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Notes

Phytoplankton growth dynamics in offshore Lake Erie during mid-winter

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ABSTRACT

The phytoplankton community in offshore Lake Erie in mid-winter was active but little net growth was occurring which suggests that high reported accumulations of phytoplankton in this lake in February are likely the product of previous bloom conditions. We measured phytoplankton dynamics as size-specific growth and loss rates of phytoplankton using dilution assays and antibiotic assays in ice-covered offshore waters of Lake Erie during the mid-winter period in 2008, 2009, and 2010. Total chlorophyll-*a* specific rates (average ± standard deviation) measured using dilution assays for growth ([0.72 ± 0.35/d]) and loss ([0.98 ± 0.36/d]) were closely matched. Growth and loss rates of picocyanobacteria determined using an antibiotic technique ranged from −0.10 to 1.22/d and −0.11 to −2.35/d, respectively. The results indicate a trend of higher grazing rate than growth rate but that this difference is not significantly different from zero, suggesting a state of phytoplankton population size equilibrium at this time of year in the waters sampled.

Introduction

The majority of what we know about growth and grazing losses of phytoplankton in temperate dimictic lakes is focused on the ice-free period (Wetzel, 2001). In the North American Great Lakes this period is from March to December. Difficulties inherent to sampling during winter, and more so for conducting experimentation necessary to measure the rate variables needed to describe plankton community dynamics, make information from this season rare. However, there is a definite need to examine winter limnology more fully if we expect to understand lake ecosystem function (Salonen et al., 2009).

With an average depth of 19 m, Lake Erie is the shallowest of the Laurentian Great Lakes; and accordingly, forms extensive stable ice cover over the majority of the lake in most winters. Relatively dense algal blooms have been observed recently during mid-winter in Lake Erie; these conditions are hypothesized to result from extensive phytoplankton growth that occurs before the onset of extensive ice cover (Twiss et al., 2012a) and to be linked to summer hypoxia (Lashaway and Carrick 2010; Wilhelm et al., 2013). Offshore phytoplankton biomass in surface water, reflected by chlorophyll-*a* (Chl-*a*) concentrations, has been observed to be as great as 14 μg/L in March 2010 (McKay et al., 2011) and exceed 120 μg/L in discrete accumulations present in February under ice (Binding et al., 2012; Smith, 2011) termed 'caches' (Twiss et al., 2012a). While conditions during ice cover in Lake Erie are not expected to be ideal for blooms due to low levels of photosynthetically available radiation attributable to ice, snow cover and high water column turbidity, the availability of potentially limiting nutrients is high and the crustacean macrozooplankton density is low (Twiss et al., 2012a). These observations leave the high accumulations of phytoplankton throughout the lake during this time of year unexplained.

We tested the hypothesis that winter blooms in Lake Erie are the result of net phytoplankton growth resulting from a greater specific growth rate of phytoplankton relative to the specific loss rate attributable to microzooplankton. The objective of this study was to establish rates of phytoplankton growth and losses during the period of maximum ice cover (typically >90%) that occurs during mid-winter (February). To assess the rate variables of phytoplankton growth and microzooplankton growth rates we used two established assay techniques, the dilution assay (Landry and Hassett, 1982) and antibiotic assay (Campbell and Carpenter, 1986).

Materials and methods

Water column sampling

Several stations were sampled in the offshore region of Lake Erie (Fig. 1) in February of 2008, 2009, and 2010. Not each station was sampled every year due to the varied cruise track of the ship that was duly tasked with ice-breaking. During sampling the lake was 70 to 90% ice covered.

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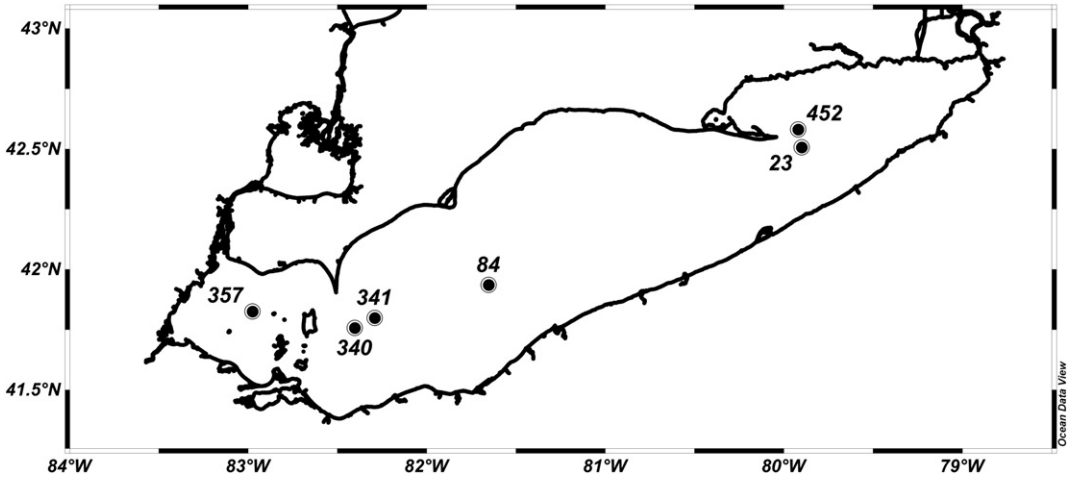

Fig. 1. Map of study stations in Lake Erie. An additional station was sampled in the Detroit River (42.1005 N, 83.1135 W; not shown).

Limnological conditions were evaluated aboard by the Canadian Coast Guard icebreaker *Griffon*. At each station, water column profiles for temperature, dissolved oxygen, chlorophyll fluorescence, and conductivity were logged from surface to near bottom using a Seabird CTD (model SBE-19) through a gap in the ice cover caused by the ship; typical data are presented in Twiss et al. (2012a). Since the water column was isothermal or weakly inversely stratified we selected a depth of 1 m to sample water. Water samples were collected using a submersible pump; previous studies indicate that the pump did not negatively affect plankton (Twiss et al., 2012a).

Chlorophyll-a analysis

Size-fractionated Chl-*a* concentrations were measured in duplicate using parallel filtration, wherein Chl-*a* content in each size class was determined by difference. The pico- (0.2–2 μm), nano- (2–20 μm), and microphytoplankton (>20 μm) size classes were determined using the corresponding pore-size, 47-mm diameter filters (polycarbonate membrane filters for 0.2-μm pore size ([prod. no. GTTP 04700, Millipore], 2-μm pore size [prod. no. TTTP 04700, Millipore], and woven nylon filters for 20-μm pore size [prod. no. NY200 4700, Millipore])). Particles retained on the filters were extracted in 10 mL of 90% acetone in the dark at 4 °C for 12–24 h. Chl-*a* in the extract was measured by fluorometry (Welschmeyer, 1994) using a calibrated fluorometer (Turner Designs model TD-700; Sunnyvale, CA) onboard the research vessel. Chl-*a* extracted in this manner was multiplied by a correction factor of 1.34 to reflect an increase in efficiency of Chl-*a* extraction in 90% acetone if filters were frozen (−15 °C) for 5 days prior to extraction and measurement as mentioned above (Smith, 2011).

Grazing assays

We measured Chl-*a* size-specific growth and loss rates of phytoplankton using a dilution assay technique (Landry and Hassett, 1982) on surface water (Fig. 1) in February 2008, 2009, and 2010 ($n = 9$ experiments). A second set of experiments conducted in 2008 and 2010 employed antibiotic assays ($n = 5$ experiments); endpoints in these experiments were rate changes specific to picocyanobacteria.

For the dilution assays, rates were estimated by diluting un-screened lake water with lake water that passed through a 0.45-μm pore size high capacity, groundwater capsule filter (Millipore) to achieve a series of six dilutions (100%, 66%, 41%, 33%, 19%, and 8% unscreened lake water) in 1.215-L polycarbonate bottles. Previous measurements during ice cover on Lake Erie in February 2007 and 2008 showed no phosphorus limitation (as determined by no detectable alkaline phosphatase activity in the plankton community; Twiss et al., 2012a) thus, no nutrients were added to account for nutrient regeneration resulting from grazing or viral and fungal induced lysis. Size-fractionated Chl-*a* concentrations (>20 μm, 2–20 μm, 0.2–2 μm) were determined in each dilution at the beginning and end of the incubation period (see below).

The antibiotic assays used the prokaryotic inhibitor, ampicillin to arrest cytokinesis, from which growth and loss rates were deduced (Campbell and Carpenter, 1986). In support of the use of this antibiotic was the known inhibitory effect of ampicillin on a Lake Huron isolate of *Synechococcus* in log-phase growth; previous studies showed that the inhibitor arrested cytokinesis without causing cell lysis (Fahnenstiel et al., 1991). Experiments were performed here by dispensing unscreened lake water into duplicate 1-L polycarbonate bottles; ampicillin was added (5 mg/L) to one set of bottles while the second set served as controls ($n = 4$ for each experiment). Samples were removed from each experimental bottle at the start and termination of each experiment; these samples were preserved with 1% glutaraldehyde to subsequently determine the abundance of dominant picocyanobacteria present in these samples. Phototrophic picoplankton (0.2 to 2.0 μm) abundance measurements were made on samples (2–10 mL) concentrated onto 0.2-μm pore-size, black polycarbonate filters (Fahnenstiel and Carrick, 1992). Slides were enumerated by counting >200 cells using a Leica DM5000 research microscope (1000×) equipped for Chl-*a* autofluorescence (450–490 nm excitation and >515 nm emission) and the determination of phycoerythrin (530–560 nm excitation and >580 nm emission). Counting error was estimated from Poisson counting statistics and the mean of replicate counts; in either case errors were <10% (Lund et al., 1958; Sandgren and Robinson, 1984).

Experimental bottles were incubated (24 to 31 h) in a temperature and light-controlled incubator (Percival; model E-30B) on the ship set to mimic the depth of sampling and the day length. Light levels were 15–25 μmol photons/m^2/s provided by an equal number of Cool White (FT20T12-CW) and aquarium plant growth (F15T8-PL/AQ) fluorescent bulbs attenuated with neutral density screen. Temperature was maintained at 1–2 °C (to prevent freezing of the water in bottles). In both types of experiments (dilution, ampicillin), growth and loss rates were calculated in each treatment, assuming exponential rate changes over time using the following Eq. (1):

$$\mu = \left(ln[B]_{\text{final}} - ln[B]_{\text{initial}}\right)/t \quad (1)$$

where B was the concentration of Chl-*a* or picocyanobacteria. In the dilution experiments, Chl-*a*-specific growth rates (μ) were determined where $[B]_{\text{initial}}$ was the Chl-*a* concentration in a given size fraction at the start of the incubation period, $[B]_{\text{final}}$ was the Chl-*a* concentration in a given size fraction at the end of the incubation period, and t was the duration of the incubation. The intrinsic specific growth rate was