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RESEARCH ARTICLE

Complex distribution of ancient carbon between tributaries of the Upper Lena seen in radiocarbon dates of modern fish

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Abstract
The results of radiocarbon dating of modern fish bone collagen from the Upper Lena River have identified a large and highly variable freshwater reservoir effect, with a maximum offset age of 2389 ± 19 ^{14}C yr BP. Variable contributions from both dissolved bedrock carbonate and permafrost soil melt were identified as the drivers for these reservoir offsets using a combination of bulk and amino acid specific stable carbon and nitrogen isotopes, as well as the novel application of strontium isotope ratios (^{87}Sr/^{86}Sr) to the study of reservoir effects. Strontium isotope ratios were used as a means of identifying the contributions of dissolved limestone and dolostone carbonate to the fish tissues in comparison to their associated radiocarbon (^{14}C) offset ages. An updated model for δ^{13}C and ^{14}C age offsets in fish bone collagen was produced to interpret the potential combined contributions of old carbon from both permafrost soil melt and carbonates from bedrock erosion. The wide range of ^{14}C offset ages identified in this study poses challenges to producing robust corrections for both modern and archaeological reservoir effects in human populations. Specifically, there is a need to address the potentially wide range of ^{14}C ages which fish could represent, rather than using reservoir effect correction models which function best with uniform endmember contributions of old carbon.

Introduction

The equal availability of the radioactive isotope ^{14}C across all environments is a key principle of radiocarbon (^{14}C) dating that is required to provide an accurate estimate of the age of carbon-based tissues (Barker 1958; Libby 1967). This principle is violated when there is either a delay in the mixing of atmospheric ^{14}C to an organism's environment or old carbon is released into these environments and becomes incorporated into the tissues of living organisms. These carbon reservoirs have an especially strong impact on aquatic environments in which there is either a slow mixing of water layers with atmospheric carbon (Arnold and Anderson 1957; Craig 1957; Revelle and Suess 1957) or an introduction of ^{14}C-depleted carbon (Deevey et al. 1954; Godwin 1951). However, freshwater reservoir effects (FRE) can be corrected to improve local archaeological chronologies (Arundale 1981; Harp 1976; Lanting and van der Plicht 1995/1996, 1998; Schulting et al. 2022). To ensure these corrections are as accurate as possible each freshwater system must be studied separately to account for the unique properties of individual rivers, lakes and wetlands, and the relatively rapid changes they may undergo.

Recent research in the Cis-Baikal region of Siberia has produced substantial knowledge on correcting human radiocarbon ages for FRE (Bronk Ramsey et al. 2014; Schulting et al. 2015, 2014, 2018, 2022;

Weber et al. 2016). A current limitation in our knowledge of the Upper Lena reservoir effect is that it has predominantly been characterized by comparisons made between archaeological samples of human and terrestrial faunal bone through paired dating (Schulting et al. 2015), with only a single date directly analysing fish from the river. Freshwater resources from the Upper Lena contributed to the diets of mid-Holocene hunter-gatherer communities as observed through stable carbon and nitrogen isotope analysis of human bone (Schulting et al. 2015). This is associated with a radiocarbon reservoir effect that appears to be unique to this microregion, and differing from those of Lake Baikal and the upper reaches of the Angara River (Schulting et al. 2022). By studying the current reservoir effect on fish from the Upper Lena system a better understanding can be gained of its impacts on radiocarbon dating of skeletal remains from prehistoric hunter-gatherer groups of this region. This research also contributes to our understanding of modern carbon cycling in the Upper Lena by providing insight into the flow of ancient carbon into the freshwater ecosystem.

The Upper Lena in scientific literature refers to the upper reaches of the Lena River, a 1530 km long section from its source approximately 10 km north of Lake Baikal to the Vitim River tributary (Pavlovskii 1929). The Upper Lena is separated from Lake Baikal by the Primorskii and Baikal'skii mountain ranges and its sources of old carbon are, therefore, independent of the lake. The waters of the Upper Lena are constantly flowing so delayed mixing with atmospheric ^{14}C cannot account for the observed radiocarbon reservoir effects. Instead, sources of old carbon must have entered the river and its tributaries and become incorporated into the tissues of freshwater plants and fish.

Sources of old carbon

Many potential sources of old carbon can enter freshwater environments and produce radiocarbon reservoir effects. Carbon may be incorporated from dissolved carbonate bedrock (Deevey et al. 1954; Godwin 1951; Turner et al. 1983); deep lake sediments may hydrate methane gasses (Kalmychkov et al. 2006; Prokopenko and Williams 2004); the groundwater supplying a river may be ancient (Riggs 1984); carbon from glacial meltwater can introduce old carbon (Doran et al. 1999; Hendy and Hall 2006); or old organic carbon could be released from peat and/or melting permafrost during periods of climatic warming (Guo et al. 2004; Gustafsson et al. 2011). Along with providing a characterisation of the current reservoir effect of the Upper Lena system through ^{14}C dating of fish bone collagen, this study seeks to determine the source(s) of old carbon that are driving the reservoir effect. The two most likely candidates for old carbon in the Upper Lena system are dissolved carbonate from bedrock and organic carbon released from peat and permafrost melt.

The Upper Lena upstream from the city of Kachug has several main tributaries (including the Anga, Manzurka, Ilikta, Chanchur, Anay and Pankucha) (Figure 1) which flow over limestone and dolostone bedrock outcrops (Figure 2A) that date back to between 488 to 600 M years ago and could release carbonates with no remaining ^{14}C. The Precambrian limestone and dolostone carbonate is much older than the limits of ^{14}C dating (>50,000 years), but when it is incorporated into the dissolved inorganic carbon (DIC) through dissolution by carbonic acid derived from atmospheric water, a maximum of 50% of the resulting DIC originates from the calcite carbonate ($CaCO_3$) in limestone (Broecker and Walton 1959). This results in a maximum reservoir offset age of 5730 ^{14}C yrs for the DIC (i.e., one half-life of ^{14}C) (see Philippsen 2013). Dolomite ($CaMg(CO_3)_2$), the mineral in dolostone, is slower to saturate into freshwater environments than calcite from limestone but will result in the same impact on the ^{14}C content of the DIC (Clark and Fritz 1997; Philippsen 2013). This DIC is incorporated into the food web through photosynthesis by phytoplankton, aquatic plants, or cyanobacteria (blue-green algae) which are then consumed by zooplankton, fish and other aquatic feeders (Clark and Fritz 1997; Philippsen 2013; Zhang et al. 2019). However, turbidity limits photosynthesis and results in low primary productivity. Where the Lower Lena drains into the Laptev Sea the phytoplankton biomass amounts are low and seasonally dependent with the highest concentrations occurring during the summer and autumn (1.0 – 4.0 mg/L) (Cauwet and Sidorov 1996). Contributions of dissolved limestone carbonate to the Upper Lena reservoir

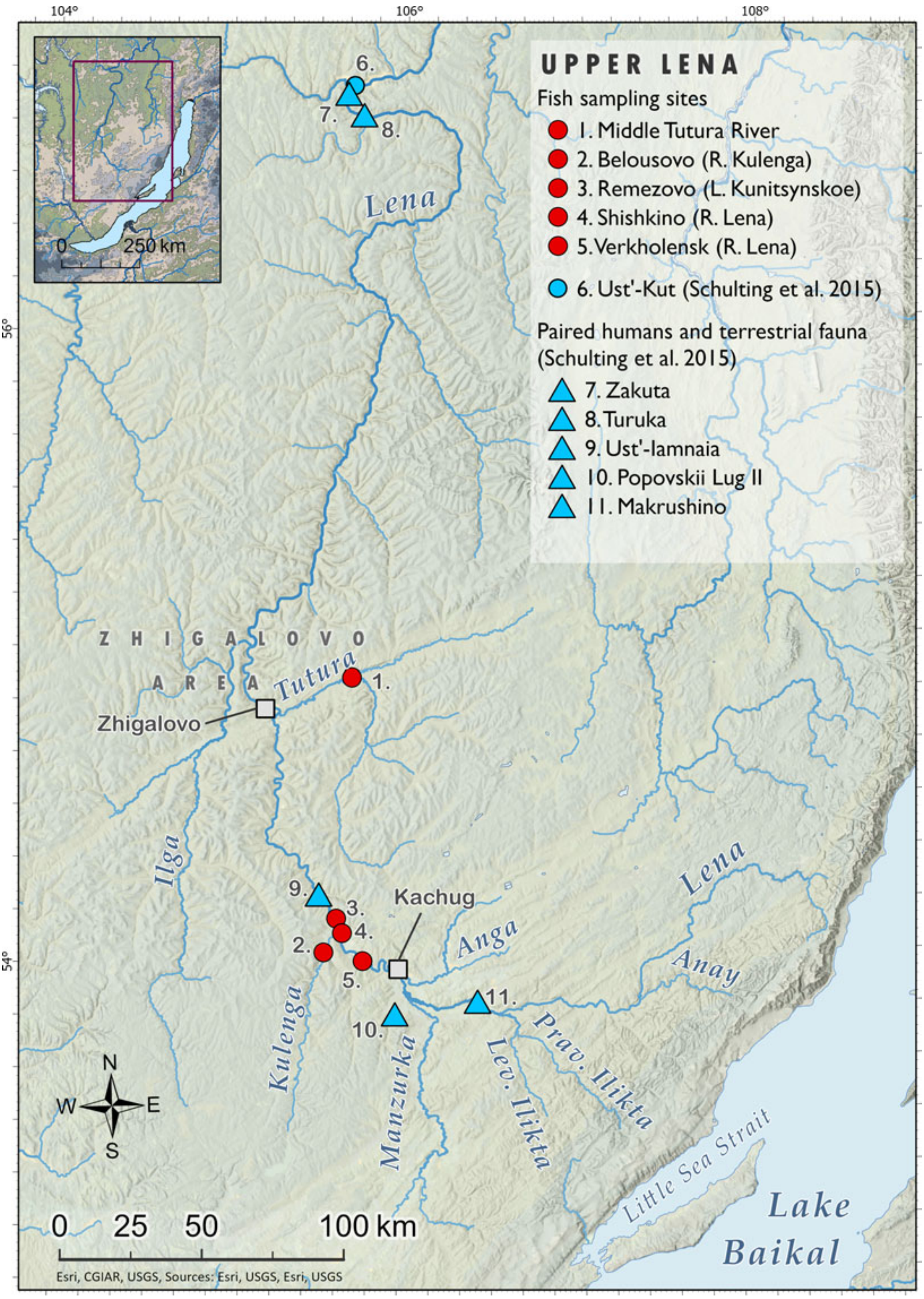

Figure 1. *Map of the Upper Lena and its various tributaries examined in this research. Locations of sampling sites for modern fish sampled for this research (1–5) and previous research (6) are indicated with circles, and previously published archaeological sites (7–11) are indicated by triangles (Schulting et al. 2015).*

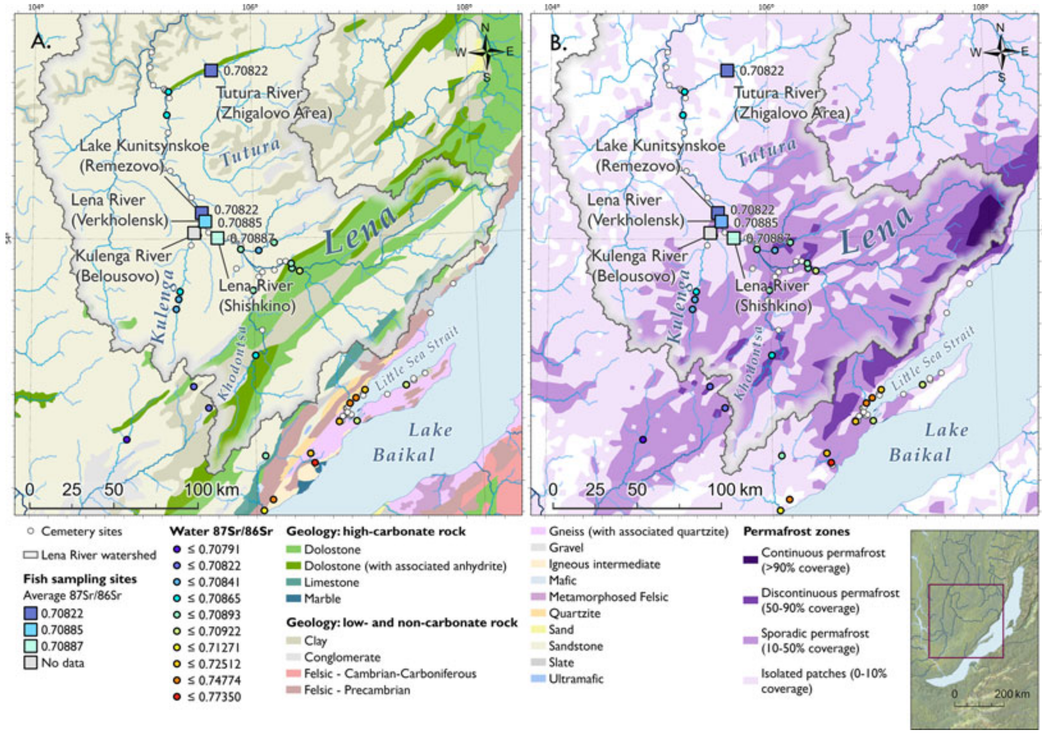

Figure 2. *Map of the underlying bedrock geology (A) over which various tributaries of the Upper Lena flow. Model of the modern extent of permafrost surrounding the watershed of the Upper Lena River system by Obu et al. (2019) (B).*

effect may vary seasonally due to the fluctuation in phytoplankton biomass brought about by seasonal changes in turbidity (Opekunova 2014), resulting in a smaller contribution to the old carbon in freshwater fish compared to organic carbon sources.

Organic carbon released from peat and permafrost melt is another likely candidate for old carbon in the Upper Lena system. While only the main headwater stream of the Upper Lena flows through continuous permafrost, much of its catchment contains sporadic (10–50%) and isolated patches (0.5–10%) of permafrost soils (Figure 2). Due to recent climate change, the permafrost soils of the Cis- and Trans-Baikal regions are melting (Boike et al. 2013; Romanovsky et al. 2010). The impact of permafrost melt on the discharge of the Lena has been well studied by ecologists tracking carbon discharge into the Arctic Ocean (Bröder et al. 2018; Costard et al. 2003, 2007; Feng et al. 2013; Fuchs et al. 2020; Vonk et al. 2012, 2013; Zhang et al. 1999). This research has included ^{14}C dating as a means of identifying the carbon released through soil permafrost melt based on its reservoir age (Ogneva et al. 2023; Shi et al. 2020; Vonk et al. 2012, 2013). Additionally, organic carbon released from peat and permafrost melt would be more easily incorporated into the aquatic food chain than DIC from dissolved carbonates. The dissolved organic carbon (DOC) from permafrost soils has a relatively low molecular weight that allows it to be transported directly through microbial cell membranes, and the limited degradation results in a high nutrient content (Mann et al. 2015; Vonk et al. 2013). Unlike inorganic carbon, organic carbon can be directly consumed by zooplankton and fish without relying on its incorporation through photosynthesis. It is, therefore, likely that the fish of the Upper Lena and its tributaries are incorporating this old carbon from permafrost melt into their tissues through their diet.

Isotope approaches

Our research distinguishes between reservoir effects driven by dissolved bedrock carbonate and permafrost soil melt using stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope analysis on bone collagen and strontium isotope ratio (^{87}Sr/^{86}Sr) analysis on bone apatite from modern fish from the Upper Lena and its tributaries. Philippsen (2015) provides a model for the impact which various old carbon sources would have on both the ^{14}C age and δ^{13}C value of fish bone collagen (Philippsen 2015: Figure 3). This model predicts that an increasing influence from fossil carbonate would result in a positive correlation between δ^{13}C values of DIC in freshwater environments and the ^{14}C age of that DIC, while the influence of the rhizosphere root zone would result in lower δ^{13}C values with lower ^{14}C age offsets. Both factors would produce a positive linear correlation between ^{14}C age and δ^{13}C values of DIC. However, the incorporation of old organic carbon from permafrost soil melt is more likely to produce a different relationship between ^{14}C ages and δ^{13}C values of bone collagen. A relationship between bulk δ^{13}C and FRE offset is anticipated from permafrost melt DOC due to the predominant C$_3$ environment of the Lake Baikal terrestrial ecosystem. This C$_3$ environment would produce δ^{13}C values around –25‰ (Cerling et al. 1997; Pessenda et al. 2016) for any terrestrial-based carbon originally incorporated into the permafrost. It is, therefore, expected that there would be a negative relationship between FRE offsets and bulk δ^{13}C values if permafrost melt is the predominant source of old carbon driving the FRE.

Amino acid specific stable carbon and nitrogen isotope analysis may further clarify whether changes in bulk δ^{13}C or δ^{15}N values are due to environmental changes or differences in individual fish diets. This technique examines the unique isotopic fractions of the individual amino acids which make up the protein structure of bone collagen. The first broad characterization of amino acids can be made between essential and non-essential amino acids (Reeds 2000; Womack and Rose 1947). Non-essential amino acids are those that the body can metabolize from other amino acids within the body and thus produce them *in vivo*. However, essential amino acids cannot be produced by the body and can only be acquired through diet. Some amino acids may be referred to as conditionally essential which means that the body can metabolize the amino acid, but either due to high demand or stressful conditions not enough of the amino acid is produced to meet the body's needs and instead relies more heavily on dietary sources (Lacey and Wilmore 1990; Young and El-Khoury 1995). Categories of essential and non-essential amino acids work well to characterize the excepted pattern in δ^{13}C values of individual amino acids (Hare et al. 1991; Macko et al. 1987). To explain amino acid δ^{15}N variation the terms source and trophic amino acids are used based on the observed δ^{15}N fractionation of these amino acids (O'Connell 2017; Popp et al. 2007). Source amino acids are amino acids that do not experience large fractionations between diet amino acid δ^{15}N values and tissue amino acid δ^{15}N values. The bonds between the nitrogen group and the amino acid are not broken between ingestion and tissue synthesis for source amino acids. Trophic amino acids are amino acids that do experience large fractionations between diet amino acid δ^{15}N values and tissue amino acid δ^{15}N values because the bonds between the nitrogen group and the amino acid are broken and remade creating the large fractionation observed in the tissue amino acid δ^{15}N values. If the essential amino acid δ^{13}C values or source amino acid δ^{15}N values vary among fish from different sampling locations this would likely reflect changes in the primary production affecting the base food web sources (Larsen et al. 2015; Lorrain et al. 2009; Ruiz-Cooley et al. 2014). Significant changes in essential amino acid δ^{13}C values with differences in ^{14}C age would indicate that the reservoir effect is likely driven by baseline food web changes such as differential inputs of a source of old carbon.

Strontium isotope analysis is based on the premise that physical and chemical erosion of bedrock leads to the strontium isotopes being transferred into the ecosystem and entering the food chain (Bentley 2006; Faure 1986; Price 2015). ^{87}Sr/^{86}Sr measured in animal and human tissues thus largely corresponds with local geology, facilitating the application of this method in provenance and mobility studies of humans and animals in the present as well as in the past (e.g. Barakat et al. 2023; Hegg et al. 2013; Koch et al. 1995; Reich et al. 2021; Scharlotta and Weber 2014; Snoeck et al. 2018). A good understanding of the local geology is of paramount importance since the ^{87}Sr/^{86}Sr distribution in the environment depends largely on the age of the underlying bedrock and its mineralogical composition (Bentley 2006; Faure 1986). The underlying bedrock geology impacts not only the soil, but also ground and surface waters, and by inference, local aquatic vertebrates, which absorb through the gills 80% to 88% of their strontium from the rivers and streams in which they live, the remaining strontium being absorbed through the gastrointestinal tract (Chowdhury and Blust 2011; Farrell and Campana 1996; Klaczek et al. 2022; Tchaikovsky et al. 2017). $^{87}Sr/^{86}Sr$ values in the analyzed fish are therefore considered geological signals of the underlying upstream geology and hence possible indicators of the presence of precipitating carbonates that are likely to impact the FRE.

The headwater tributary of the Upper Lena flows over a mixed carbonate and sandstone geology (Figure 1). Sandstones of different ages, are found on the eastern periphery of the Upper Lena microregion, have higher median $^{87}Sr/^{86}Sr$ of 0.71095 to 0.71143, with the highest median values noted in the Lena watershed (Cameron-Werens et al. in prep). The Cambrian and Precambrian limestone and dolostone further downstream the Lena and its tributaries towards the west have median $^{87}Sr/^{86}Sr$ values ranging from 0.70940 to 0.71006. The surface water values, and consequently fish values in the Upper Lena, are expected to display intermediate strontium isotope ratios between the two formations as a result of mixing of old sandstone and high-carbonate rock upstream from Kachug. The Kulenga River, which is Lena's left tributary ~25 km downstream from Kachug, flows over younger low-carbonate sandstone (Cheremkhovskaya formation) that extends over most of the central Cis-Baikal (median $^{87}Sr/^{86}Sr$ 0.71014, mean absolute deviation $MAD = 0.00052$). Similarly, the Tutura River (~100 km from Kachug) in the northern part of the Upper Lena microregion flows over the same Cheremkhovskaya formation sandstone, but also sporadic outcrops of Cambrian dolostone with associated anhydrite (median $^{87}Sr/^{86}Sr$ 0.70940, $MAD = 0.00016$). These various formations have discrete variability in their $^{87}Sr/^{86}Sr$ values, which means that the contribution and impact of different geologies will vary.

Materials and Methods

Sample locations

A total of 37 modern fish samples were collected from five sites along the Upper Lena during 2021 and 2022 (Figure 1). For discussion on the potential for bomb pulse carbon to influence the radiocarbon dates of these fish see Supplementary Information SI 1.9. Four of these sites are located along the Upper Lena and its tributaries, and one is a small oxbow lake alongside the Upper Lena. The Shishkino and Verkholensk sampling locations are near prehistoric burial sites of the same names. These two sites are downstream from the linear folds comprised of formations of Precambrian sandstones intertwined with high-carbonate bedrock, and their catchment areas include continuous, discontinuous and isolated patches of permafrost soils (Obu et al. 2019) (Figure 2A). Belousovo is located along the Kulenga River which passes over sandstone bedrock and through areas of sporadic and isolated permafrost soils. The farthest downstream sampling location is at the Tutura River (Middle Tutura), located c. 100 km north of the city of Kachug (Figure 1). The Tutura River flows mainly over areas of sandstone with some outcrops of dolostone bedrock, and areas with soils that range in permafrost coverage from none to sporadic and isolated patches (Figure 2A). Lake Kunitsynskoe (Remezovo sampling site), while close to Verkholensk, is not connected to the Upper Lena system (Figure 1).

Fish species

Multiple modern fish samples of seven species (*Brachymystax lenok, Esox lucius, Hucho taimen, Leuciscus leuciscus, Perca fluviatilis, Phoxinus* sp.*, Thymallus arcticus*) were collected from these locations based on their availability (Table 1). Some of these species (i.e., *Perca fluviatilis, Brachymystax lenok, Esox lucius, Hucho taimen*) are obligatory predators, while others (i.e., *Phoxinus* sp.*, Leuciscus leuciscus, Thymallus arcticus*) have mixed feeding diets which may include zoobenthos, insects, larvae, worms, plankton, diatoms, etc. (Supplementary Information S1.1). Most have either localized ranges or semi-migratory ranges in which the fish go into tributaries to spawn (Supplementary Information S1.1). The northern pike (*Esox lucius*) has a localized range within the Upper Lena, but can sometimes migrate up to 200–300 km (Egorov 1985; Popov 2007; Pronin et al. 2007). A range of life expectancies are represented by these species with most between 10–15 years (Supplementary Information S1.1). All samples were caught as live fish, length was recorded (Supplementary Information Table S1), the flesh was stripped from the bones by immersion in boiling water for ~1 min and the bones were dried.

Radiocarbon dating

The samples were prepared for ^{14}C dating in two separate batches according to the protocol AF for bone collagen outlined by Brock et al. (2010). The first group (OxA- 42043–42272) represent eight samples from the Lake Kunitsynskoe (Remezovo), Kulenga River (Belousovo), and Tutura River (Middle Tutura) sites. The samples from this first batch were prepared for ^{14}C dating following the ORAU standards for bone samples with an additional step for lipid removal (Brock et al. 2010) (Supplementary Information, SI 1.2–1.3). All remaining samples underwent collagen extraction based on the protocols for stable carbon and nitrogen isotope analysis by the Oxford Stable Isotope Lab (SI 1.4). The prepared Ezee-filtered collagen was then weighed out to undergo a radiocarbon combustion (see Brock et al. (2010:110)) in the same manner as the first batch.

Collagen was flash combusted in a EA-IRMS system alongside alanine reference standards to produce the δ^{13}C values used in the stable carbon isotope fractionation correction applied to the ^{14}C measurement according to Stuiver and Polach (1977) (Brock et al. 2010). These δ^{13}C values are provided in Table S3. A fraction of the CO_2 gas produced at the same time was captured in a liquid nitrogen trap and then graphitized, before being pressed into targets and then dated using the MICADAS 200 kV AMS system (Ionplus AG) at ORAU (Brock et al. 2010). A matrix-matched (i.e., collagen) background standard was then subtracted from the corrected age. OxA- and OxA-X codes were assigned to the resulting dates based on established collagen quality control criteria. Samples received an OxA-X designation when the collagen extraction did not meet the collagen quality standards of a wt % yield > 1.0%, a C:N$_{\text{atomic}}$ ratio between 3.0 – 3.4 (Wood et al. 2023, 579), or ≥ 5% wt% N. When samples fall outside of these quality controls it suggests the sample may not represent well isolated collagen free from lipids or non-collagenous proteins.

Bulk stable carbon and nitrogen isotope analysis

When possible, the excess collagen produced during the preparation of samples for ^{14}C dating was analyzed separately for stable carbon and nitrogen isotope analysis on a Sercon 20/20 EA-IRMS at the Oxford Stable Isotope Lab. When samples from the first chemical pretreatment did not provide enough excess collagen (< 1.0 mg) an additional bone sample was taken for a new collagen extraction. For two samples (E2021.0012, E2021.0013), insufficient bone remained for a second collagen extraction. Four samples from the first chemical pretreatment required an additional collagen extraction and had remaining bone material to do so (E2021.0007, E2021.0008, E2021.0018, E2021.0019). Samples requiring a second bone collagen extraction and all the samples from batch two were prepared using the bone collagen preparation protocol. This standard procedure was altered for the solvent extraction to allow for a secondary examination of the impact of 2:1 chloroform:methanol solvent wash on the bulk δ^{13}C and δ^{15}N values of bone collagen samples (Hyland et al. in prep). In this altered protocol seven samples did not undergo a solvent extraction before demineralization. All of the remaining samples underwent a solvent extraction using a 2:1 v/v chloroform:methanol solution as indicated in Table 1. For a detailed summary of the sample preparation see SI 1.4.

Table 1. *Radiocarbon dating, bulk stable carbon and nitrogen isotope results and collagen quality indicators for the modern fish bone collagen. Values with * fall outside of the collagen quality control metrics (DeNiro 1985; Guiry et al. 2020; van Klinken 1999; Wood et al. 2023:579) and values ~~struck out~~ have been removed from analyses. Solvent wash acronyms: AMC = Acetone, Methanol, Chloroform; 2:1C:M = 2:1 (v/v) Chloroform: Methanol. Values with º refer to either $\delta^{13}C$ value or C:N$_{atomic}$ produced during EA-IRMS analysis for radiocarbon dating*

BAP Sample ID	Site	Species	Common name	OxA–	^{14}C yr	±	Solvent wash	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰)	Yield (wt%)	%C	%N	C: N$_{atomic}$
E2021.0007	Lake Kunitsynskoe (Remezovo)	*Perca fluviatilis*	Freshwater perch	42267	692	19	AMC	–19.36	+7.64	12.5	42.6	15.6	3.20
E2021.0008	Lake Kunitsynskoe (Remezovo)	*Perca fluviatilis*	Freshwater perch	42268	650	19	AMC	–19.71	+7.51	10.2	42.0	15.4	3.19
E2021.0010	Lake Kunitsynskoe (Remezovo)	*Phoxinus*? sp.	Minnow	43120	317	16	2:1C:M	–22.17	+8.61	23.0	41.7	14.7	3.31
E2021.0011	Lake Kunitsynskoe (Remezovo)	*Phoxinus*? sp.	Minnow	43121	925	16	2:1C:M	–26.57	+13.41	21.5	42.1	14.5	3.39
E2021.0012	Lake Kunitsynskoe (Remezovo)	*Phoxinus*? sp.	Minnow	42043	1019	22	AMC	–25.9º		3.5			3.4º
E2021.0013	Lake Kunitsynskoe (Remezovo)	*Phoxinus*? sp.	Minnow	42044	271	21	AMC	–21.7º		5.7			3.3º
E2021.0014	Lake Kunitsynskoe (Remezovo)	*Phoxinus*? sp.	Minnow	43126	459	20	2:1C:M	–24.01	+8.63	22.6	42.7	14.9	3.34
E2022.0239	Lena River (Shishkino)	*Brachymystax lenok*	Lenok	43127	2269	21	2:1C:M	–25.42	+10.88	20.6	44.3	16.1	3.21
E2022.0240	Lena River (Shishkino)	*Brachymystax lenok*	Lenok	43128	2253	21	2:1C:M	–24.60	+11.51	21.8	43.9	16.4	3.12
E2022.0241	Lena River (Shishkino)	*Brachymystax lenok*	Lenok	43129	2231	21	2:1C:M	–25.53	+10.27	20.1	43.9	16.2	3.17
E2022.0243	Lena River (Shishkino)	*Brachymystax lenok*	Lenok	43130	2269	21	2:1C:M	–25.94	+10.96	20.9	47.1	17.4	3.16
E2022.0237	Lena River (Verkholensk)	*Brachymystax lenok*	Lenok	43131	2076	20	2:1C:M	–25.00	+10.62	18.6	44.9	16.3	3.21
E2022.0238	Lena River (Verkholensk)	*Brachymystax lenok*	Lenok	43132	2255	22	2:1C:M	–25.14	+11.61	21.9	43.0	15.9	3.17
E2022.0249	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	43133	2107	21	2:1C:M	–26.26	+10.01	25.7	46.2	15.9	3.39

E2022.0250	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	X–3213–37	2169	21		~~–26.25~~	+10.31	15.0	47.1	14.6	3.75*
E2022.0251	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	43122	2173	17	2:1C:M	–25.00	+10.11	18.7	44.9	16.0	3.28
E2022.0252	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	X–3215–39	2230	17		~~–25.57~~	+9.86	16.4	47.6	16.0	3.47*
E2022.0254	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	X–3217–16	2389	19		~~–26.40~~	+10.45	17.3	49.6	14.9	3.88*
E2022.0255	Lena River (Verkholensk)	*Esox lucius*	Northern Pike	43170	1930	18	2:1C:M	–24.51	+12.19	23.0	44.5	15.6	3.33
E2022.0256	Lena River (Verkholensk)	*Esox lucius*	Northern Pike	X–3217–18	2308	19	2:1C:M	–24.28	+12.29	26.0	44.6	15.5	3.36
E2021.0003	Kulenga River (Belousovo)	*Perca fluviatilis*	Freshwater perch	43064	929	19	2:1C:M	–25.90	+8.83	20.9	42.9	15.1	3.32
E2021.0020	Kulenga River (Belousovo)	*Perca fluviatilis*	Freshwater perch	42271	665	19	AMC	–22.69	+7.07	10.9	42.0	15.4	3.17
E2021.0021	Kulenga River (Belousovo)	*Perca fluviatilis*	Freshwater perch	42272	602	19	AMC	–22.44	+6.54	13.3	42.7	15.7	3.17
E2021.0018	Tutura River (Middle Tutura)	*Brachymystax lenok*	Lenok	42269	1860	15	AMC	–27.28	+11.75	19.6	45.0	16.3	3.23
E2021.0019	Tutura River (Middle Tutura)	*Brachymystax lenok*	Lenok	42270	1950	20	2:1C:M	–28.31	+10.79	21.2	44.9	16.3	3.21
E2022.0244	Tutura River (Middle Tutura)	*Thymallus arcticus*	Arctic grayling	43065	1712	19	2:1C:M	–28.13	+9.60	19.1	42.5	14.6	3.40
E2022.0245	Tutura River (Middle Tutura)	*Thymallus arcticus*	Arctic grayling	43066	2026	19	2:1C:M	~~–30.61~~	+9.70	23.0	43.6	14.7	3.46*
E2022.0246	Tutura River (Middle Tutura)	*Thymallus arcticus*	Arctic grayling	43067	1804	19	2:1C:M	–28.13	+9.61	18.6	45.7	16.0	3.32
E2022.0247	Tutura River (Middle Tutura)	*Thymallus arcticus*	Arctic grayling	43068	1732	20	2:1C:M	–28.40	+9.75	23.3	45.4	15.9	3.33
E2022.0248	Tutura River (Middle Tutura)	*Thymallus arcticus*	Arctic grayling	X–3212–37	1798	19		~~–29.31~~	+9.55	16.6	48.3	15.6	3.61*

Stable carbon and nitrogen isotope values were calibrated to international scales of VPDB and AIR using USGS40 (–26.39 ± 0.04‰ δ^{13}C, –4.52 ± 0.10‰ δ^{15}N) and USGS41 (+37.63 ± 0.05‰ δ^{13}C, +47.57 ± 0.20‰ δ^{15}N) as calibration standards. Internal check standards of SEAL (–12.54 ± 0.05‰ δ^{13}C, +16.14 ± 0.05‰ δ^{15}N) and COW (–24.30 ± 0.05‰ δ^{13}C, +7.86 ± 0.05‰ δ^{15}N) bone collagen were used alongside alanine (–27.11 ± 0.10‰ δ^{13}C, –1.56 ± 0.20‰ δ^{15}N) which further acted as a drift correction standard. Analytical uncertainty was calculated using the protocols described by Szpak et al. (2017).

Amino acid specific stable carbon and nitrogen isotope analysis

Six of the Upper Lena fish samples were selected as a part of a larger research project for amino acid-specific stable carbon and nitrogen isotope analysis. The results of the Upper Lena fish are presented here for a detailed evaluation and comparison against the bulk stable isotope values. All samples were prepared and analyzed at the University of Bristol School of Chemistry. For a detailed summary of the collagen sample preparation for amino acid specific stable carbon and nitrogen isotope analysis refer to SI 1.5. Analytical error for each amino acid δ^{13}C and δ^{15}N value was calculated using root sum squared [$RSS = \sqrt{\sum \sigma^2}$] to combine the standard deviation (σ) from the repeated measurements of the amino acid standard solution and duplicate samples (SI 1.6).

Strontium isotope ratio analysis

^{87}Sr/^{86}Sr was measured in bone apatite from modern fish which had not been exposed to any burial environment and, therefore, were not at risk of post-depositional contamination. The fish selected for ^{87}Sr/^{86}Sr analysis had been caught in the Lena River near the prehistoric cemeteries of Verkholensk ($n = 3$) and Shishkino ($n = 2$), as well as in the Tutura River (Middle Tutura site, $n = 4$), and Lake Kunitsynskoe (Remezovo site, $n = 2$). Samples were processed and ^{87}Sr/^{86}Sr ratios were measured at the Archaeology, Environmental Changes and Geo-Chemistry (AMGC) Research Unit, Vrije Universiteit Brussel (VUB), Belgium. Sample digestion and column extraction (chromatographic separation of strontium) were performed using standard methods (cf. Míková and Denková (2007); Snoeck et al. (2015)). The full method is described in detail in SI 1.7.

Results

Quality control indicators—bone collagen

Of the 37 analyzed samples, 29 were within the quality control range for high quality isolated collagen extraction (Table 1). All samples had wt%N 14–18% and wt%C 41–50% that fall near the ranges Guiry et al. (2020) provide for modern fish collagen (15.40 ± 0.20 wt%N, 41.91 ± 0.39 wt%C). Two samples (E2021.0012, E2021.0013) had wt% collagen yield of less than 10%, however, these samples had low starting amounts (91 and 60 mg respectively). The low yields are likely a result of sample loss during the many chemical and Milli-Q water rinses. Both samples had C:N$_{\text{atomic}}$ within 3.3–3.4 suggesting that the extracted collagen had negligible lipid content. These samples are included in these analyses although both lacked sufficient bone material for additional collagen extraction for stable carbon and nitrogen isotope analysis.

Thirty-two samples fell within the C:N$_{\text{atomic}}$ range of 3.1–3.4 which is slightly higher than the 3.0–3.3 range for modern fish collagen proposed by Guiry et al. (2021). Five samples had larger C:N$_{\text{atomic}}$ values (3.46–3.88) strongly suggesting that lipids were still present in the extracted collagen. The high C:N$_{\text{atomic}}$ values and presence of lipids were expected for three of these four samples because they did not receive a solvent wash during collagen extraction. These five samples were given OxA-X numbers rather than OxA numbers (Table 1) (Sample E2022.0256 was given an OxA-X for a C:N$_{\text{atomic}}$ of 4.8 produced as part of the radiocarbon sample preparation; however, the stable isotope sample preparation

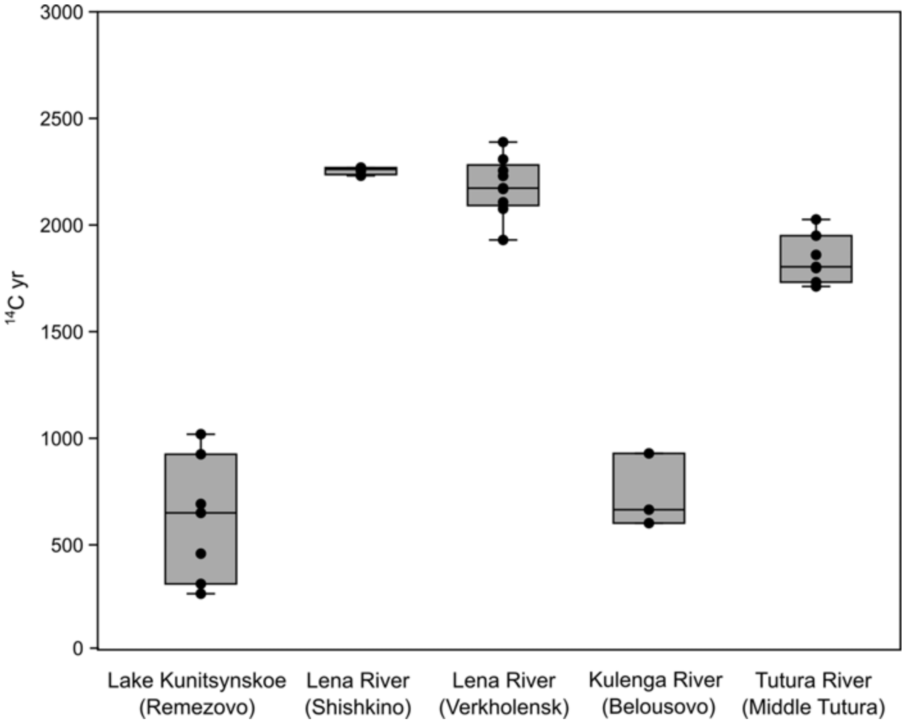

Figure 3. *Variation in* ^{14}*C yr of modern fish samples by sampling locations.*

included a solvent wash which resulted in an improved C:N$_{\text{atomic}}$ of 3.36 when measured for stable isotope analysis). The presence of lipids in these modern samples should not pose a concern for the accuracy of the radiocarbon dates as the lipids would be endogenous and should not differ from bone collagen in ^{14}C concentration. The presence of lipids is a concern for the bulk δ^{13}C values as high lipid content in modern bone has been shown to be correlated with lower δ^{13}C values (Guiry et al. 2020; Guiry et al. 2016; Hyland et al. 2022). Therefore, the radiocarbon dates for these four samples are included in the discussion, but the bulk δ^{13}C values were excluded from further analysis. All of the samples selected for amino acid specific stable isotope analysis had C:N$_{\text{atomic}}$ values between 3.19 and 3.23; however, the derivatization and analysis of amino acids in this technique would have excluded any lipids from affecting the stable carbon isotope results, regardless.

Radiocarbon dating

Highly variable reservoir offsets were observed from the uncalibrated radiocarbon ages of the modern fish samples (Table 1). The lowest offset age was 271 ± 21 BP, while the oldest was 2389 ± 19 BP. The ^{14}C ages of the modern fish samples varied based on sampling location within the Upper Lena (Figure 3). The fish from the Lena River (Shishkino and Verkholensk) and Tutura River (Middle Tutura) sites had ^{14}C ages > 1500 BP (median: 2138, IQR: 377) while the Lake Kunitsynskoe (Remezovo) and Kulenga River (Belousovo) sites had much lower ages between 271–1019 BP (median: 658, IQR: 502) (Mann-Whitney $U = 0$, p (same med.) < 0.001).

The species of fish varied across sampling locations. The three sites with the greatest ^{14}C ages included lenok (*Brachymystax lenok*), while no lenok were caught at Lake Kunitsynskoe and the Kulenga River sites. It did not appear that the inclusion of lenok was solely responsible for the larger ^{14}C yr offset between sites since non-lenok fish from the Tutura River and Lena River sites have ^{14}C dates consistent with the lenok. At the Lena River (Verhkolensk) site, the Eurasian dace (*Leuciscus leuciscus*)

Table 2. *Additional stable carbon and nitrogen isotope results for modern fish from the Upper Lena. These samples were treated with a 2:1 Chloroform:Methanol solvent wash during collagen extraction for bulk stable isotope analysis*

Sample ID	Site	Species	Yield (wt%)	$\delta^{13}C_{VPDB}$ (‰)	$\delta^{15}N_{AIR}$ (‰)	%C	%N	C:N_{atomic}
E2021.0004	Kulenga River (Belousovo)	*Perca fluviatilis*	23%	–22.51	+7.66	43.6	15.5	3.29
E2021.0005	Kulenga River (Belousovo)	*Perca fluviatilis*	24%	–22.94	+6.64	42.9	15.3	3.28
E2021.0006	Lake Kunitsynskoe (Remezovo)	*Perca fluviatilis*	22%	–19.48	+9.11	46.6	16.8	3.23
E2021.0015	Tutura River (Middle Tutura)	*Brachymystax lenok*	21%	–26.68	+11.29	44.2	15.8	3.25
E2021.0016	Tutura River (Middle Tutura)	*Brachymystax lenok*	20%	–27.26	+10.43	42.7	15.8	3.15
E2021.0017	Tutura River (Middle Tutura)	*Brachymystax lenok*	19%	–27.17	+11.14	42.5	15.8	3.14
E2022.0242	Lena River (Shishkino)	*Hucho taimen*	22%	–23.98	+12.01	45.5	16.7	3.17

ranged 2107 to 2389 BP (n = 4) which was comparable to the two lenok values of 2076 and 2255 BP from this site. On the Tutura River, the Arctic grayling (*Thymallus arcticus*) had a range of ^{14}C ages from 1712 to 2026 BP (n = 5) which was comparable to the two lenok values of 1860 and 1950 BP from this site. Based on these comparisons, we propose that the differences in ^{14}C age between sites are locationally driven rather than a result of heterogeneous species representation within each sample location. Further research with a larger data set of multiple species at each location is warranted to provide additional support.

Bulk stable carbon and nitrogen isotope analysis

The calculated analytical error for the bulk stable carbon and nitrogen isotope runs was 0.18‰ for $\delta^{13}C$ and 0.20‰ for $\delta^{15}N$. The modern fish had a wide range of both bulk $\delta^{13}C$ values (–28.40 to –19.36‰), and bulk $\delta^{15}N$ values (+6.54 to +13.41‰) (Tables 1 and 2, Figure 4). The range in $\delta^{13}C$ and $\delta^{15}N$ values for this dataset was much larger than the range previously published by Katzenberg et al. (2012). The latter was based on only four modern fish samples from the Upper Lena (three *Brachymystax lenok* and one *Leuciscus baicalensis*) with a tight range of $\delta^{13}C$ values between –27.0‰ and –25.6‰ and $\delta^{15}N$ values between +10.2‰ and +11.9‰. The larger range of $\delta^{13}C$ and $\delta^{15}N$ values in the present study is likely driven by the inclusion of different fish species, especially the freshwater perch that had higher $\delta^{13}C$ values (–25.90‰ to –19.36‰) and lower $\delta^{15}N$ values (+6.54 to +9.11‰) than the previous range (Tables 1 and 2). Additionally, the fish from Lake Kunitsynskoe had higher $\delta^{13}C$ values (–26.57 to −19.36‰, median: –20.94‰, n = 6) compared to the riverine fish from the Upper Lena (Verkholensk, Shishkino), Kulenga River and Tutura River (–22.44 to –28.40‰, median: –25.00‰, n = 10) (Mann-Whitney $U = 21$, $p = 0.005$) (Figure 4). This difference in $\delta^{13}C$ values is expected as previous research has shown that algae and aquatic plants in fast-moving waters tend to have lower baseline $\delta^{13}C$ values than seen in still-water environments (France 1995; Keeley and Sandquist 1992). Slow-moving waters can create resistance in the diffusion of carbon that results in more complete isotopic reactions and lower rates of fractionation against ^{13}C producing higher $\delta^{13}C$ values in plants and algae (Osmond et al. 1981).

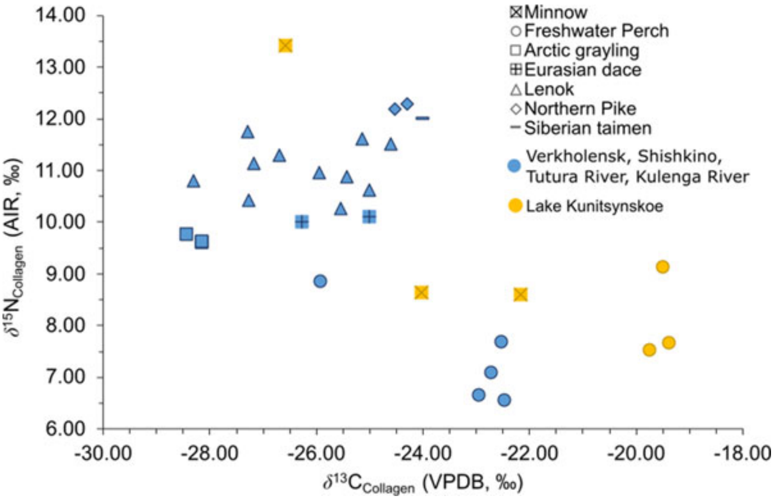

Figure 4. *Bulk stable carbon and nitrogen isotope values for fish species from the Upper Lena River. Lake Kunitsynskoe fish are distinguished from the riverine locations (Verkholensk, Shishkino, Tutura River, Kulenga River).*

Amino acid-specific stable isotope analysis

Amino acid derivatization was successful for all six selected Upper Lena fish samples. There was good separation of the amino acid gas peaks to produce δ^{13}C and δ^{15}N values for alanine, glycine, valine, leucine, threonine, serine, proline, hydroxyproline and phenylalanine (See SI 2 for sample chromatographs). During acid hydrolysis, some amino acids are converted into other amino acids of interest. This is the case for Glx and Asx which represent the combination of glutamine to glutamic acid and asparagine to aspartic acid respectively. Both Glx and Asx had sufficient gas abundance and peak separation to produce δ^{13}C and δ^{15}N values. The gas peaks for isoleucine were sufficient for only δ^{13}C analysis. This is unsurprising given that isoleucine represents only 1.1 ± 0.2% of the amino acids in bone collagen (Guiry et al. 2020). The analytical uncertainties are represented by the error bars in our associated figures and any differences in amino acid δ^{13}C or δ^{15}N values less than that amino acid's analytical uncertainty are not considered meaningful.

The amino acid specific δ^{13}C and δ^{15}N values of the six individual fish samples mirrored their bulk collagen δ^{13}C and δ^{15}N values (Tables 3 and 4). The δ^{13}C values for the essential amino acids (Val, Leu, Ile, Thr, Phe), tended to be lower for samples with lower ^{14}C ages, but these differences were not always greater than the analytical uncertainty (Phe: ± 2.1‰; Val: ± 0.8‰; Ile: ± 0.6‰; SI 1.6) (Table 3 and Figure 5). The δ^{15}N values for the source amino acids (Gly, Ser, Phe) did not show differences based on ^{14}C age offsets that were greater than the associated analytical uncertainties (Gly: ± 1.9‰; Ser: ± 1.2‰; Phe: ± 2.2‰; See SI 1.6, Figure S1).

Correlation between stable isotope values and reservoir offsets

When the data from all sampling locations were examined together, a linear negative correlation was found between the uncalibrated radiocarbon ages of the modern fish samples and the bulk δ^{13}C values ($n = 23$; Pearson's $r = -0.569$; $p = 0.005$). When results were divided by sampling location, the samples from river locations that flowed over dolostone or limestone bedrock (Shishkino and Verkholensk on the Lena River; and Tutura River) showed a positive linear correlation between bulk δ^{13}C values and ^{14}C yr ($n = 15$; $r = 0.797$; $p < 0.001$) (Figure 6). In contrast, samples from Kulenga River (Belousovo) had a negative linear correlation between bulk δ^{13}C values and ^{14}C yr ($n = 3$; $r = -0.993$; $p = 0.075$) (Figure 6).

Table 3. *Amino acid specific stable carbon isotope results for modern fish from the Upper Lena microregion. All amino acid δ^{13}C values are provided in per mil (‰) and calibrated to VPDB international reference standard. *Essential Amino Acids*

Baikal ID	E2021.0007	E2021.0008	E2021.0020	E2021.0021	E2021.0018	E2021.0019
site	Lake Kunitsynskoe (Remezovo)	Lake Kunitsynskoe (Remezovo)	Kulenga River (Belousovo)	Kulenga River (Belousovo)	Tutura River (Middle Tutura)	Tutura River (Middle Tutura)
species	*Perca fluviatilis*	*Perca fluviatilis*	*Perca fluviatilis*	*Perca fluviatilis*	*Brachymystax lenok*	*Brachymystax lenok*
OxA	42267	42268	42271	42272	42269, X-3169-16	42270
Ala	–17.57	–16.87	–21.17	–21.06	–24.46	–27.20
Gly	–11.48	–10.51	–14.13	–13.23	–18.59	–21.07
Val*	–37.70	–35.21	–39.94	–38.36	–40.10	–41.31
Leu*	–29.23	–26.48	–30.73	–31.28	–34.44	–36.41
Ile*	–26.54	–22.64	–28.48	–29.93	–30.25	–33.14
Thr*	–11.22	–8.23	–12.51	–8.69	–15.14	–17.47
Ser	–11.91	–6.16	–9.78	–10.77	–17.99	–17.35
Pro	–21.10	–20.30	–23.56	–22.00	–28.40	–28.53
Asx	–21.84	–17.95	–22.33	–20.92	–28.19	–30.67
Glx	–20.68	–18.07	–23.09	–21.02	–26.74	–30.50
Hyp	–20.62	–19.51	–23.28	–21.36	–25.98	–29.10
Phe*	–26.93	–30.76	–32.87	–33.10	–32.59	–40.64
$\Delta^{13}C_{Gly\text{-}Phe}$	15.45	20.25	18.74	19.88	14.01	19.58
^{14}C yr	692	650	665	602	1872	1950
±	19	19	19	19	15	20

Table 4. *Amino acid specific stable nitrogen isotope results for modern fish from the Upper Lena microregion. All amino acid $\delta^{15}N$ values are provided in per mil (‰) and calibrated to AIR international reference standard. *Source amino acids*

Baikal ID	E2021.0007	E2021.0008	E2021.0020	E2021.0021	E2021.0018	E2021.0019
Site	Remezovo	Remezovo	Belousovo (Butui)	Belousovo (Butui)	Middle Tutura River	Middle Tutura River
Species	*Perca fluviatilis*	*Perca fluviatilis*	*Perca fluviatilis*	*Perca fluviatilis*	*Brachymystax lenok*	*Brachymystax lenok*
OxA	42267	42268	42271	42272	42269, X-3169-16	42270
Ala	16.21	17.68	18.02	15.59	21.29	19.40
Gly*	1.91	3.04	2.58	2.26	6.79	5.95
Val	15.36	16.16	16.23	15.58	20.93	11.24
Leu	15.56	18.84	18.46	16.10	20.62	20.11
Thr	–17.61	–11.12	–15.75	–14.26	–10.96	–21.32
Ser*	3.61	5.54	6.45	5.44	8.12	6.91
Pro	12.49	13.20	13.19	12.47	20.59	19.75
Asx	12.88	14.78	14.68	12.74	24.29	22.80
Glx	16.08	17.82	19.34	17.48	22.96	22.09
Hyp	11.60	13.19	12.42	12.21	20.63	19.20
Phe*	–2.32	4.36	3.43	0.91	3.74	3.30
$\Delta^{15}N_{\text{Glx-Phe}}$	18.40	13.45	15.91	16.56	19.22	18.79
^{14}C yr	692	650	665	602	1872	1950
±	19	19	19	19	15	20

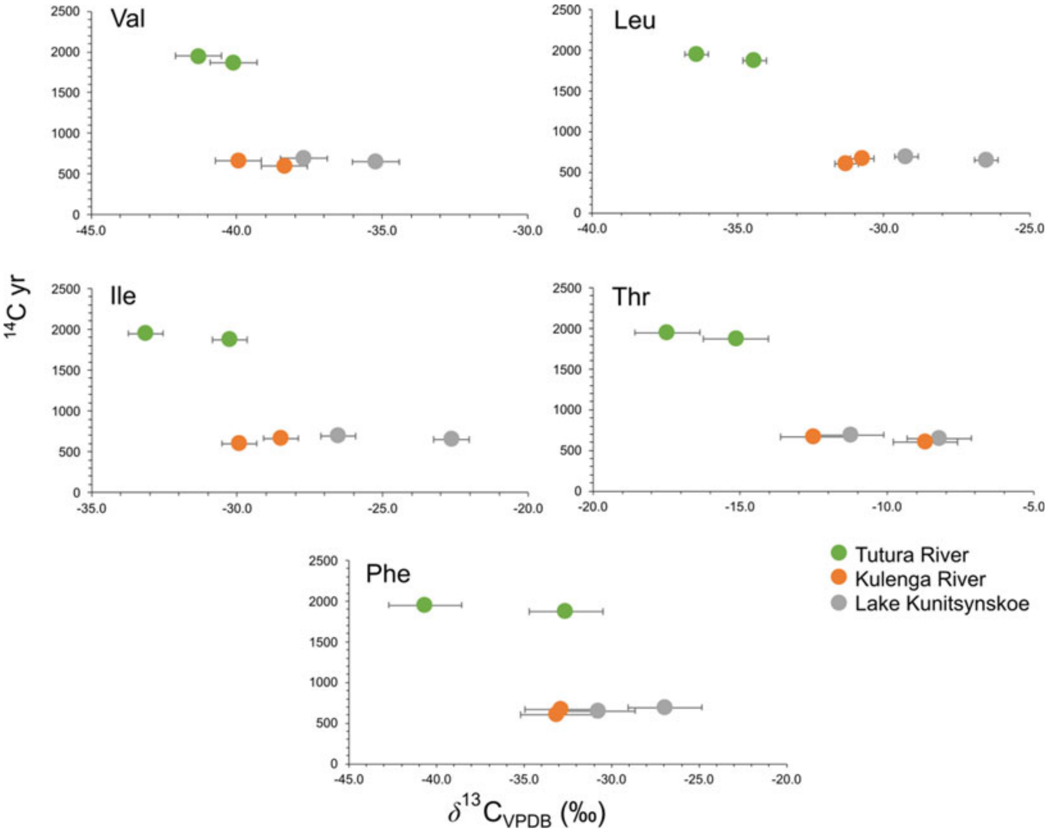

Figure 5. *Relationship between essential amino acid $\delta^{13}C$ values (Table 4) and radiocarbon age (^{14}C years) for modern Upper Lena fish. Error bars represent the calculated analytical error for each amino acid (SI 1.6: Table S2).*

A positive correlation was observed between the uncalibrated radiocarbon age and the bulk $\delta^{15}N$ values ($n = 28$; $r = 0.649$, $p < 0.001$) (Figure 6). However, this positive correlation does not suggest that the observed ^{14}C offsets are influenced by the trophic position of the fish. Within a single site location there is no strong relationship between trophic position and ^{14}C offsets. While the radiocarbon offset ages of the minnows (*Phoxinus?* sp.) are generally smaller (271–1019 BP) than the offset ages for fish taxa with mixed (1712–2389 BP) and predator (602–2308 BP) dietary types (Supplementary Information S1.1), the minnows and freshwater perch caught at Lake Kunitsynskoe had comparable ^{14}C offsets (minnows: 271–1019 BP; freshwater perch: 650–692 BP) despite their different trophic levels. The positive trend between the bone collagen $\delta^{15}N$ values and observed ^{14}C offsets is largely driven by the differences in $\delta^{15}N$ values between samples from the Kulenga river and Lake Kunitsynskoe which generally had $\delta^{15}N$ values of $< +10‰$ (although sample E2021.0011 had a $\delta^{15}N$ value of $+13.41‰$) and those of the Lena River and Tutura River sampling locations which had $\delta^{15}N$ values $> 9.5‰$. This current study is unable to evaluate this trend in further detail because our sampling strategy did not target fish taxa of varied trophic level across all sample sites.

Strontium isotope ratio analysis

The highest $^{87}Sr/^{86}Sr$ values were observed in fish samples from the Lena River in Shishkino and Verkholensk, averaging 0.70887, SD = 0.00003 ($n = 2$) and 0.70884, SD = 0.00004 ($n = 3$), respectively (Table 5). The Middle Tutura samples ($n = 4$) and Lake Kunitsynskoe (Remezovo)

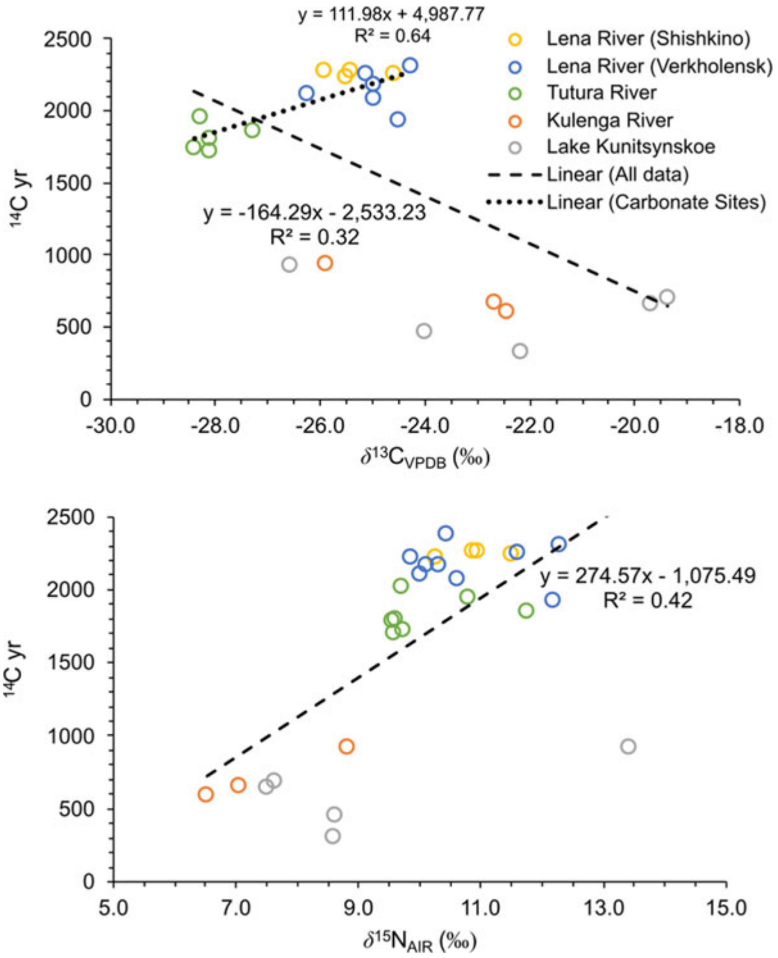

Figure 6. *Bulk δ^{13}C and δ^{15}N collagen values compared to radiocarbon age (^{14}C yr) for fish from sampling locations along the Upper Lena.*

samples (n = 2) had the same ^{87}Sr/^{86}Sr average of 0.70822, with SD = 0.00001 and SD < 0.00001, respectively.

Only eight samples have both ^{87}Sr/^{86}Sr and ^{14}C data available, all of which came from the Lena and Tutura Rivers. While the sample size is small, all fish from the two locations of upstream Lena (n = 4) and the Tutura River (n = 4), show a distinct trend. Based on ^{14}C age and ^{87}Sr/^{86}Sr, the samples can be separated by their watercourse, with the Tutura River samples displaying mean dates younger by 400 years than the Lena River samples from near Verkholensk and Shishkino (Figure 7). With the caveat that the statistical test may not be very robust due to sample size, the ^{87}Sr/^{86}Sr ratios measured in radiocarbon dated samples from the Tutura and those from the Lena River are sufficiently different to suggest that different sources of carbon, organic or inorganic may be contributing to the FRE offset (Mann-Whitney U Test, $p = 0.017$).

Discussion

Identification of a large modern reservoir offset

Our results identified a highly variable modern FRE for the Upper Lena aquatic ecosystems. The Upper Lena reservoir effect resulted in a maximum radiocarbon age in modern fish bone collagen of 2389 ± 19

Table 5. *Strontium stable isotope results for fish from the Upper Lena River system. Samples with ^{87}Sr/^{86}Sr values ≥ 0.70880 are indicated with**

BAP ID	Site	Species	Common Name	OxA-	[Sr] ppm	^{87}Sr/^{86}Sr	2SE	^{14}C yr	±
E2021.0006	Lake Kunitsynskoe (Remezovo)	*Perca fluviatilis*	European perch		656	0.708223	0.000010		
E2021.0009	Lake Kunitsynskoe (Remezovo)	*Perca fluviatilis*	Freshwater perch		905	0.708219	0.000008		
E2022.0242	Lena River (Shishkino)	*Hucho taimen*	Siberian taimen		447	0.708892*	0.000011		
E2022.0243	Lena River (Shishkino)	*Brachymystax*	Lenok	43130	472	0.708847*	0.000010	2269	21
E2022.0237	Lena River (Verkholensk)	*Brachymystax*	Lenok	43131	431	0.708887*	0.000010	2076	20
E2022.0251	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	43122	693	0.708846*	0.000009	2173	17
E2022.0252	Lena River (Verkholensk)	*Leuciscus leuciscus*	Eurasian dace	X-3215-39	605	0.708800*	0.000010	2230	17
E2021.0018	Tutura River	*Brachymystax lenok*	Lenok	42269, X-3169-16	244	0.708228	0.000008	1872	15
E2021.0019	Tutura River	*Brachymystax lenok*	Lenok	42270	179	0.708213	0.000011	1950	20
E2022.0246	Tutura River	*Thymallus arcticus*	Arctic grayling	43067	184	0.708211	0.000010	1804	19
E2022.0248	Tutura River	*Thymallus arcticus*	Arctic grayling	X-3212-37	232	0.708213	0.000009	1798	19

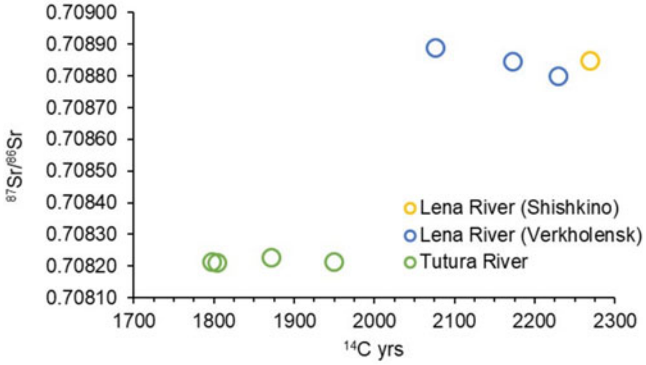

Figure 7. *$^{87}Sr/^{86}Sr$ values compared to radiocarbon offset age (^{14}C yr).*

BP. The reservoir effect did not have a uniform impact on all fish. Large differences in ^{14}C age were observed both within and between species and sampling locations. Fish from Lake Kunitsynskoe (Remezovo) displayed a 748 ^{14}C yr age difference within this single location (Table 1). ^{14}C ages were generally more consistent within fish of the same species than between species; however, a maximum difference of 397 ^{14}C yr was observed between lenok from different sampling locations (Table 1). The large differences observed in ^{14}C ages between sampling locations suggest that the old carbon source(s) responsible for the reservoir effect are unevenly distributed throughout the Upper Lena system. The observed relationship between essential amino acid δ^{13}C values and ^{14}C offset ages (Figure 5) further supports the hypothesis that the old carbon source(s) driving the reservoir effect are being introduced at the base of the aquatic food webs and thus impacting the baseline δ^{13}C values for fish. The two candidates for the source(s) of this old carbon that will be explored in the following discussion are dissolved carbonate and old carbon from the melting of permafrost soils.

Dissolved carbonate as an old carbon source

The results of this study suggest that limestone carbonate is contributing to the oldest radiocarbon age offsets observed in these samples. The largest ^{14}C yr offset ages ($>$ 1500 BP) were observed only at sampling locations in the Lena River and Tutura River which had access to waters flowing over high-carbonate bedrock. The Kulenga River does not flow over carbonate bedrock and these fish have much smaller FRE offset ages (ca. 602 to 929 BP) than those of the Tutura River and Lena River (Verkholensk and Shishkino) sites. Notably, the waters of Lake Kunitsynskoe are unconnected to the Upper Lena and the lake itself is located solely within an area of younger sandstone. There is no known carbonate bedrock contribution at these locations, so, unsurprisingly, the offset ages for these fish are closer to the radiocarbon ages of the Kulenga River fish.

Additionally, the results of the ^{87}Sr/^{86}Sr analysis provide further support that limestone or dolostone-originating material entered the tissues of the fish through their diet. Fish samples with ^{87}Sr/^{86}Sr values greater than 0.70880 were only observed at the Lena River (Verkholensk and Shishkino) downstream from the dolostone and limestone bedrock formations on the eastern fringe of the Upper Lena microregion (Table 5, Figure 2A). While the Tutura River watershed also encompasses outcrops of dolostone bedrock, its catchment is predominantly sandstone bedrock. This may explain why the fish from the Tutura River had ^{87}Sr/^{86}Sr values $<$ 0.70880, thus close to values from Lake Kunitsynskoe, indicating that the carbonate contribution is far less here than in the main river course of Lena.

As would be expected given the close relationship between ^{87}Sr/^{86}Sr in fish and water, the water ^{87}Sr/^{86}Sr from related areas (Scharlotta and Weber 2014; Figure 1) shows the same pattern between sampling sites. The waters of the Kulenga ($n = 5$), Tutura ($n = 1$) and Anga ($n = 2$), all in areas of

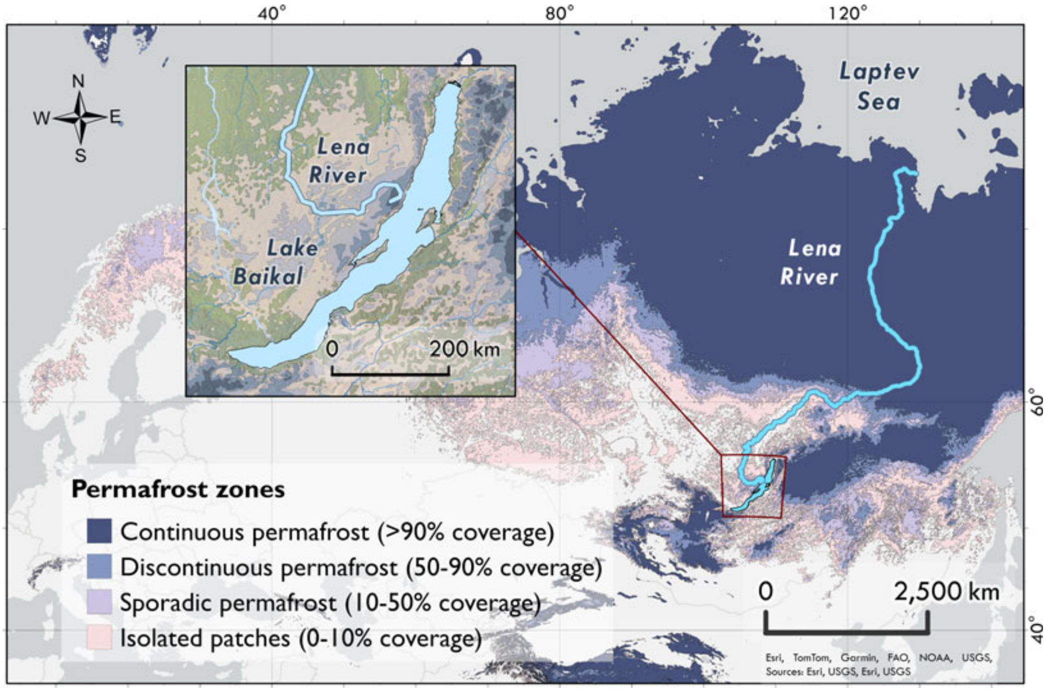

Figure 8. *Model of the modern extent of permafrost along the Lena up to the Lena Delta at the Laptev Sea (after Obu et al. 2019).*

younger sandstone, have the lowest mean $^{87}Sr/^{86}Sr$ values of 0.70835, 0.70848 and 0.70854, respectively (Figure 2B). The highest $^{87}Sr/^{86}Sr$ measurements, reaching 0.70917, were observed in the Lena River before being joined by the Anga and Manzurka tributaries, in waters flowing through the old sandstone of the Primorskii and Baikal'skii mountain ranges. The Verkholensk and Shishkino fish have intermediate $^{87}Sr/^{86}Sr$ values, as expected because these sampling locations are from the Lena downstream from Kachug where the waters from the Lena, Manzurka, and Anga have already mixed.

A comparison of fish and water $^{87}Sr/^{86}Sr$ measurements from different locations revealed that samples in low-carbonate waters are distinguished by their $^{87}Sr/^{86}Sr$ values from samples observed downstream of geological formations with high $^{87}Sr/^{86}Sr$ (Table 5, Figure 2B). This pattern is interpreted as indicating a contribution of bedrock to the biochemistry of the waters, not only regarding strontium isotopes, but also other particles, including the carbonates dissolved in these waters. In this way, the $^{87}Sr/^{86}Sr$ becomes a marker of geological formations and the carbonates that impact FRE offset in fish and water samples.

The results presented in this paper offer a rare insight into the smaller-scale contributions from different sources of old carbon in this previously under-researched area, including the use of $^{87}Sr/^{86}Sr$ as a marker of the potential source of DIC. Most research on the Lena River biogeochemistry focuses on its lower course in the permafrost-taiga zone stretching up to the delta by the Laptev Sea (e.g. Fedorova et al. 2015; Huh and Edmond 1999; Ogneva et al. 2023; Pipko et al. 2010). These sampling sites along the Lower Lena are c. 3,500 km downstream from the northernmost sampling locations in this study (Tutura River) and 78% to 93% of the Lena basin is located within the permafrost zone (Figure 8) (Chalov and Prokopeva 2022; Matveev et al. 1989). This paper supports and adds to the observations of marked variability in the $^{87}Sr/^{86}Sr$ observed in the Upper Lena's waters (Scharlotta and Weber 2014) compared to the Lower Lena (Rachold et al. 1997), as well as the ^{14}C offsets in freshwater fish, increasing with the flow towards the north (Schulting et al. 2015; Svyatko et al. 2015; Svyatko et al. 2017).

It is important to recognize that the ^{87}Sr/^{86}Sr signature from the fish could represent either the incorporation of dietary carbon originating from dissolved carbonates or the consumption of terrestrial matter (including that derived from permafrost) that grew on carbonate soils. Plant ^{87}Sr/^{86}Sr values are primarily representative of the soil on which that the plant grew (Bentley 2006; Capo et al. 1998). We would not expect any relationship between the fishes' ^{87}Sr/^{86}Sr values and ^{14}C offset age if they only reflected the inputs from terrestrial matter in permafrost soil melt. While the ^{87}Sr/^{86}Sr value would indicate plant (and therefore permafrost soil) location, only the age of the permafrost soil would impact the ^{14}C offset age. The age of the permafrost soil melt is not believed to correlate with the underlying bedrock composition in any way. If the ^{87}Sr/^{86}Sr signature reflects the incorporation of dissolved carbonates, then a relationship would be expected in which fish downstream from limestone and dolostone formations would have larger ^{14}C offset ages produced by the incorporation of larger amounts of the dissolved carbonate in their diet. A relationship between the ^{87}Sr/^{86}Sr values of the fish and their ^{14}C age was observed in which fish with ^{87}Sr/^{86}Sr values closest to those of limestone or dolostone ($>$0.70880) had the largest offset ages ($>$2000 BP) (Figure 7). This supports the hypothesis that within the Lena River dissolved carbonate is likely contributing to the observed reservoir effect in the modern fish.

A closer examination of the δ^{13}C results provides further support for this position. When only sites that have access to limestone and dolostone waters are examined (Upper Lena's Verkholensk and Shishkino, and Tutura River), the relationship between bulk δ^{13}C and ^{14}C offset age is positive ($n = 15$; $r = 0.797$; $p < 0.000$) (Figure 6). This positive relationship aligns with the model that Philippsen (2015) proposed for the impact of limestone carbonate as a source of old carbon. Overall, dissolved inorganic bicarbonates are a probable driver for the observed reservoir offset based on: 1) the examination of the radiocarbon ages concerning the potential for catchments flowing over dolostone and limestone bedrock; 2) evidence from strontium isotope analysis; and 3) the relationship between bulk δ^{13}C values and observed radiocarbon offset ages. However, limestone or dolostone carbonate is unlikely to be the source of old carbon for the Kulenga River and Lake Kunitsynskoe, and the fish from these sampling locations still had substantial offset ages ranging from 271 to 1019 BP.

Permafrost soil melt as an old carbon source

Old carbon released during permafrost soil melt is the likely source of old carbon driving the reservoir effect observed at the Kulenga River (Belousovo) and Lake Kunitsynskoe (Remezovo). While the fish from these two locations had much smaller ^{14}C offset ages than sites downstream from limestone and dolostone formations, the offsets were still substantial and wide-ranging within each site (Kulenga River: 602–929 BP, $n = 3$, mean $= 732 \pm 173$ BP; Lake Kunitsynskoe: 271–1019 BP, $n = 7$, mean $= 619 \pm 288$ BP). These sampling locations are surrounded by areas of sporadic (10–50%) and isolated patches (0.5–10%) of permafrost soils (Figure 2A) (Obu et al. 2019) that could be releasing old organic matter directly into the waters of the Kulenga River and Lake Kunitsynskoe sampling locations.

The sample sizes within these river locations were small (Kulenga River near Belousovo $n = 3$; Lake Kunitsynskoe near Remezovo $n = 7$) and this current study is unable to provide a robust means of testing the relationships between the radiocarbon dates and other isotopic proxies. Nevertheless, they may still provide some insights as to the source of old carbon. The three fish from the Kulenga River (Belousovo) show a trend toward lower δ^{13}C values with higher ^{14}C offset ages (Table 1). The freshwater perch from Lake Kunitsynskoe (Remezovo) had bulk δ^{13}C values within a very similar range (–19.36 to –19.71‰) and their radiocarbon ages were relatively similar (692 ± 19 and 650 ± 19 BP, respectively). The minnows from Lake Kunitsynskoe (Remezovo) showed a trend toward a negative relationship between bulk δ^{13}C values and ^{14}C offset ages (Table 1). The largest offsets for these minnows correspond to the lowest δ^{13}C values (925 ± 16 BP, –26.57‰; 1019 ± 22 BP, –25.9‰ δ^{13}C value produced during the radiocarbon combustion via CF-IRMS). This trend toward a negative relationship between bulk $\delta^{13}C$ values and ^{14}C ages matches the model Philippsen (2015) proposed for the inclusion of old organic matter as a driver of reservoir offsets. Further studies with a larger sample size from these locations are required to provide more robust support for the relationship between bulk $\delta^{13}C$ values and radiocarbon ages.

Unlike the process of dissolving limestone or dolostone carbonate, which results in an upper boundary of approximately 5730 years for the radiocarbon age of the resulting DIC (See Philippsen 2013), organic matter from permafrost soils have no limit to their reservoir ages (beyond those imposed by ^{14}C itself). The age of organic matter depends on the length of time that it has been trapped in permafrost soils. This results in potentially very old ^{14}C ages for DOC from permafrost soils, such as > 21,000 ^{14}C yr reported for the Kolyma River flowing over large areas of Yedoma deposits (Vonk et al. 2013). Models predicting the ^{14}C ages of soils globally also acknowledge the impact that permafrost soils have on ^{14}C ages with the Arctic having much older soil ages than other regions of the world (Shi et al. 2020). If old organic carbon from permafrost soil runoff is responsible for the observed reservoir effects at the Kulenga River (Belousovo) and Lake Kunitsynskoe (Remezovo) sites, the permafrost soils must be relatively young, or contributing only a small proportion of the carbon to the fish since their radiocarbon ages range from 271 ± 21 to 1019 ± 22 BP. Both are plausible, given the irregular distribution and relatively limited extent of permafrost in Cis-Baikal, both spatially and by depth, compared to the permafrost-taiga zone to the north (Figure 8).

The presence of bomb carbon in soil profiles is a potential source of "contamination," which would increase the variability of ^{14}C ages from the soil organic matter introduced into the Upper Lena through soil erosion and permafrost soil melt. Research studying the carbon outflows of the world's major river systems by Raymond and Bauer (2001) found variable impacts of bomb carbon, with the York, Parker, Potomac and Amazon rivers containing evidence of "bomb" ^{14}C. In these results, DOC preferentially retained the signals of the bomb carbon and influenced the overall age of riverine carbon (Raymond and Bauer 2001). Research in Canada has also shown the presence of bomb pulse carbon in the top 20 cm of soil, although its presence is highly variable between different soil layers and is not easily predicted based on the features of the soil (Mahaney and Stewart 2023; Milton and Kramer 1998). Trumbore (2009) provided models for the expected changes in soil organic matter (SOM) radiocarbon ages between 1910 to 2005, with the estimated impact on SOM in 2005 to be between 66 to 85‰ $\Delta^{14}C$ (~ –513 to –655 ^{14}C yr). These models showed a declining impact of bomb carbon on SOM radiocarbon ages since its peak between 1960–1970 (Trumbore 2009). It is likely that the impact of bomb carbon on SOM would be lower for the decades preceding our sampling of fish in the Upper Lena (~2010–2021) which aligns with more recently updated models produced by Brunmayr et al. (2024). Additionally, the contamination of bomb carbon is not uniform across hemispheres (Genty et al. 1998) and can be further reduced by the influence of low ^{14}C industrial carbon emissions (Mahaney and Stewart 2023, 1337). The overall impact of bomb pulse carbon on the radiocarbon ages of SOM from the Upper Lena watershed is currently unknown and direct dating of soil samples would be required to confirm the extent of its influence.

Recent research on particulate organic carbon (POC) at northern sampling sites from Yakutsk along the Lena main stem toward Stolb Island (62.16686–70.95567°N) reported ^{14}C ages between 1288 and 2041 BP (personal communication from Gesine Mollenhauer; Ogneva et al. (2023)) and modeled the contributions from Holocene permafrost soils to be 56 ± 12% for riverine POC. All of Siberia is currently experiencing a thawing of permafrost beginning with the end of the Little Ice Age (Romanovsky et al. 2010) which aligns with these results. There is also an interesting negative correlation between DIC and DOC along the course of the Lena, first observed by Pipko et al. (2010) in the permafrost areas ($r = -0.39$, $n = 26$) and confirmed by an observed decrease in pH and a fivefold decrease in DIC concentration between Lena's headwaters (first 500 km) and the middle Lena (Vorobyev et al. 2021). This suggests that along the course from the headwaters of the Upper Lena through to the Lower Lena contributions of old carbon from permafrost soils increase while the contributions from carbonates decrease.

Mix of carbonate and permafrost contributions to old carbon

An important tool in interpreting the results of this research has been the model presented by Philippsen (2015) on the impact of different old carbon sources to DIC δ^{13}C values. To understand more clearly the impact that old carbon sources would have on both the ^{14}C and δ^{13}C values of fish bone collagen we have expanded on Philippsen's model to account for the potential contributions from carbonate-influenced atmospheric carbon (with and without interactions from the rhizosphere), permafrost dissolved organic carbon (DOC), and contemporary terrestrial DOC. Three separate models were created to account for situations in which: 1) permafrost soils are present and interact in processes with carbonate bedrock (Permafrost and Carbonate Combined Model; 2) permafrost soils are present but do not interact in processes with carbonate bedrock (Permafrost and Carbonate Separate Model); and 3) permafrost soils are the only contribution of old carbon (Permafrost Only Model). The exact modeled changes in both ^{14}C and δ^{13}C values based on food source are provided in SI 1.8: Table S4. The final values from Table S4 were used to determine a wide range of potential fish collagen δ^{13}C and ^{14}C values as mixtures of each of the four food sources using the equations below. The equation to calculate $^{14}\mathrm{C}_{\mathrm{Fish\ Bone\ Collagen}}$ is a rearrangement of the equation to calculate the age of the sample using sample and standard absolute activity A (equation 19 of Stenström et al. 2011, 7) in which the OxI standard (Oxalic acid I) absolute activity is assumed to be ~1.0 based on the reduction of bomb carbon in the atmosphere during the years of sampling (2021–2022).

$$\delta^{13}C_{Fish\ Bone\ Collagen} = \sum\left(proportion\ of\ food\ source\ \times \delta^{13}C\ of\ food\ source\right)$$

$$^{14}C_{Fish\ Bone\ Collagen} = -19035 \times \log \sum(proportion\ of\ food\ source \times A\ of\ food\ source)$$

In which: $1 = \sum proportion\ of\ food\ source$

A = specific activity A. see Stenström et al. (2011, 7, equation 19)

A representation of the maximum potential range of δ^{13}C and ^{14}C yr in fish bone collagen for these three models was produced using SIBER (Jackson et al. 2019) and includes convex hulls for the maximum potential values and ellipses set to contain 60% of the outputs from each model (Figure 9).

Just as Philippsen's (2015) model suggested, our model predicts fish with a higher proportion of old organic matter in their diet would have lower δ^{13}C values and increased ^{14}C age, and a higher proportion of food sources with carbon derived from carbonate in the diet would result in higher δ^{13}C and ^{14}C values. A higher proportion of food sources with carbon originating from root zone CO_2 (rhizosphere) is predicted to result in lower δ^{13}C and ^{14}C values, but this was only included as a variable in the Permafrost Only Model in which the rhizosphere was modeled with a modern radiocarbon age and no mixing occurred with carbonate bedrock. Removing the interaction between the root zone and carbonate bedrock in the Permafrost Only Model allowed for lower δ^{13}C values between –40 and –37‰, but all other models saw an increase in δ^{13}C values in root zone CO_2 food sources (–26.5 to –23.5‰) due to the modeled interaction with the 0 to +3‰ values of the carbonate bedrock. Increased contributions from modern terrestrial resources were predicted to lead to increased δ^{13}C values (up to –20‰ δ^{13}C) and lower ^{14}C values in the fish bone collagen which was the case for all three models.

Comparing the fish results from this study to these models shows that all the analyzed Upper Lena samples had δ^{13}C and ^{14}C values that fit within the potential range of the Permafrost Only Model (Figure 9). However, the samples from regions suspected of carbonate contributions (Lena River, Tutura River) had radiocarbon ages at the model's upper limits. This included a comparative pike (*Esox lucius*) from Schulting et al. (2015) from the Upper Lena near Ust'-Kut (c. 230 km further north downstream from the mouth of the Tutura River) that aligned well with our measured values (–24.6‰ δ^{13}C, 1981 BP) (SI 1.8: Table S5). The samples from tributaries with lower suspected carbonate contributions have lower radiocarbon ages and higher δ^{13}C values. These values align with comparative archaeological fish data from northeastern Kazakhstan where less carbonate was present in the local bedrock compared to the Cis-Baikal area and the reservoir effect in turn showed a negative correlation

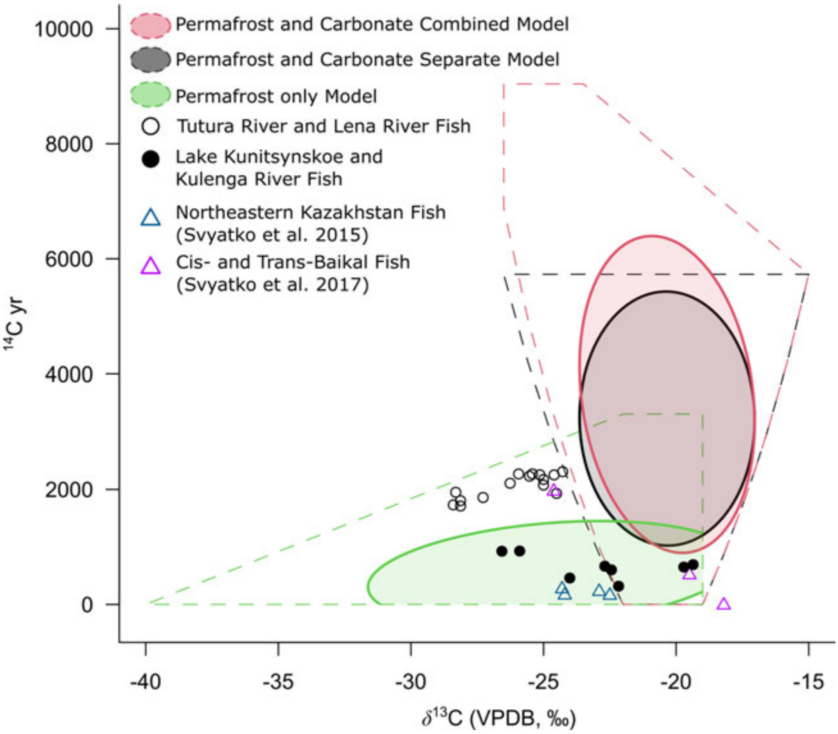

Figure 9. *Modeled* $\delta^{13}C$ *and* ^{14}C *yr values for fish diets consuming a combination of resources in three different environment models (See SI 1: Table S4). Dotted lines show the convex hull of modeled ranges and color ellipses represent 60% of the modeled values within each model. Results of modern fish bone collagen* $\delta^{13}C$ *and* ^{14}C *yr values are distinguished by sampling locations with potential contribution from dissolved carbonates (white) and with less potential contribution from dissolved carbonates (black). Comparative Eurasian data from Svyatko et al. (2015); Svyatko et al. (2017) (blue and purple triangles respectively) (See SI 1: Table S5).*

between $\delta^{13}C$ values and radiocarbon offset ages for archaeological human paired dating (Svyatko 2016; Svyatko et al. 2015, 2017) (SI 1.8: Table S5).

These results suggest that the radiocarbon ages and stable carbon isotope values could be explained using a model in which the sole contribution of old carbon is from permafrost soil melt. However, this model is very sensitive to the estimated age of the permafrost soil and if a younger soil age were used, the values from the Lena and Tutura River fish would fall outside of this model. Additionally, our models have not considered the combination of both modern root zone CO_2 and carbonate bedrock-derived food sources together in a fish's diet. This combination may better account for the observed values from the Lena and Tutura River fish. The high radiocarbon ages of the Lena and Tutura River fish and their $^{87}Sr/^{86}Sr$ values suggest that food sources with carbonate-derived carbon are contributing to their diet and the subsequent isotopic composition of their bones. The results of this model suggest that terrestrial-based carbon resources (modern terrestrial DOC or permafrost soil DOC) are contributing to the diets of the Upper Lena fish since the majority of sample values fall outside the range of the two models that include carbonate- derived carbon food sources.

Implications for archaeological radiocarbon dating

The level of variability and the magnitude of the reservoir effect observed in modern Upper Lena fish provides an interesting comparison to the freshwater reservoir offset ages in archaeological populations documented by Schulting et al. (2015). The archaeological samples that fall within this paper's study region of the Upper Lena (Makrushino, Ust'-Iamnaia, and Popovskii Lug 2 archaeological sites) ranged in paired human and terrestrial animal offset ages from 255 to 913 BP (Schulting et al. 2015). The large offset age of 913 ^{14}C yr in human bone collagen suggests that there must have been a much larger reservoir effect for the freshwater fish this individual was eating, considering that terrestrial food sources with no associated reservoir offset would also have contributed to their diet. This matches the higher reservoir offsets observed in this research for modern fish from the Upper Lena. Additionally, Schulting et al. (2015) found a moderate but significant negative linear relationship between human-animal offsets in ^{14}C yrs and human bone collagen δ^{13}C values (r = –0.70, $r^2 = 0.490$, p =0.016, $df = 10$) whereas there was no significant relationship to δ^{15}N values ($r^2 = 0.001$, $p = 0.946$, $df = 10$). The negative relationship between human bone collagen δ^{13}C values and human-animal offset ^{14}C yrs led Schulting et al. (2015) to suggest permafrost soil melt was the major contributing source of old carbon to the Upper Lena watershed and impacted the archaeological samples from this microregion. The archaeological individuals from the north of the Upper Lena area (Turuka, Zakuta) tend to have greater radiocarbon offsets than seen further south on the river (Schulting et al. 2015). This aligns not only with the increasing distribution of permafrost towards the north, especially beyond latitude 60°N (Matveev et al. 1989), but also agrees with the modern pike from Ust'-Kut (56.9°N) with an offset of 1981 BP (Schulting et al. 2015). The differences in ^{14}C and δ^{13}C between the sampling sites in the south and in the north, located c. 230 km apart, point towards increasing contribution of DOC associated with thawing permafrost, and decreasing impact of DIC (cf. Vorobyev et al. 2021).

A combination of carbonate-rich bedrock carbon and permafrost soil melt may have been the source of the archaeological reservoir offsets previously documented for the Upper Lena microregion populations. Carbon from limestone and dolostone bedrock impact the main course of the Lena and the fishes from these waters. However, there is evidence that during the period of archaeological interest, the warmer climate had moved the permafrost soil line further north such that the upstream tributaries may have eroded permafrost soils into the river system (Anisimov et al. 2002). The permafrost soils which may have begun to melt during the regional Holocene climatic optimum (ca. 8000 – 4200 cal BP) (Bezrukova et al. 2011; Kobe et al. 2022) would have included organic matter trapped during the previous maximum permafrost extent during the Younger Dryas cooling period approximately 12,900–11,700 cal BP (Bakke et al. 2009). The maximum age for this organic matter would thus be between 8700 and 3700 years during the Holocene climatic optimum. Even a small proportion of this old carbon in freshwater fish could produce observable radiocarbon offsets in hunter-gatherers that consumed them. A high level of variability in the ^{14}C offsets of fish within the Upper Lena during this period of archaeological interest could have been produced by the contribution of both limestone/dolostone carbonates and permafrost soil melt into the freshwater fish.

While changes in permafrost soil melt over time were suggested to explain the variability in the archaeological human dataset spanning from the Late Mesolithic to the Early Bronze Age (Schulting et al. 2015), this study has shown how modern fish from a relatively short time interval can show a wide range of both ^{14}C yr offset ages and δ^{13}C values of fish within the Upper Lena. The archaeological relationship between δ^{13}C values of human bone collagen and their associated human-animal ^{14}C yr offsets could reflect differential access to fish with higher or lower δ^{13}C values and ^{14}C offset ages along different tributaries of the Upper Lena, in addition to or in contrast to variable dietary preferences over time. Radiocarbon reservoir corrections for the archaeological populations of the Upper Lena microregion have been largely based on simple linear regression models using bulk δ^{13}C and δ^{15}N values of human bone collagen (Schulting et al. 2015), although stable hydrogen isotope values have also been more recently applied to the prehistoric cemetery of Shamanka II located in southwest Lake Baikal (Schulting et al. 2018). These models function best when the contribution of old carbon to human diet is represented by a freshwater food source that is both consistent in the relationships between δ^{13}C, δ^{15}N values and ^{14}C offset age and is distinct in its stable isotope values from the terrestrial food sources. This method of correcting for the reservoir effect would be challenging to use based on our modern fish samples because the freshwater food sources have overlapping δ^{13}C values with the terrestrial resources and the freshwater food sources have a wide range of ^{14}C offset ages.

Archaeological reservoir effect corrections seek a means of tracing the contribution of old carbon to the tissues analyzed in ^{14}C dating. The present research identifies a number of challenges in using bulk δ^{13}C and δ^{15}N values to distinguish either freshwater fish consumption or the extent of ^{14}C offset ages of freshwater fish as a food source for human diet. Moving forward, reservoir corrections for the Upper Lena will need to apply new methods of tracking freshwater fish consumption, such as stable hydrogen or sulfur isotope analysis, as well as account for the variability in ^{14}C offset ages that likely characterized archaeological fish. Corrections which allow for a range of potential ^{14}C offset values for fish food sources or use other isotopic measurements to estimate the magnitude of fish ^{14}C offsets would be useful in creating more robust means of correcting archaeological radiocarbon chronologies. However, the extreme variability in potential offset ages will result in lower precision for any regression equations and hence to corrected radiocarbon dates on humans. Additional research in which archaeological fish bones are recovered from undisturbed and sealed archaeological contexts with terrestrial animal bones would greatly assist in evaluating the extent to which the modern reservoir effect matches the reservoir effect during the periods of archaeological interest. Unfortunately such contexts are very rare.

Implication for modern permafrost soil research

The results of this study have implications which go beyond the study of the ancient past. Current impacts of climate change have begun to increase the amount of permafrost melt and subsequent erosion of old organic carbon into the waters of the Upper Lena system (Dzhamalov et al. 2012; Opekunova 2014). ^{14}C dating is currently used as an important tool to identify the sources of DIC and DOC in river systems (Raymond and Bauer 2001), but additional research is needed to understand how this ancient carbon is then incorporated into the biosphere (Guillemette et al. 2017). Recent research by Manlick et al. (2024) has examined the flow of ancient carbon in terrestrial ecosystems through small rodent populations, while our results show that ancient carbon is captured in the tissues of fish in aquatic ecosystems. The well-established techniques of bone collagen ^{14}C dating could benefit from additional stable isotope analyses (carbon, nitrogen, strontium, sulfur, hydrogen, amino acid specific approaches) to better distinguish and study the flow of ancient carbon across vertebrates in freshwater environments. The ability to apply these techniques to museum and archaeological faunal specimens would further allow for far greater time depth to the analysis of the contribution of permafrost melt to historic and ancient ecosystems. Comparing the current permafrost soil melting rate and its impact on the biosphere with those of historic and ancient times could further identify the need for action and the severity of the modern climate crisis. Stable isotope analyses of ancient and museum faunal skeletal collections have already been conducted to contextualize the modern climate crisis within a deeper human past (Routledge et al. 2023). This research could similarly be applied to expand the current discussion of changes in permafrost melt rate to span the entirety of human influence across time.

Conclusion

The results of ^{14}C dating, bulk and amino acid specific stable carbon and nitrogen isotope analysis of bone collagen and strontium isotope analysis of bone apatite have uncovered complex FREs for the Upper Lena. Contributions of old carbon from both dissolved bedrock carbonate and permafrost soil melt are likely responsible for the reservoir effects observed across multiple tributaries of the Upper Lena. These old carbon sources have resulted in some of the oldest recorded radiocarbon offset ages for fish of 2389 ± 19 ^{14}C yr BP. The wide range of radiocarbon offset ages produced by variable inputs of these old carbon sources to modern fish tissues poses challenges to producing robust corrections for both modern and archaeological reservoir effects in human populations. Specifically, there is a need to address a wider potential range of ^{14}C ages for fish rather than using models which function best with uniform endmember contributions of old carbon.

The utility of strontium isotope ratio analysis to identify and distinguish the contribution of limestone and dolostone carbonate as a potential source of old carbon is novel to this research as well. This technique is likely to be most useful in regions where the bedrocks of river catchments have variable, well-characterized, and distinct ^{87}Sr/^{86}Sr signatures. Benefiting from an environmental bioavailable strontium baseline, this research estimated the likely origin of the ^{87}Sr/^{86}Sr values observed in fish captured in waters downstream from old sandstone and carbonate bedrock. Additionally, alternative lines of evidence such as ^{14}C dating will need to be used to distinguish the contributions of dissolved carbonates and local plants to the fish ^{87}Sr/^{86}Sr signatures.

Research is currently underway to analyze more modern fish from across Cis- and Trans-Baikal as well as expand to include additional tributaries along the Upper Lena. A limitation of the current study was the small sample size which may not have captured the full variation across fish species at each sampling location. Despite these limitations, the multiple lines of analyses have come together to provide an improved understanding of the range of the reservoir effect along the Upper Lena and identified the contributions from both permafrost soil melt and carbonate bedrock erosion that are likely driving it.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/RDC.2026.10219

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Karolina Cameron-Werens: collected data, created maps, performed analysis, wrote section of the paper, edited the paper.
Christophe Snoeck: conceived and designed the analysis, collected data, contributed to data analysis, edited the paper.
Aleksander Shchetnikov: contributed environmental data.
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