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Age and growth comparisons of Hovsgol grayling (*Thymallus nigrescens* Dorogostaisky, 1923), Baikal grayling (*T. baicalensis* Dybowski, 1874), and lenok (*Brachymystax lenok* Pallas, 1773) in lentic and lotic habitats of Northern Mongolia

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Summary

Despite concern over the conservation status of many Mongolian salmonids and the importance of their ecological role in Mongolia's aquatic ecosystems, little is known about their basic biology. Hovsgol grayling (*Thymallus nigrescens*) is endemic to Lake Hovsgol, Mongolia and listed as endangered on the Mongolian Red List. Baikal grayling (*T. baicalensis*) and lenok (*Brachymystax lenok*) are found in lakes and rivers throughout the Selenge drainage. A detailed study of the age and growth of these three salmonids was conducted based on 1,682 samples collected from July 2006 to July 2013 in Lake Hovsgol, its outlet the Eg River, and one of the Eg's largest tributaries, the Uur River. Our results suggest that Hovsgol grayling in particular can reach a much older maximum age (17 years in our samples) than previously believed based on aging from scales. Female Hovsgol grayling were heavier at a given length than their male counterparts. Lenok had a greater average length-at-age in Lake Hovsgol compared to the rivers and greater weight-at-length in the warmer Uur River than in the Eg; female lenok from the rivers had a greater average length-at-age than their male counterparts. This study provides critical new information for the management and conservation of these threatened salmonid species in Mongolia.

1 | INTRODUCTION

Salmonids are frequently an important target of commercial and recreational fisheries and are among the fishes likely to be most vulnerable to climate change (Wenger et al., 2011). Research in North America and Western Europe has elucidated the life history (Mangel, 1994), biogeographic (Keleher & Rahel, 1996), and habitat availability (Isaak et al., 2010) consequences of climate change for salmonids in these regions. However, much less is known about the likely impacts of climate change on Asian salmonids, several of which are listed on national or global red lists. A prerequisite for predicting the impacts of climate change or fishing on these species is an understanding of their basic biology, including growth and reproduction, in different environments. In particular, growth rates of some salmonids have been shown to differ markedly between lentic (pond or lake) and lotic (stream or river) environments, e.g. Atlantic salmon (Halvorsen & Svenning, 2000).

Grayling (*Thymallus* spp.) and lenok (*Brachymystax* spp.) are two genera of freshwater salmonids that are widely distributed in Northeast Asia and are often threatened by habitat loss, overfishing, and climate change. In Northern Mongolia, Lake Hovsgol and its only outlet, the Eg River, are home to two species of grayling: Hovsgol grayling (*T. nigrescens*, considered a subspecies, *T. arcticus nigrescens*, by some authorities, e.g. Knizhin, Weiss, and Susnik (2006)) and Baikal grayling (*T. baicalensis*), and one species of lenok: *B. lenok* (hereafter 'lenok'). Hovsgol grayling are endemic to Lake Hovsgol, morphologically distinct from other grayling in the Lake Baikal drainage (Knizhin et al., 2006), and are listed as Endangered on the Mongolian Red List of Fishes (Ocock et al., 2006), with climate change considered the primary threat (drying of tributaries in which they spawn) followed by fishing. Baikal grayling, found throughout the Selenge River watershed in Mongolia, are not specifically considered in the Mongolian Red List, but the nominative species, Arctic grayling (*T. arcticus*), is considered as Near-Threatened (Ocock et al., 2006). Lenok are widely distributed in Northern Mongolia, eastern Siberia, and parts of Kazakhstan, China, and Korea (Froufe, Sefc, Alexandrino, & Weiss, 2004) and are listed as Vulnerable on the Mongolian Red List (Ocock et al., 2006) and the red lists of China and Russia (Xu, Wang, Liu, Li, & Mou, 2009), with fishing considered the primary threat followed by habitat degradation. Management of all three of these salmonids is currently hampered by a poor understanding of their age, growth, and fecundity (although some information has been published in technical reports, e.g. Dulmaa (1999)). In particular, the limited literature on age and growth of these fishes in the wild (Baasanjav et al., 1985; Dulmaa, 1999; Sideleva, 2006) is likely based entirely on ages determined from scales (although the descriptions of the methods are insufficient to establish this conclusively), which have been demonstrated to be less accurate than otoliths for aging Arctic grayling (DeCicco & Brown, 2006) and other salmonids (Sharp & Bernard, 1988).

The goal of this study is to understand age and growth of Hovsgol grayling, Baikal grayling, and lenok in lentic and lotic habitats of the Lake Hovsgol–Eg River watershed. Specifically, we evaluated whether growth rates and length–weight relationships differ between: (i) males and females, (ii) rivers within the watershed, and (iii) lentic and lotic habitats.

2 | MATERIALS AND METHODS

Fish communities were sampled in the Lake Hovsgol–Eg River watershed in July 2006, 2009, and 2011–2013 (Figure 1; Table 1). Lake Hovsgol (surface area: 2,760 km^2, maximum depth: 262 m) is the 17th largest freshwater lake in the world by volume and the largest lake in Mongolia (Goulden, Sitnikova, Gelhaus, & Boldgiv, 2006). It is also a National Park and an International Long-term Ecological Research (ILTER) site. Lake Hovsgol drains into the Eg River, which joins with the Selenge River before flowing into Lake Baikal. The Uur River is the largest tributary of the Eg and a fisheries research laboratory owned by the Taimen Conservation Fund has been established near the confluence of the Eg and Uur rivers (50°19′11″N; 101°52′45″E).

Fish sampling took place at eight locations throughout Lake Hovsgol (see Ahrenstorff, Jensen, Weidel, Mendsaikhan, & Hrabik, 2012; for further details). Lake Hovsgol is generally ice-free from early June to early November (Hatgal Meteorological Station, unpubl. data). Fish sampling in the Eg and Uur rivers took place within 20 km upstream of their confluence. This region of the Eg River is characterized by a high gradient, numerous groundwater springs, and a partial canopy of willow and larch (Gilroy et al., 2010). The section of the Uur River in our study area is wider and lower in gradient than the Eg and predominately fed by surface flow. Maximum summer water temperatures observed during 2011–2013 were 18.4°C in the Eg and 23.7°C in the Uur (B. Mendsaikhan, unpubl. data). Air temperatures in the region have risen by 2.1°C over the last 70 years (Dagvadorj,

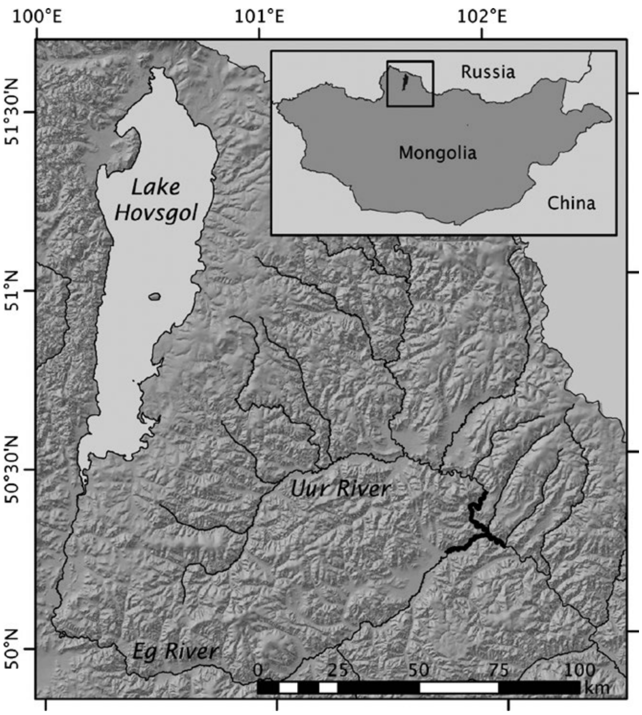

FIGURE 1 Study area in northern Mongolia. Samples were collected from Lake Hovsgol and the confluence of the Eg and Uur rivers indicated in bold

TABLE 1 Sample size of fish with length–weight and length-age (in parentheses) measurements by species and year

Species	2006	2009	2011	2012	2013	Total
Hovsgol grayling (*Thymallus nigrescens*)	30	386 (36)	201 (3)	226 (32)	222 (22)	1,065 (93)
Arctic grayling (*Thymallus baicalensis*)	0	9 (2)	41 (9)	140 (72)	13	203 (83)
Lenok (*Brachymystax lenok*)	9	56 (1)	79 (12)	209 (93)	61 (17)	414 (123)
Total	39	451 (39)	321 (24)	575 (197)	296 (39)	1,682 (299)

Natsagdorj, Dorjpurev, & Namkhainyam, 2009). Fish species richness is relatively low in both Lake Hovsgol with 10 species (Sideleva, 2006) and the Eg-Uur watershed with 12 species (Mercado-Silva et al., 2008).

Fish were collected in Lake Hovsgol using gillnets with mesh sizes ranging from 12.7 to 88.9 mm bar mesh. Because of their endangered status, Hovsgol grayling captured in the gillnets were released alive whenever possible, and only those that were dead when gillnets were retrieved were retained. In the Eg and Uur rivers, Baikal grayling and lenok were collected by angling. Fish were measured to the nearest mm (total length), weighed to the nearest gram (fish > 300 g) or 0.1 gram (fish < 300 g); for those fishes retained, their sagittal otoliths (Figure 2) were removed and the gonads examined macroscopically to determine their sex.

The relationship between total length (L, cm) and weight (W, g) was described using the standard length–weight equation: $W = aL^b$ (Ricker, 1975). Analysis of covariance (ANCOVA, lm package in R v3.0.2) was applied to the linearized form of the length–weight equation (ln (W) = ln (a) + b*ln (L)) to assess whether either of the parameters differed by sex or location for each species or between the two species of grayling.

Thin sections through the core of the otoliths in the transverse plane were prepared and examined under a compound microscope (50×) using transmitted light. Alternating light and dark circuli were interpreted as annuli by an experienced salmonid otolith reader. In several cases, annuli near the core were difficult to discern and therefore the otolith radius of young-of-the-year (measured using Image Pro Plus, Media Cybernetics) was used to establish the location of the first annulus.

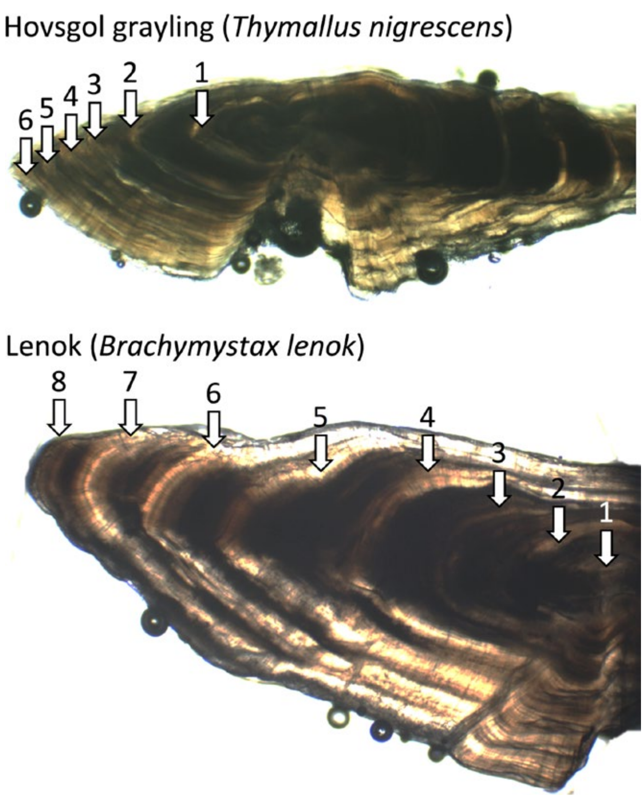

FIGURE 2 Sagittal otolith in 6-year-old Hovsgol grayling (*Thymallus nigrescens*, top) and an 8-year old lenok (*Brachymystax lenok*, bottom) under a compound light microscope; arrows = presumed annuli

A von Bertalanffy (VB) growth model of length at age (L_a):

$$L_a = L_\infty \left(1 - e^{-K(a-a_0)}\right)$$

where L_∞ is the average maximum size, K is the rate at which L_∞ is approached, and a_0 is the age at which a fish would be zero length, was fit to the age (a) and length data for each species (Hovsgol grayling, Baikal grayling, and lenok) × location (Eg River, Uur River, and Lake Hovsgol) × sex (male or female) combination. In many cases, the fish sample <10–20 cm in total length was insufficient to estimate a_0 meaningfully; in those cases, a_0 was fixed at 0. Likelihood ratio tests were used to test for overall growth differences (i.e. differences in predicted length-at-age, not in individual parameters of the growth model) between species, sex, and location (Haddon, 2001; Kimura, 1980). The method is based on the equation:

$$\chi^2_k = -N \times \ln\left(\frac{RBS_\Omega}{RBS_\omega}\right)$$

where k is the degrees of freedom (the number of constraints placed on the fit; 3 if $a0$ is estimated and 2 if a_0 is fixed at 0), N is the total observations from both curves combined, RRS_Ω is the total sum of squared residuals derived from fitting both curves separately (i.e. the minimum sum of squares from each curve added together), and RRS_ω is the total sum of squared residuals derived from fitting the curves with all constraints hypothesized as equal (Haddon, 2001).

We were not able to evaluate a potential year effect on the growth or length–weight relationships due to the short temporal span of sampling and the otolith sample sizes (effectively, 2009–2013; Table 1). Any effect of change in abiotic or biotic conditions, such as those associated with climate change, would be obscured by the fact that many of the sampled fish had overlapping life spans, i.e. they had lived through the same conditions.

3 | RESULTS

3.1 | Length–weight relationships

Length–weight regressions were constructed for each species overall and for comparisons between sexes, rivers, and lentic and lotic habitats within species using 1,065 Hovsgol grayling samples (468 males, 323 females, 274 immature/unknown), 203 Baikal grayling (41 males, 44 females, 118 immature/unknown), and 414 lenok (128 males, 79 females, 207 immature/unknown; Table 2).

Length–weight relationships (Figure 3) were significantly different between male and female Hovsgol grayling (p < .001), with a significant interaction (p = .004) between length and sex. Females were generally heavier at a given length than males across the range of observed lengths (Figure 3a). There were no significant differences in

TABLE 2 Length–weight and age-length (von Bertalanffy) model results for all three species

	Length–weight models*				Age-length models (von Bertalanffy)				
	n	Length range (cm)	*a*	*b*	*n*	Age range (years)	L_∞ (cm)	*K*	a_0
Hovsgol grayling (*Thymallus nigrescens*)									
Lake Hovsgol									
All	1,065	10.8–48.4	0.0042	3.15	93	1–17	30.7	0.32	Fixed at 0
							33.7	0.19	−1.63
Male	468	13.2–48.4	0.0024	3.31	45	3–17	32.0	0.29	Fixed at 0
Female	323	13.2–37.8	0.0058	3.06	37	1–13	31.3	0.28	Fixed at 0
Baikal grayling (*Thymallus baicalensis*)									
All water bodies									
All	203	11.5–38.2	0.0068	3.05	83	1–11	29.8	0.68	Fixed at 0
							33.2	0.42	−0.47
Male	41	15–33.4	0.0080	3.01	24	1–6	32.7	0.55	Fixed at 0
Female	44	13.7–38.2	0.0065	3.07	28	1–11	28.4	0.82	Fixed at 0
Rivers									
All	159	12.2–32.2	0.0058	3.11	68	1–5	28.6	0.77	Fixed at 0
Male	26	15.2–31	0.0061	3.10	20	1–5	30.6	0.67	Fixed at 0
Female	25	13.7–32.2	0.0041	3.23	19	1–5	26.2	1.14	Fixed at 0
Eg River									
All	85	12.5–29.6	0.0061	3.09	40	1–4	28.6	0.76	Fixed at 0
Male	17	15.2–29.6	0.0078	3.02	16	1–4	32.0	0.60	Fixed at 0
Female	15	13.7–27.9	0.0042	3.21	13	1–4	25.5	1.20	Fixed at 0
Uur River									
All	74	12.2–32.2	0.0054	3.14	28	1–5	29.0	0.77	Fixed at 0
Male	9	15.9–31	0.0032	3.30	4	2–5	28.6	0.84	Fixed at 0
Female	10	19–32.2	0.0042	3.22	6	1–5	28.1	0.98	Fixed at 0
Lake Hovsgol									
All	23	20.1–38.2	0.0104	2.90	8	2–11	33.5	0.47	Fixed at 0
Male	7	26.1–33.3	0.0366	2.53	1	4–4			
Female	12	22.1–38.2	0.0179	2.73	6	2–11	32.1	0.60	Fixed at 0
Lenok (*Brachymystax lenok*)									
All water bodies									
All	414	5.8–59.5	0.0064	3.08	123	1–10	78.1	0.15	Fixed at 0
							74.2	0.17	0.14
Male	128	23.3–56.9	0.0045	3.18	37	2–9	62.8	0.21	Fixed at 0
Female	79	20–59.5	0.0043	3.19	39	3–10	65.9	0.22	Fixed at 0
Rivers									
All	178	8.1–56.9	0.0073	3.05	64	1–9	75.1	0.16	Fixed at 0
Male	39	23.3–56.9	0.0075	3.04	20	3–9	67.0	0.18	Fixed at 0
Female	21	29.1–50.5	0.0077	3.04	15	3–7	53.3	0.32	Fixed at 0
Eg River									
All	47	25.8–56.9	0.0050	3.15	20	3–7	81.8	0.14	Fixed at 0
Male	15	31–56.9	0.0042	3.19	3	4–7	626.5	0.01	Fixed at 0
Female	11	37.9–50.5	0.0112	2.95	7	4–7	47.0	0.50	Fixed at 0

(Continues)

TABLE 2 (Continued)

	Length–weight models*				Age-length models (von Bertalanffy)				
	n	Length range (cm)	a	b	n	Age range (years)	L_∞ (cm)	K	a_0
Uur River									
All	131	8.1–53	0.0076	3.03	44	1–9	73.6	0.16	Fixed at 0
Male	24	23.3–53	0.0086	3.00	17	3–9	61.7	0.21	Fixed at 0
Female	10	29.1–50.1	0.0105	2.94	8	3–6	73.6	0.16	Fixed at 0
Lake Hovsgol									
All	232	5.8–59.5	0.0043	3.19	59	2–10	76.1	0.17	Fixed at 0
Male	88	24.6–53.5	0.0033	3.27	17	2–7	56.1	0.27	Fixed at 0
Female	57	20–59.5	0.0037	3.24	24	3–10	69.8	0.20	Fixed at 0

*r^2- and p-values omitted for length–weight regressions because all values were highly significant ($r^2 > .90$ and p-values $<.01$).

length–weight relationships between male and female Baikal grayling ($p = .486$) or lenok ($p = .760$).

There was a significant interaction between length and river ($p = .034$) in the length–weight relationship between the Eg and Uur rivers for lenok, with lenok in the Uur being generally heavier at a given length than lenok in the Eg (Figure 3d). There was no significant difference ($p = .781$) in the length–weight relationship between the Eg and Uur rivers for Baikal grayling. However, when data from the Eg and Uur rivers were combined and compared to data from Lake Hovsgol, Baikal grayling were significantly ($p < .001$) heavier at a given length in the rivers than in Lake Hovsgol (Figure 3b). For lenok, there was a significant interaction ($p < .001$) between length and habitat (lentic vs. lotic). There was also a significant difference in the length–weight relationship ($p = .01$) between Baikal grayling and Hovsgol grayling in Lake Hovsgol, with Baikal grayling being slightly heavier at a given length (Figure 3c).

3.2 | Age-length relationships

The von Bertalanffy age-length models were constructed for each species overall and for comparisons between sexes, rivers, and lentic and lotic habitats within species using samples of 93 Hovsgol grayling (45 males, 37 females, 11 immature/unknown), 83 Baikal grayling (24 males, 28 females, 31 immature/unknown) and 123 lenok (37 males, 39 females, 47 immature/unknown; Table 2; Figure 4). Sufficient sample sizes were available for 12 comparisons.

There was no difference in the age-length relationship of male and female Hovsgol grayling in Lake Hovsgol ($p = .5593$; Figure 4) or male and female Baikal grayling in rivers ($p = .1303$) or across all water bodies ($p = .3670$; Figure 4b). Although there was no difference in the age-length relationship of male and female lenok in Lake Hovsgol ($p = .1952$), there was a significant difference between the sexes

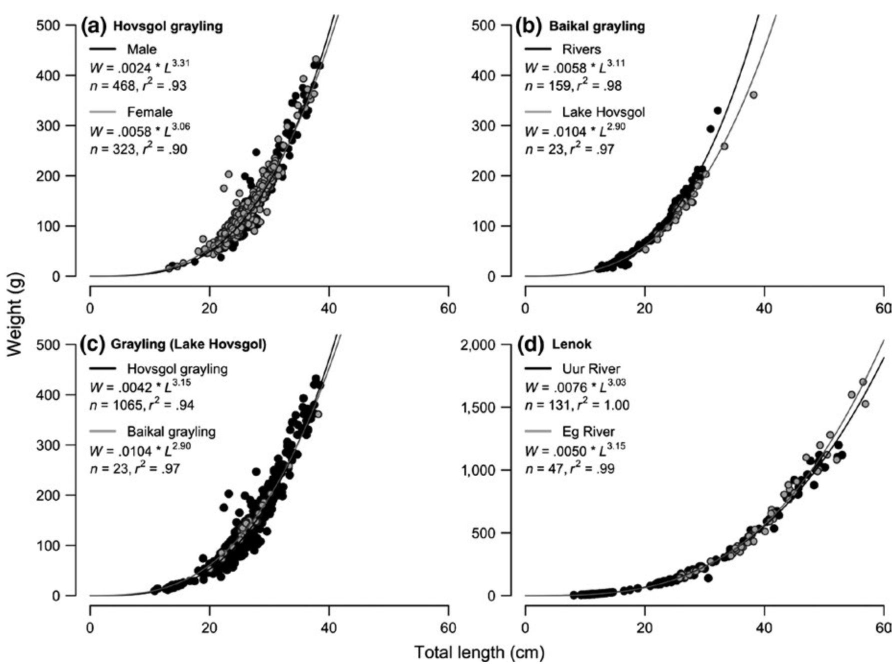

FIGURE 3 Length–weight regressions (LWRs) for (a) Hovsgol grayling males (dark) and females (light), (b) Baikal grayling in the rivers (both Eg and Uur) (dark) and Lake Hovsgol (light), (d) Hovsgol (dark) and Baikal (light) grayling in Lake Hovsgol, and (d) lenok in the Uur (dark) and Eg (light) rivers. All LWR comparisons were significantly different

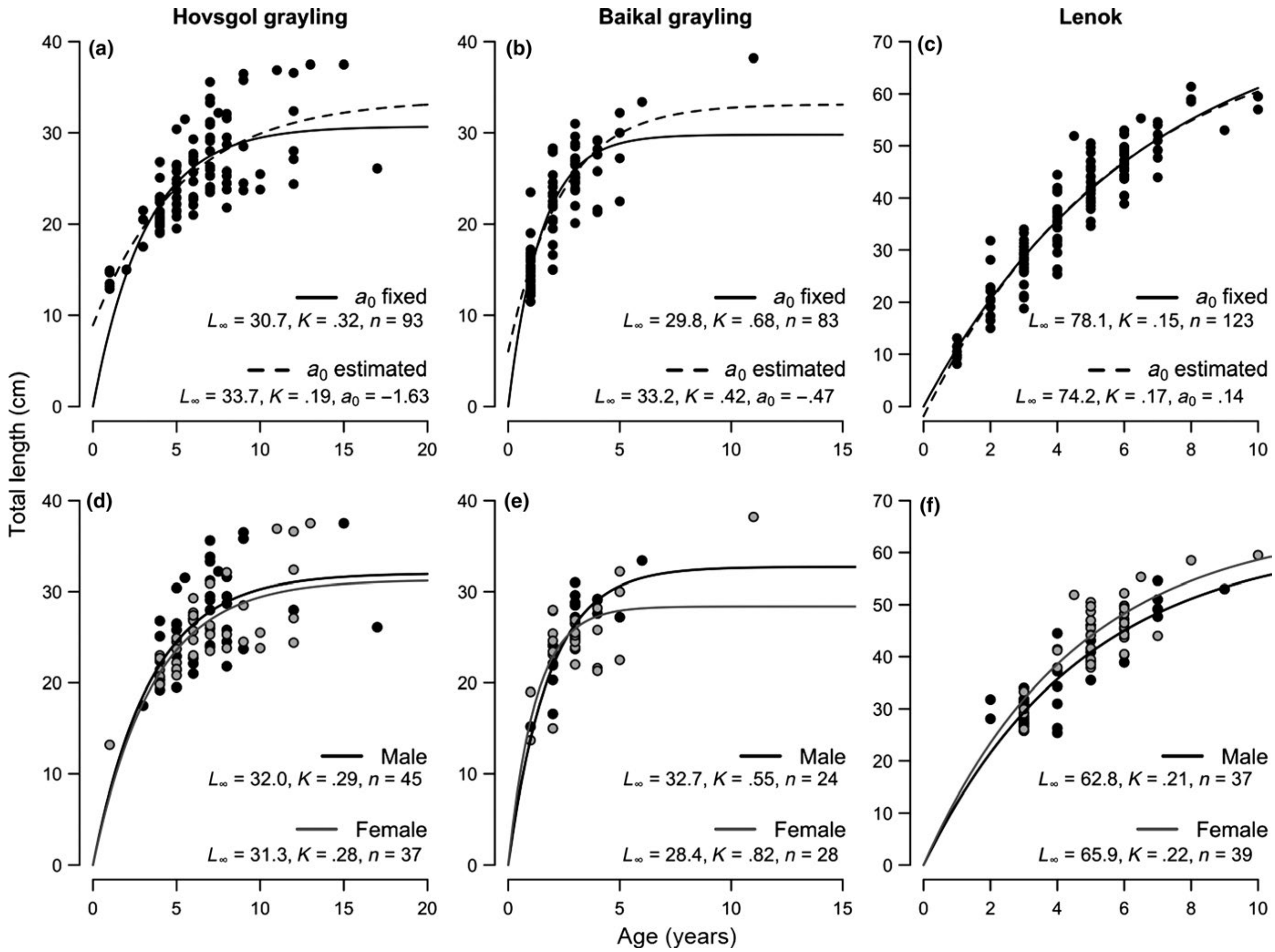

FIGURE 4 Overall length-at-age for (a) Hovsgol grayling, (b) Baikal grayling, and (c) lenok followed by length-at-age by sex (males = dark, females = light) for the same species. In a–c, solid and dashed lines = von Bertalanffy growth curves with a_0 fixed at 0 and a_0 fit as a parameter, respectively. In d–f, all lines indicate von Bertalanffy growth curves with a_0 fixed at 0. There was a significant difference in the age-length relationship of male and female lenok, with females being generally larger at age (f). None of the other age-length relationships were significantly different by sex

across all rivers (p = .0487) and across all water bodies (p = .0489; Figure 4f), with females generally being larger at age.

There was no difference in the age-length relationship of Baikal grayling between Lake Hovsgol and the rivers (p = .4309; Figure 5a) or in the Eg compared to the Uur (p = .8727; Figure 5c). There was a significant difference in the age-length relationship of lenok between Lake Hovsgol and the rivers (p = .0194; Figure 5b) with lenok in Lake Hovsgol generally being larger at age. There was no difference in the age-length relationship of lenok between the Eg and Uur rivers (p = .1301; Figure 5d).

There was a significant difference in the age-length relationship of Hovsgol and Baikal grayling (p < .0001), with Baikal grayling generally being larger at age (Figure 4).

4 | DISCUSSION

Our results provide the first estimates of growth for lenok and grayling in Mongolia based on otoliths. Qualitative comparison with earlier growth estimates for these species (Sideleva, 2006), presumably based on scales, suggests that our growth estimates are roughly similar at younger ages. For example, Sideleva (2006) indicated that lenok in Lake Hovsgol mature at age 5 (with a corresponding length of 350 mm) and Dulmaa (1999) reported an average length of 344 mm for an age 5 lenok in Lake Hovsgol. Our results show that age 5 lenok in Lake Hovsgol average slightly over 400 mm. Similarly, for Hovsgol grayling, Sideleva (2006) indicated an average length of 225–250 mm at age 4, while our results from otoliths show an average length of slightly over 200 mm at that age.

Greater differences between otolith-based and scale-based length-at-age estimates are apparent for older individuals, however. For example, Dulmaa (1999) reported an average length of 463 mm for an age 9 lenok in Lake Hovsgol, while our results suggest a length of nearly 600 mm. Scale-based ages also appear to underestimate the maximum age. Dulmaa (1999) reported a maximum age of 11 years for Hovsgol grayling, while the oldest individual in our sample was 17 years of age.

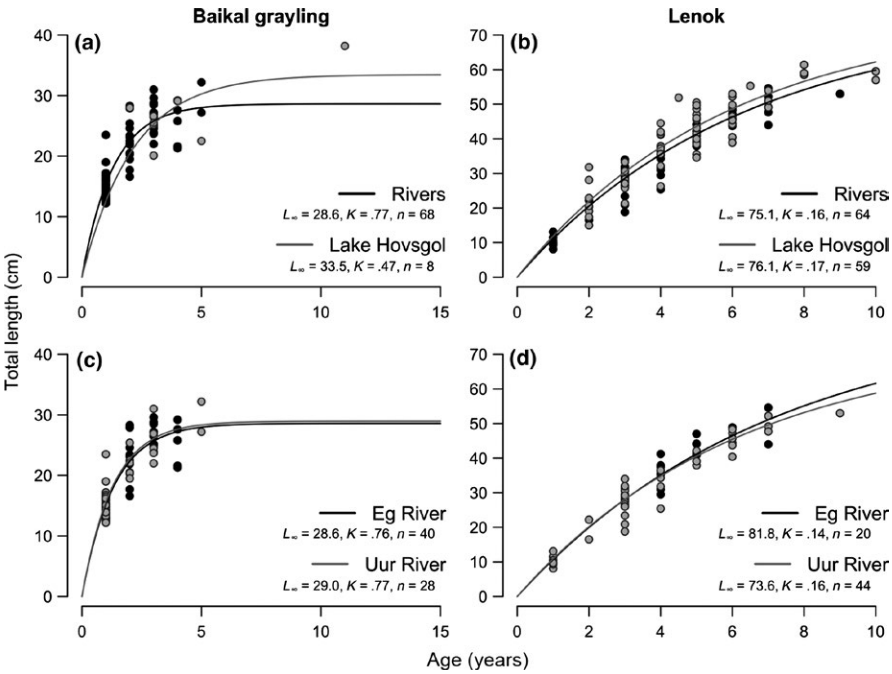

FIGURE 5 Length-at-age in rivers (both Eg and Uur) (dark) and Lake Hovsgol (light) for (a) Baikal grayling and (b) lenok followed by length-at-age in the Eg (dark) and Uur (light) rivers for the same species. All lines indicate von Bertalanffy growth curves with a_0 fixed at 0. There was a significant difference in the age-length relationship of lake and river lenok, with lenok in Lake Hovsgol generally being larger at-age (b). None of the other age-length relationship comparisons were significantly different (a, c, d)

Sexually dimorphic growth has been reported in many salmonids from other parts of the world, but has not been evaluated for the species considered here. Faster growth in males has been observed for Arctic grayling *T. arcticus* (Barndt & Kaya, 2000; Carl, Walty, & Rimmer, 1992) and for European grayling *T. thymallus*, (Nygard, 2012). We found no significant difference in male versus female growth rate for Baikal or Hovsgol grayling, although female Hovsgol grayling were heavier at a given length. Sexual dimorphism in lenok growth has not been evaluated previously, and we found that females generally attain a greater length than males at a given age in the rivers, although no significant difference was apparent in individuals from Lake Hovsgol.

Despite substantial differences in peak summer temperatures (B. Mendsaikhan, unpublished data) between the Eg and Uur rivers, we found no differences in growth rates between the two rivers for either Baikal grayling or lenok. There are numerous springs and seeps where ground water enters the warmer Uur River and it is possible that use of these thermal refugia allows fish to experience average temperatures similar to the cooler Eg River. Alternatively, potential differences in food availability between the two rivers could mask temperature effects on growth. Lenok generally showed better body condition (weight at length) in the warmer Uur River, but no difference was seen in Baikal grayling. Bioenergetic models would be useful for understanding the difference in body condition observed for lenok, but have not yet been developed for either of these species.

We found significantly greater length-at-age for lenok in Lake Hovsgol than in the two rivers. There was no difference in Baikal grayling growth between the two habitats, but individuals were significantly heavier at a given length in the rivers compared to Lake Hovsgol. A relatively large body of literature compares growth rates of fish between lentic and lotic environments, with results often differing by species (Blanck & Lamouroux, 2007). For many salmonids such as Atlantic salmon *Salmo salar* (Halvorsen & Svenning, 2000) and brown trout *Salmo trutta* (Blanck & Lamouroux, 2007), growth is greater in lakes than in rivers. Our results for lenok are consistent with this pattern. Lake habitats offer at least two distinct growth advantages: lower energy expenditure without the need for constant active swimming and a choice of temperatures during the thermally stratified period. Despite these perceived advantages, Baikal grayling showed better body condition in the rivers compared to the lake.

This study provides critical, but previously missing, information for management and conservation planning of these threatened salmonid species in Mongolia. Understanding species-specific growth rates and body condition are critical to effective planning and management for those species. For example, most stock assessment methods require knowledge of the stock's somatic growth rate, and many explicitly incorporate the von Bertalanffy *K* parameter. As climate change and other anthropogenic changes (e.g. fishing and land use change) continue, this work will also provide a baseline for evaluating the impacts of these changes on growth and condition. Endemic species, such as the Hovsgol grayling and those in high elevation or headwater habitats such as Lake Hovsgol, are less able to adapt to climate change by shifting their geographic distributions (Meyer, Sale, Mulholland, & Poff, 1999) and thus merit particularly close monitoring of changes in their growth and condition.

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