Feeding ecology of lenok (*Brachymystax lenok*), Hovsgol grayling (*Thymallus nigrescens*) and Baikal grayling (*Thymallus baicalensis*) from the Eg-Uur Watershed, Mongolia

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
OF THE UNIVERSITY OF MINNESOTA
BY

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IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
MASTER OF SCIENCE

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May, 2014

family's guidance and support has not only helped me complete this work but helped me focus on what is truly important.

ABSTRACT

The Eg-Uur Watershed of Northern Mongolia is home to several unique salmonid species which are believed to be declining due to the rapid industrial development currently taking place in Asia. Until recently, there has been an absence of scientific literature describing the diets of lenok (*Brachymystax lenok*), Baikal grayling (*Thymallus baicalensis*) and Hovsgol grayling (*Thymallus nigrescens*), three of the most prevalent salmonids in the watershed. We used a combination of stomach contents and stable isotopes of carbon and nitrogen to examine the degree of dietary niche overlap of lenok, Baikal grayling and Hovsgol grayling in lake and stream habitats of the Eg-Uur Watershed. Lenok and grayling exhibited vertical partitioning of prey resources despite differences in prey availability between lake and stream habitats. Benthic prey was consistently more abundant in the diets of lenok, while grayling were more reliant upon prey suspended in the water column or near the water's surface. Within stream habitats, prey availability was positively related to diet overlap, suggesting that competition is involved in the resource partitioning we observed. Our analysis also revealed the presence of specialist planktivores within the Hovsgol grayling population. The results from this study provide a baseline description of prey utilization and partitioning between lenok and grayling (*Thymallus spp.*) which may be used to guide management and future research of these declining species.

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CHAPTER 1: Dietary niche partitioning in lenok (*Brachymystax lenok*) and grayling (*Thymallus spp.*) from the Eg-Uur Watershed, Mongolia

1.1 Introduction:

The Eg-Uur Watershed, located in Northern Mongolia, is considered one of the least impacted watersheds in the world (Mercado-Silva et al. 2008). The remote location of the watershed and historical predominance of Buddhism in the region have allowed several salmonid species to persist in the near absence of exploitation (Mercado-Silva 2008, Chimedsengee et al. 2009, Jensen et al. 2009). Unfortunately, the rapid development and climate change currently taking place in Mongolia have resulted in habitat loss and overharvest of several species, threatening the unique salmonid community present within this watershed (Ramankutty et al. 2002, Ocock et al. 2006, Nandintsetseg et al. 2007). Three species present in the watershed, Taimen (*Hucho taimen*), Hovsgol grayling (*Thymallus nigrecens*) and lenok (*Brachymystax lenok*), are currently listed as threatened in Mongolia's Red List (Ocock et al. 2006). Additionally, lenok and taimen, which occur outside Mongolia, face threats from climate change, development and overharvest throughout their ranges in Northeast Asia (Xu et al. 2009, Haugen and Jensen 2013).

Until recently, there have been few scientific studies available in the literature on the ecology of some of these salmonid species. Previous research has focused on the ecology and management of the taimen, a long-lived, top predator (Gilroy et al. 2010, Jensen et al. 2009). There is a lack of information available on the ecology of lenok, Hovsgol grayling, and Baikal grayling (*Thymallus baicalensis*), three of the most common salmonids in the Eg-Uur watershed (Mercado-Silva et al. 2008, Aherenstorff et al. 2011). Specifically, very few studies have examined the diets of lenok, Biakal grayling and Hovsgol grayling and determined whether prey

resources are partitioned between these salmonid species (Nakano 1999a, Northcote 1995, Ahrenstorff et al. 2011).

Partitioning of resources (prey, habitat and time) is thought to be the mechanism facilitating the coexistence of fish species (Ross 1986). Species that occur in sympatry and have similar fundamental niches are predicted to segregate resources to avoid competitive exclusion and allow coexistence if possible (Hardin 1960, Schoener 1974). Partitioning of available resources may be determined by differences in morphology, physiology or behavior, which allow a species to exploit a portion of the available niche more efficiently than co-occurring species (Tilman 1987). Resource partitioning has been demonstrated in lake, stream, intertidal and reef fish communities (Nilsson 1963, Anderson et al. 1981, Paine et al. 1981, Mittelbach 1984, Grossman 1986).

Salmonids of Europe and North America have frequently been used as a model to examine niche partitioning (Andrusak and Northcote 1971, Hindar et al. 1988, Langeland et al. 1991, Haugen and Rygg 1996). Some of the earliest studies to explicitly examine resource partitioning in fish compared differences in prey and habitat use in sympatric and allopatric populations of trout (*Salmo trutta*) and charr (*Salvelinus alpinus*) in Scandinavian lakes (Nilsson 1963, 1965). Following this initial research, many observational and experimental studies have demonstrated partitioning of prey resources between salmonids in lake and stream environments (Eloranta et al. 2011, Mookerji et al. 2003, Fausch et al. 1997). In streams, prey resources are often partitioned between co-occurring invertivorous salmonids through differential use of drifting and benthic invertebrates (Nakano et al. 1992, Mookerji et al. 2003, Nakano 1999a, Dineen et al. 2007). In lake habitats, prey resources are commonly partitioned by differential use of pelagic and littoral prey (Nilsson 1963, Amundsen 2010, Eloranta et al. 2011, Langeland et al. 1991). Yet, few studies have compared prey partitioning between salmonid species across both lake and stream habitats with varied prey abundances and composition.

Niche theory predicts that overlap in species diets will decline as prey availability becomes limiting and interspecific competition more intense (Lack 1946). Several observational studies of resource use by freshwater fish have supported this prediction (Ross 1986). More recently, Nakano et al. (1999b) have described how varying levels of drifting prey influence diet overlap and competitive interactions between two char species (*Salvelinus spp.*). During periods of high drift availability, both species utilized drifting invertebrates, but as drift abundance decreased to moderate levels interference competition ensued and the species less adapted to drift foraging shifted to benthic foraging (Nakano et al. 1999b). Similarly, Amundsen et al. (2010) observed high dietary overlap between three salmonid species in lentic habitat when prey were abundant and strong partitioning when prey abundance was low.

Lenok and grayling occur sympatrically throughout the Eg-Uur Watershed. Lenok occur throughout the watershed, while Hovsgol grayling are restricted to Lake Hovsgol and Baikal grayling are largely restricted to stream habitats (Sidelva 2006). The sharp-nosed form of lenok, the only form in the Eg-Uur, have an inferior mouth, likely suited to benthic foraging (Nakano 1999a), while both species of grayling have small terminal mouths, likely suited for foraging within the water column or near the water's surface (Helfman et al. 2009). Although functional morphology differs between lenok and grayling, it appears that there may be considerable overlap in their diet niches (Sidelva 2006, Chandra et al. 2005). Reports of stream dwelling lenok and Baikal grayling diet indicates that stream benthos and terrestrial invertebrates are common in the diets of both species (Chandra et al. 2005, Sidelva 2006, Nakano 1999a). The limited information available on the diets of lake dwelling lenok indicates a diverse array of benthic prey occur in the diet (Sidelva 2006), while small Hovsgol grayling consume zooplankton but grayling larger than 200mm shift to a diet similar to that of lenok (Ahrenstorff et al. 2011). Despite apparent similarities in diet niche, there are no studies that explicitly examine partitioning of prey resources between lenok and grayling.

The Eg-Uur watershed includes three unique river systems with distinctive hydrology and riparian habitat and Lake Hovsgol, a large, deep, ultra-oligotrophic lake. Lenok and grayling occur sympatrically throughout the watershed, providing a unique opportunity to examine resource use and prey partitioning between habitats in species that have received relatively limited study. In the present study we describe the diets of lenok and grayling in lentic and lotic habitats of the watershed, examine prey partitioning of sympatric lenok and grayling, and compare degree of prey partitioning to prey availability. Based on differences in morphology, we hypothesize that grayling and lenok will partition prey resources with lenok primarily consuming bottom dwelling prey and grayling consuming prey suspended within the water column or near the water's surface. However, we predict that the degree of niche partitioning will be influenced by prey availability if competition is involved in prey partitioning. We applied a combination of stable isotope and stomach content analysis to examine niche partitioning in lenok and grayling.

1.2 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 (1500m) and located in the transition of Mongolian steppe and Taiga forest. Sampling took place at three waterbodies located in the watershed: the Upper Eg River (Egiin gol, 50°16'58"N, 101° 54'6"E), Uur River (Uur gol, 50°18'35"N, 101°53' 43"E) and Lake Hovsgol (50°58'12" N, 100° 24'0"E). Within our study reach, the Eg River is a high gradient with dense willow and larch riparian forest. The reach also receives substantial groundwater inputs through several spring-fed side channels. In contrast, the Uur River is low gradient with riparian zones composed of willow, larch and actively grazed steppe pasture with no obvious groundwater inflows. Lake Hovsgol is a large ultra-oligotrophic lake located at the headwaters of the Eg River. It is a deep rift lake (maximum depth = 262 m,

mean depth = 138 m), with an area comparable to that of Lake Erie (volume 480 km^3). The fish community of the Eg-Uur Watershed is dominated by lenok *Brachymystax lenok* and grayling *Thymallus spp.*. Burbot *Lota lota*, Taimen *Hucho taimen* (Eg and Uur Rivers only), stone loach *Barbatuli toni*, roach *Rutilus rutilus* (Lake Hovsgol only), phoxinus minnow *Phoxinus phoxinus* and Eurasian Perch *Perca fluviatilis* are also present.

Fish and Invertebrate Collection

Fish and invertebrate prey availability samples were collected at 15 sampling locations in the Eg-Uur Watershed during the summers of 2011 and 2012. Six sites were selected on the Uur River, three on the Eg River and six on Lake Hovsgol (Fig 1.1). At river sites, study reaches were restricted to riffle and run habitats between 0.1 - 0.5km in length and selected to optimize spatial coverage based on time and travel constraints. Sites on Lake Hovsgol were distributed around the lake, following long term sampling locations (Ahrenstorff et al. 2011). A total of 156 lenok and 140 Baikal grayling from the Uur River and 38 lenok and 80 Baikal grayling from the Eg River were captured via angling gear. In Lake Hovsgol, a total of 92 lenok, two Baikal grayling and 118 Hovsgol grayling were captured using experimental mesh horizontal gillnets set perpendicular to shore in depths less than 10m. Following capture, total length, fork length and weight were measured on each fish. Stomach contents were removed through the use of a gastric lavage or by stomach dissection. An efficiency trial performed on 35 lenok revealed that there was no significant difference in removal efficiency among common prey categories (Kruskal-Wallis, df =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 m^2, 500µm mesh). Substrate within the sample area was disturbed and brushed clean by hand over a 2 minute time interval. Samples were spaced evenly within each sampling site. At river sites, six drift samples

were also collected. 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, in order to sample the

entire water column. Six samples were collected at each site over a period of 6 hours. Water

velocity was measured directly in front of the drift net opening at 40% of the total depth with a

Swoffer current velocity meter in order to estimate drift rate.

Following collection, all diet and prey availability samples were preserved in 95%

ethanol, examined using a dissecting microscope, identified to family or order and enumerated. In

each sample, the total length or head width was measured on a subsample (n=5) of individuals

from each prey category, measurements were recorded to the nearest 0.1 mm. In order to

estimate proportion by mass of each prey type in diet samples, the mean of head width or total

length was converted to dry mass following existing length-mass regressions (e.g. Benke et al.

1999) and multiplied by the number of prey items in each diet.

Data analysis

Mean proportion of prey taxa by number (Guy and Brown 2007) in diet and prey

availability samples was calculated following:

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

where P is the number of fish with food in their stomachs and N_{ij} is the weight of prey type i in

the diet of fish j. Propensity of prey taxa to occur in the drift was calculated following the

equation:

$$A_p = A_d (A_b + A_d)^{-1}$$

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 0-1 with higher values indicating greater drift propensity.

Mean proportion of each prey taxa in the diet by weight was then calculated following:

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

where P is the number of fish with food in their stomachs and W_{ij} is the weight of prey type i in the diet of fish j. Dietary overlap of lenok and grayling was assessed using Schoeners measure of proportional overlap:

$$C_{xy} = 1 - \frac{1}{2} (\sum_{i} |p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the proportion of a prey item i by weight in the diets of species x and y. 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 Chessons Alpha (1983):

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

where r_i is the proportion of prey is type i in the diet and n_i is the proportion by number of prey type i in drift or benthic samples. Possible values range from 0 to 1, with values greater than $1/m$ indicating positive selection. Dietary niche width was estimated using Levin's index (1968):

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

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

Differences in diet and available prey composition were analyzed using non parametric Mann-Whitney U tests as 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 total, 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 comparisons were carried out using linear regression and one-way analysis of variance (ANOVA). When comparisons were made between >2 groups, Tukey's HSD was used following ANOVA to identify significant differences among groups. A significance level of $\alpha = 0.05$ was used for all comparisons.

1.3 Results:

Composition and abundance of invertebrate prey community

Mean benthic prey density (number/0.1 m^2) was similar between rivers (mean ± 1 S.E, Eg River = 38 ± 11, Uur River = 27 ± 11; Tukey's HSD, p=0.8) but significantly higher in the near shore of Lake Hovsgol (mean ± 1 S.E = 73± 12) than the Uur River (Tukey's HSD, p = 0.03). The benthic prey community in the Eg and Uur Rivers was primarily comprised of immature stages of Trichoptera, Ephemeroptera and Diptera, while Diptera larvae and gammarus dominated the benthic prey community of Lake Hovsgol (Fig. 1.2). Between rivers, 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, df=1, p=0.01). Trichoptera were more common in the Eg River (0.16) than the Uur river (0.04), but the difference was not significant based on a Bonferroni corrected alpha level (Mann-Whitney U-test, H=5.50, df=1, p=0.02).

Drifting prey abundance was not significantly different between rivers (Uur River = 0.12 $\pm$ 0.05 number/m^3, Eg River = 0.46 $\pm$ 0.20 number/m^3; ANOVA, $F_{1,9}$=2.56, p=0.15). Aquatic and terrestrial stages of invertebrates (e.g. adult Ephemeroptera) and terrestrial invertebrates comprised the largest portion of the drifting prey community (Fig. 1.3). Overall, terrestrial invertebrates and adult and pupal stages of aquatic invertebrates exhibited the highest drift propensity (1.00 and 0.68, respectively), while aquatic stages of Ephemeroptera, Trichoptera and Plecoptera exhibited lower drift propensity (Fig 1.4).

Dietary analysis

Aquatic invertebrates composed the largest portion of lenok, Baikal grayling and Hovsgol grayling diets by weight (Fig 1.5). Aquatic invertebrates composed 85%, 68% and 73% of Lenok, Baikal grayling and Hovsgol grayling, respectively. Invertebrates of terrestrial origin comprised 7%, 25% and 17% of lenok, Baikal grayling and Hovsgol grayling diets respectively. Piscivory was uncommon in both lenok and grayling (*Thymallus spp.*), but was more common in lenok (lenok = 5% occurrence, grayling= 1% occurrence). Dietary overlap between lenok and grayling was 51% on average, below the threshold considered ecologically significant (60%). Diet overlap ranged from 24%-77% across sites and was not significantly different among waterbodies (ANOVA, $F_{2, 13}$= 0.49, p=0.62; Table 1.2).

Lake Hovsgol

Mean diet overlap between lenok and Hovsgol grayling in Lake Hovsgol was 48%, primarily due to the prevalence of gammarus (*Gammarus spp.*) in the stomach contents of both species (Fig 1.5). Benthic prey types (e.g. gastropod, gammarus) comprised the largest portion of lenok diets in Lake Hovsgol (78% by weight), while a mix of benthic invertebrates, zooplankton and neustonic prey (e.g. terrestrial invertebrates, adult and pupae stages of aquatic invertebrates) comprised 37%, 10% and 50% of Hovsgol grayling diets by weight respectively. Zooplankton,

terrestrial invertebrates and pupae and adult stages of aquatic invertebrates comprised a significantly larger portion of Hovsgol grayling than lenok diets (zooplankton, H=9.82, df =1, p=0.002; terrestrial invertebrates, H=5.60, df=1, p=0.018; pupae and adult stages of aquatic invertebrates, H =8.3, df=1, p= 0.004), while gastropods composed a significantly larger portion of lenok diets (H=9.82, df=1, p=0.002).

Both lenok and Hovsgol grayling exhibited shifts in diet composition with length. Smaller lenok (<300mm) consumed primarily gammarus and aquatic stages of aquatic insects, while diets of larger lenok (>300mm) were more heterogeneous, composed of gastropods, fish, gammarus, and pupae and adult stages of aquatic invertebrates (Fig. 1.6). Hovsgol grayling diets also shifted with size as zooplankton made up a large portion of small grayling (<250mm) diets but were nearly absent in the diets of large grayling (>250mm; Fig. 1.6).

Prey availability estimated from benthic samples revealed that Hovsgol grayling selected for pupae and adult stages of aquatic invertebrates and against benthically associated Ephemeroptera nymphs and Trichoptera larvae, while lenok exhibited neutral selection for most prey types available in the benthos, excluding grayling eggs which were selected against (Table 1.3). Diet overlap of Lenok and Hovsgol grayling diets did not appear to be influenced by near shore benthic prey density (r^2=0.16, p=0.43).

Eg and Uur Rivers

Lenok and Baikal grayling in the Eg and Uur Rivers also exhibited dietary segregation. Lenok diets from the Eg and Uur Rivers were composed primarily of benthic insects (80% by weight), while Baikal grayling diets were composed of benthic insects (49% by weight) and prey types typically found in the drift (e.g. terrestrial invertebrates and adult stages of aquatic invertebrates; 50% by weight). As a result, the diet niche of Baikal grayling was significantly larger than lenok at river sites (Figure 1.7; H=5.50, df=1, p=0.02).

Lenok and Baikal grayling in the Uur River exhibited the highest diet overlap of the three waterbodies sampled (56%), largely due to the high proportion of Ephemeroptera nymphs in both species diets (Fig. 1.5). Though prey types associated with the drift composed a much larger portion of Baikal grayling diets from the Uur River by weight, these differences were not significant (terrestrial invertebrates, H=5.03, d.f.=1, p=0.03; adult and pupae stages of aquatic invertebrates, H=5.77, d.f.=1, p=0.02). However, benthic dwelling Trichoptera larvae composed a significantly larger portion of lenok than Baikal grayling diets from the Uur River (H=7.41, d.f. =1, p=0.007). Similar to the Uur River, benthic prey composed a larger portion of lenok diets from the Eg River, while drifting prey composed a larger portion of grayling diets on average. However, these differences were not significant based on a Bonferroni correct alpha level.

Analysis of stomach contents by size class revealed that lenok and Baikal grayling exhibited shifts in stomach composition with length. In lenok, the proportion of Ephemeroptera nymphs in the diet decreased with total length, while the proportion of Trichoptera larvae in the diet increased (Fig. 1.8, 1.9). Larger Baikal grayling from the Uur River consumed proportionally more terrestrial invertebrates and fewer benthic insects than smaller size classes (Fig. 1.8). In contrast, the importance of Dipteran larvae increased in the diets of Eg River Baikal grayling with length, while terrestrial invertebrates composed only a small portion of large Baikal grayling diets (Fig. 1.8).

Based on drifting prey availability, 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 1.3). 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. Using 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 1.3). 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 1.3). Lenok also exhibited neutral selection for all other prey types, while Baikal grayling selected for pupae and adult stages of aquatic invertebrates.

Diet overlap between river-dwelling lenok and Baikal grayling was positively correlated to drift abundance, suggesting increased utilization of drifting prey by both species during periods of high drift availability (linear regression, r^2=0.53, p=0.018, Fig. 1.10). In particular, proportion of benthic dwelling invertebrates in the diets of both species increased as they became more abundant in the drift (lenok, r^2=0.52, p=0.018; Baikal grayling, r^2=0.60, p=0.009; Fig. 1.11). However, the slopes of these regression lines were significantly different, as benthic dwelling invertebrates composed a large portion of lenok diets even at low abundance in the drift (homogeneity of slopes test, F=11.29, p<0.001).

2.4 Discussion:

Lenok and grayling exhibited vertical partitioning of invertebrate prey resources in both lake and river habitats of the Eg-Uur, despite differences in prey availability. Grayling displayed a generalized foraging strategy, utilizing both benthic and prey suspended in the water column or near the water's surface (e.g. terrestrial invertebrates and zooplankton), while lenok relied upon prey sources associated with the benthic profile (e.g. Trichoptera larvae, gastropods and gammarus). Furthermore, vertical partitioning of prey within stream habitats increased as prey availability declined, suggesting that interspecific competition is involved in the diet segregation we observed (Zaret and Rand 1971). Similar evidence was not found in Lake Hovsgol. This discrepancy is likely attributed to our limited measure of prey availability in Lake Hovsgol,

which only reflected near-shore benthic prey availability, leaving competition, predator avoidance or selective differences between lenok and grayling as possible explanations for resource partitioning.

Lake Hovsgol

Lenok from Lake Hovsgol were generalist benthivores, utilizing primarily benthic prey and exhibiting neutral selection for most benthic prey taxa. Gammarus and gastropods were the two most prevalent taxa in lenok diets, composing more than half of lenok stomach contents by weight. Reliance on benthic prey is consistent with the limited diet information available from other parts of the lenok's range (Shved'ko et al. 1997, Nakano 1999b, Chandra et al. 2005, Sidelva 2006). Similar to ontogenetic diet shifts described in other salmonids, fish and large benthic prey taxa (e.g. gastropods) were more prevalent in diets of larger lenok, likely related to increased gape size (Keeley and Grant 2001).

Hovsgol grayling exhibited a wide dietary niche, utilizing prey types associated with feeding in the water column (e.g. zooplankton, terrestrial invertebrates and adult stages of aquatic invertebrates) and benthic prey. Zooplankton were important in the diets of grayling < 250mm. Ahrenstorff et al. (2011) described a similar shift in diets between size classes. This shift may be due to changes in zooplankton foraging ability with size (Schmidt and O'Brien 1982) or predation avoidance by smaller Hovsgol grayling (Ahrenstorff et al. 2011). Alternatively, recent stable isotope and morphological analysis suggests the presence of larger benthivorous and smaller planktivorous morphotypes of Hovsgol grayling, present in both littoral and pelagic habitats (Olson et al., unpublished data). In either case, these results indicate that Hovsgol grayling are likely an important link between pelagic and littoral productivity in Lake Hovsgol (e.g. McIntyre et al. 2006).

Eg and Uur Rivers

Lenok from the Eg and Uur Rivers relied upon benthic invertebrates. Immature stages of Trichoptera, Ephemeroptera and Diptera were the dominant prey taxa. Lenok exhibited strong positive selection for Trichoptera larvae, which may be attributed to their inferior mouth, suited for foraging on benthic prey (Nakano 1999b). In an adjacent watershed, Chandra et al. (2005) reported that benthic invertebrates and fish were an important component of stream-dwelling lenok diets based on evidence from stable isotopes. Though inconsistent with results from our stomach content analysis, this may indicate that fish are an important component of lenok diets earlier in the year as diets inferred via isotopes reflect prey consumption over a period of months to a year (Hesslein et al. 1992, Church et al. 2009). The composition of benthic prey in lenok diets appeared to vary between rivers based on differences in benthic prey availability, suggesting a somewhat generalized benthic feeding strategy. For example, Ephemeroptera nymphs were more common in the Uur River benthic samples and comprised a larger portion of lenok diets than lenok from the Eg River. River dwelling also exhibited a diet shift, similar to lenok from Lake Hovsgol. Generally, the proportion of larger, armored benthic prey (e.g. gastropods and most Trichoptera) increased as lenok increased in size. This may be related to increased gape size or biting pressure of larger fish (Johansson 1989).

Baikal grayling in the Eg and Uur Rivers exhibited a wider diet niche based on Levin's index than lenok and did not exhibit consistent selection for specific prey taxa. Baikal grayling also appeared to be more reliant upon benthic prey as the proportional abundance of benthic invertebrates in grayling diets was correlated to their abundance in the drift. This is consistent with other species of stream dwelling grayling, which exhibit highly variable diets based on prey availability (Brown 1938, Northcote 1995). Similar to lenok, Ephemeroptera nymphs were more prevalent in the diets of smaller Baikal grayling while prey types with high drift propensity (i.e. terrestrial invertebrates, Diptera larvae and adult and pupa stages of aquatic invertebrates) were more common in the diets of larger size classes. Similar to dominance hierarchies documented in

other salmonids, large grayling generally occupy the best drift feeding locations within a stream to the exclusion of smaller fish, and this may explain the higher proportional contribution of prey with high drift propensities to their diets (Hughes 1992).

Prey resource partitioning of grayling and lenok

Lenok and grayling exhibited partitioning of prey resources in both Lake Hovsgol and the Eg and Uur Rivers. Though prey availability varied across habitats (particularly when comparing lentic and lotic habitats), lenok consistently relied on benthic prey while grayling more strongly utilized prey suspended in the water column. Such vertical partitioning (sensu Dineen et al. 2007) has been documented in multiple sympatric pairs of salmonids (e.g. Johnson and Ringler 1980, Hindar and Jonsson 1988, Nakano et al. 1992, Negus and Hoffman 2013). In observational studies, including the present study, it is often difficult to determine if interspecific competition is the cause of niche partitioning as evolved selective foraging differences could also explain niche partitioning (Ross 1984). Previous authors have compared species in sympatry and allopatry (Nilsson 1963, Ross 1984) or across a gradient of resource availability (Zaret and Rand 1971, Fobert et al. 2011) 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 (Lack1946, Ross 1984, Bohn and Amundsen 2001).

Our results indicate that the diets of river-dwelling lenok and grayling diverged as drifting prey availability declined; inferring that differences in prey utilization are the result of competition. Through a combination of stream observations and experimental depletion of drifting prey Nakano et al. (1999a) and Fausch et al. (1997), described similar divergence in diets of Japanese char as prey declined. The authors found that competitive interactions increased with declining prey availability and the subordinate, less efficient drift foraging species, shifted to

benthic foraging. Though our results lack direct observations, stomach contents infer a similar pattern in lenok and Baikal grayling.

In contrast to lotic habitats, there was no correlation between prey availability and diet overlap of lenok and Hovsgol grayling in Lake Hovsgol. It is possible that our measure of near shore benthic invertebrate density did not accurately reflect prey availability to lenok and grayling as suspended or surface prey were not captured. Given this limitation we cannot invoke or rule out competition as the cause of diet partitioning. Similar to river habitats, evolved differences in feeding morphology are likely involved in the differences in diet observed. Lenok have an inferior mouth suited to benthic foraging, while Hovsgol grayling have a small terminal mouth typically associated with feeding on prey suspended in the water column (Nakano 1999a, Helfman et al. 2009). Although both species exhibit flexible feeding strategies, differences in functional feeding structures lend themselves to differential use of the available prey (Helfman et al. 2009). Additionally, more closely spaced gill rakers allow Hovsgol grayling to utilize zooplankton (Schmidt and O'Brien 1982), a prey source unavailable to lenok.

Conclusion

We identified the primary prey sources of lenok, Baikal grayling and Hovsgol grayling and described how prey resources are partitioned between species. Lenok were reliant upon benthic invertebrates, while both species of grayling exhibited a generalized diet and more strongly utilized prey sources suspended in the water column or near the water's surface. These results indicate that lenok and grayling partition prey resources vertically in both lentic and lotic habitats.

Stomach contents also revealed ontogenetic diet shifts in lenok, Baikal grayling and Hovsgol grayling. Lenok shifted to larger benthic prey with size, larger Baikal grayling were more reliant upon drifting prey than smaller fish, and Hovsgol grayling exhibited a diet shift from

zooplankton to larger invertebrate prey with size. However, the difference may also be explained by trophic polymorphism in the population. In either case, Hovsgol grayling appear to be an important link between benthic and pelagic productivity, warranting further examination of this result.

Our measure of prey availability was negatively related to diet overlap in lotic habitats, suggesting competition is involved in resource partitioning, while there was no relationship in lentic habitats, possibly influenced by our limited measure of prey availability. Overall, competition, selective differences or predator avoidance may all influence resource partitioning observed in lenok and grayling. Future research on the feeding interactions of these salmonids should include direct observation of species interactions to examine differences in feeding modes and the influence of antagonistic competition on niche partitioning in lenok and grayling. Further, future work should include greater coverage of the Eg and Uur Rivers and partitioning during other seasons.

Table 1.1. Number and mean total length of fish sampled for stomach contents from the Eg-Uur Watershed.

Waterbody	Year	N			Mean TL (mm)		
		Lenok	B. grayling	H. grayling	Lenok	B. grayling	H. grayling
Lake Hovsgol	2011	39	0	41	421	-	264
	2012	53	2	77	363	276	269
Uur River	2011	24	5	0	345	201	-
	2012	94	55	0	270	175	-
Eg River	2011	15	12	0	456	175	-
	2012	23	68	0	369	207	-
	Total	**248**	**142**	**114**	(270-456)	(175-276)	(264-269)

Table 1.2. Shroener's measure of dietary overlap for lenok and grayling in the Eg-Uur Watershed. Biologically significant overlap (>0.6) indicated in bold.

Year	Waterbody	Site(s)	Overlap
2012	Uur R.	U1	0.43
2012	Uur R.	U2	**0.64**
2012	Uur R.	U3	0.60
2012	Uur R.	U4	0.43
2012	Uur R.	U5	**0.67**
2011	Uur R.	U6	0.56
2012	Eg R.	E1	0.54
2012	Eg R.	E2	**0.66**
2012	Eg R.	E3	0.45
2011	Eg R.	E4	0.29
2012	Lk. Hovsgol	H1	0.24
2012	Lk. Hovsgol	H2	**0.77**
2012	Lk. Hovsgol	H3	0.54
2012	Lk. Hovsgol	H4	0.38
2012	Lk. Hovsgol	H5	0.60
2012	Lk. Hovsgol	H6	0.35
2011	Lk. Hovsgol	H7	0.46
	Uur R.	All	0.56
	Eg R.	All	0.49
	Lk. Hovsgol	All	0.48
	Grand mean		0.51

Table 1.3. Chesson's index of selectivity for lenok and grayling from the Eg-Uur Watershed using benthos or drift as a measure of prey availability. Astrics signify negative selection and crosses signify positive selection. Ephemer = Ephemeroptera nymphs, Trichop = Trichoptera larvae, Diptera = Diptera larvae, Plecop = Plecoptera nymphs, Gamm= *Gammarus spp.*, Gast = Gastropods, Eggs = grayling eggs. A and P = adult and pupae stages of aquatic invertebrates, Terres = terrestrial invertebrates.

Species	Waterbody	Prey Sample	1/m	Chesson's α (95% Confidence intervals are given in parentheses)								
				Ephemer	Trichop	Diptera	Pelcop	Gamm	Gast	Eggs	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)
H. Grayling	Hovsgol	Benthos	0.14	**0.2[*]** **(± 0.04)**	**0.04[*]** **(± 0.04)**	0.09 (± 0.10)	-	0.13 (± 0.22)	0.07 (± 0.09)	0.09 (± 0.11)	**0.53[†]** **(± 0.31)**	-
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)**
Lenok	Hovsgol	Benthos	0.14	**0.05[*]** **(± 0.09)**	0.23 (± 0.21)	**0.03[*]** **(± 0.06)**	-	0.29 (± 0.24)	0.19 (± 0.09)	**0.04[*]** **(± 0.08)**	0.27 (± 0.30)	-
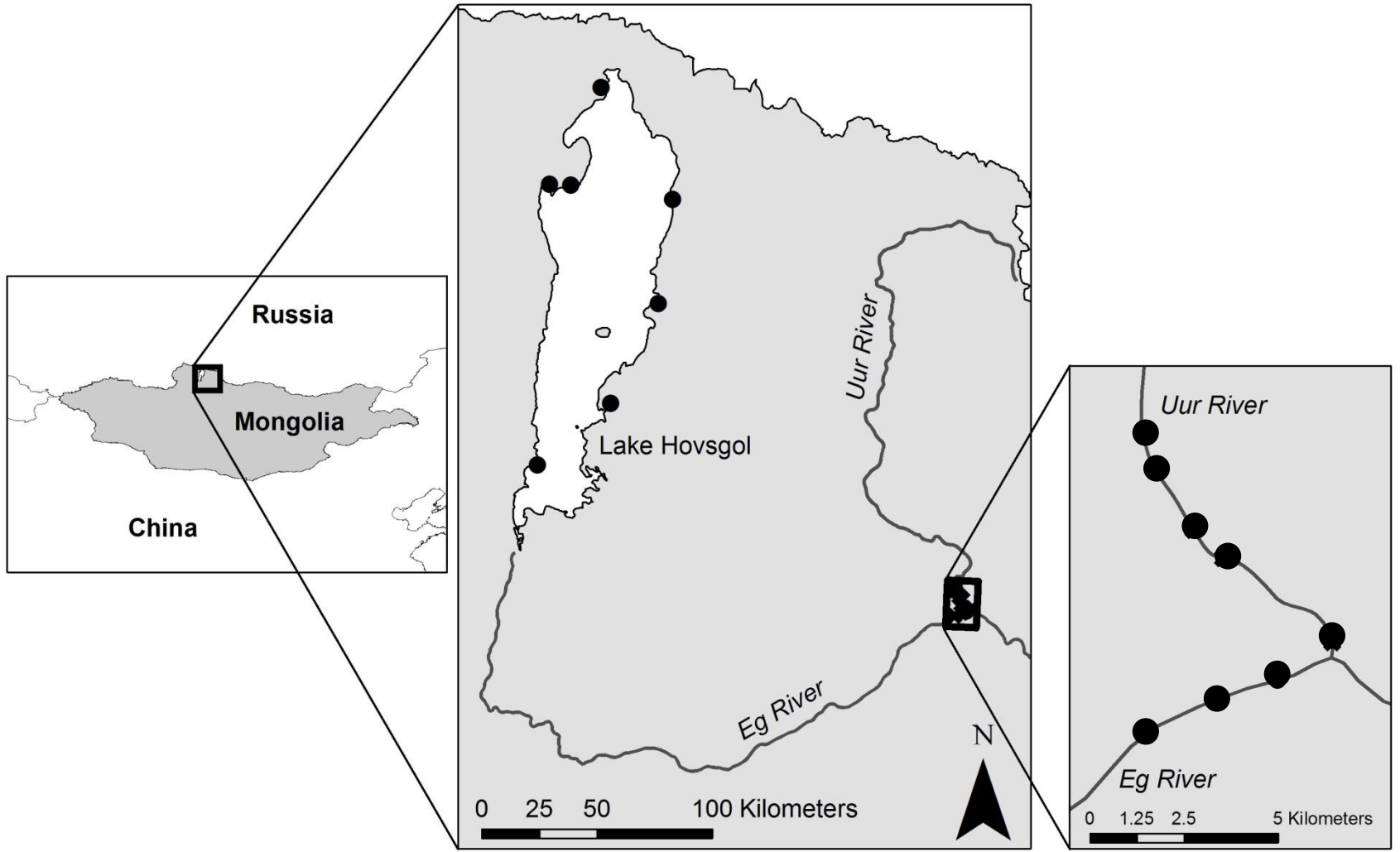
Figure 1.1. Location of the Eg-Uur Watershed andsampling sites on Lake Hovsgol, Eg and Uur.
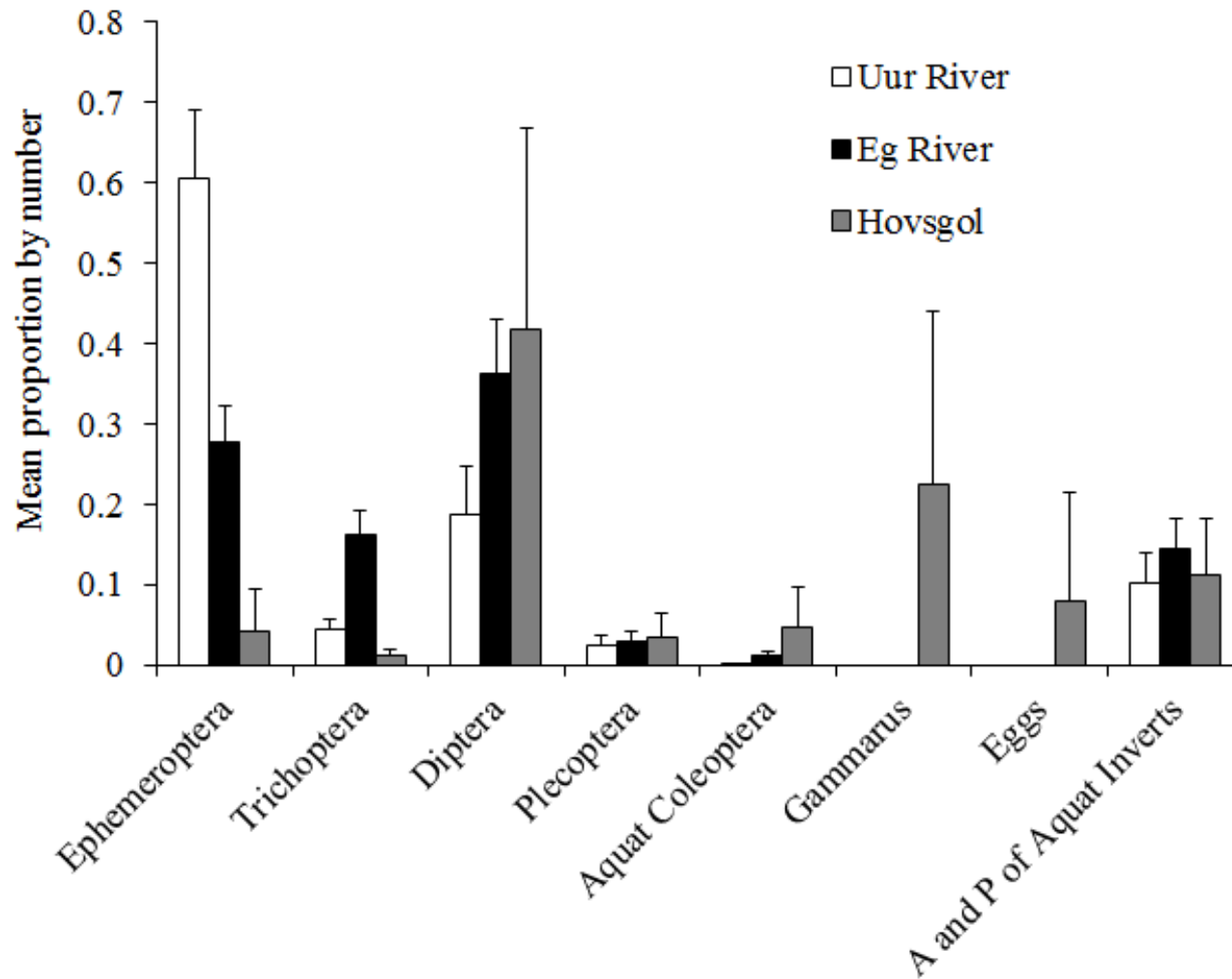
Figure 1.2. Mean proportion of prey taxa by number (±1 S.D.) in benthic samples from the Uur River, Eg River and Lake Hovsgol. Ephemeroptera = Ephemeroptera nymphs, Trichoptera = Trichoptera larvae, Diptera = Diptera larvae, Plecoptera = Plecoptera larve, Aquat Coleoptera = aquatic Coleoptera, Gammarus = *Gammarus spp.*, Eggs= grayling eggs, A and P of Aquat Inverts = Adult and pupae stages of aquatic invertebrates.
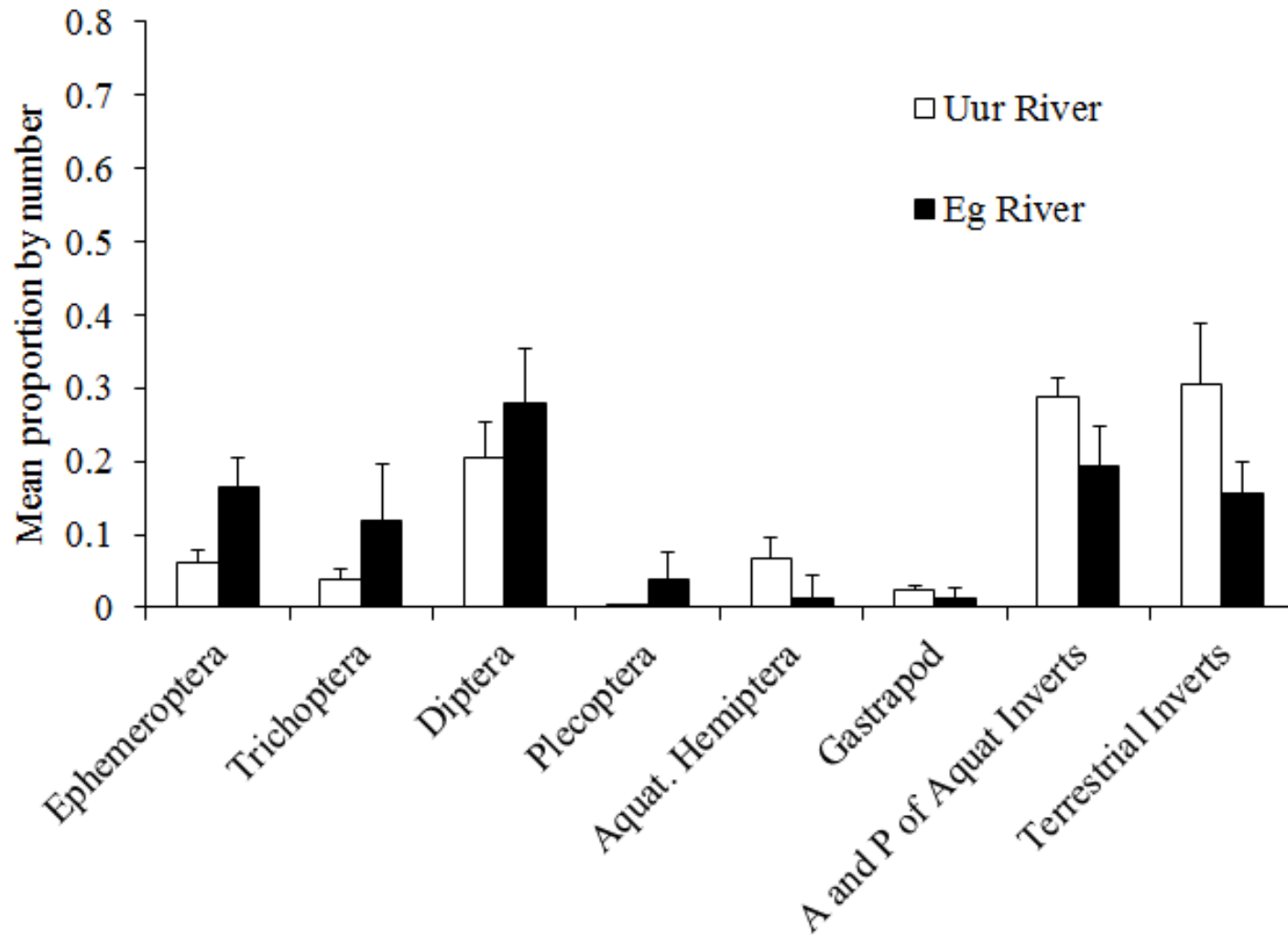
Figure 1.3. Mean proportion of prey taxa by number (±1 S.D.) in drift samples from the Uur and Eg Rivers. Ephemeroptera = Ephemeroptera nymphs, Trichoptera = Trichoptera larvae, Diptera = Diptera larvae, Plecoptera = Plecoptera larvae, Aquat hemiptera = aquatic Hemiptera, A and P of Aquat Inverts = Adult and pupae stages of aquatic invertebrates.
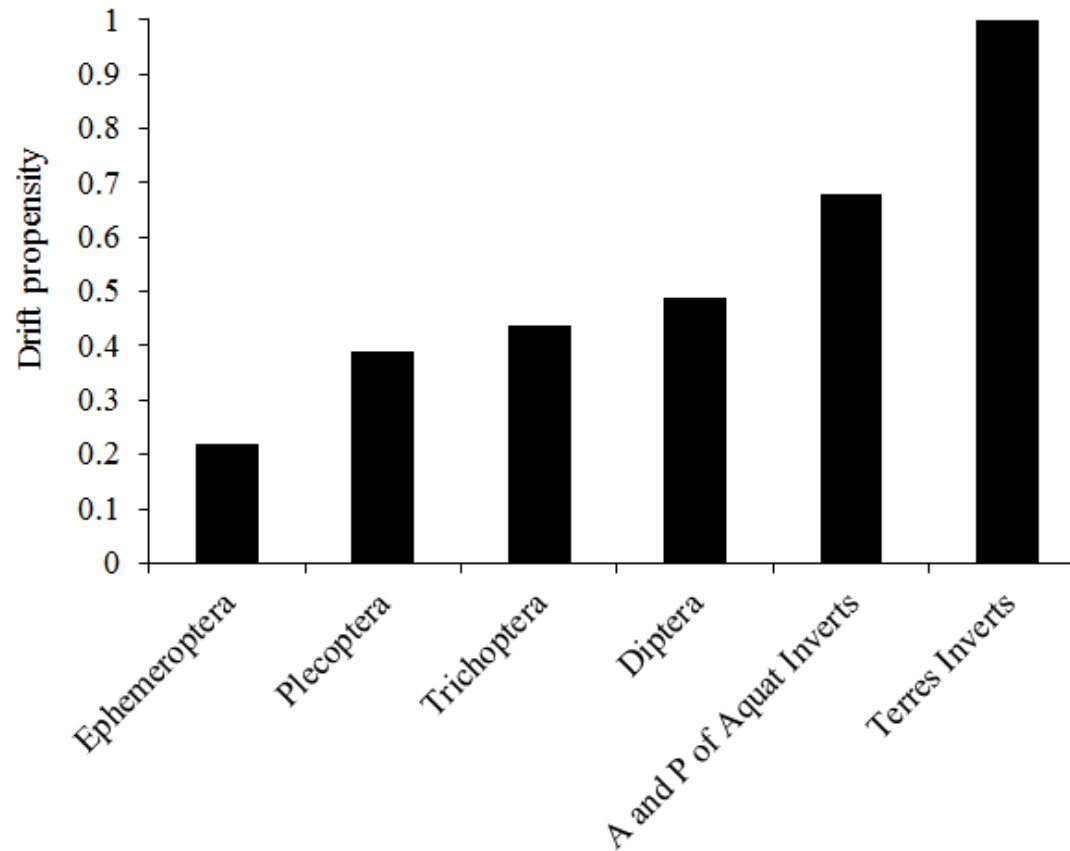
Figure 1.4. Drift propensity of invertebrate prey from the Eg and Uur Rivers. Ephemeroptera = Ephemeroptera nymphs, Trichoptera = Trichoptera larvae, Diptera = Diptera larvae, Plecoptera = Plecoptera larvae, A and P of Aquat Inverts = Adult and pupae stages of aquatic invertebrates.
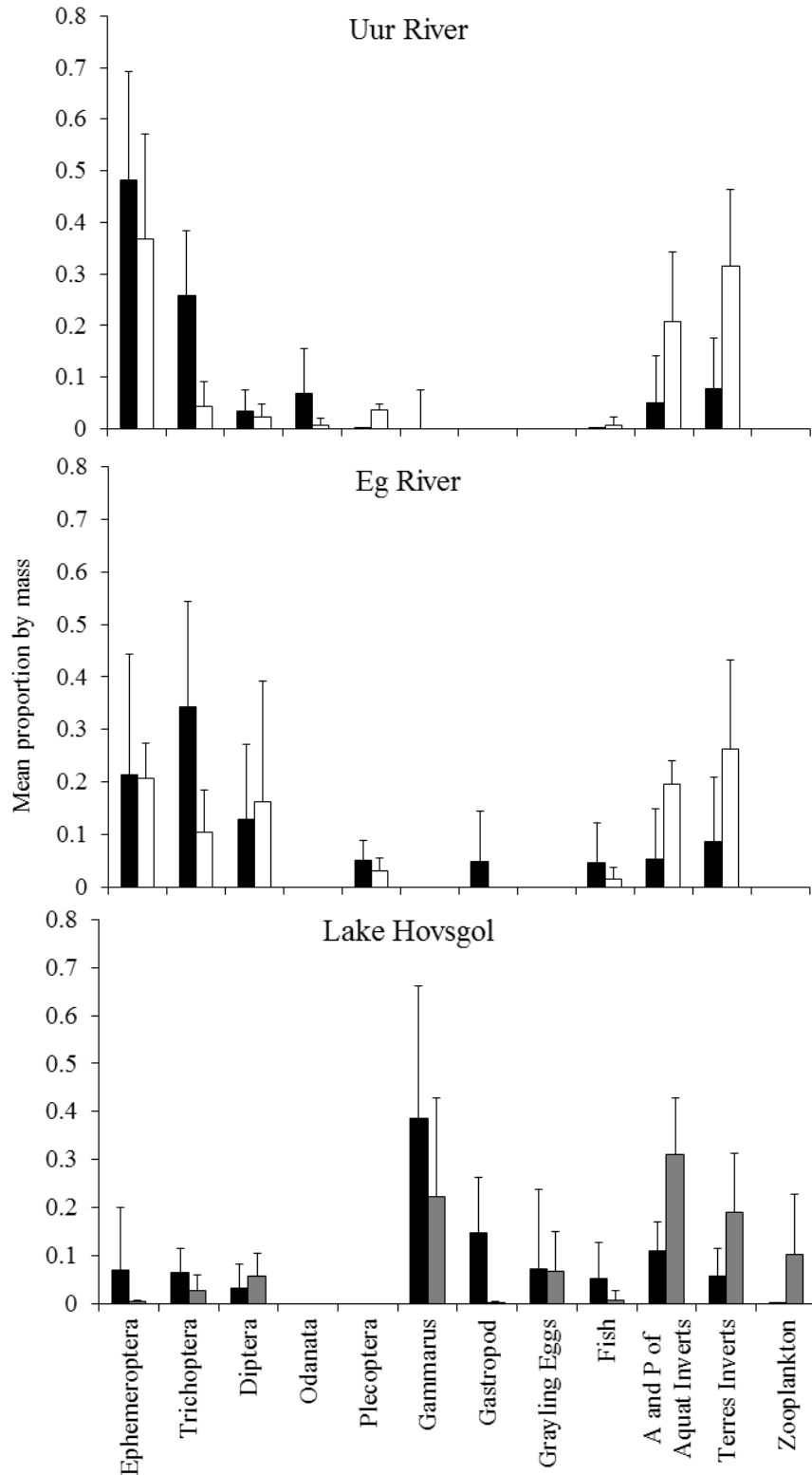
Figure 1.5. Mean proportion by weight of prey taxa (±1 S.D.) composing Baikal grayling (□), Hovsgol grayling (▨) and lenok (■) stomach contents. Ephemeroptera = Ephemeroptera nymphs, Trichoptera = Trichoptera larvae, Diptera = Diptera larvae, Plecoptera = Plecoptera larvae, A and P of Aquat Inverts = Adult and pupae stages of aquatic invertebrates.
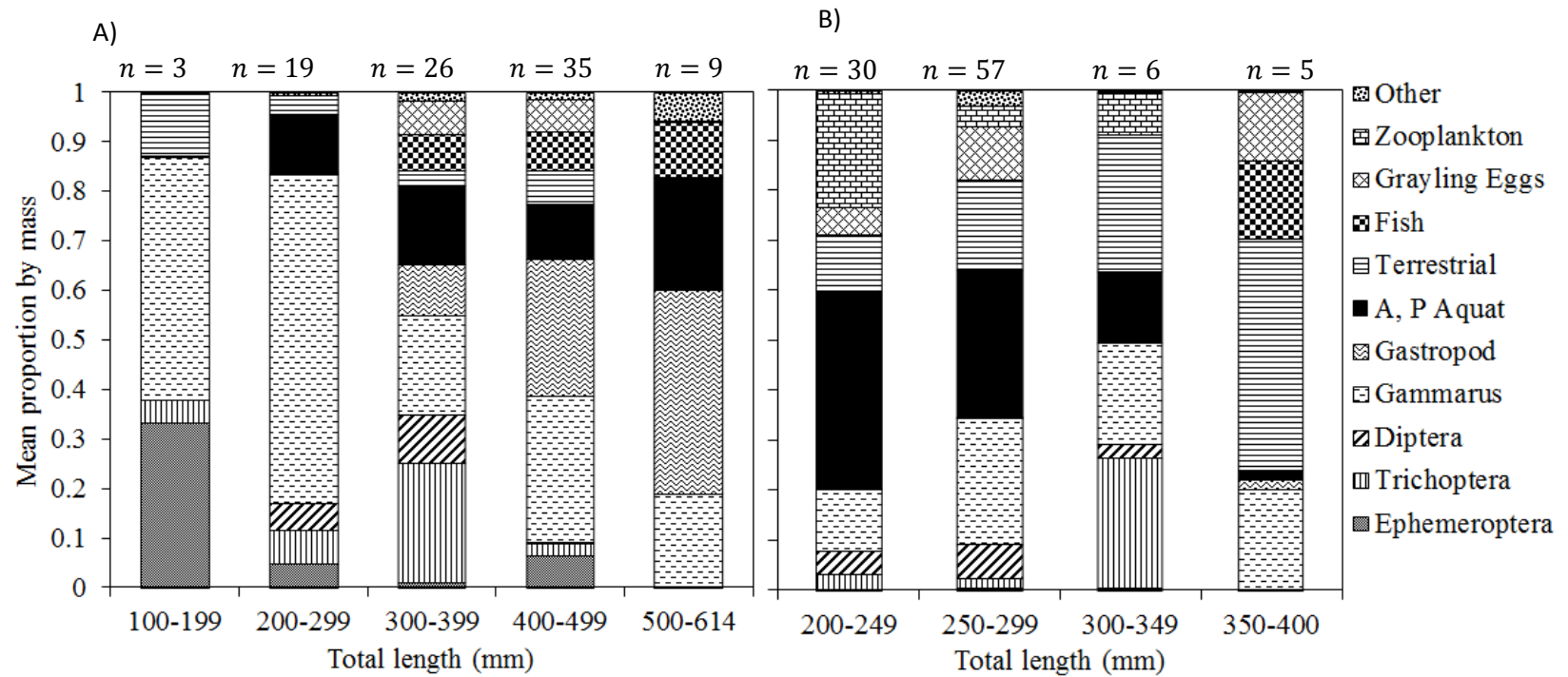
Figure 1.6. Proportional abundance (by mass) of prey taxa in lenok (A) and Hovsgol grayling (B) from Lake Hovsgol. Terrestrial = terrestrial invertebrates, A, P Aquat = Adult and pupae stages of aquatic invertebrates, Gammarus = *Gammarus spp.*, Diptera = Diptera larvae, Tichoptera = Trichoptera larvae, Ephemeroptera = Ephemeroptera nymphs.
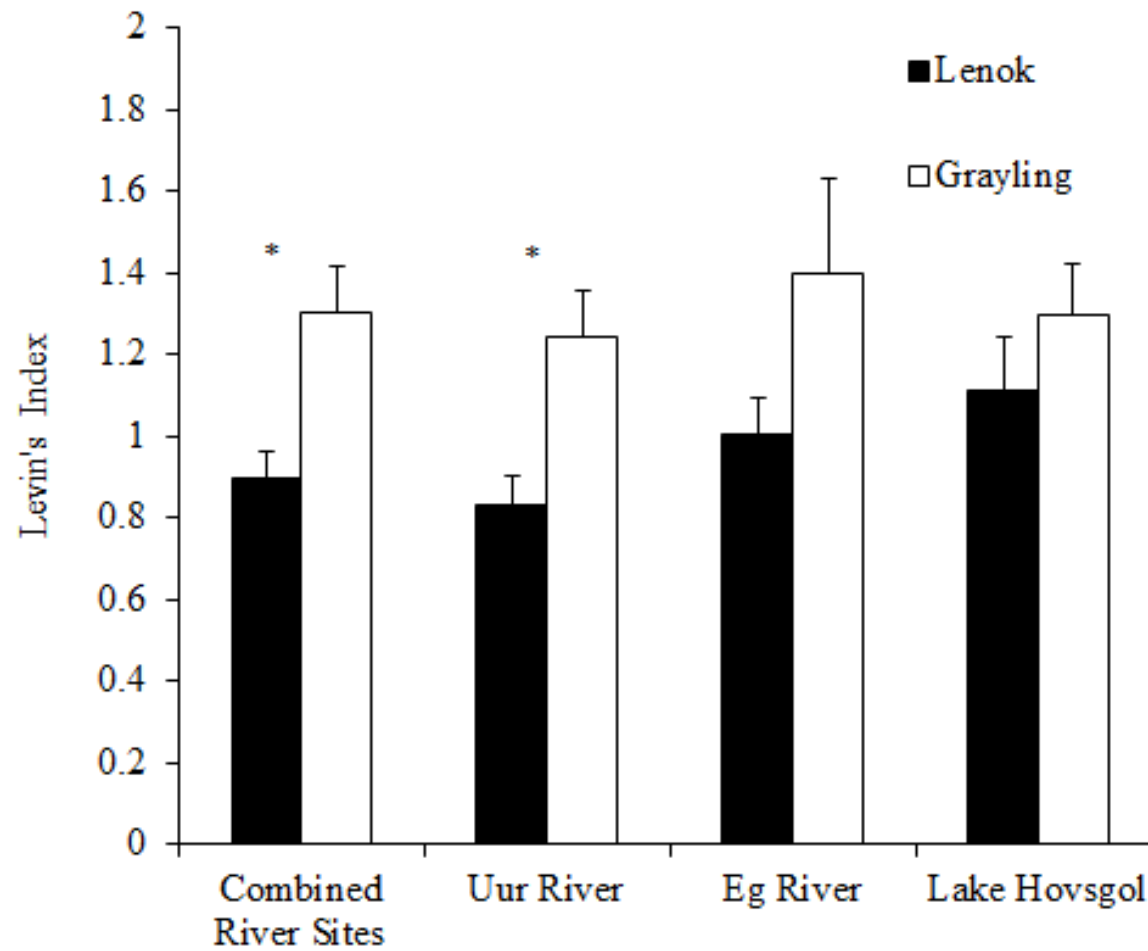
Figure 1.7. Mean dietary niche width (±1 S.D.) of lenok and grayling from the Uur River, Eg River and Lake Hovsgol based on stomach contents. Astrics indicate significant differences from one-way ANOVA.
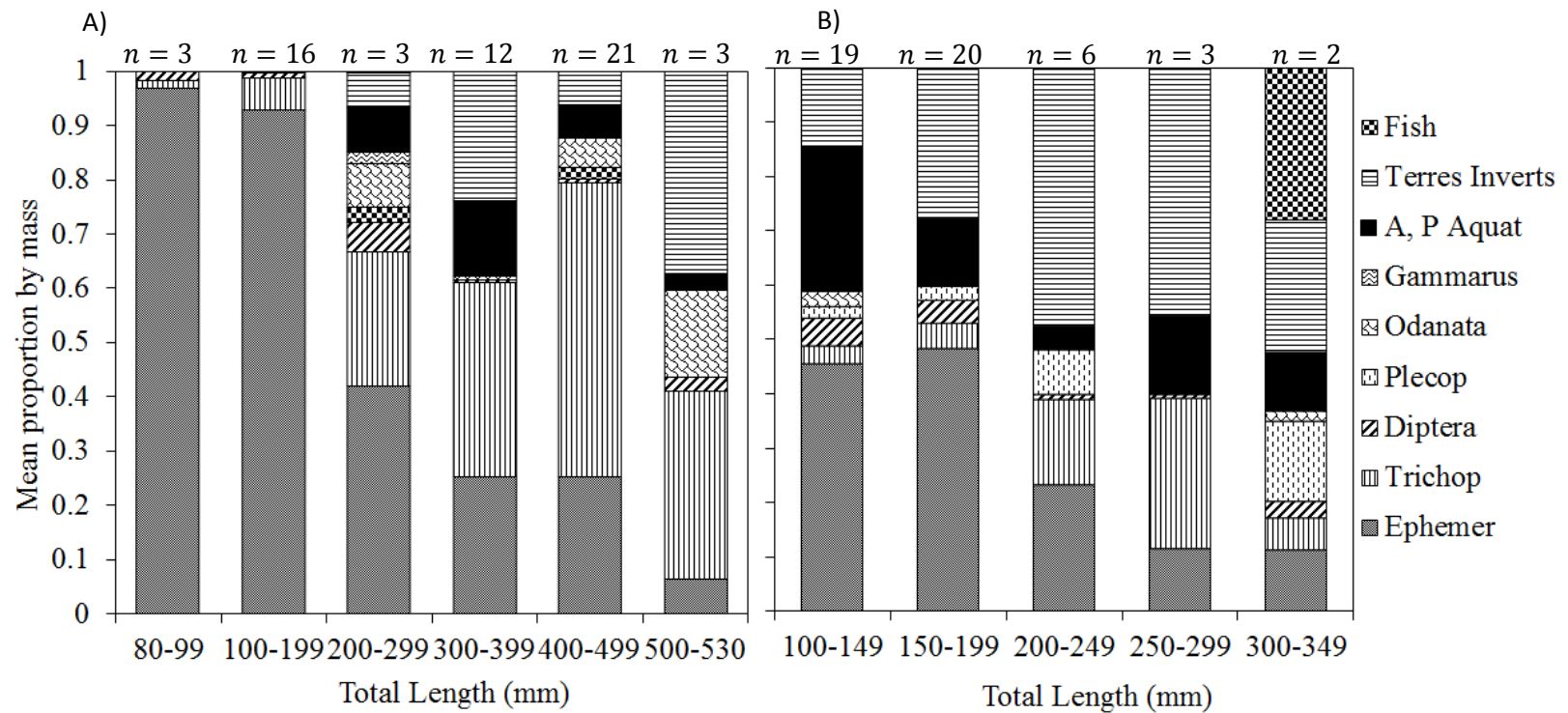
Figure 1.8. Proportional abundance of prey taxa in lenok (A, n = 94) and Baikal grayling (B, n = 50) stomachs from the Uur River. Terres Inverts = terrestrial invertebrates, A, P Aquat = Adult and pupae stages of aquatic invertebrates, Odanata = Odanata nymphs, Gammarus = *Gammarus spp.*, Diptera = Diptera larvae, Tichoptera = Trichoptera larvae, Ephemeroptera = Ephemeroptera nymphs.
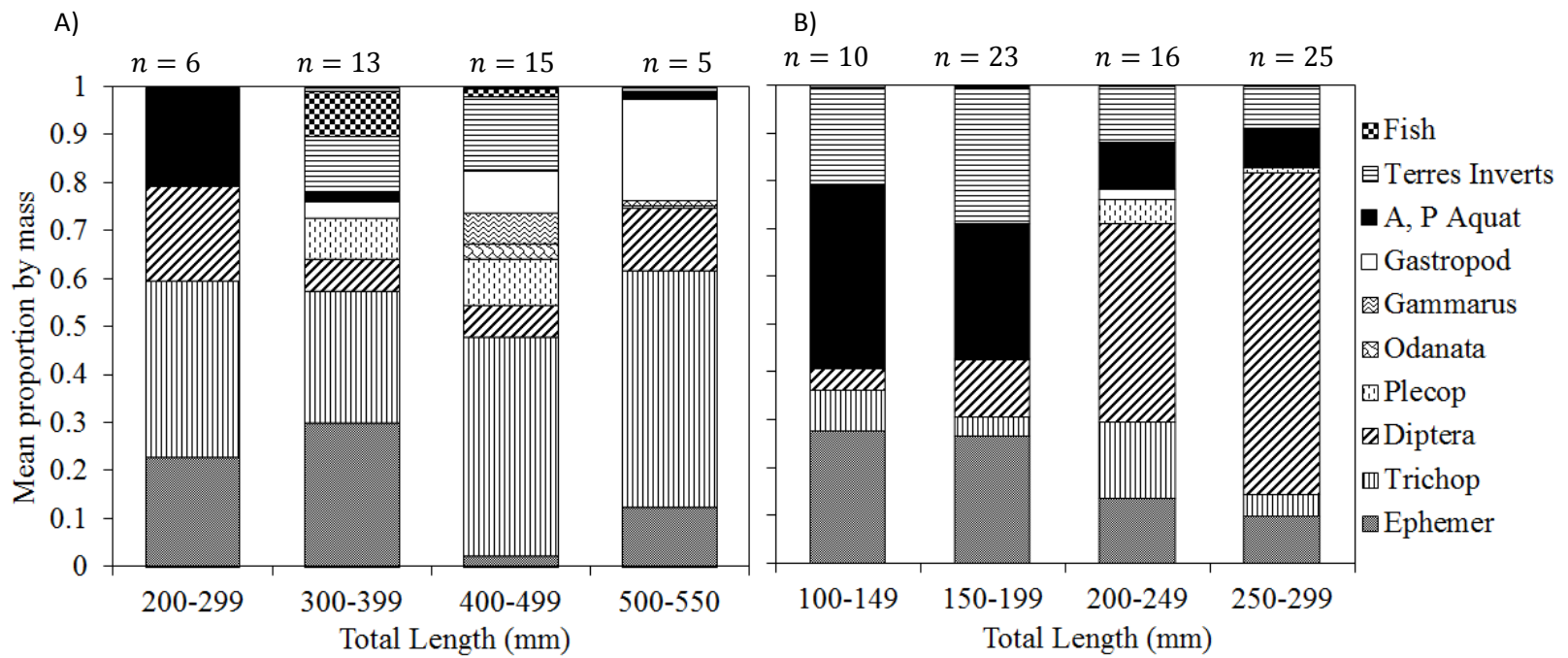
Figure 1.9. Proportional abundance of prey taxa in lenok (A, n = 38) and Baikal grayling (B, n = 68) stomachs from the Eg River. Terres Inverts = terrestrial invertebrates, A, P Aquat = Adult and pupae stages of aquatic invertebrates, Odanata = Odanata nymphs, Gammarus = *Gammarus spp.*, Diptera = Diptera larvae, Tichoptera = Trichoptera larvae, Ephemeroptera = Ephemeroptera nymphs.
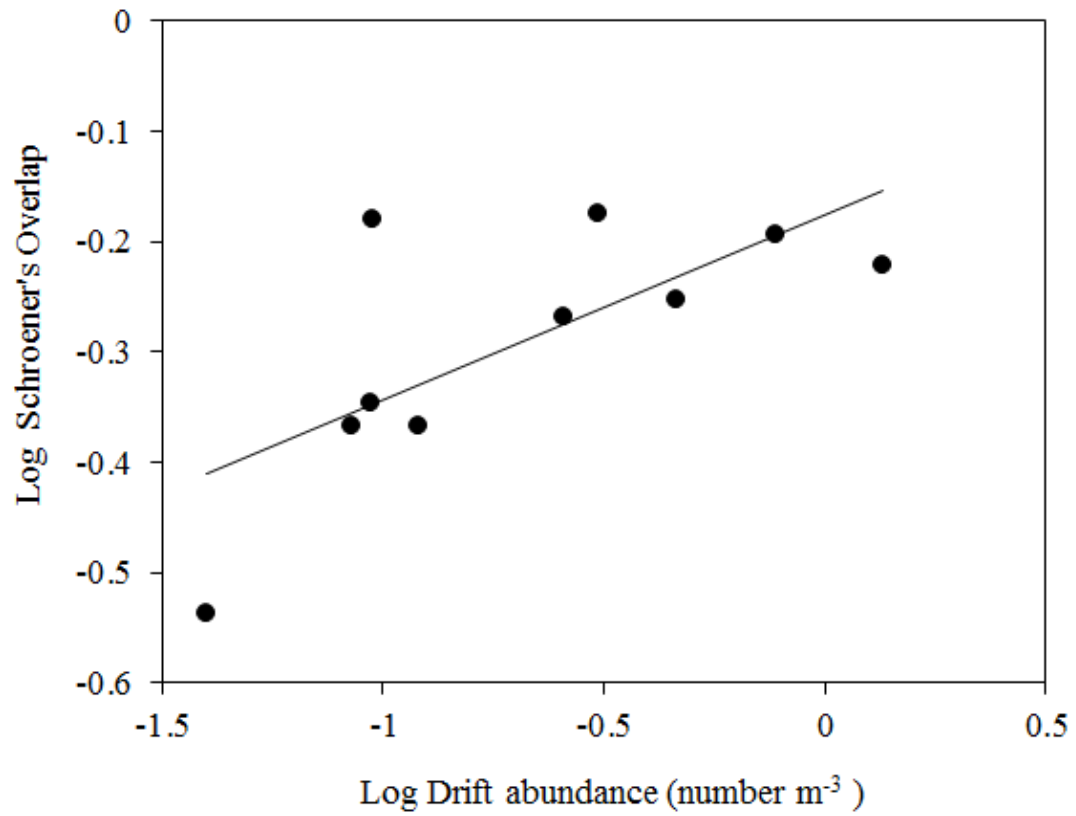
Figure 1.10. Relationship of drift abundance to proportional diet overlap between lenok and Baikal grayling from the Eg and Uur Rivers.
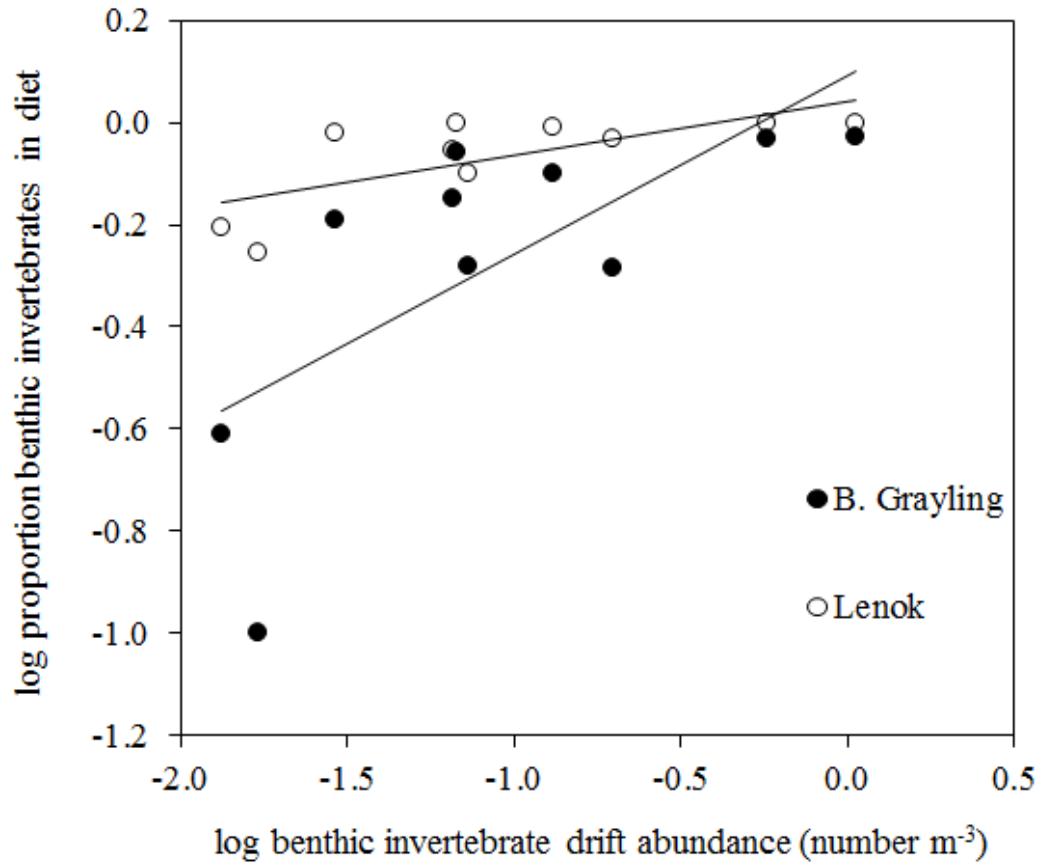
Figure 1.11. Relationship of benthic invertebrate drift abundance to proportion by weight in stomach contents of lenok and Baikal grayling from the Eg and Uur Rivers.

CHAPTER 2: Stable isotopes of carbon and nitrogen reveal sustained resource partitioning between lenok (*Brahcymystax lenok*) and grayling (*Thymallus spp.*) from the Eg-Uur Watershed.

2.1 Introduction:

The Eg-Uur Watershed, located in Northern Mongolia is home to several salmonid species that are currently declining throughout large portions of their range (Ocock et al. 2006, Xu et al. 2009). These include: lenok (*Brachymystax lenok*), Baikal grayling (*Thymallusbaicalensis*) and Hovsgol grayling (*Thymallus nigrescens*). Previously, the limited information available on the feeding ecology of these species indicated that lenok and grayling (*Thymallus spp.*) utilize similar prey resources (Chandra et al. 2005, Sideleva 2006, Ahrenstorff et al. 2011). In contrast, a recent analysis of stomach contents revealed that grayling and lenok exhibit vertical partitioning of invertebrate prey and the degree of partitioning is negatively related to prey availability, suggesting competition is involved (Olson et al. unpublished).

Although previous analyses of diet via stomach contents have provided an important detailed description of prey utilization and resource partitioning by lenok and grayling, stomach contents only reflect prey consumed over a short time frame and are influenced by the digestibility of different prey types (Bowen 1983, Vinson and Budy 2009). Additionally, the diets of lenok and grayling likely fluctuate with seasonal prey availability, similar to feeding patterns of other salmonids (Haugen and Rygg 1996, Amundsen et al. 2010).

Stable isotopes of carbon and nitrogen, in contrast, reflect prey assimilation over a period of months to a year (Hesslein et al. 1992, Church et al. 2009). The ratio of naturally occurring stable isotopes of carbon (^{13}C and ^{12}C) are particularly useful for tracking energy flow in freshwater ecosystems because the relative abundance of ^{13}C (i.e., ^{13}C: ^{12}C) carbon signatures often varies between habitats and undergoes minimal fractionation as it moves from prey to

predator (Hesslein et al. 1992, Finlay 2001). Stable isotopes of nitrogen (^{15}N and ^{14}N) are also commonly used in concert with carbon isotopes as the ratio^{15}N to ^{14}N increases with each trophic level (Hecky and Hesslein 1995, Vander Zanden and Rasmussen 1999, Fry 2006). In addition to basic comparisons of stable isotope signatures between fish, stable isotope mixing models have been developed to estimate the proportional contribution of different prey sources to a consumer's diet, allowing a more direct comparison to studies using stomach contents (Phillips and Gregg 2001, Phillips and Gregg 2003, Moore and Siemens 2008).

In this study, we used stable isotope ratios of carbon and nitrogen to examine the dietary niche and degree of niche partitioning between lenok and grayling from lentic and lotic habitats of the Eg-Uur Watershed. Assuming benthic and surface oriented prey have distinct ratios of carbon or nitrogen, we expect stable isotope ratios and mixing model estimates to be consistent with a recent description of vertical partitioning between lenok and grayling from the Eg-Uur Watershed determined through stomach content analysis (Olson, Chapter 1).

2.2 Methods:

Study Area:

The study was conducted in July of 2011 and 2012 in the Eg-Uur Watershed of Northern Mongolia (Fig. 2.1).The study area (elevation 1500m) is located in the transition of Mongolian steppe and Taiga forest. Sampling took place at three waterbodies located in the in the watershed: the Upper Eg River (Egiin gol, 50°16'58"N, 101° 54'6"E), Uur River (Uur gol, 50°18'35"N, 101°53' 43"E) and Lake Hovsgol (50°58'12" N, 100° 24'0"E). Within our study reach, the Eg River is high gradient with dense willow and larch riparian forest. The reach also receives substantial groundwater inputs through several spring fed side channels. In contrast, the Uur River is low gradient with riparian zones composed of willow, larch and actively grazed steppe pasture with no obvious groundwater inflows. Lake Hovsgol is a large ultra-oligotrophic lake

located at the headwaters of the Eg River. It is a deep rift lake (maximum depth = 262 m, mean depth = 138 m), with a total volume comparable to that of Lake Erie (volume = 480 km^3). The fish community of the Eg-Uur Watershed is dominated by Lenok *Brachymystax lenok* and grayling *Thymallus spp.*. Burbot *Lota lota*, Taimen *Hucho taimen* (Eg and Uur Rivers only), stone loach *Barbatuli toni*, roach *Rutilus rutilus* (Lake Hovsgol only), phoxinus minnow *Phoxinus phoxinus* and Eurasian Perch *Perca fluviatilis* are also present.

Fish and Invertebrate Collection

Fish and invertebrate samples were collected at 15 sampling locations in the Eg-Uur Watershed during the summer of 2012. Six sites were selected on the Uur River, three on the Eg River and six on Lake Hovsgol (Fig. 2.1). At river sites, study reaches were restricted to riffle and run habitats between 0.1 - 0.5km in length and selected to optimize spatial coverage based on time and travel constraints. Sites on Lake Hovsgol were distributed around the lake, following long term sampling locations (Ahrenstorff et al. 2011). A total of 43 lenok and 50 Baikal grayling were captured from the Eg and Uur Rivers via angling gear. In Lake Hovsgol, a total of 20 lenok, three Baikal grayling and 43 Hovsgol grayling were captured using horizontal and vertical gillnets (Table 2.1). Following capture, total length, fork length and weight were measured on each fish.

Invertebrate prey were collected at sampling sites using a Surber-sampler (0.1 m^2, 500μm mesh). Riparian invertebrates were collected in terrestrial vegetation by hand or sweeping vegetation with a 500 μm mesh D-net (Table 2.2).

Stable Isotopes

1-5 g (wet weight) white muscle samples were removed from each fish near the base of the dorsal fin. Samples were taken from a total of 63 Lenok, 52 Baikal grayling and 43 Hovsgol grayling (Table 2.1). Invertebrates were analyzed whole, excluding calcified shells. In some

cases, several individuals from the same taxon were pooled in order to achieve large enough sample weight. All samples were dried at 60°C in convection oven and homogenized. Samples were analyzed for stable isotopes of ^{13}C:^{12}C and ^{15}N:^{14}N 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}C:^{12}C and ^{15}N:^{14}N are reported in delta notation (δ), which is defined by the equation:

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

Where R_{sample} is the ratio of $^{13}C/^{12}C$ or $^{14}N/^{15}N$ in the sample and $R_{standard}$ is the ratio of $^{13}C/^{12}C$ or $^{14}N/^{15}N$ of the standard. Vienna PeeDee Belemnite and atmospheric N_2 are 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 generalized correction for fish tissue published in Hoffman and Sutton (2010):

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

Where $\delta^{13}C_{protein}$ is the corrected δ^{13}C value, $\delta^{13}C_{bulk}$ is the uncorrected δ^{13}C value and $C:N_{bulk}$ is the molar C:N ratio of the sample.

Age Analysis

Saggital otoliths were randomly collected from 18 Hovsgol grayling. Cross sections of otoliths were prepared and examined under a compound microscope (50x) and annuli were counted by a single, experienced otolith reader. After a period of at least two weeks, otoliths were validated by the same reader.

Stable Isotope Mixing Model

Isosource and three-source mixing models were applied to isotope data to estimate the proportional contribution of prey to the diets of each fish species. When feasible, a three source mixing model was applied to our data and prey contributions were estimated for individual fish. When prey types exceeded the number of isotopic tracers +1, Isosource was used to estimate the probability distribution of proportional prey contributions to each group of fish. Isosource calculated all feasible solutions in 1% increments within a tolerance of 0.1‰. Consumers were adjusted for trophic fractionation of $\delta^{13}C$ and $\delta^{15}N$ prior to application of the Isosource and three-source mixing models (Phillips and Gregg 2001, Phillips and Gregg 2003). Trophic fractionation values for $\delta^{13}C$ and $\delta^{15}N$ typically range from 0-1.3‰ and 2.3-3.4‰, respectively (Vander Zanden and Rasmussen 2001, McCutchan et al. 2003). A mean $\delta^{15}N$ fractionation (± 1Standard Deviation) value of 2.9 ± 0.47‰ was used based on model fit. Mean fractionation of $\delta^{13}C$ value was assumed to be between 0.4‰ for all fish.

Data analysis

Prior to analysis, Hovsgol grayling were separated into two categories (A and B) because the species exhibited a bi-modal distribution by $\delta^{13}C$ values and were not distinguishable by size or age (Fig. 2.2). Differences in isotope or diet composition estimated through three source isotope mixing models were compared between species using one-way ANOVA. When comparisons were made between more than two groups, Tukey's HSD was used subsequent to ANOVA. The relationship of $\delta^{13}C$ or $\delta^{15}N$ values to total length was examined using simple linear regression. A significance level of $\alpha = 0.05$ was used for all comparisons.

2.3 Results:

Lake Hovsgol:

Overall, Baikal grayling had the most enriched ^{13}C value of the four groups of fish, while Hovsgol grayling group B (HGB) had the most depleted (Baikal Grayling = -20.25 ± 0.47‰,

HGB = -24.83 ± 0.17‰; Tukey's HSD, p<0.05; Fig. 2.4). Hovsgol grayling group A (HGA) and lenok exhibited similar $\delta^{13}C$ values, intermediate to Baikal grayling and HGB (lenok = -21.59 ± 0.18‰, HGA = -21.80± 0.18‰; Tukey's HSD, p<0.05). The $\delta^{13}C$ value of lenok, Baikal Grayling and HGA were similar to littoral prey types, while the $\delta^{13}C$ value of HGB was intermediate to littoral and pelagic prey types. Lenok were significantly enriched in ^{15}N relative to both groups of Hovsgol grayling but similar to Baikal grayling, indicating their higher trophic position (lenok: $\delta^{15}N$ = 7.20 ± 0.11‰, HGB: $\delta^{15}N$ = 6.22 ± 0.11‰, HGA: $\delta^{15}N$ = 6.51 ± 0.10‰, B. Grayling: $\delta^{15}N$ = 7.02 ± 0.28‰; Tukey's HSD). Lenok total length was positively correlated with $\delta^{15}N$ values, while no relationships were observed in HGA or HGB (r^2=0.42, p=0.002).

Isosource mixing model results indicated that benthic invertebrates were an important component of lenok, HGA and HGB, composing at least 39% of each groups diet (Fig. 2.5). Lenok and HGB were most reliant on benthic prey, though gastropods appeared to be more important in the diets of lenok, composing at least 40% of their diet. HGB was the only group that utilized zooplankton, which contributed at least 25% to their diets. Isotopic signatures of Baikal grayling fell outside the mean isotopic values of prey, precluding an estimate of prey contributions to their diet.

Eg and Uur Rivers:

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. 2.6, 2.7) but there was no difference in $\delta^{13}C$ 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 $\delta^{15}N$ and $\delta^{13}C$ values were not significantly correlated with total length, indicating similar prey utilization across sizes.

Three-source mixing model results from the Uur River identified fish and aquatic invertebrates as the primary component of lenok diets (Fig. 2.8). The proportion of fish in lenok diets was positively correlated to size (Fig. 2.10, r^2=0.37, p=0.002). In contrast, Baikal grayling consumed 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 the Eg River were not bound by the prey sources we sampled, specifically δ^{13}C signatures of grayling and lenok were highly variable and often fell outside the mean isotopic values of prey included in the analysis (Fig. 2.9). This precluded the use of a mixing model on Eg River fish.

2.4 Discussion:

Overview

Diet composition inferred through stable isotope analysis revealed that aquatic and terrestrial invertebrates were the primary prey source of Baikal grayling, Hovsgol grayling and lenok in the Eg-Uur watershed. Diets inferred from stable isotopes were generally consistent with Olson's (Chapter 1) description of diets and resource partitioning via stomach content analysis, indicating a greater reliance of lenok on benthic prey than grayling in both lentic and lotic habitats. However, stable isotopes of carbon and nitrogen also revealed: diet specialization within Hovsgol grayling, importance of piscivory in large lenok and contribution of prey from side channel habitats to diets of lenok and grayling in Eg River.

Lake Hovsgol

Consistent with Olson's (Chapter 1) assessment of lenok diets through stomach contents, δ^{13}C values of lenok indicated reliance upon littoral prey sources. This result was supported by estimates of diet contribution from Isosource mixing models, which indicated that benthic gastropods composed at least 40% of the lenok diets. Reliance on benthic prey is in agreement

with the limited information available in the literature describing lenok diets (Shved'ko et al. 1997, Nakano 1999, Chandra et al. 2005, Sideleva 2006). $\delta^{15}N$ values were positively related to size in lenok, indicating that piscivory was more common in larger fish. Although this trend was not observed in Olson et al.'s (unpublished) recent stomach content analysis, it is consistent with ontogenetic diet shifts described in many other lake-dwelling salmonid species (Mittlebach and Persson 1997, Keely and Grant 2001).

Stable isotopes revealed a bi-modal distribution of individual Hovsgol grayling by $\delta^{13}C$ values, possibly indicating the presence of two specialist feeding groups with differential reliance upon pelagic prey sources (e.g. zooplankton). Hovsgol grayling group A (HGA) was the only fish category utilizing zooplankton, which composed between 25-41% of their diets. In contrast, Hovsgol grayling group B (HGB) exhibited $\delta^{13}C$ values in line with littoral prey use and mixing model results indicated that zooplankton contributed little to their diets (range = 0-9%). Differential use of zooplankton between small and large size classes of Hovsgol grayling have been previously described by Ahrenstorff et al. (2011), and attributed to an ontogenetic diet shift from zooplankton to larger benthic prey with size. In contrast, our analysis suggests the presence of littoral and pelagic specialists within the Hovsgol grayling population as there was no difference in age and large size overlap between feeding groups.

Baikal grayling were rare in Lake Hovsgol (n=3) and only captured near shore in horizontal gillnets. Baikal grayling were more enriched in ^{13}C than both lenok and Hovsgol grayling. The mean $\delta^{13}C$ value of Baikal grayling was too high to fit within our prey polygon. However, their signature falls within the range of benthic gastropod $\delta^{13}C$ values, possibly indicating reliance on benthic littoral prey.

Stable isotope evidence from Lake Hovsgol indicates that lenok and grayling exhibit sustained partitioning of prey resources. Lenok were enriched in ^{15}N relative to both groups of

Hovsgol grayling. Additionally, mixing model outputs indicate that lenok are more reliant upon benthic gastropods or other obligate algal scrappers (which would be expected to exhibit similar stable isotope ratios to gastropods) and are possibly more piscivorous than Hovsgol grayling. Similar to a recent analysis of diets through stomach contents, the overall diet niche of Hovsgol grayling is wider than that of lenok. However, the overall niche width of grayling has a high between-phenotype component (sensu Amundsen et al. 1996) as individual grayling appear to be pelagic or littoral invertebrate specialists. Of the two specialist foraging groups of Hovsgol grayling, HGA was the most ^{13}C depleted and only group of fish utilizing pelagic prey and habitat. Similar to lenok, HGB utilized littoral prey resources, but were less reliant upon fish and gastropods, indicating that littoral prey was partitioned between HGB and lenok. Greater use of gastropods or other algal scrapers (e.g. Heptageniidae mayflies) by lenok may be attributed to its sub-terminal mouth, suited for foraging on prey items attached to substrate (Keast and Webb 1966, Malmquist 1992).

Uur and Eg Rivers

Within the Eg and Uur Rivers, lenok δ^{13}C and δ^{15}N values indicated a reliance on benthic invertebrates and fish. Additionally, our three-source mixing model identified aquatic invertebrates (50%) and fish (30%) as the primary components of lenok diets. This was inconsistent with Olson's (Chapter 1) recent stomach content analysis, in which fish composed <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 δ^{15}N value of lenok muscle tissue indicated that fish were more common in their diets than was determined via stomach content analysis. Because stable isotope ratios reflect prey assimilation over a period of months to years (Hesslein et al. 1993, Church et al. 2009), this may indicate that piscivory is more common during the winter, spring and early summer.

Baikal grayling from the Eg and Uur Rivers were depleted in ^{15}N relative to lenok, suggesting a lower degree of piscivory or increased predation on terrestrial invertebrates. Mixing model results from the Uur River identified aquatic (46%) and terrestrial invertebrates (34%) as the primary prey of Baikal grayling. These results were consistent with a recent analysis of Baikal grayling diets determined through stomach contents (Olson, Chapter 1), but indicate a much lower contribution of aquatic invertebrates and higher contribution of terrestrial invertebrates than was described in Baikal grayling diets from an adjacent watershed (Chandra et al. 2005). Grayling commonly exhibit highly variable diets influenced by prey availability (Northcote 1995). Therefore, it is most likely that the incongruity between our analysis and Chandra et al.'s (2005) is due to differences in prey availability between sampling periods and locations.

Mixing models were not applied to stable isotope data from the Eg River because both lenok and Baikal grayling δ^{13}C and δ^{15}N values were often far outside of the prey mixing polygon. Overall, variability in δ^{13}C was greater in both lenok and grayling in the Eg River. A possible explanation for this is the presence of large spring side channels within our sampling reach that were not included in our prey sampling protocol. Substantial groundwater inputs influence δ^{13}C values (Rounick and James 1983). Groundwater is typically supersaturated in respiratory CO_2 which is highly depleted in ^{13}C (Rounick and James 1983). As a result, benthic algae growing in areas of substantial groundwater inflows typically exhibit low δ^{13}C values (Finlay 2001). The potential influence of groundwater-fed side channels on δ^{13}C values of benthic algae and its herbivores may be responsible for the wider variation of δ^{13}C values observed in lenok and grayling from the Eg River and lack of model fit.

Within the Eg and Uur Rivers lenok exhibited were enriched in ^{15}N indicating a greater reliance on fish prey or benthic invertebrates than Baikal grayling. Similarly, our mixing model from the Uur River indicated that Baikal grayling utilized terrestrial invertebrates to a greater

degree (34%) than did lenok (20%). This supports Olson's (Chapter 1) assessment of vertical prey partitioning as terrestrial invertebrates are most frequently found in the drift or near the surface of the water column. Though application of a stable isotope mixing model was not feasible in the Eg River, similar patterns in ^{15}N between lenok and grayling in the Eg and Uur Rivers suggest that diet differences are similar.

Conclusion

Through our analysis of carbon and nitrogen stable isotopes, we identified the feeding niche of Baikal grayling, Hovsgol grayling and lenok. Similar to Olson's (Chapter 1) description of lenok and grayling diets, we determined that lenok were primarily benthivorous, while grayling diets were more diverse, including prey taxa commonly associated with feeding in the water column. However, our analysis also revealed that the diet niche width of Hovsgol grayling is attributed to the presence of a pelagic and littoral specialist, and not a generalist foraging strategy among all fish. Our analysis also indicated that prey associated with spring side channels in the Eg River may be important component of lenok and grayling diets and that lenok may be more piscivorous than previous stomach content analyses suggest.

Future studies of Hovsgol grayling should examine the morphological and genetic differences between Hovsgol grayling feeding groups described here as we might expect differences in phenotype due to the different selective pressures of pelagic and littoral habitats (Robinson and Wilson 1994). In addition, future isotope work in the Eg River should take into account the influence of spring side channels and specifically collect prey within these habitats to estimate their importance as invertebrate and fish habitat.

Table 2.1. Total number of fish captured in horizontal and vertical gillnets (number captured in vertical gillnets signified with an asterisk) and mean total length of fish sampled for stable isotopes from the Eg-Uur Watershed.

	N				TL (±1 S.D.)			
	Lenok	B. grayling	H. grayling (A)	H. grayling (B)	Lenok	B. grayling	H. grayling (A)	H. grayling (B)
Lake Hovsgol	20	2	4, 16*	20, 3*	394 (±95)	311 (±63)	234 (±22)	288 (±41)
Uur River	29	24	0	0	306 (±113)	187 (±55)	-	-
Eg River	14	26	0	0	403 (±84)	195 (±38)	-	-
Total	**63**	**52**	**20**	**23**				

Table 2.2. Total number of invertebrates and primary producer samples collected for anlysis of carbon and nitrogen stable isotopes.

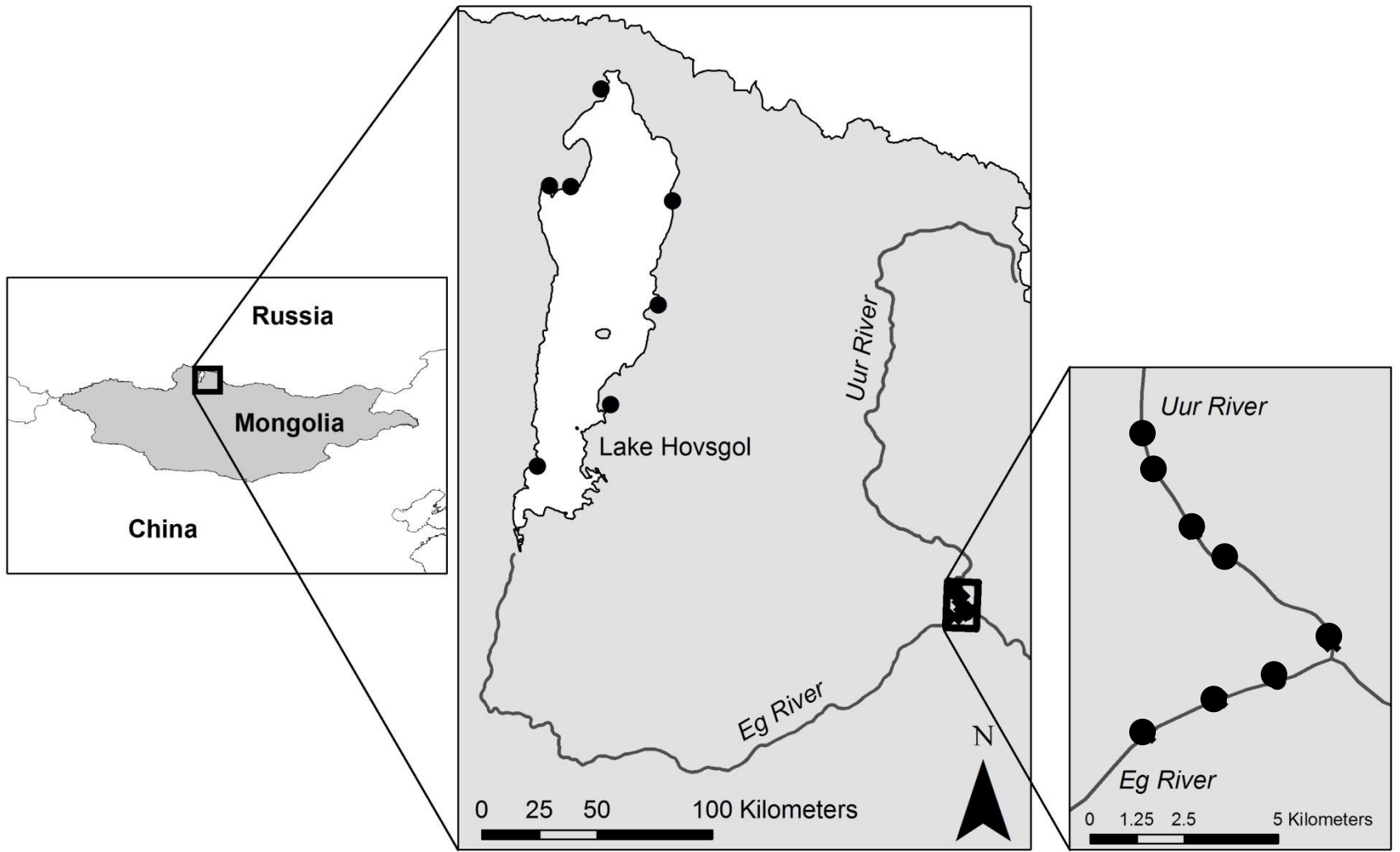| Taxa	Waterbody		
	Hovsgol	Eg	Uur
Terres Inverts	3	6	5
Gastropods	4	0	0
Gammarus	3	0	0
Coleoptera	3	0	0
Zooplankton	4	0	0
Trichoptera	1	3	5
Plecoptera	2	1	1
Diptera	3	3	3
Ephemeroptera	0	5	12
Periphyton	3	0	0
Macrophytes	2	0	0

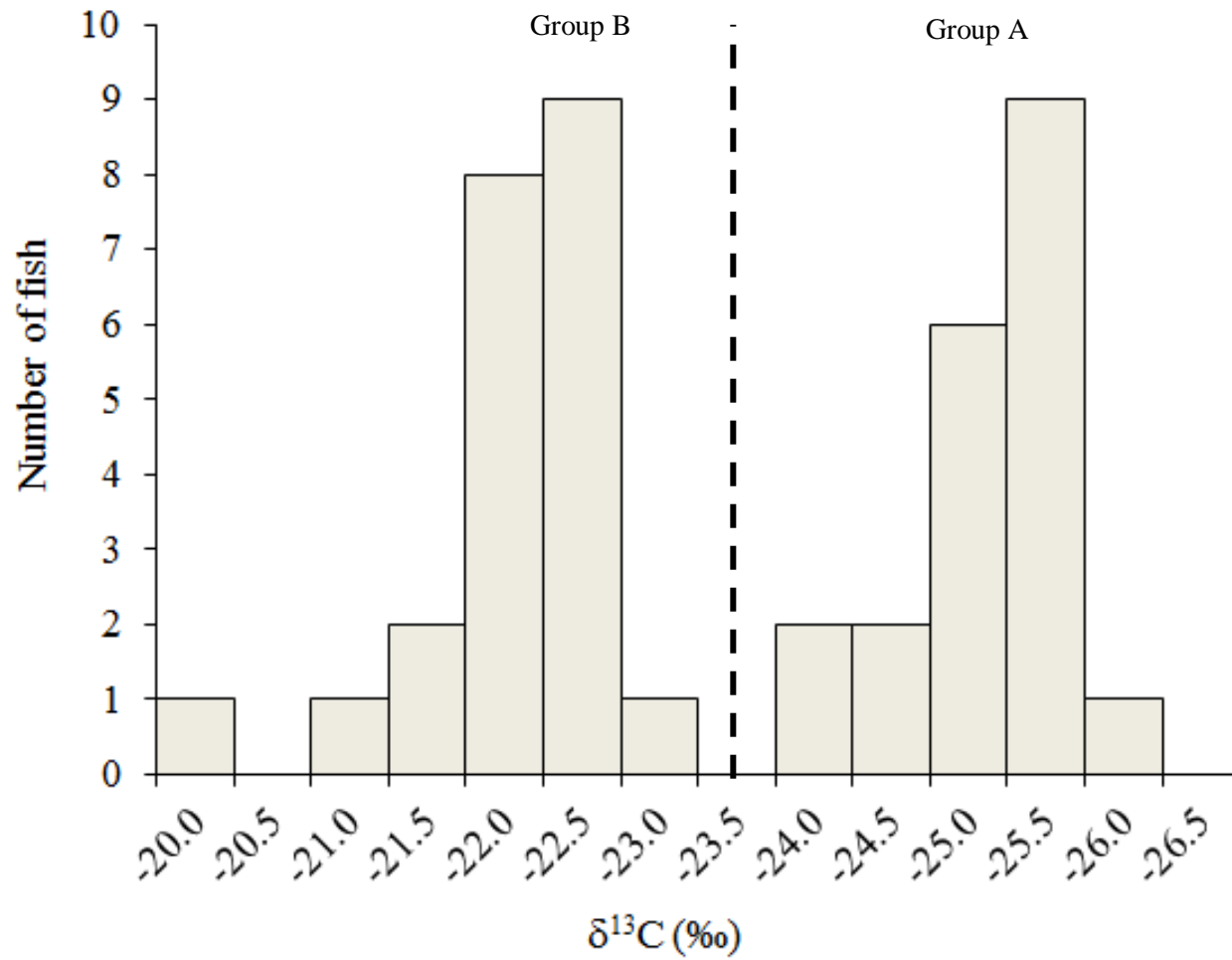**Figure 2.1.** Location of the Eg-Uur Watershed and sampling sites on Lake Hovsgol, Eg and Uur Rivers.

Figure 2.2. Histogram of δ ^{13}C values from 43 Hovsgol grayling captured in horizontal and vertical gillnets in the summer of 2012.
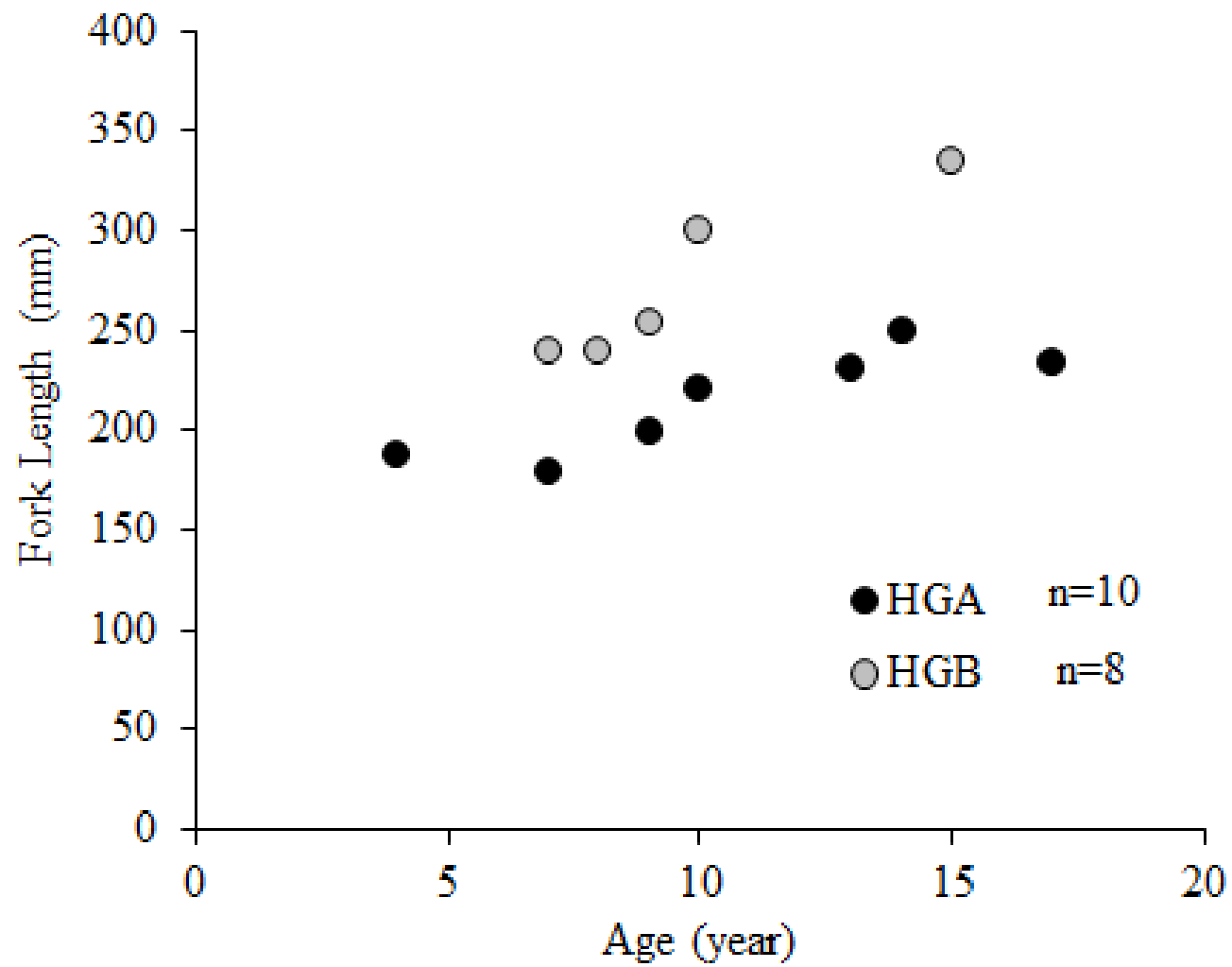
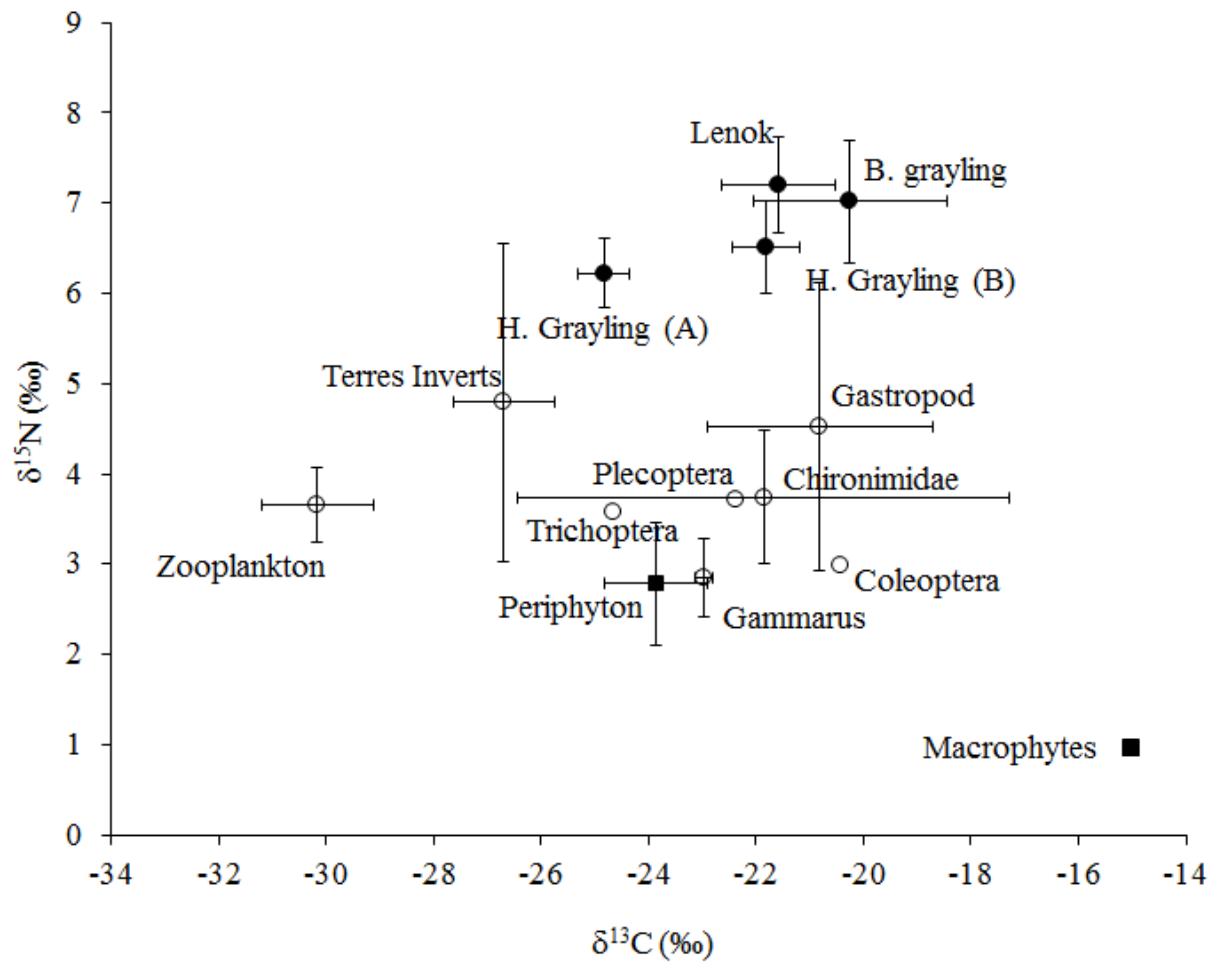**Figure 2.3.** Mean fork length (mm) at age for Hovsgol grayling group A (HGA) and Hovsgol grayling group B (HGB).

Figure 2.4. Mean $\delta^{13}C$ and $\delta^{15}N$ values of fish (closed circles), prey taxa (open circles) and others (closed squares) from Lake Hovsgol. B.Grayling = Baikal grayling, Terres Inverts = terrestrial invertebrates, H.Gralyling (A) = Hovsgol grayling group A, H. Grayling (B) = Hovsgol grayling group B.

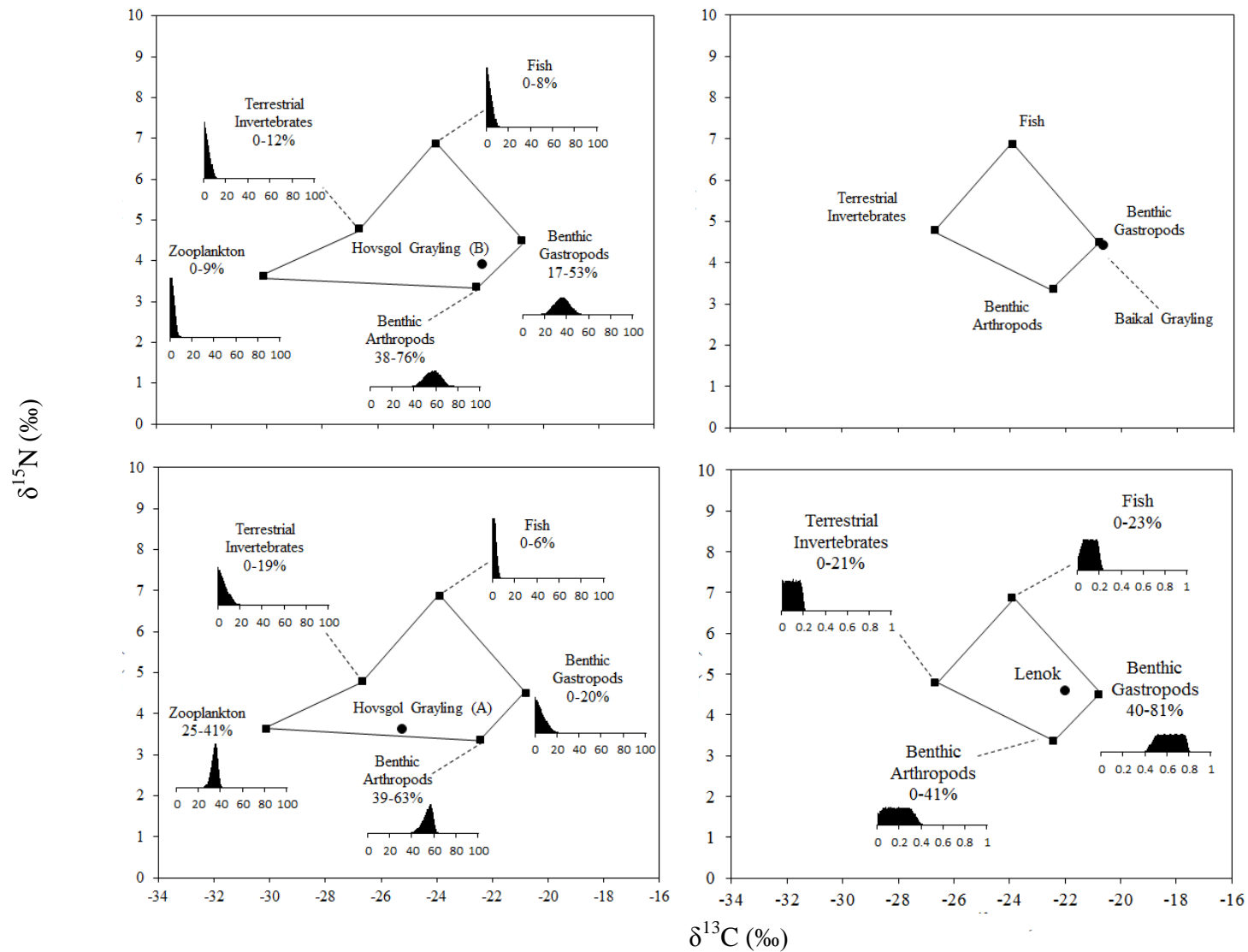**Figure 2.5.** Mixing polygon for $\delta^{13}C$ and $\delta^{15}N$ values of common prey taxa. Histograms display the range of possible contributions to the fish's diet estimated from the isosource mixing model.
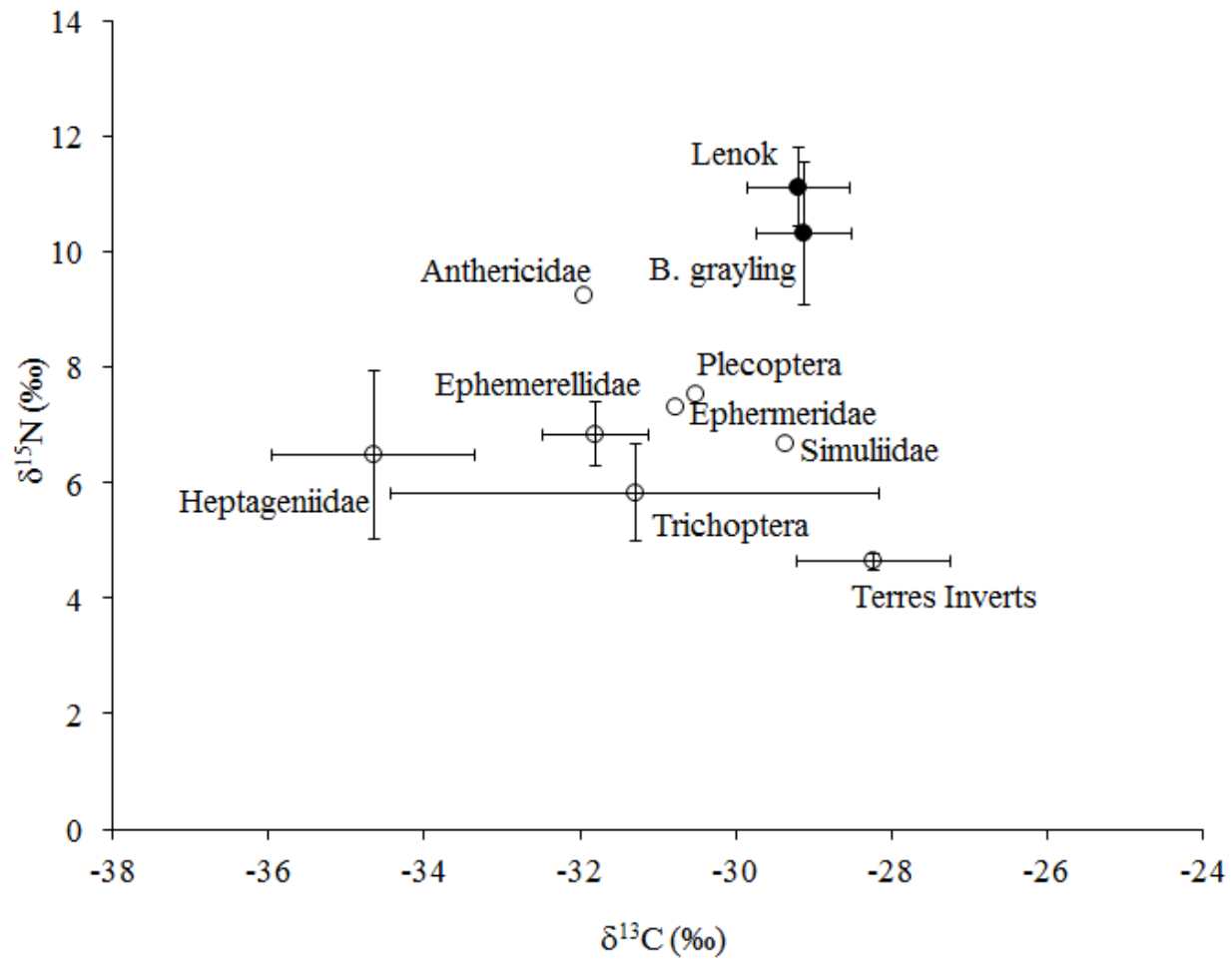
Figure 2.6. Mean $\delta^{13}C$ and $\delta^{15}N$ values of fish (closed circles) and prey taxa (open circles) from the Uur River. B. Grayling = Baikal grayling, Terres Inverts = terrestrial inverts.
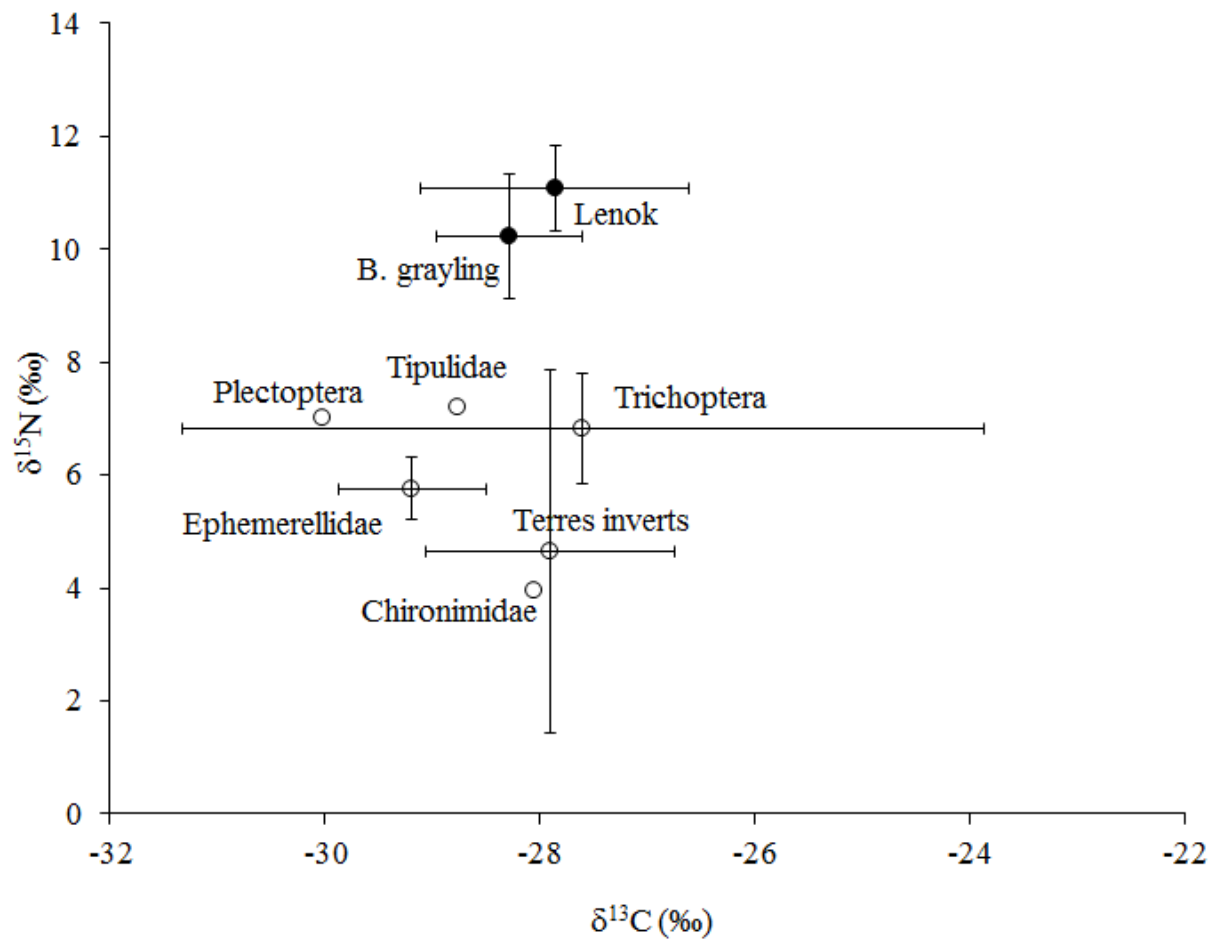
Figure 2.7. Mean $\delta^{13}C$ and $\delta^{15}N$ values of fish (closed circles) and prey taxa (open circles) from the Eg River. B. Grayling = Baikal grayling, Terres Inverts = terrestrial inverts.
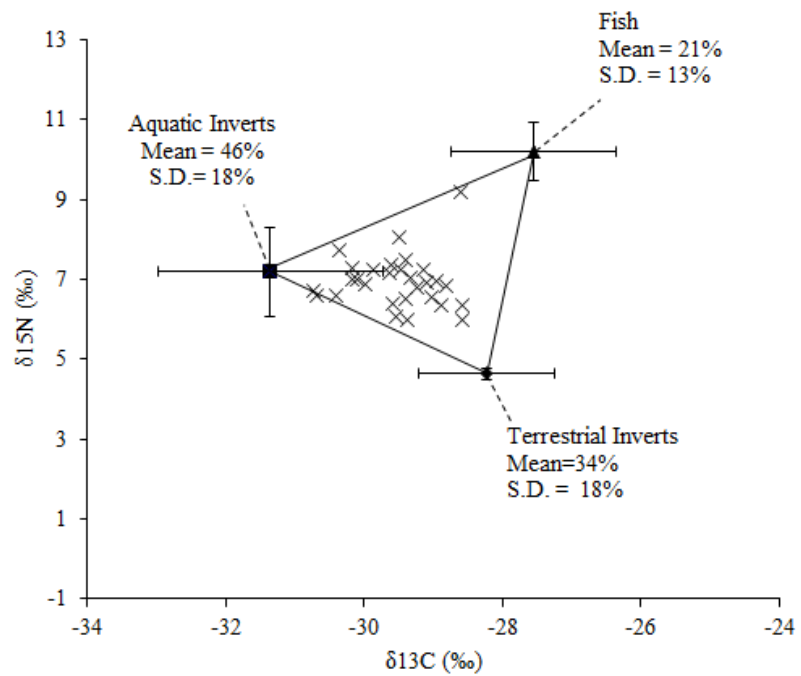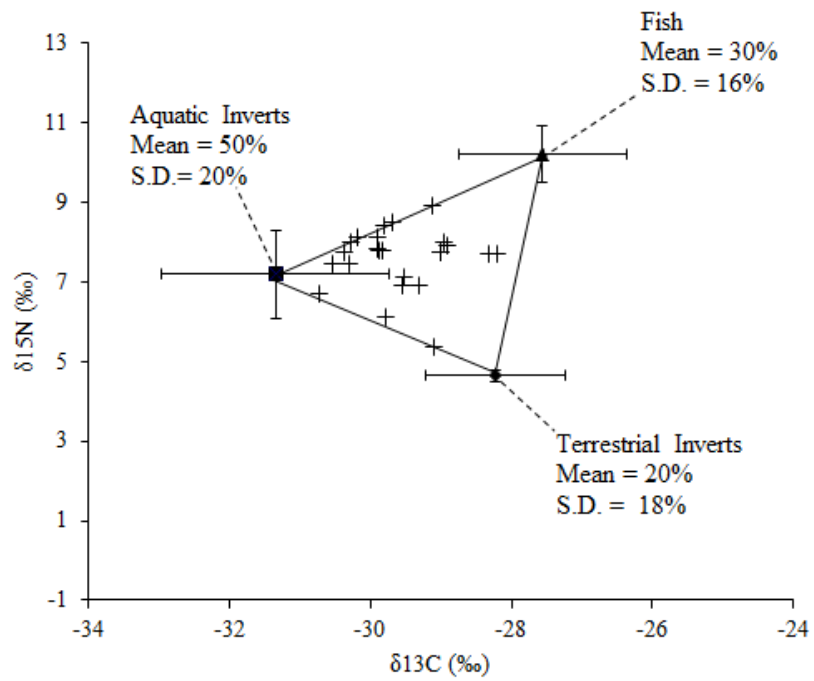
Figure 2.8. Mixing polygon for $\delta^{13}C$ and $\delta^{15}N$ values of three common prey taxa and their contribution to lenok (top) and Baikal grayling (bottom) diets from the Uur River. Inverts = invertebrates.

Figure 2.9. Mixing polygon for δ^{13}C and δ^{15}N values of three common prey taxa, lenok (top) and Baikal grayling (bottom) from the Eg River. Inverts = invertebrates.
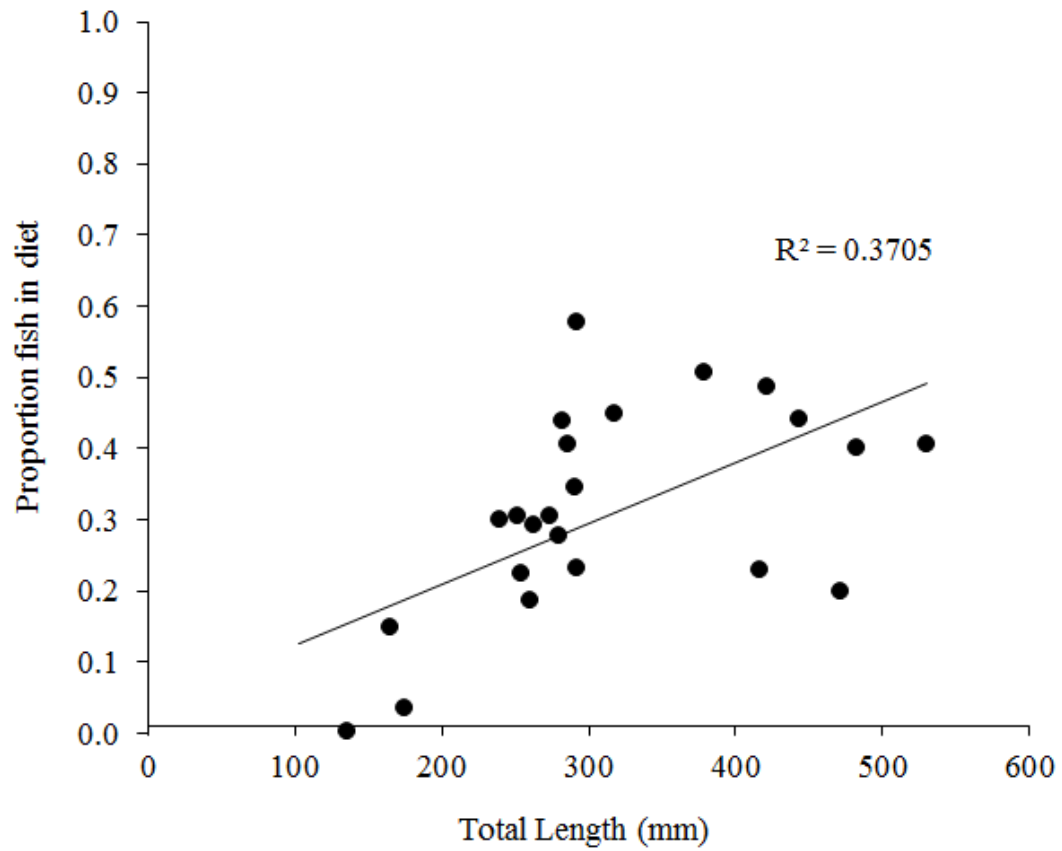
Figure 2.10. Relationship of lenok length to contribution of fish prey to the diet based on results from three-source mixing model, Uur River.

LITERATURE CITED

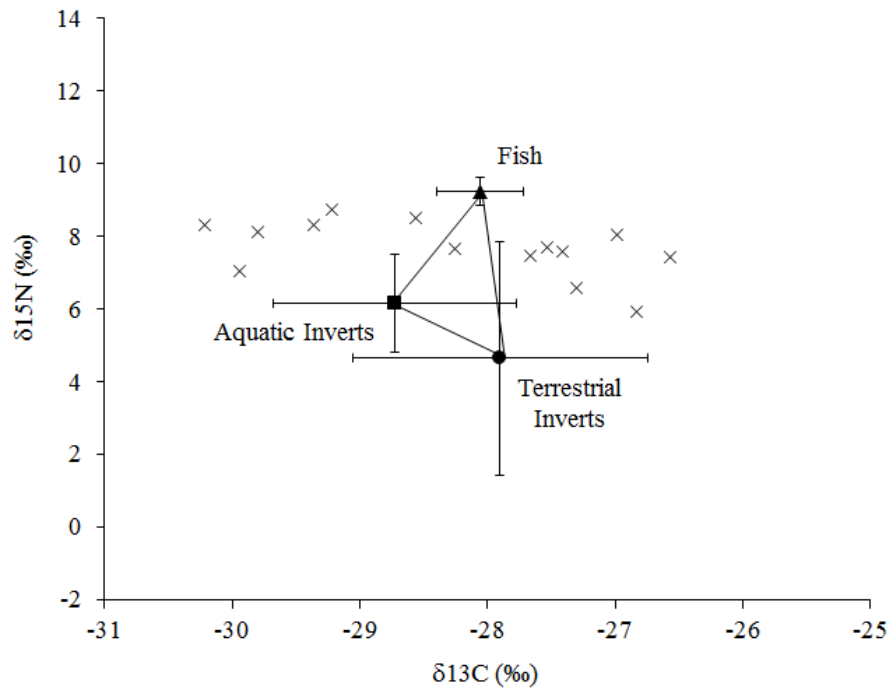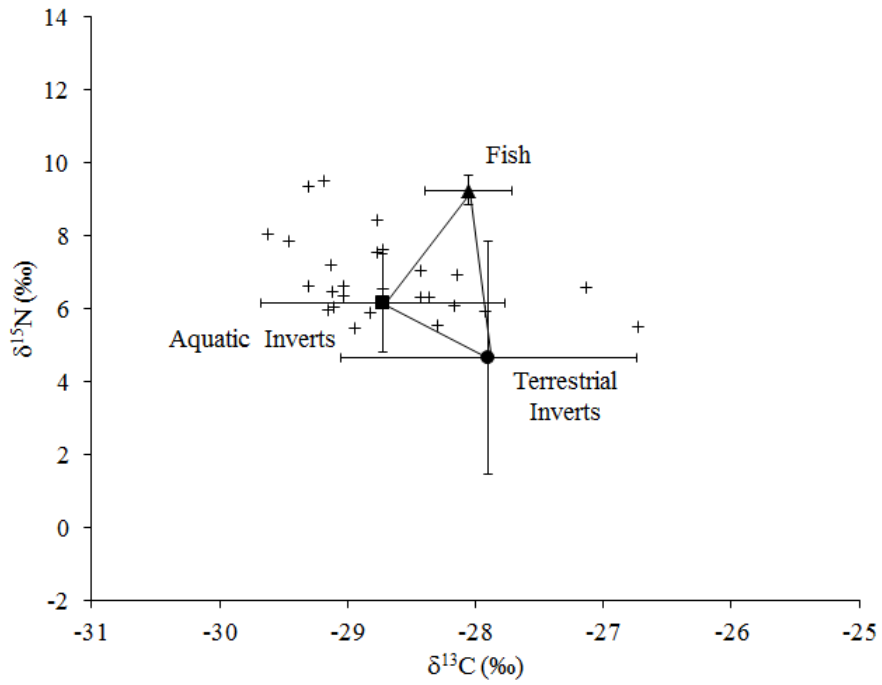Amundsen, P. A., H. M. Gabler, and F. J. Staldvik. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology.* 48:607-614.

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