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Natural isotopic composition of carbon ($\delta^{13}C$) correlates with colony size in the planktonic cyanobacterium *Gloeotrichia echinulata*

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Abstract

To assess variability in carbon isotope signatures ($\delta^{13}C$) between and within populations under natural conditions, with a particular emphasis on colony size, we repeatedly collected planktonic colonies of a freshwater cyanobacterium *Gloeotrichia echinulata* in two lakes, Pyhäjärvi (southwest Finland) and Erken (southeast Sweden). Despite substantial differences in the average $\delta^{13}C$ signature of *Gloeotrichia* between lakes (−6.9‰ in Pyhäjärvi and −20.7‰ in Erken), a similar, systematic increase in $\delta^{13}C$ with colony size was observed in both lakes (of 2–3‰ in Pyhäjärvi and 3–5‰ in Erken). This suggests declining isotope fractionation with increasing colony size, probably related to diffusion limitation of carbon availability. Temporal variation explained a minor fraction of total subsample variability (range $\delta^{13}C$ ~4‰ in Pyhäjärvi and ~6‰ in Erken). Isotopic ^{13}C fractionation in *Gloeotrichia* was likely affected both by carbon source and by colony size.

Recent studies have reported a high variability in stable carbon isotope signatures ($\delta^{13}C$) of natural phytoplankton population over time, and within and among lakes (Falkowski 1991; Gu and Schelske 1996; Vuorio et al. 2006). Application of the stable isotope approach in studies of carbon cycling and food web dynamics in lacustrine systems requires an improved understanding of the factors controlling this variability.

The primary determinants of the isotopic composition of phytoplankton are the isotopic composition of the different forms of dissolved inorganic carbon (DIC: CO_2, CO_3^{2-}, and HCO_3^-) and their availability, as well as isotopic fractionation during assimilation (Peterson and Fry 1987; Goericke et al. 1994; Gervais and Riebesell 2001). CO_2 is the only form of DIC that freely penetrates cell membranes. During C assimilation phytoplankton fractionates against the heavier ^{13}C isotope and thereby becomes depleted in ^{13}C relative to the C source. Conversely, diffusion limitation may lead to low phytoplankton fractionation against ^{13}C (Popp et al. 1998). The relative contributions of diffusion and energy-dependent C acquisition are strongly dependent on the size of algal cells (Wolf-Gladrow and Riebesell 1997), and therefore cell size is an important determinant of stable isotope fractionation (Popp et al. 1998; Burkhardt et al. 1999). Small phytoplankton with high surface area : volume ratios may more effectively take up nutrients by molecular diffusion and should, thus, have a lower susceptibility to transport limitation of nutrients. Smaller cells should, therefore, also have higher fractionation (and hence more negative isotopic signatures) than larger cells with a lower surface area : volume ratio and greater boundary-layer thickness (Korb et al. 1996; Popp et al. 1998; Burkhardt et al. 1999). If passive CO_2 influx is the dominant mechanism of carbon transport, there should thus be an inverse linear relationship between isotopic fractionation against ^{13}C and cell size, provided cell geometry remains constant (Rau et al. 1996; Popp et al. 1998; Burkhardt et al. 1999).

The planktonic cyanobacterium *Gloeotrichia echinulata* (Smith) Richter forms rather large colonies, mostly >0.5 mm in diameter, which are relatively easy to isolate under a dissection microscope in amounts sufficient for stable isotope analysis. Most importantly, colony size in *Gloeotrichia* varies widely, allowing variability in colony $\delta^{13}C$ signatures between lakes and within populations to be studied, with a particular focus on changes in ^{13}C fractionation with colony size.

Methods

Study organism—Gloeotrichia echinulata forms free-swimming, spherical, gelatinous colonies with many trichomes radiating from a common center. The species occurs in mesotrophic waters in Northern temperate zone, but is relatively uncommon. The epilimnetic growth of *Gloeotrichia* is mostly reliant on internal P reserves accumulated during the benthic stage (Istvánovics et al. 1993), rather than on inorganic P assimilation. Declining internal phosphate concentration induces hair cell formation (Livingstone et al. 1983), and thus the growth of hair cells may be a sign of P-limitation. *Gloeotrichia* also has specialized cells (heterocysts) that are able to fix dinitrogen (N_2); thus, deficiency in inorganic nitrogen is unlikely to limit its growth.

Study areas—Gloeotrichia echinulata colonies were collected from two mesotrophic lakes (Table 1): Pyhäjärvi, in southwest (SW) Finland (61°00′N, 22°17′E) and Erken, in southeast (SE) Sweden (59°25′N, 18°15′E). *G. echinulata* mass occurrences have been frequent since 1993 in Pyhäjärvi and since at least the late 1940s in Erken.

Samples—Natural populations of *Gloeotrichia* were sampled five times in July–August 2002 with a plankton net (mesh size 250 μm) from a 0–2-m-deep-water column. Samples were preserved with nitrogen- and carbon-free

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Table 1. Basic limnological features (means ± SD) of the study lakes Pyhäjärvi (SW Finland) and Erken (SE Sweden) in July–September 2002.

		Pyhäjärvi	Erken
Catchment area	km^2	461	141
Lake area	km^2	154	24.2
Max. depth	m	26	20.7
Retention time	a	3.2	7.4
Total phosphorus	mg m^{-3}	19±5	21±5
PO_4–P	mg m^{-3}	1.4±0.9	2.1±1.2
Total nitrogen	mg m^{-3}	470±35	736±105
$(NO_2^- + NO_3^-)$–N	mg m^{-3}	3.0±0.0	4.3±2.1
Chl *a*	mg m^{-3}	8.7±2.9	4.3±1.6
Alkalinity	mmol $L^{-1} CaCO_3$	0.2	0.9±0.06
Conductivity	m S m^{-1}	8.0±0.0	27.7±0.4
DIC*	mg C L^{-1}	5.3±0.1	21.6±0.0
pH*		7.5±0.2	8.2±0.2

* DIC = dissolved inorganic carbon; pH = potential hydrogen.

alkaline Lugol's solution. Prior to stable isotope analysis, the *Gloeotrichia* colonies were rinsed in distilled water and sorted manually into four size groups (diameters 250–500, 500–750, 750–1000, and >1000 μm) under a dissection microscope. Colony diameter was measured without including hair cells, and colonies with and without hair cells were separated into two subgroups. A known number of colonies of each subgroup were transferred into tin capsules and dried at 60°C (1–4 mg dry wt.).

Chemical and physical analyses—Analyses of chlorophyll *a* (Chl *a*), total phosphorus (TP), phosphate phosphorus (PO_4–P), total nitrogen (TN), nitrate and nitrite-N (as a sum of $(NO_2^- + NO_3^-)$–N for Pyhäjärvi), ammonium-N (NH_4^+–N), Chl *a*, potential hydrogen (pH), and alkalinity of lake water were performed according to standard methods (Blomqvist et al. 1989; Niemi et al. 2001). During field-sampling concentrations of the main components of dissolved inorganic carbon of the lake water (i.e., CO_2 and HCO_3^- were calculated from alkalinity and pH values). Dissolved inorganic carbon was acidified and then analyzed following Salonen (1981). New alkalinity and acidity measurements were performed in August 2006 to confirm the CO_2 and HCO_3^- concentration calculations in each lake. Measurements of alkalinity and pH corrected for water temperature were converted to partial pressure of CO_2 (pCO_2) using an appropriate Henry's law constant, corrected for temperature and atmospheric pressure (Rantakari and Kortelainen 2005).

Stable isotope analysis—Samples were analyzed for organic carbon and nitrogen using an Integra Elemental Analyser, and C and N concentrations per colony were calculated by dividing by the number of colonies in each sample. Carbon isotopic composition of *Gloeotrichia* ($\delta^{13}C_{Ge}$) was determined with a Europa Scientific Hydra 20–20 continuous-flow isotope-ratio mass spectrometer (precision ± 0.1‰) at the Stable Isotope Facility of the University of California, Davis, U.S.A. Results are expressed as δ values given as parts per thousand (‰). These represent the deviation in ratios of the heavy carbon (^{13}C) isotope to the lighter carbon (^{12}C) isotope relative to the standard, Pee Dee Belemnite limestone carbon. Measurements of stable carbon isotope signatures of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) were not taken at the time of *Gloeotrichia* sampling. However, DIC measurements were taken later, in August 2006 (analyses were run at the Department of Biological and Environmental Sciences, University of Jyväskylä, Finland). The amount of DIC is usually rather constant over time, especially in well-buffered lakes such as Erken. The main sources of DIC are geogenic or atmospheric, and changes in the isotopic composition of DIC entering our study lakes are relatively unlikely. Consequently, the $\delta^{13}C_{DIC}$ in these lakes, although seasonally variable due to selective uptake by phytoplankton (Jones et al. 2001), is unlikely to have changed significantly between 2002 and 2006.

Results

Lake physical and chemical characteristics—During the study, TP concentration was ~20 mg m^{-3} in both lakes, and both PO_4–P and the combined $(NO_2^- + NO_3^-)$–N concentrations were close to the analytical detection limits. Ammonium-N concentration was ~10 mg m^{-3} in Pyhäjärvi and 31 mg m^{-3} in Erken. Total N concentration in Erken, 640–970 mg m^{-3}, was almost twice that in Pyhäjärvi, 420–490 mg m^{-3}. In Erken, pH ranged from 7.9 to 8.4 and was higher than in Pyhäjärvi where it ranged from 7.3 to 7.7. During field sampling water temperature increased from ~19°C to 22°C in both lakes. Conductivity values were quite stable in both lakes, at ~28 mS m^{-1} in Erken and 8 mS m^{-1} in Pyhäjärvi. In Erken, mean alkalinity was 0.9 mmol L^{-1} $CaCO_3$ (SD = 0.06). Alkalinity in Pyhäjärvi was not measured during our study, but the long-term average has been ~0.2 mmol L^{-1} $CaCO_3$ (SD = 0.05), a value confirmed by measurements taken in August 2006 (0.21 ± 0.003 mmol L^{-1}). The *Gloeotrichia* bloom was accompanied by a two- to three-fold increase in Chl *a*, from 3 μg L^{-1} to 5–6 μg L^{-1} in Erken and from 3 μg L^{-1} up to 9 μg L^{-1} in Pyhäjärvi, while changes in pH from 7.3 to 7.7 in Pyhäjärvi suggest a simultaneous drop in CO_2 concentration from two- to four-fold supersaturation to 100–150% saturation. The corresponding drop in pCO_2 was from $1.66 \times 10^5 \pm 0.97 \times 10^5$ to $0.60 \times 10^5 \pm 0.27$ Pa. Higher pH values in Erken suggest that almost all the DIC was bicarbonate, a suggestion confirmed by zero acidity. The partial pressure of CO_2 in Erken, calculated from alkalinity, suggested a similar drop in pCO_2 (from $1.17 \times 10^5 \pm 0.47 \times 10^5$ to $0.65 \times 10^5 \pm 0.12 \times 10^5$ Pa) before and during the *Gloeotrichia* bloom to that observed in Pyhäjärvi. Supplementary measurements of alkalinity in 2006 suggested rather similar pCO_2 values in both lakes, $0.49 \times 10^5 \pm 0.0\,2 \times 10^5$ and $0.46 \times 10^5 \pm 0.06 \times 10^5$ Pa in Pyhäjärvi and Erken, respectively.

Elemental composition and stable carbon isotope signatures of Gloeotrichia—Most colonies had hair cells throughout the study (Table 2). In Erken, the average diameter of the largest colony size group was ~1000–

Table 2. Colony size classes, presence (+) or absence (−) of hair cells, and $\delta^{13}C$ signatures (mean ± SD) of *Gloeotrichia echinulata* during July–August 2002 in two lakes: Pyhäjärvi (SW Finland) and Erken (SE Sweden).

Lake	Colony diameter (μm)	Hair cells	n	$\delta^{13}C$ (‰)
Pyhäjärvi	>1000	+	5	−5.3±0.4
	750–1000	+	5	−6.6±0.7
	750–1000	−	3	−7.3±0.7
	500–750	+	5	−7.4±0.9
	500–750	−	3	−7.5±0.3
	250–500	+	4	−7.8±0.9
	All		25	−6.9±1.1
Erken	>1000	+	4	−18.6±0.8
	750–1000	+	4	−19.5±0.8
	750–1000	−	1	−18.4
	500–750	+	5	−21.4±0.9
	250–500	+	4	−22.8±0.5
	250–500	−	4	−22.3±1.4
	All		25	−20.7±1.8

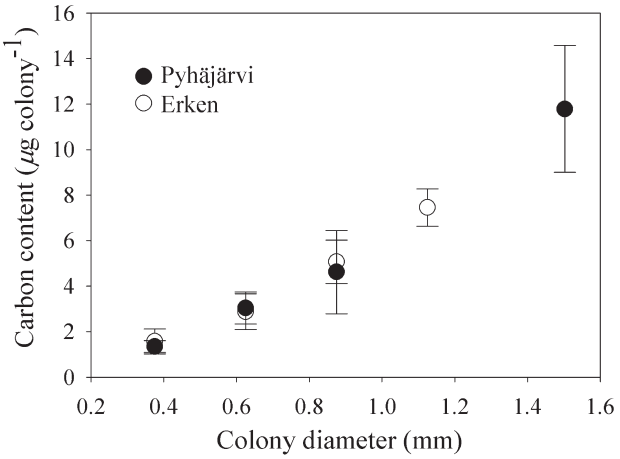

Fig. 1. Colony biomass of the cyanobacterium *Gloeotrichia echinulata* (carbon content in μg, means ± SD) in each of four colony size-classes in lakes Pyhäjärvi (SW Finland) and Erken (SE Sweden) in July–August 2002.

1250 μm, while in Pyhäjärvi it was considerably larger, at 1400–1600 μm. $\delta^{13}C_{DIC}$ signatures in 2006 were similar in both lakes, at −3.2 ± 0.2‰ in Pyhäjärvi and −3.4 ± 0.2‰ in Erken.

Carbon concentration per colony increased significantly with colony size in both lakes (Fig. 1; ANOVA, $p < 0.001$, $F_3 = 34.95$ in Pyhäjärvi and $F_3 = 19.79$ in Erken). The C : N molar ratio of colonies (5.2 ± 0.7 and 5.1 ± 0.4 in Pyhäjärvi and Erken), did not differ between lakes but seemed to decline with colony size, although this trend was not statistically significant.

We observed substantial differences in $\delta^{13}C_{Ge}$ between lakes (Fig. 2). In Pyhäjärvi, the $\delta^{13}C_{GE}$ ranged from −4.8‰ to −8.9‰ (mean = −6.9‰ ± 1.1, $n = 25$). In Erken, the $\delta^{13}C_{GE}$ was considerably lower, at between −24.3‰ and −17.8‰ (mean = −20.7 ± 1.8, $n = 25$). These between-lake differences were highly significant (ANOVA, $p < 0.001$, $F_1 = 1176.18$).

Wide variability was also found among simultaneously collected colonies, with $\delta^{13}C_{Ge}$ increasing systematically with colony size, by 2–3‰ in Pyhäjärvi and 3–5‰ in Erken, from the smallest to the largest size group. Between-size group variation was highly significant (Pyhäjärvi $p < 0.001$, $F_3 = 34.95$, Erken $p = 0.001$, $F_3 = 19.79$). Differences between colonies with and without hair cells were not statistically significant. Temporal changes in $\delta^{13}C_{Ge}$, which averaged 1–2‰ in both lakes, were moderate relative to the total range of variation (≈4‰ in Pyhäjärvi and ≈6‰ in Erken).

There was a linear relationship between $\delta^{13}C_{Ge}$ signature and colony diameter (d) in both lakes (Fig. 3), explaining 64% of the variability in the $\delta^{13}C_{Ge}$ signature in Pyhäjärvi and 74% in Erken. The slope of this relationship was slightly higher in Erken (ANOVA, $p = 0.043$, $F_1 = 4.30$).

Discussion

$\delta^{13}C$ values of colonies of the planktonic cyanobacterium *Gloeotrichia echinulata* ranged from −8.9‰ to −4.8‰ in Pyhäjärvi and from −24.3‰ to −17.8‰ in Erken. The mean difference in $\delta^{13}C_{Ge}$ of 13.5 ± 1.0‰ between Pyhäjärvi and Erken was consistent across all colony size groups. Although the DIC concentration in Erken was around four times higher than that in Pyhäjärvi, the $\delta^{13}C_{DIC}$ signatures of the two lakes were similar.

Thus, the large between-lake difference in $\delta^{13}C_{Ge}$ signatures was not explained by differences in their $\delta^{13}C_{DIC}$ signatures. Several alternative mechanisms could, however, lead to between-lake differences in the $\delta^{13}C$ signatures of phytoplankton.

First, when pH is high and the concentration of CO_2 is low, many phytoplankton species, in particular cyanobacteria, are able to assimilate HCO_3^-, which is isotopically relatively heavy. However, even if uptake of HCO_3^- (7–9‰ heavier than CO_2) accounted for all C assimilation in our study species, it could not wholly explain the difference in the $\delta^{13}C_{Ge}$ between lakes. Moreover, this mechanism should lead to ^{13}C enrichment in Erken; a situation opposite to that observed. Furthermore, pH is relatively low (~7.5) in Pyhäjärvi and, hence, HCO_3^- is probably not a significant carbon source.

Low concentrations of total DIC, as observed in Pyhäjärvi, could potentially result in active transport of either CO_2 or HCO_3^- to the cell, which could increase fractionation by phytoplankton, leading to depleted ^{13}C signatures (Keller and Morel 1999). Nonetheless, this mechanism would also work in the opposite direction to that observed, yielding depleted ^{13}C signatures in Pyhäjärvi.

Low $\delta^{13}C$ signatures have sometimes been attributed to the use of atmospheric CO_2 by cyanobacteria (*Microcystis aeruginosa* and *Anabaena flos-aquae*) that form surface blooms (Zohary et al. 1994; Gu and Alexander 1996). *Gloeotrichia* is, however, unlikely to form surface blooms in the pelagial, and therefore atmospheric CO_2 at the air–water interface is probably not an important C source for this species. Moreover, this mechanism would not explain the difference between Erken and Pyhäjärvi. Significantly lighter $\delta^{13}C$ signatures (−24.0 to −28.7‰) in other

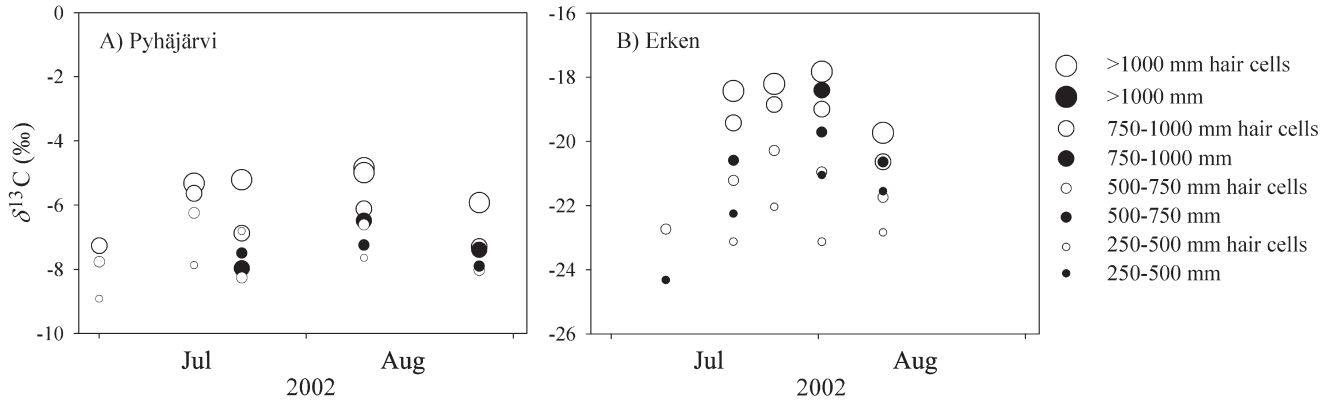

Fig. 2. Stable carbon isotope signatures ($\delta^{13}C$) in different size classes of *Gloeotrichia echinulata* colonies (with and without hair cells) in lakes (A) Pyhäjärvi (SW Finland) and (B) Erken (SE Sweden) in July–August 2002. Note different scales on the $\delta^{13}C$ axis.

phytoplankton taxa in Pyhäjärvi (Vuorio et al. 2006) do not indicate assimilation of isotopically heavy DIC deriving from methanogenesis, either, as was suggested by Gu et al. (1996) for a hypertrophic lake.

Despite the absolute difference in the $\delta^{13}C_{Ge}$ signatures between lakes, ^{13}C enrichment increased significantly, and at a relatively similar rate, with colony size in both lakes. Similar ^{13}C enrichment with increasing colony mass has been demonstrated with *Trichodesmium* colonies off Bermuda, Atlantic Ocean (Tchernov and Lipschultz 2008). The reduction in surface area : volume ratios with increasing colony size and increasing boundary-layer thickness should limit the diffusion of CO_2 into larger colonies (Wolf-Gladrow and Riebesell 1997; Burkhardt et al. 1999) and should lead to enriched $\delta^{13}C$. Moreover, laboratory experiments have demonstrated that a linear decline in stable isotope fractionation with increasing colony size applies even in the case of active HCO_3^- uptake (Keller and Morel 1999). Indeed, the observed variability in $\delta^{13}C_{Ge}$ among simultaneously collected colonies suggests a moderate decline in stable isotope fractionation with increasing colony size in both lakes, consistent with an expected simple linear relationship between CO_2 uptake rate and $\delta^{13}C_{Ge}$ signatures (Popp et al. 1998).

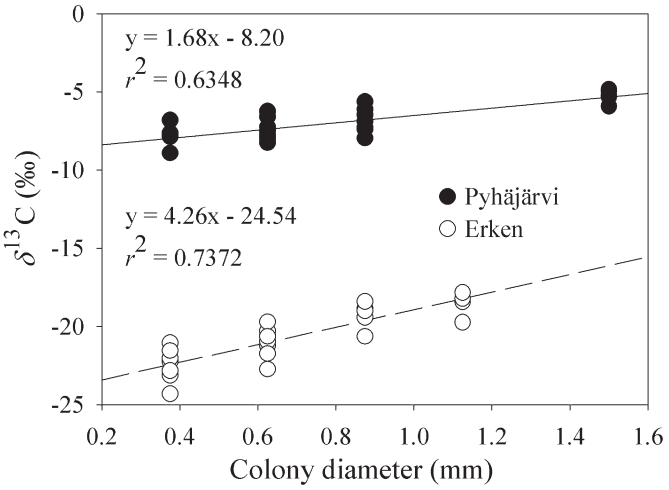

Fig. 3. Relationship between the stable carbon isotope signature ($\delta^{13}C$) and colony diameter of *Gloeotrichia echinulata* in lakes Pyhäjärvi (SW Finland) and Erken (SE Sweden) in July–August 2002.

The large difference in the $\delta^{13}C$ signatures of *Gloeotrichia* between lakes could not be explained. It was not due to differences in their $\delta^{13}C_{DIC}$ signatures, but might arise from differences in the dominant inorganic carbon source in the two lakes, although the mechanisms involved remain obscure. Data from other hardwater and softwater lakes are required to settle this issue. Regardless of this difference, however, the $\delta^{13}C$ signatures of *Gloeotrichia* were consistently correlated with colony size. It is likely that similar relationships commonly affect stable carbon isotopic fractionation by phytoplankton under natural conditions.

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