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Commentary

Research needs to better understand Lake Ontario ecosystem function: A workshop summary

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ABSTRACT

Lake Ontario investigators discussed and interpreted published and unpublished information during two workshops to assess our current understanding of Lake Ontario ecosystem function and to identify research needs to guide future research and monitoring activities. The purpose of this commentary is to summarize key investigative themes and hypotheses that emerged from the workshops. The outcomes of the workshop discussions are organized under four themes: spatial linkages and interactions, drivers of primary production, trophic transfer, and human interactions.

Introduction

The rapid rate of ecological change characteristic of Lake Ontario is in sharp contrast to the slower pace of scientific synthesis and communication of new knowledge. Public awareness of the complexity and interconnectedness of ecosystems and ecosystem services has increased (Christensen et al., 1996) leading to increased emphasis on ecosystem-level monitoring and science. The Great Lakes Water Quality Agreement between the United States and Canada has been recently updated (http://www.ijc.org/en_/Great_Lakes_Water_Quality, accessed November 2012). The agreement commits the signatories to identify binational science priorities, through the Lakewide Action and Management Plan (LAMP) process, and to support a binational Cooperative Science and Monitoring Initiative (CSMI) for each Great Lake on a five-year rotational basis. Lake Ontario was the first to initiate a science priority setting process and CSMI under the new agreement. Recently, the Lake Ontario LAMP facilitated two scientific workshops — one at the Canada Centre for Inland Waters (CCIW), Burlington, ON in November, 2011 and another at the Cornell University Biological Field Station, Bridgeport, NY in April 2012.

The focus of the workshops was on issues of lake-wide concern for Lake Ontario. The information reviewed included annual reports of the Lake Ontario Committee to the Great Lakes Fishery Commission by the Ontario Ministry of Natural Resources (www.glfc.org/**lake**com/loc/mgmt_unit/index.html, accessed Feb 2012) and the New York State Department of Environmental Conservation (http://www.dec.ny.gov/outdoor/27068.html accessed Feb. 2012), a synthesis report for the Lake Ontario Lower Trophic Level Assessment in 2008 with associated datasets (Rudstam et al., 2012), and published literature. Normal lags in synthesizing and publishing scientific findings meant that the participants additionally relied on workshop presentations of un-reported data. Where possible, peer-reviewed manuscripts developed from the same data sources and published subsequent to the workshop are referenced herein.

To more effectively advance our knowledge and support a science-based management approach, the workshops relied on expert opinion supported, where possible, by published and unpublished information. The purpose of this commentary is to summarize key investigative themes and hypotheses that emerged from the workshops, which if investigated, will contribute to an improved understanding of lakewide ecosystem function. The outcomes of the workshop discussions are organized under four themes: spatial linkages and interactions, drivers of primary production, trophic transfer, and human interactions.

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Spatial linkages and interactions

To facilitate discussion of spatial linkages and interactions we adopted an existing spatial framework developed for Lake Ontario (Minns and Wichert, 2005) with a few refinements. In this framework, the *inshore* zone is defined as <5 m depth. The inshore zone is further sub-divided based on degree of exposure to wave-induced disturbance into three zones; *embayments*, *exposed shorelines,* and *sheltered shorelines* (Minns and Wichert, 2005). The shoreside, recently defined as the wadeable depth from the shoreline to a depth less than 1 m (Makarewicz et al., 2012a) was added as an additional subdivision of the inshore zones. The nearshore zone (>5 and <25 m; Minns and Wichert, 2005), is a transitional zone between the inshore and offshore (>25 m).

A key to understanding the changing ecology of Lake Ontario is to focus research and monitoring efforts on specific ecological zones, such as the inshore and nearshore, but to also make efforts to better understand physical, chemical and biological interactions and linkages among spatial zones. In some regions of the lake, localized sources of tributary nutrients drive inshore and nearshore water quality and production (Makarewicz et al., 2012b), whereas in other regions incursions of offshore water may be an equal or dominant driver of local conditions (Howell et al., 2012a, 2012b). Nutrient inputs from Lake Erie via the Niagara River declined through the 1980s, but input via the Niagara River remains an important source of nutrients to Lake Ontario (Chapra and Dolan, 2012). In contrast, the influence of interlake flows on nutrient loading in the upper Great Lakes are negligible (Chapra and Dolan, 2012) Although total phosphorus (TP) loadings have declined in all the Great Lakes in recent decades, Lake Ontario TP loadings were consistently higher than in Lakes Michigan and Huron (Chapra and Dolan, 2012). Lake Erie flows could also be contributing to increases in water clarity and decreased frequency of whiting events in Lake Ontario due to calcium uptake in Lake Erie by dreissenid mussels (Barbiero et al., 2006). However, research subsequent to the workshop suggests that the frequency of whiting events has not changed in Lake Ontario (Watkins et al., 2013).

Both primary and secondary production are being spatially redistributed compared to recent historical conditions. For example, in many inshore and nearshore regions of the lake, nutrients and benthic algal biomass are increasing (Higgins et al., 2012) while at the same time offshore nutrient levels and production indicators are unchanged (Holeck et al., 2015). The depth of the deep-chlorophyll maximum and relative levels of hypolimnetic zooplankton biomass are increasing (Rudstam et al., 2015; Watkins et al., 2015). This may mean that a higher proportion of total production in the lake now occurs in deeper, offshore waters that were not traditionally monitored. The deep-chlorophyll layer (DCL) has been well studied in Lake Michigan (Moll and Stoermer, 1982; Moll et al., 1984; Fahnenstiel and Scavia, 1987). In Lake Michigan, 30–60% of areal primary production has been attributed to the DCL (Moll et al., 1984; Fahnenstiel and Scavia, 1987). Less is known about the observed DCL in Lake Ontario (Barbiero and Tuchman, 2001) especially the magnitude of DCL production, the possible changes in importance associated with increased water clarity through the 2000s, and the efficiency of trophic transfer of DCL production to higher trophic levels.

Planktivorous fishes such as alewife (*Alosa pseudoharengus*) rely primarily on epilimnetic zooplankton prey but have shown an ability to shift to deeper strata, and farther offshore (O'Gorman et al., 2000; Boscarino et al., 2010) and to exploit alternative food sources (Stewart et al., 2009; Stewart et al., 2010b). Coincident with declines in epilimnetic zooplankton biomass and production (Stewart et al., 2010a), alewife abundance and condition increased (O'Gorman et al., 2008; Walsh and Connerton, 2012). Similar declines in epilimnetic zooplankton in Lake Huron were followed by a collapse of the alewife population (Barbiero et al., 2011a) without changes in alewife growth (Dunlop and Riley, 2013). These observations suggest that alternative pathways and sources of production are present in Lake Ontario and are being exploited by alewife.

The hypotheses deduced from these discussions were:

1) Total offshore primary and secondary production has not declined but has shifted spatially into deeper water where it is exploited by alewife to sustain high levels of abundance and growth.
2) Maintenance of relatively high nutrient loading from Lake Erie has buffered Lake Ontario from production declines and associated disrupted food web changes observed in Lakes Huron and Michigan.

Drivers of primary production

Understanding the major drivers of primary production is needed to effectively integrate management of nutrients, water quality, aesthetics, and fisheries. Recent studies suggest that the dominant processes driving primary production are changing and are not well understood. Increased transparency is allowing benthic and pelagic production to occur at greater depths in the nearshore (Malkin et al., 2012; Higgins et al., 2012). Nutrient concentrations in the inshore are higher than observed in the nearshore and offshore (Makarewicz et al., 2012a). These changes have been attributed to dreissenid mussels as abundances are high in the inshore and their filtering and excretion activities have been hypothesized to stimulate algal growth through increased light penetration, increased nutrient availability, and altered habitat use (Hecky et al., 2004; Auer et al., 2010; Higgins et al., 2008; Higgins et al., 2012). However, recent observations in Lake Ontario suggest that mussel effects on nutrient dynamics are not adequate to explain regional variation in water quality and *Cladophora* biomass (Howell et al., 2012b). Complicating the issue is a possible change in the form of phosphorus entering the lake from the watershed. Lake Erie studies have demonstrated record high levels of soluble reactive phosphorus (SRP) in agricultural loadings to Lake Erie (Baker, 2010). Similar land-use factors could be operating directly in the Lake Ontario basin or Niagara River flows from Lake Erie could be contributing to elevated levels of SRP in Lake Ontario. Discerning the relative importance of the different mechanisms driving primary production is not only important for our understanding of the Lake Ontario ecosystem, but will also influence management actions. For example, while it is not possible to suppress dreissenid mussel populations, a better understanding of sources and chemical composition of nutrients could focus attention on other management actions that may decrease nutrient loading from point and non-point sources or affect change through altered land-use practices.

The hypotheses deduced from these discussions were:

3) Dreissenid mussel activity in the inshore and nearshore has increased light penetration due to one or several of the following mechanisms:
   i) increased grazing of phytoplankton by dreissenid mussels,
   ii) decreased re-suspension associated with sediment trapped in mussel beds, and
   iii) decreased occurrence of whiting events associated with calcium uptake by dreissenids to build shell material while recycling of calcium from dead mussel shells is reduced through burial of the shells in the sediment.
4) Increased nutrients in the inshore and nearshore promoting *Cladophora* growth is due to one or both of the following mechanisms:
   i) increased nutrient loading from the Niagara River and/or local sources.
   ii) redistribution of nutrients to the lake bottom due to dreissenid water column grazing and consequent benthic excretion and deposition of pseudofeces
5) Dreissenid mussel influence on offshore pelagic nutrients has increased because offshore production now also occurs below the thermocline in the DCL, deep chlorophyll layer where it is more accessible to dreissenid mussels.