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Patterns in the crustacean zooplankton community in Lake Winnipeg, Manitoba: Response to long-term environmental change

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ABSTRACT

Changes in the crustacean zooplankton community composition and abundance in Lake Winnipeg (1969–2006) provide a rare opportunity to examine their response to environmental changes in the largest naturally eutrophic lake on the Canadian prairies. Since 1929, zooplankton species composition in Lake Winnipeg has changed little except for the addition of the invasive cladoceran, *Eubosmina coregoni* in 1994. The dominant taxa in the lake in summer include: *Leptodiaptomus ashlandi*, *Acanthocyclops vernalis*, *Diacyclops thomasi*, *Daphnia retrocurva*, *Daphnia mendotae*, *Diaphanosoma birgei*, *Eubosmina coregoni*, and *Bosmina longirostris*. Climate-accelerated nutrient loading to southern Lake Winnipeg over the last two decades has led to increased phytoplankton abundance and higher frequency of cyanobacterial blooms especially in its northern basin. Crustacean zooplankton have likewise increased especially in the North Basin, but less so in the more nutrient rich South Basin, possibly as a consequence of higher densities of pelagic planktivorous fish and light-limited primary production compared with the more transparent North basin (Brunskill et al., 1979, 1980). Calanoid copepods play a larger role in the South basin food web in contrast to cyclopoid copepods and Cladocera in the North basin. The study begins to fill the recognized gap in understanding of Lake Winnipeg's food web structure and provides a baseline for evaluating ongoing changes in the zooplankton community with the arrival of new non-indigenous taxa, e.g. *Bythotrephes longimanus* and *Dreissena polymorpha*. It reinforces previous work demonstrating that zooplankton provide valuable indices toward evaluating the health of an ecosystem.

Introduction

Zooplankton are essential components of the pelagic food web of aquatic ecosystems, comprising a vital intermediate trophic link, subject to both top-down predation as well as bottom-up dietary factors driven by nutrient availability. Changes in predators and food quality or quantity combine to influence the abundance and composition of the zooplankton community that reflect changes occurring in the lake ecosystem. Zooplankton can serve as indicators of climate change in Canadian lakes as regional climate is known to be the main driver of variation in crustacean community structure (Pinel-Alloul et al., 2013). Zooplankton can also be an excellent, cost-efficient indicator for assessment of eutrophication in lake ecosystems (Ejsmont-Karabin, 2012; Ejsmont-Karabin and Karabin, 2013; Jeppesen et al., 2011; Caroni and Irvine, 2010; Mimouni et al., 2015).

Lakes and their biotic communities act as sentinels of climate change (Adrian et al., 2009; Leavitt et al., 2009). Climate change has influenced Lake Winnipeg in several ways, including increased mean annual water temperatures and elevated precipitation in its southern Red River catchment. This has led to higher flow rates in the Red River over the last two decades (particularly in 1997 and 2005), more severe floods and droughts, altered sediment, detritus, nutrient, and contaminant loading (Stewart et al., 2000, McCullough et al., 2012). Variation in water residence time of Lake Winnipeg has occurred, as well as increased duration of the open water period (Environment Canada and Manitoba Water Stewardship, 2011; Cushing, 1998). All of these factors have interacted to affect the water chemistry and biota in the lake. Several non-indigenous species have entered Lake Winnipeg in recent years, including white bass (*Roccus chrysops*) in the 1960s (Stewart and Watkinson, 2004), rainbow smelt (*Osmerus mordax*), and the cladoceran, *Eubosmina coregoni*, in the 1990s (Franzin et al., 1994; Salki, 1996; Suchy et al., 2010).

Lake Winnipeg, like many prairie lakes, has been mildly naturally eutrophic for centuries (Bunting et al., 2011; Kling et al., 2011). Accelerated nutrient loading over the last two decades has led to increased phytoplankton abundance (Kling et al., 2011) and higher frequency, extent, and duration of cyanobacterial blooms (McCullough et al., 2012). In 1969, cyanobacteria constituted only 56% of the total heterogeneous phytoplankton community; however, since that time, cyanobacteria

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have increased to comprise 90% of the total phytoplankton biomass, especially during mid-summer (Kling et al., 2011; Environment Canada and Manitoba Water Stewardship, 2011).

In order to develop effective adaptive lake management strategies, climate indices must be teased apart from confounding and interacting biotic factors, e.g. eutrophication, fishery management, and invasion of non-indigenous species, for which an extensive temporal record is required. Long-term datasets for extant biotic communities and their associated environmental variables in lakes are few (Shurin et al., 2010), but even more rare for large lakes. Substantial changes have been documented in the zooplankton community of some larger, shallow lakes such as Lake Champlain, Lake Balaton, and especially Lake Erie among the Laurentian Great Lakes (Davis, 1969; Fahnenstiel et al., 1998; Madenjian et al., 2002; Stewart et al., 2010; Johannsson et al., 2000; Makarewicz, 1993; Barbiero and Rockwell, 2008; Kane et al., 2004; Miller et al., 2010). These changes have been correlated with effects on commercial fisheries and water quality from prolonged nutrient loading. However, identification of primary and secondary drivers of such changes remains a daunting task.

Whereas the cladoceran component of the zooplankton community is amenable to analysis over the long term using sedimentary remains (Alric et al., 2013), copepods are much less well preserved, and both are subject to differential preservation in the sediment record. Hence, decades-long records of extant crustacean zooplankton communities that encompass both Cladocera and Copepoda provide an invaluable opportunity to investigate the impact of the interactions among species and environmental variables over a time span that encompasses pre- and post-disturbance periods (Battarbee, 2000). Lake Winnipeg is unique in providing that opportunity.

There is a critical need for a detailed study of temporal changes in the zooplankton community of Lake Winnipeg, particularly to serve as a baseline in light of the quite recent invasion of spiny waterfleas (*Bythotrephes longimanus*) and zebra mussels (*Dreissena polymorpha*) and their potential impact on the food web. The main question to be addressed is how has the overall crustacean zooplankton community changed in response to environmental stressors such as nutrient loading (leading to cultural eutrophication) and climate change in Lake Winnipeg over the last 40 years?

Methods

Study site: Lake Winnipeg

Lake Winnipeg is the largest remnant of glacial Lake Agassiz (Patalas, 2006), and is now a eutrophic prairie lake, 10th largest by surface area in the world. The lake is relatively shallow (mean depth = 12 m) with a long fetch (Brunskill et al., 1980); hence it is well mixed and rarely stratifies during the open water period. The North basin is deeper (mean depth = 13.3 m) than the South basin (mean depth = 9.7 m) (Brunskill et al., 1980). Limnological and water quality characteristics that differentiate the two basins are well established: the North basin is cooler, more transparent, and less nutrient enriched than the South basin (Brunskill et al., 1979; Lumb et al., 2012; McCullough et al., 2012). Although records are sparse, there was no evidence of bottom water hypoxia (<2 mg O_2/L) during the period 1964–2002; in 2003 hypoxia was detected in summer in the North basin (Wassenaar, 2012). There is growing evidence from forage fish and cormorant diets obtained via stable isotopes (Hobson et al., 2012; Ofukany et al., 2015) that the North and South basins of Lake Winnipeg are biologically distinct. Hence, the zooplankton communities characterizing the two basins were analyzed separately.

The Lake Winnipeg watershed (one million km^2) is 40 times larger than the lake surface area, the highest ratio among the world's great lakes. The lake receives water and nutrients via >60 rivers, but the Nelson River is the exclusive outflow (Rosenberg et al., 2005). Half of the water inflow to the South Basin comes from the Winnipeg River draining the Precambrian Shield; however, the majority of nutrients come from the Red River and agricultural regions to the south (68% of total phosphorus; Environment Canada and Manitoba Water Stewardship, 2011). Since 1990, an escalation in Red River nutrient loading, caused by climate-related increased precipitation, runoff, and flooding of farmland and urban areas, is mainly responsible for the intensification of eutrophication of Lake Winnipeg (McCullough et al., 2012). The main water inflow into the North Basin is the Saskatchewan River. It carries only a modest nutrient load despite draining a much larger watershed than the more southern rivers, largely as a consequence of the construction of the Cedar Lake-Grand Rapids impoundment that reduced sediment inputs and increased transparency of the North basin in the 1960s (Patalas and Salki, 1992). Water levels in Lake Winnipeg have been regulated since 1976 (see McCullough et al., 2012).

Because Lake Winnipeg zooplankton community diversity is generally highest during the summer period (Patalas and Salki, 1992) and summer samples were collected in each of the 8 survey years, this investigation focussed on changes in the summer zooplankton community. We hypothesised that the summer crustacean zooplankton community would have increased in abundance as a consequence of eutrophication (McCauley and Kalff, 1981; Hanson and Peters, 1984; Patalas and Salki, 1992). Whereas an increase in nutrient loading may be expected to lead to higher primary producer biomass, the consequences of possible changes in N:P ratio and predominance of possibly inedible and/or toxic cyanobacteria may offset the benefits of increased nutrient loading for zooplankton (Haney, 1987; Ferrao-Filho et al., 2007; Bednarska et al., 2011, Kling et al., 2011). Lake Winnipeg also supports the second largest inland commercial fishery in North America with average round weight production, largely walleye, of 12.8 million kg/yr during the 2000s (Manitoba Conservation and Water Stewardship, Fisheries Branch, 2012). Walleye catch rates recently (1998–2008) have been at an unprecedented high level (Ayles et al., 2011), an order of magnitude higher than in 1969 (W. Lysack, Manitoba Water Stewardship, Fisheries Branch), exerting substantial predation pressure on the ecosystem.

Environmental variables

To evaluate potential drivers of patterns of change in zooplankton species composition and abundance over the years, a suite of relevant environmental variables was assessed. Basin-volume weighted total phosphorus (TP) data, chlorophyll *a* concentrations, phytoplankton biomass (whole lake), and plankton (phytoplankton + zooplankton) biovolume (whole lake) from mid-summer surveys were reported in McCullough et al. (2012). Surface water temperatures (SWTemp), Secchi transparency (Secchi), total nitrogen (TN), cyanobacterial biomass (whole lake), and TP loadings from the Red River (into the South basin) were summarized from the State of Lake Winnipeg 1999 to 2007 Report (Environment Canada and Manitoba Water Stewardship, 2011). Planktivorous fish biomass (whole lake) was reported in Lumb et al. (2012) and walleye landings (whole lake) were extracted from Ayles et al. (2011). TP and TN showed collinearity (see 'Results'), so only TP was used in analyses. Similarly, chlorophyll *a*, phytoplankton biomass, and cyanobacteria biomass showed collinearity, and only cyanobacteria biomass was used in the analysis.

Zooplankton datasets

To examine long-term summer patterns in zooplankton species composition and abundance in Lake Winnipeg, historical datasets were compared with samples collected over the last decade:

1) 1928–29: Semi-quantitative sampling of the lake by Bajkov (1934) included both pelagic and littoral samples.
2) 1969: Six lake-wide field surveys conducted at approximately monthly intervals throughout the open water season at 83