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Abundance, spatial distribution, and diet of endangered Hovsgol grayling (*Thymallus nigrescens*)

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Abstract The Hovsgol grayling, endemic to Lake Hovsgol, Mongolia, is considered endangered, but published descriptions of the species abundance, distribution, or behavior do not exist. We used hydroacoustics, vertical and horizontal gillnetting, zooplankton sampling, and stomach content analysis to characterize abundance, distribution, prey availability, and diet of Hovsgol grayling. Pelagic Hovsgol grayling densities averaged 34.2±6.8 individuals•ha^{-1} (biomass of 4.4±0.9 kg•ha^{-1}) and were concentrated along the western and northern areas of the lake. Gillnet catch rates were 7.5 times higher for littoral sets than pelagic sets. Pelagic vertical distributions of zooplankton and Hovsgol grayling were concentrated above 50 m, with grayling exhibiting diel vertical migrations from 15 m at night to 30 m during the day. Smaller Hovsgol grayling fed primarily on zooplankton while larger individuals fed more heavily on benthic prey in littoral and pelagic areas. The results from this study may be used to guide conservation management and monitoring strategies for Hovsgol grayling, and provide a conservation reference point as human population growth and environmental change continues in the Lake Hovsgol catchment.

Keywords Hydroacoustics · Hovsgol · Grayling · Diel vertical migration · Endangered species

Introduction

Anthropogenic environmental changes are increasing worldwide and causing decreases in biological diversity in both terrestrial and aquatic ecosystems (Vitousek 1994). Freshwater ecosystems may be particularly vulnerable (Abell 2002). Conservation of endangered species in the face of increased anthropogenic influences requires knowledge of basic species demographics, including abundance, spatial distribution, and behavior (Campbell et al. 2002). Conservation action plans for threatened and endangered Mongolian fishes (e.g. Hovsgol grayling) have been initiated but there is little direct monitoring and

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limited ecological understanding of these fish populations (Ocock et al. 2006a). This is cause for concern given that Mongolia had one of the fastest growing human populations in the 20th century (Ramankutty et al. 2002) and is undergoing rapid environmental changes characterized by an increase in the average annual air temperature by 1.66°C in the last 60 years (Punsalmaa et al. 2005), shortened ice cover duration in rivers and lakes (Punsalmaa et al. 2004), increasing precipitation (Namkhaijantsan 2006), and changing stream flow regimes (Ma et al. 2003).

The Hovsgol grayling (*Thymallus nigrescens*) is listed as an endangered species on Mongolia's Red List (Ocock et al. 2006b), and is endemic to Mongolia's largest lake, Lake Hovsgol, yet no peer-reviewed publications exist about its ecology in the English-language literature. As a taxonomic group, grayling can be susceptible to anthropogenic influences as has been seen with the extirpation or reduction in population sizes of North American Arctic grayling (*Thymallus articus*) in Montana and Wyoming (Northcote 1995). The Hovsgol grayling is closely related to the Arctic grayling. Some researchers designate the Hovsgol grayling as a subspecies of the Arctic grayling (Reshetnikov et al. 2002), some classify it as its own species (Berg 1962; Scott and Crossman 1998; Kottelat 2006), and others await additional morphological and genetic analyses before making subspecies or species classifications (Froufe et al. 2005). Most of what is known about the Hovsgol grayling is based on informal reports and unpublished studies, briefly summarized in Dulmaa (1999) and Sideleva (2006). While empirical evidence is lacking, it is thought that Hovsgol grayling primarily inhabit the littoral zone and surface layers of the pelagia of Lake Hovsgol, as well as inflowing rivers mainly during the early-summer spawning period (Dulmaa 1999). It is also thought that they are omnivorous, feeding mostly on zooplankton (Sideleva 2006). There has been no assessment of their abundance, lakewide distribution, vertical distribution, diel vertical migration tendencies, or ontogenetic or habitat-related diet shifts.

Densities, distributions, and feeding behaviors of planktivores in large lake ecosystems are typically controlled by a host of factors, such as resource limitation from the bottom-up (Power 1992), top-down control from piscivores (McQueen et al. 1986), the amount of available habitat (Magnuson et al. 1979), and direct exploitation (Post et al. 2002). Lake Hovsgol is a large, ultra-oligotrophic (Urabe et al. 2006) body of water. Although still relatively pristine owing to its remote location, it faces a number of anthropogenic pressures including changing habitat conditions due to global climate change (Punsalmaa et al. 2005) and increasing exploitation caused by an increase in tourism and population growth (Ramankutty et al. 2002; Yu and Goulden 2006). However, unlike most large lake ecosystems, Lake Hovsgol has very few piscivores present in the pelagia, with much higher densities in littoral areas. The low pelagic piscivore density provides a low predation risk scenario in the pelagia for Hovsgol grayling, which may influence their distribution, diel vertical migration behavior, and ultimately the consumption of prey resources (Carpenter and Kitchell 1993).

The purpose of this study was to characterize the ecology of the endemic, endangered Hovsgol grayling population in Lake Hovsgol. Specifically, our objectives were to (*i*) assess lakewide densities of two size classes of Hovsgol grayling (small, 100–170 mm; large, > 170 mm), (*ii*) describe their vertical and horizontal distributions during day and night, and (*iii*) examine their feeding behaviors in littoral and pelagic areas. Given the potential for rapid environmental change in this region and the limited ecological understanding of Hovsgol grayling, our research provides a baseline for interpreting the effects of future environmental changes and implementing proper conservation and monitoring strategies.

Materials and methods

Study site

Lake Hovsgol, Mongolia (51°05′50.00″ N, 100°30′00.00″ E), is located in the mountains of northern Mongolia, at the southern edge of the Siberian taiga forest. It is the 19th largest lake in the world by volume (480 km^3), with a maximum depth of 262 m, and a surface area of 2760 km^2 (Herdendorf 1982; Goulden et al. 2006). For size reference, Lake Hovsgol is similar to Lake Erie in volume (545 km^3). Lake Hovsgol is dimictic, with ice cover from November to June, an established thermocline by late July (10–14 m depth), and summer surface water temperatures reaching 14–15°C (Edlund et al. 2003;

Urabe et al. 2006). It is an ultra-oligotrophic lake; characterized by low primary production (2–5 mg $C{\cdot}m^{-3}{\cdot}day^{-1}$), high oxygen content year-round throughout the water column (8–11.5 mg $O_2{\cdot}l^{-1}$), and clear water (Secchi disk readings commonly up to 20 m) (Kozhova et al. 1994; Urabe et al. 2006). The abundance of submergent and emergent vegetation is low throughout the lake, except near inflowing streams and rivers.

Biological sampling

We sampled the lake from July 20th to July 30th, 2009, and collected data on Hovsgol grayling population densities, vertical and horizontal distribution patterns, and feeding behaviors. Specific sampling techniques employed horizontal gillnets ($N=8$ locations), vertical gillnets ($N=6$ locations), hydroacoustics ($N=8$ locations), and staged vertical zooplankton net tows ($N=2$ locations) (Fig. 1). The various locations were selected in order to sample the entire lake at littoral and pelagic areas, as well as points and embayments.

The littoral fish community was sampled at eight locations using three monofilament experimental horizontal gillnets (Fig. 1). Two of the gillnets were 2 m deep and 20 m long, made up of 4 m panels of 25.4, 38.1, 50.8, 63.5, and 76.2 mm bar mesh. The other gillnet was 2 m deep and 28 m long, consisting of 4 m panels of 12.7, 25.4, 38.1, 50.8, 63.5, 76.2, and 88.9 mm bar mesh. The gillnets were deployed using a stationary bottom set, perpendicular to shore, in water less than 10 m deep (Hubert 1983). Nets were fished throughout the night, for 8.5–11.5 h, at each location. All fish captured were measured to the nearest mm in total length, weighed to the nearest gram, and stomach contents were removed and analyzed from grayling ranging in total length (described below).

The pelagic fish community was sampled using vertical gillnets at six locations distributed throughout the lake (Fig. 1). The vertical gillnets were 40 m long by 4 m wide, with spreader bars placed every 10 m. At station 2, we used a 19.1 and 38.1 mm bar mesh gillnet. At station 5, we used a 12.7, 19.1, 25.4, and 38.1 mm bar mesh net. Finally, at stations 4, 7, 8, and 9 we used a 12.7, 19.1, 25.4, and 31.8 mm bar mesh net. The vertical gillnets were deployed with the top of the net at the surface and the bottom of the net at 40 m, in bottom depths ranging from 40 to 110 m. We set each net in the evening and fished them for 7–13.5 h. Upon retrieval, fish were identified, measured to the nearest millimeter (total length), weighed to the nearest gram, had their stomachs dissected, and had the depth of capture measured to the nearest 0.5 m. Horizontal and vertical gillnet catch rates ($ind.{\cdot}h^{-1}{\cdot}m^{-2}$) with associated standard errors were calculated to compare the littoral and pelagic areas.

Entire stomachs were removed from the Hovsgol grayling caught in horizontal and vertical gillnets, and stomach contents were identified, enumerated, and weighed (to the nearest 0.1 mg wet weight). To examine ontogenetic and habitat related diet shifts, we examined the diet composition (% by mass) of at least 5 grayling (range: 5–39) in each 50 mm length bin (e.g. 100–150 mm) captured in the horizontal and vertical gillnets. Diet items were classified into major taxonomic categories as follows: primarily benthic invertebrates (Amphipoda, Chironomidae, Ephemeroptera, Hirudinea, Mollusca, Plecoptera, Simuliidae, and Trichoptera), zooplankton (Calanoida, Cyclopoida and Cladocera) and terrestrial insects (Coleoptera, Diptera adults, Ephemeroptera adults, and Hymenoptera).

Hydroacoustic data to determine the size distribution, density, and vertical distribution of the pelagic fish community were collected concurrently with gillnet sampling. For all hydroacoustic sampling we used a 120 kHz Biosonics DTX hydroacoustic echosounder (Biosonics, Inc., Seattle, Washington) mounted on a 1.75 m tow body. Eight transects were sampled during the day or night to examine lakewide densities and diel changes in vertical distributions (Fig. 1). Each transect was sampled for between 30 and 300 min with bottom depths ranging from 26 m to 222 m (Table 1). Data were collected according to Rudstam et al. (2009). The acoustic signals were collected with Biosonics Visual Acquisition Software (version 4.1) and saved to a computer hard drive for later analyses. At the beginning and end of the research cruise, a standard sphere calibration of the hydroacoustic system was performed and little difference (< ± 1 dB) was detected in the observed and theoretical target strength of the calibration sphere.

Fish densities were estimated from the hydroacoustic data using Echoview software (version 4.10, SonarData Ply Ltd., Tasmania). Post-processing procedures included removing bottom dead zone echoes, the

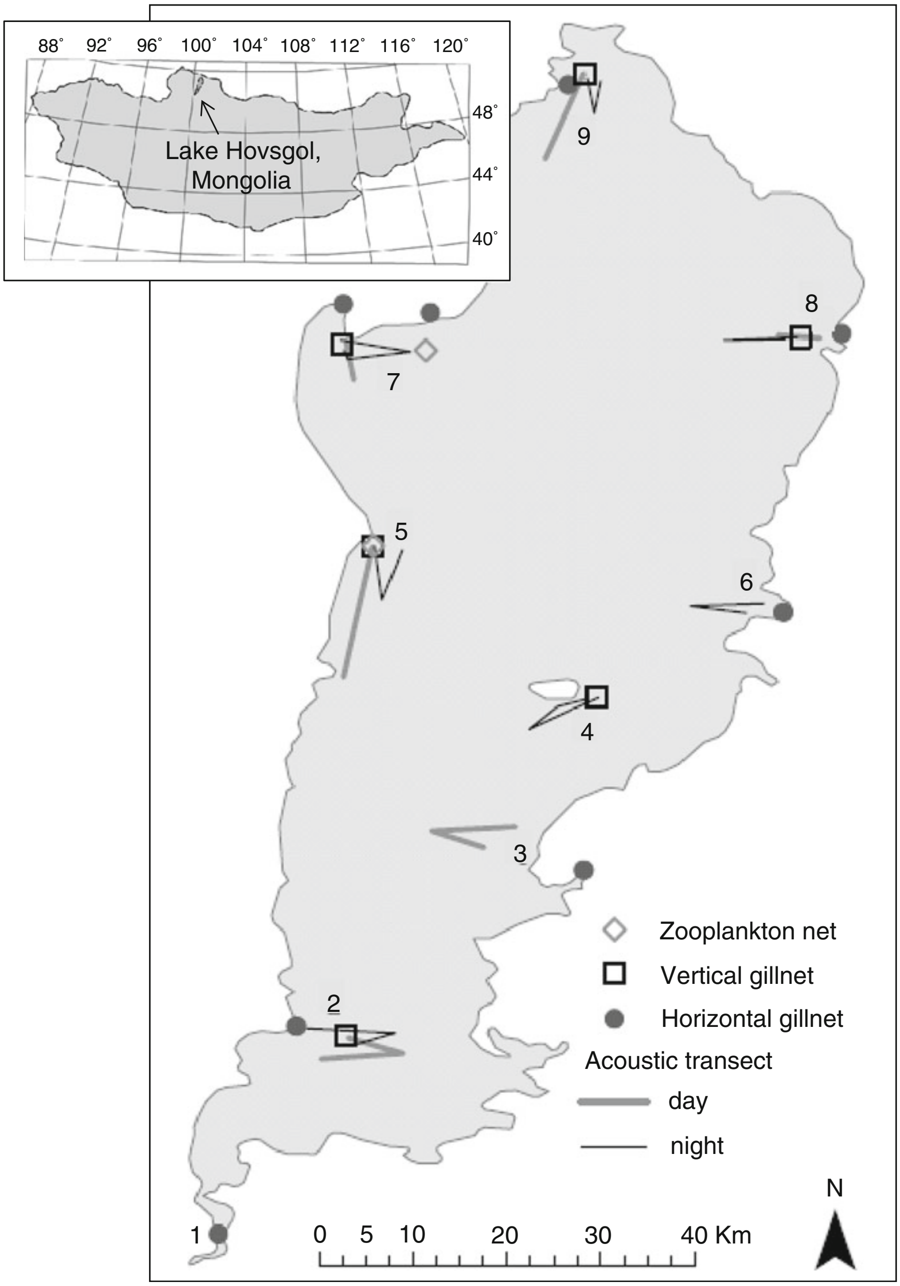


Fig. 1 Areas of Lake Hovsgol, Mongolia, sampled using hydroacoustics, vertical and horizontal gillnetting, and zooplankton net tows

near-field exclusion zone, and non-fish echoes. Data were classified into 5 m depth bins from just below the near-field exclusion zone (~ 2 m) to the maximum depth for each transect. For each depth bin, within each transect, densities of Hovsgol grayling were calculated. Based on length modes in the vertical gillnet catch data (Fig. 2b), and because only Hovsgol grayling were captured in the vertical gillnets, we classified grayling into two size groups: 100–170 mm (smaller) and> 170 mm (larger). In the absence of a target strength to length relationship for grayling, we chose to use the general equation provided in Love (1977) for measurements of fish in the dorsal aspect. The lengths in each size category correspond to target strengths ranging from −44.77 to −40.37 dB for smaller sized grayling and>−40.37 dB for larger sized grayling.

To calculate densities of smaller and larger grayling in each depth bin, we first calculated the

Table 1 Physical and biological characteristics of the hydroacoustic transects sampled. Smaller grayling are considered to be 100–170 mm, while larger grayling are >170 mm

Transect	Day/ Night	Time sampled (minutes)	Minimum depth (m)	Maximum depth (m)	Smaller grayling density (ind.•ha^{-1})	Larger grayling density (ind.•ha^{-1})
2	D	160	103	123	10.8	10.9
2	N	140	40	130	17.5	25.5
3	D	60	145	207	5.8	3.0
4	N	170	32	119	5.1	9.0
5	D	180	62	175	17.9	14.9
5	N	120	67	78	23.7	22.4
6	N	300	53	152	9.5	14.0
7	D	110	41	112	18.5	22.8
7	N	150	51	95	23.6	34.4
8	D	30	26	51	3.2	6.8
8	N	140	65	131	5.3	5.5
9	D	130	26	95	11.3	12.1
9	N	170	65	222	21.0	22.6

proportion (P_s) and mean target strength ($\overline{TS}_s$; dB re 1 m^2) for each size class (s) in each bin using a single target analysis with single target detection parameters described in Rudstam et al. (2009). If fewer than 30 single targets were present in a depth bin shallower than 50 m we used an average P_s and $\overline{TS}_s$ value for all organisms in less than 50 m of water along that transect. Likewise, if fewer than 30 single targets were present in a depth bin greater than 50 m of water we used an average P_s and $\overline{TS}_s$ value for all organisms in greater than 50 m of water along that transect. We used 50 m as a cutoff because proportionally more small individuals were present below 50 m causing differences in P_s and $\overline{TS}_s$. Next, we used P_s, $\overline{TS}_s$, and s_V, which is the linear mean volume backscattering coefficient determined from the echo integration file for the echogram (m^2•m^{-3}), to calculate the volumetric fish density (P_{VS}; ind.•m^{-3}) for each size class in each bin using the following equation:

$$P_{VS} = \frac{P_s}{\sum\left(P_s \times 10^{\left(\frac{\overline{TS}_s}{10}\right)}\right)} \times s_V \qquad (1)$$

Volumetric fish densities (ind.•m^{-3}) were converted to areal densities (ind.•ha^{-1}) when necessary by summing volumetric fish densities in each meter of the water column and multiplying by 10 000 (10 000 m^2= 1 ha). Only night estimates were used when estimating Hovsgol grayling population densities throughout

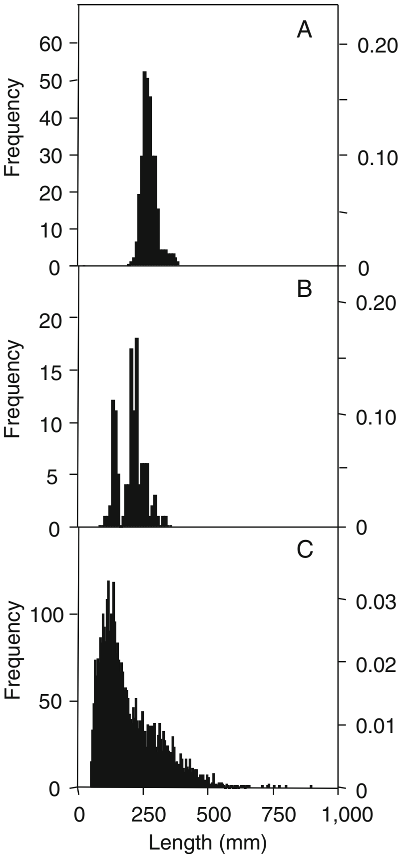


Fig. 2 Length-frequency distributions for Hovsgol grayling (*Thymallus nigrescens*) sampled with **(a)** horizontal gillnets (N=301), (**b**) vertical gillnets (N=118), and (**c**) hydroacoustics (N=3,618)

the lake because fish forming large and dense schools during the day could potentially lead to inaccuracies (Appenzeller and Leggett 1992). However, this does not appear to be a major concern given the similar day and night density estimates between most transects (Table 1). Due to these similarities, day and night density estimates were used to evaluate diel vertical migration patterns. All density estimates are accompanied by estimates of one standard error. Two-sample Kolmogorov-Smirnov tests were used to compare day *versus* night vertical distributions of smaller and larger Hovsgol grayling for each transect when the data were available.

We used staged vertical plankton net tows to gather information on the species composition, abundance, and vertical distribution of the zooplankton community. We sampled the zooplankton community at 2 locations, providing day and night samples (Fig. 1). At each location, a 0.25 m opening, 153 ųm conical mesh plankton net was deployed and retrieved at a speed of ~1 m•s^{-1}. Staged net tows were used with three replicates collected at each depth. We took replicates from 5 m off the bottom to the surface, 50 m to the surface, and 20 m to the surface. Zooplankton samples were preserved with 95% ethanol. We analyzed each zooplankton sample by identifying and counting all of the organisms in four 5 ml subsamples. Cladocerans were identified to family and copepods were identified to order. This coarse taxonomic resolution was appropriate given that our study objectives focused on zooplankton only as a component of grayling diets.

Results

Species composition, size distributions, and catch rates

We captured 565 fish at the eight littoral stations using horizontal gillnets. Hovsgol grayling represented a little more than half of all the fish captured in littoral areas (*N*=301; 53.3%). Other species captured less frequently included burbot (*Lota lota*; *N*=90; 16%), roach (*Rutilus rutilus lacustris*; *N*=65; 11.5%), lenok (*Brachymystax lenok*; *N*=57; 10.1%), Eurasian perch (*Perca fluviatilis*; *N*=51; 9%) and stone loach (*Barbatula toni*; *N*=1; <1%). A length-frequency distribution for Hovsgol grayling caught in the littoral zone was unimodal (270 mm, Fig. 2a) and ranged from 207 to 385 mm with a mean of 272 mm.

We captured 127 fish (all Hovsgol grayling) in the vertical gillnets. The pelagic Hovsgol grayling population showed a bimodal length distribution, with modes at 140 mm and 230 mm (Fig. 2b). The smaller size group ranged between 108 and 156 mm (mean= 138 mm) while the larger group was between 175 and 339 mm (mean=230 mm).

The mean gillnet catch rate of Hovsgol grayling, standardized for soak time and net area, was 7.5 times lower in pelagic set vertical gillnets (0.0031±0.001 ind.•h^{-1}•m^{-2}, *N*=22) compared to the littoral horizontal gillnets (0.0234±0.004 ind.•h^{-1}•m^{-2}, *N*=24). Pelagic vertical gillnet catch rates were 4 times higher along the western and northern shore stations 2, 5, 7, and 9 (0.004±0.001 ind.•h^{-1}•m^{-2}, *N*=14) compared to the eastern shore stations 4 and 8 (0.001±0.0004 ind.•h^{-1}•m^{-2}, *N*=8). Littoral horizontal gillnet catch rates did not vary between the western/northern shore and the eastern shore stations (0.023 and 0.024 ind.•h^{-1}•m^{-2}, respectively).

Hovsgol grayling diet composition

Diet composition (% by mass) of Hovsgol grayling varied as a function of length and habitat (littoral vs. pelagic). In pelagic vertical gillnets, 65 diets were analyzed from grayling between 108 and 339 mm, including 13 fish<150 mm, 5 fish from 150 to 199 mm, 25 fish from 200 to 249 mm, 17 fish from 250 to 299 mm, and 5 fish>300 mm. Diets of smaller grayling caught in pelagic vertical gillnets were dominated by zooplankton (Calanoida, Cyclopoida, and Cladocera). Larger grayling, however, consumed proportionally more benthically associated invertebrates (e.g. Amphipoda, Chironomidae, Ephemeroptera, Hirudinea, Mollusca, Plecoptera, Trichoptera, and Simuliidae) (Fig. 3a). Terrestrial insects (e.g. Coleoptera, Diptera, and Hymenoptera) made up about 20% or less of pelagic grayling diets regardless of size. From the littoral horizontal gillnets, 73 diets were analyzed from grayling between 210 and 385 mm, including 13 fish from 200 to 249 mm, 39 fish from 250 to 299 mm, 14 fish from 300 to 349 mm, and 7 from fish>350 mm. Only larger Hovsgol grayling (>200 mm) were captured in the horizontal gillnets set in littoral areas and their diets

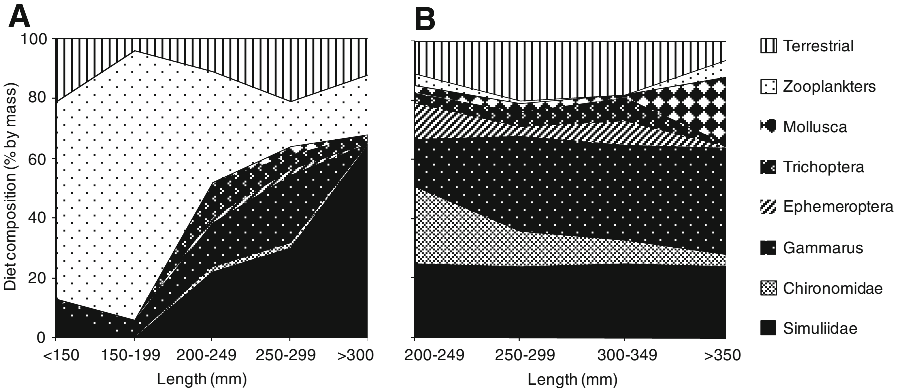


Fig. 3 Diet composition (% by mass) of Hovsgol grayling (*Thymallus nigrescens*) caught in **(a)** pelagic vertical gillnets and **(b)** littoral horizontal gillnets. Diet items present at less than 5% of the total biomass are not shown

were dominated by species associated with the bottom (~75%), followed by terrestrial insects (~20%), and zooplankton (~5%) (Fig. 3b).

Hovsgol grayling densities and diel vertical migrations

Hovsgol grayling densities calculated using hydroacoustics at night averaged 34.2±6.8 ind.•ha^{-1} (4.4±0.9 kg•ha^{-1}), however, densities of smaller and larger individuals varied throughout the lake (Fig. 4; Table 1). Smaller grayling densities ranged between 5.1 and 23.7 ind.•ha^{-1} (averaged 15.1±3.1 ind.•ha^{-1}) for transects sampled at night. Nighttime densities of larger individuals ranged between 5.5 and 34.4 ind.•ha^{-1} and averaged 19.1±3.8 ind.•ha^{-1}. Although similar depths were sampled, stations located on the western and northern shores (stations 2, 5, 7, and 9) contained higher average densities of smaller and larger Hovsgol grayling (21.5±1.5 and 26.2±2.8 ind.•ha^{-1}, respectively) compared to average densities (6.6±1.4 and 9.5±2.5 ind.•ha^{-1}, respectively) from the eastern shore stations 4, 6, and 8.

Hydroacoustic sampling over a day-night cycle allowed examination of changes in vertical distribution over changing light levels. We observed diel vertical migrations of smaller and larger Hovsgol grayling at the majority of the stations sampled (Fig. 5). For all transects with complimentary day and night data, the distribution of Hovsgol grayling during the daytime was significantly deeper compared to night distributions for both size classes (Kolmogorov-Smirnov test, all P values$<$0.05). For most transects, nighttime distributions of smaller grayling were concentrated around 15 m although they ranged between about 2–40 m. During the day densities were highest in deeper water along most transects, with modal peaks near 30 m, and the majority of the population present between 10 and 50 m. Vertical migration patterns of larger individuals were similar to smaller individuals, with densities concentrated around 15 m at night and 30 m during the day. Similar nighttime vertical distributions of both sizes of grayling were observed using vertical gillnets and hydroacoustics (figure not shown).

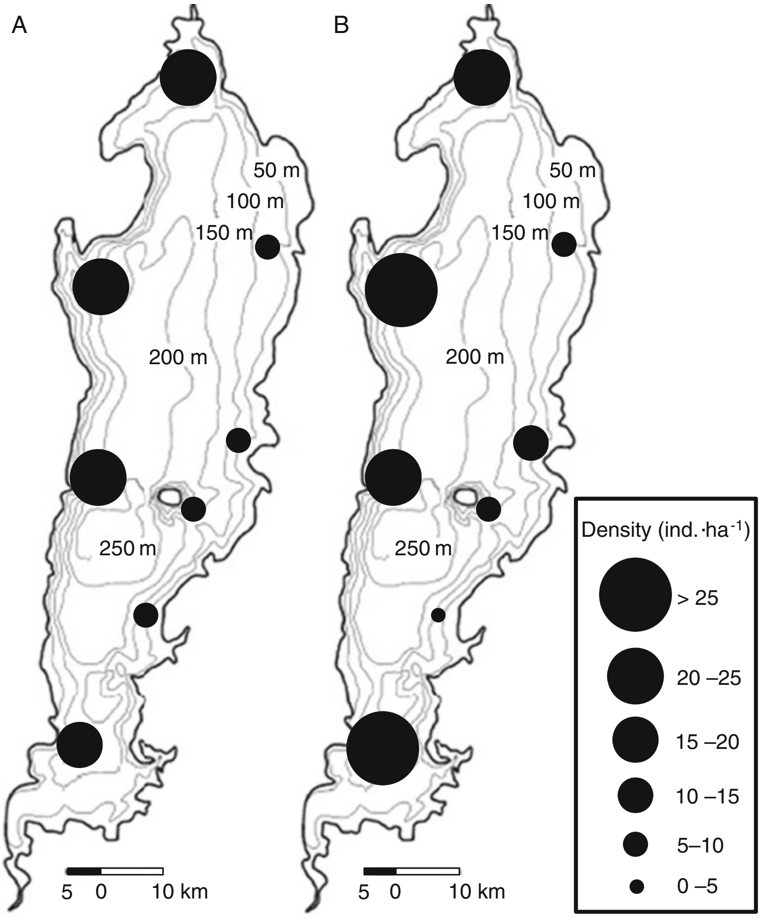
Zooplankton population characteristics

The deepwater zooplankton community was dominated by cyclopoid copepods, calanoid copepods, and the cladoceran families Bosminidae and Daphniidae. Copepod average volumetric densities were approximately 100 times greater than cladoceran densities (1,145 and 11 ind.•m^{-3}, respectively). We observed diel vertical migrations for calanoid copepods, *Bosmina* spp., and *Daphnia* spp. where densities were highest between 0 and 20 m in depth at night and 20–50 m in depth during the day (Fig. 6a, c, d). The vertical distribution of cyclopoid copepods did not appear to differ between day and night (Fig. 6b).

Discussion

Hovsgol grayling biomass estimates were low (4.4±0.9 kg•ha^{-1}) compared to fish populations in other large oligotrophic lakes. For example, Lake Superior, the most oligotrophic Laurentian Great Lake, has planktivore densities about 3.5 times higher than Lake Hovsgol, averaging 15.6 kg•ha^{-1} (Mason et al. 2005). Other more productive Laurentian Great Lakes, such as Lakes Michigan and Ontario, historically had

Fig. 4 Transect mean density estimates (ind.·ha^{-1}) of **(a)** smaller (100–170 mm) and **(b)** larger (> 170 mm) Hovsgol grayling (*Thymallus nigrescens*) in Lake Hovsgol, Mongolia



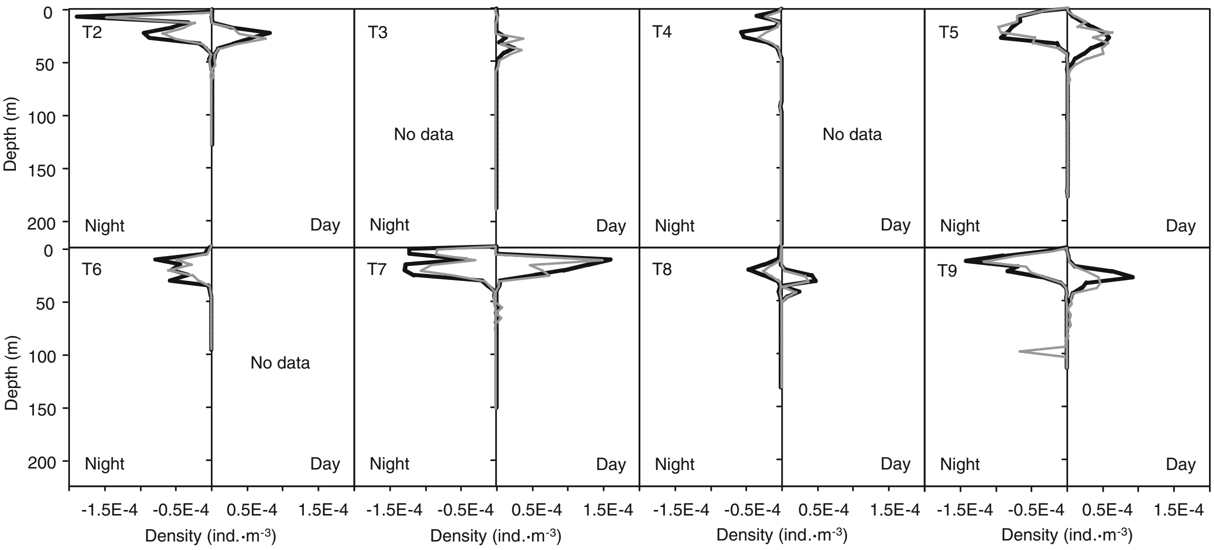


Fig. 5 Day and night vertical distributions of smaller Hovsgol grayling (gray line; 100–170 mm; *Thymallus nigrescens*) and larger Hovgsol grayling (black line; > 170 mm) at 8 transects (e.g. T2, T3, etc.) throughout Lake Hovsgol, Mongolia. No acoustic collections were made for those dates and times noted as "No data" in the figure

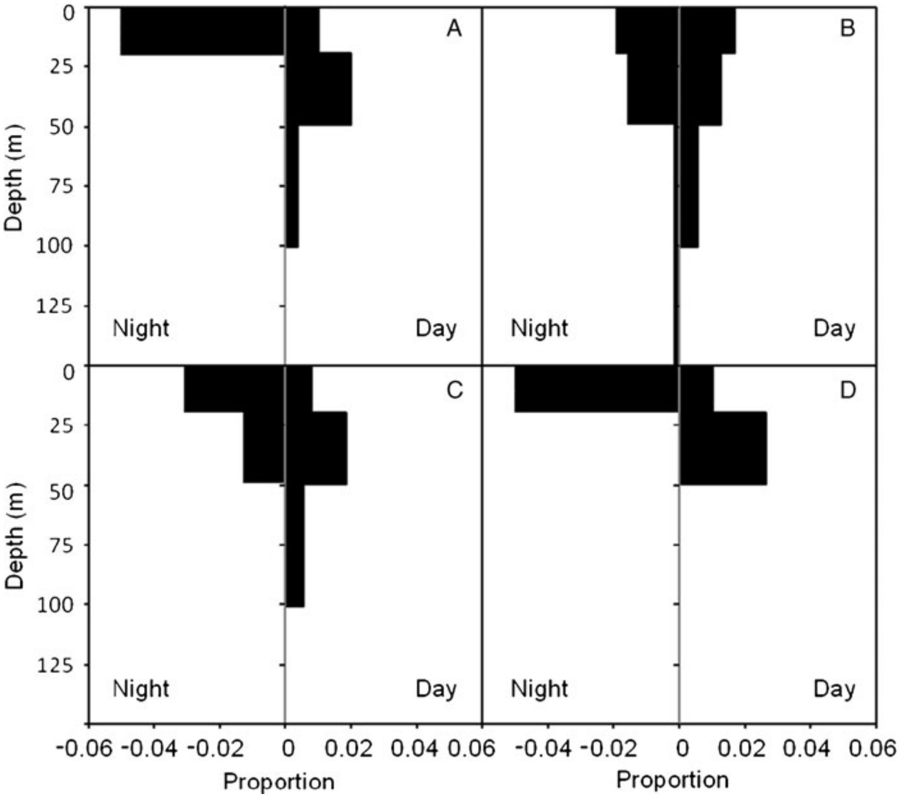


Fig. 6 Day and night vertical migrations, by proportion in each meter of the water column, of the zooplankton community consisting of **(a)** calanoid copepods, **(b)** cyclopoid copepods, **(c)** *Daphnia* spp., and **(d)** *Bosmina* spp

pelagic fish biomass estimates about 20–40 times higher than Lake Hovsgol, at 94 and 191 kg•ha^{-1}, respectively (Brandt et al. 1991; Mason et al. 2001). In Lake Tanganyika, near the peak of the seasonal biomass pulse, fish densities have been estimated at 880 kg•ha^{-1} using hydroacoustics (Coulter 1977). With no previous quantitative fish sampling in Lake Hovsgol available for comparison, it is unclear whether this low pelagic fish density represents the natural ultra-oligotrophic condition of the lake or whether it is the result of anthropogenic change. Given the lack of large scale fisheries (small scale, nearshore gillnetting and angling were occasionally observed) and invasive species, it seems likely that the low fish density is natural.

Pelagic grayling densities concentrated along the western and northern areas of the lake suggest that catchment morphometry or landscape-scale factors may influence Hovsgol grayling distributions in Lake Hovsgol. The western portion of the catchment is steeper than the eastern shore and soils may potentially experience a greater amount of weathering and therefore deposit more mineral nutrients on the western side of the lake. Alternatively, the prevailing west wind in conjunction with the steeper western shorelines may result in more terrestrial insects being deposited on the western shores. Interestingly, despite the difference in pelagic fish densities, there was little difference in grayling catch rates nearshore along the western/northern areas compared to the eastern areas. While our data suggests a difference in grayling densities in pelagic areas, it is important to recognize that our observations represent a single, seasonal snapshot of densities at the lakewide scale. Future work should determine if this large-scale spatial pattern is consistent across seasons and years and explore potential causal mechanisms.

Littoral areas had more Hovsgol grayling than pelagic areas; however, smaller grayling were only present in pelagic areas where predator densities were low. Piscivores (e.g. burbot, lenok, and Eurasian perch) were abundant in littoral samples but entirely absent pelagically. We speculate that smaller grayling, and many larger grayling, use the pelagia as a predation refuge or low risk, low reward (because of presumably lower food density than in the littoral zone) habitat. In smaller lakes, similar ontogenetic shifts between littoral and pelagic habitats occur for bluegill balancing the foraging rate—predation risk trade-off (Werner and Hall 1988).

Diel vertical migration is another common mechanism by which pelagic fish balance predation risk and growth opportunities. For example, amphipods (*Macrohectopus branickii*) in Lake Baikal and juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia lakes, undergo diel vertical migrations to increase consumption and decrease predation risk in pelagic areas (Clark and Levy 1988; Rudstam et al. 1992). In Lake Hovsgol, since there appear to be few pelagic predators of grayling, the presumed goal of migrating vertically is to track vertically migrating zooplankton resources. Although our zooplankton data were collected at a relatively coarse vertical resolution, it is apparent that most zooplankton show similar vertical migrations as grayling. The observed DVM trajectories of Hovsgol grayling are notably shallower (change in depth of ~15 m) than the observed DVM trajectory of other species, such as amphipods in Lake Baikal (change of ~100 m) (Rudstam et al. 1992) and kiyi (*Coregonus kiyi*) in Lake Superior (change of ~150 m) (Stockwell et al. 2010; Ahrenstorff et al. 2011), which may be due to the lack of predators in the pelagic areas of Lake Hovsgol. It is unclear why large Hovsgol grayling undergo similar vertical migrations as small individuals since they do not feed heavily on zooplankton resources. Perhaps the input of terrestrial invertebrates at night and subsequent death and sinking during the day plays a role in the similar movements because the percentage of terrestrial invertebrates consumed is similar (~20%) among all size classes of grayling. The movement pattern of larger individuals may also be a lasting relict of migrating when younger, or could provide a growth or a bioenergetic benefit due to the temperature differences experienced by grayling during migrations (Bevelhimer and Adams 1993).

The ontogenetic diet shift of Hovsgol grayling observed in our study has also been observed in studies on Arctic grayling in inland lakes. Juvenile Arctic grayling are commonly planktivorous (Schmidt and O'Brien 1982; Merrick et al. 1992), while adults rely more heavily on benthic production (O'Brien et al. 1979; Sierszen et al. 2003). In fact, Schmidt and O'Brien (1982) found that grayling larger than 170 mm could not be enticed to feed on zooplankton in the laboratory. Arctic grayling gill raker spacing increases with body size, up to 130 mm, suggesting a morphological mechanism for the shift in diets (Schmidt and O'Brien 1982).

Diets from larger Hovsgol grayling collected offshore suggest that they rely heavily on benthic production. However, we rarely observed grayling of any size below 50 m during the day or night. This is unlikely to be a physiological limitation as water temperatures and oxygen levels below 50 m are sufficiently high (> 4°C and>8 mg $O_2 \cdot l^{-1}$). The predominance of benthic invertebrates in larger grayling diets suggests that they are either migrating to littoral areas to feed benthically or are consuming emerging or vertically migrating benthic organisms in the water column. The former is not likely given that day and night density estimates were similar for grayling at most transects and depths. The latter is more likely given the diversity of bottom invertebrates, approaching 300 known species in Lake Hovsgol, some of which migrate off the bottom at night to feed or emerge as adults (Erbaeva et al. 2006; Erbaeva and Safronov 2006; Safronov 2006). Our fine mesh zooplankton net was likely unsuitable for capturing these larger organisms. Future research should include sampling with larger nets and mesh sizes.

Because Hovsgol grayling use a variety of habitats (e.g. littoral and pelagic areas) they are vulnerable to a variety of threats (e.g. climate change, invasive species, poaching, etc.). This emphasizes the importance of effective monitoring and management strategies (Grumbine 1994), which should be based on the results found here. Given the relatively low population densities of grayling, and the threat of a changing climate around Lake Hovsgol (Punsalmaa et al. 2005), we recommend regular lakewide monitoring of the grayling population. In addition to climate change, the introduction of invasive species to Lake Hovsgol offers significant threats to grayling, because they are the only fish species present in the pelagia. A successful introduction of a competitor, such as omul (*Coregonus migratorius*), or a predator, such as lake trout (*Salvelinus namaycush*), could significantly reduce the forage base available for grayling or increase their predation risk in pelagic areas. Interestingly, omul were introduced to Lake Hovsgol from Lake Baikal in 1956–1957 (Sideleva 2006) but we found no evidence of their presence. Prevention of the spread of invasive species should come in the form of education and awareness in high-use areas of the lake (e.g. in the towns of Hatgal and Khankh). Illegal fishing, gillnetting, and beach seining also threatens the grayling population, despite the closure of the fishery in 1995 when Hovsgol National Park was established. The minimal resources available for enforcement of current regulations should focus on areas with highest grayling densities which, based on our results, are located in littoral areas along the western shores of the lake.

Our study indicates that Hovsgol grayling densities are low compared to pelagic fish densities in other large lakes; however, this difference may simply represent the natural ultra-oligotrophic conditions of Lake Hovsgol. Hovsgol grayling diets and spatial distributions suggest that they are generalists, able to feed on a variety of food resources in different habitats throughout their lives. Despite this, it is important to develop conservation strategies to ensure the long-term health of this species. Specifically, conservation decisions should consider the primary threats to grayling in regards to their current lakewide densities and distributions. While our study provides important knowledge not previously documented, future research should investigate seasonal and yearly changes to the grayling population throughout the lake and in its in-flowing streams and rivers. In addition, examining Hovsgol grayling reproduction in terms of spawning site fidelity and success rates of in-lake *versus* stream spawning would be beneficial. Ultimately, a better understanding of the broader ecology and food-web of Lake Hovsgol will improve our ability to manage and monitor Hovsgol grayling and this unique ecosystem.

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