Microevolutionary processes in Asian sockeye salmon *Oncorhynchus nerka* populations during Late Pleistocene climatic oscillations

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Sockeye Salmon Range
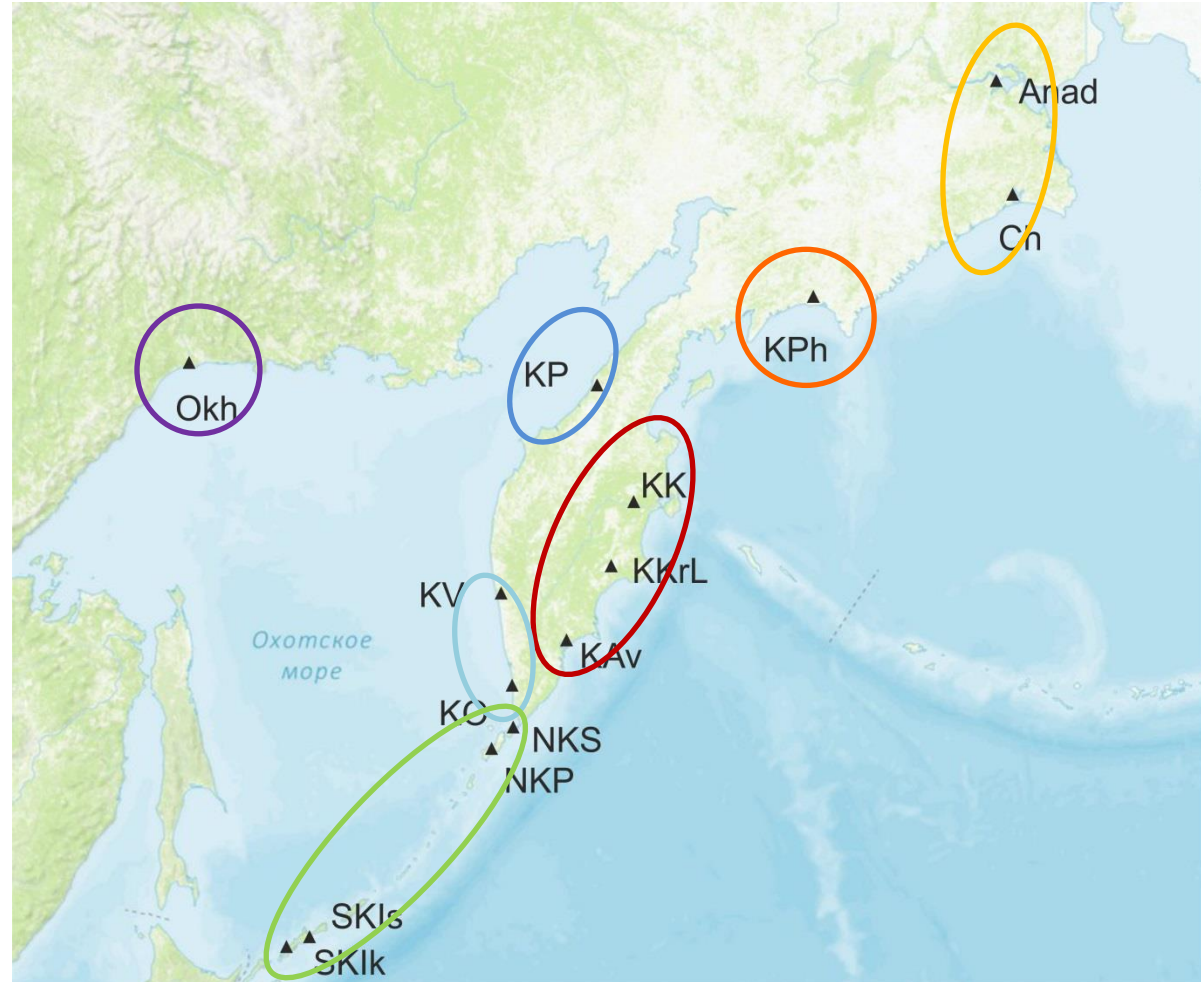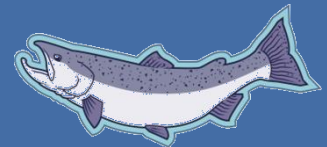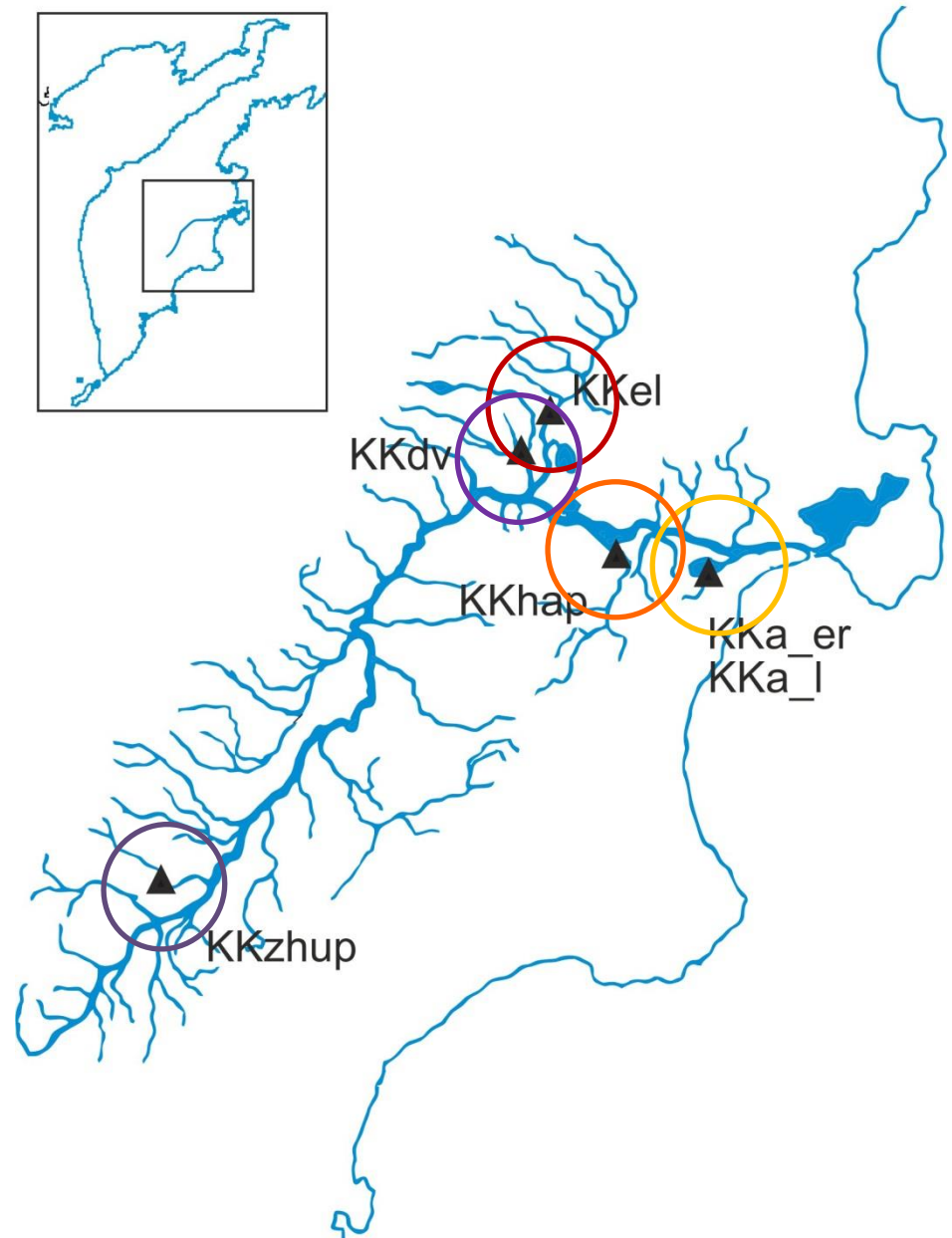
Study area and sampling locations

- **Chukotka , Anadyr and Navarinskiy region**
- **Northeastern Kamchatka, Olyutorskiy Bay, Pakhacha River**
- **East Kamchatka, Avacha River, Kronotskoye Lake, and Kamchatka River basin**
- **Continental coast of the Sea of Okhotsk, Okhota River**
- **Northwestern Kamchatka, Palana River**
- **Western and Southwestern Kamchatka, Ozernaya River, and Vorovskaya River**
- **Kuril Islands, Shumshu Island (Bettobu Lake), Paramushir Island (Glukhoye Lake), Iturup Island (Krasivoye Lake and Sopochnoye Lake)**
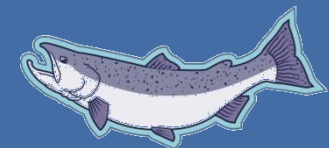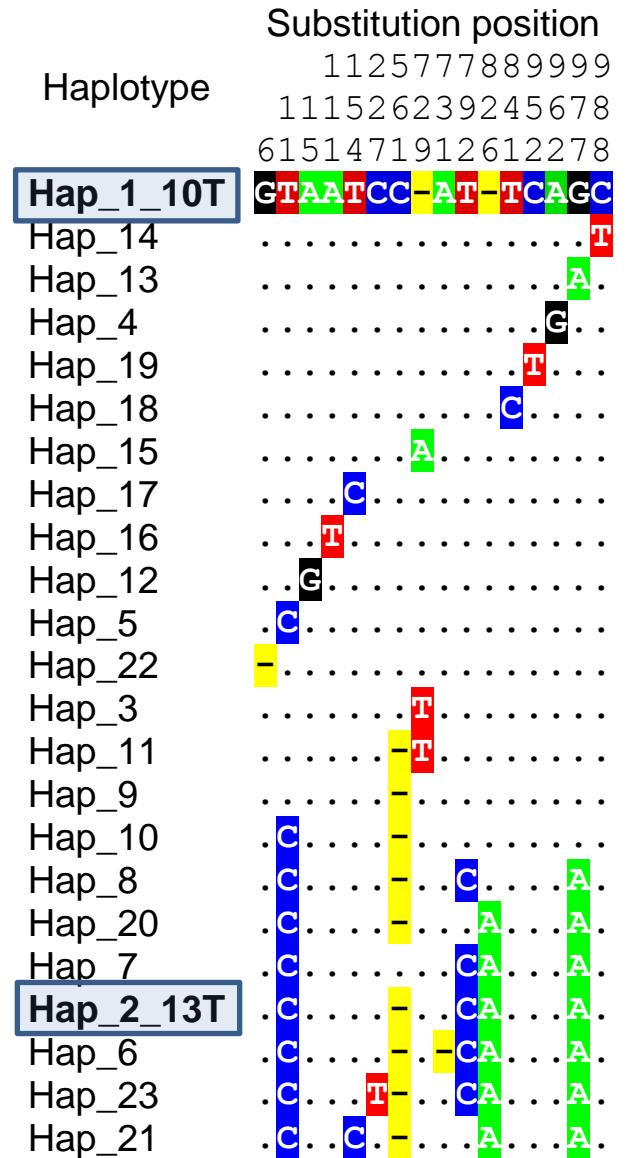
Sampling locations in Kamchatka River watershed

- **KKa_er – Azabachye Lake (early run)**
- **KKa_l – Azabachye Lake (late run)**
- **KKhap – Hapiza River**
- **KKel – Elovka River**
- **KKdv – Dvu'yurta River**
- **KKzhup – Zhupanka River**

Experimental design

o Sanger sequencing of mtDNA control region (entire D-loop,1010 bp)

o 172 specimens from 20 samples collected in 2003-2017
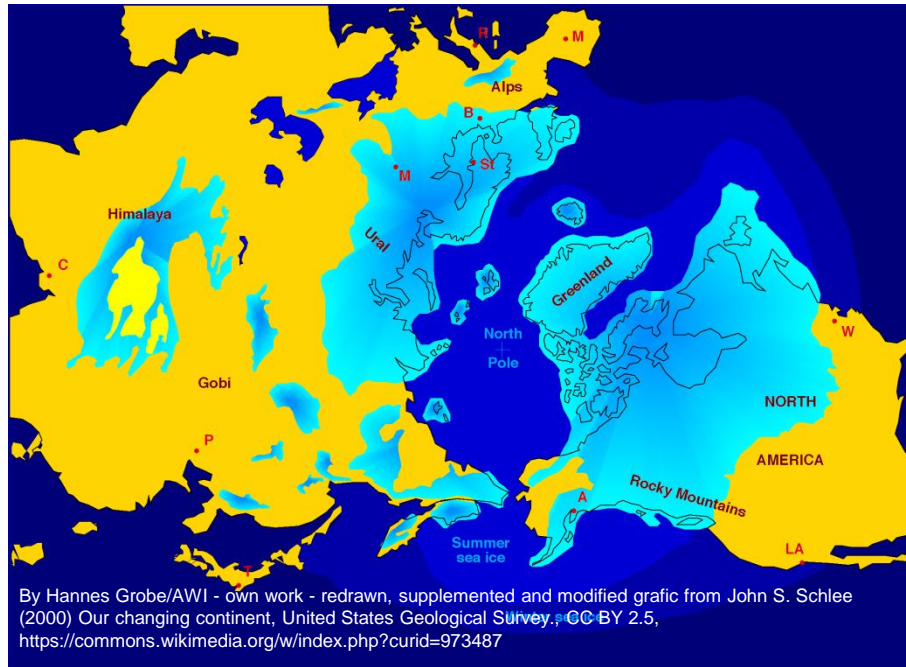
Oncorhynchus nerka

mtDNA

Haplotypes of the Asian sockeye salmon mtDNA control region

16 polymorphic sites were identified in sockeye salmon D-loop. Among the substitutions there were 10 transitions, 2 transversions and 5 indels (insertions or deletions). Most of substitutions and indels were detected in the first and the last quarters of the D-loop sequence, one indel was registered in the poly-T region. 14 haplotypes were revealed by substitutions only and 23 haplotypes were haplotypes with indels. 2 mass haplotypes (Hap1_10T and Hap2_13T) were detected.
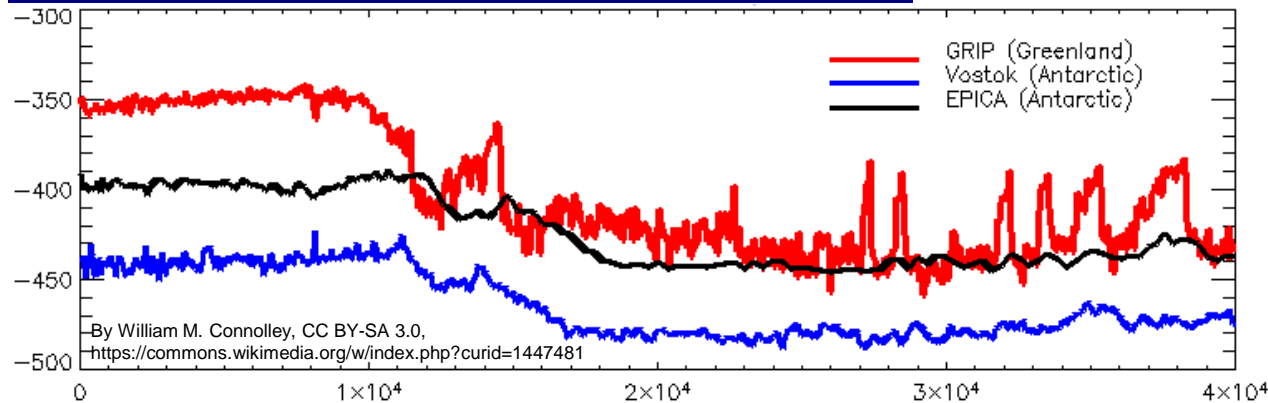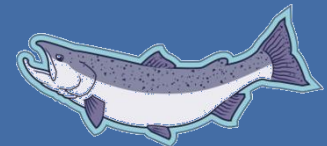
The derivation of sockeye salmon population structure was closely associated with climate oscillations in the Upper Pleistocene (between c. 129,000 and c. 11,700 years ago).

During periods of the Last Pleistocene glaciation, significant areas of the sockeye salmon range were covered with ice. Only a few populations survived in ice-free territories (refugia). During periods of climatic minimums (sea regressions), rapid divergence of populations accompanied by allopathic morphogenesis occurred in refugiums due to isolation and population decline, during optimum periods (postglacial transgressions), the populations survived were actively dispersed and mixed in newly colonized territories

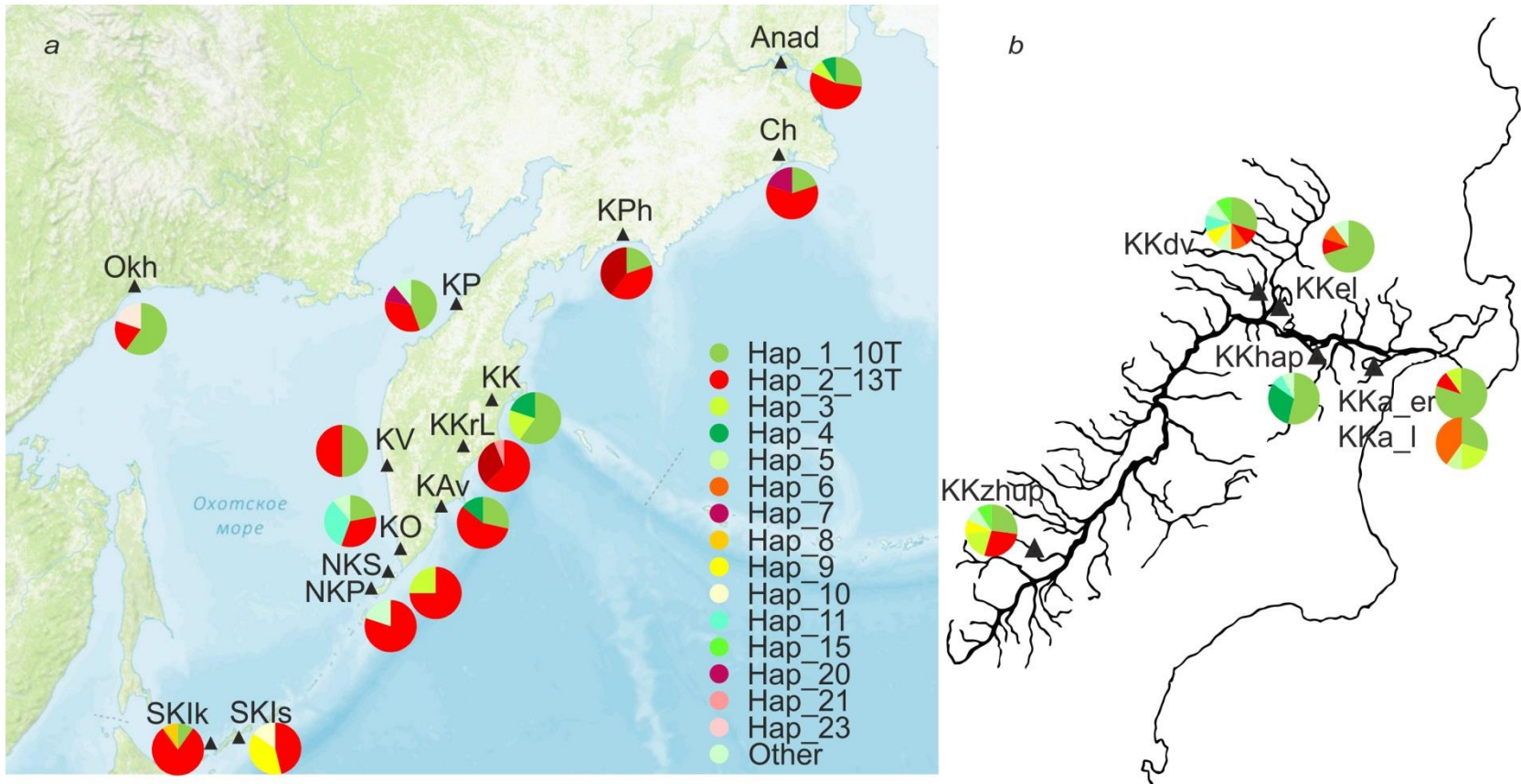**Temperature proxies for the last 40,000 years.**

Speculations supported by geological data have repeatedly been expressed about the existence of a refugium in the Central Kamchatka depression, as well as about the Beringian origin of all Kamchatka populations. In this study, we test the last two hypotheses.
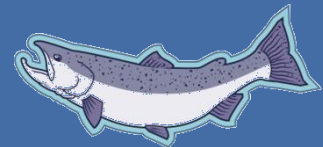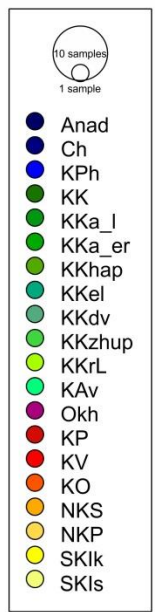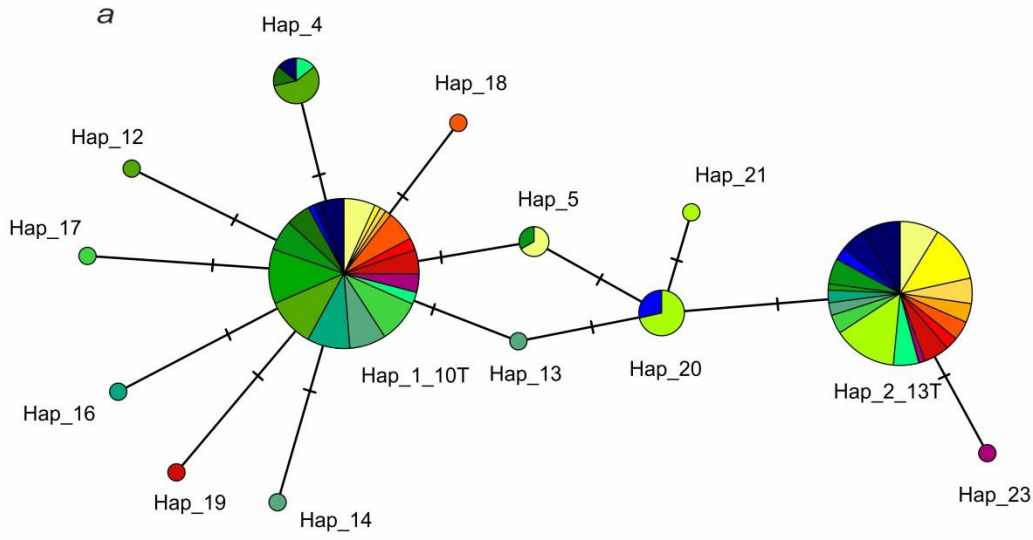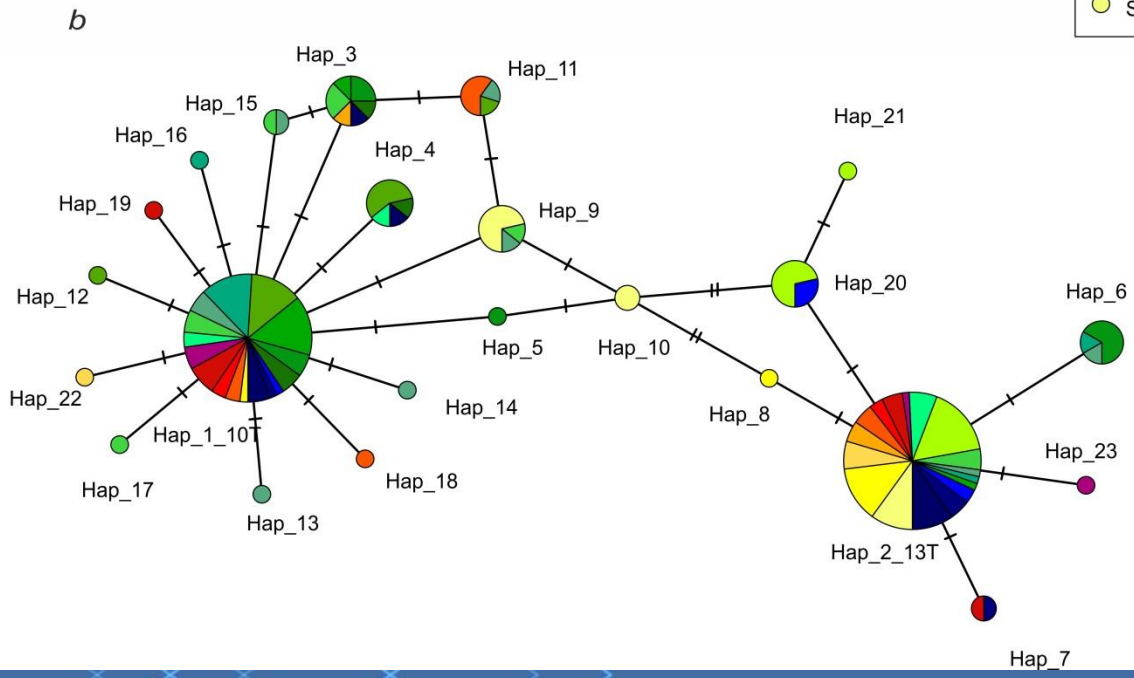
Along the Asian coast of the Pacific Ocean, the frequencies of the haplotypes are distributed rather mosaic, there is no clearly pronounced clinal character in the change in frequencies. However, the presence of both haplogroups in most populations in approximately equal proportions indicates that the entire Asian part of the sockeye range is a zone of secondary contact.
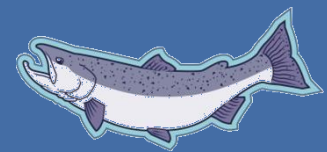
Genealogical networks of sockeye salmon D-loop haplotypes, built on the base of the minimum number of nucleotide substitutions (MST-tree): a − excluding indels, b − including indels. The size of the circles and the area of the sectors are proportional to the haplotypes frequency in the corresponding samples.

All sequences variants were distributed among two haplogroups: in the first one the central haplotype was Hap_1_10T, in the second one – Hap_2_13T, and both haplogroups formed star-shaped topology, unique haplotypes differed from central ones in one substitution or indel
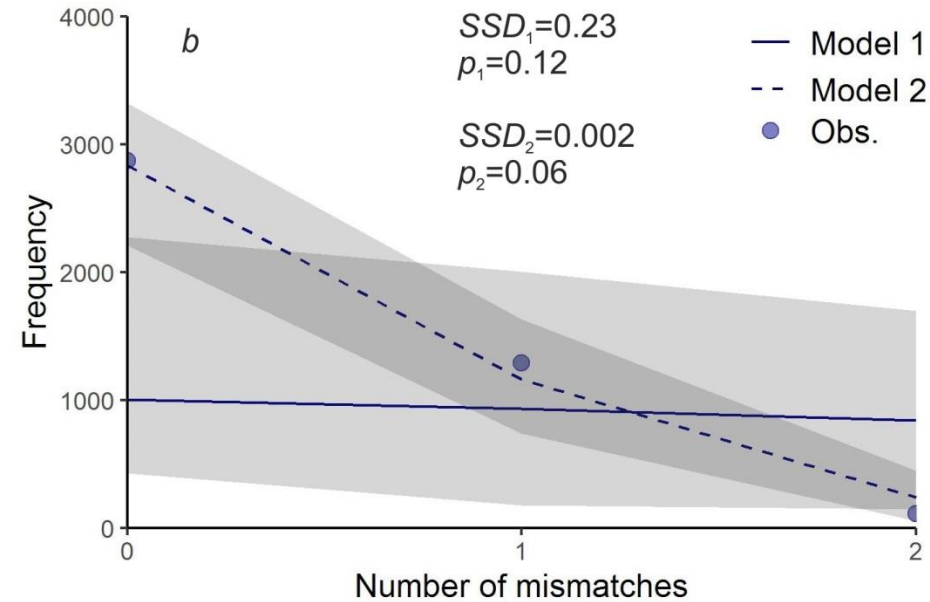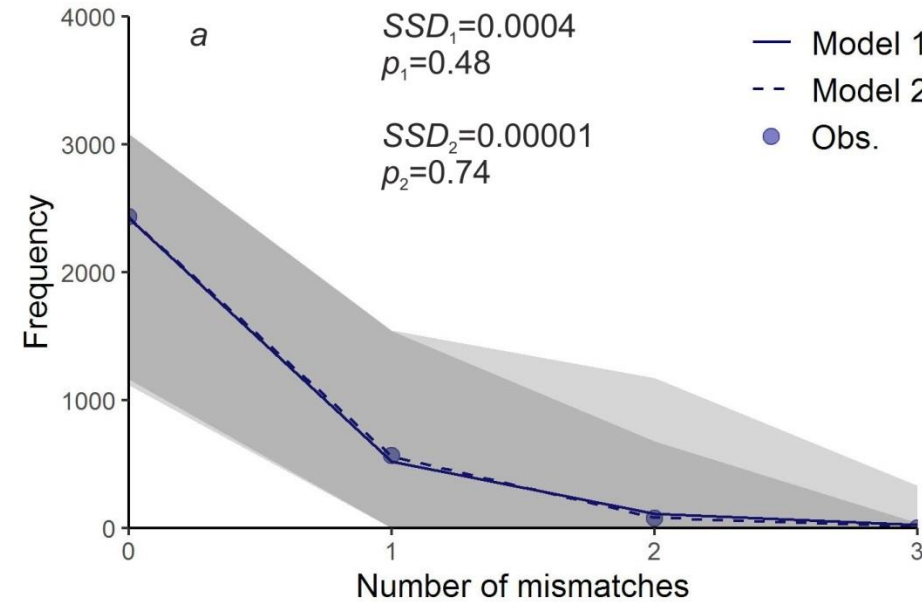
The star-shaped topology of the haplotype network indicates a fast and significant increase in the diversity of groups, assuming a rapid expansion of the species after a decrease in its number due to climatic oscillations of the Pleistocene.
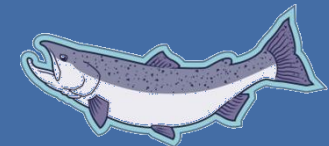
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Mismatch distribution (substitutions' frequencies distribution) analysis of the two phylogenetic lineages of sockeye salmon:
a – haplogroup 1, b − haplogroup 2. The solid lines represent the expected distributions under a sudden expansion model (Model 1), the dashed line − the expected distributions under a spatial expansion model (Model 2), dots − the frequencies of the observed pairwise differences.
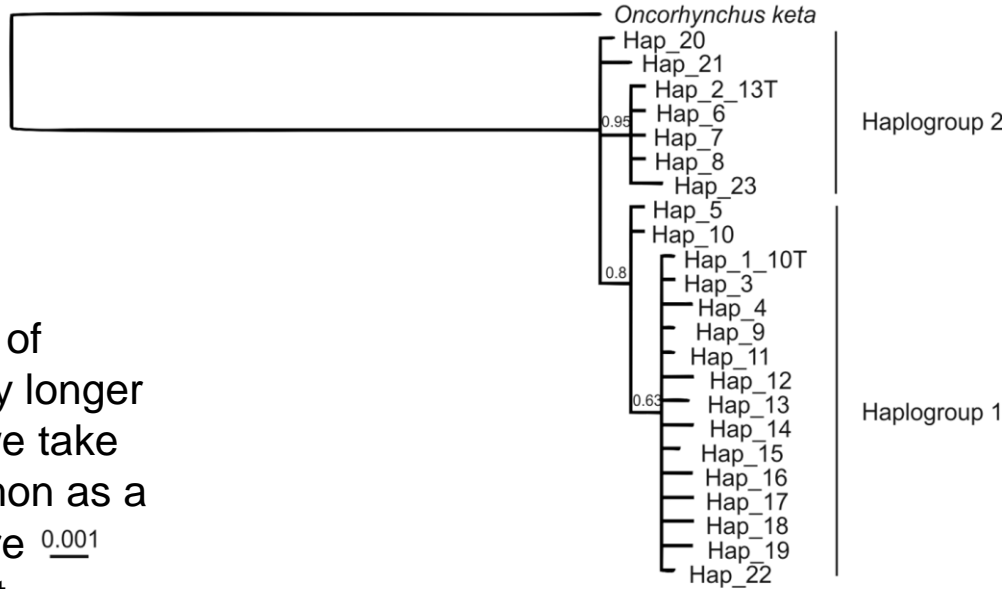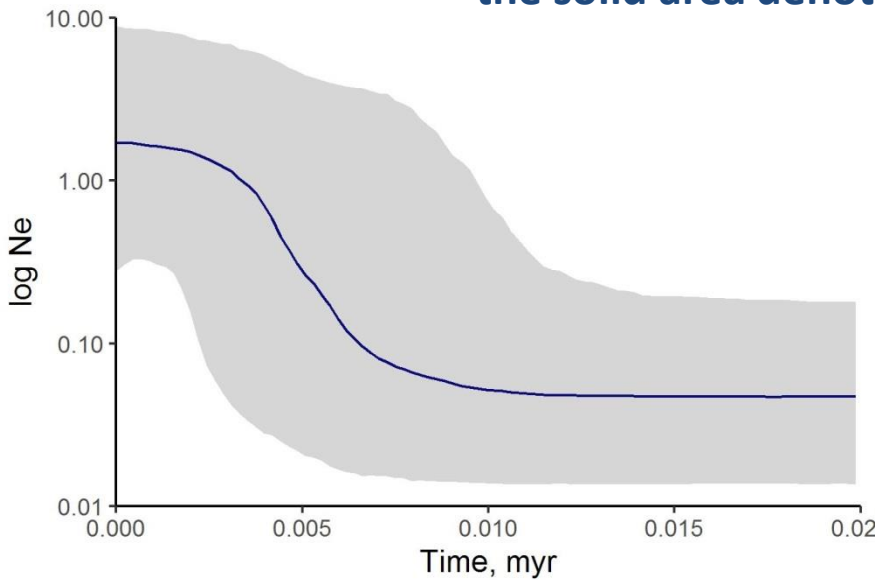

Recent demographic expansion from small founder populations was also revealed by mismatch distributions analysis. A good fit of both sudden population expansion model and spatial expansion model was observed for both haplotypic lineages. All the results point to a rapid postglacial expansion event in the Asian part of the range.
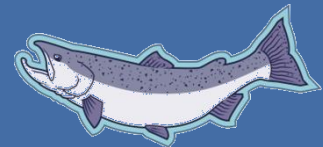
All the results point to a rapid postglacial expansion event in the Asian part of the range. The time at which the event took place was dated by the Bayesian skyline plot analysis indicated rapid abundance growth in the Early Holocene (starting up ≈11700 years ago).

Bayesian tree of D-loop haplotypes of sockeye salmon

The branches length, representing the number of changes that occurred in a lineage, is obviously longer for the Hap_1_10T, so it branches off later (if we take the divergence time of chum and sockeye salmon as a reference point) and can be considered as more recent, whereas Hap_2_13T – as more ancient.
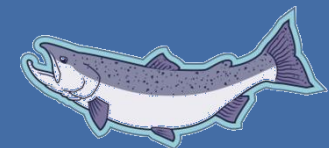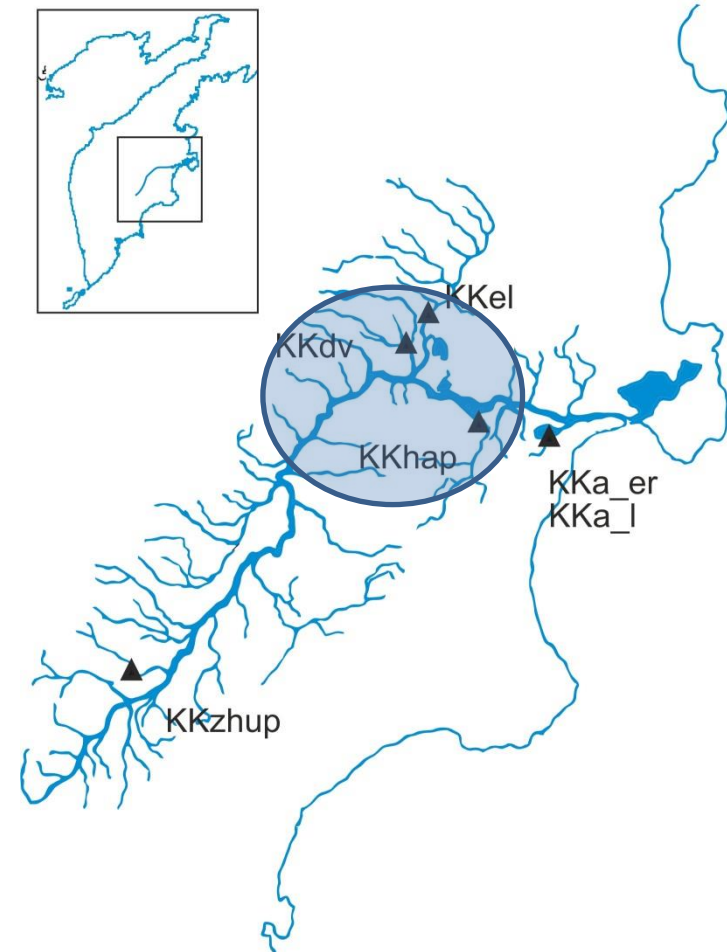
In the majority of the populations examined, in addition to two mass haplotypes, there are also 1-2 derivatives of them, which, in general, confirms the earlier hypothesis about their historical age, which we attributed to the beginning of the Holocene transgression (≈11700 years ago).

The exception, apparently, is the sockeye salmon from the Kamchatka River basin, where in addition to the two main haplotypes, 12 derivatives were found. We have every reason to believe that the vast paleobasin in the middle and upper reaches of the Kamchatka River (a deep lake in the Kamakovskaya Lowland and its tributaries) was one of the refugia in the Asian part of the sockeye salmon range (Braitseva et al., 1968), where, from the time of the Sangamon (Eemian) interglacial period (130-115 thousand years ago) and throughout the last glaciation, a large population existed.

Literature and our results allow us to consider a scenario of modern diversity of sockeye salmon mtDNA haplotypes formation, implying recurrent colonization of Asia by this species. The Hap_2_13T haplotype seems to have a more ancient origin apparently associated with the American continent. Probably, the first wave of invasion of the species into Asia, which followed the Middle Pleistocene the Illinoian Stage (the Riss glaciation) (240-140 thousand years ago), led to the spread of the Hap_2_13T haplotype along the entire Asian-Pacific coast up to the northern islands of the Japanese archipelago. Most likely the Hap_1_10T formed later, probably in Asia, because almost all transitional haplotypes (Hap_8, 9, 10) between haplogroups are found in the Iturup Island populations.

Schematic map of a refugium location in the Kamchatka River basin

KKel
KKdv
KKhap
KKa_er
KKa_l
KKzhup

Thank you
for your attention!