Overall Assessment

Status: Good

Trends:

10-Year Trend: Unchanging


Rationale: Based on the Oligochaete Trophic Index (OTI) scores, the status and trends in the trophic condition of the lakes are generally considered to be good and unchanging for long-term (1998 - 2019), 10-year (2010-2019), and short-term (2017-2019) time periods. Offshore sites in the Great Lakes are generally oligotrophic, but Lake Erie and some nearshore (<30m) stations in lakes Ontario, Huron, and Michigan are assessed as poor and the trends (both long-term and 10-year) are indicative of increased eutrophication. Overall, an increasing OTI score reflects an increase in trophic condition (more eutrophic).

Status and Trend assessment definitions are included following the Lake-by-Lake Assessment section.

Lake-by-Lake Assessment

Lake Superior

Status: Good

10-Year Trend: Unchanging


Rationale: All nearshore and offshore stations in Lake Superior were classified as oligotrophic, based on OTI scores, both long-term (1998-2019) and in recent years (2017-2019). No significant long-term or 10-year trends were observed in the trophic condition of the lake. The endpoint for this sub-indicator is to maintain oligotrophic conditions in the open waters of Lake Superior.

Lake Michigan

Status: Good

10-Year Trend: Unchanging


Rationale: Since 1998, the majority (13 out of total 16) of stations in Lake Michigan had OTI scores below 0.6 indicating an oligotrophic condition. Of the nine nearshore stations, two were mesotrophic (0.6 < OTI < 1.0), and one was eutrophic (OTI scores > 1.0). Significant long-term trends of increasing eutrophication are evident at six nearshore stations, and trends of increasing oligotrophication were found at two offshore stations and one station in Green Bay. Overall, no significant long-term or 10-year trends were observed in the trophic condition of the lake. The endpoint for this sub-indicator is to maintain an oligotrophic state in the open waters of Lake Michigan.
Lake Huron

Status: Good

10-Year Trend: Unchanging


Rationale: Almost all stations in Lake Huron are oligotrophic, except for three eutrophic nearshore stations. The trophic condition of the lake, as measured by OTI scores, has not changed significantly since 1998. The endpoint for this sub-indicator is to maintain an oligotrophic state in the open waters of Lake Huron.

Lake Erie

Status: Poor

10-Year Trend: Unchanging


Rationale: Almost all stations in Lake Erie are eutrophic, and two have a long-term trend of increasing OTI scores. Overall, no significant long-term or 10-year trends in trophic condition were observed. The endpoint for this sub-indicator is to maintain mesotrophic conditions in the open waters of the western and central basins of Lake Erie, and oligotrophic conditions in the eastern basin of Lake Erie.

Lake Ontario

Status: Fair

10-Year Trend: Unchanging


Rationale: OTI scores indicate that all deep-water stations (>80 m) in both the western and eastern basins of Lake Ontario are oligotrophic, and all the nearshore stations are eutrophic. In the last three years, three eutrophic nearshore stations in the western basin showed long-term trends of increasing eutrophication. Overall, no significant decreasing trends were found in the trophic condition of the lake either since 1998 or in the last 10 years.

Status Assessment Definitions

Good: OTI score of less than 0.6 (oligotrophic conditions)

Fair: OTI score of 0.6 to 1.0 (mesotrophic conditions)

Poor: OTI score of greater than 1.0 (eutrophic conditions)

Undetermined: Data are not available or are insufficient to assess condition of the ecosystem components.
Trend Assessment Definitions

The desired trend is toward an oligochaete open water community indicative of oligotrophic conditions throughout the lakes, with the exception of the nearshore waters of all lakes and open waters of the western and central basins of Lake Erie, where mesotrophic conditions are desired.

Improving: a decrease in the OTI indicating declining eutrophication (i.e., increasing oligotrophication)

Unchanging: OTI score is not changing

Deteriorating: an increase in the OTI indicating increasing eutrophication (i.e., declining oligotrophication)

Undetermined: metrics do not indicate a clear overall trend, or data are not available to report on a trend

Endpoints and/or Targets

Maintain an oligotrophic state consistent with healthy aquatic ecosystems in the open waters of Lakes Superior, Michigan, Huron and Ontario; maintain mesotrophic conditions in the nearshore waters of all lakes and open waters of the western and central basins of Lake Erie, and oligotrophic conditions in the eastern basin of Lake Erie.

Sub-Indicator Purpose

The purpose of this sub-indicator is to assess trends in trophic conditions in the Great Lakes using oligochaete diversity, abundances, and the individual species responses to organic enrichment. We also report general trends in the full benthic community; although these supplementary data are not used directly in the indicator assessment, they provide useful context.

Ecosystem Objective

The Ecosystem Objective is that the benthic community in the Great Lakes should be comparable to unimpaired waters with similar depth and substrate.

This sub-indicator most closely aligns with General Objectives #5 and #6 of the 2012 Great Lakes Water Quality Agreement, which states that the Waters of the Great Lakes should “support healthy and productive wetlands and other habitats to sustain resilient populations of native species” and “be free from nutrients that directly or indirectly enter the water as a result of human activity, in amounts that promote growth of algae and cyanobacteria that interfere with aquatic ecosystem health, or human use of the ecosystem”.

This sub-indicator evaluates trophic conditions in the Great Lakes using oligochaete diversity, abundances, and the individual species responses to organic enrichment.

Measure

This sub-indicator (OTI) evaluates trophic conditions in the Great Lakes using oligochaete diversity, abundances, and the individual species responses to organic enrichment. In addition to the assessment of lake trophic status using OTI, we are providing summary data on status and trends in the whole benthic community and its role in food webs for additional context.
Calculation of the OTI

To evaluate trends in the trophic conditions of the Great Lakes based on status of benthic community, an OTI is used. The OTI was initially described by Mosley and Howmiller (1977) with subsequent modifications by Howmiller and Scott (1977), Milbrink (1983), and Lauritsen et al. (1985). This sub-indicator primarily follows Milbrink’s formula (Burlakova et al. 2018a) with several modifications. Here we use the old division of Oligochaeta by Enchytraeidae, Lumbriculidae, Naididae and Tubificidae, comparable with historical data, despite the fact that only three orders are currently recognized (Enchytraeida, Lumbriculida and Tubificida) and former families of Naididae and Tubificidae in the order Tubificidae are now combined in one family Naididae (Erseus et al., 2008). Therefore for practical reasons and clarity Tubificidae was retained for the analyses. Oligochaetes (tubificids and lumbriculids) are classified into four ecological classes relative to their tolerance to organic pollution, from 0 indicating intolerant of enrichment to 3 indicating tolerant of enrichment. The index ranges from 0 to 3; scores less than 0.6 indicate oligotrophic conditions; scores above 1 indicate eutrophic conditions; and scores between 0.6 and 1.0 indicate mesotrophic conditions. The index is calculated as:

\[ c \times \frac{1/2 \sum n_0 + \sum n_1 + 2 \sum n_2 + 3 \sum n_3}{\sum n_0 + \sum n_1 + \sum n_2 + \sum n_3} \]

where

- \( n_0, n_1, n_2, \) and \( n_3 \) indicate the abundances of organisms in each of the four trophic categories (see Table 1)
- \( c \) is a density coefficient that scales the index to absolute densities (m\(^{-2}\)) of tubificids and lumbriculids. The \( c \) coefficient is as follows (Milbrink 1983):
  - \( c = 1 \) if \( n > 3,600 \)
  - \( c = 0.75 \) if \( 1,200 < n < 3,600 \)
  - \( c = 0.5 \) if \( 400 < n < 1,200 \)
  - \( c = 0.25 \) if \( 130 < n < 400 \)
  - \( c = 0 \) if \( n < 130 \)

There are several parts of the OTI calculation that were interpreted as follows (Riseng et al. 2014):

- only lumbriculids and tubificids were used to calculate the index;
- all immature lumbriculids were classified as Stylodrilus heringianus;
- the \( c \) coefficient was estimated from abundances (\( n \)) of mature and immature lumbriculids and tubificids.

Milbrink (1983) assigned the tubificid Tubifex tubifex dual classifications depending on the dominance of S. heringianus or Limnodrillus hoffmeisteri. The dual classification was formalized as follows: if the ratio of abundances of \( n_0 \) oligochaetes to \( n_3 \) oligochaetes (\( L. hoffmeisteri) < 1 \) then \( T. tubifex \) is classified as a 3; if the ratio is \( >1 \) then \( T. tubifex \) is classified as a 0; however, if the ratio is close to one (0.75 to 1.25) then \( T. tubifex \) is a 3 if \( c \geq 0.5 \) and a 0 if \( c < 0.5 \); if \( L. hoffmeisteri \) density is zero and \( n_0 \) is relatively high and/or total density is low, then \( T. tubifex \) is 0, otherwise 3; and if the total density of oligochaetes is zero, then the index is zero.

Trophic classifications were obtained from literature for the Great Lakes and are shown in Table 1.

For each lake or sub-basin, a graph showing the OTI values on the \( y \)-axis and years on the \( x \)-axis is presented to illustrate the changes in species metrics over time (Figure 1). A map is used to show the major, within lake, spatial-temporal differences (Figures 2 and 3).

Data are sourced from the long-term benthic monitoring program of U.S. EPA Great Lakes National Program Office (GLNPO) which samples 57 stations annually within the five Great Lakes during summer (August).
monitoring program started in 1997, data from 1997 are omitted from the status and trends assessments in this report due to unreconcilable discrepancies. The GLNPO benthic station ON64 was discontinued in 2016; prior to 2016 a total of 58 long-term monitoring stations were sampled and included in the OTI calculations. Less frequent but more spatially intensive sampling of all Great Lakes is now undertaken during Cooperative Science Monitoring Initiative (CSMI) field years to enhance lake-wide estimates of changes in benthic community diversity and abundance.

**Ecological Condition**

State of the Great Lakes Reporting uses the modified oligochaete-based trophic condition index (OTI, Milbrink 1983; Howmiller and Scott 1977) to assess trophic status of each station. Benthic invertebrate data for OTI calculation are collected annually at 57 permanent GLNPO sampling stations (Lakes Superior and Huron: 11 stations each, Michigan: 16, Erie: 10, and Ontario: 9 stations) located mostly offshore (Figure 2). The OTI is calculated based on known organic enrichment tolerances and abundances of aquatic annelid worms (Oligochaeta) (see the Measure section for more information). As organic pollution increases, oligochaete species with different physiological tolerances to water and sediment pollution replace each other and the community composition shifts. Overall, an increasing OTI means increasing eutrophication or increasing trophic conditions. The OTI scores range from 0 – 3: scores less than 0.6 (the lower blue line in Figure 1) indicate oligotrophic conditions; scores above 1 (the top red line in Figure 1) indicate eutrophic conditions; and scores between 0.6 and 1 suggest mesotrophic conditions. Scores approaching 3 indicate high densities of oligochaetes dominated by the pollution tolerant tubificids.

Because we expect nearshore and offshore stations to support different benthic communities, we make the distinction between offshore and nearshore zones when using the OTI to assess overall lake-wide trends in trophic conditions. The original GLNPO sampling program design established two components (offshore and nearshore) with different objectives: the offshore component is intended to assess the benthic invertebrate community as an indicator of basin-wide cumulative stressors, while the nearshore component serves as an indicator of more localized environmental stressors (Barbiero et al., 2018). For example, some of the benthic stations were chosen near tributary mouths that deliver organic matter to the lake. In general, Oligochaeta distributions exhibit depth-specific patterns, with species that are tolerant of organic enrichment found only at depths <70m. As a result, many nearshore stations will be classified as eutrophic. Because the offshore component of the monitoring program is designed to be used as an indicator of basin-wide cumulative stressors, the offshore data most directly address the goal of this indicator.

A consistent difference in trophic conditions among and within the Great Lakes was found during the study period (1998– 2019) (Figure 1). Trophic condition was significantly inversely related to station depth ($r = -0.61, P < 0.001$), with Lake Erie being the most eutrophic lake, followed in order of decreasing trophic condition by lakes Ontario, Michigan, Huron, and Superior. To assess the temporal trends in OTI scores at each station, we used linear regression, and trends were considered significant if $P < 0.05$. No significant lake- or basin-wide long-term trends of increasing trophic condition were found since 1998, but localized positive or negative trends in OTI scores over time were found at some stations in Lake Erie, Michigan, Huron, and Ontario (Figure 3).

All 11 stations in Lake Superior were oligotrophic based on OTI scores since 1998, and there were no significant long-term or 10-year trends in OTI scores either lake-wide scale or at specific stations (Figure 3), consistent with the 2019 report. Densities of major taxonomic groups, including *Diporeia*, an indicator of oligotrophic conditions and an important lipid-rich fish prey item, were stable in Lake Superior from 1998 (Figure 4). The Lake Superior total benthos biomass is the lowest of all Great Lakes, but *Diporeia* comprised over 50% of the biomass (Figure 5).
Almost all stations in northern and central Lake Michigan, as well as deep stations in the southern part of the lake (13 of 16 total stations) are oligotrophic (Figure 2). Of the 9 nearshore stations one in southeastern Michigan (MI48 near the Kalamazoo River outlet) was eutrophic and two stations (MI49 in Green Bay and MI46 near the Grand River outlet) were mesotrophic. Five nearshore stations and one offshore station (MI151, 106 m) had significant long-term trends of increasing eutrophication (P < 0.03) in 2017-2019, compared to four nearshore stations in the 2019 report. At the same time, two deep stations (MI18 and MI47, P < 0.04), along with one station in Green Bay (MI49, 44 m, P < 0.001), showed signs of increasing oligotrophication (Figure 3). Overall, no significant lake- or basin-wide long-term trends of increasing trophic condition were found in the lake since 1998. Along with Lake Ontario and Lake Erie, Lake Michigan exhibits the highest lake-wide density and biomass of Dreissena of all invaded Great Lakes (Figures 5, 6). The majority of Lake Michigan’s non-dreissenid biomass is comprised by Oligochaeta (Figure 5). Nearshore Diporeia in Lake Michigan underwent large declines in early 2000s, followed by declines in offshore populations in the mid-2000s, but have remained relatively stable at depths >90 m since 2005. Despite the declines in Diporeia, high total benthic biomass (including Dreissena) in Lake Michigan can likely support abundant benthic fish populations and native fish that feed on benthos and/or bottom fish. The percent of Oligochaeta comprising the non-dreissenid community increased with the decline in Diporeia and Sphaeriidae that began in early 2000s (Figure 4).

Most of the stations in northern and central Lake Huron (8 of 11 total stations) are oligotrophic (Figure 2). Of the five nearshore stations, three were classified as eutrophic (Figure 2). One of these stations (HU96, near the outlet of Saugeen River in Ontario, Canada) was classified as mesotrophic and had an increasing eutrophication trend in the previous reporting period. The total density of Oligochaeta, including species tolerant of organic pollution, increased at this station 20-fold since the early 2000s, which resulted in an increase the OTI score. The other two eutrophic stations are located in the southern part of the lake and in Saginaw Bay (Figure 2). Since the 2019 reporting, one additional nearshore station in central basin (HU06) showed signs of eutrophication, while one offshore station in northern Huron (HU61) displayed a trend toward oligotrophication (Figure 3). Overall, no significant lake- or basin-wide long-term trends of increasing trophic condition were found in the lake since 1998. The Lake Huron benthic community, including Diporeia, has undergone similar changes as in Lake Michigan, but the lake-wide density and biomass of Dreissena is lower than in lakes Michigan and Ontario (Figures 5, 6). Currently, the majority of Lake Huron non-dreissenid biomass is comprised by Oligochaeta (Figure 5). The percent of Oligochaeta in non-dreissenid community increased with the decline in Diporeia and Sphaeridae that began in late 1990s (Figure 4).

In Lake Erie all stations are shallower than 70m deep. Eight stations were classified as eutrophic and two stations that were eutrophic in the 2019 report (ER63 and ER91) were classified as mesotrophic in 2017-2019. No significant trends of increasing eutrophication were found lake-wide in the trophic condition during both the long-term and in the last 10 years. Only two stations showed significant long-term trends of increased OTI scores (ER15 and ER43, P < 0.025), compared to four stations in the 2019 report. One eastern nearshore station (ER 63) showed a decline in OTI score (P = 0.004, Figure 3), consistent with trends recorded in 2013-2016. Due to large declines in Dreissena in Lake Erie in the last decade caused by hypoxic events in the central and western basins, the lake-wide dreissenid density and biomass in these two basins are now the lowest of all invaded lakes, but the biomass in the eastern basin is still high (Karatayev et al., 2018, 2021a). Biomass of non-dreissenid benthos is the highest among all other lakes and is largely comprised by Oligochaeta in the eastern and central basins, and Hexagenia in the western basin. The largest density of Oligochaeta in the lake was found in 2000s. Diporeia has not been found in Lake Erie samples since the beginning of GLNPO monitoring in 1997, but abundant benthic communities can support large fish populations. Overall, due to shallow depths and high productivity, Lake Erie has higher benthic biomass and species richness than the other Great Lakes (Burlakova et al., 2018b).
All deep-water stations in Lake Ontario have remained oligotrophic throughout the 1998-2019 reporting period, and no significant trends in the trophic condition were found lake-wide both long-term and in the last 10 years. All the four nearshore stations are eutrophic (Figure 2). Three of these stations are located in the western basin and displayed a trend toward increasing eutrophication since 1998 (likely being affected in the southern shore by the outlet of the Niagara River, and on the northern shore by the Toronto metropolitan area) (Figure 3). Compared to the previous report, two stations changed status from mesotrophic to eutrophic in 2017-2019. However, deep stations, for the most part, remain oligotrophic and unchanging both the long-term and within the last 10 years. Lake Ontario has the largest biomass and the second largest density of Dreissena among the Great Lakes, and dreissenid populations are stable (Figures 5, 6). The replacement of Diporeia with quagga mussels and Oligochaeta began in Lake Ontario in the 1990s, which was earlier than in the other deep lakes, and very few Diporeia have been recorded in the samples since the late 2000s. As in the other lakes, both density and biomass of non-dreissenid benthos are now dominated by Oligochaeta.

Overall, benthic communities in lakes Ontario, Michigan and Huron have shifted from dominance by Diporeia to dreissenids and oligochaetes during the time series. Dreissenid populations continue to increase in deep regions of Lake Michigan, Huron and Ontario and decline in shallow areas of deep lakes as well as in Lake Erie, but non-dreissenid populations have exhibited relative stability over the past decade. Dreissenids were the largest contributor of biomass (>99%) in all lakes except Superior. Following the patterns of declining benthic diversity and density with depth, Lake Erie benthos is the most abundant and diverse, and supports the most productive Great Lakes fishery. In lakes where Diporeia no longer constitutes a significant part of benthic community (all lakes except Lake Superior), current benthic populations (including dreissenids) can still sustain substantial amount of benthivorous fish, transferring the energy from the lower to the upper trophic levels (Madenjian et al., 2010).

**Linkages**

Linkages to other sub-indicators in the indicator suite include:

- **Dreissenid Mussels** – the relative abundance of non-native suspension feeding benthic species such as zebra and quagga mussels can dramatically change the structure of aquatic communities (both benthic and pelagic), affect ecosystem functioning, and alter lake trophic state. In addition to direct local effects (e.g., creating additional habitat and enhancing food supply for some benthic species), dreissenid mussels also affect other sub-indicators such as Nutrients in Lakes, Chlorophyll, Phytoplankton, Zooplankton, and Diporeia, and they alter the amount of available food for some profundal taxa. In addition, dreissenids together with other benthic taxa abundant in mussel aggregations serve as food for fish, including round goby, that in turn are preyed upon by many other fish species (e.g., lake sturgeon, walleye, salmon, smallmouth and largemouth bass, lake trout, whitefish and yellow perch). There are strong interactions between these sub-indicators that are not well understood and require further investigation.

- **Nutrients in Lakes (open water)** – as a natural and essential part of aquatic ecosystems, nutrients play an important role in supporting the production of aquatic plants and algae, which provide food and habitat for planktonic and benthic organisms at the base of the food chain. The addition of nutrients affects the structure, abundance, and population dynamics of the benthic community, changing the proportion of tolerant and intolerant species, but the magnitude of changes varies depending on the depth and lake trophic status. Since the OTI was designed to reflect community changes following organic enrichment, it is expected to co-vary with an increase in nutrients. Indeed, the OTI positively correlates with the amount of Total Phosphorus and Total Soluble Phosphorus measured in near-bottom waters (Burlakova et al., 2017).
On the other hand, dreissenids can alter the amount and turnover of nutrients in the water and sediments (Li et al. 2021).

- **Diporeia (open water)** – Diporeia is a benthic macroinvertebrate in the cold, deep-water habitats of all the Great Lakes (except Lake Erie, where it is extirpated). It is an indicator of oligotrophic conditions, and an important fish food item. Historically Diporeia had been a dominant benthic macroinvertebrate in profundal regions of all five of the Great Lakes (Cook and Johnson, 1974). Proliferation of dreissenid mussels coincided with significant declines in Diporeia in Lakes Ontario, Michigan, and Huron, but the nature of these interactions is still not well-understood. While the abundance of Diporeia is not included and not necessarily responsive to the OTI, a significant increase in organic enrichment may negatively affect Diporeia.

- **Climate change** – increasing water temperatures may affect survivorship and increase the developmental rate, the timing of development, spawning, and food availability for benthic taxa. As a result, there may be potential shifts in distribution and abundance of oligochaetes, affecting the performance of the OTI index, driven directly by water temperature. Both abiotic changes and biological responses in the lakes are complex, and changes in water chemistry, hydrology, etc. may also be important for the growth and survival of benthic organisms. Synergistic effects between climate and other anthropogenic variables and sub-indicators (i.e., establishment and spread of invasive species, nutrients) will likely exacerbate climate-induced changes in the oligochaete community.

This sub-indicator also links directly to the other sub-indicators in the Habitat and Species indicator.

### Assessing Data Quality and Data Availability

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<th>Neutral or Unknown</th>
<th>Disagree</th>
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<td>Data used in assessment are openly available and accessible</td>
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Clarifying Notes:
*The annual benthic monitoring program design of U.S. EPA GLNPO samples 10-16 stations per lake, larger spatial coverage provided by CSMI surveys.

Data Limitations

The OTI index used in this assessment is based on only 27 out of total 66 species, all belonging to a single subclass, Oligochaeta. The performance of the OTI was recently evaluated against lake productivity and two more indices (an improved index, iOTI, based on a larger number of Oligochaeta species, and a modified trophic index, mTI, based on all benthic species) have been proposed for use (Burlakova et al., 2018a). In addition, the National Coastal Condition Assessment (NCCA) is considering improvements to the OTI for the nearshore zone where it fails to perform at a large number of sites due to absence of Oligochaeta. A better performing index or indices should be developed and applied to the 2025 sub-indicator report to improve classification of the trophic condition of the lakes and assessment of trends in benthic community.

The OTI was developed to characterize situations of organic enrichment due to anthropogenic eutrophication, which was an important issue addressed by the Great Lakes Water Quality Act in 1972. Currently, the Great Lakes open waters are undergoing a reverse trend of gradual oligotrophication due to the combined effect of nutrient mitigation and dreissenids (Evans et al., 2011). Therefore, excessive eutrophication remains an issue only in some nearshore areas and shallow bays (e.g., western Lake Erie, Saginaw Bay, Green Bay), but is no longer a concern at lake-wide scales or in profundal areas, limiting the utility of the OTI for this sub-indicator. In addition, the current index does not allow for assessment of the status and trends in the whole benthic community, which is a gap given the whole benthic community’s role in food webs. For example, dreissenids are now an essential part of the benthic community and Great Lakes food webs, but they are not included in the OTI nor are other important (non-oligochaete) components of benthic community. Therefore, this sub-indicator would be improved by using an index or indices that account for the whole benthic community.

Two important factors should be considered while using the OTI to evaluate lake trophic conditions. First, due to species-specific patterns of Oligochaeta distribution with depth, most of the species tolerant of organic enrichment are found at depths <70 m (Burlakova et al., 2018b). Secondly, some of the benthic stations were deliberately positioned next to mouths of large tributaries that deliver large amounts of organic matter to the lake (Barbiero et al., 2018). As a result, many nearshore stations will be classified as eutrophic. The ratio of nearshore (≤70 m) to offshore stations varies by lake (100% in Lake Erie, 56% in Michigan, 45% in Huron, 44% in Ontario, and 18% in Superior) and may therefore additionally affect the overall OTI score and our estimates of trophic condition of the lake.

Additional Information

Benthic invertebrate biomonitoring has long been a tool of choice in assessing anthropogenic impacts on aquatic systems due to species’ relative longevity, limited mobility, and wide range in tolerance to environmental stressors. Abundant, pollution-tolerant benthic species indicate degraded habitats. Increasing species diversity and decreasing abundance of pollution-tolerant species indicate return to healthy habitats. In addition, benthic secondary production plays a central role in supporting higher trophic level production, comprising over half of total consumption of fishes common to north-temperate lakes of North America (Vander Zanden and Vadeboncoeur, 2002). The benthic community serves as a good indicator of overall ecosystem health as it integrates water,
sediment and habitat qualities. Changes in the benthic community closely reflect shifts in the overall productivity of the system.

The oligochaete sub-indicator used for the State of the Great Lakes report assesses trophic status of the lakes and may suggest pressures due to organic enrichment. Most of the stations that showed increasing eutrophication are located near large river mouths, suggesting that pollution abatement efforts in the upland watersheds could help to improve water quality and sediment conditions at these stations. Other pressures not accounted for in the OTI include invasive species, regional climate change, water level changes, and toxic or other contaminants. The tendency of OTI to decrease with depth (due to the lack of pollution-tolerant species residing deeper than 70 m) may affect lake-wide index values, depending on the ratio of deep to shallow stations sampled in each lake. Non-native species that strongly affect freshwater ecosystems (e.g., *Dreissena* spp.) can alter the composition and abundance of benthic communities, affecting behavior of benthic indices, and can modify the response of communities to trophic state.

There is an emerging realization of the importance of benthic processes and pathways within a whole-lake context (Vander Zanden and Vadeboncoeur 2002). A recent analysis of long-term dynamics of major trophic levels in the Laurentian Great Lakes revealed a far greater prevalence of bottom-up regulation since 1998, as a result of long-term declines in total phosphorus (TP) inputs and the more recent proliferation of nonindigenous dreissenid mussels (Bunnell et al. 2013). Filter feeding Ponto-Caspian bivalves *Dreissena polymorpha* and *D. rostriformis bugensis* are powerful ecosystem engineers that affect both abiotic (e.g., enhance water clarity and alter nutrient cycling) and biotic (e.g., reduce abundance of phytoplankton and microzooplankton, enhance benthic algae and macrophytes, induce changes in benthic community) components of the ecosystem (Karatayev et al. 1997, 2002; Higgins and Vander Zanden 2010; Burlakova et al., 2018b). Dreissenid tissues and shells now contain nearly as much phosphorus as the entire water columns of the impacted Great Lakes, and mussels have become a major agent of phosphorus cycling, offsetting or overshadowing the effects of external loading (Li et al. 2021). Filter-feeding activity, sediment deposition and habitat provided by dreissenids directly affect benthic macroinvertebrate community abundance and composition by promoting epifaunal predators, scavengers and collectors while replacing native filter feeders (e.g., Karatayev et al. 1997; 2002; Burlakova et al. 2012; Ward and Ricciardi 2007; Higgins and Vander Zanden 2010). However, most of the changes in benthic community structure following dreissenid invasion are described for the littoral zone rich in epifaunal species while changes in profundal infaunal community are poorly understood (Burlakova et al. 2014; Karatayev et al. 2015). After the Dreissena invasion, the abundance of non-dreissenid taxa (e.g., *Diporeia*, Sphaeriidae) declined in profundal habitats (Nalepa et al. 2007, 2009; reviewed in Karatayev et al. 2015) where quagga mussels compete for space and food resources with most of native invertebrates. This may be a result of system-wide (e.g. food interception effect, resulting in strong decline of spring phytoplankton blooms) vs. local Dreissena (e.g. enrichment of sediments with biodeposits) effects. The resulting effect of Dreissena on the oligochaete community (e.g., increasing amount of both tolerant and intolerant Oligochaeta in the presence of Dreissena, Burlakova et al., 2018b) may induce changes in the OTI that will not reflect the changes in the trophic status of the ecosystem. Therefore, more data on the effect of dreissenids on species composition and abundance of benthic invertebrates in profundal vs. nearshore zone are needed to fully understand dreissenid impacts on benthic communities.

The number of permanent stations visited by U.S. EPA GLNPO allows for a cost-effective benthic monitoring program each year. Less frequent (once every 5 years) but more spatially explicit sampling of all Great Lakes occurs during the Cooperative Science and Monitoring Initiative intensive field years to assess changes in benthic community diversity and abundance. These lake-wide samplings of historical stations and other stations of concern allow the diversity, density and biomass of benthic community to be monitored in each lake and enable the
estimation of lake-wide population changes of invasive and native indicator species (e.g., dreissenids, Hexagenia, Diporeia; Mehler et al., 2020; Karatayev et al., in press; Burlakova et al., in press).

Values of the Benthos sub-indicator representative of the nearshore are very important, as nearshore benthos are more diverse and are also affected more quickly and more directly (than offshore benthos) by inputs from adjacent watersheds, including runoff of nutrients. However, different indicators and indices would need to be developed for the assessment of status and trends in the nearshore benthic community, since many of the nearshore substrates lack the Oligochaete species used in the calculation of the current benthic index (OTI) for State of the Great Lakes reporting. In addition, the current index does not allow for assessment of status and trends in the whole benthic community and its role in food webs.

Acknowledgments

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coefficient $c$ but only mature specimens were used to calculate the number belonging to each ecological group of oligochaetes (see the description of index calculation in the Measure section).


**Figure 2.** Map of the Great Lakes showing the mean trophic condition at each sampling station calculated for 2017-2019. Trophic condition was based on the modified Oligochaete Trophic Index based on Milbrink (1983).


**Figure 3.** Maps of the Great Lakes showing stations with significant temporal trend in trophic condition between 1998 and 2019. Stations without significant changes in oligochaete trophic index with time ("no change", $P > 0.10$, linear regression), with significant trends ("increasing eutrophication" or "oligotrophication", $P < 0.05$) are indicated.


**Figure 4.** Trends in benthos areal density (bottom panels) and percent areal density (top panels) of major taxonomic groups in Great Lakes (1998–2019). These values exclude *Dreissena* spp. that was monitored only after 2003, and Bivalves include only Sphaeriidae. Error bars represent one standard error.


**Figure 5.** Absolute and percent areal biomass of benthos by major taxonomic group excluding *Dreissena* spp. (bottom and middle panels) and areal biomass of *Dreissena* spp. (top panels) at stations averaged across 2017-2019. Error bars represent one standard error. Bivalves in the lower graph include only Sphaeriidae.


**Figure 6.** Changes in density (2003–2019) of dreissenid mussels in Lakes Erie, Michigan, Ontario, and Huron. Dreissenid mussel populations are not established in Lake Superior. Error bars represent one standard error.


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<table>
<thead>
<tr>
<th>SPECICODE</th>
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<th>SPECIES</th>
<th>Trophic Class</th>
<th>Source</th>
<th>Comment</th>
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<td>RHYCOC</td>
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<td>Same as Milbrink 1983</td>
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<td>claparedeianus</td>
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<td>udekemianus</td>
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<td>bedoti</td>
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<td>POTMOLD</td>
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<td>moldaviensis</td>
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<td>Milbrink 1983</td>
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<td>vejdosvkyi</td>
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<td>LIMHOFF</td>
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<td>hoffmeisteri</td>
<td>3</td>
<td>Milbrink 1983</td>
<td>Differs from classification in Lauritsen et al. 1985</td>
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<td>TUBTUBI</td>
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<td>tubifex</td>
<td>0 or 3</td>
<td>Milbrink 1983</td>
<td>Depends on densities of LIMHOFF and STYHERI and total oligochaete density</td>
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</table>

Table 1. Trophic classifications for select mature lumbriculids and tubificids taken from Howmiller and Scott (1977), Milbrink (1983) with additions from Krieger (1984), and Lauritsen et al. (1985). If Milbrink classifications differed from Howmiller and Scott, Howmiller and Scott was used. Species are classified into four ecological classes relative to their tolerance to organic pollution, from 0 indicating intolerant of enrichment to 3 indicating tolerant of enrichment. Source: Riseng et al. 2014.
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