



Regime shifts in satellite-derived chlorophyll within the Laurentian Great Lakes[☆]

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ABSTRACT

As a result of implementation of nutrient management following the binational Great Lakes Water Quality Agreement in 1972, the ecosystems within the Laurentian Great Lakes were gradually transforming to lower trophic regimes. This transformation dramatically accelerated in the late 1980s after the introduction of two invasive species of filter-feeding mussels of the genus *Dreissena*. We performed a detailed analysis of spatial and temporal patterns of this transformation using remotely sensed surface chlorophyll-a concentration (*Chl-a*) from the multi-satellite long-term Ocean Colour Climate Change Initiative (OC-CCI) dataset as a proxy of ecosystem state. We analyzed 25 years (1997–2022) of monthly composites covering most of the Great Lakes' area detecting regime shifts in *Chl-a* employing an integrated approach combining Seasonal-Trend decomposition (STL) and Sequential T-test Analysis of Regime Shifts (STARS). The results identified the timings (shift points) when *Chl-a* stabilized at new lower trophic regimes, the magnitudes of *Chl-a* decrease across various lake regions and depths, and the changes in *Chl-a* seasonal cycles. In Lakes Michigan, Huron, and Ontario, the timings and magnitudes of regime shifts and vanishing of spring phytoplankton bloom suggest that dreissenid mussel presence was a primary driving factor of the observed transformation. We demonstrate that the OC-CCI dataset is a reliable source of information that enables the detection of these regime shifts in major lakes, with only minor effects of inconsistencies resulting from the biases between different satellites collecting data during different time periods.

1. Introduction

Decreases in phytoplankton biomass and productivity in the Laurentian Great Lakes over the past decades demonstrate a cumulative effect of significant reduction of nutrient loads and the introduction of invasive species. Since European settlement through to the early 1980s, the Great Lakes experienced progressive eutrophication (Stoermer et al., 1990), with phosphorus as the major nutrient limiting primary production (Schelske et al., 1974). In response to the deteriorating state of water quality in these lakes, the binational Great Lakes Water Quality

Agreement (GLWQA), a commitment between the US and Canada to provide a framework for identifying binational priorities to improve and protect water quality, was signed in 1972 (International Joint Commission, 1972). As a result of the control programs, phosphorus loadings to the lakes substantially decreased during the 1970s and 1980s (Bunnell et al., 2014), resulting in significant lake-wide reductions in phytoplankton biomass (Millard et al., 1996; Stevens and Neilson, 1987).

The decrease of phytoplankton biomass in the Great Lakes dramatically accelerated in the 1990s after the colonization of the lakes by two

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species of filter-feeding mussels: zebra mussel *Dreissena polymorpha* (Pallas) and quagga mussel *D. rostriformis bugensis* (Andrusov), hereafter referred to collectively as “dreissenids.” As suspension filter-feeders, the magnitude of their impact on pelagic ecosystems results from their ability to filter massive volumes of water (Diggins, 2001; Horgan and Mills, 1997; Kryger and Riisgård, 1988). A little selection of particle size or quality is performed during filtration, so more water is filtered than would be required to feed an individual, and not all filtered particles are consumed. Excess food and particles that are too large or are of low food quality are bound in mucus and expelled as pseudofeces (Padilla et al., 1996). As a result, these mussels affect pelagic ecosystems through both top-down control by feeding on planktonic organisms and bottom-up control by sequestering phosphorus that otherwise would be available to phytoplankton (Bunnell et al., 2014). The total impact of an individual mollusk on the planktonic community is, therefore, much greater than the impact of the same biomass of other predators (e.g., zooplankton).

The effect of zebra and quagga mussels on the Great Lake ecosystem included an increase in water transparency (Binding et al., 2015; Son and Wang, 2019; Yousef et al., 2017), a decrease in the biomass/abundance of phytoplankton and chlorophyll-a (Fahnenstiel et al., 2010; Reavie et al., 2014; Vanderploeg et al., 2010), decline in zooplankton (Barbiero et al., 2011; Kerfoot et al., 2010; Kovalenko et al., 2018; Pothoven and Fahnenstiel, 2015) and prey fish (Bunnell et al., 2014; Madenjian et al., 2015), and changes in the structure of the nearshore benthic community (Hecky et al., 2004; Nalepa et al., 2009; Pillsbury et al., 2002).

It is unclear whether the reduction in phytoplankton biomass and increase in water clarity result primarily from the regulation of nutrient discharge, or if the heterotrophic pressure of mussels on phytoplankton biomass plays a dominating role in the observed transformation in the Great Lakes. The effect of nutrient regulation is expected to result in a gradual decrease of phytoplankton biomass over most of the lakes’ area. In contrast, the effect of mussel feeding is expected to be correlated with the steps of colonization of the lakes by dreissenids documented in previous studies (Karataev and Burlakova, 2022; Karataev et al., 2021; Nalepa et al., 2010, Nalepa et al., 2009).

The details of the transformation of the pelagic ecosystems of the Great Lakes to new lower trophic regimes are described in numerous publications based on field sampling (Bunnell et al., 2014; Fahnenstiel et al., 2010; Kovalenko et al., 2018; Madenjian et al., 2015; Mida et al., 2010; Pothoven and Vanderploeg, 2020) and satellite radiometry (Fahnenstiel et al., 2016; Rowe et al., 2015; Son and Wang, 2020, 2019; Yousef et al., 2014, 2017). Binding et al. (2015) used an empirical algorithm relating water clarity (Secchi disk depth) to reflectance measured in the green bands of Coastal Zone Color Scanner (CZCS), Sea-viewing Wide Field-of-view Sensor (SeaWiFS), and Moderate Resolution Imaging Spectroradiometer on Aqua platform (MODIS-Aqua), and showed a long-term increase (up to 62 %) in water transparency comparable to the changes in Chl-a as reported in this study. However, most published results were focused either on separate lakes or over relatively short time periods, and many provided assessments averaged over an entire lake and/or depth zone. Furthermore, most published works conclude that this transformation is ongoing (Nalepa et al., 2010, 2009; Reavie et al., 2014; Rowe et al., 2017, 2015). It is thus unknown if phytoplankton biomass has stabilized to new lower trophic regimes and what the final magnitude of that decrease was.

The questions of “when and where trophic status changes are occurring” can be addressed using estimates of surface chlorophyll-a concentration derived from visible measurements collected by Earth-observing satellites. Remotely sensed water color represents a unique source of information for quantitative assessment of interannual variations of large-scale aquatic ecosystems (including ocean and large lakes), especially in the regions where detailed monitoring based on field surveys is unavailable (Calamita et al., 2024). However, combining the data collected by different satellites into one time series may

introduce abrupt shifts and inconsistencies resulting from the differences in accuracy and resolution (spatial, temporal, and spectral) between satellite sensors.

The merged dataset produced by the Ocean Colour Climate Change Initiative (OC-CCI) project includes data corrected for the biases between the reflectances measured by different satellite sensors (Sathyendranath et al., 2019). The most recent version (v.6.0) of the OC-CCI dataset covers >25 years (1997–2022) of continuous global observations and can be used to analyze long-term interannual variations in different aquatic regions. It is important to keep in mind that the early stages of the oligotrophication process in the Great Lakes are not quantified in this study. The OC-CCI dataset started more than two decades after the beginning of nutrient discharge regulation and several years after the first reports of the introduction of dreissenids.

This study provides a detailed analysis of spatial and temporal variations of remotely sensed chlorophyll-a concentration (*Chl-a*) in the five North American Laurentian Great Lakes (Superior, Michigan, Huron, Erie, and Ontario) using a consistent methodology for detecting regime shifts. We performed a quantitative assessment of regime shifts based on *Chl-a*, thus enabling estimation of the timing of shift points between the regimes and the differences between the mean levels of the regime indicator. The objectives of our study include: 1) addressing the question of whether the biases between the data collected during different periods by different satellites can be misinterpreted as regime shifts; 2) estimating the timings (shift points) when different regions of the lake ecosystems stabilized at new lower trophic regimes; 3) quantifying the magnitudes of the *Chl-a* decrease in different geographic and bathymetric zones of the lakes; and 4) analyzing the effect of regime shift on *Chl-a* seasonal cycles in different parts of the lakes. Below, we describe the study area, steps of colonization of dreissenids in the Great Lakes, and details the OC-CCI dataset and statistical methods of data processing and regime shift detection before presenting the results of the study and discussing the findings.

2. The study region: The Laurentian Great Lakes

The Laurentian Great Lakes (Fig. 1) is one of the largest freshwater systems in the world, with a total lake surface area of 244,000 km² and a catchment area of approximately 1 million km². The lakes contain 22,000 km³ of water, which is 84 % of North America’s surface fresh water and 21 % of the world’s surface fresh water supply (Sterner et al., 2017), with the lowest nutrient loads in mass per unit time entering Lake Superior and the largest nutrient load entering Lake Erie (Sterner, 2021). The Great Lakes basin is home to almost 40 million people, or roughly 10 % of the US and 32 % of Canada’s population (Méthot et al., 2015). The lakes differ in size (from 18,960 km² for Lake Ontario to 82,100 km² for Lake Superior (Bunnell et al., 2014)), mean depth (from 7 m for western Lake Erie to 147 m for Lake Superior (Bunnell et al., 2014; Sterner, 2021)), hydraulic residence time (from about 200 years for Lake Superior to about 3 years for Lake Erie (Quinn, 1992)), and levels of primary production (from the ultra-oligotrophic Lake Superior to the periodically hypereutrophic waters of western Lake Erie (Bunnell et al., 2014; Dove and Chapra, 2015)).

Biogeochemical properties of the Great Lakes vary over a broad range of temporal and spatial scales (Sterner, 2021). Among the features potentially encouraging the colonization by dreissenids are relatively high pH and dissolved inorganic carbon (DIC) resulting from a high abundance of limestone and carbonate weathering in all lakes except for Lake Superior (Lin and Guo, 2016), a factor supporting the growth of invasive mussels (Hincks and Mackie, 1997). On the other hand, a negative factor affecting benthic organisms is hypolimnetic hypoxia, which is a regular seasonal event in some shallow embayments (Sterner, 2021), as well as the central basin of Lake Erie, where hypoxia sometimes extended up to 60 % of the surface area (Zhou et al., 2013). The spatial distribution of dreissenids in Lake Erie has been clearly connected to the occurrence of hypoxia (Karataev et al., 2018a).

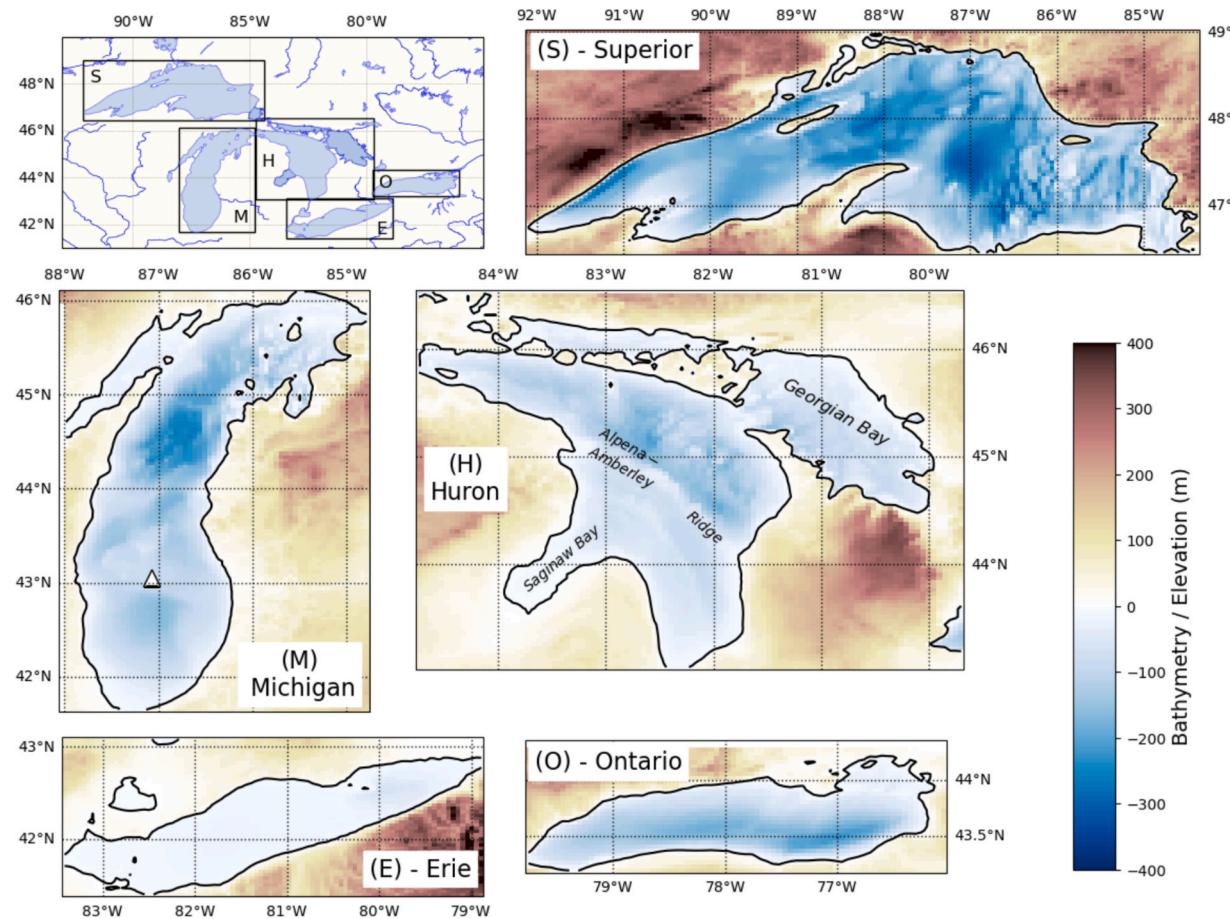


Fig. 1. Bathymetric maps of the Laurentian Great Lakes: (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. Depth/elevation grids from <https://www.ngdc.noaa.gov/mgg/greatlakes/>. White triangle in (M) indicates the center (the location with maximum distance offshore) of Lake Michigan used later in Fig. 2 and Fig. 3.

Because of their large size, the five lakes are often considered “inland seas,” requiring a scientific approach with attributes similar to those of oceanography (Sterner et al., 2017). One of these approaches is using satellite remote-sensing imagery, providing regular synoptic coverage and the opportunity for comprehensive assessment of lake-wide water quality and robust determination of spatial and temporal trends (Binding et al., 2015).

3. Colonization of the Great Lakes by dreissenids

The introduction and expansion of zebra and quagga mussels in the Great Lakes has been well documented and represents one of the most dramatic and impactful colonizations of invasive species in modern times (Evans et al., 2011; Lower et al., 2024; Ricciardi and MacIsaac, 2000). These small (maximum size 50 mm) mollusks were introduced with the release of ballast waters from commercial vessels (Ricciardi and MacIsaac, 2000). The first occurrence of zebra mussels was noted between April and November 1986 in the western basin of Lake Erie (Carlton, 2008), followed by its formal (i.e., published) discovery on 1 June 1988 in Lake St. Clair, a small lake between Lakes Huron and Erie (Hebert et al., 1989). The zebra mussel extended its distribution beyond Lake Erie and was found in 1989 in three other lakes: Michigan, Huron, and Ontario (Griffiths et al., 1991; Karatayev et al., 2021). 1989 also marked the first record of the quagga mussel in North America when a single specimen was found in Lake Erie (Benson, 2014). The discovery of quagga mussels in Lake Ontario followed soon after in 1990 (Benson, 2014). In 1997, quagga mussels appeared in northern Lake Michigan and eastern Lake Huron (Karatayev et al., 2021). Zebra mussels and then

quagga mussels were discovered in Lake Superior proper in the early 2000s (Grigorovich et al., 2008, 2003), but marginal calcium levels have dampened their expansion (Trebitz et al., 2019).

The process of colonization and the dynamic between the two dreissenid species is influenced by how their differing physiologies react to environmental conditions. Zebra mussels have lower filtration rates (Diggins, 2001) and assimilation efficiencies (Baldwin et al., 2002), as well as higher respiration rates (Karatayev et al., 2015; Stoeckmann, 2003) when compared to quagga mussels. Quagga mussels are capable of spawning at colder temperatures (Claxton and Mackie, 1998; Roe and MacIsaac, 1997) and can adapt to soft substrate (Karatayev and Burlakova, 2022). Accordingly, zebra mussels are better equipped for warmer, more productive nearshore environments, while quagga mussels can readily inhabit cold, deep waters (Karatayev et al., 2015; Strayer et al., 2019).

Lake morphometry largely dictates the outcome of dreissenid mussel composition and distribution (Karatayev et al., 2021; Strayer et al., 2019). In shallow, productive regions such as the western basin of Lake Erie and Saginaw Bay in Lake Huron, zebra mussels peaked by the early 1990s and then have been able to persist after quagga mussels arrived, albeit at lower densities (Karatayev et al., 2021). In contrast, quagga mussels are competitively superior to zebra mussels in deeper, oligotrophic waters (Nalepa et al., 2010). In Lake Ontario, Lake Huron, and Lake Michigan, quagga mussels virtually displaced zebra mussels by 1997, 2003, and 2005, respectively, all within 8 years of their arrival (Karatayev et al., 2021). Further, the biomass attained by quagga mussels in these three lakes in 2018, 2017, and 2015 was more than 10 times the maxima attained by zebra mussels in 1995, 2000, and 2000,

respectively (Karatayev et al., 2022, 2021). As a result, the quagga mussel invasion waves caused stronger lake-wide ecosystem impacts compared to the more limited nearshore impacts of zebra mussels (Karatayev et al., 2022). The steps of colonization by both quagga and zebra mussels in shallow and deep basins of the Great Lakes are clearly illustrated in maps produced by Karatayev et al. (2021), which have been reproduced in Electronic Supplementary Material (ESM) Fig. S1a and Fig. S1b for ease of reference.

4. Data and methods

4.1. Ocean Colour Climate Change Initiative (OC-CCI) dataset

Surface chlorophyll-*a* concentration (*Chl-a*) is a proxy for phytoplankton biomass and one of the most widely used satellite ocean color products that are monitored by Earth-orbiting satellites (IOCCG, 2008). Multiple studies have used *Chl-a* to identify global trends and regime shifts in aquatic ecosystems (Behrenfeld et al., 2006; Chavez et al., 2011) and to monitor ecosystem health due to its direct link to aquatic net primary productivity and biomass (Wang and Convertino, 2023). Historical importance and availability of multi-decade *Chl-a* records motivated including it into the list of Essential Climate Variables (ECV), a limited set of variables deemed critical to the characterization of Earth's climate (Bojinski et al., 2014; GCOS, 2011).

The Ocean Colour Climate Change Initiative (OC-CCI) project of the European Space Agency (ESA) provides a consistent, long-term continuous dataset of merged ocean-color products created by integrating remote sensing reflectances (*Rrs*) from individual sensors (Table 1) and retrieving various ocean-color parameters via selected in-water algorithms (Lavender et al., 2015; Sathyendranath et al., 2019).

As different ocean color sensors often measure radiances at different wavebands, the input radiometric measurements were band-shifted to a common set of bands corresponding to the Medium Resolution Imaging Spectrometer (MERIS) on ENVISAT platform. The non-reference sensors of SeaWiFS, MODIS, VIIRS, and OLCI (though OLCI already contains the MERIS bands so this was not required) were band shifted to the six main MERIS bands (412, 443, 490, 510, 560, 665 nm) by computing Quasi-Analytical algorithm (QAA) (Lee et al., 2002) Inherent Optical Properties (IOP) and back computing the *Rrs* bands using a high-resolution spectral model (European Space Agency, 2022). Then, overlapping data were used to correct for mean biases between sensors, the corrected *Rrs* were merged by averaging all available data at every pixel with equal weight given to each available sensor, and the blended *Chl-a*

algorithm (Jackson et al., 2017) was applied to the merged data to generate maps of chlorophyll concentration. The merged products were validated against a global dataset comprising in situ measurements collected from multiple sources (Valente et al., 2022).

Monthly *Chl-a* data at 4-km spatial resolution of the latest OC-CCI version 6.0 (September 1997–December 2022) were obtained from the OC-CCI dataset (<https://climate.esa.int/en/projects/ocean-colour/>).

In 2002, SeaWiFS had been operational for 5 years when MODIS-Aqua and MERIS were launched, and the total number of collected images dramatically increased. From 2012 to 2013, MERIS ceased operations, and Visible Infrared Imaging Radiometer Suite on the Suomi National Polar-orbiting Partnership platform (VIIRS-SNPP) was launched (Table 1). Starting in 2020, MODIS-Aqua and VIIRS-SNPP were not used in the OC-CCI dataset due to sensor degradation problems. Inter-mission differences in the merged OC-CCI *Chl-a* dataset may not have been completely corrected and may consequently be misinterpreted as trends and abrupt shifts (Hammond et al., 2018; Mélin, 2016; Mélin et al., 2017; Yu et al., 2023).

To evaluate if any spurious artifacts were introduced during merging, we compared OC-CCI *Chl-a* time series to the single-mission *Chl-a* time series of SeaWiFS, MERIS, and MODIS-Aqua obtained from the Ocean Biology Processing Group at NASA Goddard Space Flight Center archive (<https://oceandata.sci.gsfc.nasa.gov/>). Monthly Level-3 Standard Mapped Image (SMI) *Chl-a* products with spatial resolutions at 4 km for MERIS (April 2002 to April 2012) and MODIS-Aqua (July 2002 to December 2022) and 9 km for SeaWiFS (September 1998 to December 2010) were examined. The *Chl-a* products in these datasets were derived using a combined *Chl-a* algorithm of OC3/OC4 (OCx) band ratio (O'Reilly and Werdell, 2019) and the color index (CI) algorithms (Hu et al., 2019). All satellite data were subsampled for the Great Lakes region (41.0–49.0 N, 92.5–76.0 W) and remapped with the standard cylindrical projection on 4-km resolution grids. For increased computational efficiency during statistical analysis, the resolution of all 4-km grids was reduced by a factor of three in each direction with a resulting cell represented as 3×3 median value (hereafter called 12-km grid cells).

Although many authors have questioned the absolute accuracy of the standard NASA *Chl-a* retrievals in the Great Lakes (Bergmann et al., 2004; Budd and Warrington, 2004; Moore et al., 2017; Mouw et al., 2017, 2013; Sayers et al., 2019; Watkins, 2009), other studies have indicated that the default iterative atmospheric correction is adequate for all the Great Lakes (Shuchman et al., 2013) and standard NASA band-ratio algorithms produce chlorophyll estimates that are linearly related to the *Chl-a* concentrations measured in the field (Lesht et al., 2013). Also, most of the areas analyzed in this study (excluding Lake Erie) are optically deep; therefore, waters where the band-ratio method may be compromised by the presence of confounding substances (primarily embayments and shallow waters) constitute a comparatively small fraction of the Great Lakes (Lesht et al., 2013; Shuchman et al., 2013). Nevertheless, it is likely that increased uncertainty exists in the OC-CCI *Chl-a*, particularly in turbid or eutrophic conditions and the nearshore, relative to other algorithms specifically tuned to optically complex waters. Utilizing the OC-CCI dataset for detecting regime shifts in the Great Lakes' ecosystems, we therefore focus on relative temporal (interannual and seasonal) variations of remotely sensed *Chl-a* rather than assessment of the *Chl-a* absolute values.

4.2. Statistical methods of data analysis

This study focused on quantitative analyses of the ecosystem's regime transformation in the Great Lakes, both from a whole lake and spatially explicit perspective. To quantify these changes, we applied the statistical method detecting a breakpoint between two periods: an early period characterized by a continuous stepwise decrease of *Chl-a* followed by a period of stable or increasing *Chl-a*. For this purpose, we selected the method that can evaluate two basic metrics of *Chl-a*

Table 1

Sensor data used in the construction of the Ocean Colour Climate Change Initiative (OC-CCI) Version 6.0 dataset.

| Sensor | Satellite | Agency | Data Used in OC-CCI v.6.0 | References |
|----------------------|----------------------|-------------------|---------------------------|--|
| SeaWiFS ^a | SeaWiFS ^a | NASA ^b | 1997–2010 | (McClain et al., 2004; McClain et al., 1998) |
| MODIS ^c | Aqua | NASA ^b | 2002–2019 | (Esaias et al., 1998; Parkinson, 2003) |
| MERIS ^d | Envisat | ESA ^e | 2002–2012 | (Rast et al., 1999) |
| VIIRS ^f | SNPP ^g | NASA ^b | 2012–2019 | (Cao et al., 2014, 2013) |
| OLCI-A ^h | Sentinel-3A | ESA ^e | 2016–2022 | (Donlon et al., 2012; Nieke et al., 2012) |
| OLCI-B ^h | Sentinel-3B | ESA | 2018–2022 | (Donlon et al., 2012; Nieke et al., 2012) |

^a Sea-viewing Wide-Field-of-view Sensor.

^b National Aeronautics and Space Administration

^c MODerate-resolution Imaging Spectroradiometer.

^d MEedium spectral Resolution Imaging Spectrometer.

^e European Space Agency.

^f Visible and Infrared Imaging Radiometer Suite.

^g SUOMI National Polar-Orbiting Partnership.

^h Ocean and Land Colour Instrument.

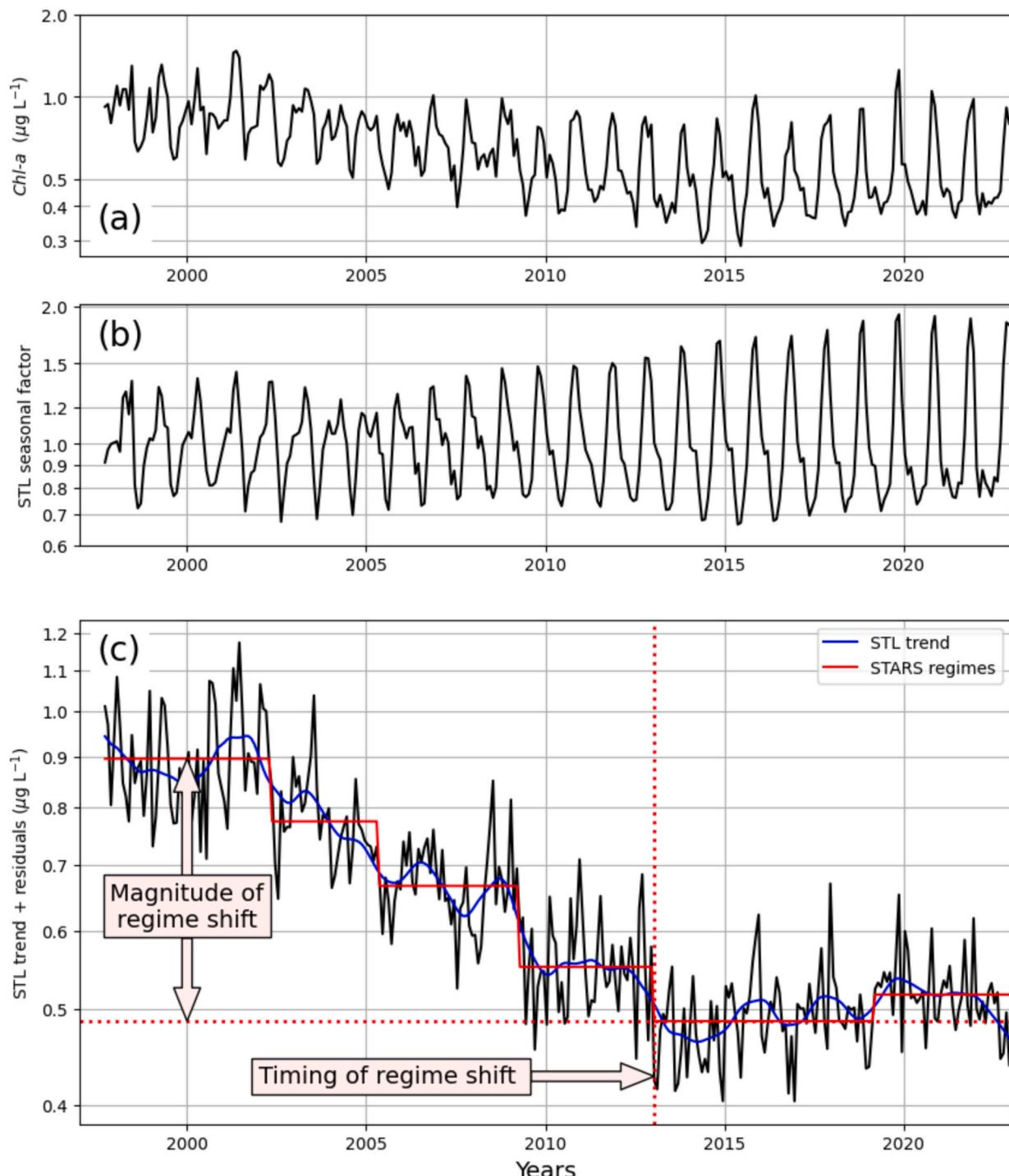


Fig. 2. An example of using (a) the time series of chlorophyll concentration ($\text{Chl-}a$; $\mu\text{g L}^{-1}$) in the center of Lake Michigan (latitude 43.047; longitude -87.070 ; depth 81 m; white triangle in Fig. 1M) to determine the Seasonal-Trend decomposition using LOESS (STL). The $\text{Chl-}a$ time series is split into the (b) seasonal factor ($\mu\text{g L}^{-1}$) and (c) smoothed trend (blue line; $\mu\text{g L}^{-1}$) and residuals (black line; $\mu\text{g L}^{-1}$). Regime shifts (solid red lines in (c)) are detected in the “deseasonalized” time series (the sum of trend and residuals) using the Sequential T-test Analysis of Regime Shifts (STARS) method. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

decrease: 1) the timing (shift point) when the transformation from one regime to another is completed; and 2) the magnitude of this transformation (Fig. 2c). The model is based on our understanding that oligotrophication was a dominant process over most of the Great Lakes. The selected model, however, may not apply to some regions for two reasons. First, some regions may not be affected by oligotrophication. Second, the process of regime transformation, which started in the late 1980s in some areas, could be completed earlier than the OC-CCI dataset

started in September 1997. The examples are Lake Superior, whose trophic status did not change (Binding et al., 2015; Fahnenstiel et al., 2016), and Lake Erie, which has undergone a period of re-eutrophication (Scavia et al., 2014; Watson et al., 2016).

The Sequential T-test Analysis of Regime Shifts (STARS; Rodionov, 2004) identifies timing(s) when a system attribute—in our study, $\text{Chl-}a$ —undergoes a persistent change. The basic constraint regulating the durations of the detected regimes is the regime's cut-off length, the

parameter similar to the cut-off point in low-pass filtering. In this study, the regime's cut-off length was determined through practical testing as 5 years (60 months). STARS sequentially analyzes each observation in the time series by testing whether it is statistically different from the current regime by calculating a Regime Shift Index (RSI) based on the Student's *t*-test to confirm or reject the existence of a regime change (Rodionov, 2004; Rodionov and Overland, 2005). Many authors used this method for detecting abrupt changes in paleoecological records (Espinoza et al., 2022), climate (Marty, 2008; Reid et al., 2016), marine ecosystems (Conversi et al., 2010; Greene et al., 2013; Möllmann and Diekmann, 2012; Möllmann et al., 2009; Tian et al., 2008), and many other studies.

Before applying STARS, seasonal variability was removed from each analyzed time series of *Chl-a* using the Seasonal-Trend decomposition using LOESS (STL) method (Cleveland et al., 1990). This filtering procedure decomposes a time series into the three components—trend, seasonal, and remainder—by extracting smoothed estimates of each component using a locally estimated scatterplot smoothing (LOESS) method based on local polynomial regressions. A salient feature of STL is that it allows amplitude variation in the seasonal component for a given period (e.g., annual), which helps capture a more significant portion of total variance than amplitude alone (Vantrepotte and Mélin, 2009). We did not use the “pre-whitening” approach recommended by Rodionov (2006) because preliminary analysis revealed that in the monthly data examined, the components generated by stationary red noise processes were not misinterpreted as “climatic regimes.” Instead, we focused on removing seasonal variations, which contributed substantially to the variability and hindered the identification of statistically significant shift points. For this, each time series (e.g., Fig. 2a) was decomposed by STL into trend (blue line in Fig. 2c), seasonal (Fig. 2b), and remainder (residual) components and then residuals were added to the trend, and the resulting “deseasonalized” time series (black line in Fig. 2c) was analyzed by STARS. Each *Chl-a* time series was log-transformed prior to STL and STARS analysis, and the outputs were inverse-transformed because the *Chl-a* values vary over several orders of magnitude and because log-transformed *Chl-a* is more normally distributed than the untransformed data (Campbell, 1995).

We applied the integrated STL-STARS algorithm to the time series of median *Chl-a* for individual lakes and each 12-km grid cell within each lake with at least 120 monthly observations, i.e., twice the regime's cut-off length, the parameter regulating minimum regime duration in STARS algorithm. In each location, transformation to a lower trophic regime was typically a gradual process that took several years and, as such, the STARS method detected a cascade of regime shifts (Fig. 2c). For individual lakes and grid cells, the STARS method identified the timings when the cell experienced its ‘initial’ and ‘final’ decreasing regime shifts. The ‘final’ shift timing is when *Chl-a* stabilized (saturated) at its ‘final’ concentration, after which no other decreasing shift in *Chl-a* was detected. Two parameters were documented from the ‘initial’ and ‘final’ regimes: 1) the year of the ‘final’ regime shift, i.e., ecosystem stabilization (months were ignored); and 2) the magnitude of *Chl-a* decrease during the regime transformation, which was calculated as the percentage difference between the chlorophyll concentrations of the ‘initial’ and ‘final’ regimes (Fig. 2c).

The relationship between detected regime shifts and lake depth was analyzed using bathymetric data of the Great Lakes obtained from the NOAA National Centers for Environmental Information (NCEI) Marine Geology and Geophysics online archive (<https://www.ngdc.noaa.gov/mgg/greatlakes>). The grids of scale 1:250,000 were reprojected to 12-km resolution similar to the resampled OC-CCI and single-mission satellite data.

The annual cycles of monthly median *Chl-a* were examined in each location during the ‘starting’ (1998–2002) and ‘ending’ (2018–2022) 5-year periods of the 25-year OC-CCI time series. The timings of *Chl-a* monthly maxima were estimated from the 5-year medians of monthly medians either in entire lakes or in spatially explicit (i.e., 12-km grid

cells) perspective during the ‘starting’ and ‘ending’ 5-year periods. The timings of monthly *Chl-a* maxima were computed using the “centroid” method to yield a center of gravity in polar coordinates. Using the center of gravity (and viewing the results in polar coordinates) is deemed a better estimate for this purpose than other estimates, such as a simple average or a center of gravity in linear coordinates (Colebrook, 1979; Edwards and Richardson, 2004; Meis et al., 2009). Fig. 3 is an example of this estimation for the grid cell located farthest from shore in the southern part of Lake Michigan (Fig. 1M). The center of gravity (Fig. 3b) of maximum average monthly median *Chl-a* was estimated to be mid-March (month 3.5) for the period from 1998 to 2002 and late October (month 10.8) for the last 5-year period, 2018–2022, which were similar though not exactly the same as the *Chl-a* maxima assessed visually (Fig. 3a). It is worth mentioning that although we operate monthly data (i.e., the times are integers), the resulting assessments of the centers of gravity can include decimal fraction leading to conclusions at sub-monthly time scale.

5. Results

5.1. Inter-mission artifact or shift to a different trophic state?

Although the potential of discontinuities of *Chl-a* (and other derived bio-optical properties) and incorrectly detecting them as regime shifts in *Chl-a* was higher when satellite sensors changed or merged (ESM Fig. S2), the analysis of the individual mission *Chl-a* time series collected by the three satellites operating during the beginning of the observed period (i.e., SeaWiFS, MODIS-Aqua, and MERIS), and used in the creation of OC-CCI, revealed decreasing trends and successive regime shifts similar to those detected in the merged OC-CCI dataset. This is particularly evident in Lakes Michigan and Huron (Fig. 4). Furthermore, in most time series collected by single satellite sensors, regime shifts were detected in 2005 (Fig. 4), when sources of data from satellite sensors in OC-CCI dataset did not change (ESM Fig. S2a).

As the trends and shifts observed in chlorophyll concentrations of the OC-CCI dataset are similar to those observed in the single satellite missions, we conclude that they are real and not artifacts introduced during the creation of the OC-CCI dataset.

5.2. Timings and magnitudes of regime shifts in *Chl-a*

The median concentrations of *Chl-a* in Lakes Michigan, Huron, and Ontario gradually decreased during 1997–2012 (Fig. 5). In Lakes Michigan and Huron, the integrated STL-STARS method detected a cascade of three regime shifts to a lower trophic state followed by a small shift to higher trophic state between 2014 and 2016 (Fig. 5M, H). In Lake Ontario, a cascade of two regime shifts to lower trophic state was detected (Fig. 5O). No decrease of *Chl-a* was observed in Lakes Superior and Erie (Fig. 5S, E), though small but significant increases of *Chl-a* were detected in Lake Erie in 2002 and in Lake Superior in 2014.

The year when chlorophyll concentration reached its ‘final’ stable levels (i.e., *Chl-a* no longer declined) differed regionally within and between each of the Great Lakes (Figs. 6 and 7). In Lakes Michigan, Huron, and Ontario, *Chl-a* decreased between 2002 and 2020 over most of the lakes’ areas. In Lake Superior, only the western portion of the lake experienced a decrease in *Chl-a* during the first decade of the observed OC-CCI time series, 2002–2008; (Fig. 6S). The majority of Lake Erie also exhibited limited shifts in *Chl-a*, occurring along its western Canadian shore early in the OC-CCI time series and along the Michigan shore and in Lake St. Clair during the latter part of the dataset (Fig. 6E). In Lake Huron, a lower trophic regime was achieved earlier (in 2002–2005) in Georgian Bay than in the northeast, then in the southern and northwestern nearshore zones and along the Alpena-Amberley Ridge (marked in Fig. 1H). Circa 2012, *Chl-a* decreased to its ‘final’ level in the remaining open parts of the lake (Fig. 6H). Over most of Lake Ontario, the process to the new regime was slow. Over most of the lake, the *Chl-a*

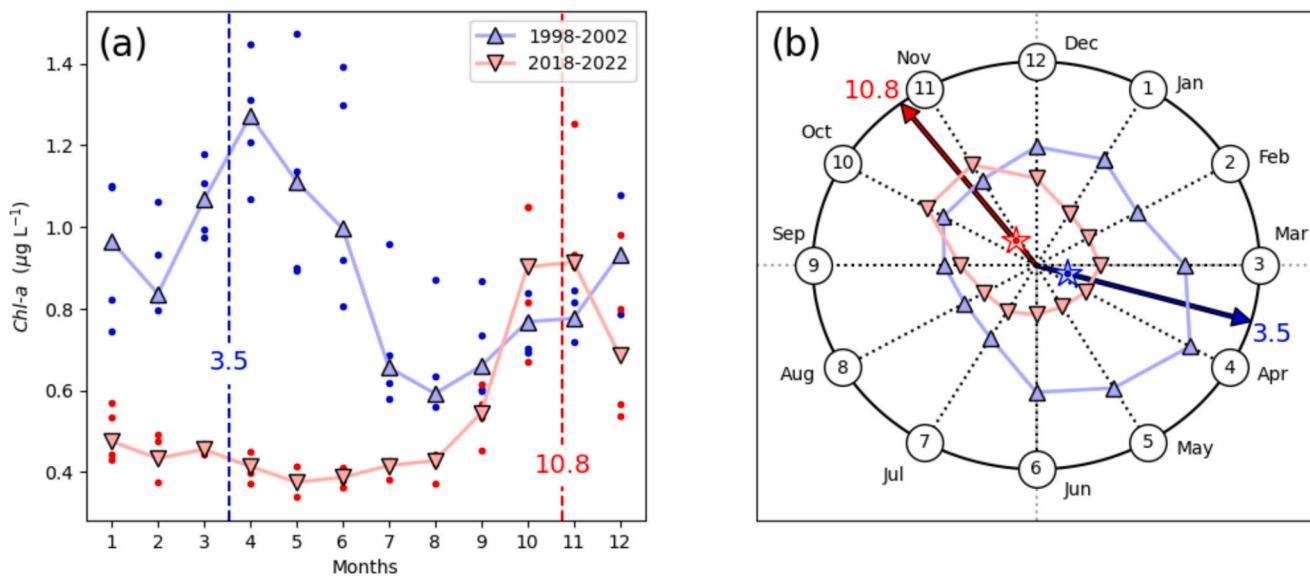


Fig. 3. (a)—Monthly median chlorophyll concentrations (dots) and its 5-year median (filled triangles) in the center of southern Lake Michigan (white triangle in Fig. 1M) for the ‘starting’ 1998–2002 (blue line; upward pointing triangles) and ‘ending’ 2018–2022 (red line; downward pointing triangles) 5-year periods of OC-CCI observations. (b)—Median monthly mean chlorophyll concentrations (blue polygon 1998–2002; red polygon 2018–2022) and the timings of annual maxima (arrows pointing through the centers of gravity represented by blue and red stars to the external circle representing a 12-month cycle) plotted in polar coordinates. The magnitude of average monthly median Chl-a is represented as the distance from the center of polar coordinates. In both 3a and 3b, the values of 3.5 and 10.8, indicate the timings in months of Chl-a maximum during 1998–2002 and 2018–2022, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

achieved a stable regime as late as 2015–2020 (Fig. 6O). Only the small central-eastern region of the lake experienced the regime shift earlier, in 2002.

In Lake Michigan, the Chl-a level stabilized first in the nearshore regions north of 44°N (Fig. 6M). From 2010 to 2012, a new regime was established offshore in the northern part of the lake, and it started spreading to its southern part, first along the western and eastern shores and then offshore. Offshore in the southern portion of the lake, the level of Chl-a stabilized as late as 2020.

Similar to the timing, the magnitude of the reduction in Chl-a between its ‘initial’ and ‘final’ stabilized concentrations also varied regionally within and between each of the Great Lakes. In Lakes Superior and Erie, where regime shifts were rarely found, the magnitudes of detected regime shifts were typically below 10 % (Fig. 7S, E). In Lake Michigan, Chl-a decreased 10–25 % north of 44°N and 35–45 % in the south (Fig. 7M). Both the timing (Fig. 6M) and magnitude of Chl-a decrease indicate that to the north of 44°N , transformation of the ecosystem from an eutrophic to oligotrophic state started before the start of the OC-CCI dataset in 1997 and was completed a few years earlier than in the south and that a substantial part of this process was not captured in our analysis. In Lake Huron, the reduction in Chl-a varied between 20 and 40 %, with a maximum in its deeper southern portion (Fig. 7H). Lastly, in Lake Ontario, the magnitude of Chl-a reduction was about 10 % in the eastern part of the lake and 20–30 % in its western part (Fig. 7O).

The relationship between the timing (year) when Chl-a reached stable levels and lake bathymetry showed no apparent pattern (not shown), whereas the difference in its magnitude did (Fig. 8). In Lake Superior, the difference in Chl-a between the ‘initial’ and ‘final’ regimes clearly decreased with increasing depth until it exceeded ~ 100 m. In Lakes Michigan and Huron, the lakes that exhibited the most evident regime shifts, the difference in Chl-a was most pronounced in water between 30 and 100 m deep. No clear-cut relationship was observed in Lakes Erie and Ontario, the former likely due to its limited depth range.

5.3. Chlorophyll concentration phenology

Analyzing seasonal cycles of Chl-a in the Great Lakes based on OC-CCI data, we have to bear in mind that the number of images collected during winter was much lower compared to other seasons due to data gaps associated with cloud and ice coverage (see ESM Fig. S3). The number of images acquired during December–January was low over all five lakes, especially over Lakes Superior and Huron (ESM Fig. S3S, H).

Significant changes in seasonal cycles of Chl-a over the entire lake areas were observed in Lakes Michigan (Fig. 9M, Fig. 10M1, M2) and Huron (Fig. 9H, Fig. 10H1, H2). In Lake Michigan during 1998–2002, two maxima of median Chl-a were observed in April–June and August (Fig. 9M); the plot of the timings of Chl-a seasonal maxima demonstrates that these two maxima were observed in different parts of the lake: in April–June in the southern part and in August in the northern part (Fig. 10M1). In 2018–2022, the timing of the seasonal maximum changed to October over the entire lake (Fig. 9M, Fig. 10M2). In Lake Huron during 1998–2002, the median (averaged over the entire lake) Chl-a maximum was in winter–spring (March–June; Fig. 9H); a spatially explicit view revealed the winter maximum in nearshore parts of the lake and spring maximum in open waters (Fig. 10H1). By 2018–2022, the timing of the seasonal maximum changed to fall (October–December). In both Lakes Michigan and Huron, the changes in the timings of seasonal maxima occurred between 2002 and 2004 (Fig. 9a).

We speculate that a seasonal maximum in northern Lake Michigan may not have been observed in spring (in contrast to its southern part; Fig. 10M1) because, during the beginning of the OC-CCI dataset, local ecosystems had already undergone most, if not all, of the regime transformation. This explanation agrees with early stabilization and low magnitude of regime shifts observed there (Fig. 6M, Fig. 7M).

In Lake Superior, the timing of the Chl-a maximum (October–December) did not change, but its magnitude substantially decreased (Fig. 9S, O). The differences in the timing and magnitude of winter maxima in Lake Superior in 1998–2002 (fall maximum in its northern part and winter maximum in the south, and a strong maximum in 1998–2002 vs. a small maximum in 2018–2022) can be attributed to

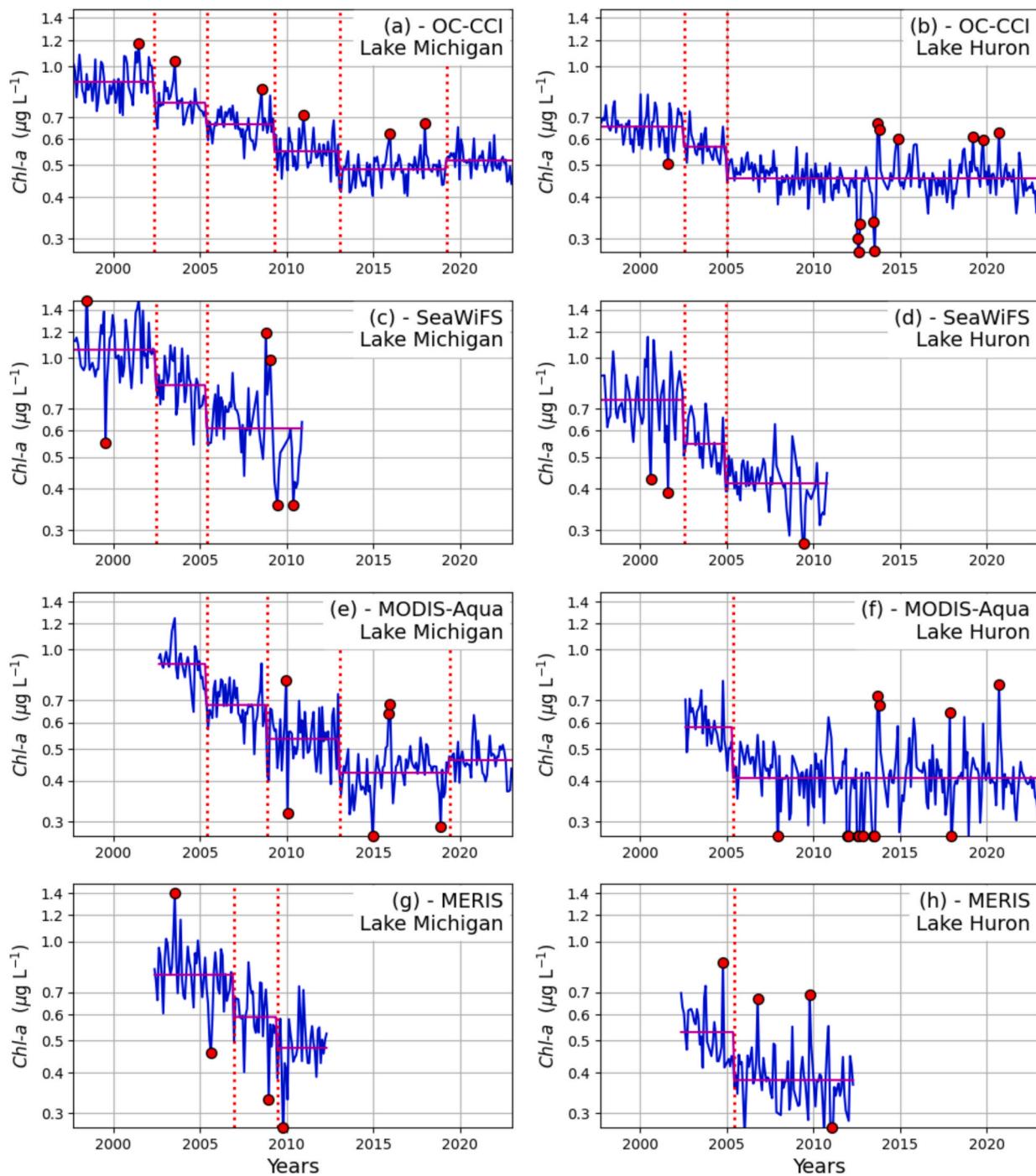


Fig. 4. Trends and regime shifts detected by the integrated STL-STARS method in median chlorophyll concentration (Chl-a) of (a, c, e, g) Lake Michigan and (b, d, f, h) Lake Huron based on observations of (a–b) OC-CCI, (c–d) SeaWiFS, (e–f) MODIS-Aqua, and (g–h) MERIS. Red circular markers indicate outliers (i.e., the values exceeding two standard deviations). Red dotted vertical lines indicate regime shifts; red horizontal lines indicate regime means. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

flaws in the OC-CCI data resulting from a very low number of satellite images acquired over Lake Superior during winter seasons 1998–2002 when the maxima were detected and only one satellite (SeaWiFS) collected data.

In Lake Erie, the Chl-a maximum in 1998–2002 was observed in winter (Fig. 10E1), and its timing did not change by the end of the observed period (Fig. 10E2). Similarly, in Lake Ontario, the timing of the Chl-a summer maximum remained unchanged (June–September; Fig. 9O, Fig. 10O1, O2).

During the ‘ending’ (2018–2022) 5-year period, we see an almost

complete disappearance of a spring bloom, typical of temperate waters, replaced with an autumn bloom. In 2018–2022, seasonal Chl-a cycles in four lakes (Superior, Michigan, Huron, and Ontario) were characterized by a maximum in late fall (October–December; Fig. 10S2, M2, H2, O2). The vanishing of spring maxima can be explained by the strong effect of mussel filtration on phytoplankton in the entire water column, including the near-surface layer, during spring when the water column is well mixed (see Discussion).

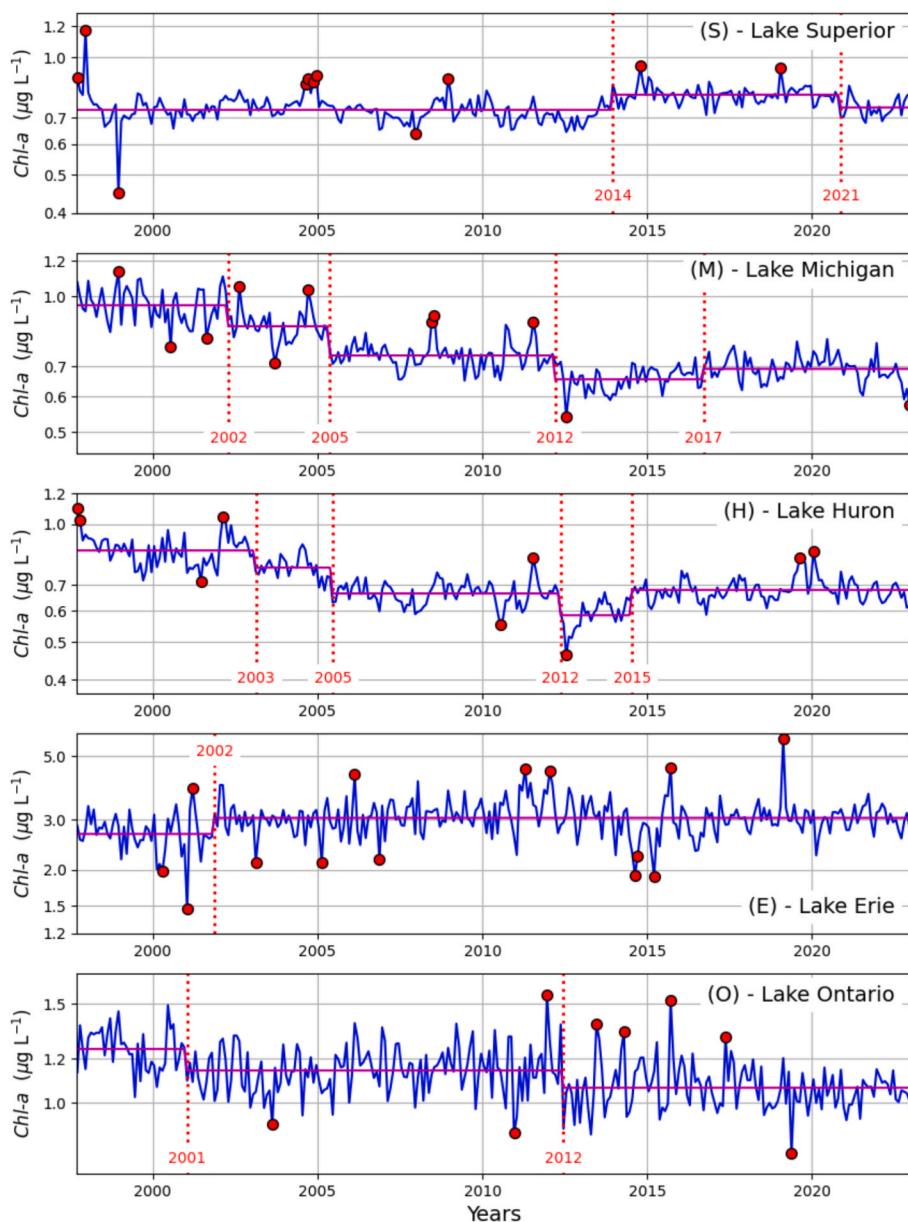


Fig. 5. Trends and regime shifts detected by the integrated STL-STARS method in OC-CCI median chlorophyll concentration (Chl-a) in Lakes (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. Red circular markers indicate outliers (i.e., the values exceeding two standard deviations). Red dotted vertical lines indicate regime shifts; red numbers indicate the years of regime shifts; red horizontal lines indicate regime means. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

6. Discussion

To our knowledge, this is the first study to analyze a relatively long-term continuous and internally consistent time series of satellite-derived chlorophyll concentration to identify statistically significant, abrupt changes of chlorophyll concentration in a spatially explicit manner in all of the Laurentian Great Lakes during the same period. This approach permits us to examine inter- and intra-lake differences in the timing and magnitude of changes in chlorophyll concentration, and explore potential factors related to these changes.

6.1. Transformations to lower trophic regimes in the Great Lakes

The spatial and temporal features of regime transformation in the Great Lakes described in this paper agree with the previously published information about the proliferation of dreissenid mussels, supporting

the hypothesis that colonization of the lakes by dreissenids was a primary driver of this transformation. A shift to the lower trophic state was evident in three initially mesotrophic deep lakes (Michigan, Huron, and Ontario) and small or absent in the consistently oligotrophic Lake Superior and regionally eutrophic Lake Erie. These results do not deny the role of nutrient management in improving water clarity in the Great Lakes, but they indicate that mussel presence was an important driving factor of this oligotrophication.

6.1.1. Lake Superior

The magnitudes of regime shifts detected in Lake Superior were small compared to the other three deep lakes (Michigan, Huron, and Ontario). These assessments agree with the information that dreissenid mussels invaded Lake Superior in very low numbers (Grigorovich et al., 2008; Karatayev and Burlakova, 2022). Also, even before the dreissenid invasion, Lake Superior was characterized as the clearest of the Great

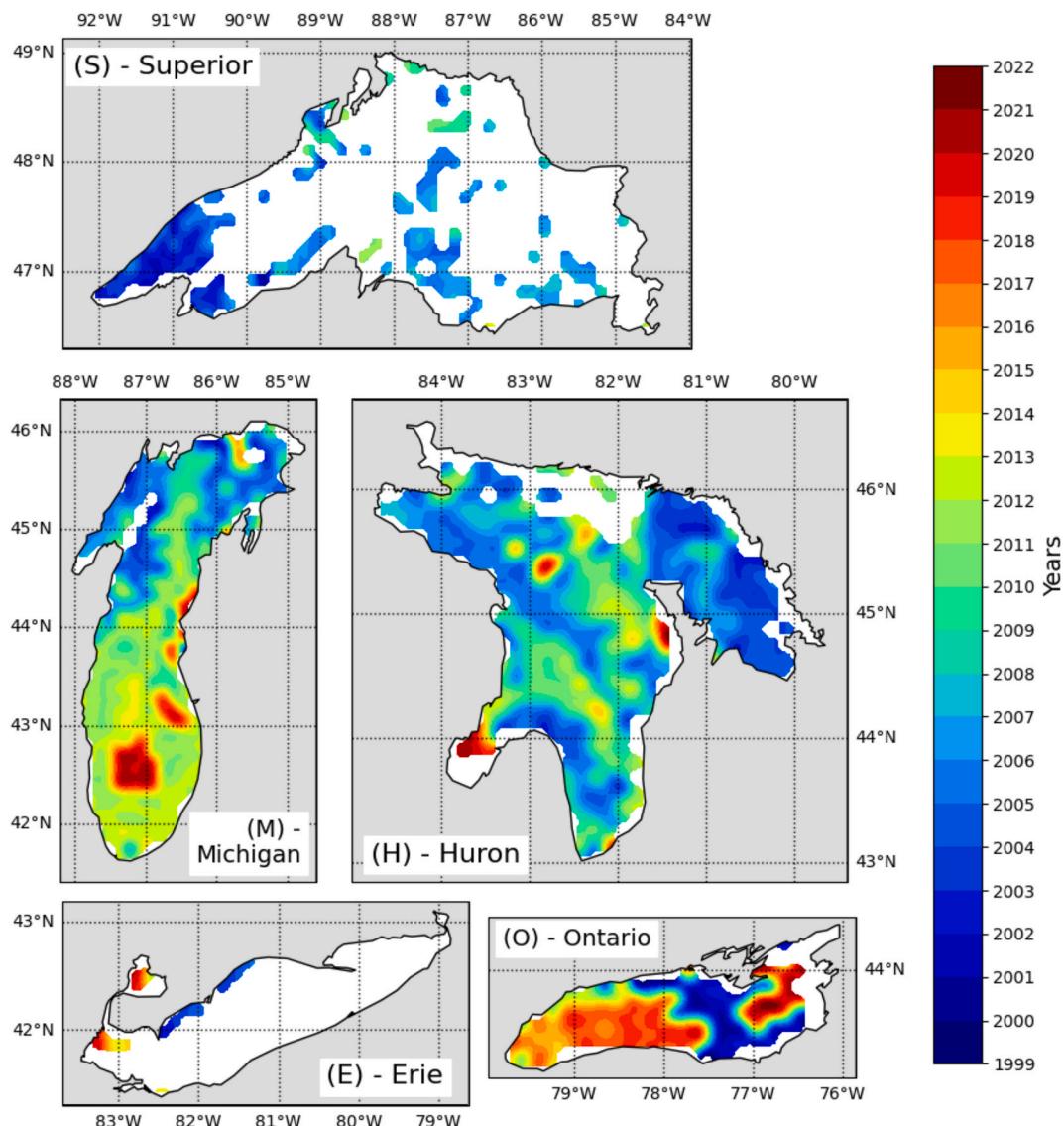


Fig. 6. Maps of the year in which chlorophyll concentrations (*Chl-a*) stabilized at a lower level in Lakes (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. White indicates that no significant decrease in *Chl-a* was detected during the period examined (1997–2022).

Lakes, in terms of water transparency (Binding et al., 2015), phytoplankton/chlorophyll/primary production (Vollenweider et al., 1974), and zooplankton biomass (Barbiero et al., 2012). As a result, no differences between pre-mussel and post-mussel periods were found in water clarity (Binding et al., 2015; Yousef et al., 2017), phytoplankton (Kovalenko et al., 2018; Reavie et al., 2014), zooplankton (Kovalenko et al., 2018), chlorophyll (Barbiero et al., 2012; Fahnstiel et al., 2016), and total phosphorus concentrations (Bunnell et al., 2014).

At the same time, small magnitudes of regime shifts detected in Lake Superior may be a result of less accurate (as compared with other deep lakes) *Chl-a* detection by the algorithms utilized in OC-CCI dataset. Mouw et al. (2017, 2013) indicated that, in Lake Superior, band-ratio algorithms significantly overestimate *Chl-a* because light absorption in its waters is dominated by colored dissolved organic matter (CDOM), while a very small contribution of phytoplankton and non-algal particles to overall absorption poses a challenge to deriving these parameters from reflectance spectra (Mouw et al., 2017, 2013), making the conclusions about temporal (seasonal and interannual) variations of *Chl-a* in that lake less reliable.

Recent observations in western Lake Superior documented cyanobacterial blooms in the narrow nearshore zone, a phenomenon never

observed before 2012 (Sterner et al., 2020). These blooms may result in a positive regime shift in median *Chl-a* averaged over the entire lake including the nearshore (Fig. 5S). Some authors attribute these recent changes in Lake Superior to atmospheric and lake warming (Reavie et al., 2014) extending its short (as compared to other lakes) period of summer stratification (Fahnstiel et al., 2016).

6.1.2. Lake Michigan

The details of regime transformation revealed by our spatially explicit analysis agree with the introduction and spread of dreissenids described in numerous publications (Evans et al., 2011; Madenjian et al., 2015; Nalepa et al., 2010, 2009; Rowe et al., 2015). Specifically, a significant number of dreissenids were first recorded in the northern nearshore regions in about 2000. By 2005, they had spread to the south nearshore, and by 2010, they had colonized offshore regions that resulted in a decrease in phytoplankton/chlorophyll biomass and an increase in water clarity. By 2015, however, maximum concentrations of dreissenids in the shallow regions slightly decreased (from 10^4 – 10^5 to 10^3 – 10^4 mussels m^{-2} (Karatayev et al., 2021)).

In the northern basin, Reavie et al. (2014) noted that a decline in spring phytoplankton occurred by 2002, followed by no statistically

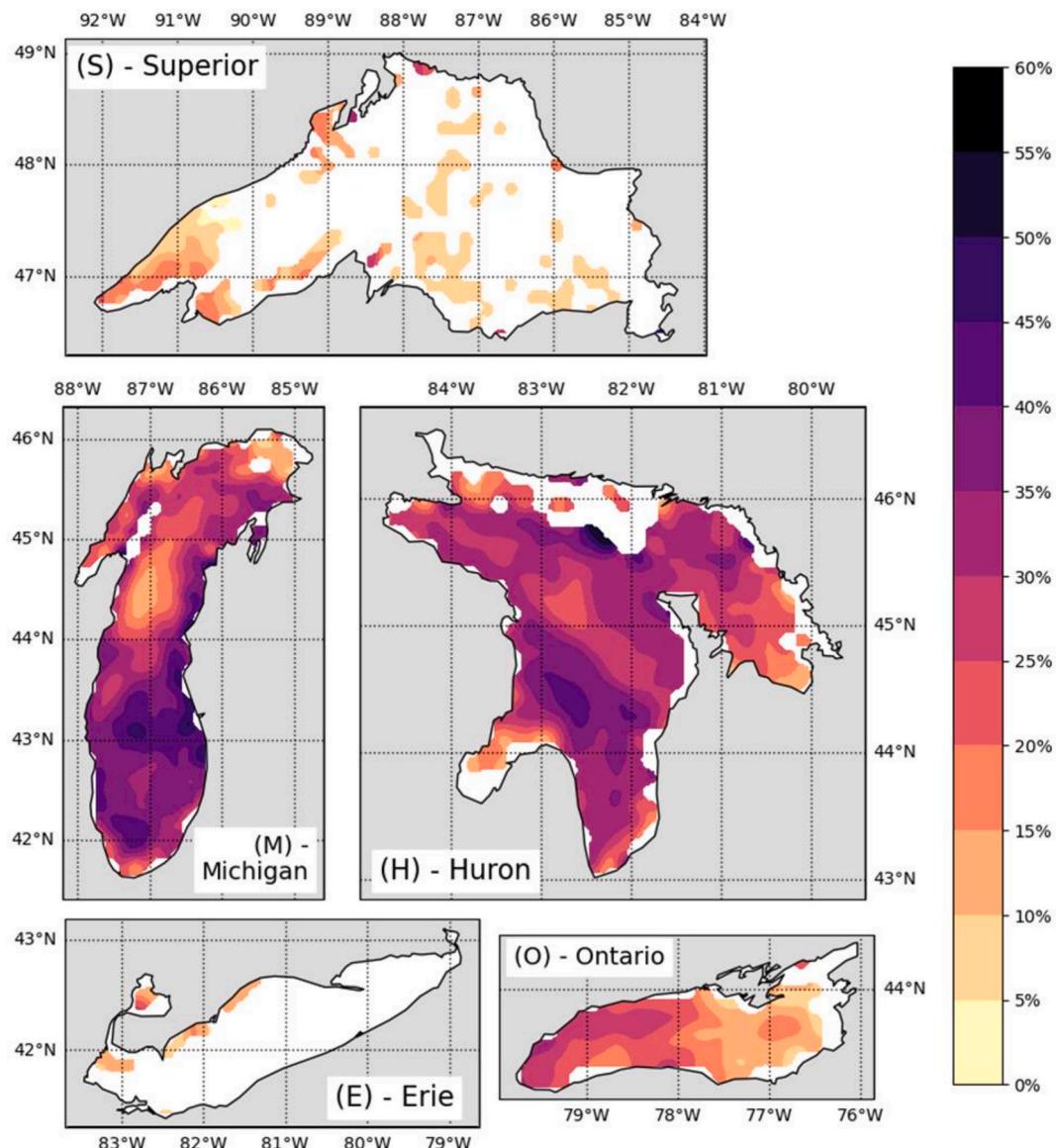


Fig. 7. Maps of the difference (in percent) of chlorophyll concentration (*Chl-a*) between the ‘initial’ (starting 1997) and ‘final’ (see Fig. 6) regimes in Lakes (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. White indicates that no significant decrease in *Chl-a* was detected during the period examined.

significant long-term trend, while in the southern basin, a significant drop in phytoplankton biovolume occurred between 2004 and 2005. Fahnstiel et al. (2010) demonstrated in the southern basin small or no decreases in *Chl-a*, phytoplankton biomass, and water column primary productivity between 1983–1987 and 1995–1998, followed by their substantial decrease by 2007–2008. In the same area, *Chl-a* decreased by 50 % between 1995–2000 and 2007–2011 (Pothoven and Fahnstiel, 2013). Yousef et al. (2017, 2014) reported a decrease in the diffuse attenuation coefficient (a proxy of water clarity based on SeaWiFS and MODIS-Aqua ocean color data) during 1998–2012 in the central part of the southern basin and no changes in the northern part of the lake. At the same time, Sayers et al. (2020) found no increasing or decreasing linear trends in remotely sensed *Chl-a* in all five Laurentian Great Lakes during 2003–2018.

Comparison between the results mentioned above and our assessments demonstrate the advantage of the approach used in this study (i.e., detecting a breakpoint between a decreasing trend followed by a stable regime) over the trend-detection method based on a linear model. The latter approach revealed significant changes in water clarity only in the offshore southern basin where, according to our results, *Chl-a* was

decreasing during most of the OC-CCI period. Also, no linear trend was detected in the northern part of the lake and in the southern basin nearshore, where, according to our results, transformation took place during the initial part of the observed period until a stable regime was achieved.

6.1.3. Lake Huron

Lakes Huron and Michigan experienced significant expansion of dreissenid populations, so it is not surprising that there are some similarities in their phytoplankton changes (Reavie et al., 2014). Previous studies documented a significant increase in water clarity associated with the deepening of the mean euphotic depth (from 41 m in 1998–2002 to 51 m in 2003–2010), which continued increasing in deeper (>30 m) regions (Yousef et al., 2017). In 2003, a dramatic reduction in the size of the spring phytoplankton maximum was reported in the entire lake (Barbiero et al., 2011; Reavie et al., 2014).

The decline in Lake Huron’s spring phytoplankton biovolume occurred earlier and was more severe than that in Lake Michigan despite a faster and more abundant dreissenid invasion in the latter (Reavie et al., 2014). One possible reason for a lower density of mussels having a

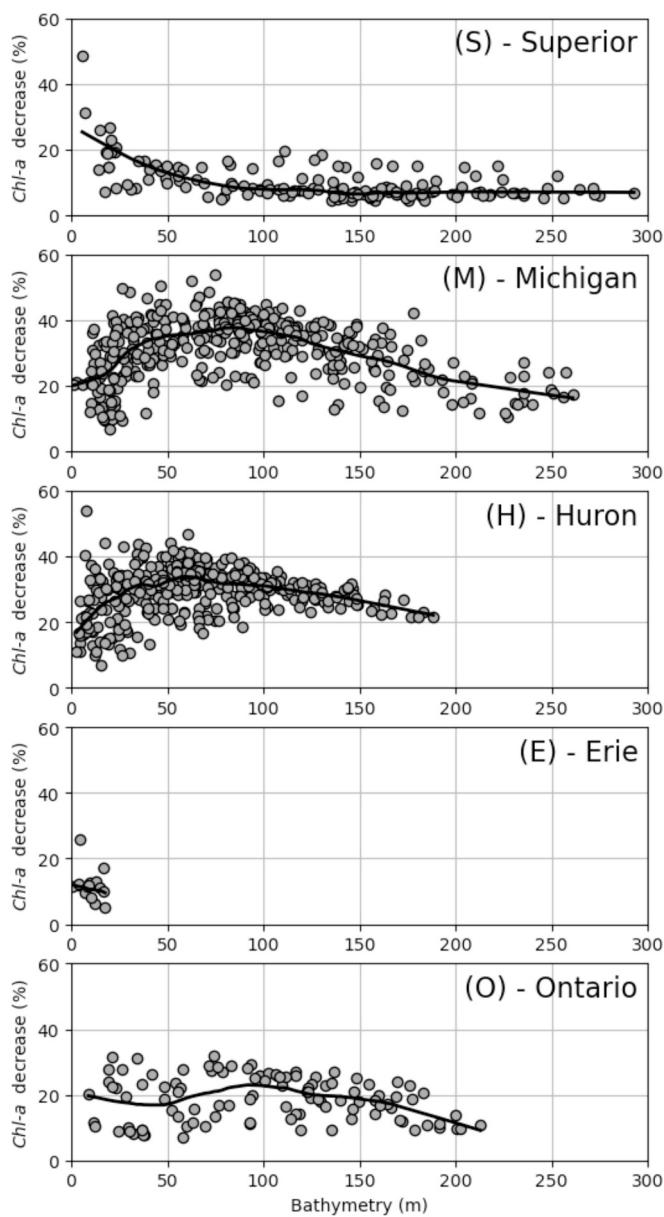


Fig. 8. Difference (in percent) of chlorophyll concentration (*Chl-a*) between the ‘initial’ and ‘final’ regimes (Fig. 7) in relation to bathymetry in Lakes (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. The magnitudes of *Chl-a* decrease in 12-km grid cells (circles) were smoothed with LOESS function (black lines).

larger impact is that Lake Huron had a lower phytoplankton abundance prior to quagga mussel colonization, and it is shallower than Lake Michigan (Yousef et al., 2017).

6.1.4. Lake Erie

Lake Erie is very different from other Great Lakes in terms of its shallow bathymetry (mean depth 7 m to 24 m from west to east (Bunnell et al., 2014)), mineral turbidity, and high bioproductivity, especially in its western basin (Allinger and Reavie, 2013; Reavie et al., 2014; Vollenweider et al., 1974). No regime shift to a lower trophic state was detected in that lake. Several studies documented a significant decrease in phytoplankton/chlorophyll concentration in some regions of Lake Erie within a few years of the establishment of large populations of zebra mussels (Allinger and Reavie, 2013; Holland, 1993; Makarewicz et al., 1999; Nicholls et al., 1999), yet this transformation may have occurred prior to the period comprising the OC-CCI dataset and hence could not

be detected in this study.

During the two most recent decades of the OC-CCI time series examined, phytoplankton biomass in Lake Erie remained high and even increased, attributable primarily due to blooms of blue-green algae (cyanobacteria) observed in both nearshore and open parts of the lake (Reavie et al., 2014; Twiss et al., 2012; Yuan et al., 2021). These blooms can be explained by increasing phosphorus loading to the western basin resulting in re-eutrophication of the lake (Michalak et al., 2013; Scavia et al., 2014; Watson et al., 2016). These blooms dramatically compromise optical signal, because cyanobacteria often exhibit unique backscatter and absorption features due to the presence of gas vacuoles, variable pigmentation, or colonial aggregation into floating mats (Binding et al., 2019; Moore et al., 2017). These unique optical properties lead to several-fold underestimation of *Chl-a* by standard blue to green ratio-based algorithms (Binding et al., 2019; Stumpf et al., 2016, 2012; Wynne et al., 2021), especially during summer when blooms are most abundant (Son and Wang, 2019; Stumpf et al., 2012; Wynne and Stumpf, 2015). The peak chlorophyll observed in winter in this study is nevertheless in agreement with the extremely high biomass diatom blooms observed in Lake Erie during the winter (Binding et al., 2012a; Twiss et al., 2012), outside of the summer cyanobacteria bloom monitoring period typically reported on using satellite observations of the lake. However, given the known uncertainties of ratio-based *Chl-a* retrieval algorithms in highly turbid waters, the seasonal cycles of *Chl-a* obtained by the OC-CCI products may also reflect seasonal variability in mineral sediments rather than chlorophyll concentration (Binding et al., 2019, 2012b), with the maximum in winter and minimum in summer. It is therefore important to consider further year-round validation of the OC-CCI *Chl-a* retrievals in these optical extremes in order to provide confidence in results in the case of the turbid eutrophic waters of Lake Erie.

6.1.5. Lake Ontario

Over most areas of Lake Ontario, the process of transformation to a lower trophic regime detected by the integrated STL-STARS method continued until the end of the OC-CCI dataset, 2020–2022. These assessments are corroborated by the conclusion that colonization of Lake Ontario by dreissenid mussels was slow compared to the other Great Lakes. One reason could be that a high proportion of Lake Ontario is deep (> 90 m), and mussels at greater depths exhibit very slow growth rates (Elgin et al., 2022b). Karataev et al. (2022) noted that the lake-wide biomass of dreissenids continued increasing since its arrival (1989 for zebra mussels and 1990 for quagga mussels) and reached an all-time high in 2018 (the most recent whole-lake data available at this time). Our assessments agree with the conclusion of Karataev et al. (2022) that the ecological effects of quagga mussels in Lake Ontario will likely continue into the foreseeable future.

A slow rate of regime transformation in Lake Ontario detected by the integrated STL-STARS method applied to OC-CCI data agrees with the data reported by Reavie et al. (2014), who noted little overall change in total algal abundance during 2001–2011, with some changes taking place in the composition of the phytoplankton assemblages.

6.2. Effect of dreissenid filtration in different depth zones

This study supports the hypothesis that the impact of dreissenid filter-feeding on pelagic ecosystems depends on lake bathymetry, and this effect is nonlinear, with a maximum in the mid-depth range (about 30–100 m) and a smaller effect in shallower and deeper waters. Similar conclusions were reached earlier by several studies using a variety of approaches: by Vanderploeg et al. (2010) estimating the clearance rates of quagga mussels; by Kerfoot et al. (2010) and Yousef et al. (2014) from their assessments of decreasing rates of remotely sensed *Chl-a* in southern Lake Michigan; and by Karataev and Burlakova (2022) in their review of dreissenid mussel biology in the Great Lakes.

The comparatively small impact of dreissenid mussels in the shallow

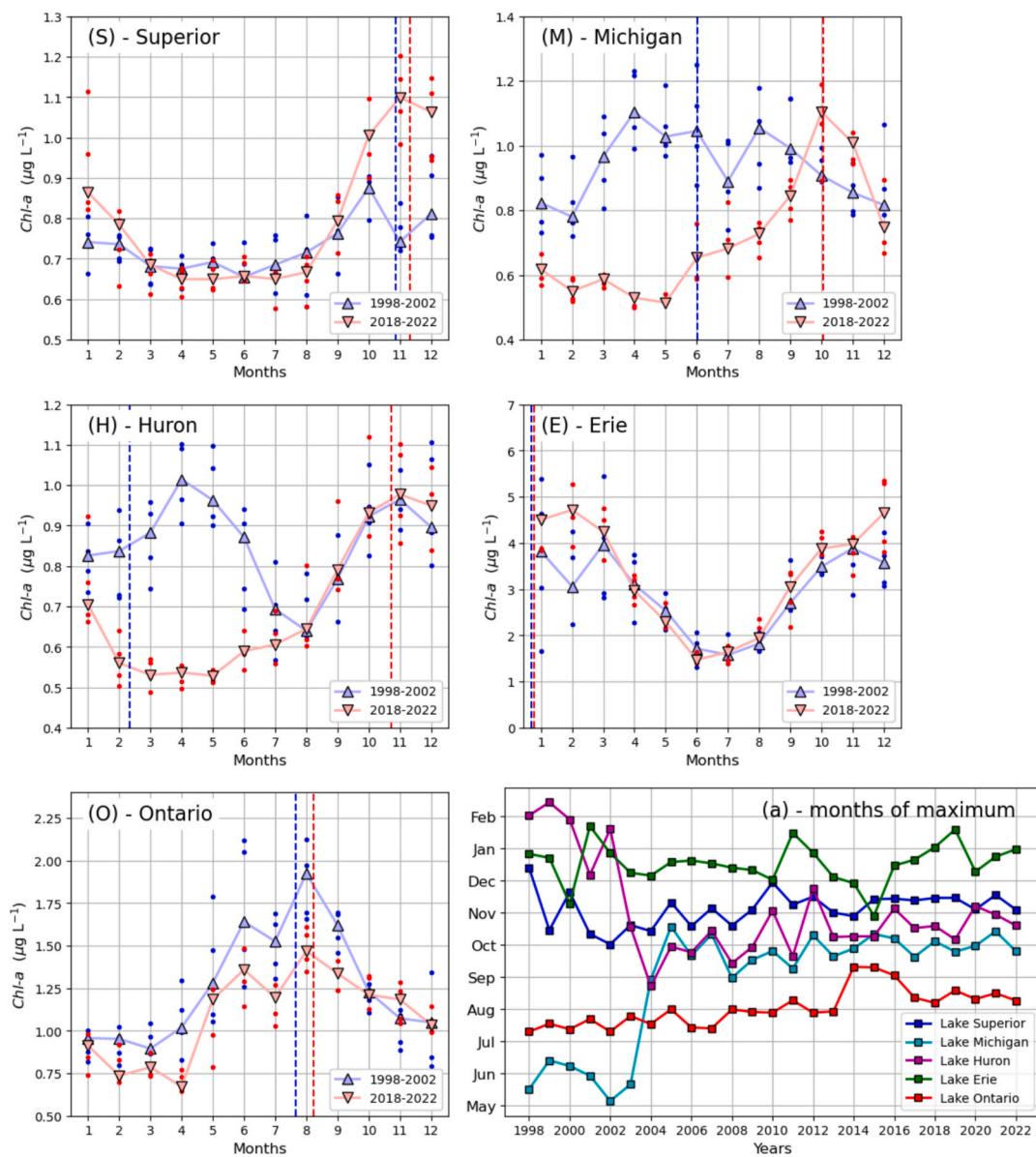


Fig. 9. Seasonal cycles of monthly median chlorophyll concentrations (*Chl-a*) in the ‘starting’ 1998–2002 (blue line; upward pointing triangles) and ‘ending’ 2018–2022 (red line; downward pointing triangles) 5-year periods of the Ocean Colour Climate Change Initiative (OC-CCI) dataset in Lakes (S) Superior, (M) Michigan, (H) Huron, (E) Erie, and (O) Ontario. Vertical dashed lines indicate the timings of seasonal maxima estimated by the “center of gravity” method. (a)—The months of *Chl-a* maximum estimated by the “center of gravity” method for each year in Lakes Superior, Michigan, Huron, Erie, and Ontario. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

zone is explained by their lower density resulting from unstable sandy substrate, physical disturbance by waves and currents, thermal instability, and fish predation (Glyshaw et al., 2015; Nalepa et al., 2010; Vanderploeg et al., 2010).

In deeper waters, the impact of dreissenid mussels on phytoplankton biomass is reduced by vertical extension of the water column (i.e., greater biomass of dreissenids is required to filter the same fraction of the water column due to greater volume per unit bottom habitat) and slower rates of mussel filtration associated with low temperature and limited food availability. At temperatures typical of shallow water, the filtration rates of dreissenids measured in experiments achieved $400 \text{ mL h}^{-1} \text{ mussel}^{-1}$ (about $10 \text{ L day}^{-1} \text{ mussel}^{-1}$) (Diggins, 2001; Horgan and Mills, 1997; Kryger and Riisgård, 1988). However, the filtration activity of mussels significantly (2- to 10-fold) decreases at lower temperatures (Vanderploeg et al., 2010; Xia et al., 2021), reducing the volume of food consumed by mussels. Low food concentrations also negatively affect dreissenid filtering activity (Karatayev et al., 2018b; Malkin et al., 2012;

Xia et al., 2021). Furthermore, during summer, the upper euphotic layer where phytoplankton is concentrated is isolated by seasonal stratification from the hypolimnion affected by mussel filtration. The effect of thermal stratification limiting the impact of filtration by benthic organisms on the pelagic community in the Great Lakes was highlighted by several authors (Fahnenstiel et al., 2010; Karatayev et al., 2021; Malkin et al., 2012; Vanderploeg et al., 2010).

Although the filter-feeding activity of dreissenids is most prominent in the mid-depth zone, it also impacts offshore regions by reducing the amount of phytoplankton biomass transported from the nearshore zone (Hecky et al., 2004; Kerfoot et al., 2010; Pothoven and Vanderploeg, 2020; Vanderploeg et al., 2010), where phytoplankton growth is stimulated by seasonal tributary inputs and resuspension of nutrients (Johengen et al., 2008; Rowe et al., 2017; Vanderploeg et al., 2007). At the beginning of regime transformation, dreissenids were concentrated in the shallow zone and nutrients (primarily phosphorus) from allochthonous sources were retained in the nearshore, thus impacting

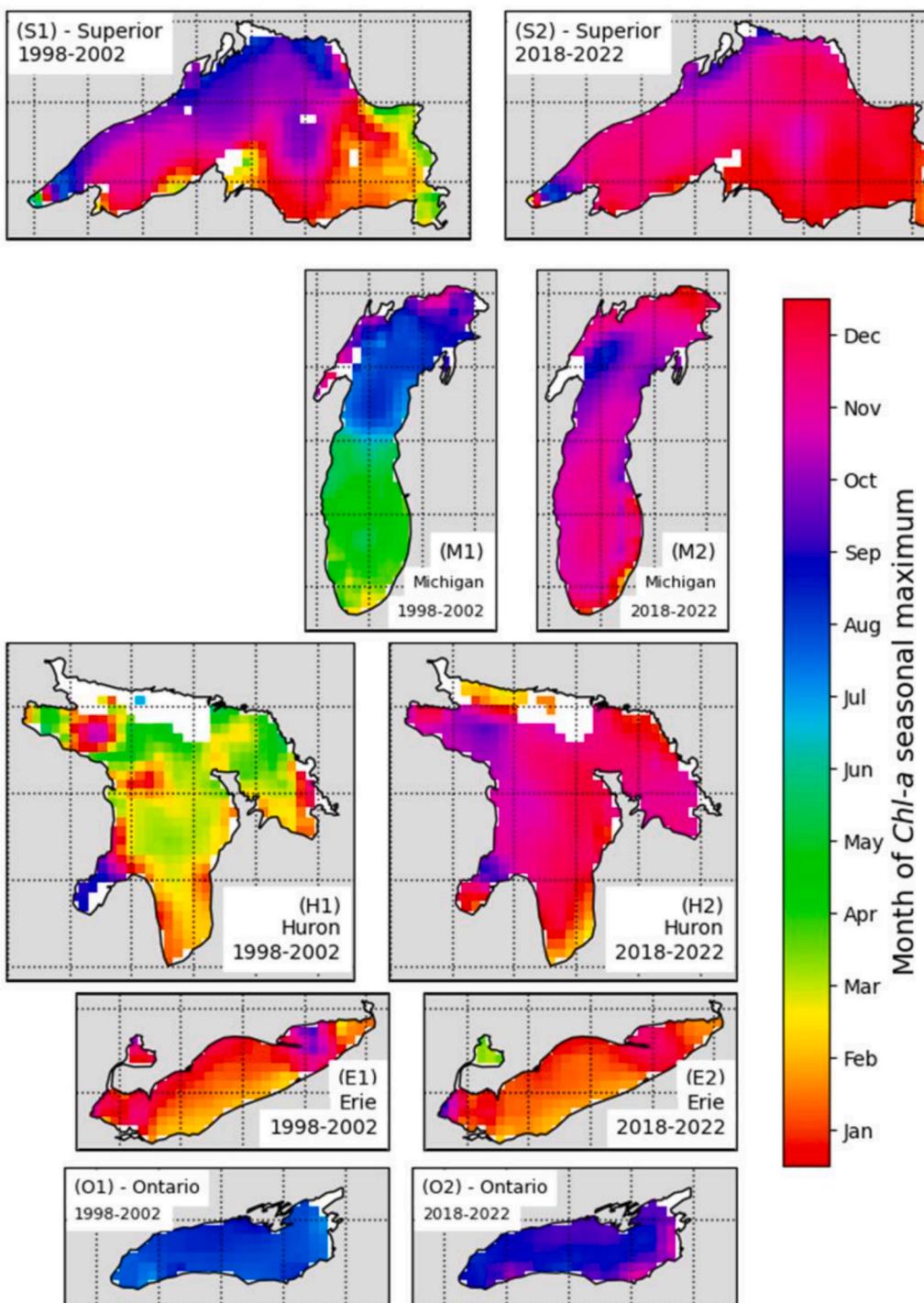


Fig. 10. Maps of the month of maximum monthly median chlorophyll concentration estimated by the “center of gravity” method for the ‘starting’ 1998–2002 (left column) and ‘ending’ 2018–2022 (right column) 5-year periods of the Ocean Colour Climate Change Initiative (OC-CCI) dataset in Lakes Superior (S1, S2), Michigan (M1, M2), Huron (H1, H2), Erie (E1, E2), and Ontario (O1, O2).

offshore pelagic communities through a “nearshore phosphorus shunt” (Hecky et al., 2004). The shift in the bulk of mussels from the nearshore to the mid-depth zone (30–50 m) resulted in the fraction of the water column cleared at mid-depth greatly exceeding phytoplankton growth, while the rates of seston uptake nearshore and offshore were lower (Vanderploeg et al., 2010). This pattern of seston uptake at different depths affected not only the mid-depth region, but also the offshore region “downstream” of the mid-depth zone, suggesting a new “mid-depth carbon and phosphorus sink” hypothesis (Vanderploeg et al.,

2010). Further expansion of mussels to deep regions and declining density and biomass in the shallowest zone resulted in the “offshore carbon and phosphorus sink” hypothesis (Karatayev and Burlakova, 2022).

6.3. Effect of dreissenids filtration on phytoplankton phenology (seasonal cycles)

The disappearance of spring *Chl-a* maximum in Lakes Huron and

Michigan corresponds closely with the dreissenid invasion, and argues strongly for top-down control through filtration. Bottom-up control through the reduction of nutrient input from the watershed and its sequestration nearshore may have contributed to this, as well as climate changes, though we cannot ascertain this in our study.

Climate change is an important factor affecting aquatic food webs (Adams et al., 2022; Behrenfeld et al., 2006; Edwards and Richardson, 2004); however, the timings of ecosystem transformations observed in the Great Lakes do not appear to be a direct consequence of global warming. Although previous studies indicated that, since 1985, water temperature in the Great Lakes was increasing even more rapidly than regional air temperature (Austin and Colman, 2008; O'Reilly et al., 2015; Schneider and Hook, 2010), the most abrupt warming occurred from 1997 to 1998 (Gronewold et al., 2015; Van Cleave et al., 2014; Zhong et al., 2016), that is, in the beginning of the period analyzed in this study. The 1997/1998 warming started with an anomalously warm El Niño winter over the northern US (Assel et al., 2000; Kumar et al., 2001), followed by a long-term shift toward a negative phase of the Pacific Decadal Oscillation (PDO) associated with an abnormally cold eastern Pacific Ocean and warm western-central North Pacific Ocean (Mantua et al., 1997; Newman et al., 2016; Zhang et al., 1997).

Warming of the upper layer results in an earlier onset of springtime stratification in the Great Lakes (Calamita et al., 2021; Fichot et al., 2019; Kayastha et al., 2023; Zhong et al., 2016). Under pressure by dreissenid mussels, the role of seasonal stratification is different from the role it usually plays in phytoplankton phenology. Typically, stratification retains phytoplankton cells in the euphotic zone where production by photosynthesis is balanced by loss processes, sinking, and heterotrophic grazing. With shallowing of the seasonal thermocline in spring, phytoplankton receive more solar energy while nutrient concentrations are still high; as a result, photosynthetic growth exceeds loss processes producing a spring ('vernal') phytoplankton bloom (Siegel et al., 2002; Sverdrup, 1953). In the regions where the abundance of filter-feeding mussels is high and the water column is well mixed (e.g., in winter-spring before the formation of seasonal thermocline), intensive heterotrophic pressure in the near-bottom layer reduces net primary production in the entire water column and, as a result, a spring maximum is not formed (Fahnenstiel et al., 2010; Reavie et al., 2014; Rowe et al., 2015; Kerfoot et al., 2010; Vanderploeg et al., 2010).

In summer, when nutrients in the upper mixed layer are depleted, the thermocline plays the role of a barrier between the subsurface euphotic layer and deep waters rich in nutrients, often resulting in the formation of deep chlorophyll maximum (DCM), regularly observed in the Great Lakes (Barbiero and Tuchman, 2004; Fahnenstiel and Scavia, 1987; Fraker et al., 2021; Malkin et al., 2012; Scofield et al., 2020). With a seasonal decrease in solar heating, erosion of the thermocline increases the nutrient supply to the upper mixed layer, resulting in the autumn phytoplankton maximum observed in remotely-sensed *Chl-a* imagery. However, in the waters affected by dreissenids, summer stratification not only retains photosynthetic algae in the euphotic layer and controls vertical nutrient flux but also separates phytoplankton from benthic filter-feeders (Fahnenstiel et al., 2010; Karatayev et al., 2021; Rowe et al., 2017, 2015). As such, erosion of stratification is expected to produce both positive (by nutrient supply) and negative (by grazing) effects on phytoplankton dynamics.

It is unclear why in the Great Lakes, in fall, when the seasonal thermocline is eroding, a positive effect of nutrient flux to the euphotic zone outweighs the negative effect of filter-feeders. A possible explanation is that an increase of near-surface *Chl-a* concentration in fall may result from shoaling DCM rather than phytoplankton growth associated with increased nutrient flux to the euphotic layer.

6.4. OC-CCI dataset as a source for regime shifts detection

The OC-CCI *Chl-a* dataset appears to be a suitable source of information for detecting trends and regime shifts in aquatic regions when

transformations are as dramatic as those observed in the Great Lakes. This is corroborated by Henson et al. (2016, 2010), who estimated that the minimum length of a time series required to detect *Chl-a* trends in the open ocean was 15–60 years based on the amplitude of trend to natural variability. The present duration of the OC-CCI dataset (25 years) is clearly within these limits, and the magnitude of observed changes in *Chl-a* are much larger than those in the open ocean driven by global warming.

Unfortunately, the OC-CCI dataset only begins in 1997 when regular satellite-derived estimates of *Chl-a* are available, and we are unable to analyze changes in *Chl-a* during the previous two decades when nutrient discharge regulation began and before the dreissenid mussel invasion in the Great Lakes started in 1988. Previous studies based on reflectances measured by satellite sensors operating during that period, such as the Advanced Very High Resolution Radiometer (AVHRR, operating since 1981) and Coastal Zone Color Scanner (CZCS; 1978–1986) demonstrated a significant increase in water clarity of the Great Lakes (Binding et al., 2015; Budd et al., 2001). Unfortunately, estimates of *Chl-a* from AVHRR imagery used by Budd et al. (2001) are unreliable because it does not possess the required wavebands used to derive *Chl-a*; it possesses only one visible (630 nm) channel (Stumpf and Pennock, 1991, 1989; Woodruff et al., 1999). The "proof-of-concept" CZCS mission (1978–1986) onboard the Nimbus-7 satellite was focused on estimates of ocean color, including assessments of *Chl-a* (Hovis et al., 1980). However, the attempts to compare *Chl-a* derived from CZCS to the more recent dedicated ocean color sensors resulted in ambiguous conclusions (Antoine et al., 2005; Gregg et al., 2003; Martinez et al., 2009), and the lack of overlap between CZCS and SeaWiFS prevented including CZCS in the OC-CCI *Chl-a* time series.

Other merged ocean color satellite datasets are available and could potentially be used to detect *Chl-a* trends. Of these, the most prominent is the Copernicus Marine Environmental Monitoring Service (CMEMS) GlobColour processor (Garnesson et al., 2019; Maritorena et al., 2010), where the continuous dataset of *Chl-a* was generated by combining *Chl-a* products computed for each sensor using different algorithms. We chose not to use the GlobColour dataset, because it was not explicitly bias-corrected and revealed higher discontinuities as compared with OC-CCI (Hammond et al., 2018).

OC-CCI is a developing project whose future versions will comprise additional satellite information, including reprocessed VIIRS SNPP after 2020, and two new VIIRS sensors onboard NOAA-20 (launched November 2017) and NOAA-21 (launched November 2022). These and other datasets with improved correction of inter-mission differences (Yu et al., 2023) will provide advanced possibilities to detect trends and regime shifts in different aquatic regions effectively.

6.5. Potential Issues

We cannot be entirely certain that all biases introduced by the merging of observations collected by different satellite sensors were completely removed from the OC-CCI *Chl-a* dataset and hence could not be misinterpreted by the STARS method as regime shifts. However, any artifacts resulting from the compilation are likely minimal and did not affect the assessments of the timings and magnitudes of this transformation; the same trends and timing of shifts in chlorophyll concentration observed in the individual sensor data were also detected in the OC-CCI dataset.

Overall, we think that STARS is a good and appropriate method to detect and quantify the timings of regime shifts. We assume the regime cut-off length parameter we set to 5 years (60 months) was sufficient. Stirnemann et al. (2019), using the experiments with synthetic time series including artificial change points (APs), demonstrated that STARS detected regime shifts within a temporal range of ± 12 time units (months) from (typically 1–3 time units before) AP and recommended caution to be used in the intra-annual (phenological scale) interpretations of the results when monthly time series is used. This

recommendation agrees with the accuracy we used in this study, analyzing the calendar years of regime shifts and ignoring the months.

As stated previously, though we analyzed the longest time series of *Chl-a* currently available, the lakes have undoubtedly undergone changes prior to the 25 years comprising the OC-CCI dataset. For instance, the oligotrophication in lakes may have begun and ended earlier than the first year of the OC-CCI dataset (i.e., 1997). Furthermore, the monthly resolution of the OC-CCI will not capture details of short-lived events. Yet, for the purposes of this study, it provides a synoptic view at a sufficient temporal scale to document the mean environment and its changes over a year.

Another issue related to the application of OC-CCI dataset to near-shore shallow parts of the Great Lakes is that OC-CCI was not well calibrated for turbid shallow waters. Field samples for OC-CCI calibration were collected over depths > 50 m (Sathyendranath et al., 2019). Similarly, the adopted *Chl-a* retrieval algorithm (a blended combination of the OC band ratio and color index) is optimized for both low *Chl-a* and typically Case-1 waters (where phytoplankton dominates the optical properties) and has been shown to carry larger uncertainties in optically complex Case-2 waters (where inorganic particles dominate) such as observed in Lake Erie (Binding et al., 2019). The ratio between total suspended solids (TSS) and *Chl-a* in Lake Erie is also higher than in other Great Lakes (Xu et al., 2022), making the assessments of remotely sensed *Chl-a* less reliable. This kind of product uncertainty may contribute to the result that no regime shifts were detected in Lake Erie.

7. Conclusions

The results of this study demonstrate that the combined effect of regulation of nutrient loads enhanced by the invasion of non-native filter-feeding mussels affected the ecosystems of the Great Lakes differently. In two of the five lakes (deep, cold, and already oligotrophic Lake Superior and shallow eutrophic Lake Erie), the regime shift was either small, not detectable due to uncertainties of algorithm performance in those optical water types, or completed before 1997, outside the temporal coverage of the analyzed time series. Over most of Lakes Michigan and Huron, pelagic ecosystems stabilized at a new lower trophic regime from 2005 to 2015. In a few locations (the central part of Lake Michigan, Saginaw Bay in Lake Huron, and most of Lake Ontario), regime transformation either occurred prior to the timeframe of this study or is ongoing and may continue in the future. The last few rounds of whole lake benthic surveys have shown that dreissenid mussels have stabilized in many locations in the Great Lakes (Elgin et al., 2022a). However, it is still unclear how the dreissenid populations will progress in these areas and what changes in the community structure and functioning are expected in the future.

This study proves that inconsistencies in the OC-CCI dataset resulting from the biases between different satellites collecting data during different periods are minor compared to regime transformations observed in the Great Lakes during the recent two and a half decades. Given that so far only 9 % of the studies focused on regime shifts in lakes use satellite data as the main data source (Calamita et al., 2024), this study demonstrates that the OC-CCI dataset is a reliable source of data that enables the detection of regime shifts in different regions of the world, including major lakes.

CRediT authorship contribution statement

Nikolay P. Nezlin: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Formal analysis, Conceptualization. **SeungHyun Son:** Writing – review & editing, Data curation, Conceptualization. **Christopher W. Brown:** Writing – review & editing, Methodology, Conceptualization. **Prasanjit Dash:** Writing – review & editing, Methodology, Conceptualization. **Caren E. Binding:** Writing – review & editing, Conceptualization. **Ashley K. Elgin:** Writing – review & editing. **Andrea VanderWoude:** Writing – review & editing,

Conceptualization.

Declaration of competing interest

The author Caren E. Binding is an Associate Editor for the Journal of Great Lakes Research and was not involved in the editorial review or the decision to publish this article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2025.102573>.

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