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## The deep chlorophyll layer in Lake Ontario: extent, mechanisms of formation, and abiotic predictors

Anne E. Scofield<sup>a,\*</sup>, James M. Watkins<sup>a</sup>, Brian C. Weidel<sup>b</sup>, Frederick J. Luckey<sup>c</sup>, Lars G. Rudstam<sup>a</sup>

<sup>a</sup> Department of Natural Resources and the Cornell Biological Field Station, Cornell University, Ithaca, NY 14850, USA

<sup>b</sup> U.S. Geological Survey, Great Lakes Science Center, Lake Ontario Biological Station, 17 Lake Street, Oswego, NY 13126, USA

<sup>c</sup> United States Environmental Protection Agency, Region 2, New York, NY, USA

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### ABSTRACT

Epilimnetic production has declined in Lake Ontario, but increased production in metalimnetic deep chlorophyll layers (DCLs) may compensate for these losses. We investigated the spatial and temporal extent of DCLs, the mechanisms driving DCL formation, and the use of physical variables for predicting the depth and concentration of the deep chlorophyll maximum (DCM) during April–September 2013. A DCL with DCM concentrations 2 to 3 times greater than those in the epilimnion was present when the euphotic depth extended below the epilimnion, which occurred primarily from late June through mid-August. In situ growth was important for DCL formation in June and July, but settling and photoadaptation likely also contributed to the later-season DCL. Supporting evidence includes: phytoplankton biovolume was  $2.4\times$  greater in the DCL than in the epilimnion during July, the DCL phytoplankton community of July was different from that of May and the July epilimnion ( $p = 0.004$ ), and there were concurrences of DCM with maxima in fine particle concentration and dissolved oxygen saturation. Higher nutrient levels in the metalimnion may also be a necessary condition for DCL formation because July metalimnetic concentrations were  $1.5\times$  (nitrate) and  $3.5\times$  (silica) greater than in the epilimnion. Thermal structure variables including epilimnion depth, thermocline depth, and thermocline steepness were useful for predicting DCM depth; the inclusion of euphotic depth only marginally improved these predictions. However, euphotic depth was critical for predicting DCM concentrations. The DCL is a productive and predictable feature of the Lake Ontario ecosystem during the stratified period.

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### Introduction

Peaks in chlorophyll concentration commonly occur below the surface mixed layer in nutrient-poor lakes and oceans, but the causes and ecological importance of these deep chlorophyll layers (DCLs) are highly variable among systems. There are a number of non-exclusive physical and biological processes that can cause a DCL to form, including in situ phytoplankton growth at depth, settling of algal cells along the pycnocline, photoadaptation by phytoplankton (increased cell chlorophyll:carbon), and high zooplankton grazing rates in the epilimnion (Camacho, 2006; Cullen, 1982). Whether the DCL contributes significantly to total lake primary production depends on the relative importance of these processes in each system; for example, phytoplankton photoadaptation would not affect food availability for zooplankton grazers in the metalimnion, while phytoplankton growth depth may impact food web dynamics.

Efforts to study the processes forming DCLs in the Laurentian Great Lakes began in the late 1970s to 1980s (e.g. Fahnenstiel and Glime,

1983; Fahnenstiel and Scavia, 1987; Moll and Stoermer, 1982), shortly after the presence of subsurface maxima in chlorophyll and phytoplankton biomass were documented in Lake Michigan and Lake Superior (Brooks and Torke, 1977; Watson et al., 1975). These early DCL studies in the upper Great Lakes showed that in situ production was an important mechanism causing DCL formation, and  $^{14}\text{C}$ -based primary production estimates suggest that the DCL contributed from 30% to 60% of areal production in Lake Michigan at that time (Moll et al., 1984). There has been continued interest in studying DCLs in recent years (e.g. Pothoven and Fahnenstiel, 2013; Watkins et al., 2015; White and Matsumoto, 2012), partly because of growing concerns about declining primary production negatively affecting fish production, as observed in Lake Huron (Bunnell et al., 2014; Riley et al., 2008).

In Lake Ontario, increased summer production in deep chlorophyll layers (DCLs) may at least partly compensate for declines in epilimnetic production observed over the past several decades. Metalimnetic chlorophyll maxima were less common during the period of cultural eutrophication from the 1960s to 1980s, when average chlorophyll concentrations were much higher than present day. During that time, the DCLs that were observed in Lake Ontario occurred at a relatively shallow average depth of 10 m, and they had mean values of about  $9\ \mu\text{g/L}$

\* Corresponding author.

E-mail address: [as2895@cornell.edu](mailto:as2895@cornell.edu) (A.E. Scofield).

(maximum 17  $\mu\text{g/L}$ ) while surface values averaged 8  $\mu\text{g/L}$  (maximum > 14  $\mu\text{g/L}$ ) (Dobson, 1984). Maximum phytoplankton biomass was also sometimes observed in the mid-thermocline region, where the community was dominated by phytoflagellates (Munawar et al., 1974). These DCL features were absent during surveys in the 1980s (Lean et al., 1987), however, and light limitation likely restricted net phytoplankton production to the epilimnion during the 1970s–1980s. Depth-stratified production estimates from the 1970s indicate that maximal production occurred in the epilimnion (Stadelmann et al., 1974), and observations of metalimnetic oxygen depletion suggest that there was net respiration below the thermocline (Boyd, 1980). However, Lake Ontario has become considerably more oligotrophic. Spring total phosphorus concentrations declined from over 20  $\mu\text{g/L}$  in the late 1960s to between 7 and 10  $\mu\text{g/L}$  by the mid-1990s (Holeck et al., 2015; Dove and Chapra, 2015). Furthermore, the lakewide average euphotic zone has increased by over 50%, from an ice-free season (March–October) average of 9.8 m (Secchi depth 4.9 m) for the years 1978–1985 to 15.4 m (Secchi depth 7.7 m) for 2004–2015 (Binding et al., 2015). Increased transparency can be attributed to a combination of decreased epilimnetic chlorophyll concentrations, likely a result of decreased nutrients and mussel filtering (Holeck et al., 2015; Rudstam et al., 2017), and fewer summertime whiting events due to reduced production (Binding et al., 2007; Watkins et al., 2013). A deeper euphotic zone can lead to the vertical redistribution of phytoplankton biomass to the metalimnion as the water column stratifies and epilimnetic nutrients become depleted, causing a productive DCL to form when the euphotic zone overlaps with the metalimnion. Therefore, we expect that the importance of the DCL has increased in Lake Ontario in response to oligotrophication.

Consistent with this expectation, DCLs have commonly been observed in Lake Ontario monitoring data since at least 1998 (Barbiero and Tuchman, 2001), and a DCL feature was ubiquitous in offshore waters during sampling efforts in 2003 and 2008 (Watkins et al., 2015). Furthermore, measurements of phytoplankton growth and loss rates to microzooplankton suggest that production in the DCL during mid-summer is at least as high as in the epilimnion (Twiss et al., 2012), and the observation of metalimnetic peaks in dissolved oxygen saturation (DO) and beam attenuation (BAT, proxy for particle density) during sampling in July 2008 suggests a productive DCL (Watkins et al., 2015). In addition, a recent analysis of Lake Ontario phytoplankton data from April and August 2007–2012 suggests that in situ growth contributes to DCL formation. Although some relict taxa from spring were commonly observed in the DCL, the August metalimnetic community was distinct from April and August epilimnetic phytoplankton (Bramburger and Reavie, 2016), which indicates that some metalimnetic phytoplankton were produced in the DCL. The fact that the DCL in Lake Ontario appears productive has sparked continued interest in studying its dynamics, and this paper expands upon previous work by addressing two primary questions: 1) Which of the most common DCL-forming processes was dominant in Lake Ontario: photoadaptation, passive settling, or in situ growth? 2) Can we predict DCL characteristics from abiotic variables? We used data from whole lake surveys completed in 2013 to revisit the observations of DCL formation made in 2003 and 2008 (Watkins et al., 2015), expand on the seasonally-limited phytoplankton composition data in the DCL compared to the epilimnion from Bramburger and Reavie (2016), and predict the location and chlorophyll concentration of the deep chlorophyll maximum (DCM).

To investigate the conditions under which DCLs form, we used discrete-depth chlorophyll and nutrient concentrations, depth-stratified phytoplankton biomass and taxonomy data, and in situ profiles of temperature, photosynthetically active radiation (PAR), and proxies for phytoplankton biomass and production (BAT and DO, respectively). We hypothesize that the DCL in Lake Ontario is a productive feature with elevated phytoplankton biomass for most of the summer but that the DCL will no longer be productive and will dissipate if the epilimnion extends below the euphotic depth. Because nutrient limitation in the

surface is the primary explanation for the vertical redistribution of phytoplankton production, we expect to observe differences in the availability of limiting nutrients between the epilimnion and metalimnion. If in situ growth of phytoplankton in the metalimnion is important to DCL formation, we expect to observe not only greater phytoplankton biomass within the DCL compared to the epilimnion but also a DCL phytoplankton community that is distinct from both integrated spring and summer epilimnetic communities. Furthermore, a productive DCL would cause supersaturation of dissolved oxygen at depth, whereas oxygen depletion would suggest that the passive settling of senescent cells is causing the biomass peak (if present). If, however, we fail to observe greater phytoplankton biomass within the DCL, then photoadaptation is likely an important factor. It is also possible that we will observe both greater biomass and oxygen supersaturation at depth but that the maxima will be offset from the DCM. In this case, there may be several factors contributing to DCL formation and maintenance that change in relative importance with depth. Our expectation is that if the peaks are asynchronous, the productivity peak will likely be shallower than the DCM because greater production per unit chlorophyll could occur near the top of the DCL where light levels are higher than at the peak, and photoadaptation may contribute to elevated chlorophyll near the bottom of the DCL. Furthermore, we expect that the processes contributing to DCL maintenance may change over the course of the stratified season as the thermocline deepens and there is less overlap of the euphotic zone and metalimnion.

## Methods

### Sampling plan

The offshore waters of Lake Ontario were sampled from aboard the US EPA's R/V Lake Guardian during the months of April, May, July, August, and September 2013 (Fig. 1). All sites included in the present analysis had a bottom depth >40 m. Ten sites designated by the US EPA Great Lakes National Program Office (GLNPO) long-term monitoring program were visited on both April 4–5 and August 12–14. Through the Cooperative Science and Monitoring Initiative (CSMI) program for Lake Ontario, efforts to sample three south to north transects were coordinated by the US EPA GLNPO and Cornell University during May 20–23, July 19–22, and September 10–13. Profile data from three additional programs aboard the R/V Lake Guardian during the summer of 2013 were included in our analysis: the Clarkson University cruise on June 18–19, the Center for Ocean Sciences Education Excellence (COSEE) cruise on July 8–12, and the An Li Sediment Survey on July 23–25. Profile data from the R/V Lake Guardian surveys were grouped into six time periods: April (GNPO), May (CSMI), Late June–Early July (Clarkson and COSEE), Late July (CSMI and An Li Sediment Survey), August (GLNPO), and September (CSMI). Discrete-depth fractionated chlorophyll data from three sites offshore from Oswego, NY (with bottom depths of 50, 100, and 200 m) and additional samples for taxonomic analysis of phytoplankton from the deepest site (200-m) were provided by the United States Geological Survey Lake Ontario Biological Field Station (USGS-LOBS), which completed sampling on the following dates: April 10, May 15–17, June 11–14, July 9, August 8, August 27–29, and September 24.

### Field and lab methods

All R/V Lake Guardian sites were sampled with a rosette assembly consisting of a 12 Niskin bottle array and the following instrumentation: SBE-911 Conductivity Temperature Depth (CTD) profile; Seapoint chlorophyll *a* fluorometer (Seapoint Sensors, Inc., Exeter, NH); dissolved oxygen sensor (SBE 43); Biospherical/Licor sensor to measure Photosynthetically Available Radiation (PAR); and transmissometer (WETlab C-Star) to measure beam attenuation at 660 nm wavelengths. The rosette was deployed at a constant speed of 0.5 m per second for the

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