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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 Alaska

Matthew 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.



## 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, 2010). 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.

* Corresponding author. Water and Environmental Research Center, University of Alaska Fairbanks, Fairbanks, AK, 99775, USA.
*E-mail address:* mjwooller@alaska.edu (M.J. Wooller).

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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 to 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 Holartic (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., 2012b 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. A sub-sample of the collagen was analyzed for its stable nitrogen isotope composition (expressed as $\delta^{15}N$ values) (Wooller et al., 2012b). We also separated cladoceran ephippia (following Wooller et al., 2012a) 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 $\delta^{15}N$ 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 Dloop 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