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Approaching storm: Disappearing winter bloom in Lake Michigan

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ABSTRACT

Between 1990 and 2001, late-winter phytoplankton blooms were common in parts of the lower Great Lakes (southern Lake Michigan, Saginaw Bay and southern Lake Huron, and western Lake Erie), providing resources for over-wintering zooplankton. In Lake Michigan up to 2001, detailed remote sensing and ship studies documented well-developed late-winter blooms in the southern gyre (circular bloom termed the 'doughnut'). However, from 2001 to 2008, the winter blooms in Lake Michigan also supported early season veliger larvae from the introduced, cold-water adapted "profunda" morph of quagga mussels (*Dreissena rostriformis bugensis*). Remote sensing and ship studies revealed that settled mussels caused an extraordinary increase in water transparency and a simultaneous decrease of Chl *a* in the late-winter bloom. Before quagga mussels in 2001, water transparency was 74–85% at deep-water sites, whereas it increased progressively to 89% by 2006 and 94–96% by 2008. Chlorophyll *a* concentrations in the gyre rings were 1.1–2.6 μg/L in 2001, declining to 0.5–1.7 μg/L by 2006 and 0.4–1.5 μg/L by 2008. The reduction of Chl *a* in the winter bloom rings from 2001 to 2008 was 56–78% for the western limb and 74–75% for the eastern limb. Zooplankton species abundance, composition and abundance also changed, as cyclopoid copepods became very scarce and over-wintering omnivorous calanoid copepods declined. Reduction in late-winter phytoplankton and zooplankton poses a serious threat to open-water food webs.

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Introduction

Prior to the development of remote sensing, details of winter circulation and production in the Great Lakes were poorly known, in part because of hazardous ship conditions (Eadie et al., 1996; Kerfoot et al., 2004). On the National Science Foundation (NSF) and National Oceanic and Atmospheric Administration (NOAA) Episodic Events-Great Lakes Experiment (EEGLE) project, we discovered a late-winter algal bloom in southern Lake Michigan (Chl *a* 'doughnut' ring; Budd et al., 2002; Kerfoot et al., 2008). Contrary to expectations of fairly uniform open waters from February to April, sea-viewing wide field-of-view sensor (SeaWiFS) and moderate-resolution imaging spectroradiometer (MODIS) imagery uncovered spatially complex resuspended sediment, Chl *a*, and CDOM patterns in offshore waters. Apparently, phosphorus-rich coastal river waters and nearshore sediments (Biddanda and Cotner, 2002) were captured by intensified winter currents, entrained along gyre convergence zones and moved into deeper waters, stimulating a ring of offshore production (Kerfoot et al., 2004, 2008). Cross-lake surveys (April 2001, 2006) with two separate profiling instruments revealed columnar patterns consistent with a spatially complex, rotating gyre structure. Optical plankton counter (OPC) transects and zooplankton net tows indicated that spatial heterogeneity extended to higher levels of food webs.

Here we note that the late-winter blooms were not peculiar to the southern basin of Lake Michigan, but also occurred regularly in other Great Lake waters, where the geometry of bloom patterns differed due to bathymetry, circulation and lake orientation (Beletsky et al., 1999; Beletsky and Schwab, 2001). In Lake Michigan, there were indications from remote sensing and ship-board studies that the winter 'lateral nutrient displacement' phenomenon had been present for at least 25 years. Up to 2001, the late-winter bloom was probably an important feature that benefited predominately cold, deep-water native taxa (phytoplankton and zooplankton), and that normally supported over-wintering strategies.

The degree that global climate change is involved in accentuating late-winter blooms is unknown, yet global climate change appears to be reducing ice-cover (Austin and Colman, 2007) and increasing the frequency and intensity of winter storms (Schwab et al., 2006), thus promoting the observed lateral displacement of limiting nutrients by capturing river discharges, resuspended sediments, and redirecting

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coastal algae (Kerfoot et al., 2008). Usually these processes would have enhanced late-winter productivity from 2001 to 2008 in Lake Michigan. However, this has not been the case as cold-adapted veliger larvae of the introduced quagga mussel (*Dreissena rostriformis bugensis*) have also exploited the late-winter productivity pulses. Water column filtration from settled adults is now seriously compromising anticipated late-winter bloom patterns.

It is truly remarkable that one or two species of mussels can so transform the entire ecosystem. During the EEGLE study, zebra mussel effects were confined largely to coastal waters off Chicago (Nalepa et al., 1998; Vanderploeg et al., 2007). In recent years, a 'shallow-water morph' of the quagga mussel (*Dreissena rostriformis bugensis*) has begun to replace zebra mussels in shallow areas of the Great Lakes (Nalepa et al., 2009). In deeper (>30 m), cooler waters, another form of *D. rostriformis bugensis* (the 'profunda morph') has increased tremendously (Nalepa et al., 2009, 2010). Unlike the zebra mussel, the 'profunda morph' is adapted for life on soft sediments (has elongated incurrent siphon and lies on the bottom on one of its valves without attachment with byssal threads). The life history cycle for quagga mussels begins somewhat earlier than zebra mussels and under lower temperatures (e.g., Claxton and Mackie, 1998). Quagga mussel spawning occurs in early winter, late spring, late summer, and fall (Roe and MacIsaac, 1997; Claxton and Mackie, 1998; Nalepa et al., 2010). The embryos first develop into swimming larvae. In 2–9 days they develop intestines and a feeding and swimming organ known as the velum. Once the velum appears, the larvae are termed veligers. In the veliger stage they develop D-shaped (straight-hinged) shells about 70–100 µm long (Sprung, 1993). The settlement of mussels to the bottom varies as a function of temperature and food concentration. At temperatures of 22–26 °C, settlement can occur after 32 d (Wright et al., 1996), yet it can take as long as several months at low temperatures and food concentrations.

Moderately high densities of quagga veligers feed on the late-winter bloom pulse, and are dispersed by strong currents associated with winter storms (Kerfoot et al., 2008). This soft-sediment species can settle in both shallow and deep waters, reaching 5–15 thousand individuals/m^2. In Lake Michigan, adult quagga mussels increased dramatically in density between 2001 and 2006, spreading below 100 m depth (Nalepa et al., 2009; 2010). At high densities, adult quagga mussels are filtering much of the overlying water column along the coastal shelf (Vanderploeg et al., 2010), seriously reducing the typical spring bloom.

Here we first discuss long-term evidence for late-winter blooms in the Great Lakes between 1998 and 2001, then focus in on Lake Michigan. Remote sensing and coordinated ship studies document how the adult mussel filtration effects are altering late-winter waters and the circular late-winter phytoplankton bloom ('doughnut'). Our observations 1) chronicle the development of a late-winter 'bottleneck' in Lake Michigan and 2) raise grave concerns about the consequences of future productivity losses on winter pelagic foodwebs.

Methods and materials

Remote sensing (AVHRR, SeaWiFS, MODIS) imagery

As part of the NSF/NOAA EEGLE Project in Lake Michigan, we processed Advanced Very High Resolution Radiometer (AVHRR 1992–2002) and sea-viewing-wide-field-of-view sensor (SeaWiFS 1997–2002) imagery (Warrington, 2001; Kerfoot et al., 2004). Since becoming routinely available in 1992, AVHRR (NOAA TIROS-N series, NOAA-10 and NOAA-11) imagery has confirmed near-coastal and offshore sediment plumes (channel 1–3 visible bands) and corresponding temperature structure (3–5 bands) every year during late winter (March–April) in Lake Michigan (Leshkevich et al., 1993; Warrington, 2001; Budd and Warrington, 2004). SeaWiFS and MODIS imagery has also verified late-winter offshore structures, although the spatial extent and duration varies from year to year (Ji et al., 2002; Kerfoot et al., 2004, 2008; Stroud et al., 2009). Since the sensor swaths included the entire Laurentian Great Lakes region, SeaWiFS image processing (1998–2002) was extended to the other lakes.

During the early EEGLE SeaWiFS processing, we became aware of the 'doughnut-shaped' bloom pattern of Chl *a* in offshore Lake Michigan waters (Budd et al., 2002). The SeaWiFS sensor was located on the PorbView-2-satellite, which imaged the Great Lakes between 17:30 and 19:30 h coordinated universal time (Gregg, 1992; approximately the same as Greenwich mean time). The instrument had a scan coverage of 2800 km, a nadir resolution of 1.1 km^2, and contained a passive, eight-band multispectral scanner. The scanner picked up reflectance in six visible bands (412 nm, Gelbstoffe; 443 nm, chlorophyll; 490 nm, pigment; 510 nm, chlorophyll; 555 nm, sediments and pigments; and 670 nm, atmospheric correction) used for estimating pigment and total suspended material (TSM) concentrations, and two near-infrared bands (765 nm and 865 nm) used primarily for atmospheric corrections (McClain et al., 1998).

Time series SeaWiFS imagery was processed using SeaWiFSMAP image processing software (Warrington, 2001) and a modified IDL/SeaDAS (http://seadas.gsfc.nasa.gov/seadas/) code that included the 1998 sensor calibration (McClain et al., 1998) and the coastal atmospheric correction scheme (Stumpf et al., 2000, 2003; Budd and Warrington, 2004). SeaWiFS Chl *a* (OC2) maps were derived from empirical, band-ratioing algorithms, OC2v4 (O'Reilly et al., 2000a) and OC4v4 (O'Reilly et al., 2000b). The OC2v4 Chl *a* algorithm used a ratio of SeaWiFS bands 3 and 5 (O'Reilly et al., 1998; Budd and Warrington, 2004). See Kerfoot et al. (2008) for OC2, OC2v4, and OC4v4 equations and more details on procedures.

To check for long-term spatial trends in the southern Great Lakes, we utilized OC2 images and scored the incidence of late-winter bloom patterns between 1998 and 2002. Spectral reflectance (R_{RS}) at 555 nm was used to estimate total suspended matter (TSM; McClain et al., 1998). The ability to observe late-winter blooms is greatly hindered by cloud cover (Stroud et al., 2009), but the observations provided strong evidence for past widespread incidence. To provide a quantitative temporal record of Chl *a* concentration decline within the Lake Michigan 'doughnut', we superimposed the southern ship transect on SeaWiFS images between 1998 and 2008 and chose Chl *a* pixel values from the inner and outer rims of the eastern and western 'doughnut' bands. We then regressed the mean values against time, over the complete 1998–2008 interval.

Concerns about coastal suspended matter (TSM) and colored dissolved organic matter (CDOM) influencing OC2 interpretations are discussed in Stumpf (2001), Stumpf et al. (2003) and Budd and Warrington (2004). CDOM interference was severe for Lake Superior OC2 Chl *a* estimates, but not for Lake Michigan Chl *a* estimates (Budd and Warrington, 2004). The entire set of processed images bearing on pre-quagga conditions from 1998 to 2002 is posted at: http://www.geo.mtu.edu/great_lakes/lakersi/cgi-bin/seawifs.cgi.

Phytoplankton distribution and Chl a concentrations

Several cruises were used to validate SeaWiFS imagery and to determine water column variables. Ship-based Chl *a* and TSM samples were collected from January to November 1998–2000 along five transects off Racine, Chicago, Gary, St. Joseph, Muskegon, and at two central stations (Fig. 1) and used in initial Chl *a* on C_{SAT} and R_{555} (SeaWiFS) regressions (Table 1, regression 1). These initial EEGLE determinations were supplemented in later years by additional cruise measurements along the Lake Michigan southern transect. Field and laboratory calibration curves utilized a pure Chl *a* standard (*Anacystis nidulans*, Sigma C6144). Between 1 and 3 L of lake water from 0, 10, 20, to 25 m depths were filtered (preweighted Whatman GF/F 55 mm filters) at 30–40 stations along the 62-station southern transect. Both field and laboratory values for Chl *a* were run on a Turner TD-700

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