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Pelagic–littoral resource polymorphism in Hovsgol grayling *Thymallus nigrescens* from Lake Hovsgol, Mongolia

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Abstract

Resource polymorphism is a widespread phenomenon in post-glacial fishes where multiple morphotypes of a species occur sympatrically and exhibit distinct resource use. Availability of open niches and high levels of within and among species competition are thought to drive differences in morphology and may provide insights into early stages of speciation. Hovsgol grayling (*Thymallus nigrescens*) are endemic to Lake Hovsgol, a lake colonised by fish following the Pleistocene, and are threatened with habitat loss due to climate change and illegal harvest. Previous analysis of Hovsgol grayling diet inferred through C and N stable isotopes suggested the presence of littoral and pelagic foraging groups. We hypothesised that morphology of the two foraging groups would reflect predictions of functional morphology, indicating the presence of resource polymorphism. To test this hypothesis, we evaluated evidence from C and N stable isotopes, stomach contents, fish ages, capture location and morphology. Two foraging groups of Hovsgol grayling were identified through stomach content and C and N stable isotope analysis. Individuals with greater zooplankton consumption were more frequently captured in the pelagic zone, exhibited higher gill raker counts, larger orbit (eye) sizes, longer paired fins, narrower head width, larger maxilla and smaller size at age than the group with greater reliance on benthic invertebrate prey. These differences were generally consistent with those described in other fish species exhibiting littoral–pelagic resource polymorphism. Our study provides the first example of littoral–pelagic resource polymorphism in the salmonid subfamily Thymallinae and highlights the potential influence of competition on fish evolution.

KEYWORDS
fisheries conservation, functional morphology, Lake Hovsgol, resource polymorphism

1 | INTRODUCTION

Resource polymorphism, where multiple morphotypes (morphs) of a species occur sympatrically and occupy distinct ecological niches, has been described across a diverse array of freshwater fish species (Robinson & Wilson, 1996; Schluter & McPhail, 1993; Snorrason et al., 1994). This phenomenon is particularly widespread in freshwater fish species that have colonised freshwater lakes since the end of the Pleistocene (e.g., salmonids) and may lead to sympatric speciation in some cases, though considerable debate still surrounds the concept (Chavarie et al., 2017; Jonsson & Jonsson, 2001; Schluter, 2001; Ward, Webster, & Hart, 2006; Wimberger, 1994). Morphs within a population exhibit distinct phenotypes and life history attributes, allowing more efficient use of a specific habitat and

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reducing intraspecific competition (Skúlason & Smith, 1995). The degree to which differences are heritable is highly variable (Adams & Huntingford, 2004; Goetz et al., 2010; Sandlund et al., 1992), possibly reflecting a continuum of species divergence (Rundle & Schluter, 2004; Smith & Skúlason, 1996; Snorrason & Skúlason, 2004).

The occurrence of pelagic and littoral morphs is the most prevalent type of resource polymorphism described in post-glacial lake fish populations (Klemetsen, 2010; Robinson & Wilson, 1994; Schluter & Mcphail, 1992). Pelagic morphs often exhibit higher gill raker number and length, larger eyes, streamlined body shape and a more terminal mouth position when compared to littoral morphs (Bernatchez, Chouinard, & Lu, 1999; Jonsson & Jonsson, 2001; Parsons & Robinson, 2007; Rundle & Schluter, 2004) and these differences allow for more efficient zooplankton consumption (Malmquist, 1992; Roesch, Lundsgaard-Hansen, Vonlanthen, Taverna, & Seehausen, 2013; Schluter, 1993). Pelagic–littoral morph pairs have arisen among distantly related species (i.e., convergence; Robinson & Wilson, 1994) and among populations within a species (i.e., parallelism; Taylor & McPahil, 1999, Bernatchez et al., 1999, Østbye et al., 2006). These findings indicate consistent differences between morphs are likely the result of distinct selective pressures in littoral and pelagic lake habitats (Robinson & Wilson, 1994). In addition, a recent analysis identified that natural selection plays a significant role in the divergence of traits typically associated with pelagic–littoral morph pairs (i.e., body size and gill raker number; Häkli, Østbye, Kahilainen, & Amundsen, 2017).

Hovsgol grayling is considered by many to be the only endemic fish species in Lake Hovsgol (Ocock et al., 2006), though whether Hovsgol grayling represent a distinct species or subspecies of *Thymallus arcticus* is under debate (Knizhin, Weiss, & Susnik, 2006). Lake Hovsgol is a large, oligotrophic and ancient (c.a. 2–5 mya.) lake located in the Baikal rift zone (Goulden, Tumurtogoo, Karabanov, & Mongontsetseg, 2006). Lake Hovsgol's ecosystem likely collapsed during the Last Glacial Maximum and the current fish community is hypothesised to have colonised the lake sometime in the last ~13,000 years (Karabanov et al., 2004; Roman et al., 2018). Within Lake Hovsgol, Hovsgol grayling is the only species which is currently found in both the littoral and pelagic zone (Ahrenstorff, Jensen, Weidel, Mendsaikhan, & Hrabik, 2012) and a recent analysis of diet inferred from stable isotopes, suggested the presence of littoral and pelagic foraging groups (Olson, 2014).

Hovsgol grayling are listed as endangered in Mongolia due to excessive illegal harvest and drying of spawning tributaries due to climate change (Ocock et al., 2006). Illegal gill netting on Lake Hovsgol has increased in recent years and, likely the result of excessive harvest, average body size of Hovsgol grayling has declined (Free, Jensen, & Mendsaikhan, 2015). Illegal fishing on Lake Hovsgol is currently limited to near shore areas (Free et al., 2015), making littoral fish more vulnerable to harvest. Given this, determining whether pelagic and littoral morphs are present in the Hovsgol grayling population and whether they represent distinct populations is critical for understanding the impacts of increased illegal harvest and guiding future conservation efforts.

Here, we evaluate the hypothesis that morphology of the pelagic and littoral foraging groups of Hovsgol grayling reflects predictions of functional morphology and parallel those described in other pelagic–littoral morph pairs occupying post-glacial lakes (Robinson & Wilson, 1994; Smith & Skúlason, 1996). Specifically, we predicted that the pelagic foraging group would have higher gill raker counts, more fusiform body shape and larger eyes than the littoral group, reflecting the consistent divergent selective pressures of pelagic and littoral habitats.

2 | METHODS

2.1 | Study site

Lake Hovsgol is a large (276,000 ha.) and highly oligotrophic rift lake located in north-central Mongolia (Figur e 1; 51°05′50.00″N, 100°30′00.00″E). The fish fauna of Lake Hovsgol is relatively depauperate, with only nine species documented in recent sampling efforts (Young, Jensen, Weidel, & Chandra, 2015). These include Hovsgol grayling, Baikal grayling (*Thymallus baicalensis*), sharp-snouted lenok (*Brachymystax lenok*), roach (*Rutilus rutilus*), burbot (*Lota lota*), Eurasian minnow (*Phoxinus phoxinus*), Siberian stone loach (*Barbatula toni*), Siberian spiny loach (*Cobitis melanoleuca*), and Eurasian perch (*Perca fluviatilis*). Results from Mongolian and Russian research expeditions (Baasanjav et al., 1983; Mendsaikhan, Dgebuadze, Dgebuadze, & Surenkhorloo, 2017) and Sideleva (2006) indicate that *Coregonus autumnalis* and Lake minnow (*Phoxinus percnurus*) are also present in Lake Hovsgol. However, the taxonomy of Mongolian Fishes is in flux and the nomenclature of some of these species is likely to change (Kottelat, 2006).

2.2 | Fish and invertebrate collection

In late July and early August of 2011, 2012 and 2013, vertical and horizontal gill nets were set throughout the lake, following long-term sampling protocols established by Ahrenstorff et al. (2012). Horizontal gillnets were 20 m long with 4 m panels of 2.54, 3.81, 5.08, 6.35 and 7.62 cm bar mesh. Vertical gillnets were 40 m tall and 4 m wide with panels of 1.27, 1.91, 2.54 and either 3.81 or 3.18 mm bar mesh. Both horizontal and vertical nets were fished overnight (8.5–10.5 hr.) at each site. Though horizontal and vertical nets did not have all the same mesh size panels, both net types included 2.5 cm bar mesh, which is the most effective mesh size for capturing grayling in Lake Hovsgol (Free et al., 2015). Species composition and catch per unit effort for individual species are reported in Free et al. (2015).

For this study, a subsample of 92 Hovsgol grayling captured in gill nets were used for stable isotope, diet and morphological analysis (horizontal gill nets: $n = 65$; vertical gill nets: $n = 27$). Following capture, fish were sacrificed, sex and maturity determined, and morphometric measurements and meristic counts were made (Table 1). Excluding fork length, which was measured to the nearest 1 mm using a tape measure, all morphometric measurements were made

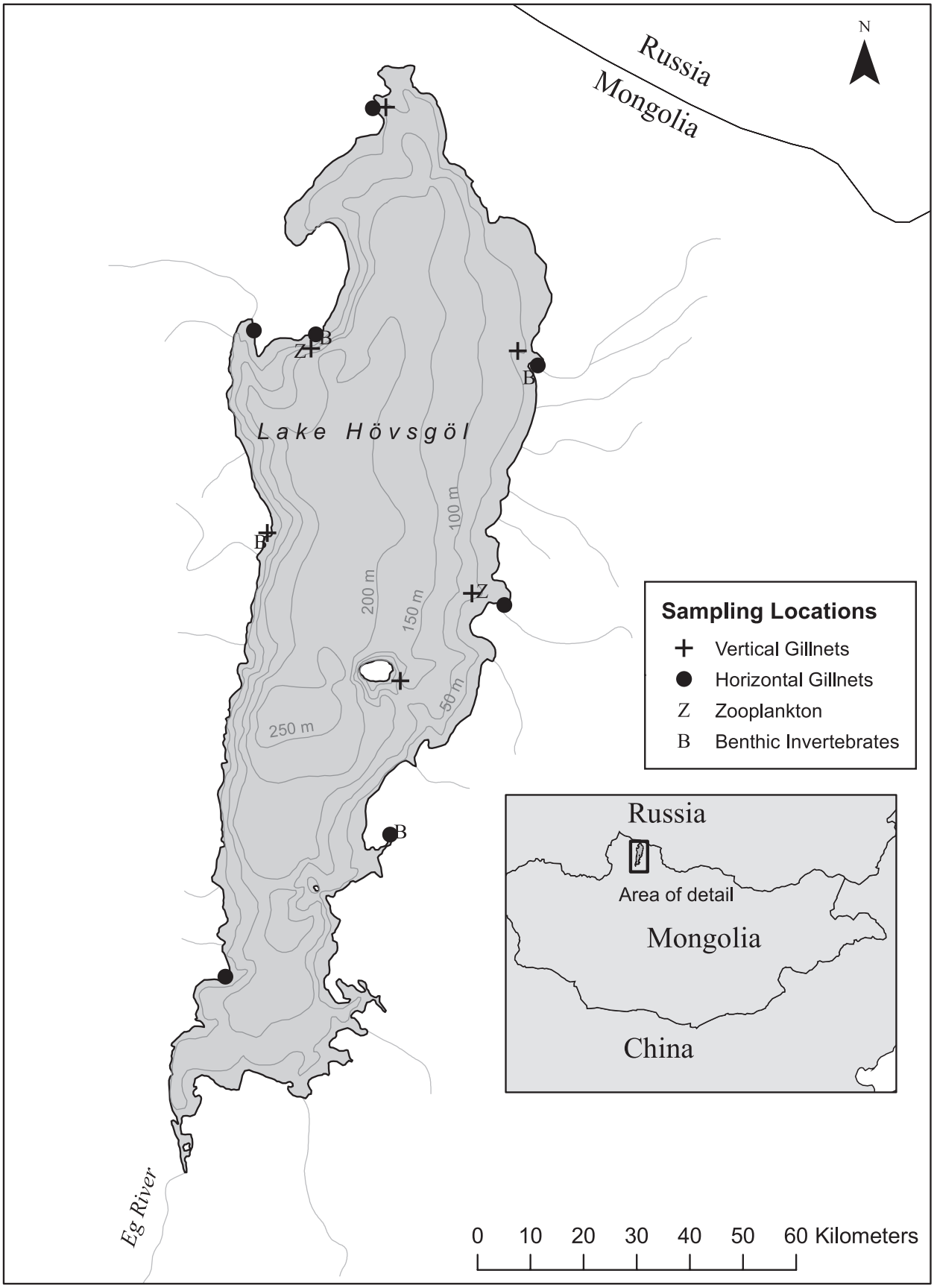

FIGURE 1 Location of horizontal and vertical gill net sampling locations on Lake Hovsgol, Mongolia

TABLE 1 Homogeneity of slopes test for the relationship between morphological characteristics and fork length compared between $\delta^{13}C$ enriched and depleted Hovsgol grayling

		Y-intercept		Slope		Homogeneity of slopes	
Attribute	*n*	Enriched	Depleted	Enriched	Depleted	*F*	*p*
Pectoral fin length	90	−1.43	−1.39	0.92	0.92	0.00	0.968
Pectoral fin width	92	−30.42	−21.90	7.10	5.56	0.17	0.681
Pelvic fin length	91	−1.16	−2.09	0.86	1.04	1.23	0.270
Pelvic fin width	91	−1.92	−1.98	0.73	0.74	0.00	0.970
Caudal peduncle depth	**89**	**−3.60**	**−2.06**	**1.13**	**0.84**	**5.56**	**0.021**
Mandible length	92	−1.81	−2.28	0.88	0.97	0.34	0.560
Maxilla length	91	−2.50	−3.76	0.95	1.19	2.04	0.157
Orbit diameter	**92**	**0.37**	**−2.18**	**0.38**	**0.85**	**11.95**	**0.001**
Body depth	92	−1.51	−2.39	0.96	1.13	0.81	0.371
Head height	91	−1.77	−2.70	0.94	1.10	1.43	0.236
Head length	87	−0.71	−0.84	0.83	0.85	0.05	0.827
Head width	**92**	**−2.21**	**3.45**	**0.76**	**−0.30**	**5.58**	**0.021**

Bold values indicate significance at the 0.05 significance level.

with a caliper to the nearest 0.1 mm. Head depth was measured along the dorsoventral axis at the posterior edge of the operculum, head width was measured along the left-right axis at the posterior edge of the eyes, head length was measured along the anteriorposterior axis from the posterior edge of the operculum to the tip of the snout, fin lengths were measured from the fin insertion to tip along the proximaldistal axis and body depth was measured along the dorsoventral axis at the anterior edge of the dorsal fin. All determinations, measurements and counts were made on all but four individuals, that were not measured for multiple morphological attributes due to errors made in the field. After measurements and counts, otoliths (n = 21), dorsal muscle samples for stable isotope analysis (n = 92) and stomach contents from dissected stomachs (n = 29) were collected opportunistically, as field conditions allowed, from a subsample of sacrificed fish.

Benthic invertebrates were collected opportunistically and concurrent with fish sampling at four littoral sites for stable isotope analysis (Figure 1). Aquatic gastropods (n = 4) and aquatic arthropods (n = 5) were collected using a Surber sampler (0.1 m^2, 500 µm mesh). Riparian invertebrates were collected in terrestrial vegetation by hand or sweeping vegetation with a 500 µm mesh D-net (n = 3). Zooplankton samples (n = 4) for stable isotope analysis were collected at two pelagic locations using an 0.5 diameter 153 µm mesh zooplankton net pulled through the top 50 m of the water column. Zooplankton samples were rinsed, and any visible vegetation removed.

2.3 | Stable isotope and stomach content analysis

A dorsal muscle sample (1–5 g, wet weight) was removed from grayling for stable isotope analysis. Invertebrate prey taxa were analysed 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.

Stable isotope ratios of ^{13}C:^{12}C and ^{15}N:^{14}N are reported in delta notation (δ), which is defined by the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1{,}000,$$

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 were the standards for ^{13}C and ^{15}N, respectively. Analytical precision was 0.09 for $\delta^{13}C$ and 0.15 for $\delta^{15}N$. Fish tissue samples were corrected for lipid content using the generalised 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 $\delta^{13}C$ value, $\delta^{13}C_{bulk}$ is the uncorrected $\delta^{13}C$ value and $C:N_{bulk}$ is the molar C:N ratio of the sample.

Isosource Mixing models (Phillips & Gregg, 2003) were applied to estimate the proportional contribution of benthic arthropods, zooplankton, terrestrial invertebrates and fish to Hovsgol grayling tissue. Hovsgol grayling signatures were adjusted for trophic fractionation of $\delta^{13}C$ and $\delta^{15}N$ prior to application of Isosource mixing models. Mean trophic fractionation values for $\delta^{13}C$ and $\delta^{15}N$ typically range from 0 to 1.3‰ and from 2.3 to 3.4‰, respectively (McCutchan, Lewis, Kendal, & McGrath, 2003; Vander Zanden & Rasmussen, 2001). Assumed trophic fractionation values for $\delta^{13}C$ and $\delta^{15}N$ were 0.4‰ and 2.6‰, respectively.

Of the Hovsgol grayling sampled for stable isotopes, stomach contents were opportunistically collected from a total of 29 fish. 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, for prey in the order Trichoptera, head width was measured on a subsample (n = 5) of individuals from each prey category. Total length and head width 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 regression equations (e.g., Benke, Huryn, Smock, & Wallace, 1999) and multiplied by the number of prey items in each diet. Mean proportion of each prey taxon in the diet by weight (MW_i, Chipps & Garvey, 2007) was then calculated following:

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

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 the total number of prey categories. Mean proportion of each prey taxon in the diet by number (MN_i, Chipps & Garvey, 2007) was then 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, N_{ij} is the number of prey type i in the diet of fish j and Q the total number of prey categories.

2.4 | Otolith age analysis

Saggital otoliths were collected opportunistically from 21 Hovsgol grayling and aged following the methods of Tsogtsaikhan et al. (2017). Thin transverse sections of otoliths were examined under a compound microscope (50× magnification) using transmitted light, and age determination was made by one experienced reader.

2.5 | Statistical analysis

Isotopically distinct groups of Hovsgol grayling were determined by visual evaluation of $\delta^{13}C$ and ^{15}N bi-plots and histograms. Groups were defined by distinct modes with non-overlapping distributions based on $\delta^{13}C$ or ^{15}N values. To evaluate whether distinct modes were the result of isotopic variability between years, we visually evaluated isotopic distributions for grayling captured in 2012 (n = 42) and 2013 (n = 46) for the presence of distinct,

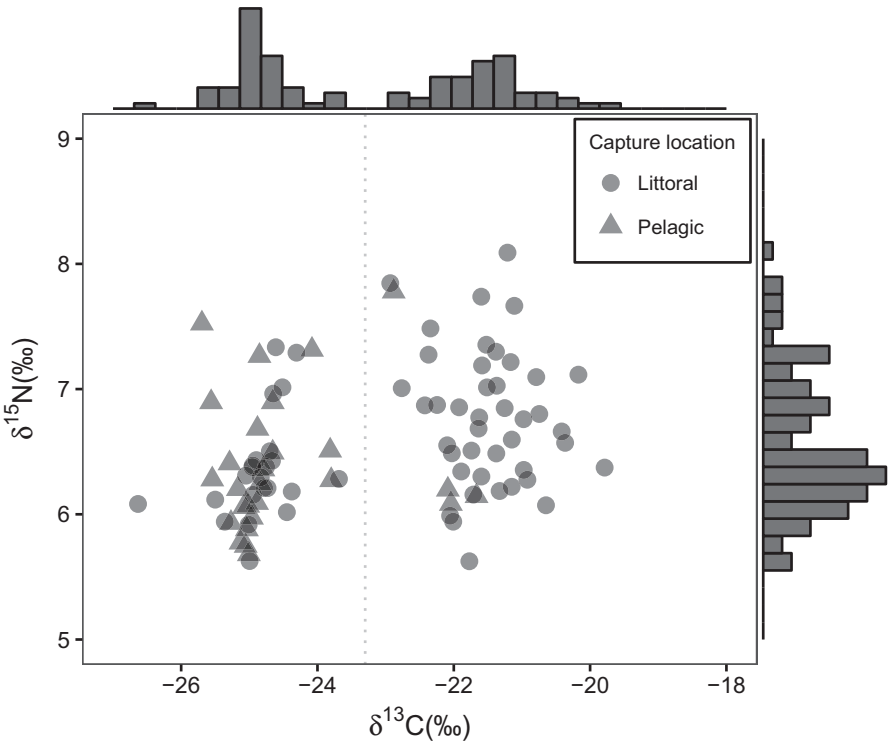

FIGURE 2 $\delta^{13}C$ and $\delta^{15}N$ values for individual Hovsgol grayling and distribution of values (gray bars). The vertical dashed line ($\delta^{13}C$ = −23.3) represents the cut-off used to classify Hovsgol grayling into $\delta^{13}C$ depleted ($\delta^{13}C$ <−23.3) and $\delta^{13}C$ enriched ($\delta^{13}C$>−23.3) groups

non-overlapping modes. Low sample size in 2011 (n = 4) precluded a comparison for that year. Analysis of covariance was used to evaluate differences in morphological attributes which were correlated with fork length between isotopic groups. Fork length and all morphological measurements were natural log transformed to meet assumptions of analysis of covariance. Analysis of variance was used to evaluate differences in gill raker number, which was uncorrelated to fork length, between isotopic groups. Extreme outliers were removed (n = 0–3) prior to analysis of covariance based on visual evaluation of bi-plots. All statistical analyses were performed in SAS-JMP (ver. 10.0) or R (ver. 3.3.1; R Core Team, 2016).

3 | RESULTS

Visual evaluation of δ^{13}C and δ^{15}N distributions for Hovsgol grayling revealed two non-overlapping δ^{13}C distributions (Figure 2). The

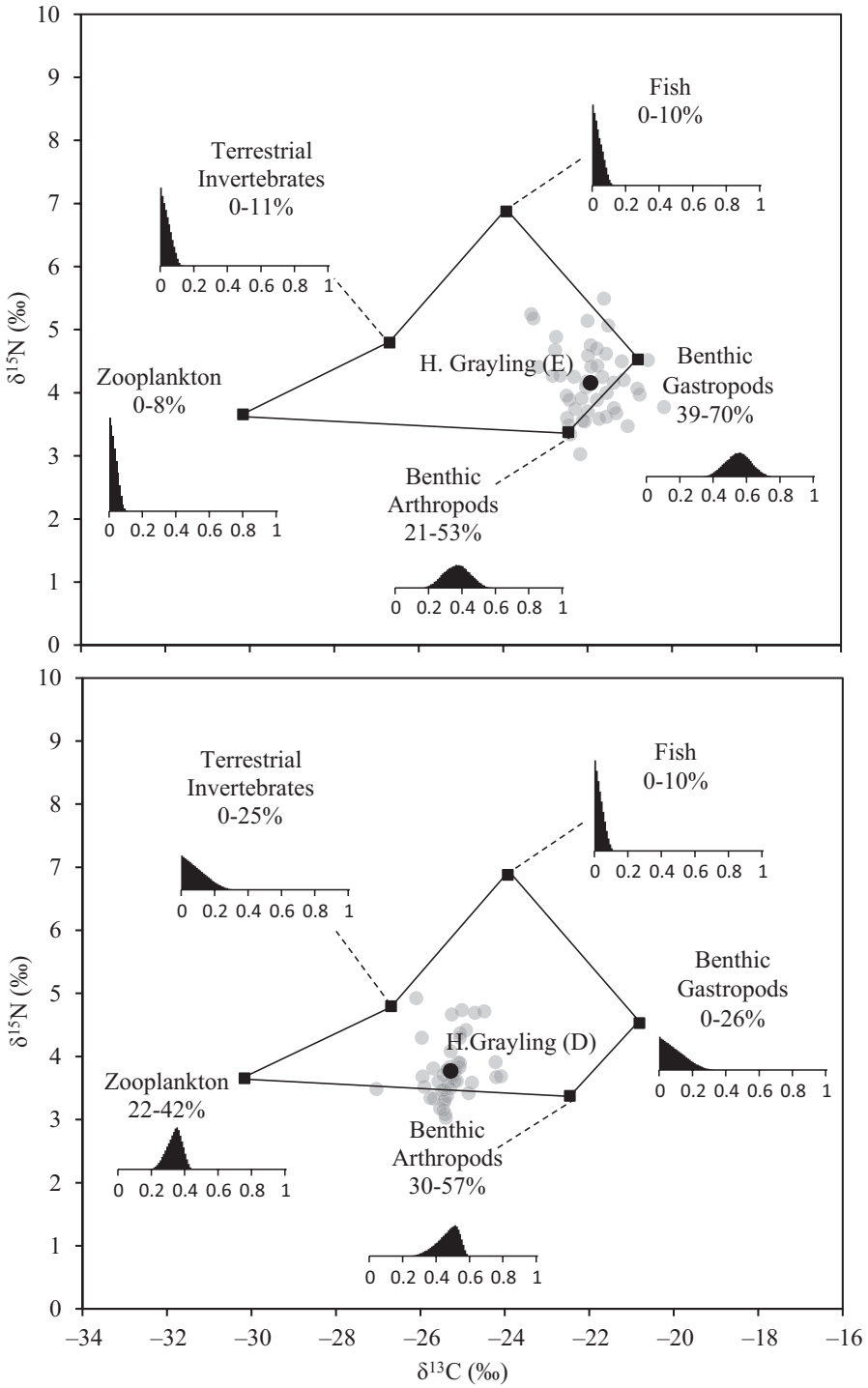

FIGURE 3 Mixing polygon for δ^{13}C and δ^{15}N values of common prey taxa and Hovsgol grayling, adjusted for trophic fractionation. Black squares represent isotope ratios of prey sources, black circles represent mean isotope ratios of δ^{13}C depleted Hovsgol grayling (D) and δ^{13}C enriched Hovsgol grayling (E), and gray circles represent isotope ratios of individual fish. Histograms display the range of possible contributions to the fish's diet estimated from Isosource mixing models

distinct δ^{13}C distributions were present in both 2012 and 2013 samples, indicating that the finding was not an artifact of differences in δ^{13}C between years.

Isosource mixing model estimates indicated that zooplankton composed on average between 22% and 42% of the diet for Hovsgol grayling within the δ^{13}C depleted distribution ("δ^{13}C depleted grayling" hereafter, Figure 3). In contrast, zooplankton were estimated to contribute between 0% and 8% of the diet for Hovsgol grayling within the δ^{13}C enriched distribution (δ^{13}C "enriched grayling" hereafter). Benthic arthropods were important components of both δ^{13}C depleted and enriched grayling, comprising between 30% and 57% of the diet for δ^{13}C depleted grayling and between 21% and 53% for δ^{13}C enriched grayling. Benthic gastropods were estimated to contribute a greater proportion to the diets of δ^{13}C enriched grayling (δ^{13}C enriched grayling = 39%–70%, δ^{13}C depleted grayling = 0%–26%). The estimated range of contribution from fish and terrestrial invertebrates to δ^{13}C depleted and enriched grayling were similar (δ^{13}C depleted: fish = 0%–10%, terrestrial invertebrates = 0%–25%; δ^{13}C enriched: fish = 0%–10%, terrestrial invertebrates = 0%–11%).

By dry mass, benthic and surface invertebrates (e.g., terrestrial invertebrates) composed most prey in the stomachs of both δ^{13}C depleted and enriched grayling (87% and 93%, respectively; Figure 4). Zooplankton composed a small portion of stomach contents in both δ^{13}C enriched and depleted grayling by mass, but constituted a larger portion in depleted grayling stomach contents (0.3% and 8%, respectively). By number, zooplankton composed a large portion of δ^{13}C depleted Hovsgol grayling diets (75%), while benthic and surface invertebrates were the dominant prey items in the stomachs of δ^{13}C enriched Hovsgol grayling (37% and 50%, respectively; Figure 4.).

Based on otoliths, a range of ages were present in both δ^{13}C depleted and δ^{13}C enriched Hovsgol grayling (δ^{13}C depleted: range = 4–17 years; δ^{13}C enriched: range = 6–12 years), with no difference in mean age between the two groups (δ^{13}C depleted = 8.6 years, δ^{13}C enriched = 7.7 years; two-sample t test, $df = 19$, $p = 0.52$). Though small sample sizes of aged individuals precluded statistical comparisons of length at age between groups, δ^{13}C enriched Hovsgol grayling typically had a greater fork length for their age than δ^{13}C depleted Hovsgol grayling (Figure 5). The ratio of male to female fish was similar between δ^{13}C depleted and δ^{13}C enriched grayling (δ^{13}C depleted: female = 41.5%, male = 58.5%; δ^{13}C enriched: female =41.4%, male =58.6%; $\chi^2 < 0.0001$, $p = 0.99$). However, five fish in the δ^{13}C depleted group were of unknown sex while sex determination was possible on all δ^{13}C enriched fish.

Gill raker counts were significantly greater in δ^{13}C depleted Hovsgol grayling (ANOVA, mean ±1 *SD*; δ^{13}C depleted = 29.0 ± 2.6, δ^{13}C enriched = 25.5 ± 2.0; ANOVA, $F_{1,90} = 51.00$, $p < 0.0001$; Figure 6). However, both groups had higher gillraker counts than sympatric Baikal grayling (*T. arcticus baicalensis*, Berg 1962; T. Krabbenhoft unpublished data). The slope of the relationship between orbit diameter and fork length was significantly greater for δ^{13}C depleted Hovsgol grayling (Table 1; Figure 7). The slopes of the relationships of head width and caudal peduncle depth to fork length were significantly lower for δ^{13}C depleted grayling (Table 1; Figure 7). δ^{13}C depleted Hovsgol grayling exhibited longer paired fin and maxilla lengths, by fork length, than δ^{13}C enriched Hovsgol grayling (Table 2; Figure 8).

The proportion of δ^{13}C depleted grayling captured offshore in vertical gillnets (0.50) was greater than that of δ^{13}C enriched grayling (0.09; $\chi^2 = 11.08$, $p < 0.001$; Figure 2) and δ^{13}C enriched Hovsgol grayling were only captured in two of six vertical gill net

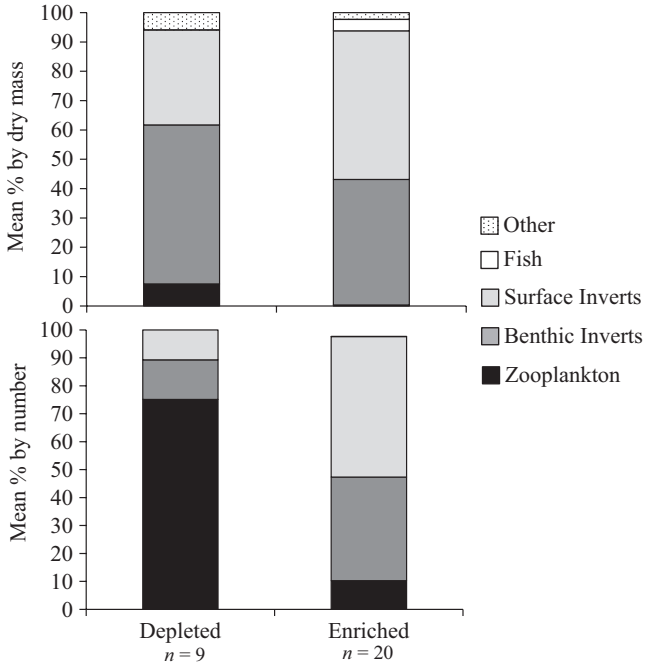

FIGURE 4 Composition of prey in δ^{13}C enriched and depleted Hovsgol grayling stomachs by dry mass (top) and number (bottom). Surface Inverts = adult and pupal stages of aquatic invertebrates and terrestrial invertebrates and Benthic Inverts = benthic dwelling invertebrates

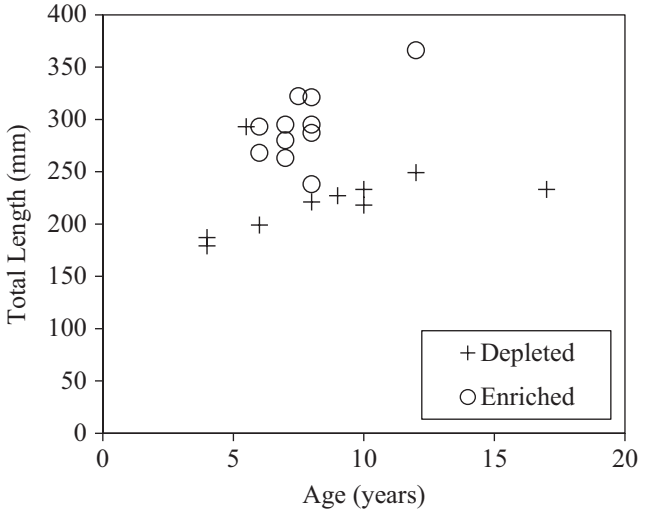

FIGURE 5 Relationship of fork length and otolith age for δ^{13}C depleted and enriched Hovsgol grayling

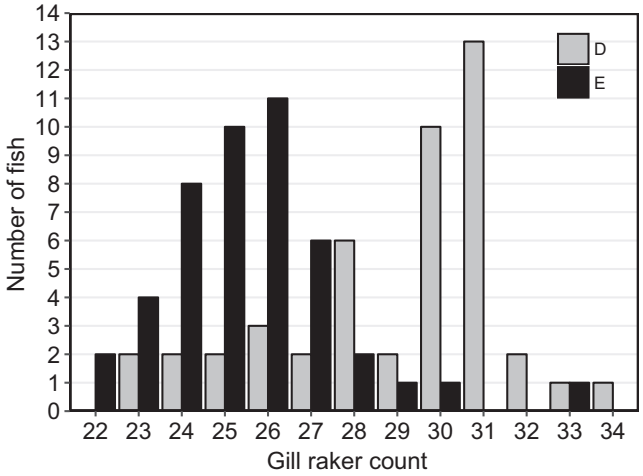

FIGURE 6 Distribution of gill raker counts for δ^{13}C depleted (D) and enriched (E) Hovsgol grayling

sites (Figure 9). Horizontal gill nets nearshore captured both δ^{13}C depleted and enriched grayling (Figure 9).

4 | DISCUSSION

Our study revealed the presence of pelagic and littoral morphs of Hovsgol grayling in Lake Hovsgol, which appears to be the first example of resource polymorphism in the salmonid subfamily Thymallinae (grayling). Through stable isotope and stomach content analysis, we also confirmed the presence of distinct foraging groups that exhibited differing levels of zooplankton consumption, a finding initially identified by Olson (2014). Evidence from the two diet measures indicated the presence of a more pelagic oriented generalist group that fed on zooplankton and benthic invertebrates and a littoral specialist that consumed benthic and surface oriented (e.g., terrestrial) invertebrates. Further, we documented agreement in diet differences inferred through stable isotope ratios and stomach contents, suggesting that diet differences were temporally stable as stomach contents reflect prey consumption over a period of hours to several days (He & Wurtsbaugh, 1993; Sweka, Cox, & Hartman, 2003), while stable isotopes in muscle tissue represent prey assimilation over a period of 6 months to 2 years (Hesslein, Hallard, & Ramlal, 1993; Weidel, Carpenter, Kitchell, & Vander Zanden, 2011). Subsequent analysis of habitat use and morphological comparisons between groups revealed that the pelagic foraging group was more frequently captured in the pelagic zone, exhibited smaller size at age, higher gill raker counts, narrower caudal peduncle, larger orbit (eye) size, narrower head width, longer paired fins and longer maxilla length; indicating the presence of pelagic–littoral polymorphism in the population.

The morphological differences we observed between Hovsgol grayling morphs were broadly consistent with those described in other species exhibiting pelagic–littoral polymorphism and with the predictions of functional morphology (Klemetsen, 2010; Robinson & Wilson, 1994; Schluter & McPhail, 1992). For example, greater gill

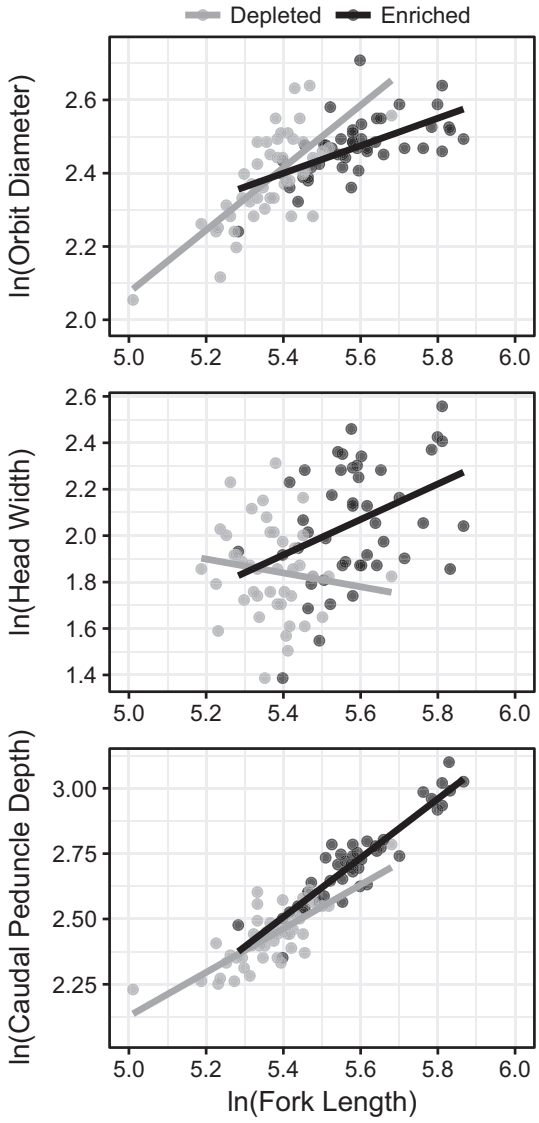

FIGURE 7 Relationship between fork length and morphological variables with statistically different slopes between δ^{13}C depleted and enriched Hovsgol grayling

raker counts, larger eye sizes and more streamlined body parts are associated with increased zooplankton foraging efficiency (Cresko & Baker, 1996; Kahilainen et al., 2011) and this was consistent with differences we observed between δ^{13}C depleted (pelagic) and δ^{13}C enriched (littoral) Hovsgol grayling morphs. The pelagic Hovsgol grayling morph also exhibited longer, more streamlined, paired fins, consistent with the expectations of increased open water swimming efficiency and differences described in pelagic and littoral pumpkinseed *Lepomis gibbosus* morphs (Robinson & Wilson, 1996). In contrast to differences described in other pelagic–littoral morph pairs (e.g., Schluter, 1993, Adams & Huntingford, 2002), the pelagic Hovsgol grayling morph exhibited a longer maxilla length than the δ^{13}C enriched (littoral) morph. Maxilla length is an indicator of gape size (Adams & Huntingford, 2002), and the larger gape size in the pelagic morph may reflect the relatively broad diet of the morph, which included a substantial proportion of larger prey types (i.e., benthic

TABLE 2 Comparison of least squares means and results of ANCOVA for morphological attributes between $\delta^{13}C$ enriched and depleted Hovsgol grayling. Least squares means represent measurements (mm) adjusted for the influence of fork length

	Least squares means		ANCOVA	
Attribute	**Enriched**	**Depleted**	***F***	***p***
Pectoral fin length	**36.3**	**38.7**	**16.48**	**<0.001**
Pectoral fin width	8.5	8.6	0.46	0.499
Pelvic fin length	**34.1**	**36.2**	**6.15**	**0.015**
Pelvic fin width	7.9	7.7	1.00	0.319
Mandible length	19.8	20.7	3.46	0.066
Maxilla length	**14.6**	**15.5**	**6.55**	**0.012**
Body depth	42.6	43.6	0.84	0.362
Head height	28.7	27.7	3.28	0.074
Head length	45.8	45.0	1.87	0.176

Bold values indicate significance at the 0.05 significance level.

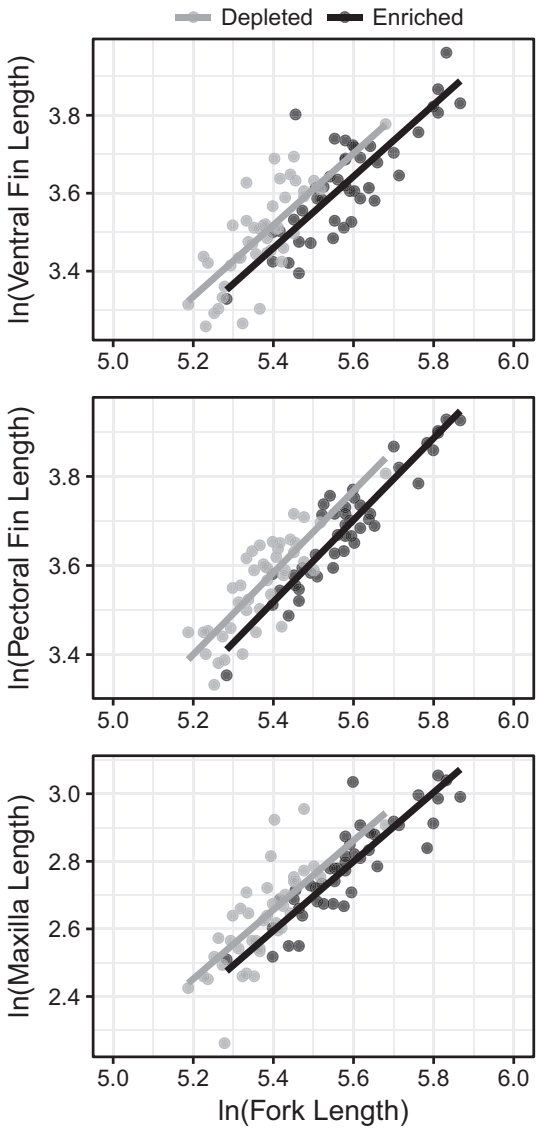

FIGURE 8 Relationship between fork length and morphological variables with statistically different y-intercepts between $\delta^{13}C$ depleted and enriched Hovsgol grayling

invertebrates), and smaller average size of the pelagic morph when compared to the littoral morph.

Size differences between littoral and pelagic morphs are ambiguous and not consistently associated with resource use (Robinson & Wilson, 1994). Klemetsen, Elliott, Knudsen, and Sørensen (2002) found that size differences between Arctic charr (*Salvelinus alpinus*) morphs were not heritable and appeared to be associated with differences in resource availability and temperature conditions between habitats. Pelagic morphs of whitefish (*Coregonus* spp.), in contrast, consistently exhibited smaller sizes than littoral forms (Bernatchez et al., 2010), and genetic differentiation (Bernatchez et al., 1999). The smaller size of the pelagic morph we observed may be related to the extremely low productivity and temperature in Lake Hovsgol's pelagic zone (Urabe et al., 2006). Lake Hovsgol's littoral habitats, in contrast, support a more diverse prey assemblage and include many river and stream mouths with seasonally warmer water temperatures, potentially providing better conditions for growth.

Though we documented significant morphological differences between pelagic and littoral specialists of Hovsgol grayling, it is worth noting that we observed substantial overlap in several traits typically associated with littoral and pelagic morphs (e.g., gill raker number, eye size, caudal peduncle depth; Robinson & Wilson, 1994). This observation may indicate that the population represents an earlier stage on the continuum of divergence, positioned somewhere between individual specialization with limited morphological differences (e.g., Kristjánsson & Leblanc, 2017) and full speciation (Smith & Skúlason, 1996).

Resource polymorphism is a widespread phenomenon in fishes that have colonised post-glacial lakes with open niches and is believed to represent an early stage of divergence that, under specific circumstances, may lead to sympatric speciation (Schluter, 1996; Smith & Skúlason, 1996). Evidence suggests that the availability of open niches and competition within and between species may be involved in the diversification observed in these lakes (Robinson & Wilson, 1994; Skúlason & Smith, 1995). Though Lake Hovsgol is believed to have formed 2–5 million years ago (Goulden et al., 2006), recent fossil diatom evidence has revealed that the lake's ecosystem collapsed during the last glacial period (Karabanov et al., 2004). In the past ~13,000 years, nine species widely distributed in northeast Asia and one endemic species have established populations in the lake. All but Hovsgol grayling exclusively inhabit the littoral zone (Ahrenstorff et al., 2012) and exhibit some degree of diet overlap (Olson, 2014; Young et al., 2015). Therefore, the pelagic zone represents an open niche, free of interspecific competition and we speculate that these conditions may have driven the divergence of the pelagic morph we observed.

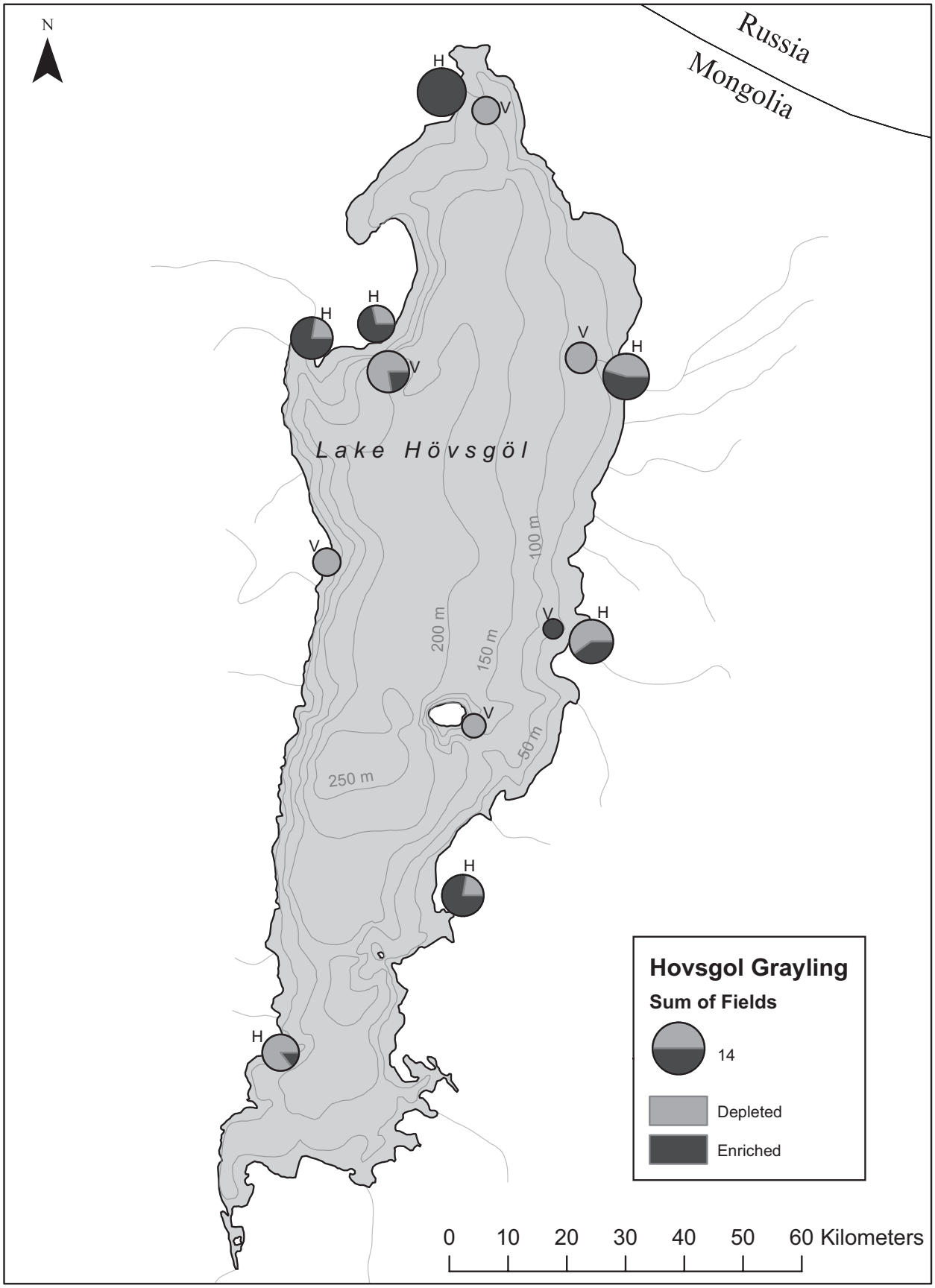

FIGURE 9 Composition of $\delta^{13}C$ depleted and enriched Hovsgol grayling captured in vertical (V) and Horizontal (H) gill nets

As with any study inferring diet through stable isotope analysis, two key assumptions are that all prey sources and any spatial and temporal isotopic variation in prey sources is accounted for (Phillips et al., 2014). In our analysis, we attempted to account for these assumptions by utilising stomach content information from this study and others (i.e., Ahrenstorff et al., 2012, Olson, 2014) to verify that prey types included in our stable isotope analysis were the primary prey types consumed by Hovsgol grayling. Lending further support to our analysis, we found consistency in the zooplankton consumption inferred through both stomach contents and stable isotopes. Though our spatial coverage for prey sampling was limited given the size of lake Hovsgol, Young et al. (2015) documented spatial and temporal consistency in the variation of δ^{13}C or δ^{15}N in pelagic and littoral primary consumers in Lake Hovsgol. It is possible that some grayling captured in the lake may have consumed prey in tributary streams, where we do not have stable isotope information from potential prey taxa. However, the δ^{13}C depleted and enriched groups of Hovsgol grayling (later identified as pelagic and littoral morphs, respectively) were not segregated by capture location, as would be expected if one group was reliant on a significant tributary habitat. Additionally, large concentrations of Hovsgol grayling in tributary streams only appear to occur during spawning, when local fishers target the species (Ocock et al., 2006, Sideleva, 2006, Free et al., 2015).

The presence of littoral–pelagic polymorphism in Hovsgol grayling is the first described in the salmonid subfamily Thymalinae (grayling). The absence of other examples of resource polymorphism in grayling is surprising given their widespread distribution in post-glacial lake and stream habitats in the northern hemisphere and prolific examples of resource polymorphism in many other salmonids. This is also surprising given that Haugen (2000) and Gregersen, Haugen, and Vøllestad (2007) documented rapid evolutionary change in European grayling *Thymallus thymallus* following the colonisation of a large freshwater lake in Norway. The presence of resource polymorphism in other grayling populations could be easily overlooked if they are subtle, like differences described here. The morphs we described were only revealed through the discovery of a distinct bimodal distribution of individual Hovsgol grayling by δ^{13}C, indicating the presence of two foraging groups, and subsequent comparison of morphological features. Future studies evaluating the presence of resource polymorphism in freshwater fish populations should consider collecting stable isotope information.

In other salmonid species that exhibit polymorphism, morphological differences between morphs may be heritable (Goetz et al., 2010; Klemetsen, 2010) or the result of phenotypic plasticity (Hindar & Jonsson, 1993). In European whitefish (*Coregonus lavaretus*), differences in gill raker counts between pelagic and littoral morphs are heritable (Østbye et al., 2006) and recent evidence suggests that these differences arose through natural selection in post-glacial lakes of the Fennoscandian Peninsula (Häkli et al., 2017). Future efforts should evaluate whether littoral and pelagic morphs of Hovsgol grayling represent genetically distinct populations. Currently, illegal gill net harvest is concentrated in the littoral zone of Lake Hovsgol, where fish densities are highest and fish are accessible to shore fishers (Free et al., 2015). Given this, the littoral morph likely composes a larger proportion of the illegal harvest than does the pelagic morph. Determining whether the two represent genetically distinct populations would have significant conservation implications.

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AUTHORS' CONTRIBUTION

TH, OJ, TK, BM and KO conceived and designed the investigation. TH, OJ, TK, BM and KO performed field and laboratory work. TK and KO analysed the data. TH, OJ, TK, BM and KO contributed materials, reagents, and analysis tools. TH, OJ, TK, BM and KO wrote the paper.

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