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A hypothesis linking chrysophyte microfossils to lake carbon dynamics on ecological and evolutionary time scales

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ABSTRACT

Chrysophyte algae are common in the plankton of oligotrophic lakes and produce a rich microfossil record of siliceous cysts and scales. Paleolimnological investigations and phytoplankton records suggest that chrysophyte populations are increasing in a wide range of boreal and arctic lakes, ultimately representing one component of the limnological response to contemporary global changes. However, the exact mechanisms responsible for widespread increases of chrysophyte populations remain elusive. We hypothesize that recent increases in chrysophytes are related to rising pCO_2 in lakes, in part because these algae lack carbon concentrating mechanisms and therefore rely on diffusive entry of CO_2 to Rubisco during photosynthesis. We assessed the abundance of modern sediment chrysophyte microfossils in relation to summer CO_2 relative saturation in 46 New England (USA) lakes, revealing significant positive relationships for both cysts and scales. These observations imply that correlations between chrysophytes and limnological conditions including low pH, oligotrophy, and elevated dissolved organic matter are ultimately underscored by the high pCO_2 associated with these conditions. In lakes where chrysophyte populations have expanded over recent decades, we infer that increasingly heterotrophic conditions with respect to CO_2 have stimulated production by these organisms. This linkage is supported by the remarkable abundance and diversity of chrysophytes from middle Eocene lake sediments, deposited under atmospheric CO_2 concentrations significantly higher than present. The Eocene assemblages suggest that any chrysophyte-CO_2 connection borne out of results from modern and sub-recent sediments also operated on evolutionary time scales, and thus the absence of carbon concentrating mechanisms appears to be an ancient feature within the group. Chrysophyte microfossils may potentially provide important insights concerning the temporal dynamics of carbon cycling in aquatic ecosystems.

1. Introduction

Chrysophytes are primarily photosynthetic, occasionally mixotrophic, heterokont algae with silica metabolism. Although chrysophytes are widely distributed, they are most commonly associated with oligotrophic, low pH, or humic lake, pond, and river ecosystems (Siver, 1995; Kristiansen, 2005). Chrysophytes include two Classes, Chrysophyceae and Synurophyceae, for which all taxa produce endogenous siliceous cysts as a resting stage, sometimes referred to as stomatocysts or statospores. Some members of the Chrysophyceae and all synurophytes also produce siliceous scales. The number of scales sheathing an individual cell varies tremendously, ranging from 25 to 200 (Siver, 1991). Together, cysts and disarticulated scales form a robust fossil record for the chrysophyte algae, from which past environmental conditions can be inferred, most notably lake water pH and covariates (Smol, 1995; Paterson et al., 2002; Siver, 2002).

Paleolimnological analyses (Wolfe and Perren, 2001; Paterson et al., 2004; Köster et al., 2005; Laird and Cumming, 2008; Ginn et al., 2010; Thienpont et al., 2013) and multi-decadal phytoplankton monitoring records (Findlay et al., 2001; Paterson et al., 2008) indicate marked recent increases in chrysophyte abundance across many arctic and boreal lake regions. These authors have advanced several hypotheses to explain this trend, including the effects of climate warming on lake stratification patterns, changes in nutrient availability, diminished grazing pressures, and altered ultraviolet radiation regimes associated with dissolved organic carbon (DOC). However, none of these explanations is entirely satisfactory because most chrysophytes are highly motile flagellates that are able to migrate opportunistically to the most suitable microhabitats in the water column (Nicholls, 1995). Furthermore, many taxa, particularly within the Chrysophyceae, supplement photosynthesis with saprotrophic or phagotrophic nutritional strategies, implying a diminished role for dissolved nutrient concentrations in these instances (Raven, 1995). Furthermore, although these changes are geographically widespread, they are not necessarily expressed in

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all lakes of a given region. This implies that the underlying mechanism is somewhat decoupled from the direct effects of climate change on limnological regimes, and instead relates to processes that may differ considerably between individual lakes, such as those underpinned by biogeochemical cycling.

A conspicuous trait of chrysophyte physiology is the lack of any known enzymatic carbon concentrating mechanism (CCM; usually one or more carbonic anhydrases) to convert HCO_3^- to CO_2 when accessing ribulose bisphosphate carboxylase–oxygenase (Rubisco; Saxby-Rouen et al., 1998; Bhatti and Colman, 2005; Raven et al., 2005). During photosynthesis, chrysophytes are therefore metabolically dependent on direct diffusive entry of CO_2 to Rubisco, which is ultimately modulated by ambient pCO_2. This biochemical pathway appears to be shared among all photosynthetic chrysophytes and likely represents a plesiomorphic character for the group as a whole (Maberly et al., 2009). This contrasts sharply with other clades of aquatic algae that rely strongly upon CCMs, including cyanobacteria, chlorophytes, diatoms, and most rhodophytes (Giordano et al., 2005). Although the exact reason for the absence of CCMs in chrysophytes remains unspecified, it may suggest that they initially evolved during high CO_2 climatic regimes (Raven et al., 2012). Accordingly, chrysophytes are predicted to be favored under conditions of high limnetic pCO_2 because they are not metabolically encumbered with the cost of expressing CCMs, as are the co-occurrent photosynthetic algae with which they compete.

From the above observations, we develop and evaluate an alternate hypothesis for the documented increase of chrysophyte populations over recent decades. We propose that rising lake water pCO_2 is the proximate cause for these observations, thereby bridging studies of chrysophyte physiology, performed on axenic cultures under controlled laboratory conditions, with detectable responses at the lake ecosystem scale. While we do not deny the potential importance of any of the limnological factors mentioned above, or of their myriad interactions in both space and time, our objective is to provide a unifying framework that is broadly applicable to the range of lake ecosystems where chrysophyte populations are expanding. In doing so, we evaluate chrysophytes as potential indicators of CO_2 dynamics in lakes, which is a topic of interest in limnology and biogeochemistry for several reasons.

It has been established that CO_2 supersaturation is very common in lakes worldwide, leading to the condition of net heterotrophy with regard to carbon cycling (Kling et al., 1991; Cole et al., 1994; Duarte and Prairie, 2005). However, it remains uncertain to what extent this condition represents a natural limnological state, or one that has been enhanced, directly or indirectly, by anthropogenic interference with the global carbon cycle (Cole et al., 2007). Two principal mechanisms may lead to increased pCO_2 in lakes: (1) continuous re-equilibration with the rising CO_2 content of the atmosphere owed to fossil fuel combustion and land-use changes (currently ~2 ppm CO_2 per year; NOAA, 2012); and (2) enhanced mineralization of organic carbon in lakes. Contributions from the latter are necessary for supersaturation to develop, and for lakes to become net sources of CO_2 to the atmosphere. It is now recognized that organic carbon mineralization rates are highly temperature dependent and therefore predicted to increase in the future (Bergström et al., 2010; Gudasz et al., 2010; Kosten et al., 2010). While the resulting increase of lake water pCO_2 can enhance whole-lake primary production (Sobrino et al., 2009; Jansson et al., 2012), it is not clear how the community structure of primary producers is affected. For these reasons collectively, it is of considerable interest to evaluate whether sediment proxies exist that track the status of lake water CO_2 through time.

2. Materials and methods

2.1. Recent paleolimnological records of chrysophyte microfossils

Recent trends in chrysophyte microfossil abundance are illustrated by stratigraphic profiles from the sediments of nine lakes, three each from the following regions: the High Arctic (northern Greenland, Ellesmere Island, and western Spitsbergen), the middle Arctic (Baffin Island and southwestern Greenland), and the boreal forest of northeastern Alberta (Fig. 1). Details concerning the various sites have been presented elsewhere (Wolfe and Perren, 2001; Michelutti et al., 2005; Hazewinkel

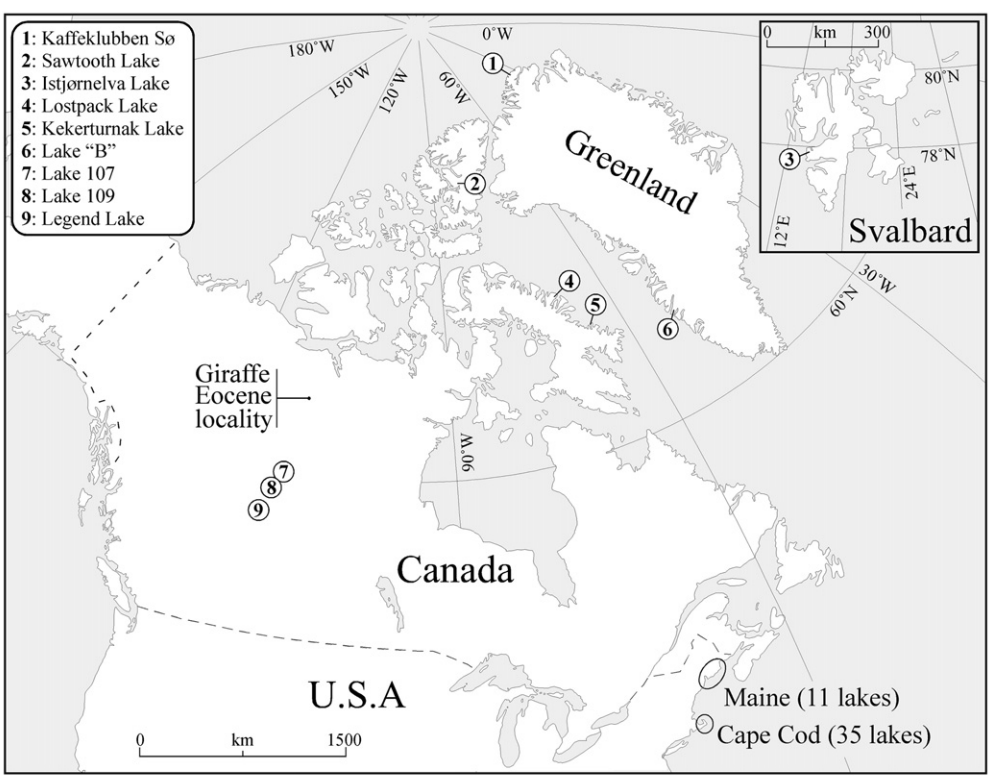

Fig. 1. Location map of the sites investigated for modern and fossil chrysophyte microfossils.