



## Widespread occurrence of distinct alkenones from Group I haptophytes in freshwater lakes: Implications for paleotemperature and paleoenvironmental reconstructions

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### ABSTRACT

Alkenones are C<sub>35</sub>–C<sub>42</sub> polyunsaturated ketone lipids that are commonly employed to reconstruct changes in sea surface temperature. However, their use in coastal seas and saline lakes can be hindered by species-mixing effects. We recently hypothesized that freshwater lakes are immune to species-mixing effects because they appear to exclusively host Group I haptophyte algae, which produce a distinct distribution of alkenones with a relatively consistent response of alkenone unsaturation to temperature. To evaluate this hypothesis and explore the geographic extent of Group I haptophytes, we analyzed alkenones in sediment and suspended particulate matter samples from lakes distributed throughout the mid- and high latitudes of the Northern Hemisphere ( $n = 30$ ). Our results indicate that Group I-type alkenone distributions are widespread in freshwater lakes from a range of different climates (mean annual air temperature range:  $-17.3$ – $10.9$  °C; mean annual precipitation range:  $125$ – $1657$  mm yr<sup>-1</sup>; latitude range:  $40$ – $81$  °N), and are commonly found in neutral to basic lakes (pH > 7.0), including volcanic lakes and lakes with mafic bedrock. We show that these freshwater lakes do not feature alkenone distributions characteristic of Group II lacustrine haptophytes, providing support for the hypothesis that freshwater lakes are immune to species-mixing effects. In lakes that underwent temporal shifts in salinity, we observed mixed Group I/II alkenone distributions and the alkenone contributions from each group could be quantified with the RIK<sub>37</sub> index. Additionally, we observed significant correlations of alkenone unsaturation ( $U_{37}^K$ ) with seasonal and mean annual air temperature with this expanded freshwater lakes dataset, with the strongest correlation occurring during the spring transitional season ( $U_{37}^K = 0.029 * T - 0.49$ ;  $r^2 = 0.60$ ;  $p < 0.0001$ ). We present new sediment trap data from two lakes in northern Alaska (Toolik Lake, 68.632°N, 149.602°W; Lake E5, 68.643°N, 149.458°W) that demonstrate the

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highest sedimentary fluxes of alkenones in the spring transitional season, concurrent with the period of lake ice melt and isothermal mixing. Together, these data provide a framework for evaluating lacustrine alkenone distributions and utilizing alkenone unsaturation as a lake temperature proxy.

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## 1. Introduction

Long-chain alkenones (LCAs) are C<sub>35</sub>–C<sub>42</sub> aliphatic unsaturated ketones that are produced by a relatively limited number of species from the Isochrysidales order of Haptophyte algae. LCAs are globally distributed in oceans, estuaries and inland lakes. They have been studied extensively because the degree of LCA unsaturation is well correlated with the temperature of the water in which the lipids are produced, providing the basis for the widely used U<sub>37</sub><sup>K'</sup> and U<sub>37</sub><sup>K</sup> temperature proxies (Brassell et al., 1986; Prahl and Wakeham, 1987).

In the global oceans, LCA production is dominated by two closely related haptophyte species – *Emiliania huxleyi* and *Gephyrocapsa oceanica* (Volkman et al., 1980, 1995; Conte et al., 1998) – that are phylogenetically classified as Group III haptophytes (Theroux et al., 2010). Algal cultures of various strains of these organisms demonstrated that the temperature sensitivity of LCA unsaturation could vary as a function of the producing species (Prahl and Wakeham, 1987; Volkman et al., 1995). However, global core-top and water column calibrations of U<sub>37</sub><sup>K'</sup> vs. sea surface temperature (SST) indicated that temperature exerts a strong first-order control on the index in most open marine settings (Müller et al., 1998; Conte et al., 2006). This suggests that changes in species composition – defined here as “species effects” – generally do not impair marine SST reconstructions.

Coastal seas, estuaries and lakes, however, contain several different species of LCA-producing haptophyte algae that collectively exhibit more genetic diversity than their open marine relatives (Coolen et al., 2004; D'Andrea et al., 2006; Theroux et al., 2010; Bendif et al., 2013). Different haptophyte species often display disparate temperature sensitivities and LCA distributions (Prahl et al., 1988; Volkman et al., 1995; Sun et al., 2007; Ono et al., 2012; Nakamura et al., 2014, 2016; D'Andrea et al., 2016; Longo et al., 2016), which have caused species effects on LCA-based temperature reconstructions in saline lakes and coastal waters (Randlett et al., 2014; Wang et al., 2015; Warden et al., 2016). The diversity of LCA-producing haptophytes in these environments necessitates that species effects and associated ecological factors (e.g., production seasonality) be accounted for before LCA-based temperature reconstructions are pursued (e.g. Wang et al., 2015).

Recent observations have suggested that LCAs from freshwater lakes feature distinct distributions (Longo et al., 2016; Song et al., 2016) and are produced by a specific phylogenetic clade of haptophyte algae – the so-called Group I phylotype (D'Andrea et al., 2006; Theroux et al., 2010; Longo et al., 2016). Group I haptophyte species have yet to be physically described, however genetic and geochemical data have shown that these organisms produce a highly specific LCA distribution (Longo et al., 2013; Dillon et al., 2016) with a narrow range of temperature sensitivities across sites (D'Andrea et al., 2016; Longo et al., 2016). These findings prompted the hypotheses that freshwater lakes are potentially immune to species effects and furthermore, that new LCA indices involving the Group I-specific tri-unsaturated isomeric LCAs (RIK<sub>37</sub> and RIK<sub>38E</sub>) could be used to identify and quantify species mixing in sedimentary records (Longo et al., 2016). These indices would thereby establish metrics to assess the validity of LCA-based temperature estimations and concurrently reconstruct salinity-induced shifts in haptophyte species assemblages. Longo et al. (2016) intro-

duced and provided support for these hypotheses from a number of Arctic lakes in northern Alaska, yet they remain to be tested on a larger scale. Here, we address these hypotheses by investigating LCA distributions in sediments and suspended particulate matter (SPM) samples from lakes distributed throughout the mid- to high latitudes of the Northern Hemisphere. Concurrently, we provide an assessment of LCA occurrence, temperature sensitivity and production seasonality in freshwater lakes.

## 2. Methods

### 2.1. Samples and sample preparation

Samples were obtained from a number of sources including SPM, sediment traps, surface sediments and archived sediment cores (Fig. 1; Tables 1, S1).

#### 2.1.1. Suspended particulate matter

SPM samples were collected from Lake Ichino-megata, Japan (39.96°N, 139.74°E) on May 1, 2013 (G-09) and June 1, 2013 (G-10) by filtration of lake water (20 L) through glass fiber (GF/F) filters. Filters were freeze-dried and lipids were extracted with dichloromethane:methanol (9:1; v/v) using an automated solvent extraction system (100 °C and 1500 psi). The extracts were saponified in 0.5 mol L<sup>-1</sup> KOH in methanol at 80 °C for 2 h. The neutral fraction was separated into sub-fractions by silica-gel column chromatography using an automated sample preparation system (Rapid Trace SPE Workstation, Zymark Corp., Hopkinton, MA, USA). The solvents and sub-fractionation steps were the same as described previously (Harada et al., 2003). SPM samples were processed at the Japan Agency for Marine-Earth Science and Technology and shipped to Brown University, USA for LCA analysis.

#### 2.1.2. Surface sediments and archived sediment core and sediment trap samples

Surface sediments were collected from lakes in Northeastern China, Germany, France, Japan and Inner Mongolia. Surface sediments were collected as the top 0–1 or 0–2 cm of sediment obtained from sediment cores collected by gravity or pole coring devices, or as Ekman grab samples. Whenever possible, sediment samples were collected from the deepest point in the lake, in order to provide an integrated signal of water column LCA production. Sediments were freeze-dried and shipped to Brown University for further processing. Extraction and purification were carried out using standard methods (Longo et al., 2016), plus an additional purification with silver-thiolate functionalized silica gel for samples that featured complex matrices. Briefly, freeze-dried sediments were extracted with dichloromethane:methanol (9:1, v/v) using a Dionex™ accelerated solvent extraction (ASE) system (120 °C and 1200 psi). The extracts were separated into acid and neutral fractions by flash column chromatography with Supelco Supelclean LC-NH<sub>2</sub> (45 μm, 60 Å). Neutral compounds were eluted with dichloromethane/isopropanol (2:1, %v/v), followed by acidic compounds with 4% glacial acetic acid in ethyl ether. The neutral fractions were further separated into alkane, ketone and polar fractions by flash column chromatography using silica gel (40–63 μm, 60 Å) and eluting with hexane, dichloromethane and methanol, respectively. The ketone fraction was saponified, then purified again

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