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Short communication

Post-glacial dispersal patterns of Northern pike inferred from an 8800 year old pike (*Esox cf. lucius*) skull from interior AlaskaMatthew J. Wooller^{a, b, *}, Benjamin Gaglioti^a, Tara L. Fulton^c, Andres Lopez^{b, d}, Beth Shapiro^c^a Water and Environmental Research Center, University of Alaska Fairbanks, Fairbanks, AK, 99775, USA^b School of Fisheries and Ocean Sciences, Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK, 99775, USA^c UCSC Paleogenomics Lab., University of California Santa Cruz, 1156 High St, Santa Cruz, CA, 95064, USA^d University of Alaska Museum of the North, University of Alaska Fairbanks, Fairbanks, AK, 99775, USA

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ABSTRACT

The biogeography of freshwater fish species during and after late-Pleistocene glaciations relate to how these species are genetically organized today, and the management of these often disjunct populations. Debate exists concerning the biogeography and routes of dispersal for Northern pike (*Esox lucius*) after the last glaciation. A hypothesis to account for the relatively low modern genetic diversity for *E. lucius* is post-glacial radiation from refugia, including lakes from within the un-glaciated portions of eastern Beringia. We report the remains of a Northern pike (*E. cf. lucius*) skull, including bones, teeth, bone collagen and ancient DNA. The remains were preserved at a depth of between 440 and 446 cm in a 670 cm long core of sediment from Quartz Lake, which initiated at ~11,200 cal yr BP in interior Alaska. A calibrated accelerator mass spectrometer (AMS) radiocarbon age of the collagen extracted from the preserved bones indicated that the organism was dated to 8820 cal yr BP and is bracketed by AMS values from analyses of terrestrial plant macrofossils, avoiding any potential aquatic reservoir effect that could have influenced the radiocarbon age of the bones. Scanning electron microscope images of the specimen show the hinged tooth anatomy typically of *E. lucius*. Molar C:N (3.5, $1\sigma = 0.1$) value of the collagen from the specimen indicated well-preserved collagen and its mean stable nitrogen isotope value is consistent with the known predatory feeding ecology of *E. lucius*. Ancient DNA in the bones showed that the specimen was identical to modern *E. lucius*. Our record of *E. lucius* from interior Alaska is consistent with a biogeographic scenario involving rapid dispersal of this species from glacial refugia in the northern hemisphere after the last glaciation.

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1. Introduction

The evolution, refugia, and dispersal of freshwater fish species during and after late-Pleistocene glaciations is relevant for how these species are genetically organized today, and how their disjunct populations need to be managed for diversity (Bernatchez and Wilson, 1998). Beringia offers a globally important case study because much of it was unglaciated during the Pleistocene and served as the primary refugium for many freshwater species during glacial periods (Cumbaa et al., 1981; Bernatchez and Wilson, 1998;

Cox and Hebert, 2001; Weider and Hobaek, 2003; Harris and Taylor, 2009). Salmonid fishes with facultative or obligatory marine stages as part of their life history dominate the freshwater fish fauna in Beringia (Oswood et al., 2000). This prevalence of salmonids highlights the fact that a large portion of present freshwater habitats in the region only became available with the retreat of ice sheets following the last glacial maximum. The presence in Beringia of salmonids and other aquatic species that tolerate saltwater at some point in their life history is most easily explained through marine dispersal. In contrast, biogeographic explanations for Beringian aquatic species with much more strict freshwater requirements, such as the Northern pike, require the historical presence of freshwater connections between linking drainages within and outside areas affected by ice sheets.

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Four of the five living species of *Esox* are found in North America and only one, *Esox reichertii*, is restricted to Eurasia. Given the phylogenetic relationships among the five species of *Esox*, the extant Eurasian forms *Esox lucius* and *E. reichertii* are most likely descendants of North American ancestors (Grande et al., 2004). However estimates of the timing for the divergence between the Holarctic/Eurasian and North American lineages of *Esox* place the occurrence that split well prior any possible influence of Pleistocene glaciations (Campbell et al., 2013) at approximately 45 mybp. Thus, questions of Northern pike (*E. lucius*) biogeography are best examined at the population level and in comparison to populations of other freshwater fishes found in Beringia.

Recent work on the distribution of genetic diversity of a Beringian freshwater endemic species and Northern pike relative, the Alaska blackfish (*Dallia pectoralis*) showed evidence of the persistence of populations of blackfish through several glacial cycles in multiple Beringian glacial refugia (Campbell and López, 2014). In contrast, the timing and genetic affinity of the specimen documented here combined with documented distribution patterns of genetic diversity in modern populations of Northern pike (Skog et al., 2014; López, unpublished data) suggest that Northern pike populations expanded rapidly following glacial retreat. There is no evidence reported to date that indicates the survival of Northern pike in Beringia through the habitat changes associated with Pleistocene glaciations. Notably, a Northern pike population in the vicinity of Yakutat is thought to represent a late Pleistocene relict, however the genetic affinities of that population have not been examined and the 'relictual' status of these aggregations remains speculative (U.S. Dept. of Interior, 1975; p. 359). How dispersals took place for species with low genetic diversity, such as Northern pike (Senanan and Kapuscinski, 2000), can be clarified by analyzing genetic material from ancient specimens that could provide the trail of genetic signatures from former populations. The late-Quaternary fossil record of fish and the paleo-genetic information that they hold is sparse in this region, but additional sites and perspectives can expand the biogeographical details of many economically important species.

Conflicting accounts exist regarding the place of origin and routes of dispersal of Northern pike in the northern hemisphere (e.g., Crossman, 1978; Raat, 1988; Miller and Senanan, 2003), an issue exacerbated by a lack of recent genetic divergence associated with this species in Eurasia and North America (Miller and Senanan, 2003). This could be explained by contact and gene flow between *E. lucius* from various refugia during Pleistocene glaciations (Raat, 1988; Miller and Senanan, 2003). Modern *E. lucius* samples have been placed into three mitochondrial DNA haplogroups, two of which are largely restricted to Europe and one that is found across the Holarctic (Skog et al., 2014). These clades became separated ~200,000 yrs BP and underwent a post-glacial expansion ~100,000 yrs BP (Skog et al., 2014), although the location of the refugia for the late-middle Pleistocene glaciations for the Holarctic clade remain unclear. Drastic population declines on a time scale of several thousand years within European populations of *E. lucius* have been ascribed to either glacial bottlenecks or postglacial founder events (Jacobsen et al., 2005). However, relatively scant paleontological data exists documenting the past geographic presence and distribution of *E. lucius* (Raat, 1988). A suite of hypothetical dispersal patterns has been proposed. The presence of Paleocene *Esox* fossils in North America (Wilson, 1980) indicates that there was access of *Esox* sp. to North America from Asia via the Bering land bridge. Alternative hypotheses include North American origins or immigrations of *E. lucius* from Europe via the deGeer route (Raat, 1988). Paleontological dentaries from deposits in the Old Crow area of the Yukon Territory indicate that Northern pike probably had crossed the Bering land bridge by

>40,000 years ago and support the idea that *E. lucius* was present in refugia in Beringia during the Wisconsin glaciation (Crossman and Harington, 1970). Fossil pike remains from a site in the southern end of lake Michigan demonstrate the occurrence of *E. lucius* during the Holocene and within the present range of the species in North America (Bland and Bardack, 1973; Teller and Bardack, 1975) and some evidence indicates that *E. lucius* may have repopulated North America from multiple southern refugia (Seeb et al., 1987). We report on the remains of a Northern pike (*E. cf. lucius*) skull, including bones, teeth, bone collagen and ancient DNA from a lake sediment core taken from Quartz Lake in interior Alaska. Our ancient DNA data from bone preserved in lake sediments also add to the currently limited, but gradually increasing, number of studies that have demonstrated the utility and viability of ancient DNA from lake sediments to inform biogeographic and paleoenvironmental reconstructions (Anderson-Carpenter et al., 2011; Parducci et al., 2012).

2. Study site, materials and methods

Here we document a fossil record of *E. lucius* in Quartz Lake (70°22.739'N, 157°20.861'W, Fig. 1), which is located north of the Alaska Range in Alaska and was part of the un-glaciated terrain in eastern Beringia during the last glaciation. No modern population of *E. lucius* exists in Quartz Lake today because this species was eradicated using rotenone in 1970 (Doxey, 1991).

A 670 cm sediment core (core code QL-2010c) was taken from Quartz Lake, interior Alaska and a chronology for the core was established (Wooller et al., 2012a,b see also Table 1). A collection of bones, some measuring ~5 cm in length, and sharp teeth were encountered (440 and 446 cm depth) in the sediment core. The bones and teeth were examined under a dissecting microscope and with a scanning electron microscope (SEM). A sub-sample of the bones was sent to BETA-analytic for collagen extraction and radiocarbon dating. All AMS radiocarbon dates were calibrated using the Calib 7.0 software (Stuiver et al., 2009). A sub-sample of the collagen was analyzed for its stable nitrogen isotope composition (expressed as $\delta^{15}\text{N}$ values) (Wooller et al., 2012b). We also separated cladoceran ephippia (following Wooller et al., 2012b) from five sediment samples (mid point depths 329.5, 369.5, 459.5, 479.5, 484.5 cm) that bracketed the depth of the bones in the core (440 cm) to generate $\delta^{15}\text{N}$ values to determine the relative trophic position of the organism represented by the bones.

DNA extraction and all pre-PCR work of the specimen was performed in a dedicated ancient DNA facility at the Pennsylvania State University that is housed in a separate building from any laboratories that perform genetic analysis. Ancient DNA protocols were strictly adhered to at all stages (Cooper and Poinar, 2000; Gilbert et al., 2005). No fish specimens have ever been previously processed in this facility. Ancient DNA extraction from bone was performed following Rohland et al. (2010), with a final elution into 50 μl TE plus 1.5 μl Tween20. An extraction negative control (no sample) was carried out simultaneously. A series of primers were designed to amplify a series of ~200 bp overlapping fragments (Table 2), targeting regions of the mitochondrial D-loop and cytochrome *b* (cytb). PCR amplifications were performed in 25 μl reactions comprising 50 μg rabbit serum albumin, 0.25 mM dNTPs, 1X High Fidelity buffer, 1.25 units Platinum Taq High Fidelity (Life Sciences), 2 mM MgSO_4 , 0.4 μM of each primer, and 0.5 μl DNA extract. Cycling conditions for all fragments were 94 °C for 90 s, 60 cycles of 94 °C for 45 s, 45 s at 54 °C, 68 °C for 90 s, with a final hold for 10 min at 68 °C. Negative PCR reactions (containing no DNA extract) were included for each amplification reaction. PCR products were cleaned using Millipore Multiscreen PCR μ96 filter plates. Each of the three fragments for each marker was amplified

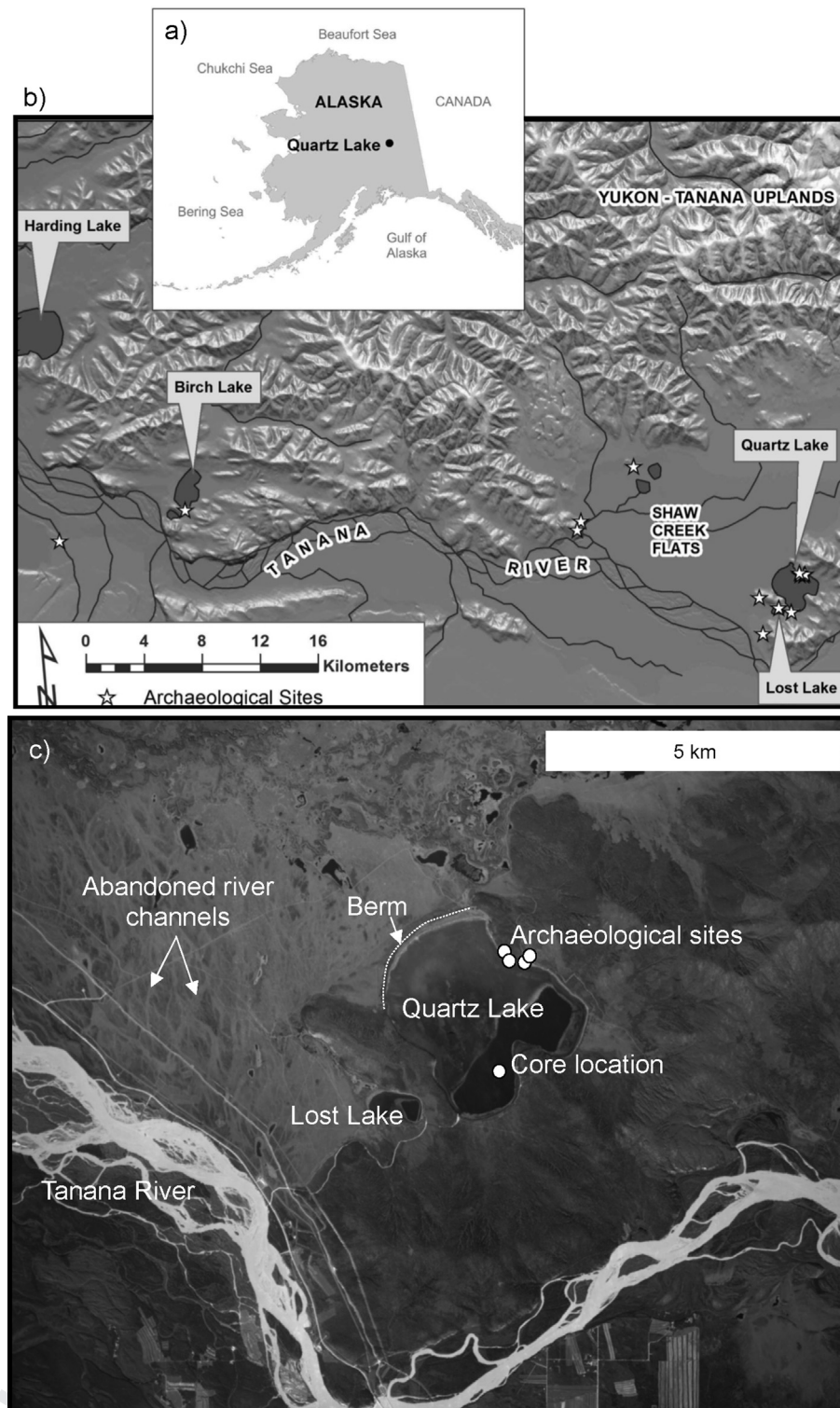


Fig. 1. Location of Quartz Lake in Alaska (inset) and locations of the coring site (QL-2010c) in the lake.

twice. To assess potential DNA damage, all amplifications were cloned using a reduced volume reaction of the TOPO-TA cloning kit (Life Sciences). Multiple clones were amplified in a 12.5 μ l total reaction volume comprising 1X Econotaq buffer (including $MgCl_2$), 0.625U Econotaq (Lucigen), 0.25 mM dNTPs, 1 μ M each M13F(-20) and M13R, and 5 μ l of the colony in water (each colony is picked

into 50 μ l water). Positive clone amplifications were sequenced with BigDye v3.1 chemistry (Life Sciences) using M13F(-20). Following ethanol/EDTA precipitation, sequences were resolved on an ABI3730xl DNA Analyzer (Applied Biosystems) at the Penn State Genomics Core Facility (University Park). All sequences were visualized and aligned using Lasergene 8 (DNASTAR).

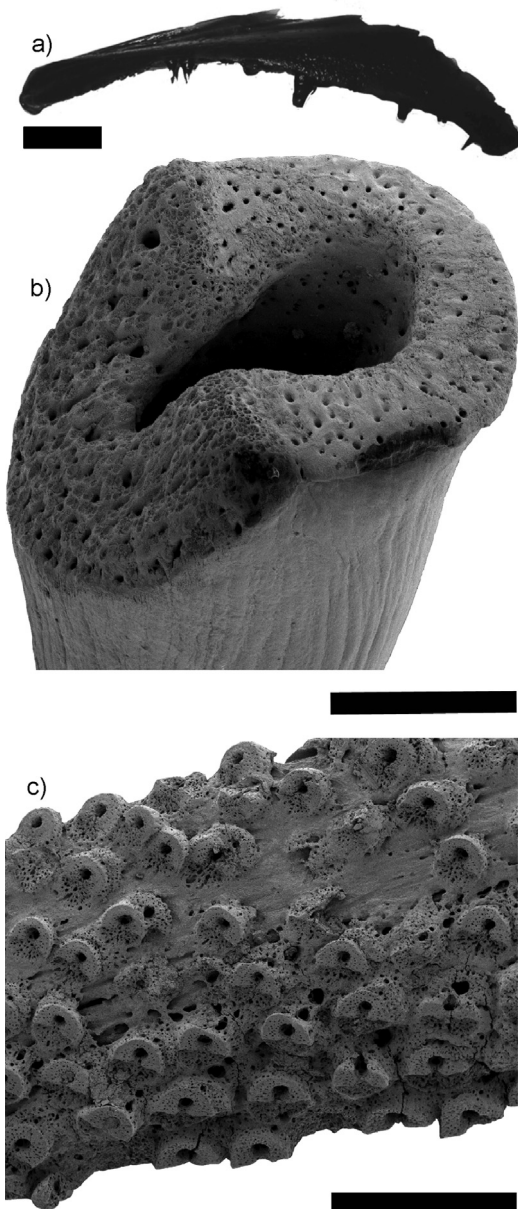


Fig. 2. a) Jaw bone with teeth from core QL-2010c (black bar = 1 cm length). b) scanning electron microscope image of the basal area of a tooth from the jaw (black bar = 2 mm length). c) scanning electron microscope image of the jaw (black bar = 1 cm).

The final sequences obtained from the ancient fish specimen were 423 base pairs (bp) of cytb and 407 bp of D-loop. DNA sequences were aligned with sequences obtained from GenBank (Accessions listed in Table S1). The final D-loop alignment was 405 bp in length, comprising 23 *E. lucius* sequences. Sequences from Maes et al. (2003) were not included in the network analysis, as the alignment had to be reduced to <300 bp to avoid sites with missing data. The final cytb alignment was trimmed to 401 bp in length, comprising 14 *Esox masquinongy*, 5 *Esox niger*, 10 *Esox americanus*, 11 *E. reichertii*, and 57 *E. lucius* sequences. Median joining networks for *E. lucius* D-loop and for cytb sequences were produced using Network v4.613 (Bandelt et al., 1999) (Fig. 3a,b). A multi-species split decomposition network was estimated using SplitsTree4 (Huson and Bryant, 2006) (Fig. 3c).

3. Results

The set of bones and teeth removed from the sediment core taken from Quartz Lake included a right dentary with four complete lateral teeth (Fig. 2a). The shape and size of the bones and teeth, and submandibular pores indicated the bones represented a member of the family Esocidae. Scanning electron microscope images of the specimen show the hinged tooth anatomy typically of *E. lucius* (Fig. 2b and c). The bones were compared with the comparative modern collection of fish specimens in the University of Alaska Museum of the North.

Twelve AMS radiocarbon analyses were previously reported from analyses of terrestrial plant material from the sediment core (Table 1), which were used to produce the chronology for the core from which the bones were removed (Wooller et al., 2012a). The bones were located at between 440 and 446 cm in the sediment core. Results from an AMS radiocarbon analysis of collagen extracted from the bones (Table 1) produced a calibrated 2σ age range of 8650–9000 cal yrs BP (mean = 8820), which overlaps the two calibrated ages produced from plant macrofossils above and below this specimen (Table 1). The age of the specimen is also consistent with the interpolated age of the specimen (8600–8800 cal yrs BP) based on its depth range (440–446 cm) from within the core and using the AMS radiocarbon chronology for the core (Wooller et al., 2014a).

The collagen from the bones had a mean ($n = 3$) molar C:N value of 3.5 ($1\sigma = 0.1$) that is typical of well-preserved collagen (2.9–3.6, Ambrose, 1990). The $\delta^{15}\text{N}$ values of the bones (9.3‰, mean of $n = 3$) were relatively high (5.0‰), compared with values from the lake sediment surrounding the bones (4.2‰, mean of $n = 3$) and aquatic invertebrate remains (cladoceran ephippia) from the same sediment (4.1‰, mean of $n = 5$), and are consistent with the elevated $\delta^{15}\text{N}$ values expected of a predatory fish, such as pike. A single trophic level can impart ~3.4‰ increase in $\delta^{15}\text{N}$ values per trophic level (Minigawa and Wada, 1984). Using the sediment and the invertebrate results as indicators of the baseline $\delta^{15}\text{N}$ value for the ecosystem at the time the ancient fish from Quartz Lake gave an estimated trophic level of between 1.8 and 2.

DNA sequences for D-loop and cytb are entered into GenBank with accessions (Supplemental documents Table 1). The DNA appeared to be exceptionally well-preserved and had very little DNA damage. One G to A transition was observed at cytb base 395 (4 clones stemming from two independent PCRs had state G, 2 clone sequences had A). Three damaged bases were observed in the D-loop fragment: G to A at base 84 (8G:2A), C to T at base 119 (11C:3T), and C to T at base 276 (13C:3T). In all cases, multiple independent amplifications confirmed the true sequence. Both the D-loop and cytb haplotype sequences are identical to many previously sequenced modern *E. lucius* individuals available in GenBank (Fig. 3) and is clearly referred to this species genetically, consistent with the morphological analyses. The D-loop sequence of the newly described specimen matches haplotype 'B' of Skog et al. (2014) found across the Holarctic including a modern Alaskan sample and haplotype Eld7 (Maes et al., 2003) from Ontario, Canada. The Maes et al. (2003) sequences were not included in the network analysis, as their inclusion led to too many sites with missing information. The cytb haplotype is common in GenBank entries from isolates deriving from across the Holarctic.

4. Discussion

Our ancient DNA and radiocarbon results show the presence of Northern pike (*E. lucius*) in Quartz Lake, Alaska at 8820 cal yr BP. Quartz Lake formed at ~11,200 cal yr BP (Wooller et al., 2012a) in one of this species' purported sub-arctic, glacial refugia (in eastern

Table 1
AMS radiocarbon ages and calibrated ages for material from Quartz Lake.

AMS laboratory accession number	Type	Depth (cm)	¹⁴ C age (yr BP)	Error	Mean calibrated age (cal yr BP)	Calibrated range (cal yr BP) 2 sigma
NSRL-19964	Charcoal/Birch Seeds	8	935	±15	855	800–920
NSRL-19965	Charcoal	150	2535	±15	2626	2510–2740
NSRL-19966	Birch Seeds and Spruce Seed	210	3620	±15	3929	3880–3980
NSRL-18167	Plant Macrofossils	215	4020	±15	4480	4430–4530
NSRL-18166	Wood	265	4170	±20	4726	4620–4830
NSRL-19968	Birch Bracts and Birch Seeds	320	5200	±15	5954	5920–5990
NSRL-19970	Birch Seeds and Spruce Seeds	416	6970	±25	7819	7720–7920
BETA-294705	Fish (Pike) Bone	440–446	7960	±50	8820	8650–9000
NSRL-18164	Spruce Cone	465	8435	±25	9476	9430–9520
NSRL-18165	Wood	533	9910	±25	11,314	11,240–11,390
NSRL-18163	Plant Macrofossils	554	10,015	±25	11,513	11,330–11,700
NSRL-18160	Wood/Charcoal	666	10,040	±30	11,555	11,360–11,750
NSRL-18161	Plant Macrofossils	681	10,945	±30	12,799	12,660–12,940

Beringia). Our dated fish specimen's D-loop and cytochrome b (cytb) haplotype clearly identify it as *E. lucius*, as it is identical to sequences obtained from modern individuals found across the Holarctic (Fig. 3a, Table S1). Although individuals deriving from this mitochondrial haplogroup are found across the Holarctic, all but one individual sequenced from a North American location from Alaska to Ontario belong to this haplogroup and are very closely related. This supports a single expansion across North America out of Alaska, likely within the last ~100,000 years based on fossil specimens and Skog et al.'s (2014) estimate of the post-glacial expansion timing of this clade. In this regard our data are consistent with fossil Northern pike remains from deposits in the Old Crow area of the Yukon Territory that support the idea that *E. lucius* was present in refugia in Beringia during the Wisconsin glaciation (Crossman and Harington, 1970). Alaska itself may have been colonized more than once from Asia, given that multiple haplogroups are observed in modern Alaskan populations. However, available genetic data from across North America are sparse. Northern pike have consistently shown low within-population variation (Miller and Senanan, 2003; Skog et al., 2014). Low genetic variation within populations may result from compounding factors of low effective population size and bottlenecks (Miller and Senanan, 2003). A glacial refugium in southern North America has been previously proposed on the basis of allozyme genetic differences in the Mississippi drainage (Seeb et al., 1987); however, DNA sequence data are lacking from this region so we cannot assess this herein. Our data certainly place Northern pike north of the Alaska Range at a date that is relatively close to the recession of glaciers in eastern Beringia.

Table 2
Ancient DNA primers.

Target region	Primer name	Primer sequence	Fragment length (bp) ^a
Cytochrome b	EsoxCytbF1	TTGTAAACTTCAACTATAAGAACT	212
	EsoxCytbR1	AGGCTGTGGAGATGTCAGAG	
	EsoxCytbF2	TRATTACACAAATCCTAACCG	176
	EsoxCytbR2	GGCGATGTGTATRTAAATRCAG	
	EsoxCytbF3	AAATATTCAYGCTAACGGTGC	204
	EsoxCytbR3	TTAGTAATTAAGTGTGCGCCT	
Dloop	Esox_DL1	GATTCTAAATTTAACTACCTCTG	174
	Esox_DL1R1	CTCGTGATTGCTTTATGTA	
	Esox_DL1F2	TTGAATTTACCCCTCATACA	208
	Esox_DL1R2	TGCACGAGTGGAACTCGTTG	
	Esox_DL1F3	AAACTCAACATCCCTACAG	196
	Esox_DL1R3	CAGATGCATACCATTCGGC	

^a Fragment length includes primers.

Freshwater habitats in Beringia during the last glaciation were fragmented on a macro scale by glaciers straddling the major mountain ranges (Manley and Kaufman, 2002), and by aridity on a micro scale. Many lakes were either dry or acted as closed basin during Marine Isotope Stage (MIS) 2 because the climate was much more continental in nature (Guthrie, 2001; Elias and Crocker, 2008). The timing and mode of post-glacial dispersal of fish out of Beringia was mediated by glacial re-advances, pro-glacial lakes, outburst floods, and habitat succession after deglaciation (Bernatchez and Wilson, 1998). For example, shortly after deglaciation, Broad Whitefish colonized the Mackenzie River basin through the Arctic Ocean and via glacial meltwater connections with the Yukon River basin (Harris and Taylor, 2009). Many freshwater species dispersing from full glacial Beringia are now widespread in North America.

The most parsimonious mechanism by which Northern pike might have gained access to Quartz Lake probably involved connectivity between Quartz Lake and the Tanana river, which is only ~3.5 km away from Quartz Lake today and may have been more connected in the past compared with its current closed-lake system status (Wooller et al., 2012a). Northern pike can certainly thrive and migrate along rivers (Rohtla et al., 2012; Engstedt et al., 2014; Pauwels et al., 2014). Since Quartz Lake is relatively close to the headwaters of the Tanana River (Fig. 1) our finding implies that Northern pike were likely also present in the substantial watershed covering much of the interior of Alaska by ~8820 cal yr BP as a result of upstream-directed connectivity, which controls the dispersal of Northern pike among lakes (Spens et al., 2007). In other words, all lakes with adequate connections to a dispersal source situated downstream are expected to have Northern pike (Spens et al., 2007).

Since the Northern pike specimen came from a previously analyzed lake-sediment core from Quartz Lake (Wooller et al., 2012a) we are able to provide some direct paleoecological context for the specimen. There appears to have been an increase in lake production that occurred after ~10,500 cal yr BP, which could have resulted from an increase in July temperature and decreased ice cover (Wooller et al., 2012a). Increased autochthonous production from ~10,300 cal yr BP peaked at ~9500 cal yr BP (Wooller et al., 2012a) and the development of this productive lacustrine environment probably provided a habitat and food web to support an aquatic predator such as a Northern pike. Certainly the trophic level of the fish specimen (1.8–2) from the core is consistent with the opportunistic, predatory feeding ecology of Northern pike (e.g., Beaudoin et al., 1999; Paradis et al., 2008; Cott et al., 2011; Sepulveda et al., 2013; Lepak et al., 2014). Our finding also shows that the pike fossils were actually present during a period of

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relatively declining lake production (from ~9500 to 6600 cal yr BP) (Wooller et al., 2012a). Modern Northern pike have been shown to adapt their feeding ecology and subsequently lower their trophic level during periods when the availability of higher trophic level diet items, such as prey fish, is reduced (Beaudoin et al., 1999; Venturelli and Tonn, 2006). The magnitude of variation in the $\delta^{15}\text{N}$ values of the sediment (range = -1.7 – 7.0‰) (Wooller et al., 2012a) and Cladoceran ephippia (range = -2.2 – 9.7‰) (Wooller, unpublished data) throughout the entire sediment core indicates that any trophic level estimation of this type is only realistic when comparing the stable isotope data from analyses of taxa from the same or similar time period/depth. In terms of trophic ecology Northern pike was also certainly featured as a food resource for past people in the circum-arctic, including those evident from archaeological sites near the Angara river (Mamontov et al., 2006) and Lake Baikal in Russia (Weber and Bettinger, 2010) and in Alaska (Holmes, 2001) during the mid-Holocene. Pike bones and dentaries have also been reported from protohistoric (from AD 1650) and mid to early Holocene-aged archaeological sites around Quartz Lake itself (Gelvin-Reymiller and Reuther, 2010). The presence of Northern pike in Quartz Lake confirms at least the availability of this freshwater food resource to ancient people that were present and using aquatic resources in Interior Alaska at times during the Holocene (e.g., Gelvin-Reymiller and Reuther, 2010). There is certainly evidence of aquatic resources present at archaeological sites in interior Alaska that pre-date the Northern pike specimen we have documented (Holmes, 2001; Potter et al., 2011). In the case of the evidence presented by Holmes (2001) the presence of Northern pike is consistent with our finding and indication of rapid dispersal of Northern pike in eastern Beringia after MIS2.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.quascirev.2015.04.027>.

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