Journal of Great Lakes Research xxx (2017) xxx–xxx

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Long-term trends in benthic invertebrate populations (1929–2013) in Lake Winnipeg

B.J. Hann [a,*], M.J. Wishart [a], S.B. Watson [b]

[a] Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada
[b] Watershed Hydrology and Ecology Research Division, Environment and Climate Change Canada, Canada Centre for Inland Waters, 867 Lakeshore Road. Burlington, ON L7S 1A1, Canada

ARTICLE INFO

Article history:
Received 16 August 2016
Accepted 9 June 2017
Available online xxxx

Keywords:
Zoobenthos
Invertebrates
Eutrophication
Lake Winnipeg
Long-term change
Regime change

ABSTRACT

Spatial, seasonal, and inter-annual variation in zoobenthos was examined in Lake Winnipeg which has experienced accelerated nutrient loading and multiple environmental stressors over the last several decades leading to increased overall productivity. Qualitative zoobenthos data (1928–29) and quantitative data (1969–2013), revealed two prevailing patterns: (1) a substantial increase in density, mainly Oligochaeta (Tubificinae), Mollusca (Sphaeriidae), and Diptera (Chironomidae) in the North basin, but a less consistent pattern of increase in density overall and of Ephemeroptera (Ephemeridae) and Trichoptera (Leptoceridae) in the South basin, and (2) disappearance of Amphipoda (*Diporeia*) from the South basin and a decline in *Diporeia* as a dominant taxon in the North basin, although it remained prevalent in the Narrows where higher total organic carbon (TOC) concentrations have persisted. Permutational analysis of variance (PERMANOVA) revealed that over time, inter-basin variation overwhelmed the seasonal component of variation in zoobenthos abundance. The benthic environment has changed (e.g. food resources, sediment particle sizes and nutrients) over the decades, contributing to the substantial changes in zoobenthos abundance and community composition that may constitute a regime change in the lake.

Introduction

Lake Winnipeg has experienced multiple environmental stressors throughout its history. Principal drivers of enhanced eutrophication of the lake are nutrient loading from its extensive watershed, particularly in recent decades, and increased hydrological forcing (Schindler et al., 2012; McCullough et al., 2012). Anthropogenic changes in the watershed have been extensive over the last decades (summarized in Schindler et al., 2012).

Investigation of the consequences of accelerated eutrophication on Lake Winnipeg has focused on the pelagic food web, particularly the primary producers, including algal pigments and microfossils in the sediment record (Bunting et al., 2012, 2016) and extant phytoplankton (Kling et al., 2011; McCullough et al., 2012). Zooplankton abundance also increased in the 1990s throughout the lake; however, the response was more substantial in the North basin than in the South basin (Hann and Salki, 2017). Pelagic planktivorous fish densities since 2000 have been greater in the South basin than in the North basin (Lumb et al., 2012).

Bunting et al. (2012, 2016) documented changes in the paleolimnological record, and established that the lake has undergone a change in state in the South basin resulting in a shift from mesotrophic to eutrophic conditions (Bunting et al., 2016). However, analyses of North basin sediments has shown a gradual, though continuous, increase in eutrophication but no parallel ecosystem shift yet in the North basin (Bunting et al., 2012) and little is known of the response of zoobenthos to these changes. In theory, responses of benthic communities to state change should be profound, as they contribute substantially to energy flow via benthic-pelagic coupling of food webs, particularly in large lakes (Lake et al., 2000; Palmer et al., 2000; Vadeboncoeur et al., 2002; Vander Zanden and Vadeboncoeur, 2002). These communities act as "ecosystem engineers" and make large contributions to lake ecosystem services such as sediment oxygenation via bioturbation, internal nutrient loading, and other biogeochemical processes (Covich et al., 1999; Hunting et al., 2012; Hölker et al., 2015). In addition, some taxa, such as chironomid pupae, are fed upon by pelagic fish as they ascend from the sediments to the water surface, thereby coupling benthic-pelagic food webs (Wagner et al., 2012; Einarsson et al., 2016). They emerge as adults resulting in a transfer of organic carbon from aquatic to terrestrial food webs (Scharnweber et al., 2014). Similarly, the mass emergence of mayflies (*Hexagenia* spp.) provides a vector for aquatic-terrestrial persistent organic contaminant transfer (Daley et al., 2011).

Examination of the long-term changes of the zoobenthos of a large, complex ecosystem is essential to describe current conditions as well as to provide a historical perspective against which future change (e.g. invasion of aquatic species) can be assessed and managed (Jackson and Füreder, 2006; Lovett et al., 2007; Lindenmayer and Likens, 2009, 2010; Dodds et al., 2012). Extensive datasets, such as

* Corresponding author.
E-mail address: Brenda.Hann@umanitoba.ca (B.J. Hann).

http://dx.doi.org/10.1016/j.jglr.2017.06.005
0380-1330/© 2017 Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

that for Lake Winnipeg (1928–29, 1969, 2002–2013), are rare and even though discontinuous, permit evaluation of the magnitude of natural variation (i.e., seasonal, inter-annual, and spatial) in the sediment-associated biotic community during periods of natural and anthropogenic environmental change (Strayer et al., 1986; Jackson and Füreder, 2006).

Zoobenthos in Lake Winnipeg was first studied by Bajkov (1930), and Neave (1932, 1933, 1934) as part of a survey of large Manitoba lakes. Bajkov assessed the contribution of zoobenthos to the productivity of lake whitefish in the lake and suggested that the North basin of the lake was more productive than the South basin on the basis of higher transparency, as well as phytoplankton and zooplankton populations and zoobenthos samples. However, Neave (1934) commented that "a noticeable feature of the lake is the turbidity of the water". The province of Manitoba (Fisheries Branch) executed limited sampling programs through the 1960s and 1970s with zoobenthos summarized in manuscript reports (Stone and Cober, 1965; Rybicki, 1966; Crowe 1969, 1972a,b,c, 1973a,b; Slack, 1973; Kristofferson et al., 1975). An extensive lake-wide Lake Winnipeg baseline survey in 1969 was executed by Department of Fisheries and Oceans Canada (Freshwater Institute, Winnipeg) with zoobenthos summarized in several manuscript reports (Flannagan, 1979; Flannagan and Cobb, 1981, 1984, 1991, 1994; Flannagan et al., 1994; Chang et al., 1992, 1993, 1994). Flannagan et al. (1994) collated all existing knowledge of Lake Winnipeg zoobenthos and attempted to evaluate future potential threats, e.g. invasive species such as zebra mussels, and climate change, threats that have been realized. Preliminary synthesis of zoobenthos data based on provincial sampling programs (1999–2007) was presented in the State of Lake Winnipeg Report (Environment Canada and Manitoba Water Stewardship, 2011).

The objective of this study was to evaluate changes in the zoobenthic community abundance and composition in Lake Winnipeg (1928–2013) in parallel with accelerating eutrophication in response to changes in the environmental conditions documented via paleolimnological and limnological studies. In particular, we test whether the response of the benthic community to eutrophication coincides with the regime change postulated to have occurred in the South basin since the 1990s, but not yet in the North basin (Bunting et al., 2012, 2016).

Methods

Study site

Lake Winnipeg, a remnant of glacial Lake Agassiz (Brunskill, 1973), is the 10th largest lake (by surface area) in the world and the seventh largest in North America (McCullough et al., 2012). The lake has a surface area of 23,750 km^2, a mean depth of 12 m, and a maximum depth of 36 m (Brunskill et al., 1980). Its watershed extends east to near Lake Superior, west to the Rocky Mountain foothills, north to the Churchill drainage basin, and south into Montana, North Dakota, and Minnesota (Flannagan et al., 1994). L. Winnipeg is bordered by the Central Plains on the south and west and by Precambrian Shield on the north and east. A Paleozoic – Precambrian boundary runs north to south down the center of L. Winnipeg (Todd et al., 1996, 1998). The western Paleozoic rock, consisting of dolomite, limestone, and minor sandstone, is of Ordovician age, whereas the eastern Precambrian (Superior Province) rock is of Archean age (Todd et al., 1996, 1998).

The lake can be subdivided into three basins (Fig. 1), with the South basin being shallower (mean depth = 9.7 m) than the larger North basin (mean depth = 13.3 m); these two basins are linked by the Narrows (mean depth = 7.2 m), a region subject to strong currents associated with seiches (Flannagan and Cobb, 1991). The South basin has a flat lake bottom, whereas the bottom of the Narrows is more variable with both very shallow and very deep portions subject to strong currents; the North basin bottom is mainly flat except along the eastern and western shores, which are uneven resulting in varying

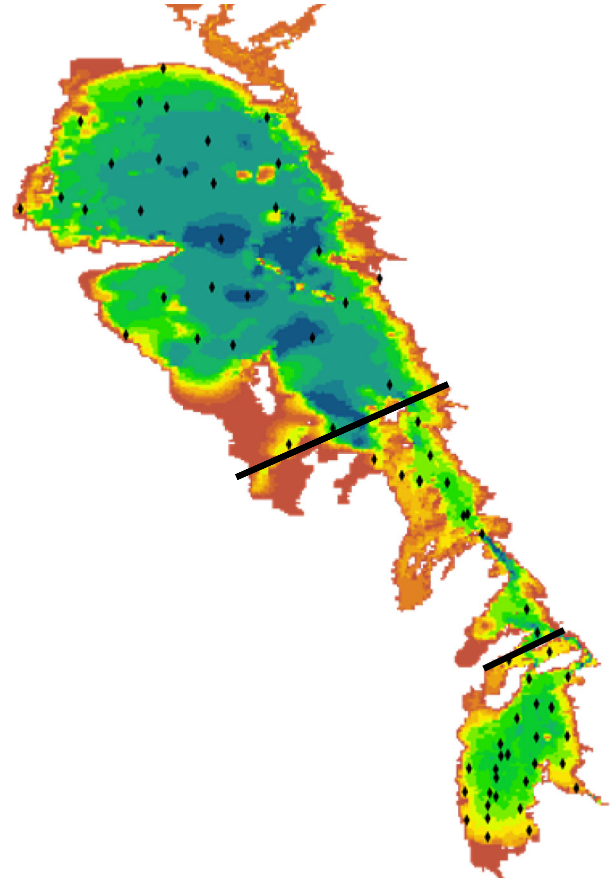

Fig. 1. Stations sampled in Lake Winnipeg in North basin, South basin, and Narrows (according to Flannagan and Cobb (1991)). Not all stations were sampled in all years. Cooler colours represent greater water depths.

depths (Fig. 1). The offshore sediments of L. Winnipeg consist mainly of silty clays and clayey silts with coarse sand, gravel, and boulders commonly found near shore or around islands, along the east side of the North basin, and at river mouths (Brunskill and Graham, 1979).

Water levels in Lake Winnipeg have been regulated since 1975 for hydroelectric power production. The Saskatchewan River was dammed in 1968 with completion of construction of the Grand Rapids hydroelectric generating station, creating Cedar Lake at the mouth of the river at Grand Rapids (Patalas and Salki, 1992); this has resulted in a reduction of sediment input to the North basin of Lake Winnipeg. Lake Winnipeg has control structures used for hydroelectric power generation on almost all major inflowing and out-flowing rivers; winter flow is increased and summer flow is reduced (Baker and Davies, 1991; Manitoba Hydro, 2005) essentially controlling water residence time or flushing time of the North basin. The Nelson River, the only outlet from the lake, flows from the North basin of Lake Winnipeg into Hudson Bay (Brunskill et al., 1980).

During the open-water period, all of L. Winnipeg is subject to frequent wind mixing and seiches, and is typically isothermal with high turbidity due to its long fetch, geography, and shallow depth. These characteristics, along with high nutrient loading from the watershed, result in L. Winnipeg being highly productive (Schindler et al., 2012; Bunting et al., 2016).

Nutrient loading to the lake from diffuse and point sources has increased total nitrogen and total phosphorus concentrations in Lake Winnipeg (McCullough et al., 2012; Schindler et al., 2012). Indications of nutrient enrichment include larger and more frequent algal blooms during the last 10 years, changes in phytoplankton species composition consistent with anthropogenic eutrophication (Kling et al., 2011), and increased abundance of zooplankton (Hann and Salki, 2017). Nutrient

Please cite this article as: Hann, B.J., et al., Long-term trends in benthic invertebrate populations (1929–2013) in Lake Winnipeg, J. Great Lakes Res. (2017), http://dx.doi.org/10.1016/j.jglr.2017.06.005