



## Comparative phylogeography of salmonid fishes (Salmonidae) reveals late to post-Pleistocene exchange between three now-disjunct river basins in Siberia

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**Abstract.** We use a comparative phylogeographical framework to evaluate the hypothesis of hydrological exchange during the Pleistocene among the now disjunct Lena, Amur, and Enisei basins in Siberia, and to provide evidence on the causal mechanism of their present day faunal dissimilarities. Approximately 600 bases of the mitochondrial control region were sequenced in five distinct lineages among three genera of salmonid fishes, *Hucho*, *Brachymystax* and *Thymallus*. All three basins were fixed for divergent (2–5.4%) lineages of *Thymallus* whereas a single shared haplotype was present in all three basins for *Hucho taimen* (Pallas, 1773) and one shared haplotype between the Lena and Amur basins out of a total of five for blunt-snouted and one out of five for sharp-snouted *Brachymystax lenok* (Pallas, 1773). For both blunt- and sharp-snouted lenok the

haplotypes found within each basin did not form clades, so no relationship between genotypes and geographical occurrence was found. Our data support relatively recent hydrological mixing of the major river drainage systems in eastern and far-eastern Siberia, congruent with the hypothesis of large-scale palaeo-hydrological exchange stemming from glacial advance, retreat and melting during Pleistocene climate fluctuations. Furthermore, these results in conjunction with a comparison of overall faunal composition suggest that environmental differences rather than historical contingency may be responsible for the faunal dissimilarities of the Amur, Lena, and Enisei river basins.

**Key words.** Amur, Baikal, *Brachymystax*, Enisei, *Hucho*, Lena, mtDNA, phylogeography, *Thymallus*.

### INTRODUCTION

Quaternary climatic oscillations have left an impressive imprint on the genetic architecture of European fauna and flora (Hewitt, 2000). Indeed, molecular-based phylogeographical studies in temperate latitudes have interpreted geographical patterns of genetic variation largely in terms of the landscape and associated biotic

changes that ice age phenomena have caused. For European freshwater fishes, both a priori knowledge and ad hoc speculation on the isolation, alteration, and redistribution of river basins have played a major role in the interpretations of numerous phylogeographical studies (Bernatchez *et al.*, 1992; Riffle *et al.*, 1995; Durand *et al.*, 1999; Weiss *et al.*, 2000, 2001, 2002). Similar studies of Siberian fauna are scarce, in part due to logistic and financial limitations of large-scale sampling in remote regions. Additionally, the

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traditional view of Siberian palaeoclimates maintained that drier climates prevented the extent of glaciation seen in North America and Europe, and thus glacial events were not expected to be a major factor influencing patterns of distribution. However, this paradigm is largely giving way to a perspective of spectacular glacial phenomena that have repeatedly reshaped some of the largest hydrological networks in the temperate latitudes (Grosswald, 1998, 1999 and references therein). While hypotheses on landscape alterations can aid phylogeographical inferences, there is also hope that sound phylogeographical inferences, especially when based on multiple species, may help support palaeoclimatic hypotheses. This seemed indeed the case where a systematic study of the genus *Thymallus* in and around Lake Baikal not only supported the timing of several palaeohydrological events, such as the isolation of Baikal from the Lena basin and the formation of the lake's only contemporary outlet (Angara River), but also suggested that Pleistocene perturbations in or around the lake may have had a predominant effect on ichthyofaunal diversity (Koskinen *et al.*, 2002a).

The Amur, Lena and Enisei rivers are among the world's 10 largest hydrological systems. The three basins are geographically close, with extensive regions of the Lena coming into close proximity of tributaries now located in both the Amur and Enisei catchments. Furthermore, the Selenga River, Lake Baikal's largest tributary system and thus ultimately part of the Enisei basin, has regions that closely border the upper Enisei, Lena and Amur basins. Enisei and Lena host essentially the same Siberian fish species; Berg (1949) included them in the Holarctic zoogeographical region, whereas he classified the Amur to the Amur (Manchurian) transitional region based on the overall dissimilarity of its highly distinct faunal assemblage, compared to Siberian drainages. Banarescu (1991) considered Eastern Asia from the Amur basin to Northern Vietnam as a subregion of the Sino-Indian region and described the area where the headwaters of the Amur and Lena are separated by the Yablonov and Stanovoi mountain ranges as the sharpest continental divide for freshwater fauna in the world, preventing mixture of the Indo-Pacific and Siberian aquatic faunal subregions. Bogutskaya & Naseka (1996) followed Berg in considering

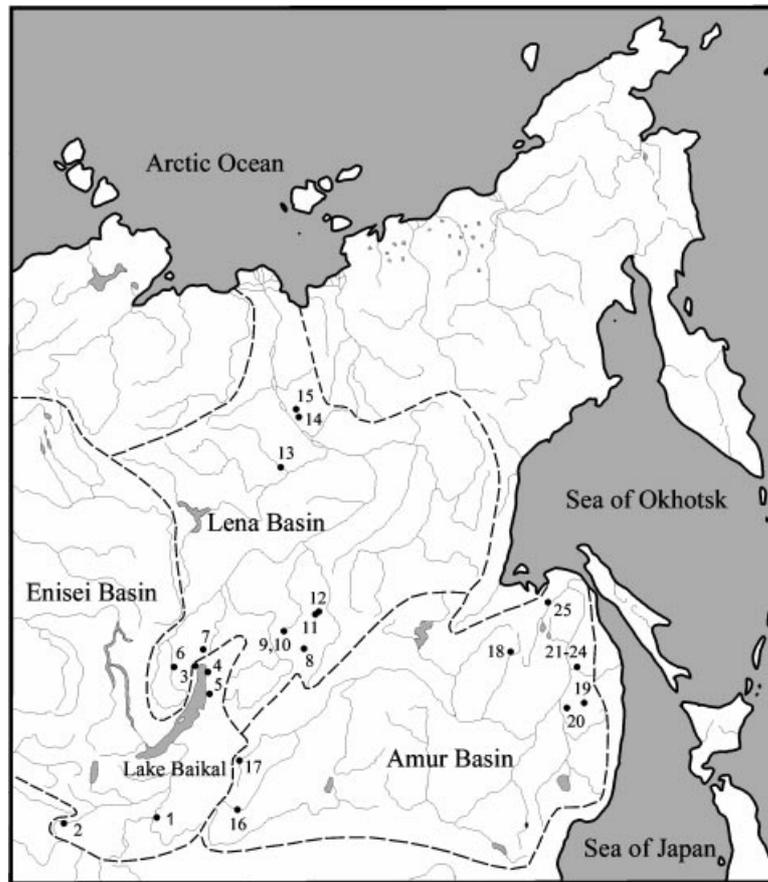
the Amur-Manchurian area as a separate zoogeographical transitional region. However, faunal exchange between the Amur and Lena basins is facilitated by the structure of the divide, with portions of these systems' headwaters sharing vast plateau regions (Berg, 1949). Palaeogeological evidence supports recent captures of the formerly Amur basin headwaters by the headwaters of the Vitim and Olekma belonging to the Lena basin (Pavlovskii, 1939; Korzhuev, 1956, 1979) as well as capture of the headwaters of the Aldan basin (tributary of Lena) by the headwaters of the Zeya river basin (tributary of Amur) (Ganeshin, 1972; Korzhuev, 1979).

According to Grosswald (1998, 1999), during the Pleistocene the Enisei and Lena basins were repeatedly connected forming part of a global trans-Siberian drainage system of periglacial lakes draining west into the Atlantic Ocean via the Mediterranean. The Amur along with the now closed basins of Central Asia belonged to another system, the Gobi-Amuran drainage discharging east into the Pacific Ocean. However, glaciation in the Baikal region periodically forced the discharge of Selenga and upper Vitim basins into the Amur and of Lake Baikal into the Lena thus playing the role of a switchboard rerouting the discharge of Central Asia between Angara (Enisei basin), Lena, and Amur rivers (Fastook & Grosswald, 1998). Thus, palaeohydrological data indicate connections between Enisei, Lena, and Amur basins in the Pleistocene.

Indeed, a number of faunal elements, including the cold-tolerant salmonid genera *Thymallus*, *Hucho*, and *Brachymystax* are shared between all three basins. Berg (1949) lists 13 common Siberian fish species in the Amur basin. In addition, one species, clearly of Amur origin (*Phoxinus lagowskii*) is found in the Lena basin. We assess the genetic divergence between several populations of the shared salmonid taxa between the Lena, Enisei, and Amur systems and evaluate the degree of phylogeographical congruency in terms of both recent palaeohydrological hypotheses, and the overall pattern of ichthyofaunal and environmental dissimilarity between these basins.

## METHODS

Five morphologically diagnosable lineages among three salmonid genera were investigated



**Fig. 1** Sample locations for this study. Basin margins are indicated by broken lines. For each basin and numbered sample site the taxa analysed are shown. **Baikal/Enisei Basin:** (1) Orkhon (sharp-snouted *B. lenok*); (2) Terkhyn (*Thymallus arcticus*); (3) Gramna (*Hucho taimen*); (4) Frolikha (sharp-snouted *B. lenok*, *Thymallus arcticus*); (5) Bolshaya (*Hucho taimen*). **Lena Basin:** (6) Kutima (*Thymallus arcticus*); (8) Kalar (sharp-snouted *B. lenok*, *Hucho taimen*); (9) Leprindokan (*Thymallus arcticus*); (10) Kuanda (sharp-snouted *B. lenok*, blunt-snouted *B. lenok*); (11) Olongdo (*Thymallus arcticus*) (14) Kundudei (blunt-snouted *B. lenok*); (15) Tirekhtyakh (sharp-snouted *B. lenok*); (7) Nomama (sharp-snouted *B. lenok*); (13) Tuyng (sharp-snouted *B. lenok*); (12) Itchilyak Lake (blunt-snouted *B. lenok*). **Amur Basin:** (16) Onon (sharp-snouted *B. lenok*, *Thymallus grubii*); (17) Sypchegurka (*Thymallus grubii*); (18) Bureya (blunt-snouted *B. lenok*); (19) Sukpai (*Hucho taimen*); (21) Gobili (sharp-snouted *B. lenok*, blunt-snouted *B. lenok*); (22) Ertukulli (sharp-snouted *B. lenok*); (24) Anui (sharp-snouted *B. lenok*, blunt-snouted *B. lenok*, *Thymallus grubii*); (23) Manoma (blunt-snouted *B. lenok*); (25) Merek (blunt-snouted *B. lenok*); (20) Khor (sharp-snouted *B. lenok*, blunt-snouted *B. lenok*).

with a total of 91 individuals sampled from 25 locations distributed among the three basins (Table 1; Fig. 1). These included *Hucho taimen* (Pallas, 1773) ( $n = 7$ ), the sharp ( $n = 20$ ) and blunt-snouted ( $n = 14$ ) lenoks; two morphs grouped together under the same taxon, *B. lenok* (Pallas, 1773; Alekseyev *et al.*, 1986; Mina, 1991),

or recognized as two different species (Kifa, 1976; Shed'ko *et al.*, 1996; Shed'ko, 1998), and two species of *Thymallus*, *T. arcticus* (Pallas, 1776) ( $n = 29$ ), which has been given numerous subspecies designations, and *T. grubii* (Dybowski, 1869) ( $n = 20$ ), which is also listed as a subspecies of *T. arcticus* by some authors. All but two of the

**Table 1** Population names, basin, sample sizes and geographical coordinates for the *Hucho taimen* (Pallas, 1773), *Brachymystax lenok* (Pallas, 1773), *Thymallus arcticus* (Pallas, 1776) and *Thymallus grubii* (Dybowski, 1869) samples used in this study

Population	Population number	Basin	Taxa (number of individuals)					Latitude	Longitude
			<i>H. taimen</i>	<i>B. lenok</i> (sharp)	<i>B. lenok</i> (blunt)	<i>T. arcticus</i>	<i>T. grubii</i>		
Orkhon River	1	Enisei → Selenga	2					49°20'	105°30'
Terkhyn River	2	Chulutyngol → Selenga → Enisei				2		47°45'	99°20'
Gramna Lake	3	Tiya → Baikal → Enisei	1					55°44'	109°06'
Frolkha Bay, Baikal	4	Enisei		2				55°31'	109°51'
Bol'shaya River	5	Baikal → Enisei	3					54°27'	109°28'
Kutima River	6	Kirenga → Lena				2		57°02'	108°36'
Nomama Lake	7	Chaya → Lena	1					56°16'	110°17'
Kalar River	8	Vitim → Lena	1					56°14'	119°32'
Leprinidokan Lake	9	Kuanda → Vitim → Lena				8		56°33'	117°29'
Kuanda River	10	Vitim → Lena	2		2			56°31'	117°26'
Olongdo Lake	11	Khani → Olekma → Lena				15		57°10'	119°41'
Itehilyak Lake	12	Olekma → Lena Basin						57°11'	119°52'
Tuyng River	13	Vilti → Lena	2					63°58'	121°30'
Kundudei River	14	Lena			2			65°47'	125°40'
Tirekhtyakh River	15	Undlung → Lena	1					66°22'	125°00'
Onon River	16	Shilka → Amur	2					48°35'	110°48'
Sypchegurka River	17	Ingoda → Amur				10		51°20'	113°26'
Bureya River	18	Amur						51°55'	134°53'
Sukpai River	19	Khor → Amur	2					47°45'	137°10'
Khor River	20	Amur		3				47°50'	135°22'
Gobili River	21	Anui → Amur		1				49°15'	138°19'
Ertukuli River	22	Anui → Amur		1				49°18'	138°03'
Manoma River	23	Anui → Amur						49°21'	137°24'
Anui River	24	Amur		2				49°17'	137°55'
Merek River	25	Amgun' → Amur			2			51°17'	134°47'

sequences for *Thymallus* are reported in Koskinen *et al.* (2002a). Whole genomic DNA was isolated from alcohol preserved tissue using a high salt extraction protocol. The complete mitochondrial (mtDNA) control region and portions of flanking tRNA gene regions were amplified for all the taxa using the LRBT-25 and LRBT-1195 primers and PCR conditions first described in Uiblein *et al.* (2001) and used in Weiss *et al.* (2002). Amplified DNA templates were purified using the QIAquick PCR Purification Kit (Qiagen) and 100 ng of purified PCR product were used in cycle sequencing reactions, using the forward PCR primer, following ABI PRISM BigDye Terminator protocols. Sequences were visualized on either an ABI-310 or ABI-373 automated sequencer and aligned by eye using the Sequence Navigator Software.

Because intraspecific dichotomous branching haplotype trees do not necessarily reflect population history (Goldstein *et al.*, 2000) and we were particularly interested in the genealogy of closely related haplotypes within basins, we used unrooted networks for evaluating genetic relationships. Networks were constructed with a 95% criterion (Templeton *et al.*, 1992) and gaps counted as events (i.e. treated as a fifth state) using TCS 1.13 computer program (Clement *et al.*, 2000). The relationship of haplotypes, or clades beyond the limit of this parsimony criterion is displayed graphically using the net nucleotide divergence (Da) between groups (Kimura two-parameter model) calculated in MEGA 2.01 (Kumar *et al.*, 2001). This metric corresponds to between-group variation corrected for within-group variation in haplotypes (Nei, 1987).

## RESULTS

For *Hucho taimen* and *B. lenok*, a total of 600 bp of the 5' end of the L-strand of the control region, including 71 bp of the flanking tRNA proline gene could be read using the forward PCR primer. An analogous length of sequence was compared among *Thymallus* samples, taken from the approximately 1100 bp-long sequences in Koskinen *et al.* (2002a).

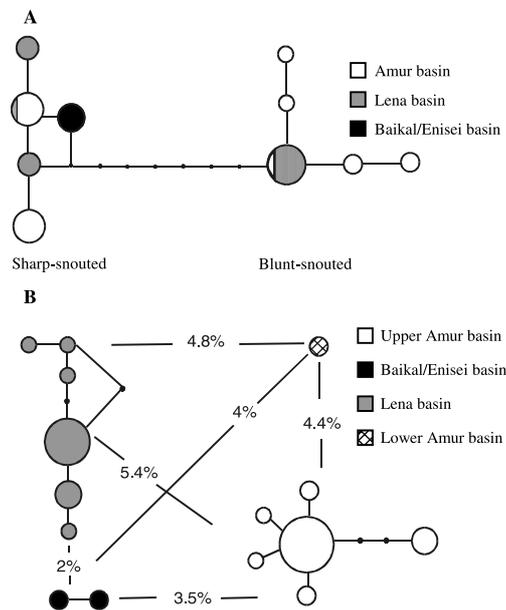
Only a single haplotype was found among the seven samples of *Hucho taimen* (GenBank accession numbers AY230447-AY230450) stemming from three distinct basins (Lena, Amur, Baikal/

Enisei). In contrast, 10 haplotypes were found in *B. lenok*, with five unique haplotypes in each form (blunt- and sharp-snouted) (GenBank accession numbers AY230451-AY230472). There was one insertion/deletion, no transversions and 14 transitions. The two lineages formed monophyletic groups with 1.4% sequence divergence (Da) between them; 0.19% within sharp-snouted and 0.23% within the blunt-snouted form. Based on the maximum parsimony network, neither form displayed geographical concordance with their respective genealogical relationship (Fig. 2a). Within each form, there was also a single haplotype, which occurred in both the Lena and the Amur basins.

In *Thymallus* a total of 15 haplotypes were resolved (six in the Lena, seven in the Amur, and two in the Enisei) (GenBank access no AY168390-99; AY168379-85; AY168368-68; AY230473). There were five insertion/deletions, 20 transversions, and 35 transitions. The maximum parsimony analysis revealed four distinct networks, each divergent beyond the limit of the 95% parsimony criterion (Fig. 2b). Each basin contained at least one fixed monophyletic clade (two within the Amur basin) with no shared haplotypes between basins. Mean pairwise divergence of haplotypes among these clades ranged from 2% (Lena-Enisei) to 5.4% (Lena-Upper Amur) (Fig. 2b).

## DISCUSSION

Variation in the genetic diversity of freshwater organisms generally tends to be distributed among basins, as dispersal is largely limited to the linear architecture of riverine drainages. Patterns of molecular diversity in European freshwater fishes, for example, are primarily interpreted in terms of the disjunct basins within which particular lineages have evolved, and the shifting drainage patterns that occur over glacial and interglacial time periods (Bernatchez *et al.*, 1992; Nesbo *et al.*, 1998; Englbrecht *et al.*, 2000). Two of the three genera investigated show a similar pattern in lacking differentiation among the major basins, strongly supporting hydrological exchange in the recent (late or post Pleistocene) past, and dismissing the notion of a sharp zoogeographical divide based on basin isolation as proposed by Banarescu (1991). This inference is



**Fig. 2** (A) Parsimony network of control region haplotypes observed in sharp- and blunt-snouted *Brachymystax lenok* (Pallas, 1773). White circles represent haplotypes from Amur basin; grey circles represent haplotypes from Lena basin; black circles represent haplotypes from Baikal/Enisei basin. (B) Parsimony networks of control region haplotypes observed in *Thymallus*. The mean sequence divergence between each group ( $D_{ij}$ ) is also shown. White circles represent haplotypes from upper Amur basin, *Thymallus grubii* (Dybowski, 1869); hatched circles represent haplotypes from lower Amur basin, *Thymallus grubii*; grey circles represent haplotypes from Lena basin, *Thymallus arcticus* (Pallas, 1776); black circles represent haplotypes from Baikal/Enisei basin, *Thymallus arcticus*. For both A and B, circle size is proportional to the observed haplotype frequencies and black points represent unobserved haplotypes and potential intermediates.

clearer for the Lena/Amur basin boundary, whereas one unique haplotype for lenok was found in the Enisey. For the third genus, however, not only is each basin fixed for at least one monophyletic clade, but the divergence between them corresponds to several million years of isolation, or a pre-Pleistocene split among basins (based on 1% divergence per Myr). Phylogeographical incongruencies based on molecular data can be based on several phenomena that are

not mutually exclusive, such as differences in the mutation rate of the sequence investigated, demographic history, and a varied colonization and dispersal history. We address these phenomena in turn and relate inferences to the overall pattern of faunal dissimilarity among these major basins, as well as current palaeohydrological hypotheses.

### Variation in the molecular clock

Several lines of evidence support that mtDNA in poikilothermic animals including salmonid fishes evolves at a considerably slower rate than in homeotherms (Martin & Palumbi, 1993; see also Steinfartz *et al.*, 2000). This assumption, combined with a fossil-based calibration (Smith, 1992), calibrations based on independent palaeohydrological hypotheses (Koskinen *et al.*, 2002a) as well as additional empirical studies (see Discussion in Weiss *et al.*, 2002) all support an approximate divergence rate of 1–2% per million years for salmonid mtDNA and more specifically approximately 1% for the entire control region (i.e. containing both hypervariable and highly conserved regions) across the genus *Thymallus*. However, body size and age at maturity have been shown to be inversely related to substitution rate (Bromham, 2002). The question is raised as to whether such differences resulting in varying substitution rate among the three genera investigated here could account for the observed phylogeographical incongruencies? While there is a general trend in increased age at maturity beginning with *Thymallus* followed by the larger *Brachymystax* and finally *Hucho*, absolute differences are negligible (e.g. age at maturity for *Thymallus* and *Brachymystax* is generally 3–6 years, and *Hucho* 4–8 years) and the ranges found among populations overlap considerably, making it doubtful that this characteristic can have much effect on molecular divergence estimates. Moreover, the percent divergence between Amur basin grayling *T. grubii* (whether from the upper or lower portions of the drainage, see Fig. 2b) and Lena, for example, is approximately 5%, or about 30 mutations across 600 bp. As there is no variation among samples of *Hucho*, and no or little genetic divergence attributable to basin isolation in *Brachymystax*, a reduction in mutation rate of at least 30 times would be required to explain these differences based on varying molecular clock alone,

far in excess of what could be explained by differences in generation time or metabolic rate.

#### Variation in demography

Fluctuations in historical effective population size affect the observed amount of genetic variation (Avice, 2000). Furthermore, based on body size and position in the food chain, *Hucho* should exist at smaller population sizes than *Thymallus*, with *Brachymystax* at intermediate sizes. However, if *Hucho* or *Brachymystax* existed in isolation for a period of several million years, it would be extremely unlikely for subsequent bottlenecks to erase the fixed differences that would occur via an accumulation of independent basin-specific mutations. For *Hucho*, we can perhaps assume that a bottleneck has occurred, or at least the species has had vastly lower effective population sizes compared to the two other genera. However, this demographic scenario needed to have only occurred in a single basin, with the genetically impoverished lineage subsequently spreading to the other basins. A bottleneck in more than one basin would have resulted in multiple lineages. *Brachymystax*, existing as two monophyletic lineages provides considerably more support for our conclusion of recent faunal exchanges, as the two lineages appear to have independently replicated their cross-basin pattern of within-clade similarity. For this genus, bottlenecks or low effective population sizes cannot explain their phylogeographical pattern in comparison to *Thymallus*.

#### Variation in dispersal history

The most parsimonious explanation for the observed incongruencies is simply differing colonization histories for each species (or lineage), based on a combination of varying migratory ability, habitat preferences and any other life-history characteristics that may contribute to natal fidelity or dispersal distance. However, in order for these biological differences to have effect, it must have been physically possible in the recent past for fish to cross the watershed divides that now exist between the Lena, Amur, and Enisei basins. The faunal dissimilarity between these basins, discussed in Banarescu (1991) may more reflect differing environmental conditions rather

than physical barriers to colonization. Reviewing the available faunal lists for Siberian fishes it is apparent that a number of taxa in addition to the salmonids studied here are shared between the Amur basin and either the Enisei or Lena, or both (Appendix I). Berg (1949) listed 13 widespread Siberian species that were present in the Amur and one present in Amur and Lena. The shared species include cold-tolerant taxa such as *Phoxinus lagowskii*, *Ph. perenurus*, *Ph. phoxinus*, *Ph. czekanowskii*, *Gobio gobio*, *G. soldatovi*, *Carassius auratus*, *Barbatula toni*, *Cobitis melano-leuca*, *Lota lota*, and *Cottus poecilopus*. The large number of taxa found in the Amur basin ( $N = 78$ , i.e. excluding introduced species) but not in other Siberian systems, primarily represents cold-intolerant cyprinids. This comparative faunal perspective supports a scenario with ample opportunities for faunal exchange between these systems, under which environmental factors have limited the shared faunal elements to primarily cold-tolerant species. The major incongruency in our data then, is not the shared haplotypes found within *Hucho* and *Brachymystax*, but rather the deep divergences displayed by *Thymallus*.

The genus *Thymallus* is widespread, and especially *T. arcticus* (within which many authors still group Amur River populations) displays a broad range originally existing from the Ural Mountains in the west, clear across Eurasia as far east as Michigan, USA. However, most recent genetic data support a general trend of higher levels of isolation and divergence even within major drainages, compared to other coexisting species. For example, European grayling *T. thymallus* display levels of within-basin fragmentation that greatly exceed that of co-occurring ecologically similar taxa (Koskinen *et al.*, 2001, 2002b; Weiss *et al.*, 2002). These authors have hypothesized that perhaps strong natal homing tendencies coupled with poor dispersal may promote inter- and intra-basin population fragmentation. In a region of central Europe, where the headwaters of three drainages come into close contact, a number of late-Pleistocene river capture events have been documented and used to explain faunal exchanges (Riffle *et al.*, 1995; Weiss *et al.*, 2000). *T. thymallus* nonetheless exhibits significant divergence between each basin (Gross *et al.*, 2001), a pattern similar to that described in this investigation in eastern Siberia. Additional studies (Froufe *et al.*, in press)

reveal reproductively isolated sympatric lineages of grayling in the lowermost reaches of the Amur basin itself. Thus, it appears that grayling lineages throughout Eurasia display a relatively fine level of population structure, and have a difficult time achieving trans-basin dispersal even when hydrological corridors have provided the suitable paths for other cold-tolerant species. Clearly, some biological mechanism promotes isolation and divergence in *Thymallus*, and thus divergence time estimates between lineages within the genus (whether considered conspecific or not) cannot be directly used to infer the permanence of basin isolation. Whereas the divergence of *Thymallus* revealed in this study most probably reflects allopatric origins, subsequent isolating mechanisms may confound the phylogeographical signal and obscure the fact that these drainage basins have had more recent physical contact, as revealed by investigating other taxa (*Hucho* & *Brachymystax*).

In summary, our data support relatively recent hydrological mixing of major river drainage systems in eastern and far-eastern Siberia congruent with the large-scale palaeohydrological patterns hypothesized by Grosswald based on glacial advance, retreat and melting during Pleistocene climate fluctuations. Further, we note that additional sampling of *Hucho* and *Brachymystax* cannot alter this result, as shared haplotypes have already been demonstrated. Additional strength for the hypothesis of a biological cause for *Thymallus*'s apparent inability to use the palaeohydrological corridors, could be built by more intensive headwater sampling and by investigating the molecular diversity of several other cold-tolerant species shared among these drainages, such as species of *Phoxinus*, *Barbatula toni*, *Cobitis melanoleuca*, *Lota lota*, and *Cottus poecilopus* and lastly, we propose that the differences in ecological demands, namely between cold-tolerant and intolerant species, may be the primary mechanism promoting the faunal distinction of the Amur among other Siberian systems, rather than a simple zoogeographical explanation based on hydrological isolation.

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**Appendix I** Checklist of the Amur, Lena and Enisei/Baikal fish fauna compiled from Berg (1949), Nikol'skii (1956), Kirillov (1972), Baasanzhav *et al.* (1983), Yegorov (1985), Karasev (1987), Bogutskaya & Naseka (1996) Kirillov (2002) & Reshetnikov *et al.* (2002a,b) with some updates, corrections and comments by the authors. The authors recognize that significant taxonomic reform and debate is ongoing within many groups.

Taxon	Amur River basin	Lena River basin	Enisei River basin	
			Baikal Lake & tributaries	The rest of the Enisei basin
<b>Petromyzontidae</b>				
<i>Lethenteron japonicum</i>	X			
<i>Lethenteron kessleri</i>		X		X
<i>Lethenteron reissneri</i>	X			
<b>Acipenseridae</b>				
<i>Acipenser ruthenus</i>				X
<i>Acipenser baerii</i>		X	X	X
<i>Acipenser schrenckii</i>	X			
<i>Acipenser medirostris</i>	X			
<i>Huso dauricus</i>	X			
<b>Salmonidae</b>				
<i>Brachymystax lenok</i>	X	X	X	X
<i>Hucho taimen</i>	X	X	X	X
<i>Oncorhynchus gorbusha</i>	X	X		
<i>Oncorhynchus keta</i>	X	X		
<i>Oncorhynchus kisutch</i>	X			
<i>Oncorhynchus masou</i>	X			
<i>Oncorhynchus tshawytscha</i>	X			
<i>Salvelinus alpinus</i>		X	X	X
<i>Salvelinus malma</i>	X			
<i>Salvelinus leucomaenis</i>	X			
<b>Coregonidae</b>				
<i>Coregonus autumnalis</i>		X		X
<i>Coregonus autumnalis migratorius</i>		(X)	X	
<i>Coregonus chadary</i>	X			
<i>Coregonus lavaretus pidschian</i>		X	X	X
<i>Coregonus muksun</i>		X		X
<i>Coregonus nasus</i>		X		X
<i>Coregonus peled</i>		X	(X)	X
<i>Coregonus sardinella</i>		X		X
<i>Coregonus tugun</i>		X		X
<i>Coregonus ussuriensis</i>	X			
<i>Prosopium cylindraceum</i>		X		X
<i>Stenodus leucichthys nelma</i>		X		X
<b>Thymallidae*</b>				
<i>Thymallus arcticus arcticus</i>			X	X
<i>Thymallus arcticus baicalensis</i>			X	
<i>Thymallus arcticus nigrescens</i>			X	
<i>Thymallus arcticus pallasi</i>		X		
<i>Thymallus grubii</i>	X			
<b>Osmeridae</b>				
<i>Osmerus mordax dentex</i>	X	X		X
<i>Hypomesus nipponensis</i>	X			
<i>Hypomesus olidus</i>	X			
<b>Esocidae</b>				
<i>Esox lucius</i>		X	X	X

## Appendix I continued.

Taxon	Amur River basin	Lena River basin	Enisei River basin	
			Baikal Lake & tributaries	The rest of the Enisei basin
<i>Esox reichertii</i>	X			
<b>Cyprinidae</b>				
<b>Leuciscinae</b>				
<i>Abramis brama</i>			(X)	(X)
<i>Aristichthys nobilis</i>	X			
<i>Elopichthys bambusa</i>	X			
<i>Hypophthalmichthys molitrix</i>	X			
<i>Leuciscus idus</i>		X	X	X
<i>Leuciscus leuciscus baicalensis</i>		X	X	X
<i>Leuciscus waleckii</i>	X			
<i>Phoxinus czekanowskii</i>	X	X	?	X
<i>Phoxinus czekanowskii ezerskii</i>	X			
<i>Phoxinus lagowskii</i>	X	X		
<i>Phoxinus perenurus</i>	X	X	X	X
<i>Phoxinus phoxinus</i>	X	X	X	X
<i>Pseudaspius leptcephalus</i>	X			
<i>Rutilus rutilus</i>		X	X	X
<i>Tribolodon brandtii</i>	X			
<i>Tribolodon hakuensis</i>	X			
<b>Cultrinae</b>				
<i>Chanodichthys dabryi</i>	X			
<i>Chanodichthys erythropterus</i>	X			
<i>Chanodichthys mongolicus</i>	X			
<i>Culter alburnus</i>	X			
<i>Hemiculter leucisculus</i>	X			
<i>Hemiculter lucidus</i>	X			
<i>Megalobrama terminalis</i>	X			
<i>Parabramis pekinensis</i>	X			
<b>Xenocyprininae</b>				
<i>Plagiognathops microlepis</i>	X			
<i>Xenocypris argentea</i>	X			
<b>Rasborinae</b>				
<i>Aphyocypris chinensis</i>	X			
<i>Ochetobius elongatus</i>	(X)			
<i>Opsariichthys uncirostris amurensis</i>	X			
<b>Acheilognathinae</b>				
<i>Acanthorhodeus asmussii</i>	X			
<i>Acanthorhodeus chankaensis</i>	X			
<i>Rhodeus lighti amurensis</i>	X			
<i>Rhodeus sericeus sericeus</i>	X			
<b>Gobioninae</b>				
<i>Abbottina rivularis</i>	X			
<i>Gnathopogon strigatus</i>	X			
<i>Gobio gobio cynocephalus</i>	X		X	X
<i>Gobio soldatovi soldatovi</i>	X			
<i>Gobio soldatovi tungussicus</i>		X		
<i>Gobiobotia pappenheimi</i>	X			
<i>Hemibarbus labeo</i>	X			
<i>Hemibarbus maculatus</i>	X			
<i>Ladislavia taczanowskii</i>	X			
<i>Microphysogobio tungtingensis amurensis</i>	X			

## Appendix I continued.

Taxon	Amur River basin	Lena River basin	Enisei River basin	
			Baikal Lake & tributaries	The rest of the Enisei basin
<i>Pseudorasbora parva</i>	X			
<i>Romanogobio tenuicarpus</i>	X			
<i>Sarcocheilichthys czerskii</i>	X			
<i>Sarcocheilichthys sinensis</i>	X			
<i>Sarcocheilichthys soldatovi</i>	X			
<i>Saurogobio dabryi</i>	X			
<i>Squalidus chankaensis</i>	X			
<b>Barbinae</b>				
<i>Ctenopharyngodon idella</i>	X			
<i>Mylopharyngodon piceus</i>	X			
<i>Squaliobarbus curriculus</i>	X			
<b>Cyprininae</b>				
<i>Carassius auratus gibelio</i> †	X	X	X	X
<i>Carassius carassius</i> †		X		X
<i>Cyprinus carpio haematopterus</i>	X		(X)	
<b>Tincinae</b>				
<i>Tinca tinca</i>			X?	X?
<b>Balitoridae</b>				
<i>Barbatula toni</i>	X	X	X	X
<i>Lefua costata</i>	X			
<b>Cobitidae</b>				
<i>Cobitis choui</i>	X			
<i>Cobitis lutheri</i>	X			
<i>Cobitis melanoleuca</i>	X	X	X	X
<i>Leptobotia mantschurica</i>	X			
<i>Misgurnus anguillicaudatus</i>	X			
<b>Siluridae</b>				
<i>Parasilurus asotus</i>	X		(X)	
<i>Silurus soldatovi</i>	X			
<b>Bagridae</b>				
<i>Leiocassis brashnikowi</i>	X			
<i>Leiocassis herzensteini</i>	X			
<i>Leiocassis ussuriensis</i>	X			
<i>Mystus mica</i>	X			
<i>Pelteobagrus fulvidraco</i>	X			
<b>Lotidae</b>				
<i>Lota lota</i>	X	X	X	X
<b>Gasteosteidae</b>				
<i>Gasterosteus aculeatus</i>	X			
<i>Pungitius pungitius pungitius</i>		X		X
<i>Pungitius sinensis</i>	X?			
<b>Percichthyidae</b>				
<i>Siniperca chuatsi</i>	X			
<b>Percidae</b>				
<i>Gymnocephalus cernuus</i>		X		X
<i>Perca fluviatilis</i>	X	X	X	X
<i>Stizostedion lucioperca</i>	(X)			
<b>Eleotrididae</b>				
<i>Micropercops cinctus</i>	X			
<i>Percottus glenii</i>	X?		(X)	
<b>Gobiidae</b>				
<i>Chaenogobius annularis</i>	X			

## Appendix I continued.

Taxon	Amur River basin	Lena River basin	Enisei River basin	
			Baikal Lake & tributaries	The rest of the Enisei basin
<i>Chaenogobius macrognathus</i>				
<i>Rhinogobius bruneus lindbergi</i>	X			
<b>Channidae</b>				
<i>Channa argus warpachowskii</i>	X			
<b>Cottidae</b>				
<i>Batrachocottus baicalensis</i>			X	
<i>Batrachocottus multiradiatus</i>			X	
<i>Batrachocottus nikolskii</i>			X	
<i>Batrachocottus talievi</i>			X	
<i>Cottocomephorus alexandrae</i>			X	
<i>Cottocomephorus grewingkii</i>			X	
<i>Cottocomephorus inermis</i>			X	
<i>Cottus poecilopus</i>	X	X		X
<i>Cottus sibiricus</i>		X		
<i>Leocottus kesslerii</i>			X	
<i>Mesocottus haitej</i>	X			
<i>Paracottus knerii</i>			X	X
<i>Triglopsis quadricornis</i>		X		X
<i>Comephorus baicalensis</i>			X	
<i>Comephorus dybowski</i>			X	
<b>Abyssocottidae</b>				
<i>Abyssocottus elochini</i>			X	
<i>Abyssocottus gibbosus</i>			X	
<i>Abyssocottus korotneffi</i>			X	
<i>Asprocottus abyssalis</i>			X	
<i>Asprocottus herzensteini</i>			X	
<i>Asprocottus korjakovi</i>			X	
<i>Asprocottus parmiferus</i>			X	
<i>Asprocottus platycephalus</i>			X	
<i>Asprocottus pulcher</i>			X	
<i>Cottinella boulengeri</i>			X	
<i>Cyphocottus eurytomus</i>			X	
<i>Cyphocottus megalops</i>			X	
<i>Limnocottus bergianus</i>			X	
<i>Limnocottus godlewskii</i>			X	
<i>Limnocottus griseus</i>			X	
<i>Limnocottus pallidus</i>			X	
<i>Neocottus thernalis</i>			X	
<i>Neocottus werestschagini</i>			X	
<i>Procottus gotoi</i>			X	
<i>Procottus gurwici</i>			X	
<i>Procottus jeittelesii</i>			X	

Latin names are given according to Reshetnikov *et al.* (2002a,b).

(X) — introduced species;

bold — endemic species;

? — not absolutely clear.

\* *Thymallus* — The authors consider this genus under revision based on their own ongoing research.

Koskinen *et al.* (2002a) demonstrate a paraphyletic status for *Thymallus arcticus*, and based on mtDNA revealed no distinction of taxa within the Selenga, Baikal, and Angara/Enisei portion of the Enisei basin, and thus for the purposes of this paper, we refer only to *T. arcticus* without concern for subspecies designations.

† According to Kirillov (1972), only one species *Carassius carassius jacuticus* is present in the Lena basin.

