



Natural trophic variability in a large, oligotrophic, near-pristine lake



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ABSTRACT

Conclusions drawn from stable isotope data can be limited by an incomplete understanding of natural isotopic variability over time and space. We quantified spatial and temporal variability in fish carbon and nitrogen stable isotopes in Lake Hövsgöl, Mongolia, a large, remote, oligotrophic lake with an unusually species-poor fish community. The fish community demonstrated a high degree of trophic level overlap. Variability in $\delta^{13}\text{C}$ was inversely related to littoral-benthic dependence, with pelagic species demonstrating more $\delta^{13}\text{C}$ variability than littoral-benthic species. A mixed effects model suggested that space (sampling location) had a greater impact than time (collection year) on both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variability. The observed variability in Lake Hövsgöl was generally greater than isotopic variability documented in other large, oligotrophic lakes, similar to isotopic shifts attributed to introduced species, and less than isotopic shifts attributed to anthropogenic chemical changes such as eutrophication. This work complements studies on isotopic variability and changes in other lakes around the world.

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Introduction

Stable isotope analysis is a powerful tool for elucidating the effects of humans on aquatic ecosystems, useful both for documenting change over time due to anthropogenic impacts and for quantifying ecosystem disturbance. Historical isotope studies have illustrated trophic shifts resulting from the introduction of smallmouth bass and rock bass into Canadian lakes (Vander Zanden et al., 1999), sea lamprey and rainbow smelt into Lake Superior (Schmidt et al., 2009), and lake trout and *Mysis* shrimp into Lake Tahoe (Vander Zanden et al., 2003). Carbon stable isotope analysis has been used to illuminate a shift in Lake Tahoe toward pelagic primary production as a result of anthropogenic eutrophication (Chandra et al., 2005b). Nitrogen stable isotopes have been used to monitor or distinguish sources of anthropogenic nitrogen in lakes (Hoffman et al., 2012), and as indicators of habitat change or restoration (Lake et al., 2001).

Interpretation of these stable isotope data remains limited, however, by our incomplete understanding of natural isotopic and trophic variability in the absence of anthropogenic disturbance. For instance, what is the significance of a trophic shift in lake trout after the introduction of sea lamprey if we do not know how much trophic variability lake trout might have demonstrated over time in the absence of sea

lamprey? A number of studies have quantified temporal and spatial isotopic variability in a range of lakes, such as Lake Superior (Harvey and Kitchell, 2000), Lake Winnipeg (Hobson et al., 2012), Lake Jyväsjärvi (Syväranta et al., 2006), Lake Kyoga (Mbabazi et al., 2010) and Lake Erie (Guzzo et al., 2011). These studies found a range of interannual and among-site isotopic variability in a wide variety of fish species. But all of these study systems have been anthropogenically modified – and in some cases, quite extensively so – by commercial fishing, development, introduced species, and dams, making it difficult to assess background variability without these human impacts.

Understanding natural trophic variability is critical not only for interpreting past anthropogenic effects on ecosystems, but also for managing current resources and planning for such effects in the future. Ecosystem and resource management are often conducted in the context of the “range of natural variability” (Landres et al., 1999), and yet scientists and managers struggle to determine the extent of that range, frequently relying on coarse-scale paleo-data, or long-term data sets begun only after major anthropogenic impacts, as proxies for such “natural variability” (Morgan et al., 1994; Smol, 1992). Increases in variability have been shown in both laboratory and field contexts to act as an indicator for large-scale ecological regime shifts (Carpenter and Brock, 2006; Carpenter et al., 2011; Dakos et al., 2009) and stable isotope ratios have been suggested as an effective early-detection indicator for environmental change (Williams et al., 2007). But any changes in variability may be hard to detect over background noise without a better understanding of baseline variability.

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In this study, we quantified natural trophic variability in the near absence of anthropogenic effects, using carbon and nitrogen stable isotopes of a fish community in a near-pristine system. Our study lake, Lake Hövsgöl (Fig. 1), is a large, deep, oligotrophic lake in Mongolia, one of the least densely populated countries in the world. Lake Hövsgöl is subject to minimal commercial or recreational fishing or development, and has only ten species of fish (including the endemic and endangered Hövsgöl grayling (*Thymallus nigrescens*)) (Ocock et al., 2006; Sideleva, 2006), offering an unusually pristine and ecologically simple study system. In addition to describing the food web of this system, we focused on two more general questions about isotopic variability:

1. Do we see any patterns of isotopic variability related to life history and ecological characteristics of a species, such as size, trophic level and trophic guild (e.g., planktivory vs. piscivory)? We might, for example, expect to see decreased $\delta^{13}\text{C}$ variability among piscivores, since any differences in $\delta^{13}\text{C}$ in prey fish would be integrated in their piscivore consumers.
2. Which has greater impact on isotopic variability: collection year (temporal or interannual variability) or collection location (spatial variability)? In other words, are spatial and temporal variability comparable in this system? Other work – using other metrics – has suggested that spatial variability exceeds temporal variability (Kratz et al., 1995, 2003; Roset et al., 2007).

Methods

Study site

Lake Hövsgöl (51.0°N, 100.5°E) (also spelled Khovsgol and Khuvsgul) is located in northern Mongolia, just south of the Russian border,

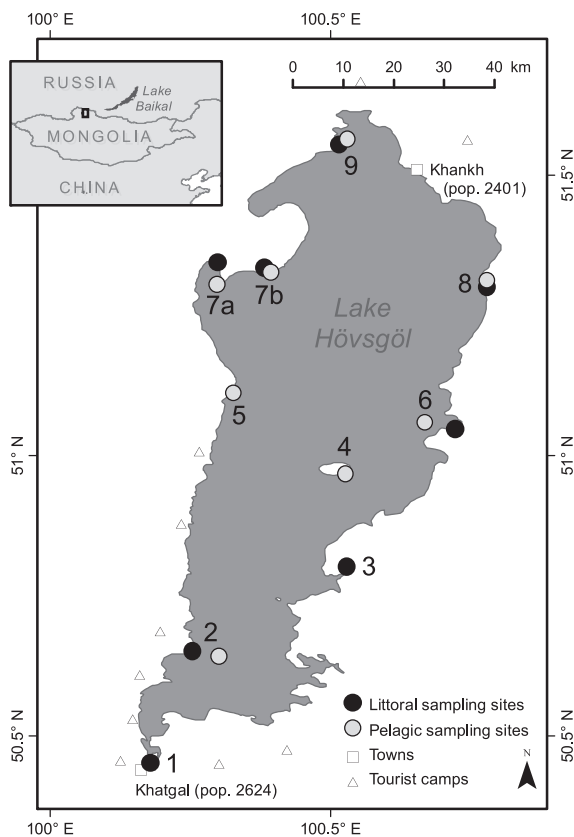


Fig. 1. Lake Hövsgöl, with collection locations. We sampled at both littoral and pelagic sites at most collection locations (2, 6, 8, 7a, 7b, 9). Two collection locations (1, 3) included only littoral sampling while two other collection locations (4, 5) included only pelagic sampling.

1645 m above sea level (Fig. 1). The lake is the nineteenth largest in the world by volume (383 km^3), 136 km long and 20–37 km wide, with a surface area of 2760 km^2 , a mean depth of 138 m and maximum depth of 262 m (Goulden et al., 2006; Herdendorf, 1982). The lake is dimictic, ice-covered from November to June, and ultra oligotrophic, with Secchi depths ranging from 14 to 30 m (Goulden et al., 2006; Goulden and Boldgiv, 2002; Kozhova and Kobanova, 2006). The lake is fed by approximately 96 tributaries and drains into the Eg River at the south end of the lake, which joins the Selenga River and flows into Lake Baikal (Goulden et al., 2006). Lake Hövsgöl lies about 200 km southwest of Lake Baikal and shares the same geological formation (the Baikal rift system), but is estimated to be much younger than Lake Baikal: 2–5 Ma old compared to Baikal's 20–65 Ma old (Goulden et al., 2006). Furthermore, geological data suggest that primary productivity in Lake Hövsgöl may have halted completely during the last glacial maximum, so that its ecosystem may only be about 10,000 years old, repopulated from nearby bodies of water after the glaciers receded (Goulden et al., 2006; Karabanov et al., 2004). This event may explain the paucity of fish species inhabiting the lake (Karabanov et al., 2004).

Ten fish species are known to inhabit the lake (Table 1), including Baikal omul (*Coregonus autumnalis migratorius*), which were introduced to the lake twice (in 1956–7 and 1980) (Dulmaa, 1999; Manchin and Dgebuadze, 2010), but are nonetheless rare or perhaps extirpated, as we did not encounter this species in five years of fish community sampling.

Lake Hövsgöl was established as a national park in 1995, and remains largely free of direct human impacts. The region is half a day's drive on unpaved roads from the nearest city (of less than 40,000) and the total population living around the lake is about 5000 (Population and Housing Census of Mongolia, 2010). A few tourist camps line the southwestern shore, and sparse mobile herding communities graze livestock along portions of both the eastern and western shores. None of the tributaries are dammed, and the lake is subject to limited fishing from shore. The region has, however, experienced unusually rapid warming in the last few decades (mean increase of $2.1 \text{ }^\circ\text{C}$ over the past 70 years) (Dagvadorj et al., 2009).

Sample collection

We collected tissue samples from six of the ten fish species known to occupy the lake (Table 1) from one to seven littoral locations around the lake in July 2006, 2009, 2011, 2012 and 2013 (mean $n = 14$ samples/species/year, total samples analyzed = 430) (Fig. 1, Table 2, Electronic Supplementary Material (ESM) Table S1). We were not able to collect every species at every location in every collection year. We collected Hövsgöl grayling at nine pelagic locations in addition to the littoral locations. We also collected Baikal grayling (*Thymallus arcticus baicalensis*), Siberian stone loach (*Barbatula toni*) and spiny loach (*Cobitis melanoleuca*), but did not include them in our analysis because the samples were not distributed adequately across years and locations. In 2006, we differentiated Hövsgöl grayling from Baikal grayling using visual identification characteristics. In all other years, we differentiated Hövsgöl grayling from Baikal grayling using gillraker counts, based on Berg (1962) and the distribution of our samples; those with greater than 23 gillrakers were designated Hövsgöl grayling (K. Olson, unpubl., T. Krabbenhoft, unpubl.).

Collection methods are described in greater detail by Ahrenstorff et al. (2011). Briefly, we collected fish primarily by nearshore horizontal gillnet (mesh size range: 12–90 mm) and supplemented with seining and minnow traps. At pelagic locations, we used vertical gillnets (mesh size range: 12–38 mm). Samples from all species, except Eurasian minnow (*Phoxinus phoxinus*), consisted of muscle tissue plugs from behind the dorsal fin. Smaller Eurasian minnows were sampled whole and larger ones were skinned and filleted. Collection locations are numbered to correspond with Ahrenstorff et al. (2011), with the exception of sites 7a and 7b, which Ahrenstorff et al. (2011) combined into a single site, 7.

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