faster than *Rhizocarpon*, giving potentially greater dating resolution over the relatively short timescales (<250 years) considered in this project. Second, a second species provided us with independent lichenometric dates, an approach advocated previously by other lichenometrists (e.g. Orombelli and Porter 1983; Winchester 1984).

We examined lichen thalli growing on boulders (defined here as any rock with a major axis >15 cm embedded in an apparently stable substrate) and bedrock outcrops. We did not stratify the samples by lithology; most rock in the study area is gneiss, with some metaquartzite and phyllite (Pavlis and Sisson 1995). At all sites, we minimized microsite variability by sampling lichens only on unshaded, upwards-facing rock surfaces with slopes less than 20°. We

attempted to sample all such rocks accessible on each dating surface. To quantify lichen density and cover, we approximated the area of each sampling unit by measuring the major and minor axes of the irregular polygon enclosing each population. We used automatically downloading Mitutoyo digital calipers to measure lichens across their major axes (largest diameters) to the nearest 0.1 mm. Bull and Brandon (1998) have shown this technique to be very precise, with a standard deviation of single lichen diameter measurements of 0.47 mm: less than 3 yrs of growth for either species (Loso and Doak 2005). We excluded lichens <1 mm diameter (these were very common), lichens growing in contact with other lichens of the same species (uncommon due to low overall lichen densities on these young surfaces), and lichens with a major axis greater than twice the length of their minor axis (rare in the >1 mm size classes). Interspecific lichen competition may have affected demographic rates of lichen thalli in contact with other species, but such cases were also very rare. Lichens with internal thallus erosion (common in *P. pubescens*) were included if a majority of the outer thallus ring was clearly distinguishable.

For analysis and modeling, we binned *Rhizocarpon* data in 2 mm size classes and *P. pubescens* data in 4 mm size classes. We normalized all lichens measured in 2003 to a standard reference year (AD 2002) by subtracting the maximum growth rate (from Loso and Doak 2005) from their measured diameters, and then calculated model ages as years prior to 2002. In all populations of both species, we found unexpectedly few individual lichens in the smallest size class. We attribute this rarity to both the difficulty of seeing extremely small thalli and the cryptic, morphologically diverse nature of young thalli (especially *Rhizocarpon*; Asta and Letrouit-Galinou 1995; Clayden 1998). Thus, although our demographic model adds new colonists as “infants” with a diameter of 0.1 mm, we excluded the smallest size class (0–2 mm for *Rhizocarpon* and 0–4 mm for *P. pubescens*) when fitting models to the data. Following Calkin and Ellis (1980), we also excluded from the final dataset 15 anomalous individuals that were over 20% larger than the next largest thallus in their respective populations. These were likely inherited from older surfaces; three of the 15 grew on the same boulder in a steep gully near the lake, and eight grew on the only large boulders remaining where Chisma Glacier’s terminal moraine was breached by a proglacial stream.

### Model calibration

Traditional lichenometric calibration curves predict the sizes of largest lichens on different aged surfaces. In comparison, our approach uses measurements of SFDs to calibrate demographic models with explicit rules for lichen colonization, growth, and survival. The best fitting model can then be used to predict the SFD of an entire population at any given surface age. Details of the model fitting process, including model structure, functional forms tested, likelihood scores, and the use of *Akaike information criterion* (AIC) weights (Burnham and Anderson 2002) to judge support for model structures of increasing complexity, are presented in Loso and Doak (2005). Here, we use the results of that analysis to present and understand the general patterns observed in our lichen populations before turning our attention to the focus of this paper: using the derived demographic model to date glacier moraines.

In total, we measured over 12,000 individual lichen thalli near Chisma Glacier and Iceberg Lake (Table 1). Nearly 5000 of these were measured on calibration surfaces, the independently dated shorelines (Loso *et al.* 2004), with the remainder constituting our primary dataset for dating terminal moraines around Chisma Glacier. On young surfaces, thallus density was low and fairly similar for the two species, but *P. pubescens* were generally two to three times more common than *Rhizocarpon* on older moraines and shore-

lines (Table 1). For both species, densities were very low on the youngest surfaces, and we found no lichens of either species on moraine 4 (terminus position E, Fig. 1). Based on aerial photos, moraine 4 was deposited sometime after AD 1972. At the maximum densities achieved on the oldest surfaces, 50 thalli m<sup>-2</sup> for *P. pubescens* and 16 thalli m<sup>-2</sup> for *Rhizocarpon*, there was still very little obvious intraspecific competition. Thallus contact never required us to exclude more than 1% of observed lichens.

The distributions of lichens from the four shorelines and moraines 1–3 are shown in Fig. 2. All the SFDs, from both species and at all ages, exhibit a consistent shape. Small lichens (<16 mm diameter for *P. pubescens*; <7 mm for *Rhizocarpon*) were most common while large lichens were rare. Older surfaces were distinguished primarily by increasing positive skewness that resulted from small numbers of increasingly large lichens. The largest *P. pubescens* found had a diameter of 121.8 mm, and the largest *Rhizocarpon* was 37.8 mm. The shapes of these distributions are consistent with those found by other investigators who have collected full-population distributions (Locke *et al.* 1979; Innes 1983; Hestmark *et al.* 2004; Mercier 2004). Our best-fit demographic models (Table 2) present strong support for the argument, first made by Farrar (1974), that the approximately log-normal SFDs demonstrate the importance of regular and ongoing thallus mortality. His interpre-

Table 1. Numbers and densities of lichens measured on calibration surfaces (shorelines, shown with ages in years AD) and dating surfaces (moraines) near Chisma Glacier, AK.

Surface	Boulders (n)	Area (m <sup>2</sup> )	Species	Thalli (n)	Density (n m <sup>-2</sup> )	Cover (cm <sup>2</sup> m <sup>-2</sup> )
Shoreline 1 (1957)	146	151	<i>Rhizocarpon</i>	185	1.2	0.1
			<i>P. pubescens</i>	269	1.8	2.3
Shoreline 2 (1867)	63	48	<i>Rhizocarpon</i>	703	14.6	3.9
			<i>P. pubescens</i>	891	18.5	76.4
Shoreline 3 (1834)	40	22	<i>Rhizocarpon</i>	348	15.8	8.6
			<i>P. pubescens</i>	1100	50.0	248.7
Shoreline 4 (1825)	40	29	<i>Rhizocarpon</i>	439	15.1	8.8
			<i>P. pubescens</i>	1059	36.5	253.8
Moraine 1	157	117	<i>Rhizocarpon</i>	1667	14.3	10.7
			<i>P. pubescens</i>	4272	36.6	208.8
Moraine 2	67	56	<i>Rhizocarpon</i>	477	8.6	3.2
			<i>P. pubescens</i>	438	7.9	33.3
Moraine 3	32	44	<i>Rhizocarpon</i>	148	3.4	0.6
			<i>P. pubescens</i>	107	2.5	4.1
Moraine 4	>50	>50	<i>Rhizocarpon</i>	0	0.0	0.0
			<i>P. pubescens</i>	0	0.0	0.0



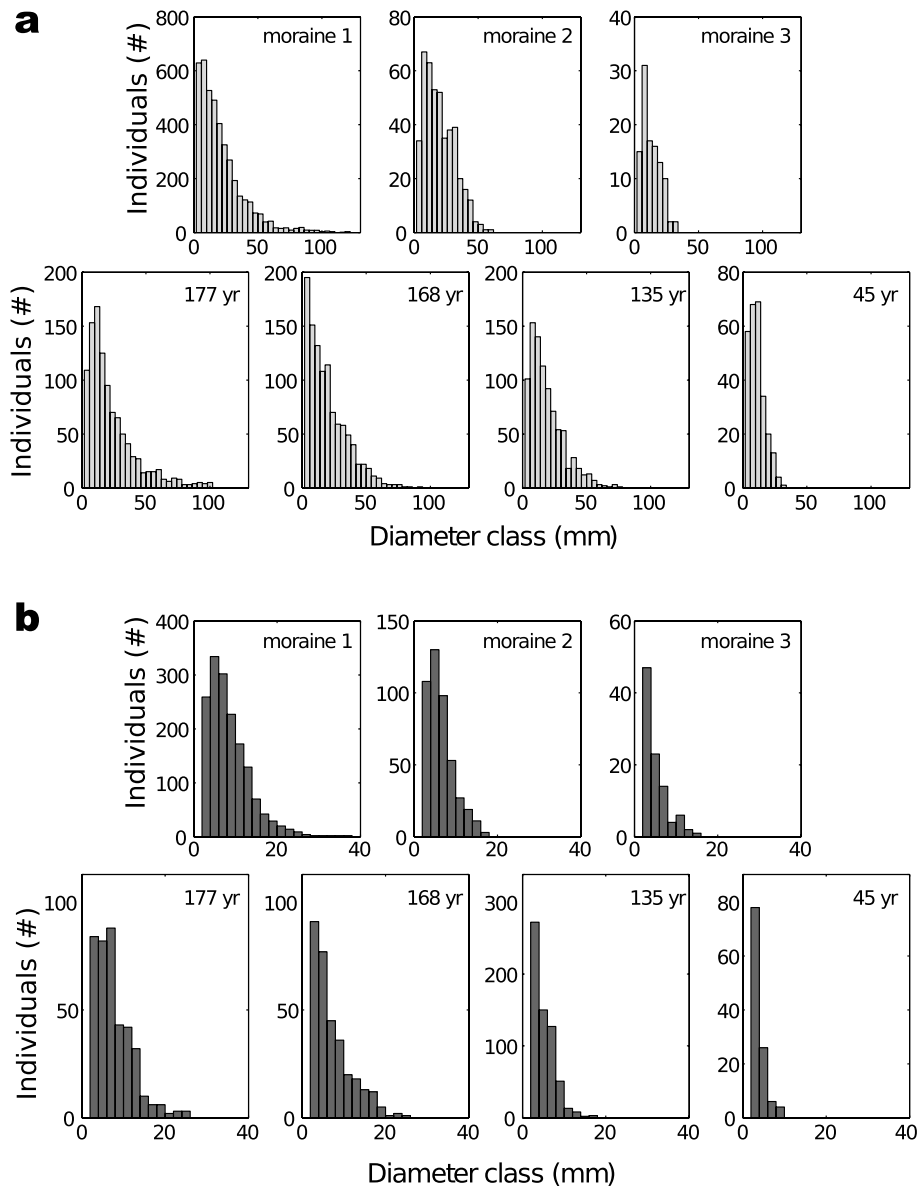


Fig. 2. Size–frequency distributions of lichens growing near Chisma Glacier. For *P. pubescens* (a) and *Rhizocarpon* (b), each set of seven panels shows distributions measured on three undated terminal moraines (above) and four independently dated shorelines (below). Each lichen thallus was measured across its major axis, and these measurements are binned in 4 mm (for *P. pubescens*) and 2 mm (for *Rhizocarpon*) size classes. Thalli in the smallest size class were difficult to locate and are not shown.

tation was debated by Innes (1983), who argued that the predominance of small lichens on successively older surfaces was evidence for a continuing exponential increase in colonization rate. Upon casual inspection of the data (Fig. 2), either explanation seems plausible, but lichen density either

increased slowly or even decreased for times greater than 135 years (Table 1). Constrained by both the SFDs and lichen densities, our maximum-likelihood models – which are based only on lichen SFDs from the calibration surfaces – provide strong support for steady and significant mortality

Table 2. Structures and best-fit parameters of the demographic models used in this paper, where  $a_1$ – $a_6$  are fitted parameters,  $n$  is population size, and  $d$  is thallus diameter (mm).

Structure	<i>P. pubescens</i>	<i>Rhizocarpon</i>
Colonization	$1000 * \left[ 1 - \exp\left(-\frac{n}{a_1}\right) \right]$	$1000 * \left[ \frac{\exp(a_1 + a_2 n - a_3 n^2)}{1 + \exp(a_1 + a_2 n - a_3 n^2)} \right]$
Growth	$a_2 * \left[ 1 - \exp\left(-\frac{d}{a_3}\right) \right]$	$a_4 * \left[ 1 - \exp\left(-\frac{d}{a_5}\right) \right]$
Survival	$a_4$	$a_6$
Parameters	<i>P. pubescens</i>	<i>Rhizocarpon</i>
$a_1$	23,917	–3.35
$a_2$	0.7148	0.00075
$a_3$	0.4667	–0.000000027
$a_4$	0.9790	0.2084
$a_5$	–	0.4000
$a_6$	–	0.9665

of 2% per year for *P. pubescens*, and 3% per year for *Rhizocarpon* (Table 2).

Other predictions of the fitted demographic models (Table 2) include colonization rates that increase rapidly in the first few decades and stabilize within a century, and maximum growth rates of 0.71 mm per year (for *P. pubescens*) and 0.21 mm per year (for *Rhizocarpon*). Colonization rate is the most poorly constrained element of these models, largely because the smallest lichens, although common, are very difficult to locate and were likely undercounted, especially in the youngest populations. Inferred growth rates are lowest for these juvenile lichens, and reach a maximum rate when the lichens are 2–3 mm in diameter. This contrasts with the common interpretation of lichenometric calibration curves as indirect evidence for rapid early “great growth”, but we note that our lichen populations are likely not old enough to display evidence of slowed growth by mature/senescent lichens (seen by some investigators in lichens greater than ~50 mm diameter; Armstrong and Bradwell 2010), if indeed that occurs.

### Dating surfaces of unknown age: Methods

While the demographic parameters predicted by our models may be of interest to lichen biologists, our purpose here is to use the SFDs (and densities) predicted by those models to date glacial moraines. To demonstrate the range of such predictions, we plot the evolution of each species’ modeled SFD from model ages of 50–325 years in Fig. 3. As

expected, these distributions mimic the patterns found in our measured datasets (Fig. 2), and serve (along with the densities and distributions predicted for all the intermediate model ages, not shown) as the basis for dating surfaces of unknown age. Next, we discuss the manner in which this comparison was made, and how we calculated the associated confidence intervals for the inferred surface ages.

### Deriving surface ages and confidence intervals

In the dating process, the best model structure and parameters were fixed, and time ( $t$ ) was the only model parameter allowed to vary as we sought the model “age” that best fits the size distribution data collected from some dating surface, like a moraine, of unknown age. For annual timesteps  $t = 1$  to some reasonable maximum, we sought to minimize the negative log-likelihood of the model:

$$\text{NLL}(M_t) \approx - \sum_{i=1}^{\max} y_{\text{dat},i} \ln \psi_{t,i} \quad (1)$$

where  $\text{NLL}(M_t)$  indicates the negative of the log of the likelihood of the modeled size distribution at time  $t$  being the actual size distribution, given the observed lichen sizes.  $y_{\text{dat},i}$  is a vector representing the measured frequency of lichens in size class  $i$  on the dating surface of interest ( $\text{dat}$ ), and  $\psi_{t,i}$  are the modeled probabilities of lichens in size class  $i$  at any given model timestep  $t$ . Note that population density was not used as a constraint in this dating phase of our technique. The value of  $t$  that

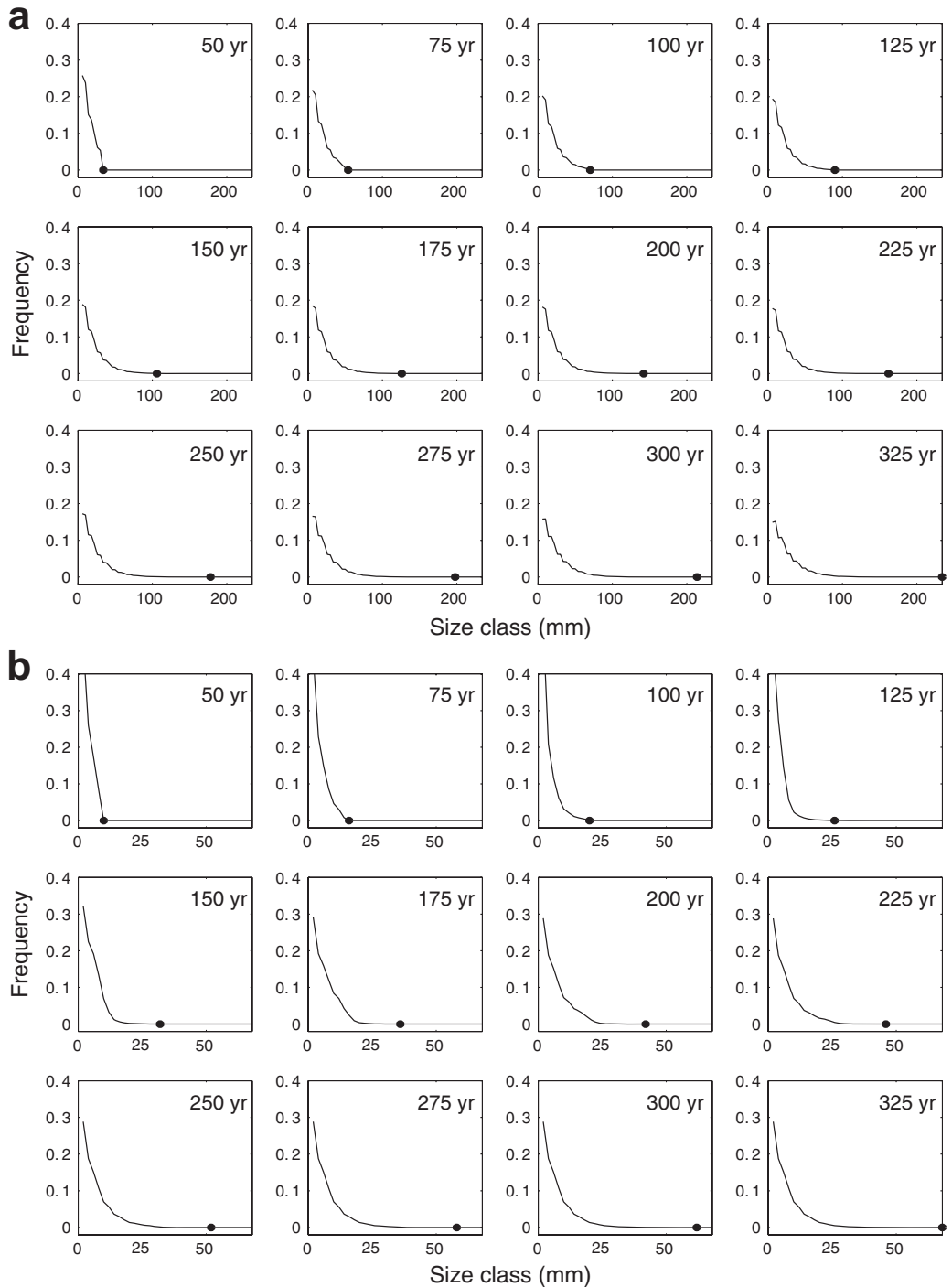


Fig. 3. Size distributions predicted by the best-fit demographic models. For *P. pubescens* (a) and *Rhizocarpon* (b), each series of 12 panels (across rows from upper left) shows SFDs for modeled population ages 50–325 in 25-year increments. At older population ages, large lichens are extremely rare and their abundance is difficult to distinguish from 0; black dot shows the size of the largest lichen predicted to be present in a population of extremely large size.



minimized  $NLL(M_t)$  was our best estimate for the age of the moraine.

Confidence intervals for our age estimates were calculated in three parts. We first relied upon the likelihood ratio test, or *G*-test (Sokal and Rohlf 1995) to determine *prediction uncertainty*: a measure of our ability, with our best-fit model, to distinguish among the fits of different model ages to a given dataset. If, when dating some surface, we saved the scores from Eqn (1) for different values of  $t$ , we could compute a likelihood profile for a range of model ages:

$$NLL(M_t) - NLL(M_{best}) \quad (2)$$

where  $NLL(M_{best})$  is the negative log-likelihood of the best-fitting model age. We were varying only one model parameter,  $t$ , so that the value

$$G = 2(NLL(M_t) - NLL(M_{best})) \quad (3)$$

had a  $\chi^2$  distribution and 1 degree of freedom. The 95% confidence interval was thus defined by all values of  $t$  where  $G < 3.84$  (Hilborn and Mangel 1997).

Because our models are imperfect representations of a complicated biological reality, a more complete estimate of uncertainty in our moraine ages must incorporate *model parameter uncertainty* and *model structure uncertainty*. We calculated these sources of uncertainty, for any given moraine, by varying the best-fit parameters and model structures of our demographic model within biologically plausible limits. The process was complicated, but importantly allowed our confidence intervals to reflect the uncertainty in our demographic models.

Model parameter uncertainty was treated first. For a single model structure  $m$ , we varied all the demographic parameters (as in Table 2) to generate 10,000 different combinations of parameter values, picking each parameter value from an independent uniform distribution within the ~90% confidence interval of its best-fit value. For each of these 10,000 variants, denoted by the subscript  $b$ , we calculated  $NLL(M_{ab})$  representing the ability of each model variant to explain observed lichen distributions on the *calibration surfaces*. For each parameter combination  $a_b$  we then fixed the parameters and allow model time to vary, calculating  $NLL(M_{tb})$  for the *dating surfaces* with Eqn (1). Each model variant (parameter combination  $b$ ) thus has an associated  $NLL(M_{ab})$ , the likelihood of that parameter combination given the lichen distribu-

tions on all calibration surfaces, and  $NLL(M_{tb})$ , the associated range of likelihoods for different model ages  $t$  given that parameter combination and the lichen distribution on a single moraine. Returning to likelihood space (recalling that  $L(M) = \exp[-NLL(M)]$ ), the first likelihood could be used to weight the latter range of likelihoods by multiplication, and the resulting likelihoods summed across all parameter combinations for each model age. In other words, the likelihood of any given estimated moraine age  $t$ , as given in Eqn (1), was refined to reflect the likelihood of the chosen model parameters as follows:

$$L(M_t) = - \sum_{b=1}^{10,000} L(M_{ab} | y_{cal}) L(M_{tb} | y_{dat}) \quad (4)$$

After taking the negative log-likelihood of Eqn (4), confidence intervals that incorporate the likelihood of variation in each fitted parameter (i.e. prediction uncertainty + parameter uncertainty) were calculated using a *G*-test as in Eqn (3). Formally, the result of Eqn (4) should first be divided through by the number of model variants to yield a weighted average. In practice, we skipped that step because the divisor became a constant when we returned to log space, and hence had no impact on the relative log likelihoods of different model ages. Model structure uncertainty was calculated in an analogous fashion. For all model structures  $m$  that have AIC weights  $>0.05$  (as listed in Table 1 of Loso and Doak 2005), we first calculated the weighted likelihoods as described in Eqn (4). Before returning to log space, however, we multiplied all weighted likelihoods,  $L(M_j)$ , from each model structure by the AIC weight of that model structure. Again, the results were converted to negative log likelihoods and confidence intervals determined by a *G*-test.

#### *How much of the distribution should we use?*

Before applying this basic approach to our data, we performed some numerical experiments to explore an important question: how *much* of the size distribution should we use? In the calibration phase, we used full-population SFDs (except for the very smallest size class) to test and fit the demographic models. These full distributions were critical for making robust inferences about the interplay of colonization, growth, and survival. However, in the dating phase, it was not clear that the full distribu-

tion was necessary, or even desirable, for comparison with predictions of the fitted demographic models.

Five reasons compelled us to explore the value of fitting partial distributions. One was the predominance of the smallest size classes at all population ages, suggesting that the left side of the distribution provides little information with which to distinguish among populations of different ages. Two, the left side of the distribution was most sensitive to changes in colonization and early lichen growth, the least well constrained elements of our demographic model. Three, the likelihood function weights each size class by the frequency of individuals in that class (the  $y_i$ 's in Eqn 1), meaning that the fit was dominated by the small (but abundant) size classes if we did not exclude them from the analysis. Four, our measurements of the smallest size classes were probably the least accurate, due to the difficulty of locating and accurately measuring such small thalli. Five, measurement of all lichens on a dating surface was very time consuming, and the workload was dominated by measurements of small lichens. This is how we collected our data (on both calibration and dating surfaces), but we were interested in determining whether we might improve the efficiency of our sampling technique (on dating surfaces only) by focusing on the larger size classes.

In practice, limiting the subpopulation of sampled lichens by some minimum diameter would be easy to apply in the field. We evaluated this approach in a series of Monte Carlo simulations where the surface age and confidence interval determination process just described was applied only to lichens above a minimum diameter ( $d_{min}$ ). We defined  $d_{min}$  as a percentage of the size of the largest lichen present at that age. On a surface with lichens up to 10 mm diameter, for example, a 50% minimum diameter (that we denote  $d_{min} = 50\%$ ) dictated measurement of all lichens in and above the size class containing 5 mm lichens. We tested seven minimum diameter cutoffs,  $d_{min} = [0, 25, 50, 60, 70, 80, 90\%]$ . To do so, we first used the best-fit demographic models to simulate large populations of both *P. pubescens* and *Rhizocarpon* on surfaces ranging in age from 50 to 300 years old (at 25-year intervals) and then recalculated model probabilities for only the size classes  $i \geq d_{min}$ :

$$\psi_i = n_i / \sum_{i \geq d_{min}}^{\max} n_i \quad (5)$$

where  $n_i$  is the number of lichens produced by our demographic model in size class  $i$ . We then simulated the collection of data from the simulated populations at each surface age by randomly selecting individuals of each species at three different sample sizes,  $N = [10, 100, 1000]$ , limiting our sampling to lichens above  $d_{min}$ . Likelihood profiles were calculated for each sample using Eqn (2), and the confidence limits determined using Eqn (3).

The 95% confidence interval ranges estimated by a likelihood ratio test, averaged over all surface ages and simulation replicates, are shown in Fig. 4a, b. We do not show the actual predicted ages because our outcomes, when averaged over 1000 simulations, were very accurate. This was expected, given that the demographic models were the source of the selected data. We focus instead on the magnitude of the prediction uncertainty calculated with a likelihood ratio test. It was highest in simulations where most or all of the population was sampled, and was minimized by large samples of the largest size classes. In other words, the largest size classes provided the greatest power to distinguish among distributions from surfaces of different ages. We interpret these results as supportive of a sampling regime (on dating surfaces) that excludes the smallest lichens. However, Fig. 4c also demonstrates the tradeoff between sample size and minimum diameter. Typical lichen probability and cumulative density functions, shown on a normalized scale that records size as a percentage of the largest lichen present, remind us that relatively few lichens are present in the very largest size classes. Samples gathered only from the extreme upper tail of the distribution (e.g.  $d_{min} = 90\%$ ) would invariably be extremely small, and thus risk substantial error due to the very small numbers of individual measurements possible.

To examine this tradeoff with real data, we next tested a range of minimum cutoff diameters on surfaces with independently known ages – the shorelines around Iceberg Lake. This was a very different test than the Monte Carlo simulation described above, where the data were simulated by selecting randomly from distributions generated by our best-fit demographic models. Because the total sample size was in this case fixed, the tradeoff just described was in effect: increasing values of  $d_{min}$  required that smaller numbers of lichens were used to predict the age of the surface. Second, the data used in this test were selected from real distributions that are only imperfectly described by the best-fit demographic models. These models performed well

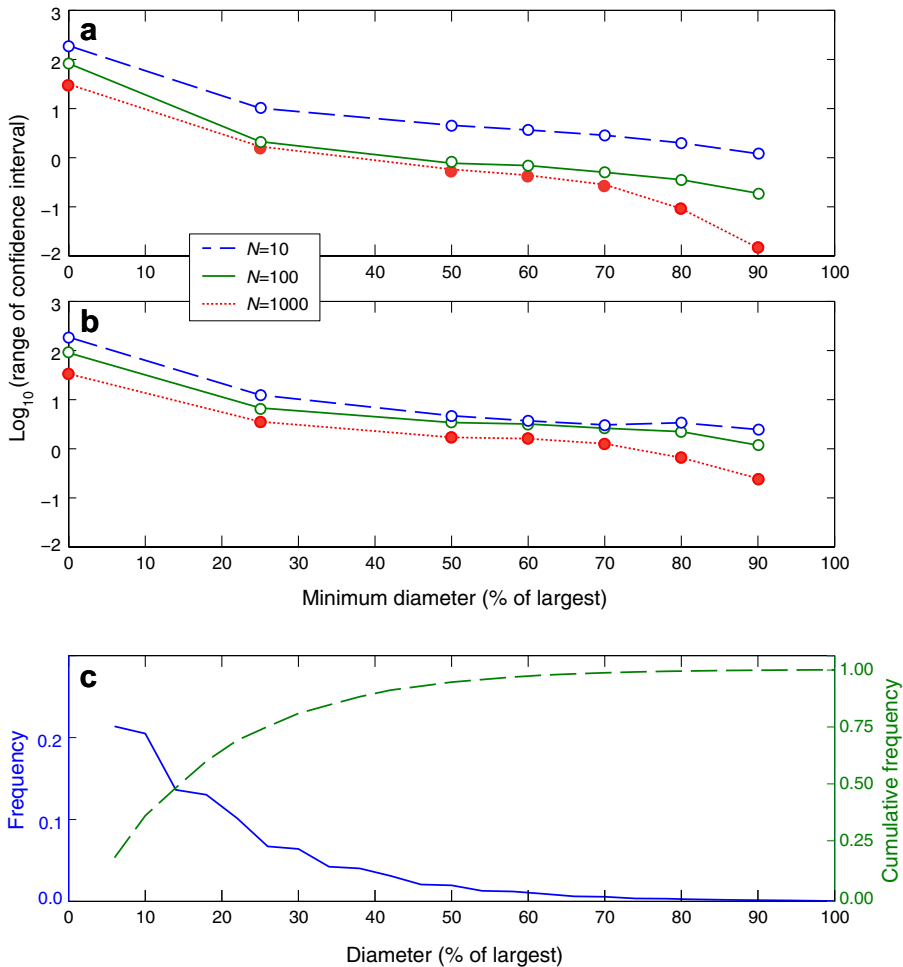


Fig. 4. Effects of sample size and minimum diameter on ranges of confidence intervals for surface age estimates. Values are derived from Monte Carlo simulations that compare random samples of lichens above some minimum diameter (defined as a percentage of the largest lichen diameter in that population) to the predictions of demographic models. Plotted results are averages of 1000 simulations on each of 11 surfaces ranging in age from 50 to 300 years old, for *P. pubescens* (a) and *Rhizocarpon* (b). Note that ranges in (a) and (b) are presented on a  $\log_{10}$  scale, and that lines only indicate trends between actual simulation results (circles). Large samples of the extreme upper tail of the distribution give the most precise results, but probability (solid line) and cumulative density (dashed line) plots of a modeled 150-year old *P. pubescens* population (c) demonstrate the difficulty of collecting large samples of lichens from only the largest size classes.

in explaining the lichen populations from Iceberg Lake's shorelines (Loso and Doak 2005), but here we asked whether they are good enough to predict the ages of those same populations, and how the predictions changed with changing values of the cutoff diameter  $d_{min}$ .

In Fig. 5, we compare the 95% prediction bounds of estimated shoreline ages with the independently known actual ages, using values of  $d_{min}$  that range from 10% to 90%. Two trends are apparent. First,

the ranges of these confidence limits did not steadily shrink with increasing values of  $d_{min}$ , as they did in Fig. 4. They actually increased slightly as  $d_{min}$  rose, largely because the sample size shrank. Second, the predicted ages were typically biased estimates that were too young when using low values of  $d_{min}$ . Accuracy improved (the correct age was more commonly enclosed within the confidence intervals) as the cutoff increased and we focused more clearly on the larger size intervals. In combination with the

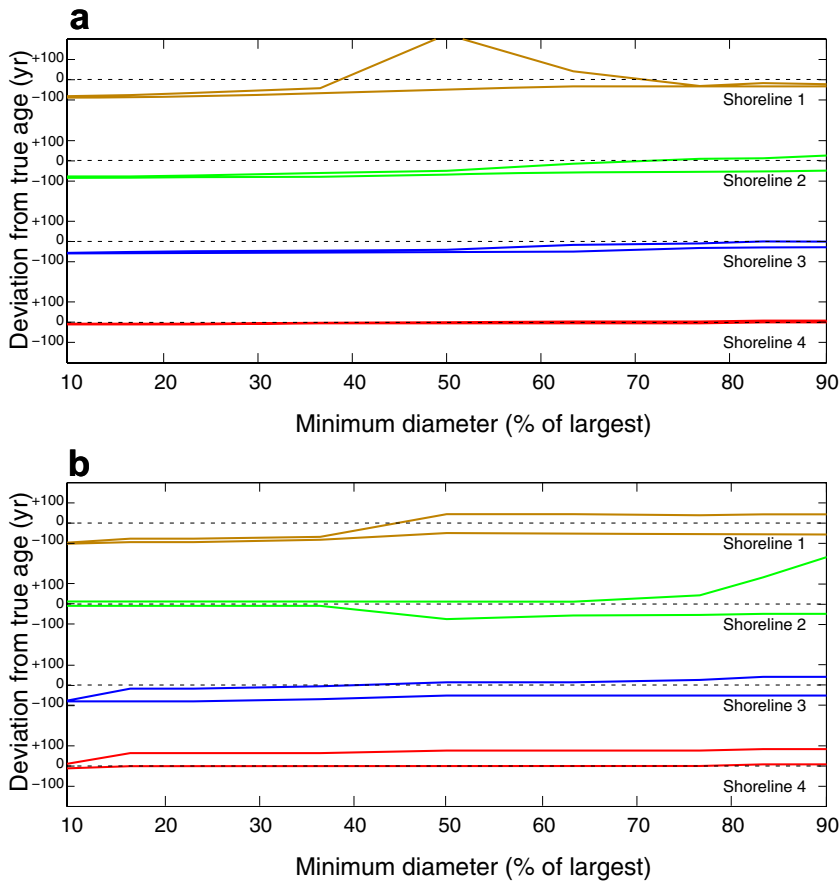


Fig. 5. Upper and lower 95% confidence intervals of surface ages estimated using lichen diameter measurements from four shorelines of known age. For both *P. pubescens* (a) and *Rhizocarpon* (b), true ages are shown with dashed lines. Generally, increasing values of  $d_{min}$ , the minimum diameter of sampled lichens, improves the accuracy of the results but in some cases increases the range of the confidence intervals.

evidence for expanded confidence intervals at low values of  $d_{min}$ , presented in Fig. 4, these results argued for the use of partial distributions that emphasize the largest size classes. This approach agrees in theory, if not in computational details, with previous workers who have dated surfaces using the slope of a portion of the lichen size–frequency distribution above the modal size-class (Bradwell 2004 and references therein). Larger sample sizes, refined demographic models, and additional theoretical work are required before we can make a general case for the “best” minimum cutoff diameter, but the accuracy of predicted ages for shorelines 1–4 were maximized around  $d_{min} = 75\%$ . We adopted this value of  $d_{min}$  in our analysis of the unknown moraine ages, presented next.

### Dating surfaces of unknown age: Results

Estimated ages, using our method and  $d_{min} = 75\%$ , are shown in Fig. 6. Best-fit ages predicted by *P. pubescens* and *Rhizocarpon*, respectively, were 156 and 280 years on moraine 1, 80 and 84 years on moraine 2, and 47 and 76 years on moraine 3. Plotted 95% confidence intervals account for all known sources of error; the cumulative effects of prediction uncertainty, model parameter uncertainty, and model structure uncertainty are shown separately in Table 3. Confidence intervals varied widely among moraines and between species, and were dominated by prediction error; the cumulative effects of model parameter error and model structure error were small. Notably, the upper confidence interval predicted by *Rhizocarpon* for moraine 1 is unbounded, indicating that the data fit

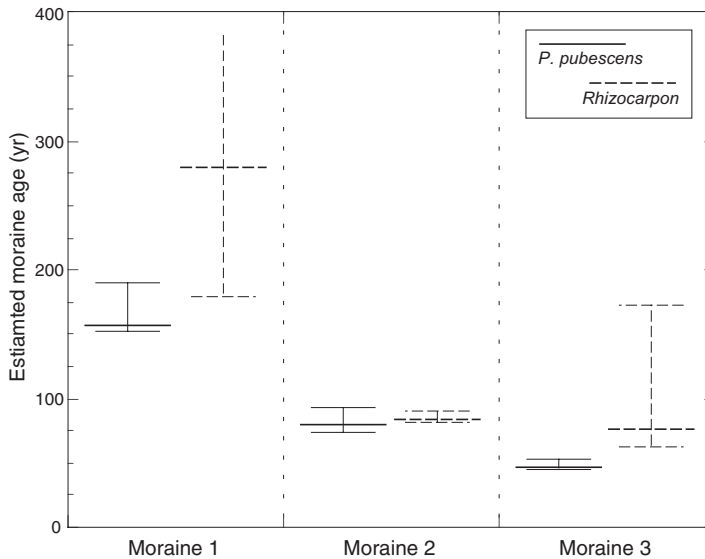


Fig. 6. Estimated ages of moraines 1–3. Dates for each moraine are derived from populations of *P. pubescens* (left, solid lines) and *Rhizocarpon* (right, dashed lines). Measured lichen distributions on moraines 1–3 were compared with a series of modeled population distributions from simulated surfaces of different ages, in each case comparing only lichens with a diameter 75% or greater that of the largest lichen present on that surface. Maximum likelihood techniques were used to select the modeled distribution that most closely fits the data. Error bars show 95% confidence interval based upon a likelihood ratio test, which estimates the cumulative effects of prediction uncertainty, model parameter uncertainty, and model structure uncertainty.

Table 3. Summary of moraine ages (in years before AD 2002) estimated by a variety of lichenometric analyses using the same data from Chisma Glacier, Alaska. Each set of three columns indicates the mean age prediction (age) bracketed by the 95% confidence limits for younger (–) and older (+) ages.

Technique	Species	Moraine 1			Moraine 2			Moraine 3		
		–	Age	+	–	Age	+	–	Age	+
Likelihood (all errors, species grouped)	Grouped	172	186	283	81	85	89	53	64	83
Likelihood (prediction error only)	<i>P. pubescens</i>	170	173	189	84	85	92	45	47	53
	<i>Rhizocarpon</i>	185	279	∞	81	84	91	72	76	171
Likelihood (prediction and parameter error)	<i>P. pubescens</i>	152	156	190	73	80	93	45	47	53
	<i>Rhizocarpon</i>	184	279	∞	81	84	91	63	76	171
Likelihood (all errors, by species)	<i>P. pubescens</i>	152	156	190	73	80	93	45	47	53
	<i>Rhizocarpon</i>	180	280	∞	81	84	91	63	76	173

nearly as well with extremely old (modeled) distributions as they did with the best-fit age.

Best-fit ages differed between the two species, with *Rhizocarpon* consistently predicting the older moraine ages: 124, 4, and 29 years older than *P. pubescens* on moraines 1–3, respectively. Ninety-five percent confidence intervals overlapped on moraines 1 and 2, but were separated by 10 years on moraine 3 (Fig. 7). For the best single estimate of each moraine's age, we combined for every model year  $t$  the likelihood calculated for each species in Eqn (4), returned the joint likelihood to

log space, and calculated the best-fit age and confidence intervals as before. Using this technique, the estimated moraine ages were 186, 85, and 64 years before AD 2002 for moraines 1–3, respectively (Table 3), or AD 1816, 1917, and 1938.

No lichens were found on moraine 4 (Table 1, terminus position E in Fig. 1), but we could crudely estimate the age of this moraine by asking how old the moraine could be before we became confident of finding lichens. Based on distributions of thalli on shorelines 1–4, we previously concluded that thalli with diameters <4 mm (for *P. pubescens*) and

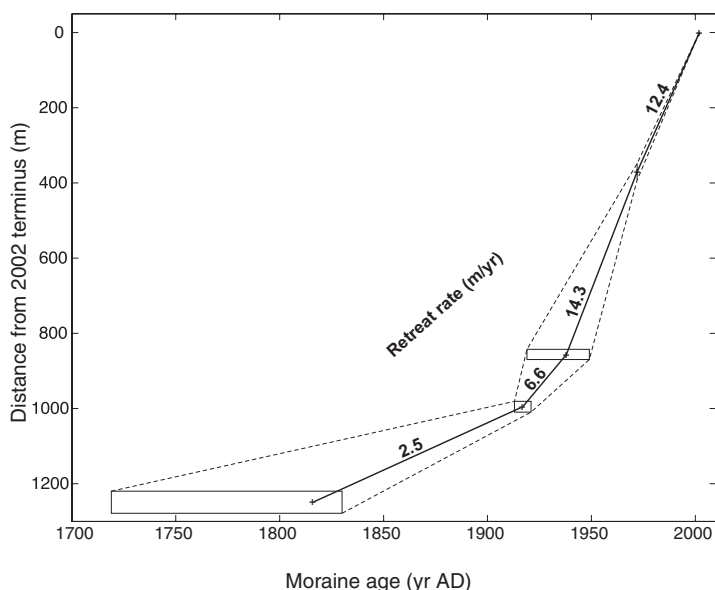


Fig. 7. Post-Little Ice Age maximum retreat history for the terminus of the Chisma Glacier. The oldest three moraine ages and confidence intervals are estimated using our new lichenometric technique; the two newer dates are from aerial photography and ground-based surveys. Distances are from Table 4, and include 95% confidence intervals based on SD of measurements from 10 transects. Dashed lines thus enclose overall confidence limits for the retreat history, and mean retreat rate for each interval is shown in bold print ( $\text{m a}^{-1}$ ).

<2 mm (for *Rhizocarpon*) were undersampled, presumably because they were often not seen in the field (Loso and Doak 2005). Based upon those estimates, we used growth rates of both lichen species to estimate the age at which lichens enter the second, easily visible size class. If lichens of either species colonized the moraine immediately and grew at the modeled growth rate, we would expect to have found lichens somewhere on that moraine no more than 8 years (*P. pubescens*) or 13 years (*Rhizocarpon*) after the moraine was abandoned by glacier retreat. This suggests a calendar age of AD 1994 or later for moraine abandonment, consistent with the well known dates of bracketing terminus positions D (AD 1972) and F (AD 2002) but with sufficient uncertainty that we excluded it from subsequent calculations of glacier retreat rates.

These age estimates permitted derivation of net glacier retreat rates for Chisma West Glacier. To calculate distances between terminus positions, we used fluting in exposed lodgement till to determine an ice flow trajectory of  $103^\circ$  and then calculated distances along that trajectory at 10 parallel transects superimposed over the terminus area (Fig. 1). Average distances between positions, with standard deviations, are reported in Table 4.

Chisma West Glacier retreated a total of 1249 m between the time of the LIA maximum advance and 2002. The estimated date of Chisma Glacier's LIA maximum advance was AD 1816, suggesting an overall net retreat rate of  $6.7 \text{ m yr}^{-1}$  (Table 4). Given the 95% confidence intervals for that age, that rate could be as high as  $7.3 \text{ m yr}^{-1}$  or as low as  $4.4 \text{ m yr}^{-1}$ . A plot of the moraine ages versus time (Fig. 7) breaks the retreat down into discrete intervals and makes it clear that retreat of the Chisma Glacier has accelerated in recent decades. We estimated a net retreat rate of  $14.3 \text{ m yr}^{-1}$  between AD 1938 and 1972, with a 95% confidence interval of  $9.2\text{--}21.2 \text{ m yr}^{-1}$ . Based upon aerial photography and ground-based surveys, the net retreat rate was  $12.4 \text{ m yr}^{-1}$  between AD 1972 and 2002. Confidence intervals that reflect uncertainty in both ages and moraine positions show that the acceleration in retreat rate took place sometime between approximately AD 1910 and 1950.

## Discussion

In a novel approach to lichenometric dating, we have estimated the ages of three terminal moraines by comparing the measured SFDs of lichens on



Table 4. Terminus positions and ages for Chisma Glacier, with calculated net retreat rates.

Terminus position	Age (year AD)	Distance between (m)	Distance between (SD)	Net retreat rate (m yr <sup>-1</sup> )
F-2002 Terminus	2002			
	>	238	39.3	12.4 <sup>a</sup>
E-Moraine 4	1994 <sup>a</sup>			
	>	133	29.6	12.4 <sup>a</sup>
D-1972 Terminus	1972			
	>	485	18.1	14.3
C-Moraine 3	1938 <sup>b</sup>			
	>	139	19.0	6.6
B-Moraine 2	1917 <sup>b</sup>			
	>	254	38.9	2.5
A-Moraine 1	1816 <sup>b</sup>			
	Total distance	1249	Average rate	6.7

<sup>a</sup> The AD 1994 date is poorly constrained, so we compute retreat rate over the interval AD 1972 to 2002.

<sup>b</sup> These dates based upon the joint likelihoods of age predictions by *P. pubescens* and *Rhizocarpon*.

those moraines to those predicted by demographic models that feature explicit rules for colonization, growth, and survival. Below, we first consider the reliability of our inferred dates, and compare them with other geological evidence from the region. Second, we probe the potential sources of uncertainty in our study, their impacts on our results, and their general implications for lichenometry. Finally, we discuss the pros and cons of our technique and the extent to which it might, with various improvements, merit the considerable effort it requires.

#### Reliability of age estimates

The calendar ages for our estimated moraine ages (AD 1816, 1917, and 1938; Table 4) are internally consistent and accord with independent geological evidence. They pass the most basic test: that ages progress chronologically from the furthest outboard moraine, 1, to the most inboard moraine, 3, as expected during a period of glacial retreat. Further, moraine 3 is older than the next terminus position further inboard (position D in Fig. 1), whose date (AD 1972) and position is known from aerial photography. The age of the furthest outboard moraine (1) sits well within the age range of the LIA maximum, as known from coastal and interior sites in the vicinity of Chisma Glacier (Wiles *et al.* 2002). It is also consistent with independent evidence for abandonment of the LIA maximum shoreline of ice-dammed Iceberg Lake – presumably due to thinning of the impounding

Tana Glacier – in AD 1825 (Loso *et al.* 2004). Finally, the temporal pattern of retreat rates shown in Fig. 7, which documents an LIA maximum advance around AD 1816 and accelerating retreat of the Chisma Glacier terminus beginning in the early to mid twentieth century, is consistent with the known patterns of Alaskan and Arctic temperature history (Davi *et al.* 2003; Kaufman *et al.* 2009).

However, our decision to independently date the moraines using two different species reveals complexities that might otherwise remain hidden. Ages predicted by *Rhizocarpon* alone are consistently older than ages predicted by *P. pubescens*, and the confidence intervals associated with those ages overlap for only two of the three moraines (1 and 2; Fig. 6). We dealt with this complication by computing joint likelihoods that combine all the evidence from both species to determine the most probable moraine ages. Had we chosen to strictly interpret every lichenometric date as a minimum age, thus using the older *Rhizocarpon* age for each moraine, we would have concluded that the LIA-maximum advance was almost 100 years earlier and the subsequent retreat rates substantially slower. We acknowledge the caution with which our results should thus be interpreted, and in the next section consider the potential sources of our errors.

#### Sources of uncertainty

We agree with others who argue that well justified confidence intervals are critical to the continued acceptance of lichenometric dates (e.g. Jomelli

*et al.* 2007), and the confidence intervals associated with our lichenometric dates are in some cases large and inconsistent between species (Fig. 6). Here we address the sources of uncertainty in our results. We begin with an acknowledgment of methodological issues unique to our particular study. Most important, perhaps, is our use of the broad *Rhizocarpon* subgenus. We initially identified our yellow-green lichens as *Rhizocarpon geographicum* (Loso and Doak 2005) but have since concluded that the lichens we sampled, particularly in the smaller and more cryptic size classes, cannot all be confidently attributed to that species. Because various species within the broader subgenus can differ substantially in their biology (Clayden *et al.* 2004), our models and likelihood-based lichenometric ages may reflect interspecific variability in demographic rates that could be eliminated with more definitive taxonomic field identification. This variability is in any case not captured in our demographic models and therefore likely contributes to the broad confidence intervals for *Rhizocarpon* on moraines 1 and 3.

The small sample sizes used for dating the moraines are also important for explaining the large confidence intervals. In the field, we measured all lichens (>1 mm diameter) on both calibration and dating surfaces. On calibration surfaces, the full distribution is clearly important for fitting the demographic models. But for dating surfaces of unknown age, we subsequently concluded that one can maximize both sampling efficiency and model accuracy by measuring only those lichens with a diameter equal to or greater than 75% the diameter of the largest lichen found. That conclusion came too late to influence the sampling design of this study, however. Of the thousands of lichens we measured on moraines 1–3, our subsequent choice of  $d_{min} = 75\%$  dictated that fewer than 200 were used for dating.

The disadvantages of such small sample sizes may be magnified by high variability in size-specific demographic rates. Aside from the potential variability introduced by use of the subgenus, already discussed, there is substantial evidence for individual intraspecific variability in *Rhizocarpon*, including growth rates (Armstrong and Bradwell 2010) and early development (Asta and Letrouit-Galinou 1995). The same is possibly true for *P. pubescens*, as well. We did not quantify that variability in our study but it highlights the desirability of larger sample sizes and, ultimately, demographic models that incorporate individual variability. Similarly, we recognize that the vital rates of individuals

in both lichen taxa used in this study are sensitive to environmental differences associated with regional/microclimate, landscape position, and substrate type (Armstrong 2011), but we controlled for this variability by sampling lichens from comparable microenvironments in both our calibration and dating populations.

While some of the sources of uncertainty just mentioned could be minimized with refined sampling techniques, other sources of uncertainty can be attributed to the demography of lichens themselves. To develop insight into the relative importance of each vital rate for estimates of moraine age, we calculated elasticity values for each parameter. Elasticities relate change in a dependent variable of interest (here, the moraine ages) to changes in independent variables, facilitating comparison among parameters of differing magnitudes by normalizing the change in each variable by its mean value (Caswell 2001; Morris and Doak 2002). To do so, we first found the 90% confidence intervals for each fitted parameter  $a_{1-6}$  (Table 2) and recalculated the moraine ages ( $t$ ) using the these slightly “unfit” parameters. For each moraine, the elasticity  $E_k$  of a given parameter  $a_k$  is then:

$$E_k = \frac{\Delta t}{t} \bigg/ \frac{\Delta a_k}{a_k} \quad (6)$$

where  $\Delta a_k$  is the difference between the best-fit parameter and the “unfit” parameter, and  $\Delta t$  is the resulting change (in years) of the calculated moraine age.

Elasticities are shown in Table 5. In general, elasticities on all moraines and for both species are highest for the survival parameter, and next highest for the growth parameter that dictates adult maximum growth rates. Stated another way, our ability to estimate correctly the moraine ages is most dependent upon our understanding of survival rates, secondarily dependent on adult growth rates, and least dependent upon our understanding of colonization and early growth. The latter point is expected – we chose to date the moraines using only the largest portion of the distribution ( $d_{min} = 75\%$ ) in part to minimize the sensitivity of our estimates to these relatively poorly constrained parameters. More surprising is the importance of survival, given the almost complete lack of attention paid to this process by most lichenometrists. Overall, the elasticity of survival is generally higher on older moraines, suggesting that as surface ages increase, the age estimates are increasingly dependent upon

Table 5. Elasticities of fitted parameters, judged by their impact upon calculated moraine ages.

Process		<i>P. pubescens</i>		<i>Rhizocarpon</i>	
		Parameter	Elasticity	Parameter	Elasticity
Moraine 1	Colonization	$a_1$	-0.42	$a_1$	-0.32
	Colonization			$a_2$	0.12
	Colonization			$a_3$	0.02
	Adult growth	$a_2$	2.71	$a_4$	-0.78
	Early growth	$a_3$	0.01	$a_5$	0.01
	Survival	$a_4$	-2.01	$a_6$	-6.95
Moraine 2	Colonization	$a_1$	-0.15	$a_1$	-0.07
	Colonization			$a_2$	0.02
	Colonization			$a_3$	0.00
	Adult growth	$a_2$	-1.05	$a_4$	-1.54
	Early growth	$a_3$	0.02	$a_5$	0.07
	Survival	$a_4$	-2.23	$a_6$	-0.47
Moraine 3	Colonization	$a_1$	-0.02	$a_1$	-0.15
	Colonization			$a_2$	0.05
	Colonization			$a_3$	0.00
	Adult growth	$a_2$	-1.11	$a_4$	-0.96
	Early growth	$a_3$	0.04	$a_5$	0.05
	Survival	$a_4$	-0.78	$a_6$	-0.52
Average	Colonization	$a_1$	-0.20	$a_1$	-0.18
	Colonization			$a_2$	0.07
	Colonization			$a_3$	0.01
	Adult growth	$a_2$	0.18	$a_4$	-1.09
	Early growth	$a_3$	0.03	$a_5$	0.05
	Survival	$a_4$	-1.67	$a_6$	-2.65

the relative density of lichens remaining from early cohorts. While this exact sensitivity result is unique to our study, the importance of large, old lichens in virtually all lichenometric techniques suggests an important general implication: lichenometric data are strongly influenced by lichen mortality, particularly on older surfaces.

This idea has received surprisingly little attention in the lichenometric literature, in part because demography in general has received little attention, but also because the absence of evidence for a maximum lifespan (based on the ubiquitous presence on old surfaces of very large individual thalli; e.g. Matthews and Trenbirth 2011) can easily be mistaken as evidence for the absence of mortality (Innes 1983). Without precluding the possibility of very long lifespans, or of other processes like fusion of small thalli (Asta and Letrouit-Galinou 1995), our previous work provided strong evidence for significant ongoing mortality in *Rhizocarpon* and *P. pubescens* (Loso and Doak 2005). A similar result was recently reported for the foliose lichen *Vulpicida pinastri* (Shriver *et al.* 2012). This mortality has little effect on young populations, where most early colonists remain, but on older surfaces lichen populations become increasingly skewed

(Fig. 2), reflecting the fact that many of the early colonists have died. The mortality reflected by these highly skewed distributions explains the infinite upper boundary of a confidence interval around the age predicted by *Rhizocarpon* for moraine 1 (Fig. 6, Table 3). The SFD that most closely matches the measured distribution of moraine 1 cannot be reliably distinguished from the SFDs expected on much older surfaces, precisely because the very large lichens that distinguish those older surfaces are so rare that their absence has almost no significance for the model fit. On surfaces slightly older than the ones we measured, a similar result might be expected of *P. pubescens*, which has a lower estimated mortality rate than *Rhizocarpon*. We make such an extrapolation cautiously, however, because we have no information about the demography of these populations after 177 years. Survival of the two species, and indeed growth and colonization rates too, almost certainly evolve over centennial timescales in ways that our models do not capture.

As a final source of uncertainty, we consider the demographic models themselves. The models we used are biologically defensible, provide a good fit to measured SFDs from the calibration surfaces,

and have tightly constrained parameters (Loso and Doak 2005). Our measures of uncertainty reflect this. For all moraines and both species, the 95% confidence intervals are dominated by prediction uncertainty, and the collective impacts of model uncertainty are small (Table 3). But because the likelihood function and AIC weights measure support for each model relative only to the other models tested, there is unavoidably an additional, unquantified error associated with the difference between our best model and the “right” model: one that perfectly describes the demographic processes of lichens growing on the undated surfaces of interest. We believe this error is small, but can only say with certainty that improved demographic models will further reduce it.

#### *The case for an explicit demographic approach*

The technique presented in this paper yields plausible moraine ages with confidence intervals that account for all knowable sources of uncertainty. It is a labor-intensive approach, however. It requires more fieldwork than single-largest lichen technique, and more analysis than multiple-largest lichen technique. With reference to other, similarly complex efforts to “improve” lichenometry, Bradwell (2009) recently asked whether such efforts are justified. In his view, one of the great merits of lichenometry is its simplicity, and we agree. There is undeniable value in the rapid results available to a field practitioner of the traditional largest lichen technique, or its variants. But when the results of lichenometric studies are published, particularly if they are pertinent (as most glacier retreat studies are) to the highly scrutinized field of climate change, we contend that the most important questions have less to do with the complexity of the methodology than with the trustworthiness of the results. In light of that, is our approach worth the trouble?

If lichenometric dates are to be regarded with the same confidence as calibrated radiocarbon dates, we believe the answer is yes. We choose the comparison to radiocarbon dating purposefully. Depending upon the time period of interest, calibrated radiocarbon dates can have large, and even multiple, confidence intervals (Stuiver and Reimer 1993). But because those confidence intervals are based upon a solid general understanding of the processes that produce  $^{14}\text{C}$  in the atmosphere, transmit it to organic materials, and break it down, calibrated radiocarbon dates are accepted with

great confidence by a variety of scientific disciplines. Equally importantly, identification of those key processes has provided direction for additional research aimed at characterizing their temporal and spatial variability. Lichenometry, by comparison, remains dependent upon a statistical correlation – usually some form of calibration curve. As already discussed, these curves are functions of complicated interactions among sampling strategy and the underlying biological/demographic processes (Innes 1984, 1985; McCarroll 1994; Clayden *et al.* 2004). The effects of these interactions are unpredictable, and their impacts on the accuracy and precision of the results cannot be quantified, even if the calibration surfaces and dating surfaces are biologically identical and sampled in exactly the same way. In comparison, the functions and fitted parameters in a demographic model describe actual biological processes that can be readily understood, tested independently, compared among different species and locations, and explicitly accounted for in the dating process. Confidence intervals can be calculated that directly reflect the influence of these processes, and situations where the technique performs poorly (on very old moraines colonized by lichens with poor survival rates, for example) can be identified and avoided. This degree of understanding is especially important if lichenometry data are used to extrapolate beyond the distribution of surface ages represented in the calibration data.

The case study presented here is only a first step in that direction. Although we succeeded in presenting internally consistent and geologically plausible dates for three moraines, our results include broad and in one case non-overlapping confidence intervals that reflect taxonomic uncertainty, an inadequate sample size in the larger size classes, high inferred lichen mortality, and a potentially oversimplistic demographic model. But this first application of the technique suggests immediate pathways for improvement: better taxonomy and higher sample sizes focused on the upper quarter of the size distribution, of course, but most importantly more sophisticated demographic data and models. This is the key advantage of our approach: because it depends on explicit, process-based models, advances in our understanding of lichen biology will translate directly into more accurate, and precise, lichenometric dates.

One approach to better demographic models is offered by incremental improvements to the model calibration technique presented in Loso and Doak (2005) and summarized here. Our demographic

models were inferred from full SFDs on independently dated shorelines using techniques proven by conservation biologists studying other species (Doak and Morris 1999; Monson *et al.* 2000), and larger calibration datasets collected from surfaces of many ages would support development of more realistic models with additional parameters (Morris and Doak 1998). Particularly valuable model improvements might include incorporation of vital rate variability; use of younger and older calibration surfaces to better characterize early and late lifespan processes; stratification of calibration data to model the influences of aspect, lithology, and other microsite characteristics; and broader geographic coverage of each lichen species' range.

Alongside such improvements, however, we note the significant opportunity of incorporating vital rate functions derived from direct studies of lichen biology. This is an important methodological point: the vital rates that comprise a demographic model (colonization, growth, and survival) need not be inferred from large calibration datasets, as we have done. Growth rates provide an example. A growing number of studies are using direct ongoing measurements of lichen thalli to estimate growth rate patterns and variability (reviewed in Armstrong and Bradwell 2010). Where ecologically and taxonomically appropriate, the functions that describe these patterns can be used directly in the demographic model used to date landforms. The same is true of colonization and survival. In this way, lichenometric dates developed using some evolution of our demography-based approach will benefit directly from advances in our understanding of lichen biology. This, we suggest, is the key to improving the accuracy, precision, and broader acceptance of lichenometry.

## Conclusions

We show that a new lichenometric technique can be employed to date surfaces by comparing lichen size distributions to the predictions of an explicit demographic model. The model uses explicit rules for colonization, growth, and survival to predict expected size distributions on surfaces of different ages. In a previous paper, we derived a demographic model from full size–frequency distributions of lichens on calibration surfaces of known age, but vital rates could instead be taken from direct biological studies. Here, we compared model predictions with lichen distributions on surfaces of unknown age, showing that the technique

is most efficient and accurate when using only lichens in the top quarter of the size distribution. Using two lichen species, our technique successfully provided surface ages for three terminal moraines in southcentral Alaska. The dates are internally consistent and geologically plausible, documenting glacier terminus retreat beginning with an LIA maximum around AD 1816 and accelerating after the early to mid twentieth century. These results demonstrate promise for our general approach, which we suggest can be improved with tighter taxonomic controls, larger sample sizes, and improved demographic models.

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Michael G. Loso, *Department of Environmental Science, Alaska Pacific University, Anchorage, AK 99508, USA*  
Email: mloso@alaskapacific.edu

Daniel F. Doak, *Environmental Studies Program, University of Colorado, Boulder CO 80309, USA*  
Email: daniel.doak@colorado.edu

Robert S. Anderson, *Department of Geological Sciences and INSTAAR, University of Colorado, Boulder, CO 80309, USA*  
Email: robert.s.anderson@colorado.edu

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