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## A comparison of phytoplankton communities of the deep chlorophyll layers and epilimnia of the Laurentian Great Lakes

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### ABSTRACT

Phytoplankton biomass and primary productivity within Great Lakes deep chlorophyll layers (DCL) remain largely uninvestigated. Consequently, the taxonomic makeup of DCL phytoplankton communities, as well as the mechanisms regulating their formation and maintenance, is poorly understood. We examined 6 years of phytoplankton compositional characteristics of Great Lakes summer DCL and epilimnetic communities as well as spring communities from isothermal water columns. DCLs were regularly observed during summer stratification in all lakes with the frequent exception of Lake Erie. Relative compositions of summer chlorophyte and cryptophyte assemblages were not different between the epilimnion and DCL, but DCL phytoplankton communities from other algal groups were distinct from their epilimnetic counterparts and comprised an integration of phytoplankton from the overlying epilimnetic assemblages and relict taxa characteristic of spring. Summer epilimnetic communities were characterized by higher abundances of cyanophytes, and centric diatom communities were dominated by *Cyclotella sensu lato* (i.e. species within *Cyclotella* and closely related genera). *Cyclotella* species exhibited distinct patterns of vertical distribution, with small-bodied taxa being partitioned heavily into the epilimnion, while larger-bodied forms tended to occupy the DCL. Vertical size partitioning was exemplified by larger mean individual cell sizes in epilimnetic siliceous algae (diatoms and chrysophytes) in the DCL compared to the epilimnion, while the opposite pattern was exhibited by cyanophytes. These findings demonstrate the importance of stratification intensity to vertical structuring of summer phytoplankton communities and imply that changing stratification regimes (such as that due to recent climate change) may exert profound effects on Great Lakes primary producer communities.

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### Introduction

In water bodies that exhibit seasonal or permanent stratification, deep chlorophyll layers (DCL) (Fahnenstiel et al., 1984; Moll et al., 1984) often occur in the water column below the thermocline (Brooks and Torke, 1977; Pilati and Wurtsbaugh, 2003). While the DCL may represent a large portion of the water column chlorophyll and can be responsible for much of the primary production of a lake, the mechanisms governing the general composition and dynamics of the DCL remain largely uninvestigated (Camacho, 2006; Moll and Stoermer, 1982; Pilati and Wurtsbaugh, 2003). There remain several potentially valid hypotheses regarding mechanisms that influence the formation and maintenance of the DCL. These include active processes such as *in situ* production in the metalimnion and hypolimnion (Cullen, 1982; Fasham et al., 1985; Venrick, 1982) and decreased grazing pressure below the thermocline (Fee, 1976), as well as active light and/or

predation avoidance by motile taxa (Campbell et al., 2009; Fiedler, 1982; Saros et al., 2005). Alternatively, DCL formation can be driven by passive mechanisms, including formation of a relict community following stratification and differential sinking of phytoplankton from the epilimnion (Kiefer and Kremer, 1981).

When they occur, DCLs can vary considerably in their taxonomic composition and structure (Cullen, 1982; Cullen and Eppley, 1981), and this can confound indirect measures of DCL productivity. Chlorophyll *a* concentrations estimated by *in situ* fluorescence, not necessarily a reliable indicator of phytoplankton biomass (Falkowski and Kolber, 1995), may be affected by several factors and can exhibit substantial heterogeneity both through space and among taxa (Yilmaz et al., 1994). Cullen (1982) cautioned that chlorophyll *a* profiles provide limited information regarding mechanisms that regulate DCL formation and maintenance. Taxonomic investigations of phytoplankton communities in both the DCL and overlying waters are necessary in order to understand the role of the DCL in vertical community structure and function.

Comprehensive taxonomic studies can provide insight into the importance of DCLs in contributing to overall water column productivity

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as well as food web function and potentially as an indicator of climate change effects on water column stratification. Although relationships between algal productivity, carbon uptake, and DCL algal communities have been investigated in marine systems (e.g., Jochem and Zeitzschel, 1993; Shulenberger and Reid, 1981; Veldhuis et al., 1997), relatively little work has been conducted on DCL productivity in lakes (Fee, 1976). Planas (1990, 1973) showed that metalimnetic carbon assimilation rates can often be higher than those observed in the epilimnion. Current understanding of what taxa are responsible for DCL productivity is minimal (Camacho, 2006). Several authors have described deep, maximal abundances of eukaryotic algal groups (e.g., Barbiero and Tuchman, 2004, 2001; Fahnenstiel et al., 1989; Pick et al., 1984; Wolin and Stoermer, 2005) within the DCL, while cyanophytes have been implicated as the primary component of DCL communities in other systems (Craig, 1987; Gervais et al., 2003; Kasprzak et al., 2000). Low grazing pressures in the metalimnion (Work and Havens, 2003) can provide refugia for palatable algal taxa capable of existing under low-light conditions (Gasol et al., 1992) and favor biomass accumulation of these forms in the DCL during stratification (Naselli-Flores and Barone, 2003). Whether these mechanisms exert sufficient influence to constrain the development of a DCL-specific algal community across multiple lakes is unknown.

The existence of DCL-specific assemblages could provide a useful indicator of prolonged stratification periods that could be linked to data from paleolimnological reconstructions. For instance, increases in *Cyclotella sensu lato* (including taxa from the genus *Cyclotella* and closely related genera) taxa in the Great Lakes (Chraïbi et al., 2014) and in other northern lakes (e.g., Leavitt et al., 2009; Rühland et al., 2008) appear to be related to increasing atmospheric temperatures that are changing the physical characteristics of lake stratification. This group includes species from the genus *Cyclotella* and other closely related genera. Examples from the Laurentian Great Lakes include *Cyclotella comensis* Grunow, *Discostella pseudostelligera* (Hustedt) Houk and Klee, and *Cyclotella cf. delicatula* Reavie and Kireta. This paleolimnological shift may be related to changing assemblage characteristics of Great Lakes DCLs, but to date, no evaluation supports such a hypothesis.

Deep chlorophyll layers have been reported from the Great Lakes (Putnam and Olson, 1966; Watson et al., 1975) and have been studied primarily within Lakes Superior (Barbiero and Tuchman, 2001; Putnam and Olson, 1966; Watib et al., 1975; White and Matsumoto, 2012), Michigan (Fahnenstiel and Scavia, 1987; Scavia and Fahnenstiel, 1987), and Huron (Barbiero and Tuchman, 2001; Fahnenstiel and Carrick, 1992). To date, investigations of DCLs within the Great Lakes have been limited to single lakes and short temporal durations. Fahnenstiel and Scavia (1987) provided a synopsis of the DCL community of Lake Michigan and its temporal trends from 1982 to 1984, while Twiss et al. (2012a) described growth and loss rates in phytoplankton communities in Lake Ontario. Barbiero and Tuchman (2001) broadly summarized physical, chemical, and biological properties of DCLs in the Great Lakes based on a single season dataset (1998).

We compared and contrasted the composition and structure of phytoplankton communities from the spring isothermal water column and summer epilimnia and DCLs of the Great Lakes during the period spanning 2007–2012, and evaluated dissimilarities between epilimnetic and DCL phytoplankton assemblages at the basin scale in order to determine whether a characteristic DCL community exists within the Great Lakes. We also described general biovolume and abundance characteristics for epilimnetic and DCL assemblages in order to provide initial insight into the relative contributions of DCL assemblages to the overall Great Lakes phytoplankton community. We hypothesize that the phytoplankton assemblages of Great Lakes DCLs are compositionally distinct from corresponding epilimnetic assemblages. We further anticipate that the same suite of taxa contributes to this dissimilarity across lakes. Additionally, we hypothesize that size differences exist between conspecific occupants of the DCL and epilimnion.

## Methods

### Sampling site locations and sample collection

A total of 1034 phytoplankton samples were collected from 71 stations within the Great Lakes during a series of twice-annual cruises (April and August 2007–2012) by the R/V *Lake Guardian* as part of the USEPA–GLNPO Monitoring Program (Fig. 1). Water quality parameters (temperature, specific conductivity, pH, irradiance, dissolved oxygen, turbidity, chlorophyll *a* by fluorescence) were measured *in situ* using a SeaBird 911 CTD equipped with auxiliary sensors. Additional parameters (total phosphorus, nitrates + nitrites, silica) were measured according to methods described in detail by the USEPA (2010) standard operating procedure. Phytoplankton samples were collected simultaneously with water quality measurements via Niskin bottle rosette. Integrated samples collected in spring (381) were produced by combining samples from discrete depths through the water column. Summer integrated epilimnetic samples (385) were produced by combining samples from discrete depths above the thermocline (surface, 5 m, 10 m, 20 m), while summer DCL samples (268) were taken from a single discrete depth associated with the fluorescence-inferred chlorophyll *a* maximum below the thermocline at each site (USEPA, 2010). When no DCL was detected at summer stations, only integrated epilimnetic samples were collected. Spring sampling cruises occurred annually in April, while summer cruises took place annually in August. This study is based on data from samples collected during the 2007–2012 cruises.

### Sample preparation and algal enumeration

Whole-water phytoplankton samples were preserved with Lugol's iodine solution and returned to the laboratory for taxonomic analysis. Subsamples for soft-bodied algal analysis were loaded into Utermöhl (1958) counting chambers for inverted light microscope (LM) analysis. Diatom samples were subjected to digestion with heated 30% H<sub>2</sub>O<sub>2</sub>. Cleaned diatom material was mounted on coverslips and counted under LM. Diatom and soft algae (all non-diatom and non-siliceous groups) samples were enumerated along transects until a total count of 250 entities for soft algae or 500 diatom valves was achieved. Both diatoms and soft algae were identified to the lowest taxonomic level possible. For diatoms, identification was to species or variety, while identification was to species, and occasionally genus for soft algae. Up to 10 individuals of each taxon were measured (length, width, depth, diameter as applicable) in order to determine taxon-specific individual biovolume (cell size) (Reavie et al., 2010). Count and measurement data were used to calculate cell density, species-relative abundance, biovolume, and individual cell biovolume. These counting methods follow the standard GLNPO phytoplankton enumeration techniques outlined by USEPA (2010). Additional details of sample processing are provided by Reavie et al. (2014a).

### Statistical analysis

Paired-sample *t*-tests were used to examine differences in water quality parameters between summer epilimnetic and DCL samples. A series of one-way analyses of variance (ANOVA) were used to evaluate differences in mean phytoplankton taxonomic richness, density, and biovolume among spring integrated (SprINT), summer epilimnetic (SumEPI), and summer DCL (SumDCL) phytoplankton samples. We employed non-metric multidimensional scaling (NMDS), coupled with analysis of similarity (ANOSIM) in order to visualize and quantify dissimilarities among spring and summer epilimnetic and summer DCL phytoplankton assemblages within each lake. Similarity percentages (SIMPER; per Clarke, 1993) were used to evaluate species' contributions to assemblage dissimilarities. We used repeated-measures analysis of variance (rANOVA) and paired-sample *t*-tests in order to examine

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