

Feeding ecology and prey resource partitioning of lenok (*Brachymystax lenok*) and Baikal grayling (*Thymallus arcticus baicalensis*) in the Eg and Uur rivers, Mongolia

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Abstract – Baikal grayling (*Thymallus arcticus baicalensis*) and lenok (*Brachymystax lenok*) are two salmonids which co-occur in lakes and rivers of the Selenga River and Lake Baikal drainage in northern Mongolia and Siberia. Populations of both species have declined due to habitat loss and overfishing. Previous studies have established that diets of both species are comprised of aquatic and terrestrial invertebrates, but none have examined how prey resources are partitioned between the species. We explored resource partitioning between these species using information from stomach content analysis and stable isotope analysis of carbon and nitrogen. Stomach content data were also compared to invertebrate prey availability estimated from drift and benthic samples. Stomach content analysis indicated that lenok were benthic specialists, while Baikal grayling exhibited a more generalised and surface-oriented diet, preying upon both terrestrial and aquatic invertebrates. In addition, drifting invertebrate prey availability was positively related to diet overlap based on stomach content analysis, suggesting that competition was involved in the prey resource partitioning we observed. Our analysis of assimilated diet using stable isotopes was generally consistent with stomach contents, indicating that prey partitioning was sustained over a period of several months, but also revealed a greater importance of fish prey to lenok diets. This study provides a baseline description of prey utilisation and prey resource partitioning between lenok and Baikal grayling, which may be used to guide management and future research of these threatened species.

Key words: feeding ecology; niche partitioning; lenok; Baikal grayling; Eg river; Uur river

Introduction

Partitioning of resources (i.e. prey, habitat and time) is thought to be a mechanism facilitating the coexistence of competing fish species when resources are limited (Ross 1986). Species that occur in sympatry and have similar fundamental niches are predicted to segregate resources to avoid competitive exclusion, possibly allowing coexistence (Hardin 1960; Schoener 1974). Partitioning of available resources may be determined by differences in morphology, physiology or behaviour, which allow a species to exploit a portion of the available niche more efficiently than competing species (Tilman 1987). Salmonids have

frequently been used as a model to examine niche partitioning (Andrusak & Northcote 1971; Hindar et al. 1988; Langeland et al. 1991; Haugen & Rygg 1996). In streams, prey resources are often partitioned between sympatric salmonids through differential use of drifting and benthic invertebrates (Nakano et al. 1992; Nakano 1999; Mookerji et al. 2004; Dineen et al. 2007). Although competition theory predicts that resource availability influences niche overlap in competing species (Schoener 1982; Wiens 1993), relatively few studies have examined how prey resource partitioning of stream-dwelling salmonids is influenced by prey availability (Fausch et al. 1997; Nakano et al. 1999). These studies indicate that prey

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partitioning between sympatric stream-dwelling salmonids may be dynamic and negatively related to the abundance of drifting invertebrate prey.

The Eg and Uur rivers of northern Mongolia support robust populations of lenok (*Brachymystax lenok*, sharp-nosed morphotype) and Baikal grayling (*Thymallus arcticus baicalensis*), which occur sympatrically in both rivers (Mercado-Silva et al. 2008). Unfortunately, lenok and Baikal grayling are declining in Mongolia due to rapid industrial development and climate change currently taking place in the country (Ramankutty et al. 2002; Ocock et al. 2006a; Nandintsetseg et al. 2007). The limited information available on the ecology of these species indicates that lenok and Baikal grayling have similar diets, composed primarily of aquatic and terrestrial invertebrates (Nakano 1999; Chandra et al. 2005; Sideleva 2006). Despite apparent similarities in diet niche, prey resource partitioning between lenok and Baikal grayling has not been studied. Sympatric populations of lenok and Baikal grayling in the Eg and Uur rivers provide a unique opportunity to examine prey partitioning in stream-dwelling salmonids which have received limited study. Dietary niche overlap between these species may also be relevant for conservation efforts targeting these two potentially competing species as human use increases within the watershed and elsewhere throughout their ranges.

In this study, we examined the feeding habits and degree of prey partitioning between lenok and Baikal

grayling in the Eg and Uur rivers. We employed stomach content and carbon and nitrogen stable isotope analysis, which allow an assessment of prey partitioning over short (days) and long (months) timescales (e.g. McIntyre et al. 2011). In addition, we incorporated measures of drifting and benthic invertebrate prey abundance to examine the influence of prey availability on diet overlap. Based on the differences in functional morphology and predictions of competition theory, we hypothesised that lenok, which exhibit a more subterminal mouth position, will prey on benthic invertebrates to a greater degree than Baikal grayling and degree of prey partitioning will be negatively correlated with drifting prey availability.

Methods

Study area

The study was conducted in July of 2011 and 2012 in the Eg-Uur watershed of northern Mongolia (Fig. 1). The study area is at high elevation (1500 m) and located in the transition of Mongolian steppe and Taiga forest. Sampling took place in the Eg River (Egiin gol, 50°16'58"N, 101°54'6"E) and Uur River (Uur gol, 50°18'35"N, 101°53'43"E). The Eg River is a high gradient river with willow and larch riparian forest, receiving substantial groundwater inputs. The Uur River is low gradient with riparian zones

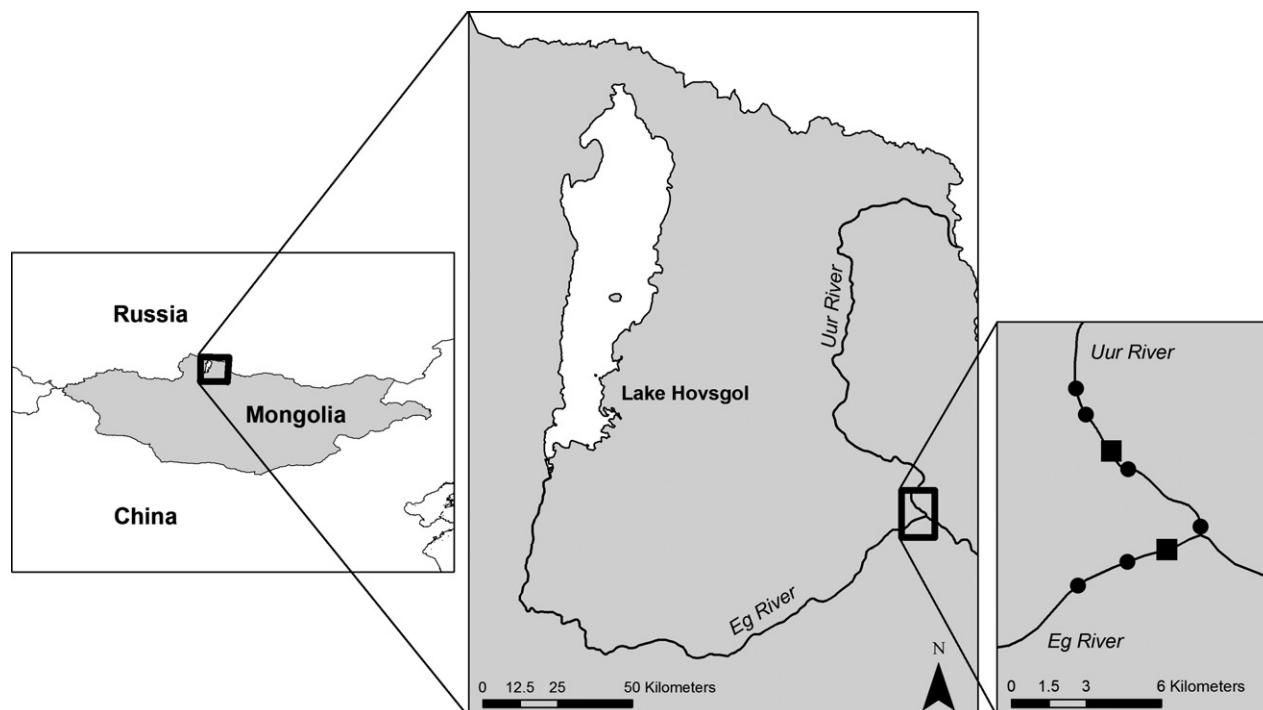


Fig. 1. Location of the Eg-Uur watershed and sampling sites on the Eg and Uur rivers. Circles signify sites sampled in 2012 and squares signify sites sampled in 2011 and 2012.

composed of willow, larch and actively grazed steppe pasture and receives most of its volume from run-off (Gilroy et al. 2010). The known fish community of the Eg and Uur rivers include lenok, Baikal grayling, burbot *Lota lota*, taimen *Hucho taimen*, loach *Barbatuli toni*, phoxinus *Phoxinus phoxinus*, Eurasian perch *Perca fluviatilis* and pike *Esox Lucius* (Mercado-Silva et al. 2008).

Fish and invertebrate collection

Fish and invertebrate prey samples were collected at eight sampling locations in the Eg-Uur watershed in July 2011 and 2012. Five sites were selected on the Uur River and three on the Eg River. A single site on each river was sampled in 2011 and all sites were sampled in 2012 (Fig. 1). Sampling occurred over the course of 1–2 days at each site between 8:00 and 21:00 and over a period of 10–12 h. Sampling reaches were restricted to riffle and run habitats between 0.1 and 0.5 km in length. A total of 107 lenok and 62 Baikal grayling from the Uur River and 38 lenok and 80 Baikal grayling from the Eg River were captured by angling with artificial lures. Following capture, total length, fork length and weight were measured on each fish. Stomach contents were removed through the use of a gastric lavage (lenok only) or by stomach dissection. On a subsample of lenok ($n = 27$), lavage efficiency was tested by comparing the composition of prey removed to prey remaining in the diet. This analysis revealed that there was no significant difference in removal efficiency among common prey categories (Kruskal–Wallis, d.f. = 6, $P = 0.31$).

Invertebrate prey availability was sampled at each site concurrent with fish sampling. Three benthic samples were collected at each site using a Surber sampler (0.1 m², 500 μm mesh). Substrate within the sample area was disturbed and brushed clean by hand over a 2-min time interval. Samples were evenly spread along each sample reach. Six drift samples were collected at each site over a period of 6 h between 8:00 and 21:00. The drift sampler (45 cm × 30 cm opening, 363 μm mesh) was placed at the upstream end of the sampling reach at approximately 0.28 m in depth, to sample the entire water column. Water velocity was measured directly in front of the drift net opening with a Swoffer 2100 current velocity meter during each drift sample, allowing an estimate of invertebrate drift rate.

Stomach content and prey availability analysis

Stomach content and prey availability samples were identified to family or order and enumerated. In each sample, total length or head width was measured on

a random subsample ($n = 5$) of individuals from each prey category, and measurements were recorded to the nearest 0.1 mm. The mean of head width or total length was then converted to dry mass following existing length–mass regressions (Sample et al. 1993; Benke et al. 1999; Sabo et al. 2002 Baumgartner & Rothhaupt 2003; Stoffels et al. 2003) and multiplied by the number of individuals in each prey category.

Mean proportion of each prey taxon in the diet by weight (MW_i , Chipps & Garvey 2007) was then calculated following the equation:

$$MW_i = 1/P \sum_{j=1}^P \left(\frac{W_{ij}}{\sum_{i=1}^Q W_{ij}} \right)$$

where P is the number of fish with food in their stomachs, W_{ij} is the weight of prey type i in the diet of fish j , and Q is the total number of prey categories. Propensity of prey taxa to occur in the drift (A_p) was calculated following the equation:

$$A_p = A_d / (A_b + A_d)$$

where A_d is the mean proportion of taxon A in the drift and A_b is the mean proportion of taxon A in benthic samples. Possible values range from 0 to 1 with higher values indicating greater drift propensity. Dietary overlap of lenok and grayling was assessed using Schoener's (1970) measure of proportional overlap C_{xy} :

$$C_{xy} = 1 - \frac{1}{2} \left(\sum_i |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the proportion of a prey item i by weight in the diets of species x and y . The value 0 indicates no overlap, while 1 indicates total overlap. Generally, overlap >0.60 is considered biologically significant (Wallace 1981). Selectivity of lenok and grayling for common prey taxa was quantified using Chesson's alpha (1983):

$$\alpha_i = \frac{\left(\frac{r_i}{n_i} \right)}{\sum_{j=1}^m (r_j/n_j)}$$

where α_i is Chesson's index of prey selectivity for prey taxon i , r_i is the proportion of prey type i in the diet, n_i is the proportion by number of prey type i in drift or benthic samples, and m is the total number of prey categories present in stomach contents and drift or benthic samples. 95% confidence intervals for Chesson's alpha were estimated for each prey taxa. Possible values of Chesson's alpha range from 0 to

1, with values $>1/m$ indicating positive selection, values $<1/m$ indicating negative selection and values equal to $1/m$ indicating neutral selection. Dietary niche width was estimated using Levin's index B :

$$B = 1 / \sum p_i^2$$

where p_i is the proportion of each prey in the diet by weight.

Stable isotope analysis

A total of 1–5 g (wet weight) white muscle samples were removed from 43 lenok and 50 Baikal grayling near the base of the dorsal fin. Representative invertebrate prey taxa were analysed as a whole, excluding the calcified shells of gastropods. In some cases, several individuals from the same taxon were pooled to achieve large enough sample weight. All samples were dried at 60 °C in a convection oven and homogenised prior to analysis. Samples were analysed for carbon (^{13}C and ^{12}C) and nitrogen (^{15}N and ^{14}N) stable isotopes using a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) at the University of California Davis Stable Isotope Facility.

Ratios of $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ are reported in delta notation (δ), which is defined by the equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000$$

where R_{sample} is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{14}\text{N}/^{15}\text{N}$ in the sample and R_{standard} is the ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{14}\text{N}/^{15}\text{N}$ of the standard. Vienna PeeDee Belemnite and atmospheric N_2 were the standards for ^{13}C and ^{15}N respectively. Analytical precision was 0.09 for ^{13}C and 0.15 for ^{15}N . Fish tissue samples were corrected for lipid content using the generalised correction for fish tissue published in Hoffman & Sutton (2010):

$$\delta^{13}\text{C}_{\text{protein}} = \delta^{13}\text{C}_{\text{bulk}} + (-6.39\text{‰} \times (3.76 - \text{C} : \text{N}_{\text{bulk}})) / \text{C} : \text{N}_{\text{bulk}}$$

where $\delta^{13}\text{C}_{\text{protein}}$ is the corrected $\delta^{13}\text{C}$ value, $\delta^{13}\text{C}_{\text{bulk}}$ is the uncorrected $\delta^{13}\text{C}$ value, and $\text{C}:\text{N}_{\text{bulk}}$ is the molar C:N ratio of the sample.

Phillips & Gregg's (2001) three-source stable isotope mixing model was used to estimate the proportional contribution of prey to the diets of individual lenok and Baikal grayling. Consumers were adjusted for trophic fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ prior to application of three-source mixing models. Mean trophic fractionation values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ typically range from 0 to 1.3‰ and 2.3 to 3.4‰ respectively (Vander Zanden & Rasmussen 2001; McCutchan et al. 2003). A mean $\delta^{15}\text{N}$ fractionation (± 1 SD) value of $3.5 \pm 0.44\text{‰}$ was used based on model fit.

Mean fractionation of $\delta^{13}\text{C}$ value of 0.4‰ was assumed for all fish.

Statistical analysis

Differences in diet and available prey composition were analysed using nonparametric Mann–Whitney U -tests when the data were not normally distributed and transformations did not improve normality. Mann–Whitney U -tests were performed on prey categories that composed $>10\%$ of the diet, treating individual sites as replicates. A Bonferroni-adjusted significance level was used in these comparisons to control for experimentwise error rate. Analysis of covariance was used to compare proportional contribution of benthic prey types to lenok and grayling diets with abundance of benthic invertebrates in the drift as the covariate. All other analyses were carried out using linear regression and two-sample t -tests.

Results

Composition and abundance of invertebrate prey community

Mean benthic prey density (number per m^2) was similar between rivers (mean ± 1 SE, Eg River = 686 ± 274 , Uur River = 470 ± 224 ; t -test, $t = 0.61$, d.f. = 8, $P = 0.56$). The benthic prey community in the Eg and Uur rivers was primarily comprised of immature stages of Trichoptera, Ephemeroptera and Diptera. Ephemeroptera were proportionally more abundant in benthic samples from the Uur River (0.60) than the Eg River (0.28; Mann–Whitney U -test, $H = 6.50$, d.f. = 1, $P = 0.01$), while Trichoptera were more common in the Eg River (0.16) than the Uur River (0.04), although this difference was not significantly based on a Bonferroni-corrected alpha level (Mann–Whitney U -test, $H = 5.50$, d.f. = 1, $P = 0.02$).

Drifting prey abundance was highly variable among sampling locations and dates (range = 0.04–6.4 prey items per m^3), but not significantly different between rivers (Uur River = 0.12 ± 0.05 number per m^3 , Eg River = 0.46 ± 0.20 number per m^3 ; t -test, $t = 0.15$, d.f. = 8, $P = 0.15$). Overall, terrestrial invertebrates, adult and pupal stages of aquatic invertebrates exhibited the highest drift propensity (1.00 and 0.68 respectively), while aquatic stages of Ephemeroptera, Trichoptera, Diptera and Plecoptera exhibited lower drift propensity (Ephemeroptera = 0.22, Trichoptera = 0.44, Diptera = 0.49, Plecoptera = 0.39).

Stomach content analysis

Within the Eg and Uur rivers, lenok diets were composed primarily of benthic invertebrates

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(mean = 84% by weight), while Baikal grayling diets were composed of benthic invertebrates (mean = 49% by weight) and prey types typically found in the drift (i.e. pupal and adult stages of aquatic invertebrates and terrestrial invertebrates; mean = 50% by weight). Fish were uncommon in the stomachs of lenok and Baikal grayling, but were more common in lenok (lenok = 5% occurrence, grayling = 1% occurrence). Overall, Baikal grayling exhibited a larger diet niche width (Baikal grayling, $B = 1.3$) than lenok ($B = 0.90$; Mann-Whitney, $H = 5.50$, $P = 0.02$). Dietary overlap between lenok and Baikal grayling was large, 53% on average, but below the threshold often considered ecologically significant (60%, Zaret & Rand 1971). Diet overlap ranged from 29 to 67% across sites and was not significantly different between the Eg and Uur rivers (two-sample t -test, $t = 0.86$, d.f. = 8, $P = 0.41$).

In the Uur River, benthic dwelling Trichoptera larvae comprised a significantly larger portion of lenok than Baikal grayling diets ($H = 7.41$, d.f. = 1, $P = 0.007$, Fig. 2). Prey types associated with the drift composed a larger portion of Baikal grayling diets from the Uur River by weight, but differences were not significant based on a Bonferroni-corrected alpha level (terrestrial invertebrates, $H = 5.03$, $P = 0.03$; adult and pupal stages of aquatic invertebrates, $H = 5.77$, $P = 0.02$, Fig. 2). Similar to the Uur River, benthic prey comprised a larger portion of lenok diets from the Eg River, while prey commonly found in the drift composed a larger portion of grayling diets on average (Fig. 2). However, these differences were not statistically significant based on a Bonferroni-corrected alpha level.

Analysis of stomach contents by size class revealed that lenok and Baikal grayling exhibited shifts in stomach composition with length. The proportion of

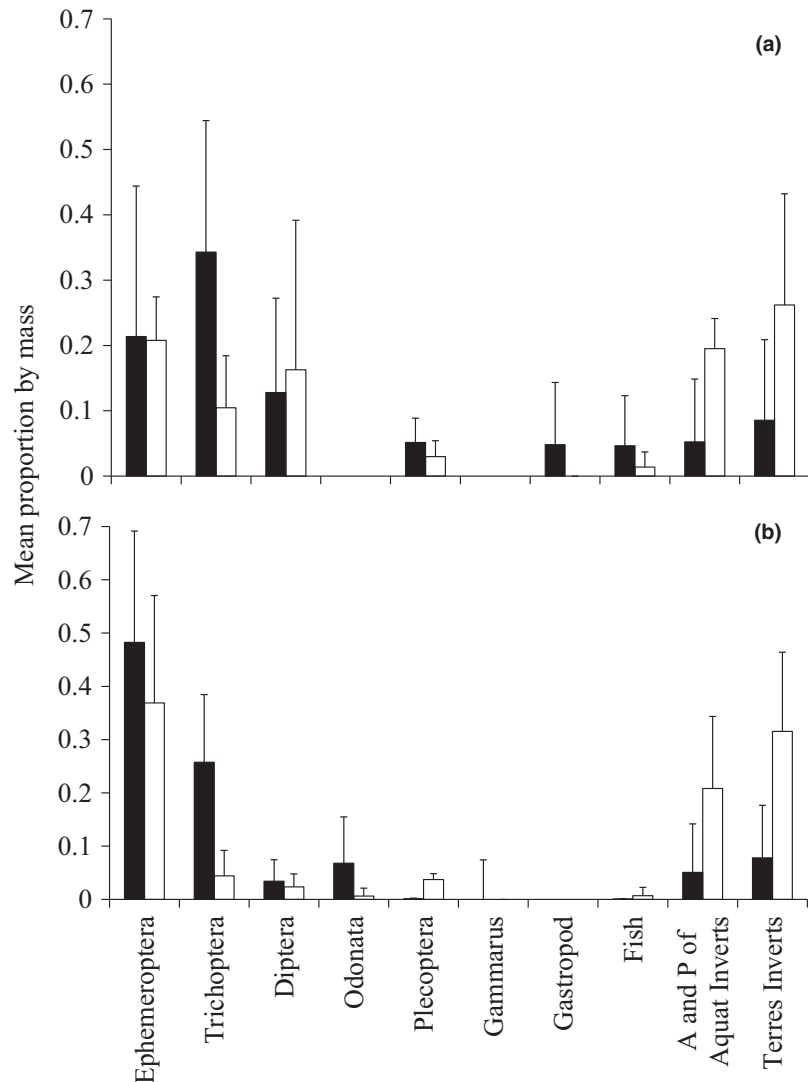


Fig. 2. Mean proportion by weight of prey taxa (± 1 SD) composing lenok (filled bars) and Baikal grayling (open bars) stomach contents in the Eg River (a) and Uur River (b).

Ephemeroptera = Ephemeroptera nymphs,
Trichoptera = Trichoptera larvae,
Diptera = Diptera larvae,
Plecoptera = Plecoptera larvae, A and P of
Aquat Inverts = adult and pupae stages of
aquatic invertebrates.

Ephemeroptera nymphs declined in both species diets with size. In lenok, the proportion of Trichoptera larvae increased, while the proportion of Diptera larvae increased in the diets of larger grayling (Fig. 3).

Based on drifting prey availability, lenok in the Eg River selected for Trichoptera larvae and against pupae and adult stages of aquatic invertebrates lenok in both the Eg and Uur rivers selected for Trichoptera larvae and against terrestrial invertebrates and pupae and adult stages of aquatic invertebrates (Table 1). Lenok also selected against Dipteran larvae in the Uur River but exhibited neutral selection for Dipterans in the Eg River. Baikal grayling exhibited neutral selection for all prey types in the Eg River but selected for Ephemeroptera nymphs and against terrestrial invertebrates, pupae and adult of aquatic invertebrates and dipteran larvae in the Uur River.

Based on benthic samples as a measure of prey availability, lenok in the Uur River selected for Trichoptera larvae and against Diptera larvae and pupae and adult stages of aquatic invertebrates (Table 1). Grayling in the Uur River also selected against Dipteran larvae and exhibited neutral selection for all other prey types. In the Eg River, both lenok and Baikal grayling exhibited negative selection for Plecoptera (Table 1). Lenok also exhibited neutral selection for all other prey types, while Baikal grayling selected for pupae and adult stages of aquatic invertebrates.

Drifting prey abundance was positively correlated with diet overlap between lenok and Baikal grayling (linear regression $r^2 = 0.50$, $P = 0.022$, Fig. 4). In addition, the density of benthic invertebrates in the

drift was positively correlated to the proportion of benthic invertebrates in grayling diets and marginally correlated to proportion of benthic invertebrates in lenok diets. (lenok $r^2 = 0.39$, $p = 0.052$, Baikal grayling, $r^2 = 0.65$, $p = 0.005$). However, the proportion of benthic invertebrates in the diets of Baikal grayling was less than that of lenok. (ANCOVA, $F = 37.15$, $p < 0.001$, Fig. 5).

Stable isotope analysis

In the Eg and Uur rivers, lenok were significantly ^{15}N -enriched relative to Baikal grayling (Uur River, $F_{1,52} = 9.15$, $P = 0.004$; Eg River, $F_{1,39} = 6.62$, $P = 0.014$; Fig. 6) but there was no difference in $\delta^{13}\text{C}$ values between species (Uur River, $F_{1,52} = 0.1468$, $P = 0.70$; Eg River, $F_{1,44} = 0.80$, $P = 0.37$). Lenok also exhibited significant enrichment in ^{13}C with total length (Eg River, $r^2 = 0.38$, $P = 0.02$; Uur River, $r^2 = 0.38$, $P = 0.002$). Grayling $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were not significantly correlated with total length, indicating similar prey utilisation across sizes.

Three-source mixing model results from the Uur River identified fish and aquatic invertebrates as the primary component of lenok diets (Fig. 7). The proportion of fish in lenok diets was positively correlated with size (linear regression, $r^2 = 0.37$, $P = 0.002$). In contrast, Baikal grayling assimilated proportionally fewer fish and more terrestrial invertebrates than lenok (fish, $F_{1,52} = 5.49$, $P = 0.023$; terrestrial invertebrates, $F_{1,52} = 8.20$, $P = 0.006$). Isotopic signatures of lenok and Baikal grayling from

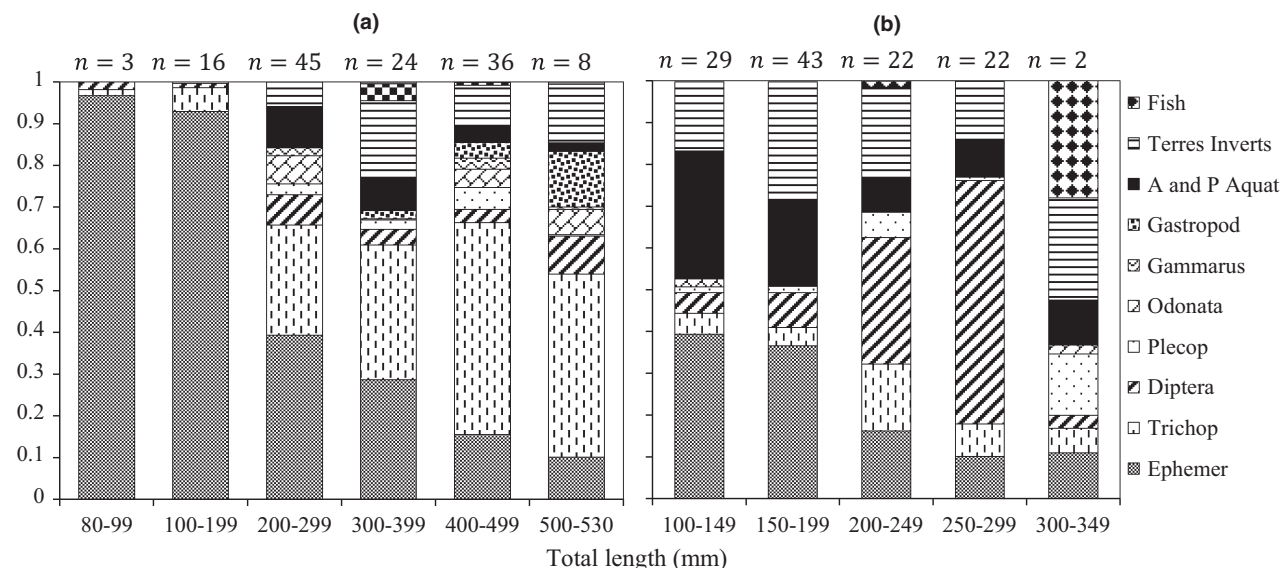


Fig. 3. Proportional abundance of prey taxa in lenok (a) and Baikal grayling (b) stomachs by length group from the Eg and Uur rivers. Terres Inverts = terrestrial invertebrates, A, P Aquat = adult and pupae stages of aquatic invertebrates, Odonata = Odonata nymphs, Gammarus = *Gammarus spp.*, Diptera = Diptera larvae, Trichoptera = Trichoptera larvae, Ephemeroptera = Ephemeroptera nymphs.

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Table 1. Chesson's index of selectivity for lenok and grayling from the Eg-Uur watershed using benthos or drift as a measure of prey availability.

Species	Waterbody	Prey sample	Chesson's α (95% confidence intervals are given in parentheses)						
			1/m	Ephemer	Trichop	Diptera	Plecop	A and P	Terres
B. Grayling	Uur River	Benthos	0.25	0.24 (± 0.14)	0.36 (± 0.18)	0.08* (± 0.06)	–	0.32 (± 0.08)	–
B. Grayling	Uur River	Drift	0.20	0.47† (± 0.16)	0.27 (± 0.18)	0.05* (± 0.06)	–	0.16 (± 0.15)	0.05* (± 0.04)
B. Grayling	Eg River	Benthos	0.20	0.19 (± 0.20)	0.24 (± 0.31)	0.21 (± 0.34)	0.03* (± 0.04)	0.34† (± 0.13)	–
B. Grayling	Eg River	Drift	0.20	0.30 (± 0.56)	0.24 (± 0.39)	0.18 (± 0.44)	–	0.16 (± 0.11)	0.11 (± 0.13)
Lenok	Uur River	Benthos	0.25	0.25 (± 0.17)	0.62† (± 0.15)	0.09* (± 0.09)	–	0.02* (± 0.02)	–
Lenok	Uur River	Drift	0.20	0.43 (± 0.24)	0.49† (± 0.24)	0.04* (± 0.04)	–	0.01* (± 0.02)	0.02* (± 0.04)
Lenok	Eg River	Benthos	0.20	0.18 (± 0.23)	0.53 (± 0.40)	0.18 (± 0.19)	0.04* (± 0.09)	0.07 (± 0.13)	–
Lenok	Eg River	Drift	0.20	0.18 (± 0.23)	0.54† (± 0.29)	0.17 (± 0.29)	–	0.5* (± 0.09)	0.03* (± 0.08)

Ephemer, Ephemeroptera nymphs; Trichop, Trichoptera larvae; Diptera, Diptera larvae; Plecop, Plecoptera nymphs; A and P, adult and pupae stages of aquatic invertebrates; Terres, terrestrial invertebrates.

Asterisks signify significant negative selection and crosses signify significant positive selection based on 95% confidence intervals. Lines indicate prey type was not present in either fish diet or prey availability sample.

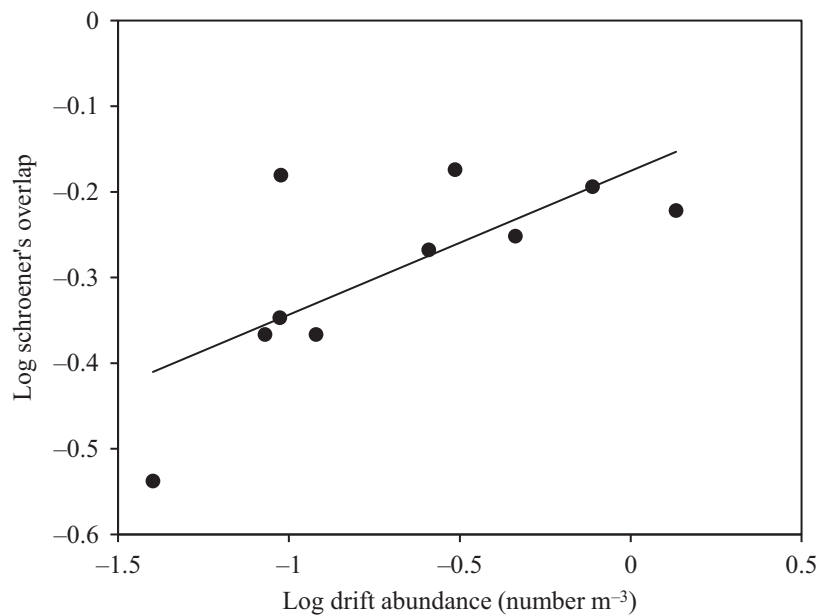


Fig. 4. Relationship of drift abundance to proportional diet overlap between lenok and Baikal grayling from the Eg and Uur rivers.

the Eg River were not bound by the prey sources we sampled. Specifically, $\delta^{13}\text{C}$ signatures of grayling and lenok were highly variable and often fell outside the mean isotopic values of prey included in the analysis. This precluded the use of a mixing model to estimate proportional assimilation of prey for Baikal grayling and lenok in the Eg River.

Discussion

Stomach content analysis

Based on stomach contents, lenok were benthic specialists, preying primarily on immature stages of Trichoptera, Ephemeroptera and Diptera and often exhibiting positive selection for Trichoptera larvae. Lenok's more underslung mouth and bulbous snout is likely more suited for foraging on benthic prey

than that of grayling (Snorrason et al. 1994; Helfman et al. 1997; Nakano 1999). Stomach contents of lenok shifted with size. As length increased, the proportion of Ephemeroptera nymphs in the diets of lenok decreased while Trichoptera larvae increased in proportion. Lower gape size and biting pressure of smaller fish may limit smaller lenok from feeding on cased Trichoptera larvae (Johansson 1991), which were observed in the diets of large lenok.

Baikal grayling stomach contents indicated a generalist feeding strategy. Baikal grayling had a wider diet niche than lenok and no consistent selection for a single prey taxon. Baikal grayling also appeared to be more reliant upon drifting prey than lenok as the proportion of benthic invertebrates in Baikal grayling diets was much lower than lenok when the density of benthic invertebrates in the drift was low. The generalist feeding habits we observed are consistent with

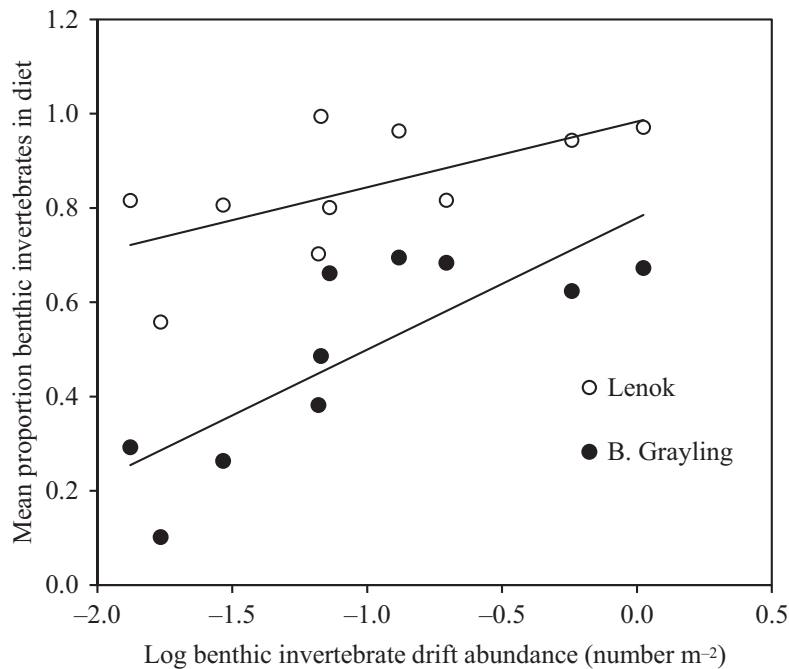


Fig. 5. Relationship of benthic invertebrate drift abundance to proportion by weight in stomach contents of lenok and Baikal grayling from the Eg and Uur rivers.

the descriptions of other stream-dwelling grayling, which exhibit highly variable diets influenced by prey availability (Brown 1938; Northcote 1995). Ephemeroptera nymphs, the prey with the lowest drift propensity, were more prevalent in the diets of smaller Baikal grayling while prey with higher drift propensities (e.g. Diptera larvae and terrestrial invertebrates) were more common in the diets of larger size classes. Similar to drift-feeding dominance hierarchies documented in other salmonids (Fausch & White 1986; Nielsen 1992), large Arctic grayling generally occupies the best drift-feeding locations within a stream to the exclusion of smaller fish (Hughes 1992), possibly leading to a higher degree of epibenthic feeding in smaller size classes of grayling. Size-based diet differences have also been observed in a closely related lake-dwelling grayling (Hovsgol grayling *Thymallus nigrescens*) higher in the Eg River watershed, which shift from a diet of zooplankton at smaller sizes to benthic invertebrates at larger sizes (Ahrenstorff et al. 2012).

The differential use of benthic and drifting prey revealed through stomach contents indicates vertical partitioning of prey resources by lenok and Baikal grayling. Lenok consistently relied on benthic prey while grayling more strongly utilised prey suspended in the water column. Such partitioning of prey in the water column has been documented in multiple sympatric pairs of salmonids (e.g. Johnson & Ringler 1980; Hindar and Jonsson 1988; Nakano et al. 1992; Negus & Hoffman 2013). In observational studies, including the present study, it is difficult to determine whether interspecific competition is the cause of

niche partitioning as evolved selective foraging differences could also explain niche partitioning (Ross 1986). Previous authors have compared species in sympatry and allopatry (Nilsson 1963; Andrusak & Northcote 1971; Jonsson et al. 2008) or across a gradient of resource availability (Zaret & Rand 1971; Liso et al. 2013) to determine the influence of interspecific competition on resource partitioning. Evidence of reduced niche overlap during periods of low prey availability is often cited as support for interspecific competition (Lack 1946; Ross 1986; Bohn and Amundsen 2001).

The positive relationship between drifting prey availability and diet niche overlap we observed indicates that differences in prey utilisation are the result of competition. Through a combination of stream observations and experimental depletion of drifting prey, Fausch et al. (1997) and Nakano et al. (1999) described similar increase in diet overlap of sympatric Japanese char as abundance of drifting prey increased. The authors found that competitive interactions increased with declining prey availability and the subordinate, less efficient drift-foraging species, shifted to benthic foraging. Although our results lack direct observations, stomach contents infer a similar pattern in lenok and Baikal grayling.

Stable isotope analysis

In the Eg and Uur rivers, lenok muscle tissue was enriched in $\delta^{15}\text{N}$ relative to Baikal grayling, indicating greater reliance upon fish and aquatic invertebrates, which were enriched in $\delta^{15}\text{N}$ relative to

Prey partitioning in lenok and Baikal grayling

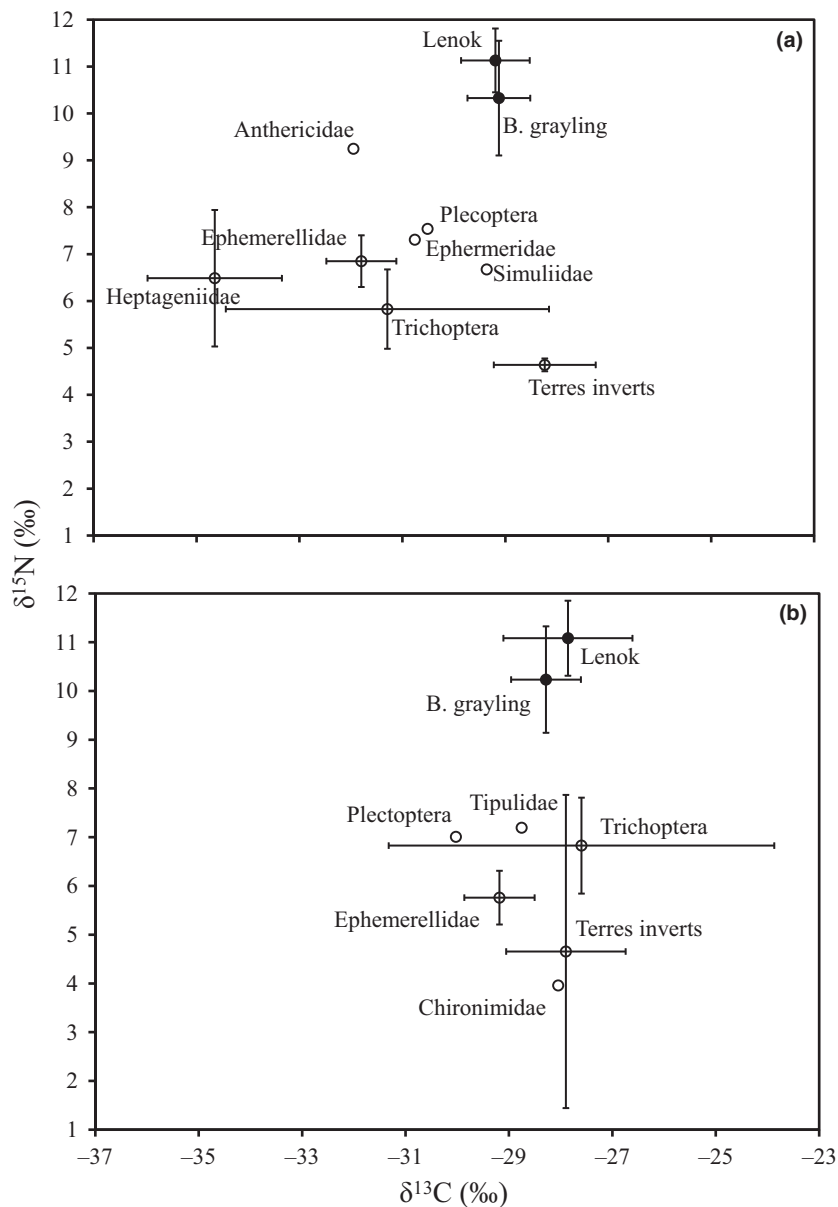


Fig. 6. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (± 1 SD) of fish (closed circles) and prey taxa (open circles) from the Uur River (a) and Eg River (b). B. Grayling = Baikal grayling, Terres Inverts = terrestrial inverts.

terrestrial invertebrates. Similarly, the Uur River three-source mixing model identified that terrestrial invertebrates made a greater contribution to Baikal grayling assimilated diet than that of lenok, while fish comprised a larger portion of lenok's assimilated diet. The greater utilisation of terrestrial invertebrates by Baikal grayling was consistent with stable isotope analysis and indicates that vertical partitioning of prey resources is sustained over several months, as stable isotope ratios in fish muscle tissue reflect prey assimilation over a period of months to years (Hesslein et al. 1993; Church et al. 2009). However, evidence from stable isotopes also indicate that piscivory was more common in lenok than revealed through stomach contents, in which fish comprised <1% of lenok diets by mass. In an

adjacent watershed, Chandra et al. (2005) reported a similar discrepancy between stomach content and stable isotope analysis as the $\delta^{15}\text{N}$ value of lenok muscle tissue indicated that fish were more common in their diets than was determined via stomach content analysis. These results may indicate that piscivory in lenok is more common in the months prior to July, when stomach contents were collected, or that fish were assimilated more readily than invertebrates.

Mixing models were not applied to stable isotope data from the Eg River because both lenok and Baikal grayling $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fell far outside of the prey mixing polygon. Overall, variability in $\delta^{13}\text{C}$ was greater in both lenok and grayling in the Eg River. A possible explanation for this is the presence

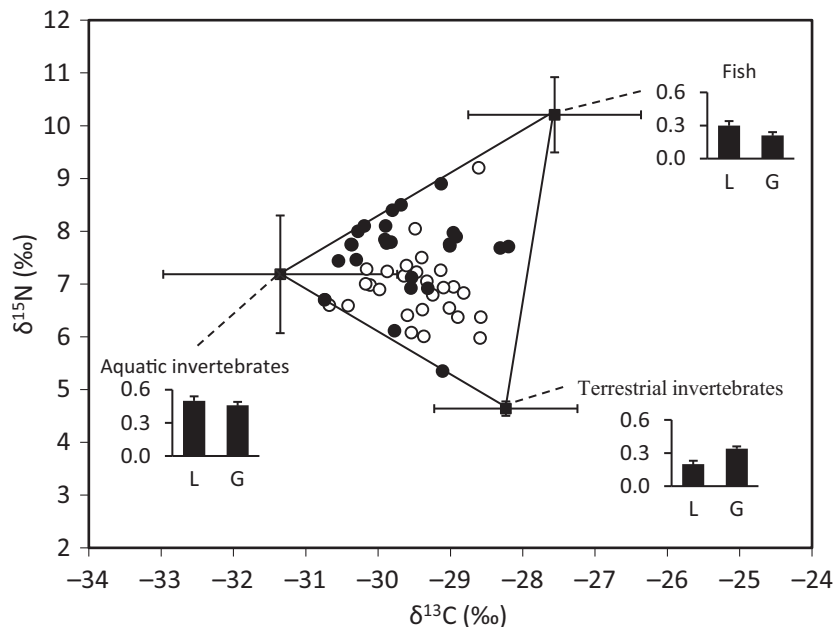


Fig. 7. Prey mixing polygon based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from fish, aquatic invertebrates and terrestrial invertebrates. Filled squares represent mean (± 1 SD) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of each prey taxa. Closed circles represent lenok and open circles represent Baikal grayling following $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Bar graphs display mean proportional contribution of each prey type (± 1 SE) to the assimilated diet of lenok (L) and Baikal grayling (G) from the Uur River.

of large spring side channels within our sampling reach, which were not included in our prey sampling protocol. Groundwater is typically supersaturated in respiratory CO_2 , which is highly depleted in ^{13}C (Rounick & James 1984). As a result, benthic algae growing in areas of substantial groundwater inflows typically exhibit low $\delta^{13}\text{C}$ values (Finlay 2001). The potential influence of groundwater-fed side channels on $\delta^{13}\text{C}$ values of benthic algae and herbivores may be responsible for the wider variation of $\delta^{13}\text{C}$ values observed in lenok and grayling from the Eg River and lack of model fit.

Conclusion

Our analysis indicates that lenok and grayling exhibit vertical partitioning of prey resources. Additionally, drifting prey availability was negatively related to diet overlap based on stomach contents, suggesting competition is involved in resource partitioning and highlighting the importance of considering drifting prey availability in future studies of resource partitioning in stream-dwelling salmonids. Direct observation of species interactions should be considered in future examinations of niche partitioning in Baikal grayling and lenok as they would allow an examination of differences in feeding modes and the influence of antagonistic and exploitation competition. Fisheries managers considering conservation actions for lenok and Baikal grayling in Mongolian rivers (e.g. Ocock et al. 2006b) should consider the potential impacts of human development on invertebrate prey densities, as declining prey density may lead to increased competitive interactions between lenok and Baikal grayling.

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