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Approaching storm: Disappearing winter bloom in Lake Michigan

W. Charles Kerfoot^{a,*}, Foad Yousef^a, Sarah A. Green^b, Judith W. Budd^c,
David J. Schwab^d, Henry A. Vanderploeg^d

^a Lake Superior Ecosystem Research Center and Department of Biological Sciences, Michigan Technological University, Houghton, MI 49931, USA

^b Department of Chemistry, Michigan Technological University, Houghton, MI 49931, USA

^c Department of Geological Engineering and Sciences, Michigan Technological University, Houghton, MI 49931, USA

^d NOAA Great Lakes Environmental Research Laboratory, 2205 Commonwealth Blvd., Ann Arbor, MI 48105, USA

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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

* Corresponding author.

E-mail addresses: wkerfoot@mtu.edu (W.C. Kerfoot), fyousef@mtu.edu (F. Yousef), sgreen@mtu.edu (S.A. Green), jwbudd@mtu.edu (J.W. Budd), david.schwab@noaa.gov (D.J. Schwab), henry.vanderploeg@noaa.gov (H.A. Vanderploeg).

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 OrbView-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

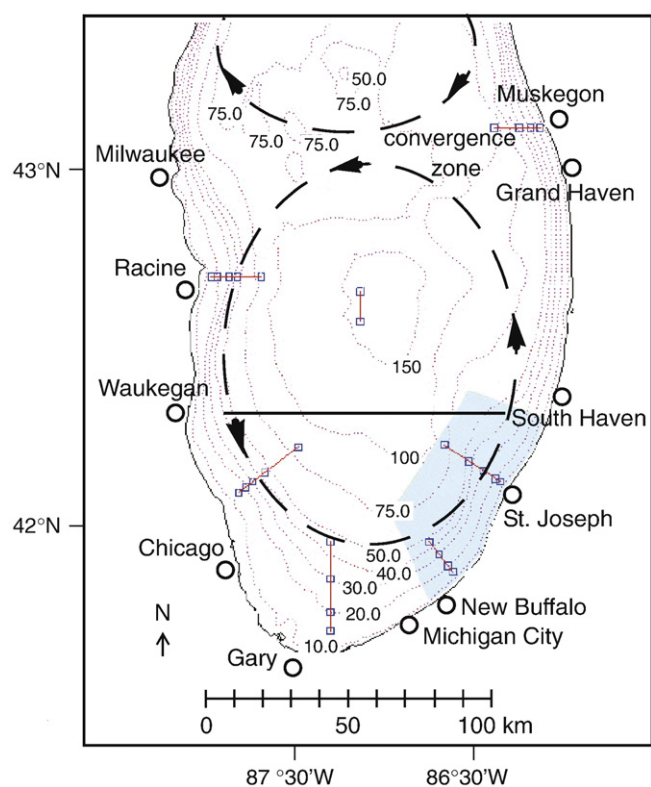


Fig. 1. Southern Lake Michigan, indicating transect stations for 1998–2000 ship-board TSM:Chl *a* validation studies (connected squares off various cities) and the April 2001, 2006, and 2008 Seabird CTD/BAT southern transects (62 stations, solid line from South Haven to Waukegan). Gyre circulation of waters after a northwest wind is indicated by arrows, with the position of the convergence zone off Grand Haven/Muskegon noted. Blue area is region of intensified monitoring during the EEGLE project and region of greatest phosphate loading from river discharges.

Fluorometer using the acid (phaeophytin) correction method (Wetzel and Likens, 2000) on 90% acetone extracts. The 2006–2008 cruises featured a combination of ship-board Chl *a* determinations supplemented by later laboratory determinations on additional filtered samples. The field and laboratory filtered samples were used routinely to calibrate CTD and Acrobat (Wet Lab ECO-AFL) fluorescence values (Table 1, regressions 3–6). In addition, CTD and Acrobat Chl *a*

Table 1

Validation and empirical relationships for southern Lake Michigan: coefficients of linear ($Y = bX - a$) regressions relating ship-sampled Chl *a* ($\mu\text{g/L}$) to C_{SAT} Chl *a* ($\mu\text{g/L}$) or CTD fluorescence (FL). In the first regression, Chl *a* measurements taken along numerous transect stations at 5–10 m depth from 22 Mar 98–11 Sep 99 are regressed on SeaWiFS C_{SAT} Chl *a* values, whereas the second regression utilizes Chl *a* measurements from the southern transect, 21–23 April 08. In the third to fifth regressions (2001, 2006, 2008), Chl *a* from southern transect stations is regressed on Seabird CTD fluorescence (FL) values. The lowest, log-linear regression (equation 6) relates SeaWiFS R_{555} values to ship-sampled TSM (mg/L ; total suspended matter). TSM measurements for R_{555} validation were taken Jan–Mar 1998 and Feb–Apr 1999 from 5 to 10 m depths at various coastal transect stations plotted in Fig. 1. All regressions are significant at the $p < 0.001$ level.

Linear regression	<i>n</i>	<i>b</i> ± SE	<i>a</i> ± SE	<i>r</i> ²
1. Chl <i>a</i> on C_{SAT} 1998–1999	18	1.079 ± 0.102	−0.087 ± 0.171	0.874
2. Chl <i>a</i> on C_{SAT} 2008	51	1.209 ± 0.058	−0.022 ± 0.082	0.900
3. Chl <i>a</i> on FL(CTD) 2001	36	23.433 ± 1.81	−0.501 ± 0.097	0.836
4. Chl <i>a</i> on FL(CTD) 2006	31	21.331 ± 2.54	−0.349 ± 0.196	0.708
5. Chl <i>a</i> on FL(CTD) 2008	52	24.274 ± 1.29	−0.398 ± 0.106	0.872
<i>Log-linear regression</i>				
6. R_{555} on log(TSM)	32	5.975 ± 0.387	2.005 ± 0.15	0.891

measures were checked by running a dilution series of previously calibrated algal cultures (*Chlamydomonas*) through the fluorescence sensors.

Near-surface Chl *a* values were used to validate SeaWiFS OC2v4 reflectance readings. Because field surface samples often showed daylight Chl *a* quenching (Kerfoot et al., 2008), which influenced CTD fluorometry readings, 10–20 m Chl *a* determinations were favored for validation regressions over surface values. However, winter Chl *a* values for 10–25 m readings were spatially similar and highly correlated. For example, on the April 2008 cruises, correlations between 10 m, 20 m, and 25 m Chl *a* values along the ship sampling transect were very high (10 m vs 20 m $r^2 = 0.976$; 10 m vs 25 m $r^2 = 0.974$; 20 m on 25 m $r^2 = 0.990$; $N = 74$), reflecting winter deep-water vertical mixing.

A previously published relationship between SeaWiFS C_{SAT} and R_{555} estimates and in situ TSM concentrations (regression 6, Table 1) was used to look at long-term trends. The ground-truth effort provided an empirical nonlinear relationship between SeaWiFS R_{RS} (555) and ship-based TSM measurements over the observed range of 1–12 mg/L. The logarithmic fit was heuristic for it covered saturating values in nearshore turbidity plumes, while revealing subtle patterns for low-concentration levels in offshore waters. Further discussion of validations used with SeaWiFS imagery during the EEGLE project can be found in Bergmann et al. (2004) and Lohrenz et al. (2008). Bergmann et al. (2004) discuss difficulties in OC2 Chl *a* determinations relating to marine versus freshwater phytoplankton species differences. Additional water column calibrations between CTD fluorometry and Chl *a* are discussed in Vanderploeg et al. (2007) and Lohrenz et al. (2008).

Chlorophyll a and zooplankton along southern Lake Michigan transect: Developing impact of quagga mussels

Four cruises (April 2001, 2006–2008) aboard the RV Laurentian compared the spatial nature of the late-winter bloom ('doughnut') in southern Lake Michigan, three along the same latitudinal transect (2001, 2006, 2008). All four cruises originated from the eastern port of Muskegon, Michigan. The three E–W cruises (Fig. 1) traversed along a mean latitude of 42.372° from South Haven to Waukegon and back, cutting across the center of the circular algal bloom on 19–21 April 2001 and along its southern ring on 12–15 April 2006 and 23–25 April 2008. Over the 3–4 day cruises, Seabird SBE 911plus conductivity-temperature-depth (CTD) full vertical profiles were taken from around 64 stations at 1.85-km (1 nautical mile) intervals (longitude 87.745°W to 86.320°W). The Seabird CTD instrument package recorded depth, temperature, Chl *a* fluorescence, photosynthetically available radiation (PAR), and water transmissivity. The device was equipped with a SeaTech transmissometer, Biospherical Instruments scalar PAR sensor (400 to 700 nm), and Wet Lab ECO-AFL fluorometer. Contour plots were generated from the vertical CTD casts using Matlab (Mathworks). The CTD data were binned at 0.5-m depth intervals from casts every 1.85 km for a total of ca. 10,400 points for each parameter. Data were interpolated in the horizontal dimension using the cubic polynomial function to provide ca. 32,000 points for contouring the cross-sections (Kerfoot et al., 2008). On April 2–3, 2007, we traversed diagonally towards the 'doughnut hole' from Muskegon harbor, taking CTD vertical profiles, but were forced off the lake by an approaching storm. On April 25, 2008, we traversed diagonally back to Muskegon along a similar transect, and then along the nearshore coastline.

In addition to CTD vertical casts, we towed a BAT (Sea Sciences Acrobat) in tow-yo undulating fashion (5–20-m depth amplitude) behind the ship in 2001 and horizontally (10–20-m depth) in 2006 and 2008. In addition to temperature, Chl *a*, and concentration of dissolved organic matter (CDOM) fluorescence estimates, the BAT contained an optical plankton counter (OPC; Mini Optical Plankton Counter, model OPC-2T, Focal Technologies) that counted and sized zooplankton. The

OPC utilized a flow-through tunnel with a thin rectangular light beam (4×20 mm cross-section) that measured the profile area of each plankton target, and converted the size into an equivalent spherical diameter (ESD). The device was towed at around 2.5 m/s (ca. 4–5 knots). Counts were binned in two different size categories (Bin 1, 0.25–0.50 mm; Bin 2, 0.5–1.0 mm). Densities (counts/m³) were plotted as a 50-interval mean and high-low range of 10-s-duration counts. On 25 April 2008, south of Muskegon, the BAT with the OPC was towed horizontally from offshore, through the thermocline region, and into the nearshore zone to record horizontal patterns for zooplankton densities.

OPC counts in Lake Michigan have been compared with plankton tows (Liebig et al., 2006; Kerfoot et al., 2008) and in the laboratory (Liebig et al., 2006). In open, dilute waters counts were reliable, whereas in nearshore turbid waters prior to 2002, they tended to be higher, by virtue of non-living particles being counted along with living plankton (Liebig et al., 2006).

In April 2006–2008, vertical zooplankton tows were taken at 24 stations along the E–W transect with a 1-m diameter Puget Sound plankton net (125 μ m Nitex). In April 2007, they were obtained along the diagonal transect out of Muskegon harbor. The vertical plankton tows were subsampled with a Hensen–Stempel pipette and counted under a 50 \times Olympus SZ30 dissection scope equipped with a 2 \times auxiliary adapter. The samples allowed calculation of species densities and indicated changes in community structure from 1998–2001 (EEGLE Project) to 2006–2008. Veliger larvae of quagga mussels also were counted in the 2006–2008 samples, although use of 125 μ m mesh meant that smaller sizes were lost. Statistical comparisons utilized *Systat* (Wilkinson, 2000).

Results

Remote sensing evidence for late-winter phytoplankton blooms

SeaWiFS imagery revealed spatially complex suspended sediment and Chl *a* patterns in several Laurentian Great Lakes during winter (January to April). The spatial patterns were first detected during the low ice-cover El Niño winter of 1998, largely because SeaWiFS imagery became available and the lakes were relatively free of ice. A SeaWiFS image from March 24, 1998, illustrates elevated Chl *a* (OC2) late-winter plumes in all ice-free lakes, but most pronounced in southern Lake Michigan (“doughnut”), southern Lake Huron and western Lake Erie (Fig. 2). In Lake Superior, elevated Chl *a* regions were found off Duluth–Superior Harbors, Chequamegon Bay, and along the southern shallow coastal shelf off the Keweenaw Peninsula. Ice-covered regions are indicated in gray. In the lower lakes, the blooms were even better developed in shallow coastal regions and were sometimes mixed with drifting ice (Green Bay; Saginaw Bay and off Port Huron, Lake Huron; western and middle basins, Lake Erie). The coastal and offshore patterns indicated a previously undetected relationship between storm-induced gyre formation, coastal water plus resuspended sediment capture, and late-winter productivity.

The cold-water blooms were not restricted to abnormally warm, nearly ice-free winters, as images from moderate ice-cover years of 2000–2002 also showed very strong suspended sediment (R_s 555) and Chl *a* (OC2) bloom patterns in late March to early May (Fig. 3, Table 2). Again, cloud or ice-covered regions (high albedo) are indicated in gray in the images. In Lake Michigan, ship surveys showed that the patterns

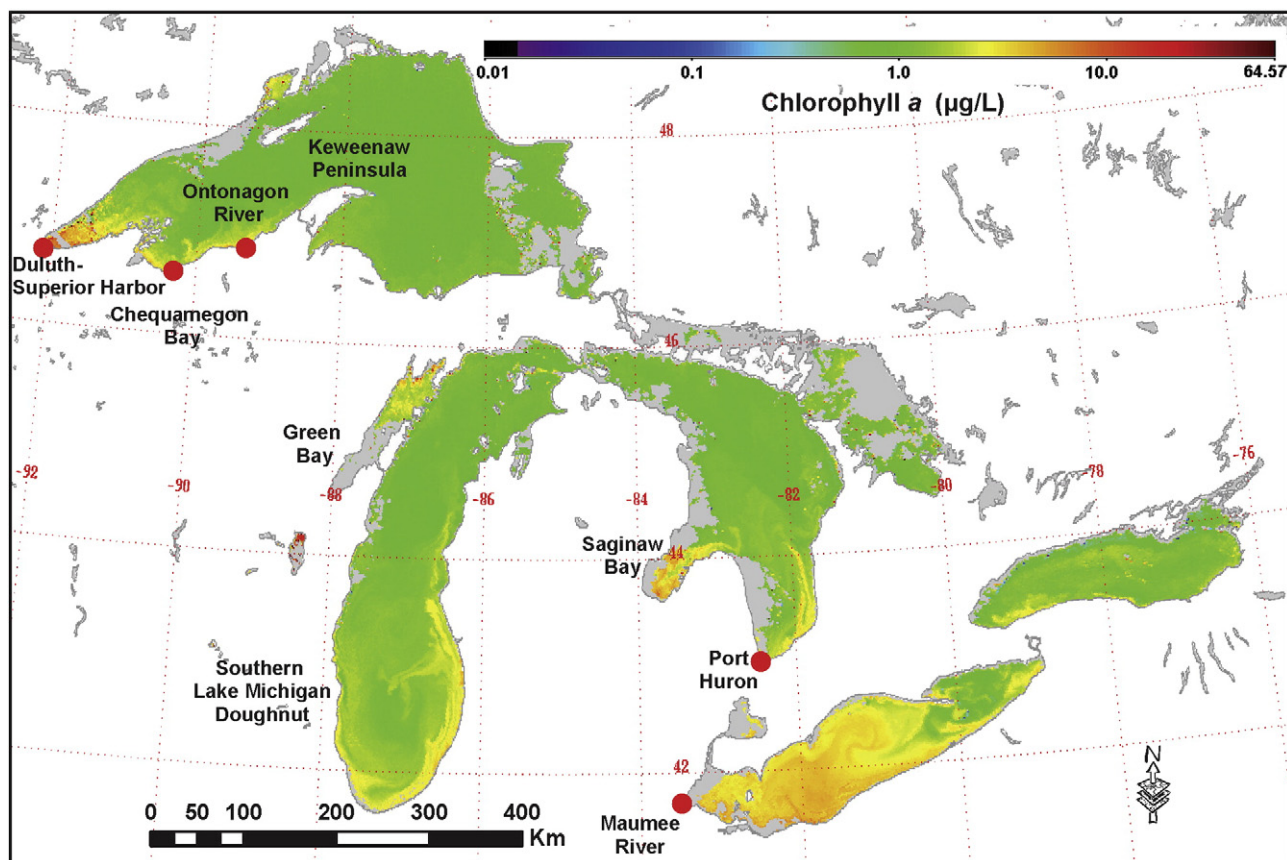


Fig. 2. Chlorophyll *a* patterns (SeaWiFS imagery) for the Great Lakes on 24 March 1998, an El Niño year. During this winter, ice development (grey area) was exceptionally scarce. Under prevailing westerly winds, note the movement of Chl *a*-rich waters out of Duluth/Superior Harbor, Chequamegon Bay, and Ontonagon River in Lake Superior; rotation of Chl *a*-rich waters into a circular ring ('doughnut') in southern Lake Michigan; movement of Chl *a*-rich waters out of Saginaw Bay and circulation around Port Huron into the southern basin of Lake Huron; intense development in the shallow southwestern basin of Lake Erie off the Maumee River, movement of waters along the northern rim into the middle basin of Lake Erie.

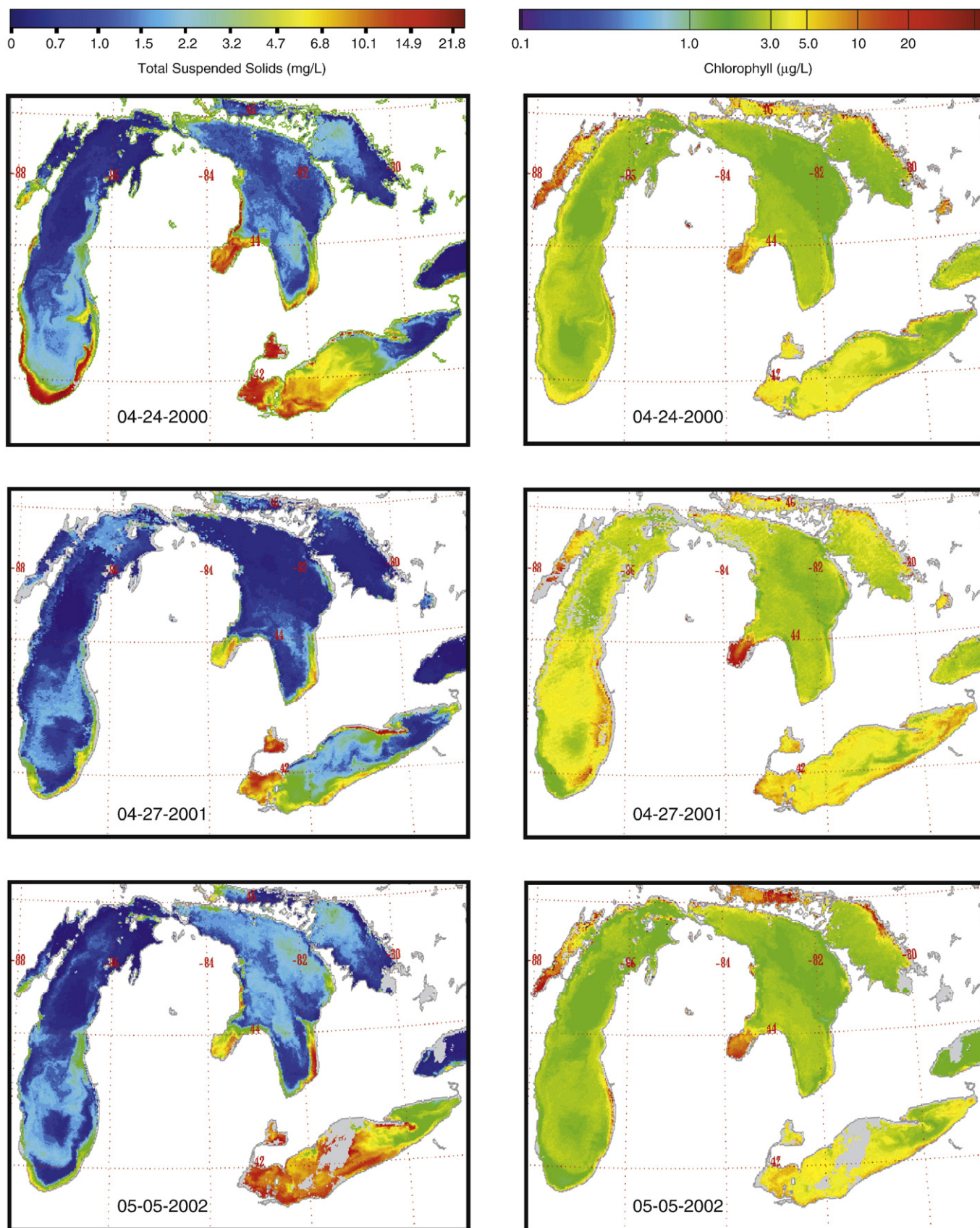


Fig. 3. Late-winter TSM and Chl *a* patterns, 2000–2002 (SeaWiFS imagery). Left column is total suspended matter (TSM), derived from SeaWiFS 555 nm band reflectance, whereas right column is Chl *a*, from OC2 equation (see Methods and materials). Scale bar is given above each column. Dates are provided for the various years.

Table 2

Using SeaWiFS imagery, we noted the number of days that winter algal blooms were seen in southern Lake Michigan, Saginaw Bay in Lake Huron, and western Lake Erie. With SeaWiFS imagery, there were two overpasses per day. The table suggests that late-winter algal blooms were relatively common in the lower Great Lakes and in lower Lake Michigan before quagga mussels began increasing. Daily cloud cover obscured many of the scenes in January and February, accounting for low early season totals, whereas clear skies were more common in March and April, allowing better detection of algal blooms.

Year	Lake Michigan				Lake Erie				Lake Huron (Saginaw Bay)			
	J	F	M	A	J	F	M	A	J	F	M	A
1998	–	–	5	4	2	–	5	9	–	–	6	7
1999	–	1	11	5	1	3	12	13	–	1	9	13
2000	–	–	7	12	1	2	11	8	–	4	10	12
2001	1	1	5	11	–	2	8	15	–	–	2	10
2002	–	5	5	5	3	10	7	9	–	2	4	11

were not image artifacts, as transects verified vertical patterns for Chl *a*, temperature, and other variables (colored dissolved organic matter, transmissivity) associated with the spatially complex, rotating surface gyre structure (Budd et al., 2002; Kerfoot et al., 2008).

The precise circulation patterns appeared to be basin-specific, subject to ice-off dates, bathymetry configuration, and prevailing wind stress and propagated currents (Beletsky et al., 1999). For example, multiple images showed that in southern Lake Huron, following ice-off, sediments moved out of Saginaw Bay counterclockwise (cyclonic) around the southern basin. They also rotated counterclockwise off Port Huron, delivering sediments and phytoplankton into deeper waters. In Lake Erie, again following ice-off, Maumee River discharges and resuspended sediments from the shallow western basin combined and moved northward and eastward (anticyclonic) into the central and eastern basins (Figs. 2 and 3). Algal growth was most pronounced in Saginaw Bay and in the western and middle basins of Lake Erie, as the latter achieved surface Chl *a* concentrations as high as 5–15 µg/L. Circulation of sediments and algae was also evident in southern Lake Michigan, moving off the eastern coastline near the convergence zone (Figs. 1–3). Algal activity within the circular offshore ring ('doughnut') in Lake Michigan appeared more diffuse than in Saginaw Bay or Lake Erie, and reached maximum Chl *a* concentrations of 2–3 µg/L during 1998–2002. The important point here is that these phytoplankton blooms were late-winter phenomena (Table 2), distinct from the traditional warmer water spring blooms that developed behind the coastal 'thermal bar' in late April to early June, and that peaked in May–early June.

Details of 'doughnut' in Lake Michigan before quagga mussels

In Lake Michigan, we studied late-winter bloom rings ('doughnut') in much greater detail than in the other lakes. In southern Lake Michigan, water circulation appeared highly episodic, because it was strongly wind driven. Wind direction during winter was predominantly from the north to northwest, propagating two counter-rotating gyres: a counterclockwise-rotating (cyclonic, south basin) gyre to the right of the wind and a clockwise-rotating (anticyclonic, north basin) gyre to the left of the wind (Fig. 1; Beletsky and Schwab, 2001; Beletsky et al., 2003; Schwab and Beletsky, 2003). After a large storm, the gyres were separated by a convergence zone (Figs. 1–3) along the downwind shore (Grand Haven to Muskegon) with resulting offshore flow and a divergence zone along the upwind shore with onshore flow. Offshore flow in the convergence zone could be seen to extend into the rotating offshore gyre (Figs. 2 and 3). Turbid water captured in the convergence zone contained very fine-grained material (grain size <20 µm), in concentrations between 1 and 5 mg/L, which could stay in suspension for weeks. Within about 2–7 days after capture, the nutrient-rich water created a doughnut-shaped algal bloom in water depths roughly between 40 and 100 m. A subsequent strong storm

could create a new nearshore turbid (resuspended sediment) region, or in the absence of a storm, the offshore 'doughnut' ring could close and dissipate.

How long has the 'doughnut' late-winter bloom been occurring? Remote sensing studies (AVHRR, SeaWiFS) in the Laurentian Great Lakes are hindered during winter by cloud cover, particularly in January–February (Stroud et al., 2009; also see Table 2). Yet inspection of AVHRR imagery confirmed TSM and temperature spatial patterns from 1992 to the present (16 years). Similar scrutiny of SeaWiFS imagery revealed winter bloom structures from 1998 until the present, a continuous 10-year interval. April sampling by GLNPO (Great Lakes National Program Office) from 1982 until the present (26 years) indicates strong horizontal patterns for Chl *a* along our E–W transect region that are very consistent with the 'hole' and circular 'doughnut' bands seen in SeaWiFS images (Glenn Warren, unpubl. data). That is, values are lowest in the 'doughnut hole', higher in the left turbid limb, and highest in the right turbid limb, where PO₄ loading from rivers is known to be greatest (St. Joseph, Kalamazoo, Grand, and Muskegon Rivers, Kreiss et al., 2004; Pauer et al., 2007).

The 'doughnut' structure can be present in January, but is most pronounced in March–April (Table 2). It can also persist through multiple storms. For example, in 2000, the circular bloom feature was present from March 7 until April 25, whereas in 2001, it extended from April 8 until April 24. If storms are not strong, or near the end of April, the structure would dissipate as rings expand to fill in the central 'hole'. On 19–22 April 01 the 'doughnut' was well formed and the cruise path cut across the hole of the structure, whereas on 12–15 April 06 and 21–23 April, 08, the ring pattern was more diffuse.

Phytoplankton in net tows and water samples from 2001 to 2008 dates documented that the species composition in the doughnut had large-bodied diatom species [*Aulacosira* (*Melosira*), *Asterionella*, *Tabellaria*, *Fragilaria*; Kerfoot et al., 2008], in addition to open-water small centric diatoms (*Cyclotella*), cryptophytes, and flagellates typically found in deep waters (Bergmann et al., 2004). Deep net tows were often clogged with *Aulacosira*. However, zooplankton samples from 2006 included substantial concentrations of quagga mussel veliger stages (Fig. 4a), although counts were low-biased because we used 125 µm netting. However, dramatic differences have now appeared in the late-winter and early spring spatial distribution of Chl *a* patterns. These transformations appear due to the spread of settled, filtering quagga mussels.

Disappearing 'doughnut' in Lake Michigan

Both remote sensing images and ship-board measurements record a major reduction in Chl *a* and a dramatic increase in water transparency since 2002, coincident with increase in dreissenid mussels. Winter veliger larvae from *D. rostriformis bugensis* were detected during the 2006 cruise (Fig. 4a). These larvae were not present during the EEGLE late-winter pelagic collections (1998–2001). In 2006, the veligers were shown to be differentially concentrated in the rings of the 'doughnut', benefiting from the late-winter productivity pulse (Kerfoot et al., 2008). During the last three years, veligers were most abundant in 2006, and declined in 2008 (Table 3).

Whereas zebra mussels (*D. polymorpha*) have a preference for hard substrates, the rounded and lighter shell and longer, more vertical siphon of *D. rostriformis bugensis* allows this species to colonize softer substrates. Individual *D. rostriformis bugensis* were capable of colonizing substrate under the doughnut, just by settling out of suspension. Over the interval from 2002 until 2006, the density of settled mussels increased exponentially (Nalepa et al., 2009). By 2006–2008, mean densities of attached mussels ranged between 6 and 19 × 10³ individuals/m² at 16–30 m depth, 12 and 13 × 10³ individuals/m² at 30–50 m depth, and 5 × 10³ individuals/m² at 51–90 m depth (Nalepa et al., 2009, 2010). As the ability of settled adults to clear the water column is related to the volume of water over the benthic interface, one

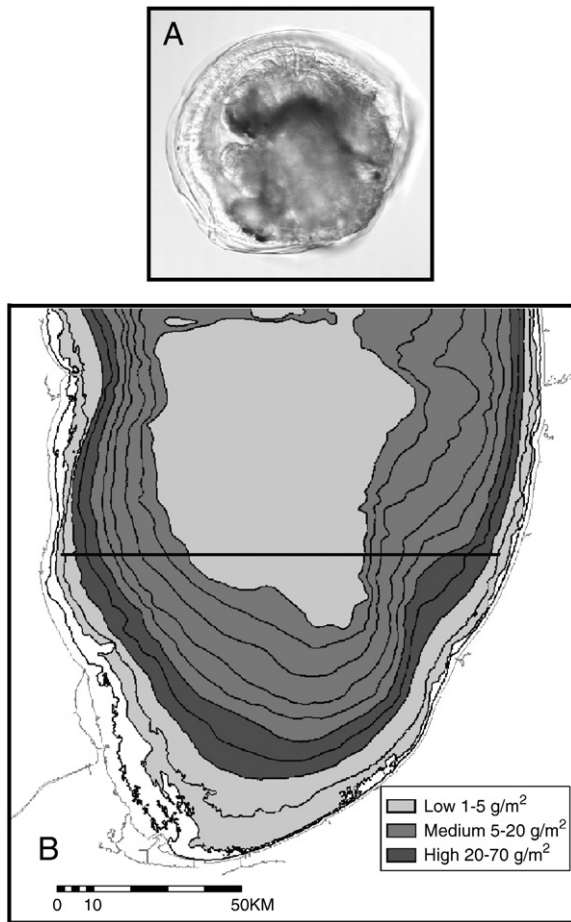


Fig. 4. Dreissenid mussels in Lake Michigan waters: A) veliger stage from April southern transect sampling; B) depth distribution of settled quagga mussels (*D. rostriformis bugensis*) in southern Lake Michigan (after Nalepa et al., 2009).

would expect filtration effects from settled adults to be most pronounced around the shallow rim of the doughnut (Fig. 4b; modified from Nalepa et al., 2009). The clearing in nearshore waters around the outer, shallow rim of the “doughnut” is evident in plots of SeaWiFS Chl *a* values through time (Fig. 5). Values from the outer edges of the “doughnut” show pronounced, highly significant (OW $_{1F_{10}}=48.0$; $p=4.05E-05$; OE $_{1F_{10}}=18.0$; $p=0.002$) declines, whereas values from inner edges show only a modest, nonsignificant decrease (IW $_{1F_{10}}=1.6$; $p=0.228$; IE $_{1F_{10}}=1.6$; $p=0.233$).

Ship-board studies complemented the remote sensing investigation. Vertical Seabird CTD casts [64 stations at 1.85 km (i.e., 1 nautical mile) intervals] and horizontal BAT tows recorded water column differences across the southern basin on a longitudinal transect, between 86.320°W

Table 3

Mean densities (number/m³) of zooplankton along cross-lake transect, S. Lake Michigan, comparing 2006 (13–14 April 06), 2007 (2–3 April 07), and 2008 (21–23 April 08) values. Densities are means ± 95% confidence limits ($n=9$, 2006; $n=7$, 2007; $n=11$, 2008); total nauplii are shown separately. Significant ($p<0.05$; *t*-test) declines between 2006 and 2008 are marked by an asterisk (*). Although veliger densities are high, these are conservative estimates, because smaller individuals passed through the 120 μm mesh.

Taxa	2006	2007	2008
Nauplii	8142 ± 2309	5721 ± 1776	6016 ± 1360
<i>Diatomus</i>	3208 ± 950	2807 ± 704	2912 ± 775
*Cyclopoids	223 ± 111	16 ± 19	14 ± 8
* <i>Epischura</i>	750 ± 445	1682 ± 2468	55 ± 29
* <i>Limnocalanus</i>	364 ± 198	85 ± 59	30 ± 12
<i>Dreissena</i>	645 ± 381	123 ± 48	448 ± 219

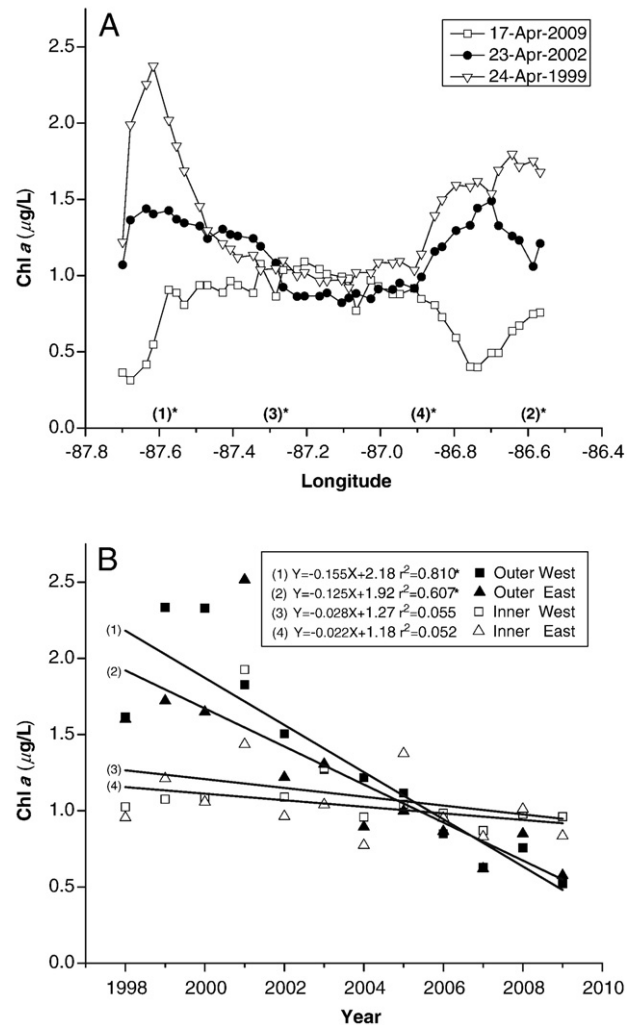


Fig. 5. Reduction of Chl *a* around the outer edge of the ‘doughnut’, estimated from SeaWiFS images: A) Chl *a* values along southern Lake Michigan transect in 1998, 2006, and 2009, taken from SeaWiFS images (mean of 4 nearby pixels per site). Numbers on top of x-axis indicate longitudinal position of the “inner” and “outer” edge regression values plotted in (B). b) Linear regressions are fit to yearly Chl *a* values in outer edge versus inner edge of rings. Paired linear regressions represent east and west limbs of the ‘doughnut’, contrasting reduction in outer (solid symbol) versus inner (hollow symbol) margin. Regression equations are given for each line (*highly significant slope, $p<0.01$).

and 87.745°W. Ship-board vertical CTD profiles for Chl *a* and water transmissivity during 2001, 2006, and 2008 across the southern transect also show pronounced clearing through time, especially along the shallow edges (Fig. 6; compare 2001 with 2006 and 2008). Both Chl *a* and water transmissivity change over the time interval, and shallow waters become less turbid. Mean CTD temperatures, depth-averaged Chl *a*, and mean water transmissivity values emphasize how values have changed (Fig. 7). Standard deviations for vertical (CTD) site profiles quantify the statistical variation of values. During the cruises, water temperature ranged between 2.8 and 4 °C in offshore waters, and above 4 °C behind the thermal bar in coastal waters. Note that the standard deviations around the mean temperature values are very narrow, underscoring the vertical mixing of the winter water column in the rotating gyre. Values for different years document highly significant temporal shifts toward increased water transparency and decreased Chl *a* along the outer edge of the eastern and western “doughnut” rings from 2006 to 2008.

In 2001, before quagga mussels, water transparency (transmissivity) varied between 74 and 85% at deep-water sites and was 80 and 82% in the western and eastern ‘doughnut’ rings. In 2001, Chl *a* ranged

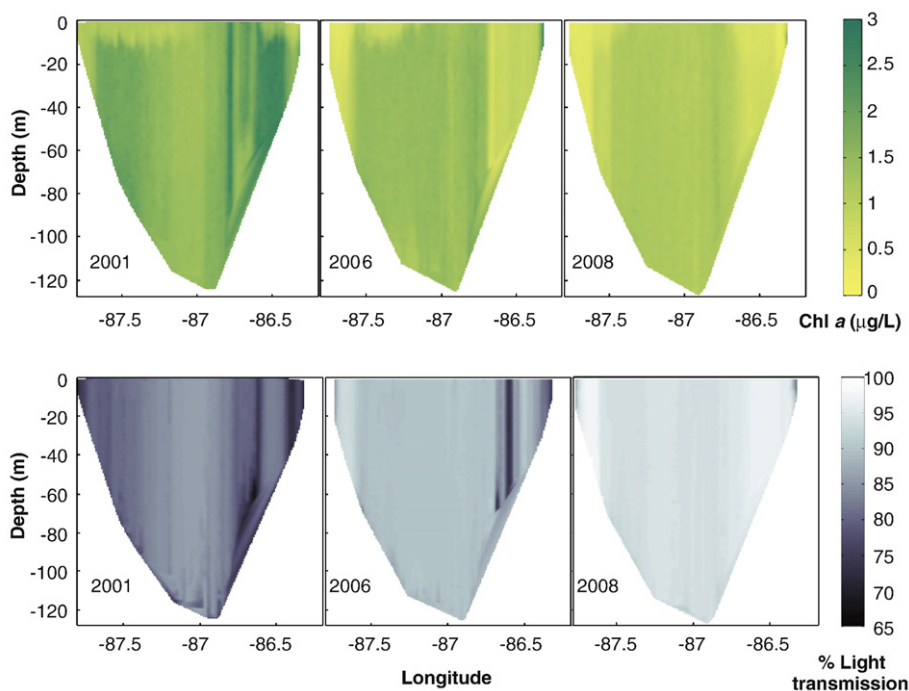


Fig. 6. Vertical clearing of water column, based on ship-board measurements. Measurements come from Seabird CTD casts taken along the southern transect (see Fig. 1) between South Haven, Michigan, and Waukegan, Wisconsin. Compare the Chl *a* and % light transmission values for 2001, 2006, and 2008.

between 1.1–2.6 µg/L and 1.8–2.6 µg/L in the western and eastern doughnut rings, respectively. After quagga mussel appearance, water transparency increased progressively to 89% by 2006 and 94–96% by 2008. Chlorophyll *a* concentrations declined to 0.5–1.7 µg/L by 2006 and 0.4–1.5 µg/L by 2008. The reduction of Chl *a* between 2001 and 2008 was 56–78% in the western limb and 74–75% in the eastern limb.

Not only did transparency increase and Chl *a* fall across all sampling stations, the spatial turbidity pattern changed dramatically (Figs. 6 and 7). The width of the “doughnut” narrowed 26% and transparency at mid-coastal regions (40–80 m depth) reversed from more turbid to less turbid (from 80–82% to 97% transmissivity). Some of the individual values are now extraordinary for Lake Michigan. Along the western shoreline in 2008, water transmissivity reached 97% and Chl *a* dropped to 0.4 µg/L, approaching water clarity and Chl *a* concentrations reported for Lake Superior.

Individual vertical CTD profiles for 2001 and 2008 document the dramatic decline in Chl *a* concentration at the shallower coastal margins of the transect, as compared to the central region, although the decline is present at all stations (Fig. 8). When the % reduction is plotted versus longitude along the southern transect, the greater reduction along shallow edges is evident (Fig. 9). Reduction of chlorophyll related to water depth and a corresponding transparency pattern suggests progressive filtration effects from settled quagga mussels. The observed results correspond closely to modeled quagga filtration effects expected from a combination of density and water column depth (Vanderploeg et al., 2010).

Zooplankton changes

Some zooplankton changes are also apparent from the cross-transect vertical tows (Table 3). From 2006 to 2008, nauplii and total herbivorous diaptomid copepods decreased in density (26% and 9%, respectively). Cyclopoid copepods were dominant in 1998–1999 (Vanderploeg et al., 2007), yet by 2008 they were severely depressed over 2006 values (94% decline), and often missing from individual vertical tows. There was also a recent reduction of large-bodied, omnivorous calanoid copepod species from 2006 to 2008 (*Limnocalanus*,

93% decline; *Epischura*, 92% decline). The recent reduction in over-wintering omnivorous (predatory) species may signal reduced energy flow up to higher trophic levels, indicating repercussions of the winter Chl *a* reduction. The *Limnocalanus* reduction from 2006 to 2008 reverses an increasing trend from 2003 to 2006 discussed by Barbiero et al. (2009). Reduced phytoplankton density may begin to have an impact on veliger densities, although the decline from 2006 to 2008 is not significant.

Comparison of OPC coastal counts also showed some differences. OPC counts were broken down into the two different-sized bins (Bin 1, 0.25–0.5 mm; Bin 2, 0.5–1.0 mm) used previously (Kerfoot et al., 2008). The smallest size category was comprised mainly of rotifers, nauplii, and immature copepodites, whereas the larger was primarily calanoid copepodites. In 2001 OPC transects, Bin 2 coastal densities ranged between 4000 and 5000 counts/m³ (mean ± SD = 4.8 ± 0.4 × 10³/counts/m³) whereas 2008 transects ranged between 2000 and 4000 counts/m³ (mean ± SD = 3.0 ± 1.9 × 10³/counts/m³), significantly lower than the earlier counts ($p < 0.0001$, t -test on 2001 vs 2008 data sets, $N = 1169$, $t = 206$). The significant count reduction occurs in the same region where there were serious reductions in Chl *a* due to quagga activity, again suggesting an impact up the pelagic food-web. This test is region-specific and hence more powerful than the vertical zooplankton tows, which are averaged across the entire transect.

In 2008, across the thermal bar off Muskegon, the smaller size category was 4-fold higher in nearshore waters (Fig. 10, Table 4) than in offshore waters. The second size category (0.5–1.0 mm) was elevated in deep offshore and declined in nearshore waters, although values peaked near the thermal bar (4 °C). Despite the lower Bin 2 values in the coastal regions, the relative Bin values were similar to previous historical comparisons, i.e. rotifers were much more abundant (2–4×) in nearshore regions (Vanderploeg et al., 2007).

Discussion

Remote sensing (SeaWiFS, MODIS) imagery from 1998 to 2003 verified spatially complex suspended sediment and Chl *a* patterns in

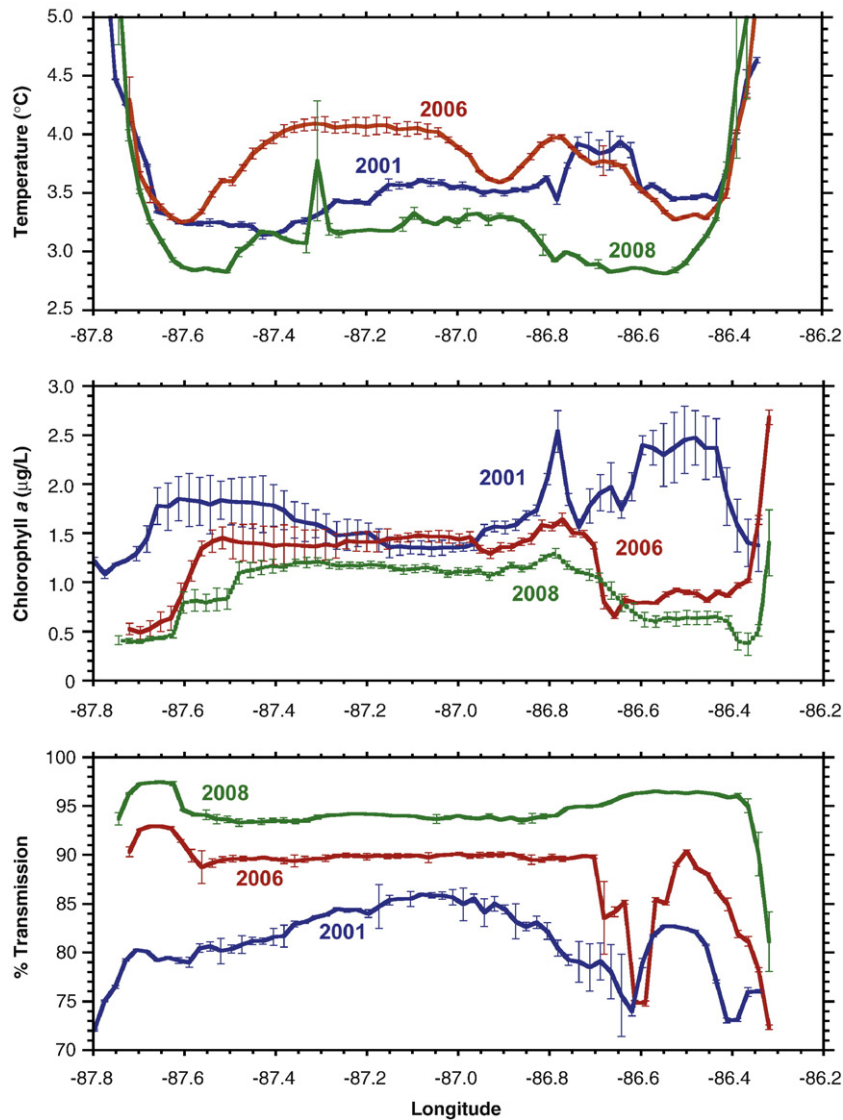


Fig. 7. Statistical plots for depth-averaged CTD values along southern Lake Michigan transect: (A) temperature, (B) Chl *a*, and (C) % light transmission. Values are means and standard deviations for vertical casts. Note the severe decrease in Chl *a* concentration in both the eastern and western shelf regions (down to 0.4 µg/L), the extreme increase in water transparency (average % transmission 93–98%), and the narrowing of the high-Chl *a* 'doughnut' region.

the Laurentian Great Lakes during late winter. These patterns suggested an important coupling between late-winter storm-induced gyre formation, coastal water plus sediment capture, and deep-water productivity (Kerfoot et al., 2008). Recent resuspended particle-based modeling efforts have successfully reproduced the resuspension and transport dynamics seen on SeaWiFS imagery for Lake Michigan (Lee et al., 2007).

Detailed inspection of river discharges and resuspended sediments along the southeastern coastline of Lake Michigan (Biddanda and Cotner, 2002) suggested high levels of dissolved organic matter and enhancement of productivity along the coastal shelf in years when the near-coastal turbidity plume did not hinder photosynthesis (Millie et al., 2002; Lohrenz et al., 2004, 2008). Here we extended the initial Lake Michigan observations to a number of the Laurentian Great Lakes. The remote sensing images revealed an important coastal-offshore linkage, one that normally benefited over-wintering planktonic species characteristic of the large lakes. In Lake Erie, the productivity pulse occurred with scattered ice and persisted into the time of the spring bloom, so that the two phenomena might be confused. High densities of late-winter algae probably contributed to the summer deoxygenation of hypolimnetic waters in the middle (summer 'Dead Zone') and eastern basins.

The magnitude of the offshore transfer of nutrients in Lake Michigan might be exaggerated by climate change, as higher temperatures and more frequent winter storms suppressed coastal ice formation and encouraged movement of nutrient-enriched river waters and sediments into pelagic waters (Kerfoot et al., 2008). The dominant algae associated with the Lake Michigan 'doughnut' ring blooms (*Aulacoseira islandica*) is the same species that recently clogged net tows during 2007–8 Lake Erie ice-breaker studies (Wilhelm, 2008). In Lake Erie, *Aulacoseira islandica* was found attached under ice and in open waters near ice, achieving near-bloom conditions (Mike McKay, unpubl. data).

The late-winter blooms were distinct from traditional spring blooms, because they occurred earlier and in cold water, away from the coastal thermal bar. Thermal bar formation and stratification, in fact, disturbs the conditions that promote offshore transfer of river waters and resuspended sediments. During low ice years, phosphorus-rich plumes (river water and coastal sediments) are transported offshore and go through a heterotrophic to autotrophic transformation between January and April in deep waters (Cotner et al., 2000; Biddanda and Cotner, 2002; Kerfoot et al., 2008). The remote sensing and ship studies have stimulated preliminary modeling reconstructions (Ji et al., 2002; Beletsky et al., 2003; Lee et al., 2007).

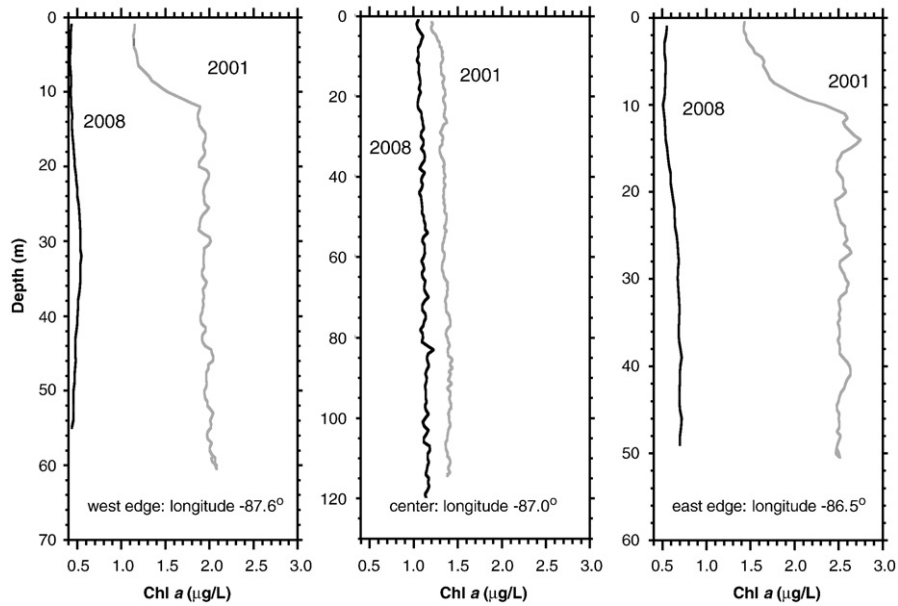


Fig. 8. Comparative depletion of Chl *a* in shallow shelf versus deep-water, central regions, showing the vertical impact. Vertical profiles for April 2001 (before quagga mussels) are compared with profiles from April 2008 (after quagga mussels) from western shelf, central, and eastern shelf regions.

Earlier optical plankton counter (OPC) transects and vertical plankton net tows in Lake Michigan documented that the lateral late-winter transfers influenced higher levels of food webs (zooplankton). Deep-water, over-wintering zooplankton species (*Leptodiptomus sicilis*, *Limnocalanus macrurus*, *Eurytemora affinis*, *Senecella calanoides*) seemed to benefit from the late-winter production, as they differentially congregated in the rings (Kerfoot et al., 2008). However, the discovery in 2006 that veliger larvae from quagga mussels were also exploiting the late-winter production pulse in southern Lake Michigan, and presumably in the other lower Great Lakes, carried disturbing implications

that are now playing out. Deep-water veligers experience a double benefit, relative to spread and growth. Not only do the suspended larvae capitalize on the late-winter productivity pulse, they also disperse in strong winter currents associated with the winter storms. Increased benthic attached mussel abundance in coastal waters behind the thermal bar seems to be severely depleting the spring bloom (Fahnenstiel et al., 2010; Nalepa et al., 2009, 2010), yet we show here that it is also reducing the winter ‘doughnut’ pulse in contiguous offshore waters. As suspended material is filtered from overlying waters,

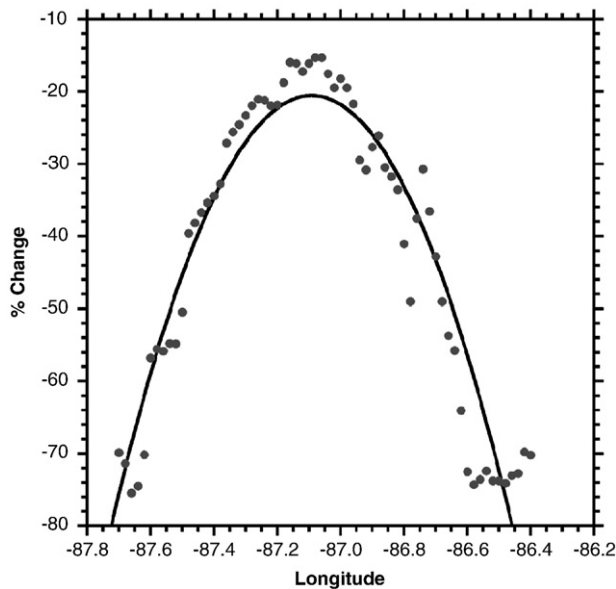


Fig. 9. Spatial pattern of Chl *a* depletion along southern transect in Lake Michigan, expressed as % change (i.e. reduction) between April 2001 sites (before quagga mussels) and April 2008 sites (after quagga mussels). The difference between the mean Chl *a* site values is plotted against longitude, along the southern ship transect. The Chl *a* reduction occurs most dramatically along the shallower rim (“edges”) on both sides, is symmetrical, and is less in the deep central basin. The fit polynomial regression ($Y = -1.127e^{06} - 25874X - 148.55X^2$) has an $r^2 = 0.901$; but more important, it shows the depth-dependent symmetry of the severe coastal reductions relative to quagga mussel abundance (see Fig. 4).

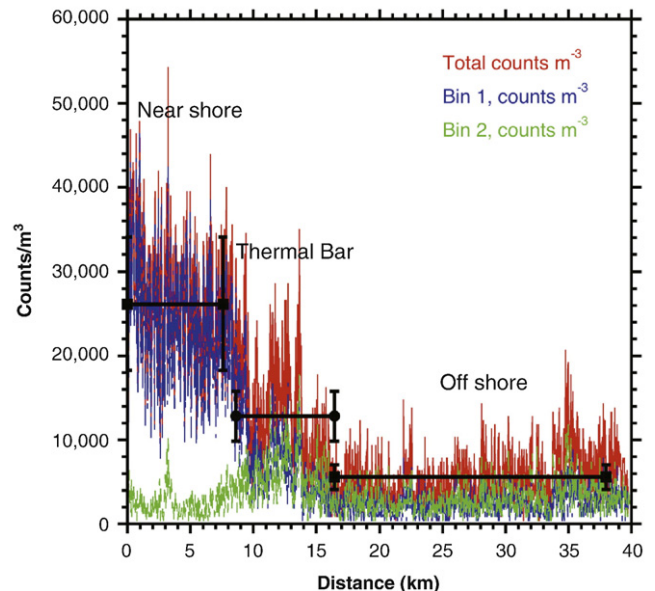


Fig. 10. Optical plankton counter (OPC) transect from nearshore into offshore waters off Muskegon, Michigan, illustrating differences in zooplankton densities on 14 April 2008. Densities are plotted as a 50-interval mean and high-low range for 10-s-duration interval counts. Total counts (red) and separate densities from two separate size bins (blue, Bin 1, 0.25–0.5 mm; green, Bin 2, 0.5–1.0 mm) are plotted. Dark lines show the mean density (all three bins) for the three intervals: nearshore (left portion), thermal bar region (middle), and offshore region (right). Bin 2 densities increase slightly in the region of the thermal bar (4 °C). Statistics are listed in Table 4.

Table 4

Grand means and standard deviations for BAT optical plankton counter tallies, nearshore into offshore waters, 14 April 2008, off Muskegon, MI. Grand means are based on a series of 50-interval means for number of individuals counted during a 10-s duration interval. Estimates of fluid volume flows are then used to convert counts into density estimates given below.

Location	Mean	Std dev
1.0–7.6 km, nearshore		
Total density ($\times 10^3/\text{m}^3$)	26.2	7.9
Bin 1 (0.25–0.5 mm)	24.2	7.4
Bin 2 (0.5–1.0 mm)	2.4	1.5
8.6–16.4 km, thermal bar		
Total density ($\times 10^3/\text{m}^3$)	13.0	6.7
Bin 1 (0.25–0.5 mm)	7.3	4.7
Bin 2 (0.5–1.0 mm)	5.4	3.0
16.5–37.9 km, offshore		
Total density ($\times 10^3/\text{m}^3$)	5.6	3.0
Bin 1 (0.25–0.5 mm)	2.5	1.5
Bin 2 (0.5–1.0 mm)	3.0	1.9

remarkable water clarity is achieved along with diminished phytoplankton abundance and productivity. The filtering attached mussels seem to be constricting the winter bloom primarily along the edges and diminishing even the deep-water algae.

Along the coastal regions of Lake Michigan, water transmissivity and Chl *a* values are now approaching Lake Superior values. Primary production estimates in 1998 ranged from 0.18 to 0.48 g C/m²/d compared to 0.18–0.24 g C/m²/d for satellite-derived values, and in 2000 ship-board studies gave 0.19–0.37 g C/m²/d compared to 0.15–0.46 g C/m²/d for satellite-derived values (Lohrenz et al., 2004, 2008). Recent offshore Muskegon site estimates suggest a 66% decline in spring Chl *a* and a 70% reduction in productivity (Fahnenstiel et al., 2010), whereas GLNPO April ship surveys show about a 72% decrease in April Chl *a* concentrations in southern Lake Michigan (Mida et al., 2010). Both these estimates are similar to our observed declines, although we document the spatial pattern across southern Lake Michigan in much more detail.

Quagga mussel filtration is influencing both nearshore and offshore productivity. Barbiero et al. (2009) argued that a combination of top-down and bottom-up effects between 1998 and 2006 led to a large increase in *Limnocalanus*. We found that since 2006, filtration from settled mussels seems to be diminishing Chl *a* concentrations for deep-water, over-wintering omnivorous zooplankton species (cyclopoid copepods; the calanoid copepods *L. macrurus* and *Epischura lacustris*). The OPC counts in sensitive regions over the coastal quagga beds document a highly significant reduction in counts. We interpret this as a reduction in zooplankton density for medium sized species and size classes (Bin 2, 0.5–1.0 mm). However one must be cautious that the reduced counts might also be correlated with inert particles and increased water transparency, since OPC counts in Lake Michigan can include particles other than live plankton (Liebig et al., 2006). The offshore depression of cyclopoid copepods may be linked to severe coastal suppression, as absolute densities of cyclopoid copepods were previously greatest in nearshore waters (Vanderploeg et al., 2007). Late-winter veliger larvae benefit from the winter production pulses because the late-winter blooms provide a primary source of food at a critical time when starvation could be important. The late-winter phytoplankton pulse allows deep-water recruitment to begin in April, before the spring bloom (Nalepa et al., 2010). In our samples, there are some indications of a plateau, or even a modest reduction in veliger density, perhaps suggesting the beginning of a late-winter density-dependent feedback. That is, diminished algae in the 'doughnut' may lower food levels for the April deep-water pulse of veligers, reducing future settlement success. Similar density-dependent feedbacks have been recorded for zebra mussels in Lake St. Clair, Saginaw Bay, Lake Erie, and Lake Champlain (Bentil et al., 2007).

Larger zooplankton (0.5–1.0 mm) seems decreased over coastal waters where quagga mussels are most abundant. Increased smaller zooplankton (especially rotifers) in nearshore waters is expected, and the ratio of small to large size categories appears as skewed in our OPC counts as before. For example, during March–April 2000 EGGLE sampling at four transects (New Buffalo, Gary, Chicago, Muskegon), relative densities of microplankton and small zooplankton to large zooplankton increased from deep to nearshore waters, along a ratio of 1.2–2.3× (Vanderploeg et al., 2007).

The implications of quagga-mediated productivity displacements in the Great Lakes are disturbing. In all probability, in Lake Michigan we are witnessing a major shift of productivity patterns in time and space largely mediated by a single species (i.e. quagga mussels). The spatial and temporal changes resemble shifts documented in Lake Erie for dreissenid filtering (Depew et al., 2006). As quagga and zebra mussels filter the overlying water column, their feces and pseudofeces contribute nutrients and organic matter to the benthic environment (Vanderploeg et al., 2002). The increased water transparency allows light to penetrate to the shelf bottom and the displaced nutrients encourage diatom and attached macrophyte growth (e.g. *Cladophora*). This process has been termed 'benthification' by Mayer et al. (2002) and the 'shunt' by Hecky et al. (2004).

The LND ('lateral nutrient displacement') observed in past late-winter SeaWiFS images should act opposite to 'benthification' effects, differentially transporting shallow-water river discharges and resuspended nutrients back out to the deep pelagic zone. Yet descending coastal shoals of quagga mussels appear to have interrupted resuspension of littoral nutrient-rich sediments and lateral transport of organic-rich river discharges. Our observations of greatly enhanced water transparency and severely decreased Chl *a* concentrations along inner (shallow) basin margins suggests serious interference with lateral transport. If the spring bloom collapses along the entire shoreline of Lake Michigan, can the remaining deep-water portion of the late-winter productivity pulse and the summer deep-water Chl *a* maximum adequately sustain the pelagic deep-water food-web?

The presence of dreissenids in the other Great Lakes has caused dramatic increases in water clarity, increased nuisance benthic plant growth, and increased harmful algal blooms, with indications of impacts on many fisheries (e.g. Vanderploeg et al., 2002; Hecky et al., 2004). We stress that the winter–spring transition is also a critical time for calanoid copepod reproduction. Deep-water calanoid copepods should be the most resilient to nearshore coastal impacts. However, any effect of cold-water dreissenid pelagic veligers or settled adults on 'doughnut' phytoplankton and microzooplankton in Lake Michigan would influence survival and subsequent reproduction of over-wintering calanoid copepods during this period, at a time when food is limiting for over-wintering plankton species, creating a winter bottleneck. Severe reduction of calanoid and cyclopoid copepodite stages would also have serious implications for fish recruitment in the spring, since young of many species draw from these over-wintering planktonic stages as their primary food source. Preliminary evidence on a few pelagic Lake Michigan fishes suggests developing impacts (e.g., alewives; Pothoven and Madenjian, 2008).

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