Forecasting the Effects of Invasive Dreissenid Mussels on Walleye (*Sander vitreus)* Habitat Occupancy and Yield

by

Marianne E. Geisler

A Thesis submitted to the Faculty of Graduate Studies of

The University of Manitoba

in partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

Department of Biological Sciences

University of Manitoba

Winnipeg

Abstract

Over the past few decades, dreissenid mussels have been introduced in North America and have caused changes in various ecosystem responses including water clarity and fish production. This thesis investigates the response of walleye populations to dreissenid invasion. A predictive model was developed to estimate increases in water clarity following dreissenid mussel invasion and extended to predict an increase in mixing depth and decrease in walleye yield from an Ontarian dataset. Observed declines in walleye yield where dreissenids have invaded were determined to be partly due to increases in water clarity, but concurrent declines in total phosphorus and angler effort likely contributed as well. Finally, walleye production models were developed for Manitoban Boreal Shield and Plains lakes, highlighting the importance of total phosphorus as an indicator of primary productivity in Plains lakes. These walleye production models were related to the water clarity model and small changes in walleye yield post-dreissenid invasion were predicted. These predictive models could prove to be useful tools to managers in uninvaded lake ecosystems.

Acknowledgements

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1: General Introduction

The introduction of non-native species outside of their natural range can pose a risk to ecosystems and the economic services they provide. Human activities have greatly accelerated the rate of introduction and spread of non-native species which can cause profound environmental change (Vitousek et al. 1997). These introductions are often mediated by anthropogenic activities that act as vectors of dispersal and facilitate spread across large geographic areas, often overcoming natural physical barriers. Native habitats, ecosystems and the native species they support can become altered with the introduction of an invasive species via both direct and indirect effects (White et al. 2006). Aquatic invasive species (AIS) can be dispersed via natural mechanisms, such as inter-connecting waterways and animals, or anthropogenic-mediated mechanisms, such as in the bilge of watercraft or attached to fishing nets and other fishing equipment (Mackie and Schloesser 1996).

Canada boasts an extensive coastline and an expanse of freshwater resources, many of which have been invaded by hundreds of non-native species. Asian carp (*Hypophthalmichthys molitrix*), spiny waterflea (*Bythotrephes longimanus*) and rusty crayfish (*Orconectes rusticus*) are among those species that have received particular attention (Department of Fisheries and Oceans Canada 2013). In North America, few have had as great an impact as the dreissenid mussels, the zebra mussel (*Dreissenia polymorpha*) and the quagga mussel (*Dreissenia rostriformis bugensis*). Both of these species of small freshwater mussels are native to Eastern Europe and were likely transported to North America via the ballast water of ocean going ships (Roberts 1990;

Griffiths et al. 1991). The first zebra mussel was detected in Lake St. Clair in 1986 (Benson 2013) and rapidly spread across waterways in the USA and Canada. A lack of natural predators, ecological adaptations for rapid dispersal that include their high reproductive capacity, ability to withstand days to weeks out of water and propensity to colonize almost any hard surface available (Benson et al. 2013) made these mussels ideally suited to exploit freshwater ecosystems (Ludyanskiy et al. 1993). Dreissenid mussels are now established in all of the Great Lakes, all large navigable rivers in the USA and Ontario, the Trent-Severn & Rideau Canal systems in Ontario, and numerous small lakes and rivers throughout the Northeastern part of the USA. On October 17, 2013 it was publicly announced that adult zebra mussels had successfully established in Western Canada, having been found in Lake Winnipeg, Manitoba (Figure 1-1) (Province of Manitoba 2013). As of 2015 zebra and/or quagga mussels were found in 744 reservoirs, impoundments and freshwater lakes in the USA in addition to the five Great Lakes (USGS 2015).

Dreissenid Life History and Economic Impacts

These two species of invasive dreissenids are morphologically similar however the quagga mussel, which also originates from Eastern Europe, is physiologically distinct from the zebra mussel. For example, the zebra mussel has evolved a keeled shape which the quagga mussel lacks, which allows the zebra mussel to anchor to the substrate via byssal threads very firmly (Mills et al. 1996). Alternatively, the quagga mussel can tolerate lower water temperatures and colonize a broader range of substrates than the

zebra mussel (Mills et al. 1996) therefore allowing it to expand into the deeper and siltier regions of lakes (Strayer 2009).

Both species are "*r* strategists" (Vanderploeg 2002; Higgins and Vander Zanden 2010) with a short maturation time (1-2 years) and high fecundity (>1 million eggs produced per female spawning event). Densities reached by these organisms can exceed 100 000 individuals/m^3 (Ludyanskiy et al. 1993), with largest reported populations near 700 000-800 000 individuals/m^3 (Kovalak et al. 1993). At such high population densities, the fouling of physical infrastructure including hydro power structures, drinking water intakes, fish hatcheries, irrigation and boating facilities can be problematic and costly. The economic impacts resulting from invasive species, specifically the zebra and quagga mussels, are extremely high and far-reaching. Recent cost estimates indicate that approximately $0.5 million is spent annually for the control of zebra mussels at each individual water system in the Great Lakes region (Chakraborti et al. 2014). As of 2004, costs associated with invasive dreissenids were estimated at $267 million to raw-water dependent infrastructure facilities, including power plants and drinking water treatment plants throughout the mussels' North American range (Connelley et al. 2007). Chakraborti et al. (2014) reported that $23.6 million was spent on upgrades at 13 hydropower facilities in the Colorado River Basin, in addition to $1.3 million spent annually on chemical treatments of these facilities.

Ecological Effects of Dreissenids

Water Transparency and Suspended Solids

Both *D. polymorpha* and *D. rostriformis bugensis* are efficient filter feeders and are credited for the increased transparency in lakes where they have invaded (e.g. Effler and Siegfried 1998; Binding et al. 2007). Individual zebra mussels are capable of filtering up to 1L/day (Benson et al. 2013) which is ~10 times the clearance rate of native unionid mussels (Strayer et al. 1999; Vanderploeg et al. 2002). Unionid filtration rates typically range between 0.01-0.3 m^3/m^2/day while dreissenids range between 0.1-5.0 m^3/m^2/day (Strayer et al. 1999). Factoring in the population densities these species reach, filtration rate of this magnitude can greatly decrease the amount of suspended solids in the water and increase water clarity.

A published meta-analysis found that dreissenid invasions were associated with significant decreases in suspended particulate matter (suspended solids and turbidity) and significant increases in water clarity (Secchi depth) in lakes and rivers (Higgins and Vander Zanden 2010). Across a diverse set of lake and river systems, mean Secchi depth increased by ~38.5% and turbidity decreased by ~40.7% (Higgins and Vander Zanden 2010). Dreissenids have a high filter area per unit mass (Vanderploeg et al. 2002), and in optimal environments can ingest and assimilate up to 40% of their body carbon per day (Vanderploeg et al. 2001).

Algae and Periphyton

Hecky et al. (2004) described the hypothesis referred to as the "nearshore phosphorus shunt" proposing the importance of dreissenids in the the translocation and retention of phosphorus in the nearshore environment which induces growth of benthic algae such as *Cladophora glomerata*. Great increases in Cladophora have been seen post-

dreissenid invasion in the Laurentian Great Lakes (Higgins et al. 2008, Auer et al. 2010).

While total phytoplankton biomass is generally reduced, there have also been instances of

blue-green algae proliferation seen following dreissenid-induced ecosystem changes such

as dreissenid promoted blooms of *Microcystis aeruginosa*, a toxic alga, as reported in

Lake Huron and Lake Erie (Vanderploeg et al. 2001).

Phytoplankton and Invertebrates

Significant declines in both phytoplankton and zooplankton biomass were

reported in both pelagic and littoral lake zones, with phytoplankton decreasing by

~58.5% and zooplankton by ~51.3% (Higgins and Vander Zanden 2010). These

dreissenid-induced declines in phytoplankton biomass can correspondingly increase

water clarity by the same magnitude or greater (Strayer et al. 1999), although this

relationship is non-linear (Higgins and Vander Zanden 2010).

The benthic communities of lakes can be drastically altered by dreissenid

invasion. Higgins and Vander Zanden (2010) showed that in the littoral zone of lakes,

there was a 1976% increase in the biomass of all benthic taxa (including dreissenids) and

the mean biomass of dreissenid mussels (220 g/m^2) was an order of magnitude higher

than the mean biomass of all other taxa combined (~10 g/m^2). However, abundance of

native unionid mussels have been dramatically reduced (Gillis and Mackie 1994) and in

some cases extirpated (Schloesser and Nalepa 1994) after dreissenid invasion. An

average unionid decline of 93.1% was reported for 11 littoral lake zones (Higgins and

Vander Zanden 2010) post-invasion, due to both fouling of unionids by dreissenids

(Gillis and Mackie 1994; Ricciardi et al. 1996) and reduction in phytoplankton (Strayer and Smith 1996, Strayer and Malcolm 2007).

Fish Populations

Effects of dreissenids on physical, chemical and various biological properties of lakes are often large and of direct relevance to fish communities. The often large effects on the physical, chemical, and biological properties that comprise the habitat and food availability or quality for resident fish species strongly suggest effects on fish could be both ecologically and economically relevant. Dreissenids have been shown to alter the foraging behaviour, growth and energetics of Great Lakes whitefish (Rennie et al. 2009; Rennie et al. 2012), increased growth rates of yellow perch (Mayer et al. 2000) and the change in behaviour and distribution patterns of the resident walleye population in the Bay of Quinte, Ontario (Hoyle et al. 2008). However, a concern relating to the invasion of dreissenid mussels is the effect on fish populations which, relative to effects on other ecosystem components (water clarity, plankton, benthos etc.), has been poorly studied (Higgins and Vanderzanden 2010; Kissman et al. 2010).

Potential effects on walleye

Walleye fisheries may be especially vulnerable to dreissenid invasion because of their known light sensitivity and the high incidence of water clarity increases associated with dreissenid establishment (Lester et al. 2004; Robillard and Fox 2006). Walleye are a pelagic, piscivorous fish species that prey on a variety of species including cisco, yellow perch, emerald shiners, trout-perch and nine-spine sticklebacks (Colby et al. 1979;

Kaufmann et al. 2006). Walleye mature between 2-5 years of age when ~200 mm in length (Henderson and Morgan 2002; Johnston et al. 2010) and spawn in shallow rocky areas, such as cobble or gravel reefs. The timing of spawning is dependent on increasing water temperature (Scott and Crossman 1973). Walleye spawn as early as late January in the southern reaches of its distribution to early June in northern Canada (Craig 1987). Adult walleye typically range from 330-508 mm total length with females commonly larger than males (Scott and Crossman 1973).

Walleye are a critically important fishery in North America and are the most lucrative in terms of commercial values and tourist dollars generated from anglers in most freshwater lakes in the northern latitudes (Frie et al. 1989). In Canada, recreational fishers spend on average $2.5 billion annually on direct recreational fishing expenditures and 23% of all fish harvested in this recreational fishery are walleye, making it the most predominant fish species caught nationally (Fisheries and Oceans Canada 2010). Commercially, an average of 7,109,000 kg of walleye are harvested nationally contributing to 40% of the national average landed value of all commercially harvested freshwater fish species and worth over $29 million (Fisheries and Oceans Canada 2007). The commercial walleye fishery in the United States produces on average 15 730 kg of walleye annually, worth almost $60 000 (National Oceanic and Atmospheric Administration 2014).

Growth and productivity of walleye have been related to lake size, climate, lake productivity and water clarity (Henderson and Morgan 2002). Early growth rates are correlated to total dissolved solids (Lester et al. 2000), an indicator of primary

productivity (Chow-Fraser 1991). Temperature has been shown to be an important factor in walleye growth, reproduction and distribution (Craig 1987). Christie and Reiger found that walleye sustainable yield was significantly correlated with thermal habitat area (1988). A study of Ontarian lakes showed that walleye production was correlated with both thermal and optical habitat conditions, with light and temperature limiting suitable adult walleye habitat (Lester et al. 2004).

Walleye are described as "eurybionts" which can survive a wide range of both physical and chemical environmental conditions with the exception of their extreme sensitivity to light (Scott and Crossman 1973; Colby et al. 1979) which is most likely the main factor dictating their distribution (Ryder, 1977; Colby et al. 1979). Typically, walleye are crepuscular or nocturnal in their feeding habits, due to a specialized visual apparatus called the *tapetum lucidum* that allows them to see well in dim-light conditions (Ali and Anctil 1977). Due to their dependency on low light conditions, walleye tend to be more active during the day in turbid lakes where surface irradiance is rapidly attenuated over depth (Arnold 1960; Ryder 1977). While in non-stratified lakes walleye appear to be distributed evenly throughout the water column, in lakes with thermal stratification are distributed based on turbidity and temperature (Olson et al. 2007). Their ability to perform in dim-light allows walleye to occupy a temporal niche which reduces their competition with other predators which are dependent on higher light intensities (Bozek et al. 2011).

Changes in a variety of ecosystem dynamics associated with dreissenids could have implications on walleye habitat, behaviour, growth and reproduction. As adults,

walleye are likely to be affected by increased water clarity induced decreased foraging efficiency and increased competition (Nate et al. 2011) as higher light levels favor other fish species which prefer these conditions. Alteration of walleye spawning habitat by colonization of dreissenids has also been proposed, but no effects to egg deposition, egg viability or interstitial dissolved oxygen on walleye spawning grounds have been found to date (Leach et al. 1993, Fitzsimons et al. 1995). Dreissenids may also affect early life stages of walleye by reduction of composition and abundance of phytoplankton and zooplankton (Nate et al. 2011) and via a non-direct effect on walleye recruitment (Quist et al. 2003). Proliferation of aquatic vegetation as a result of clearer water could increase foraging habitat for predatory competitors of walleye (Bowlby et al. 1991) and encroach on and reduce walleye habitat (Leisti et al. 2006). The effects are also hypothesized to arise from a change in thermal-optical habitat area (Lester et al. 2004) due to increased light penetration with the presence of dreissenids. Both Chu et al. (2004) and Hoyle et al. (2008) hypothesized that changes in walleye behaviour and distribution patterns in eastern Lake Ontario were caused by increased water clarity. Increased light penetration will affect walleye as their thermal-optical habitat area expands or contracts depending on light penetration and bathymetry (Lester et al. 2004). Reductions in optimal thermal habitat due to increased water clarity could result in limitations to metabolism or negative impacts on reproductive success (Craig 1987). Overall, dreissenid effects on fish communities are poorly studied relative to other ecosystem components and due to the importance of water clarity in their biology and distribution suggest that a better understanding of the linkages between dreissenids and walleye populations are needed.

Chapter Outline

      The objective of this thesis is to demonstrate how statistical modelling can be used as a predictive method of estimating dreissenid-induced changes in limnological characteristics of lakes and fisheries production, with an emphasis on the economically important walleye (*Sander vitreus*). In Chapter 2, I developed a model which, using commonly-available lake morphometric characteristics, can accurately predict the change in water clarity in freshwater lakes following the establishment of invasive dreissenid mussels. Effects on water clarity were then used to estimate changes in lake mixing depth and walleye production using previously published equations. In Chapter 3, I evaluated the predictive capacity of a commonly-used published walleye production model to accurately estimate observed changes in walleye production in North American lakes following dreissenid establishment. In Chapter 4, I examined the same walleye production model as applied to lakes on the Prairies and Boreal Plains lakes and developed a more accurate ecozone-specific model. This model was then combined with the water clarity model created in Chapter 2 to predict how much water clarity is expected to change in Manitoba with dreissenids present and what consequences that will have on the walleye fishery in Manitoba. Chapter 5 provides a summary of the main conclusions, discusses their implications and highlights gaps in knowledge where future studies should focus efforts.

References

Ali, M.A. and Anctil, M. 1977. Retinal structure and function in the walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*). J. Fish. Res. Board Can. **34**: 1467-1474.

Arnold, B.B. 1960. Life history notes on the walleye, *Stizostedion vitreum vitreum* (Mitchill), in a turbid water, Utah Lake, Utah. M.Sc. Thesis, Utah State University, Logan, Utah.

Auer, M.T., L.M. Tomlinson, S.N. Higgins, S.Y. Malkin, E.T. Howell and H.A. Bootsma. 2010. Great Lakes *Cladophora* in the 21st century: same alga – different ecosystem. J. Gr. Lakes Res. **36**(2): 248-255.

Benson, A.J. 2013. Chronological history of zebra and quagga mussels (*Dreissenidae*) in North America, 1988-2010. In: Quagga and Zebra Mussels: Biology, Impacts, and Control (Ed. by T. Nalepa & D. Schloesser), pp. 575-585. 2nd edn. London: Taylor & Francis.

Benson, A. J., D. Raikow, J. Larson, and A. Fusaro. 2013. *Dreissena polymorpha*. USGS Nonindigenous Aquatic Species Database, Gainesville, FL [online]. Available from http://nas.er.usgs.gov/queries/FactSheet.aspx?speciesID=5 [accessed 6 June 2012].

Binding, C.E., J.H. Jerome, R.P. Bukata and W.G. Booty. 2007. Trends in Water Clarity of the Lower Great Lakes from Remotely Sensed Aquatic Color. J. Great Lakes Res. 33: 828-841.

Bowlby, J. N., Mathers, A., Hurley, D. A., Eckert, T. H., 1991. The resurgence of walleye in Lake Ontario. *In* Status of Walleye in the Great Lakes: Case Studies Prepared for the 1989 Workshop. *Edited by* P.J. Colby, C.A. Lewis and R.L. Eshenroder. Great Lakes Fish. Comm. Spec. Publ. 91–1, pp 169–205.

Bozek, M.A., D.A. Baccante and N.P. Lester. 2011. Walleye and sauger life history. *In* Biology, management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries Society, Bethesda, Maryland, pp. 233-302.

Chakraborti, R.K., S. Madon, J. Kaur and D. Gabel. 2013. Management and control of dreissenid mussels in water infrastructure facilities of the Southwestern United States. *In* Quagga and Zebra Mussels: Biology, Impacts, and Control. *Edited by* T. Nalepa & D. Schloesser. 2nd edn. London: Taylor & Francis, pp. 575-585.

Chow-Fraser, P. 1991. Use of the morphoedaphic index to predict nutrient status and algal biomass in some Canadian lakes. Can. J. Fish. Aquat. Sci. **48**: 1909-1918.

Christie, G. C. and H.A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. **45**: 301-314.

Chu, C., C.K. Minns, J.E. Moore and E.S. Millard. 2004. Impact of Oligiotrophication, Temperature, and Water Levels on Walleye Habitat in the Bay of Quinte, Lake Ontario. Trans. Am. Fish. Soc. **133**: 868-879.

Colby, P . J., R. E. McNichol and R. A. Ryder. 1979. Synopsis of biological data on the walleye (Stizostedion v. vitreum) (Mitchell 1818). FAO Fisheries Synopsis No. 119. 139 p.

Connelly, N. A., C. R. O'Neill, B. A. Knuth, and T. L. Brown. 2007. Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities. Environ. Manage., **40**: 105–112.

Craig, J.F. 1987. The biology of perch and related fishes. Croom Helm, Beckenham, England. 333 p.

Department of Fisheries and Oceans Canada. 2013. Aquatic invasive species [online] Available from http://www.dfo-mpo.gc.ca/science/enviro/ais-eae/index-eng.htm [accessed 22 April 2013].

Depew, D.C., A.J. Houben, T. Ozersky, R.E. Hecky and S.J. Guildford. 2011. Submerged aquatic vegetation in Cook's Bay, Lake Simcoe: Assessment of changes in response to increased water transparency. J. Great Lakes Res. **37**(3): 72-82.

Effler, S.W. and C. Siegfried. 1998. Tributary water quality feedback from the spread of zebra mussels: Oswego River, New York. J. Great Lakes Res. **24**(2): 453-463.

Fisheries and Oceans Canada. 2007. Canadian Fisheries Statistics 2002-2004 [online]. Available from http://www.dfo-mpo.gc.ca/stats/commercial/cfs/2004/section7-3-14-eng.htm#ta3.2.1 [accessed 10 November 2014].

Fisheries and Oceans Canada. 2010. 2010 Survey of recreational fishing in Canada [online]. Available from http://www.dfo-mpo.gc.ca/stats/rec/canada-rec-eng.htm [accessed 10 November 2014].

Fitzsimons, J.D., J.H. Leach, S.J. Nepszy and V.W. Cairns. 1995. Impacts of zebra mussel on walleye (*Stizostedion vitreum*) reproduction in western Lake Erie. Can. J. Fish. Aquat. Sci. **52**(3): 578-586.

Frie, R.V., J.K. Anderson and M.J. Larson. 1989. Age Verification of Walleyes from Lake of the Woods, Minnesota. J. Great Lakes Res. **15**(2): 298-305.

Gillis, P. L., and G. L. Mackie. 1994. Impact of the zebra mussel, Dreissena polymorpha, on populations of Unionidae (Bivalvia) in Lake St. Clair. Can. J. Zool.**72**: 1260–1271.

Griffiths, R.W., D.W. Schloesser, J.H. Leach and W.P. Kovalak. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. **48**: 1381-1388.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**: 1285-1293.

Henderson, B.A. and G.E. Morgan. 2002. Maturation of walleye by age, size and surplus energy. J. Fish Biol. **61**(4): 999-1011.

Higgins, S.N., S.Y. Malkin, E.T. Howell, S.J. Guildford, L. Campbell, V. Hiriart-Baer and R.E. Hecky. 2008. An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. J. Phycol. **44**(4): 839-854.

Higgins, S.N. and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. **80:** 179-196.

Hoyle, J.A., J. N. Bowlby and B. J. Morrison. 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosyst. Health **11**(4): 403-411.

Johnston, T.A., Lysack, W. and Leggett, W.C. 2010. Abundance, growth, and life history characteristics of sympatric walleye (*Sander vitreus*) and sauger (*Sander canadensis*) in Lake Winnipeg, Manitoba. . J. Great Lakes Res. **38**: 35-46.

Kovalak, W. P., G. D. Longton, and R. D. Smithee. 1993. Infestation of power plant water systems by the zebra mussel *(Dreissena polymorpha). In* Quagga and Zebra Mussels: Biology, Impacts, and Control. *Edited by* T. Nalepa & D. Schloesser). Lewis Publishers, Boca Raton, Florida. pp. 359-380.

Leach, J.H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie. *In* Quagga and Zebra Mussels: Biology, Impacts, and Control. *Edited by* T. Nalepa & D. Schloesser. 1st edn. Lewis Publishers, Boca Raton, Florida, pp. 381-397.

Leisti, K. E., E.S. Millard and C.K. Minns. 2006. Assessment of submergent macrophytes in the Bay of Quinte, Lake Ontario, August 2004, including historical context. Can. MS Rpt. Fish. Aquat. Sci. 2762. Department of Fisheries and Oceans Canada, p.81.

Lester, N. P., Shuter, B. J., Kushneriuk, R. S. & Marshall, T. R. 2000. Life history variation in Ontario walleye populations: implications for safe rates of fishing. Percid Community Synthesis Population and Yield Characteristics Working Group Report, p. 34. Peterborough: Ontario Ministry Natural Resources.

Lester, N.P., A.J. Dextrase, R.S. Kushneriuk, M.R. Rawson and P.A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. Trans. Am. Fish Soc. **133**: 588-605.

Limburg, K.E., V.A. Luzadis, M. Ramsey, K.L. Schulz and C.M. Mayer. 2010. The good, the bad, and the algae: Perceiving ecosystem services and disservices generated by zebra and quagga mussels. J. Great Lakes Res. **36**: 86-92.

Ludyanskiy, M.L., D. McDonald and D. MacNeil. 1993. Impact of the zebra mussel: a bivalve invader. Bioscience **43**(8): 533-544.

Mackie, G.L. and D.W. Schloesser. 1996. Comparative biology of zebra mussels in Europe and North America: An Overview. Am. Zool. **36**: 244-258.

Mayer, C.M., A.J. VanDeValk, J.L. Forney, L.G. Rudstam and E.L. Mills. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the

establishment of zebra mussels (*Dreissena polymorpha*). Can. J. Fish. Aquat. Sci. **57**: 742-754.

Mills, E.L., G. Rosenberg, A.P. Spidle, M. Ludyanskiy, Y. Pligin and B. May. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. Am. Zool. **36**: 271-286.

Nate, N. A., M. J. Hansen, L. G. Rudstam, R.L. Knight and S.P. Newman. 2011. Population and community dynamics of walleye. *In* Biology, management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries Society, Bethesda, Maryland, pp. 321-374.

National Oceanic and Atmospheric Administration. 2014. Annual commercial landing statistics [online]. Available from http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings. html [accessed November 21, 2014].

Noordhuis, R., H. Reeders, and A. Bij de Vaate. 1992. Filtration rate and pseudofaeces production in zebra mussels and their application in water quality management. *In* The zebra mussel *Dreissena polymorpha*. *Edited by* D. Neumann and H. A. Jenner. New York: Gustav Fischer Verlag. pp. 101-114.

Olson, N.W., Guy, C.S. and Koupal, K.D. 2007. Interactions among three top-level predators in a polymictic great plains reservoir. N. Am. J. Fish. Manage. **27**: 268-278.

Ontario Ministry of the Environment. 2012. Ontario's Lake Partner Program [online]. Available from http://www.ene.gov.on.ca/environment/en/local/lake_partner_ program.html [accessed 19 December 2012].

Province of Manitoba. 2013. Adult zebra mussels found in Lake Winnipeg [online]. Available from http://www.gov.mb.ca/waterstewardship/stopais/pdf/zebra_mussel_ alert.pdf [accessed 17 October 2013].

Quist,M.C.,Guy,C. S., Stephen, J. L., 2003. Recruitment dynamics of walleyes (*Stizostedion vitreum*) in Kansas reservoirs: generalities with natural systems and effects of a centrarchid predator. Can. J. Fish. Aquat. Sci. **60**: 830–839.

Reeders, H. H. and A. Bij de Vaate. 1990. Zebra mussels *(Dreissena polymorpha):* A new perspective for water quality management. Hydrobiology **200**:437-450.

Reeders, H.H., A. Bij de Vaate and R. Noordhuis. 1993. Potential of the zebra mussel (*Dreissena polymorpha*) for water quality management. *In* Quagga and Zebra Mussels: Biology, Impacts, and Control. *Edited by* T. Nalepa & D. Schloesser. Lewis Publishers, Boca Raton, Florida. pp. 439-451.

Rennie, M.D., W.G. Sprules and T.B. Johnson. 2009. Resource switching in fish following a major food web distruption. Oecologia **159**: 789-802.

Rennie, M.D., T.B. Johnson and W.G. Sprules. 2012. Energy acquisition patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. Can. J. Fish. Aquat. Sci. **69**: 41-59.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1996. Impact of the *Dreissena* invasion on native unionid bivalves in the upper St. Lawrence River. Can. J. Fish. Aquat. Sci. **53**: 1434–1444.

Roberts, R. 1990. Zebra mussel invasion threatens US waters. Science **249**: 1370-1372.

Robillard, M.M. and M.G. Fox. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Can. J. Fish. Aquat. Sci. **63**: 798-809.

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34**: 1481-1491.

Scott, W.B and E.J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin. Fisheries Research Board of Canada, 184: 966 p.

Schloesser, D. W., and T. F. Nalepa. 1994. Dramatic decline of unionid bivalves in offshore waters of western Lake Erie after infestation by the zebra mussel, Dreissena polymorpha. Can. J. Fish. Aquat. Sci. **51**: 2234–2242.

Strayer, D. L. and H. M. Malcom. 2007. Effects of zebra mussels (*Dreissena polymorpha*) on native bivalves: the beginning of the end or the end of the beginning? J. N. Am. Benthol. Soc. **26**: 111–122.

Strayer, D. L., and L. C. Smith. 1996. Relationships between zebra mussels (Dreissena polymorpha) and unionid clams during the early stages of the zebra mussel invasion of the Hudson River. Freshw. Biol. **36** :771–779.

Strayer, D.L., N.F. Caraco, J.J. Cole, S. Findlay and M.L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. Bioscience **49**: 19-27.

Strayer, D.L. 2009. Twenty years of zebra mussels: lessons from the mollusk that made headlines. Front. Ecol. Environ. **7**: 135-141.

Stybel, N., C. Fenske and G. Schernewski. 2009. Mussel cultivation to improve water quality in the Szczecin Lagoon. J. Coastal Res. **56**: 1459-1463.

United States Geological Survey. 2015. Zebra mussel distribution [online]. Available from http://fl.biology.usgs.gov/Nonindigenous_Species/Zebra_mussel_distribution/ zebra_mussel_distribution.html [accessed 10 March 2015].

Vanderploeg, H. A., J. R. Liebig, W. W. Carmichael, M. A. Agy, T. H. Johengen, G. L. Fahnenstiel, and T. F. Nalepa. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic *Microcystis* blooms in Saginaw Bay (Lake Huron) and Lake Erie. Can. J. Fish. Aquat. Sci. **58**: 1208–1221.

Vanderploeg, H.A., T.F. Nalepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Liebig, I.A. Grigorovich and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **59**: 1209-1228.

Vitousek, P. M., C. M. Dantonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: a significant component of human-caused global change. New Zeal. J. Ecol. **21**: 1–16.

White, E.M., J.C. Wilson and A.R. Clarke. 2006. Biotic indirect effects: a neglected concept in invasion biology. Divers. Distrib. **12**: 443-455.

Figure 1-1. Zebra mussels found in Lake Winnipeg, October 2013. *Photo courtesy: H.*

Clark, Manitoba Water Stewardship.

Chapter 2: A predictive framework for estimating the effects of dreissenid mussels on lake water clarity and related limnological characteristics

Abstract

Optical transparency, or water clarity, is a fundamental property of lake ecosystems influencing a wide range of physical, chemical and biological variables and processes. The establishment of non-native dreissenid mussels in lake and river ecosystems across North America and Europe has been associated with often dramatic, but highly variable, increases in water clarity. The objective of this study was to develop and evaluate a model predicting dreissenid effects on water clarity within lakes. Improved and broadly applicable methods for predicting dreissenid-associated water clarity changes will assist in evaluating potential changes to freshwater ecosystems threatened by infestation. I compiled water clarity data before and after dreissenid invasion from 53 North American lakes that varied in size and nutrient status. In our dataset, water clarity increased post-invasion in >80% of lakes. An AIC model averaging approach was taken to generate post-invasion water clarity predictions based on pre-invasion water clarity and lake morphometric characteristics. A cross-validation approach confirmed the predictive efficacy of this approach as applied to independent data. Combining our model with existing empirical models, I demonstrate that increased water clarity associated with dreissenid invasion is likely to significantly increase thermocline depths and decrease walleye yield in Ontario lakes.

Introduction

Optical transparency, or water clarity, is one of the most widely reported indicators of ecosystem condition for freshwater ecosystems and is considered a state variable; defining the vertical distribution where short wave radiation is absorbed and long wave radiation is emitted and stored as heat. Variations in optical transparency drive changes in surface temperature, heat budgets, and in small lakes (<500 ha) changes in thermocline depth and thermocline stability (Mazumder et al. 1990; Fee et al. 1996). Water clarity is of direct importance to biota: defining the depth to which potentially damaging UV radiation penetrates and the maximum depth where photosynthesis can occur (Kirk 1994), determining how primary production is partitioned between benthic and pelagic energy pathways (Vadeboncoeur et al. 2008; Higgins et al. 2014), and influencing predation and reproduction for fish populations that use visual cues (Ryder 1977). Changes in the concentration of suspended particles through the process of eutrophication or the grazing action of herbivores also have a large effect on water clarity, mixing depths and have the potential for dramatic shifts in the partitioning of primary and secondary production between benthic and pelagic habitats, especially in small and shallow lakes that are prone to regime shifts (Mazumder et al. 1990; Vadeboncouer et al. 2008; Higgins et al. 2014).

The translocation and establishment of *Dreissena polymorpha* (zebra mussel) and *D. rostriformis bugensis* (quagga mussel) across Eurasia and North America has been associated with often dramatic, but highly variable, changes in suspended particle concentrations and water clarity (Higgins and Vander Zanden 2010). Such changes are

associated with two processes: a 'fast' (minutes to days) process where high dreissenid densities and filtration rates directly reduce particle concentrations and improve water clarity, and a 'slow' (months to years) process where the redistribution of nutrients from the pelagic zone to the littoral zone, and eventual burial within the sediments, reduces plankton growth and biomass (Hecky et al. 2004). Dreissenid effects on some physical, chemical and biological properties are likely to be sustained for decades (Higgins 2013). Effects of dreissenid induced changes in water clarity on aquatic ecosystems include physical processes such as mixing depth (Yu and Culver 2000) and altered patterns of habitat use and energetics of fishes (Rennie et al. 2009; Rennie et al. 2012; Rennie et al. 2013).

The effect of dreissenids on water clarity is a function of their filtration rate (Strayer et al. 1999), ecosystem size, hydrodynamics and other factors such as sediment resuspension (Vanderploeg et al. 2002). However, because dreissenid population densities at the ecosystem scale are not routinely estimated and hydrodynamics of most systems are poorly understood, it has remained challenging to estimate or predict their filtration rates, effects on water clarity, and associated limnological properties using mechanistic models. Such predictions would be useful to understand how the establishment of dreissenids might influence a wide range of physical, chemical, and biological processes in water bodies at high risk of invasion. Specifically, such estimates could be used with existing hydrodynamic models to predict changes in thermocline depth, stability and heat content, and with fisheries models (Lester et al. 2004) where yield estimates are dependent on water clarity.

The primary objective of our study is to define a predictive model for dreissenid effects on water clarity based on commonly reported limnological parameters that are likely to be included in most monitoring programs. While dreissenid densities in most invaded ecosystems are not known, it is probable that ecosystem densities and filtration rates scale with measures of ecosystem size (Higgins and Vander Zanden 2010) and I include such variables within my model selection process. As a secondary objective I extend my predictive dreissenid-water clarity model to simple limnological and fisheries models to demonstrate the potential for dreissenids to influence lake processes and biota.

Methods

Data Compilation

Data were compiled from various sources including the EPA Storet database, Cornell University Knowledge Network for Biocomplexity (KNB) database, Minnesota Pollution Control Agency (MPCA), the Michigan and Wisconsin Departments of Natural Resources, Ontario Ministry of the Environment (OMOE), the Ontario Ministry of Natural Resources and Forestry (OMNRF) and the scientific literature. Grand mean values for some Great Lakes and other freshwater lakes were obtained from published literature on dreissenid effects on water clarity (Higgins and Vander Zanden 2010). All data came from mid-continental North America (Iowa, Michigan, Minnesota, New York, Vermont, Wisconsin, and Ontario) and covered a wide range of lake morphometric characteristics (Table 2-1). Dates of invasion are based on those listed on the USGS website (http://nas.er.usgs.gov/taxgroup/mollusks/zebramussel/) for American lakes and on published invasion dates for Canadian lakes, which were cross-referenced with peer

reviewed literature where available. Though over 600 freshwater lakes were identified as being invaded by dreissenids (Benson 2013), a total of 53 North American lakes were found with sufficient data to permit an analysis of dreissenid effects on water clarity (Appendix A).

Data were constrained to include Secchi depth measured during the ice-free period at one or more sampling stations in a lake. Following the methodology of similar analyses (Higgins and Vander Zanden 2010; Higgins et al. 2011; Cha et al. 2013) data had to conform to the following criteria to be included: (*i*) data were available for both the pre- and post-invasion periods, (*ii*) pre-invasion data were from up to 15 years before invasion and post-invasion data within 25 years since invasion, (*iii*) individual data points were within ±2 standard deviations (SD) from annual mean value (to avoid the influence of outlier values), (*iv*) data were from the summer "ice-free" season (April-November) and (*v*) data were from offshore, pelagic lake stations. Lakes with more than three data points per year were included when calculating annual mean and SD values, and lakes with at least 3 annual mean data points in both the pre- and post-invasion periods were included when calculating grand mean and SD values. Zero values for Secchi depth were interpreted as measurement or reporting errors and removed from data sets prior to analyses.

For lakes that did not have reported thermocline depths or available temperature profile data, thermocline presence and depth was estimated from lake surface area using the equations of Hanna (1990). Equations in Hanna (1990) can over predict mixing depth for very large lakes because they do not account for the Coriolis effect (Fee et al. 1996)

so maximum mixing depth was set to 20 m for lakes with surface area >4000 ha that had no reported thermocline depth. Lakes with greater than 80% of lake area above mixing depth were defined as "mixed", and those with less than 80% were defined as "stratified" (sensu Higgins and Vander Zanden 2010).

Statistical Analysis

The effect of lake size, stratification and dreissenid community (zebra mussels only versus zebra and quagga mussels together) on the extent of observed water clarity changes were evaluated using *t*-tests and ANOVA. Two-sample *t*-tests used a Welch correction on the degrees of freedom to account for differences in variance between groups. Residuals were examined to ensure the satisfaction of assumptions of homogeneous variance and normality.

Standardized z-scores were used to graphically display long-term Secchi depth changes in a subset of lakes with raw annual data (*n*=42, see Appendix A). As in Higgins (2013), mean annual parameter values for each year's growing season were used to calculate the pre- and post-dreissenid invasion period grand means. Z-scores were calculated as:

$$Z = \frac{\mu_A - \mu_{Pre}}{SD_{Pre}} \qquad (1)$$

where μ_A is the annual mean, μ_{Pre} is the pre-invasion grand mean, and SD_{Pre} is the pre-invasion grand standard deviation.

Model development and selection

I evaluated models that expressed a change in water clarity following dreissenid invasion as a function of pre-invasion water clarity, lake size and depth, and thermal stratification. Generalized linear models (GLM) with a gamma error distribution were used to fit the model because the response variable variance increased with the mean. A log-link function was used to transform the data into a linear relationship. Akaike's Information Criterion (AIC) was used to determine which models best described change in water clarity following dreissenid invasion. Models were compared using the second-order Akaike's Information Criterion for smaller sample sizes (AIC_c). In this method, AIC_c is calculated for each model using the equation:

$$AIC_c = 2k - 2ln(L) + \frac{2k\,(k+1)}{n\text{-}k\text{-}1} \tag{2}$$

where *n* is sample size, *L* is the maximum likelihood and *k* is the number of parameters in the model (Burnham and Anderson 2002). Measures used to determine strength of evidence for each model include ΔAIC_c and Akaike weights ($wAIC_c$). ΔAIC_c values < 2 suggest substantial model evidence and the $wAIC_c$ of each model indicates the probability that it is the best model among the set (Burnham and Anderson 2002). The model which produced the smallest AIC value (AIC_{min}) was determined to be the "best" model (Akaike 1973). In cases where no model has overwhelming support, AIC model averaging is used where individual model parameter estimates (of post-invasion water clarity, in this case) are generated and weighted based on their $wAIC_c$, then are summed to generate a single model-averaged estimate across all models. The null model, which

consists of only the intercept and no predictor variables, was included in model

comparisons as an indicator of the relative performance of the remaining models and was

not used in model averaging.

In order to determine the predictive efficacy of our models, leave-one-out cross

validation (LOOCV) was used to assess model fits when applied to independent data and

is commonly used on small datasets with a predictive outcome. The model's predictive

accuracy is estimated using cross validation Xr^2 as:

$$Xr^2 = 1 - \frac{\Sigma\left[y_{observed} - y_{predicted}\right]^2}{SS_T} \tag{3}$$

where $y_{observed}$ is the observed value of post-invasion Secchi depth from the lake

excluded from model generation, $y_{predicted}$ is the value of post-invasion Secchi depth

predicted from the subset of data from which the observed values were excluded, and SS_T

is the total sum of squares estimated as the variance of post-invasion Secchi depth times

n-1, where n is the number of observations used to generate the model (Rennie et al.

2005).

Applications

This water clarity model was applied to a suite of lakes in Ontario using lake

morphometric information and pre-invasion Secchi depths reported by Lester et al.

(2004) in order to estimate effects on water clarity. I then extended this model to examine

how these predicted changes in water clarity affect (i) thermal structure of lakes and (ii)

walleye yield, using models defined in the literature. These particular variables were

chosen because both have published predictive models linking these responses to water clarity and they represent ecologically and limnologically important parameters in freshwater ecosystems that could potentially be affected by dreissenid invasion.

Dreissenid effects on mixing depths in 49 walleye lakes in Ontario (Lester et al. 2004) were assessed using an empirical model by Fee et al. (1996) that relates the mixing depth to water clarity. The relation of water clarity to thermal stratification depth was made by estimating light extinction coefficient (k) from reported Secchi depth (z_{sec}) (Wetzel 2001) using the equation:

$$k = \frac{1.7}{z_{sec}} \tag{4}$$

Equations from (Fee et al. 1996) were used to estimate percent light transmission ($T_\%$) from k:

$$T_\% = 100 \times e^{-k} \tag{5}$$

and mixing depth (z_{mix}) from $T_\%$:

$$z_{mix} = 2.92 + 0.0607\ A_o^{0.25} \tag{6}$$

where A_o is lake surface area. Deviations of mixing depth (E_{dev}) from the Fee et al. (1996) regression were calculated as:

$$E_{dev} = -3 + 0.80 \times e^{0.022\ T_\%} \tag{7}$$

and added to estimates of z_{mix} to determine depth of thermal stratification (z_T). This was compared for both the pre-invasion and post-invasion scenarios in order to

predict the change in estimated thermocline depth as a result of increased water clarity due to dreissenid establishment.

Estimates of walleye yield were based on Lester et al. (2004) equations (Appendix B) and reflect a change in optimal walleye habitat with changes in Secchi depth. Estimates of yield were generated and compared under scenarios with and without dreissenids present to evaluate the potential impacts of dreissenid-induced increased water clarity on walleye yield in this suite of Ontario lakes.

Results

The 53 North-American lakes included in model development spanned a wide range of size, depth and trophic status (Appendix A). Secchi depth was highly variable across systems, ranging from 0.7 to 12.7 m pre-invasion (mean $\pm$ SD, 3.1 $\pm$ 1.9 m) and 0.7 to 14.8 m (3.7 $\pm$ 2.3 m) post-invasion. Dreissenid-induced changes in Secchi depth were also highly variable across lakes, ranging from -0.69 m in North Lake, WI to +3.49 m in Lake Ontario, ON. Increases in Secchi depth following dreissenid invasion were found in 81% of lakes analyzed (Figure 2-1), with a mean increase of 0.56 m (95% CI = 0.345, 0.781).

Consistent patterns of change were seen when lakes were separated into morphometric categories based on propensity for seasonal stratification. In mixed lakes, Secchi depth increased on average 0.31 m ($t = 2.70$, df = 16, $p < 0.05$) whereas in stratified lakes, Secchi depth increased an average of 0.68 m ($t = 4.51$, df = 35, $p < 0.001$). However, there was no significant relationship between magnitude of change in

water clarity and lake size when comparing small (area <100 ha), medium size (area between 101-1000 ha) and large lakes (area >1000 ha) ($F_{1,51} = 2.05$, $p > 0.05$). A significant relationship between change in clarity and mean depth was seen when lakes were separated into shallow ($z_{mean} < 5$ m), mid-depth (z_{mean} between 5-20 m) and deep ($z_{mean} > 20$ m) ($F_{1,51} = 10.29$, $p < 0.01$).

For lakes with long term datasets available, our results indicate increased water clarity after dreissenid invasion persists for at least 20 years post-invasion (Figure 2-2). Variation in z-scores was high but the trend of an overall increase among systems is seen in the post-invasion period, with some annual post-invasion values being > 6 SD's above the pre-invasion mean.

Of the 53 lakes included in this analysis, 8 had both zebra and quagga mussels present. Lakes with both species present showed a higher degree of increase in water clarity than those with only zebra mussels ($F_{1,51} = 26.54$, $p < 0.001$). Mean absolute change of Secchi depth for lakes with only zebra mussels was 0.37 ± 0.55 m (mean $\pm$ SD, $n=45$) compared to an increase of 1.68 ± 1.16m ($n=8$) when both species of dreissenids were present (Figure 2-3).

Ranking the four models using AIC_c showed that all were found to be somewhat supported by the data (Table 2-2). The model averaged parameter estimate generated by these four models explained 91% of the variance in post-invasion Secchi depth and the predicted values were very similar to the observed values in those analyzed invaded systems (Figure 2-4). LOOCV model validation produced an Xr^2 value of 0.98, suggesting a good fit of our model against independent data. The positive coefficients of

the models generated (Table 2-2) suggest that water clarity increases on a continuous positive basis with the parameters included therein.

Applying our model to a list of Ontario lake data (Table 2 in Lester et al. 2004), I predicted increased water clarity with dreissenid invasion in all lakes with an average increase of 0.465 (95% CI = 0.431, 0.500), similar to our observed effects in the original dataset. Applying these predicted changes in water clarity to the mixing depth model, I predicted consistent increases (deepening) of thermocline depth among all stratified lakes in the Lester et al. (2004) dataset. Mean difference in mixing depth from the pre-invasion to post-invasion time period was 0.307 (95% CI = 0.276, 0.338) which is an 11% increase on average (relative to pre-invasion conditions) with a maximum estimated 23% increase in mixing depth due to increased water clarity alone. Pre-invasion Secchi depth had a significant effect on total predicted change in mixing depth with increased water clarity, though this effect was non-linear (Figure 2-5, $t = -7.86$, $df = 44$, $p < 0.001$).

On average, walleye yield was estimated to decline by 5% with increased dreissenid-induced water clarity ($t = -2.76$, $df = 48$, $p < 0.01$). However, there was a large range of predicted walleye response to dreissenids from an estimated decrease in yield of -33% to an increase of 45%. There was a statistically significant difference in pre-invasion Secchi depth between lakes with a predicted increase in walleye yield and those with a predicted decrease ($t = 2.41$, $df = 83.9$, $p < 0.01$). Lakes with a predicted decrease in yield over the hypothetical invasion were more likely to have greater pre-invasion Secchi depth (3.24 ± 1.870 m, $n = 36$) than those lakes which saw an increase in walleye yield (2.169 ± 1.153 m, $n = 13$).

Discussion

Predictive Capacity

I was successful in generating a model capable of accurately predicting lake-wide effects of dreissenids on water clarity using limited but readily available ecosystem parameters. I found that model averaging across four GLM models which incorporated pre-invasion Secchi depth, mean lake depth, lake surface area and presence of thermal stratification generated accurate predictions of post-invasion water clarity in North American lakes after invasion by dreissenid mussels. The ability to use these basic limnological characteristics to estimate potential changes in water clarity across a broad range of ecosystems should prove useful for investigators and resource managers alike, who wish to better understand the potential effects of these invasive species on aquatic ecosystems.

In accordance with results from previously published papers and meta-analyses (see Higgins and Vander Zanden, 2010), I found a nearly-consistent increase in water clarity over time in lakes with one or both species of dreissenid mussels present. The lakes in our dataset range in size, depth and trophic status, and are representative of north-temperate lakes in the area threatened by dreissenid invasion. Increases seen in water clarity were positively related to ecosystem size, depth, stratification and pre-invasion water clarity, as indicated by the high predictability and positive coefficients of the models I generated. Our results further demonstrated that dreissenid effects on water clarity were lasting, and showed no signs of diminishing within 10-15 years of invasion.

Ecosystem Responses

While differences in patterns of water clarity when comparing mixed and stratified lakes are said to be due to the greater availability of the whole water column for mussel filtration in mixed systems (Higgins and Vander Zanden 2010), the results found here show a greater increase in water clarity in stratified lakes following dreissenid establishment. This discrepancy is likely due to the fact that all lakes in our dataset that were invaded with both zebra and quagga mussels, with the exception of Oneida Lake, NY, were also stratified (Appendix A). While the zebra mussel colonizes in great numbers in the littoral area, quagga mussels tend to be found in deeper, colder water of lakes (Vanderploeg et al. 2002). Therefore the total dreissenid filtering capacity in lakes with both species present may be higher than with zebra mussels alone (Figure 2-3) and could have led to a higher water clarity increase in those systems. Mixed lakes are frequently subject to high rates of resuspension of bottom sediments by wind. This wind driven resuspension is common in shallow, turbulent systems where wave action comes in contact with the bottom and resuspends bottom sediments, including dreissenid psuedofeces (Vanderploeg et al. 2002). High loads of inorganic suspended material have been shown to impede dreissenid clearance rates and water processing potential (Madon et al. 1998).

Though zebra mussel densities and subsequent impacts on water clarity differ spatially in a lake, our model is meant to capture their broader lake-wide effect. Data points included in this exercise were limited to offshore stations, and though littoral areas will inevitably experience greater impacts in the short term due to the presence of

dreissenids mostly along the near shore, hydrodynamic mixing will incorporate this effect into a pelagic component as well. Other analyses have shown that dreissenid effects on water clarity are greatest near shore, increasing ~50-78% in the littoral zone, and less-pronounced mid-lake increases of 31-49% in the pelagic zone (Yu and Culver 2000; Higgins and Vander Zanden 2010). As such, our model is likely providing a conservative estimate of dreissenid effects on overall lake water clarity.

Dreissenid-induced water clarity responses can differ among lakes depending on the management strategies in place. If dreissenid invasion happens concurrently with phosphorus reduction strategies, which arguably was the case in Lake Erie (Phosphorus Management Strategies Task Force, 1980), there may well be a greater increase in water clarity than due solely to the filtering ability of the mussels. However, the majority of lakes used in our model development were small inland lakes which have no known phosphorus reduction strategies in place which could be contributing to observed increases in clarity (Appendix A). It is possible that management strategies associated with P reduction may have some influence on reported increases in water clarity in some of the systems included in our study, but they represent the minority of included in model generation here.

Optical transparency of natural waters are a function of both particulate and soluble (i.e. color) components. As reported elsewhere, dreissenid effects are predominantly associated with the reduction of particle concentrations (MacIsaac 1996). There is evidence that levels of suspended solids (SS) and turbidity will decrease post-invasion, but will follow a non-linear relationship between SS and Secchi depth, as

described in Higgins and Vander Zanden (2010). I tried to evaluate these parameters in the models but too few lakes had these data to permit analysis in the current study. However, I would encourage other investigators to collect such information for future analyses. Presumably, lakes where water clarity is strongly controlled by variations in dissolved organic carbon (DOC) would be less influenced by dreissenid mussel effects, due to the fact that DOC is indicative of organic loadings and would not necessarily be filtered out by mussels. While the mediating influence of DOC on water clarity changes were not directly accounted for, DOC has been demonstrated to vary with lake size and residence time (Rasmussen et al. 1989; Xenopoulos et al. 2003), though this effect was not seen consistently in a larger scale analysis (Sobek 2007). However, as our results and model are based on empirical responses across >50 natural systems across a broad geographical region, they likely also represent natural variation in DOC concentration among lakes.

Dreissenid density obviously plays a role in the magnitude of effect size, as discussed in a published meta-analysis (Higgins and Vander Zanden 2010), but the models developed here work well without that information, which is unknown in most systems. While dreissenid density may be important and is likely to contribute to the relatively small amount of unexplained variation in our predictions, our main objective for the current study was to develop a predictive model based on easily accessible ecological parameters. Accurate estimates of dreissenid density are far less common than the typical limnological characteristics included here. Further constructing models that rely on highly limited data would dramatically limit the applicability of our model for prediction purposes. Our model meets these objectives reasonably well, suggesting that

dreissenid density may be less important than, or may correlate with, the other limnological parameters I included in my predictive models.

Implications to ecosystems and management

As optical transparency is a fundamental variable of freshwater ecosystems and is a commonly used indicator of water quality, dreissenid effects on water clarity and the ability to predict such effects have a range of implications for invaded ecosystems and ecosystem management. Extending our predictive model of dreissenid effects on water clarity to other existing empirical models, I demonstrate the capacity of changes in water clarity of this magnitude and direction to have a significant influence on other ecosystem parameters, including mixing depth and walleye yield. Thermocline depth is an important limnological parameter which influences heat budget of lakes, vertical distribution of biota (Fee et al. 1996) and volume of cool-water fish habitat (Christie and Regier 1988, Lester et al. 2004).

Walleye are an important commercial and recreational fishing species in Canada and the United States. This species has been shown to exhibit movements associated with light transmission and thus are highly susceptible to changes in water clarity (Ryder 1977) which may affect foraging behaviour and reproductive capability. Our study suggests that water clarity effects on walleye are context specific, as increases in walleye yield may occur in systems which originated with low water clarity as they move toward an "optimum Secchi depth" which (depending on the bathymetry of the system) is near 2 m (Lester et al. 2004). However, in systems where optimal habitat is already constrained by high water clarity, further increases are expected to lead to reductions in yield. Any

potential decline in the harvest of this species could have great economic effects to this lucrative fishery. Because of the long lifespan of this species, empirical monitoring approaches could take years before impacts are realized. Through the application of these predictive models, fisheries resource managers can better understand which populations are most vulnerable to dreissenid-induced ecosystem changes on valuable walleye stocks, in order to inform adaptive management frameworks in anticipation of ecosystem changes and determine where management levers could be applied.

In summary, this study provides a broadly-applicable predictive framework for estimating the effects of dreissenid invasions on lake ecosystems based on limited limnological information. As dreissenids expand their range across North American ecosystems, the results of this study may provide a starting point for evaluating their effects on vulnerable ecosystems and provides examples for managers of extending those predicted effects to other ecosystem aspects beyond water clarity alone. However, while our model may provide an estimate of impacts in areas where dreissenid invasion is anticipated, extensions of the model presented here are meant only to provide a first estimate of these effects. Interactions among ecological parameters (and potential effects of dreissenids on ecosystems besides water clarity alone) likely require a closer evaluation of how extensions of our model are accurately reflected in invaded systems, and is the focus of ongoing research.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle, p. 267-281. *In* B.N. Petrov & F. Ckaski [eds.], Proceedings of the Second International Symposium on Information Theory, Akademiai Kiado.

Benson, A.J. 2013. Chronological history of zebra and quagga mussels (*Dreissenidae*) in North America, 1988-2010. *In* T. Nalepa & D. Schloesser [eds.], Quagga and Zebra Mussels: Biology, Impacts, and Control, 2nd ed. Taylor & Francis.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer.

Cha, Y., C.A. Stow and E.S. Bernhardt. 2013. Impacts of dreissenid mussel invasions on chlorophyll and total phosphorus in 25 lakes in the USA. Freshwater Biol. **58:** 192-206.

Christie, G. C. and H.A. Regier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. **45:** 301-314.

Fee, E.J., R.E. Hecky, S.E.M. Kasian and D.R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41:** 912-920.

Hanna, M. 1990. Evaluation of models predicting mixing depth. Can. J. Fish. Aquat. Sci. **47:** 940–947.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61:** 1285-1293.

Higgins, S.N. and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. **80:** 179-196.

Higgins, S.N., M.J. Vander Zanden, L.N. Joppa and Y. Vadeboncoeur. 2011. The effect of dreissenid invasions on chlorophyll and the chlorophyll:total phosphorous ratio in north-temperate lakes. Can. J. Fish. Aquat. Sci. **68:** 319-329.

Higgins, S.N. 2013. Meta-analysis of dreissenids effects on freshwater ecosystems. *In* T. Nalepa & D. Schloesser [eds.], Quagga and Zebra Mussels: Biology, Impacts, and Control, 2nd ed. Taylor & Francis.

Higgins, S.N., B. Althouse, S.P. Devlin, Y. Vadeboncoeur and M.J. Vander Zanden. 2014. Potential for large-bodied zooplankton and dreissenids to alter the productivity and autotrophic structure of lakes. Ecology **95:** 2257-2267.

Kirk, J.T.O. 1994. Light and photosynthesis in aquatic ecosystems. 2nd ed. Cambridge University Press.

Lester, N.P., A.J. Dextrase, R.S. Kushneriuk, M.R. Rawson and P.A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. T. Am. Fish. Soc., **133:** 588-605.

MacIsaac, H.J. 1996. Potential Abiotic and Biotic Impacts of Zebra Mussels on the Inland Waters of North America. American Zoologist **36:** 287-299.

Madon, S. P., D. W. Schneider, J. A. Stoeckel and R. E. Sparks. 1998. Effects of inorganic sediment and food concentrations on energetic processes of the zebra mussel, *Dreissena polymorpha*: implications for growth in turbid rivers. Can. J. Fish. Aquat. Sci. **55:** 401-413.

Mazumder A, W.D. Taylor, D.J. McQueen and D.R.S. Lean. 1990. Effects of fish and plankton on lake temperature and mixing depth. Science **247:** 312-315

Phosphorus Management Strategies Task Force. 1980. Phosphorus management for the Great Lakes. Final Report to the Great Lakes Water Quality Board and the Great Lakes Science Advisory Board. International Joint Commission, Windsor.

Rasmussen, J.B., L. Godbout and M. Schallenberg. 1989. The humic content of lake water and its relationship to watershed and lake morphometry. Limnol. Oceanogr. **34:** 1336-1343.

Rennie, M.D., N.C. Collins, C.F. Purchase and A. Tremblay. 2005. Predictive models of benthic invertebrate methylmercury in Ontario and Quebec lakes. Can. J. Fish. Aquat. Sci. **62:** 2770-2783.

Rennie, M.D., W.G Sprules and T.B. Johnson. 2009. Resource switching in fish following a major food web disruption. Oecologia, **159:** 789-802.

Rennie, M.D., T.B. Johnson and W.G. Sprules. 2012. Energy acquisition and allocation patterns of lake whitefish (*Coregonus clupeaformis*) are modified when dreissenids are present. Can. J. Fish. Aquat. Sci. **69:** 41-59.

Rennie, M.D., D.O. Evans and J.D. Young. 2013. Increased dependence on nearshore benthic resources in the Lake Simcoe ecosystem after dreissenid invasion. Inland Waters **3:** 297-310.

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. **34:** 1481-1491.

Sobek, S., L.J. Tranvik, Y.T. Prairie, P. Kortelainen and J.J. Cole. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol. Oceanogr. **52:** 1208-1219.

Strayer, D.L., N.F. Caraco, J.J. Cole, S. Findlay and M.L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. BioScience **49:** 19-27.

Vadeboncoeur, Y., G. Peterson, M.J. Vander Zanden and J. Klaff. 2008. Borders of biodiversity: life at the edge of the world's large lakes. BioScience **61:** 526-537.

Vanderploeg, H.A., T.F. Nalepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Liebig, I.A. Grigorovich and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **59:** 1209-1228.

Wetzel, R. G. 2001. Limnology: lake and river ecosystems. 3rd ed. Academic Press.

Xenopoulos, M.A., D.M. Lodge, J. Frentress, T.A. Kreps, S.D. Bridgham, E. Grossman and C.J. Jackson. 2003. Regional comparisons of watershed determinants of dissolved organic carbon in temperate lakes from the Upper Great Lakes region and selected regions globally. Limnol. Oceanogr. **48:** 2321-2334.

Yu, N. And D.A. Culver. 2000. Can zebra mussels change stratification patterns in a small reservoir? Hydrobiologia **431:** 175-184.

Table 2-1. Morphometric characteristics of 53 North American lake ecosystems used in this study to evaluate zebra mussel and quagga mussel effects on water clarity.

Characteristic	Units	Range	Mean	Median
Surface Area	ha	43.3 – 5 959 600.0	170 745.8	448.0
Max. Depth	m	2.7 - 244.0	32.0	18.3
Mean Depth	m	1.5 - 88.6	12.3	6.4

Table 2-2. AIC_c, ΔAIC_c and $wAIC_c$ values for the five AIC_c models. Pre-invasion Secchi depth (m); z_{mean}, mean depth (m); Area, lake surface area (ha); Stratification, presence of thermal stratification in summer months (stratified [1] or mixed [0]), * indicates the null model.

Model	AIC_c	ΔAIC_c	$wAIC_c$
(1) log (Post-Invasion Secchi) = 0.186 + 0.788 x Pre-Invasion Secchi + 0.106 x z_{mean}	121.56	0	0.58
(2) log (Post-Invasion Secchi) = 0.143 + 0.873 x Pre-Invasion Secchi + 0.023 x Area	122.92	1.36	0.29
(3) log (Post-Invasion Secchi) = 0.283 + 0.904 x Pre-Invasion Secchi	125.46	3.89	0.08
(4) log (Post-Invasion Secchi) = 0.265 + 0.870 x Pre-Invasion Secchi + 0.077 x Stratification	126.91	5.34	0.04
(5)* log (Post-Invasion Secchi) = 1.310	217.80	96.24	0.00
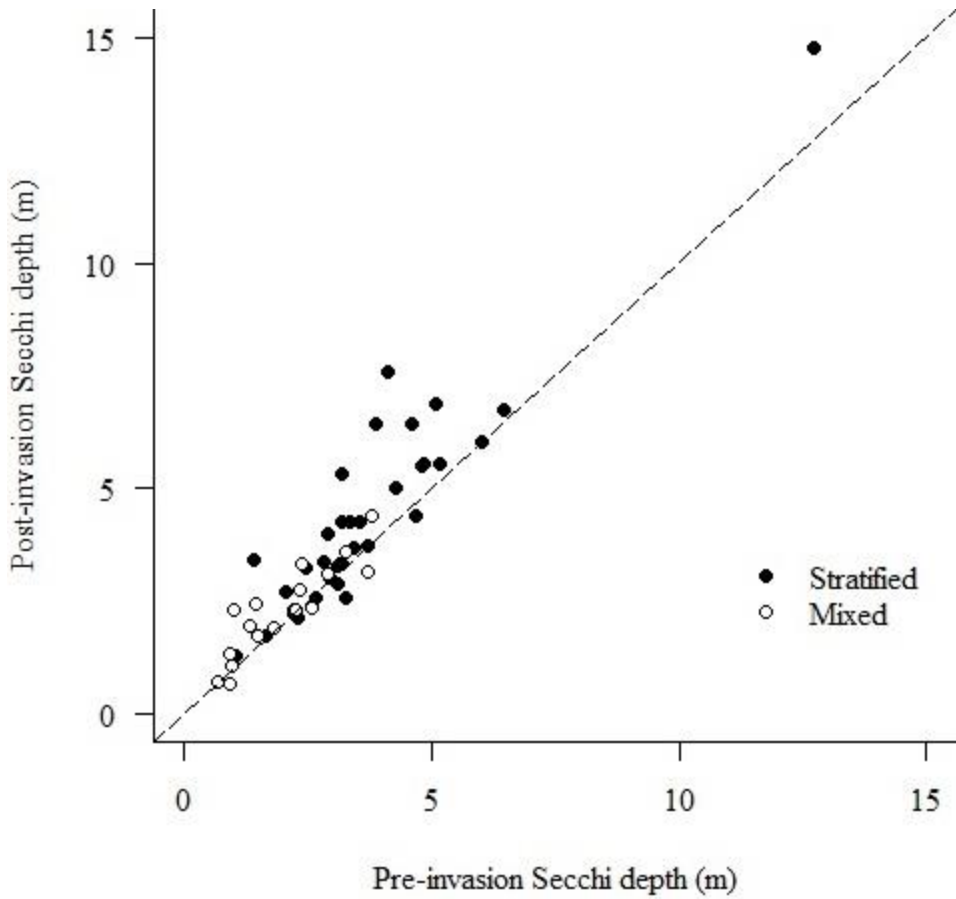
Figure 2-1. Effect of zebra mussels on water clarity (Secchi depth, m) in 53 North American lakes. Closed circles represent lakes that stratify during summer months and open circles represent non-stratified (mixed) lakes. Values above the 1:1 line (dashed line) indicate an increase in water clarity over the invasion period.
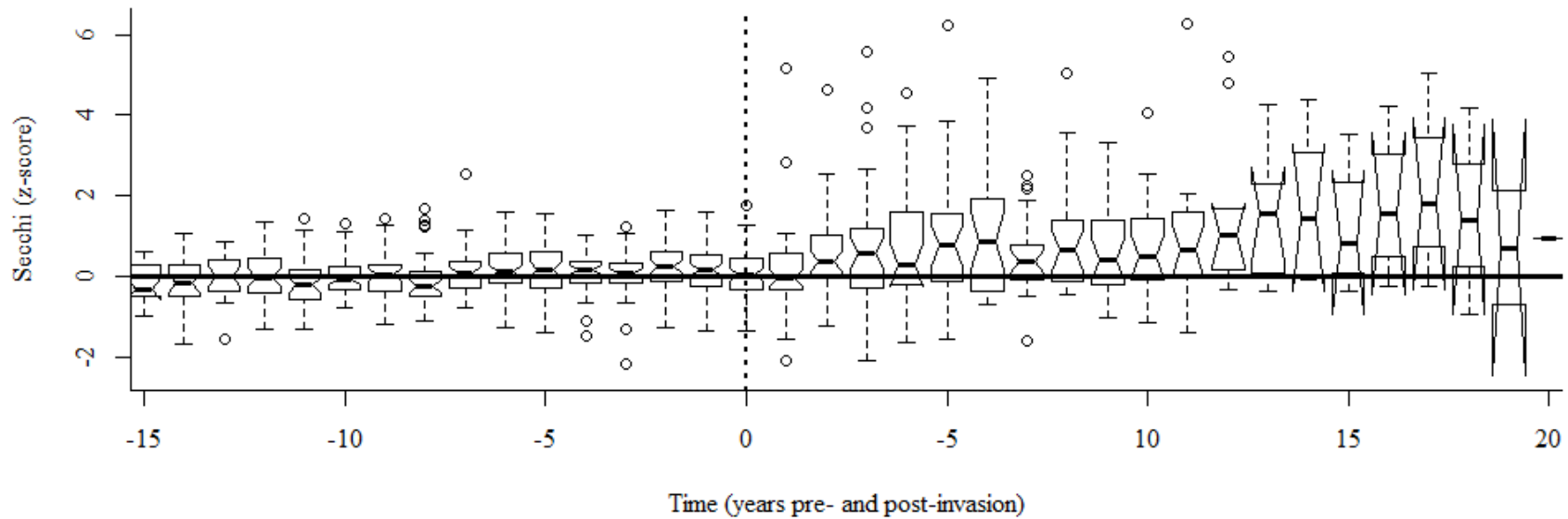
Figure 2-2. Time series effects of dreissenids on water clarity in 42 lake ecosystems with annual data available. Solid horizontal line represents the mean pre-invasion Secchi depth value, broken vertical line represents year of invasion. Box represents the range of 1st to 3rd quartile, with the median as the solid black line in the middle. Whiskers represent 1.5 x Interquartile Range (difference between 3rd and 1st quartile), open circles represent data outliers. Effects between the two time periods were considered significant where notches of boxes did not overlap between the two periods (i.e. strong evidence their medians differ). Notches overlap boxes in the last 10 years because few data points exist in that time period.
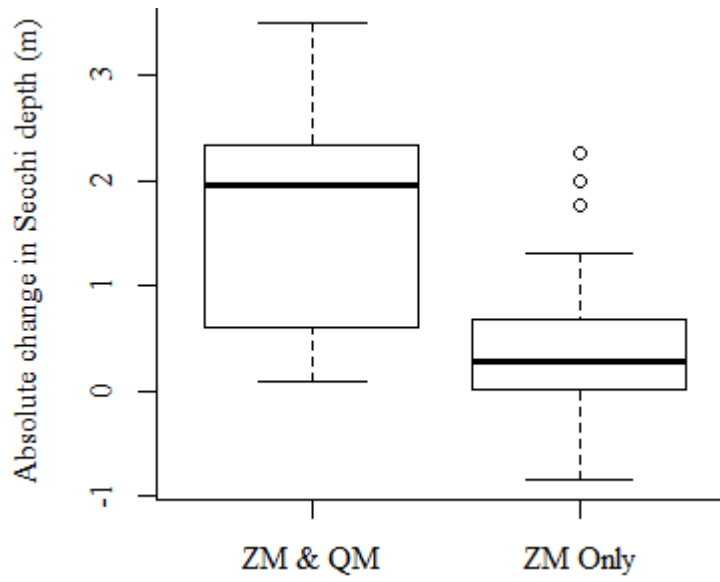
Figure 2-3. Absolute change in Secchi depth (m) pre- and post-dreissenid invasion within 53 North American lakes. ZM, lakes invaded by zebra mussels; QM, lakes invaded by quagga mussels.
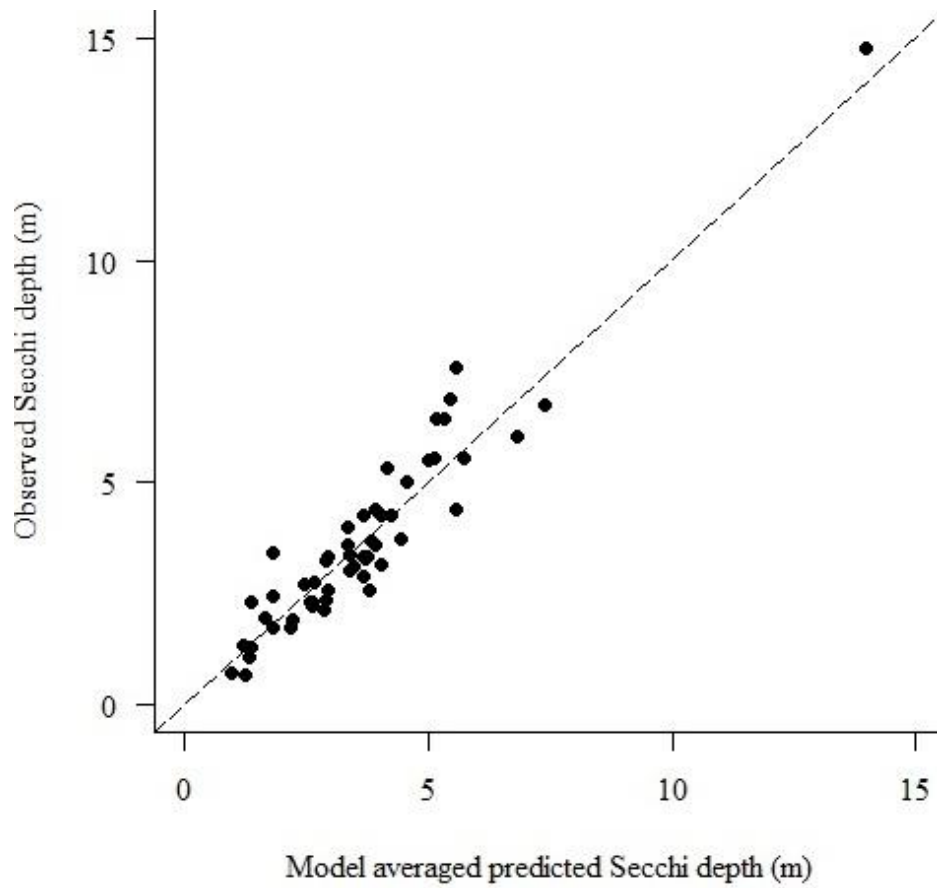
Figure 2-4. Observed versus predicted values of post-invasion Secchi depth (m) from cross-validated averaging four models using AIC model averaging. Dashed line, 1:1 line.
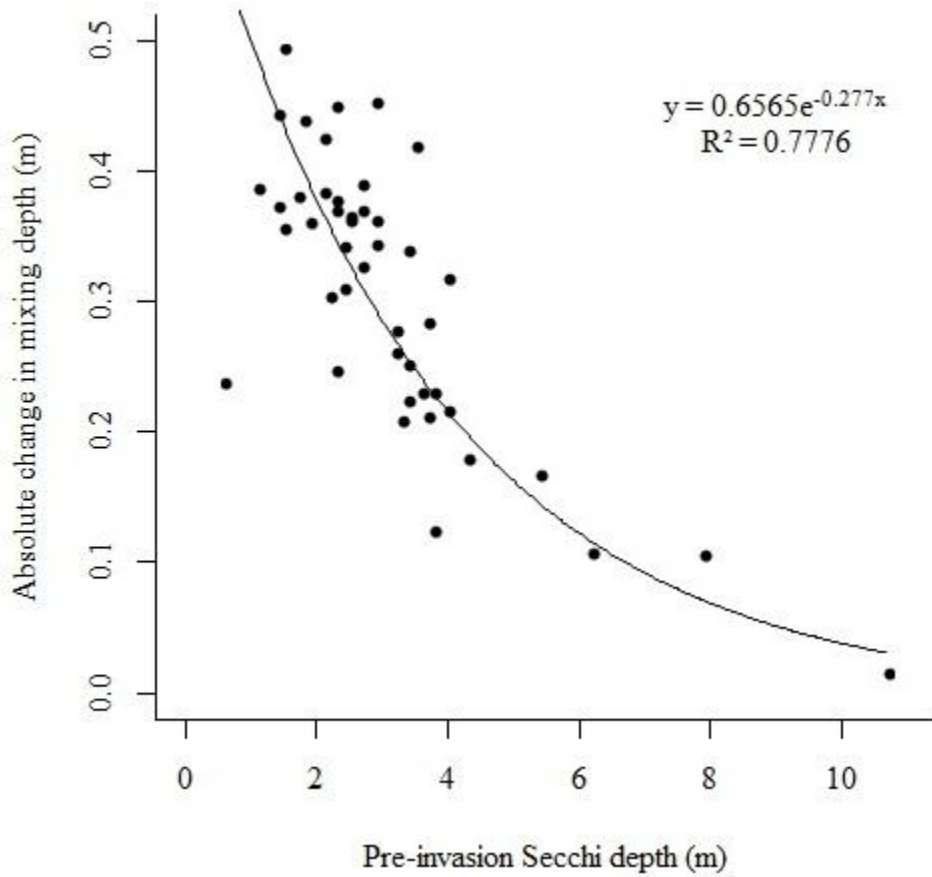
Figure 2-5. Change in predicted mixing depth (m) associated with pre-dreissenid invasion Secchi depth (m) values in Ontarian lakes (n=58).

Chapter 3: Declines in walleye (*Sander vitreus*) production following dreissenid establishment

Abstract

Walleye (*Sander vitreus*) are an important fish species in both the recreational and commercial fisheries in North America. Invasive dreissenid mussels are expanding their range across North America and are changing native ecosystems. Reports of some walleye populations near the Great Lakes region show declines in yield coincident with increases in water clarity following dreissenid establishment, but such declines have not been explicitly linked to the presence of dreissenid mussels. Using time series data from eight North American lakes where dreissenids have established, I found significant increases in water clarity concurrent with declines in walleye production, consistent with literature. A published walleye production model also predicts declines in production of this species on the basis of light-sensitivity; as water clarity increases, optimal walleye habitat decreases. However, our study demonstrated that while a portion of this decline could be explained by dreissenid-induced increases in water clarity, greater than expected declines in yield were likely also driven by coincident declines in both total phosphorus (TP) and walleye-targeted angler effort. Our results show that these three major components – water clarity, TP and angler effort – explain the majority of the observed declines in walleye yield in these ecosystems. Walleye yield declines in lakes threatened by non-native dreissenid mussels may be more profound in systems undergoing TP reduction efforts and/or changes in either the fishery or management practices.

Introduction

Walleye (*Sander vitreus*) are an important fish in North America to both commercial and recreational fishers. In Canada, walleye is the predominant freshwater species caught by anglers and the most lucrative in terms of tourist dollars generated (Frie et al. 1989) with an average of $2.5 billion spent annually on direct angling expenditures (Fisheries and Oceans Canada 2010). Canada's commercial walleye fishery contributes 7,109,000 kg to the average annual landed weight of freshwater fish harvested nationally, as well as 40% of the national average landed value (Fisheries and Oceans Canada 2007). Because of the walleye's economic importance, they are a high priority for management agencies, and changes to walleye production could have large ecological and economic impacts on both recreational and commercial fisheries.

The distribution of walleye in the water column is primarily determined by light (Moore 1944) due to the presence of a specialized visual apparatus called the *tapetum lucidum* which allows them to see well in dim light (Ali and Anctil 1977) and therefore decreases competition with other piscivorous predators (Ryder 1977). Walleye are dependent on low light levels for their spatial and temporal distribution and light levels beyond their optimum could lead to feeding inefficiency, lack of effective reproduction or higher rates of predation (Ryder 1977).

Some ecosystems have reported a decrease in walleye coincident with the increased light penetration caused by invasive dreissenid mussels, the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. rostriformis bugensis*). Increased water clarity associated with dreissenid mussels have been attributed to decreased walleye

54

yields in eastern Lake Ontario (Hoyle et al. 2008) and in the Kawartha Lakes region of

Ontario (Robillard and Fox 2006). Effects of dreissenids on fish communities are

variable, depending on the species and life stage, and are difficult to quantify due to the

complex nature of the food web in lake ecosystems. Of the few published accounts that

exist which report a decrease in walleye yield where dreissenid-induced increased water

clarity are implicated (e.g., Chu et al. 2004; Hoyle et al. 2008), none to date have

attempted to explicitly link walleye declines to water clarity increases due to dreissenid

establishment.

A model developed by Lester et al. (2004) described the relationship between

water clarity and walleye yield. Because of this relationship between dreissenid-induced

water clarity increase and change in walleye yield, the potential exists to link the Lester et

al. (2004) model with a model predicting changes in water clarity associated with the

establishment of dreissenids which could predict changes in walleye populations inherent

with dreissenid invasion. Using a statistical model that predicts a change in water clarity

following dreissenid invasion (Chapter 2), I used the Lester et al. (2004) model to predict

the outcome of dreissenid invasion in a suite of Ontarian lakes.

The goal of our study was to compile and analyze time series data on a number of

walleye lakes that have experienced dreissenid mussel establishment and evaluate

directly the effect of dreissenids on walleye production. I applied the Lester et al. (2004)

model to these same lakes to determine the degree to which changes in walleye

production might be due solely to changes in light conditions in these lakes associated

with dreissenid-induced increases in water clarity. Finally, I investigated a number of

potential factors not explicitly accounted for in the Lester et al. (2004) model that might additionally influence changes in walleye yield beyond those predicted as a result of increased water clarity following dreissenid establishment.

Methods

Study Areas

Lakes chosen for analysis were those which support a walleye fishery and were invaded by dreissenid mussels, and had also seen an increase in water clarity over the invasion period. This included Oneida Lake, NY; Bay of Quinte, Lake Ontario, ON; and 6 lakes in the Kawartha Lakes region of Ontario that were used in the original Lester et al. (2004) model generation (Balsam, Buckhorn, Chemong, Pigeon, Rice and Scugog Lakes, Table 3-1). All lakes in this analysis are located around Lake Ontario in the Great Lakes region of North America (Figure 3-1).

The Kawartha Lakes are a series of connected water bodies located in central Ontario which are mostly shallow lakes with highly productive habitat, ideally suited to walleye (Ontario Ministry of Natural Resources 2008). In the last few decades, these lakes have experienced changes in nutrient levels and water quality resulting from phosphorus load reductions (Stevens and Neilson 1987), extensive shoreline development and invasion of several non-native species including the zebra mussel (Robillard and Fox 2006). Pigeon, Buckhorn and Chemong Lakes are sometimes considered a single system ("Tri Lakes") due to their high connectivity (Ontario Ministry of Natural Resources 2008). In the instance where only one data point is available from the three, it can be used

as an approximation of the other two lakes. When the three lakes were pooled, year of dreissenid invasion was estimated to be 1996 which was the invasion year of Buckhorn Lake, the lake in the middle of the "Tri Lakes" system.

The Bay of Quinte is a z-shaped bay on the northeastern portion of Lake Ontario which is home to some of the largest stocks of walleye in Lake Ontario (Bowlby et al. 2010). The management of aquatic resources in a system like the Bay of Quinte has proven to be challenging due to dynamic ecosystem change by large scale ecological stressors like the invasion of dreissenids which started to affect the water clarity of the Bay of Quinte by the year following their proliferation (Hoyle et al. 2012).

Oneida Lake is the largest inland lake in New York and supports a year round fishery with walleye being the most sought after species (VanDeValk et al., in press). This lake is shallow, well-mixed and generally isothermal during summer and has experienced increases in water clarity since the invasion of dreissenids, which reached high densities in the lake within 3-4 years of invasion (Jackson et al. 2012).

Data compilation

Kawartha Lakes lake morphometry and climate data were reported by Ontario Ministry of Natural Resources (2008). Water quality data was made available by the Ontario Ministry of Natural Resources and Forestry (OMNRF), Kawartha Lakes Fisheries Assessment Unit (KLFAU) and the Ontario Ministry of the Environment (OMOE) Provincial Water Quality Monitoring Network (PWQMN). Walleye yield data for the Kawartha Lakes systems were taken from Ontario Ministry of Natural Resources

(2008). Bay of Quinte lake morphometry, climate and water quality data was made available by the Canadian Department of Fisheries and Oceans (DFO) and walleye yield data was provided by OMNRF. Oneida Lake lake morphometry, climate and water quality data was made available by the Cornell University Knowledge Network for Biocomplexity (KNB) database and walleye yield data was taken from VanDeValk et al. (in press).

From the data obtained, the following variables for the post-invasion periods were needed to estimate the parameters of the model: growing degree days (GDD, °C), Area (ha), proportion of lake above the thermocline, Secchi depth (m), total dissolved solids (TDS, mg/L) and mean depth (m). Thermal-Optical Habitat Area (TOHA, ha) and relative Secchi depth (m) were calculated based on equations from Lester et al. (2004; see Appendix B).

Limnological data were limited to the "ice-free" season (April to November) at one or more sampling stations in a lake. Pre-invasion data included at least 15 years before invasion and post-invasion data included up to 20 years since invasion. In Bay of Quinte where spatial resolution of water quality data was higher than walleye yield data (sampling stations in the Upper, Middle and Lower Bays as opposed to a single Bay of Quinte value), water quality data were pooled and averaged to represent the whole Bay. Thermocline data for the Bay of Quinte was calculated using mid-summer temperature profile data provided by DFO, and estimated as the depth where the temperature change per m was greatest.

Data Analysis

Water clarity data from the 8 lakes analyzed were input into the water clarity model developed in Chapter 2 to estimate effects of dreissenids on water clarity. I then compared the observed changes to predicted results by testing the difference of the relationship slope to a 1:1 line (test for heterogeneity of slope) to determine whether observed increases in water clarity were due solely to dreissenids.

Predictions of change in walleye yield due to water clarity (Secchi depth) were determined using the Lester et al. (2004) walleye production model to explore whether dreissenid induced changes in water clarity alone could account for changes in walleye yield. The fit of this model to the post-invasion data was examined when adjusting other parameters in the model (total phosphorus, TP) to improve fits, and also by incorporating other parameters not explicitly accounted for in the model (fishing effort).

A one-tailed *t* test was used for comparison of pre- and post-invasion walleye yield based our hypothesis that walleye abundance declines following dreissenid invasion, which is supported by anecdotal observations in the literature (Hoyle et al. 2008, Robillard and Fox 2006). Additionally, I was most interested in declines in walleye yield because a decline in the fishery due to effects of invasive dreissenids is of greater concert from a management perspective than an increase. Other pre- and post-invasion parameters with no expected directionality were compared using a standard paired two-tailed Student's *t* test and test for heterogeneity of slope.

Published papers on both the Kawartha Lakes and Bay of Quinte (Robillard and Fox 2006, Nicholls et al. 2011) have reported declines in total phosphorus over the same time period as observed decreases in walleye relative abundance. Though TP was not analyzed in the Nigel et al. (2004) model it has previously been linked to, and can be estimated from, TDS (Chow-Fraser 1991):

$$\log\text{TP} = 0.905 \, (\pm \, 0.081) \, \log\text{TDS} - 0.669 \tag{8}$$

Mean observed decline in TP was related to TDS via the above equation and comparative declines in TDS were input into the model to determine what proportion of yield declines could be solely attributed to changes in TP.

Fishing effort data was compiled for some Kawartha Lakes (Ontario Ministry of Natural Resources 2008), the Bay of Quinte (Hoyle et al. 2008) and Oneida Lake (VanDeValk et al., in press). The Kawartha Lakes (Ontario Ministry of Natural Resources 2008) and Bay of Quinte (Hoyle et al. 2008) data were digitized from figures in these publications using PlotDigitizer software (ver. 2.6.6), whereas raw catch data were used for Oneida Lake (VanDeValk et al., in press). A comparison of regression slopes of changes in fishing effort over time were evaluated from the years with effort data available.

Results

Across all of the lakes included in the study, mean water clarity increased significantly after dreissenids had become established (Table 3-2, paired *t* test, $t_8 = 4.42$,

$p < 0.01$). Water clarity (Secchi depth) increase averaged 0.53 m ± 0.36 m (mean ± SD), ranging from 0.01 m to 1.11 m.

No significant difference was found between the observed post-invasion Secchi values and our predicted values from the dreissenid water clarity model (paired t test, t_7 = 1.07, $p = 0.320$), suggesting that the water clarity increases I observed here are typical of other lakes that have become invaded by dreissenids. Predicted increases in water clarity based on the water clarity model for the 8 lakes in this study ranged from 0.30 m to 0.66 m (Secchi depth) with a mean of 0.41 m ± 0.12 m (mean ± SD). Observed post-invasion Secchi depth values were highly related to predicted values and resulted in an R^2 of 0.9042 (Figure 3-2, test for heterogeneity of slope, t_6 = -0.84, $p = 0.215$).

Walleye production decreased in 7 of 8 lakes following dreissenid invasion (Table 3-3). The mean observed walleye yield following dreissenid establishment was significantly lower than the mean pre-invasion observed yield (one-tailed paired t test, t_7 = 2.11, $p < 0.05$). Observed post-invasion yield data and predicted post-invasion yield data were significantly different (Figure 3-3, paired t test, t_7= -2.45, $p < 0.05$, test for heterogeneity of slope, t_6 = -3.42, $p < 0.01$). Average observed mean walleye yield across lakes declined by 51.9% of original yield values whereas model estimates based on water clarity only predicted a mean decline in yield of 17.2%. With the single exception of the Bay of Quinte fishery, the model predicted a less dramatic decline in walleye production than is currently observed in these lakes (Figure 3-3). With the Bay of Quinte excluded, the difference between observed yield and that predicted by the model in the post-

invasion period remained significant (paired t test, $t_6 = -4.54$, $p < 0.01$, test for heterogeneity of slope: $t_6 = -1.95$, $p = 0.054$).

To try and better understand discrepancies between observed declines in walleye yield and model predictions, I sought to explore other factors besides water clarity which may have exacerbated walleye declines beyond expectations. I first examined how changes in TP might impact walleye yield. Mean TP decreased by 29.7% following dreissenid invasion in 5 of the 8 lakes where data was available (Figure 3-4). TDS values were estimated using the Chow-Fraser (1991) equation and entering those values into the post-invasion estimates from the Lester et al. (2004) model, I accounted for an additional 4.7% decline in the mean predicted production of walleye (total estimated mean production decline = 21.9%).

I also examined the potential effect of changes in fishing effort on reported walleye yields. Of those lakes in the current study with fishing effort available, 5 of the 6 lakes reported declines in effort over the entire time period under investigation (Figure 3-5). Lakes with the highest declines in effort were Rice Lake and the Tri-Lakes which represents Pigeon, Buckhorn and Chemong Lakes in the Kawartha Lakes region. The Bay of Quinte was the only lake with an overall increase in effort (Table 3-4) over a similar time period. However, when focusing on effort changes seen in these lakes since the invasion of dreissenids the trends change slightly: Rice Lake no longer had enough data to constitute an analysis, Oneida Lake had an increase in effort and the Bay of Quinte had a substantial decrease in walleye targeted effort (Table 3-4).

Hoyle et al. (2008) suggested that walleye targeted effort was somewhat proportional to walleye yield in a study done on the Bay of Quinte. Average walleye targeted effort of lakes in this dataset declined by a mean of 19.3% in the post-invasion period. Using a simple additivity approach and summing the proportional contributions from decline in effort (19.3%), TP (4.7%) and water clarity (17.2%), an average of 41.2% decline in yield is explained of a total average observed decline of 51.9% across all lakes. Therefore, these three major components – water clarity, total phosphorus and angler effort – contribute to the explanation of the observed declines in walleye yield in these ecosystems.

Discussion

Our analysis demonstrated that, as predicted on the basis of water clarity alone, walleye production declined following dreissenid invasion. Unlike predictions, however, walleye production declines in our systems were far more dramatic than would have been anticipated based on water clarity alone. Assuming all else was equal, the Lester et al. (2004) model predicted a 17.2% average decline in walleye yield based solely on an increase in water clarity in the post-dreissenid time period. These declines are hypothesized to arise from a decrease in thermal-optical habitat area (Lester et al. 2004) due to dreissenid-induced increased light penetration which affects walleye prey encounter rates. However, the average observed decline in all systems analyzed was 51.9%, far greater than that predicted from increased water clarity alone. Our analyses suggest that declines in TP as well as walleye-targeted fishing effort are likely contributing factors to this exaggerated decline in walleye production.

While declines in TP in our lakes likely contributed to declines beyond those predicted by the Lester et al. (2004) model, our results demonstrate that TP alone cannot account for the additional decline in walleye production. Observed declines in TP in the lakes analyzed here accounted for an additional 4.7% decline in walleye yield, but an over two-fold increase in that TP decline would be necessary to explain observed walleye production declines. Legislation beginning in the early 1980s (Phosphorus Management Strategies Task Force 1980) changed the amounts of phosphorus which were allowed to be released from wastewater treatment plants into the streams and rivers of the Kawartha Lakes system (White 2006). Robillard and Fox (2006) described the TP concentration decreases in 4 of the 6 Kawartha Lakes described here (Balsam, Buckhorn, Rice and Scugog Lakes) and noted that they were similar in pattern to decreases in walleye abundance in these lakes. However, our analysis indicates that these observed declines in walleye abundance are not likely attributable to TP alone.

Our results indicate that declines in walleye-targeted fishing effort may also contribute to observed declines in walleye yield in our study systems. There has been a dramatic decline in walleye targeted effort seen in some of the Kawartha Lakes (Ontario Ministry of Natural Resources 2008). This could be due to the imposition of a slot size regulation on the Kawartha Lakes walleye fishery which resulted in a decline in both walleye targeted angling effort and harvest (Ontario Ministry of Natural Resources 2008). In the 1980-2003 period on Balsam, Buckhorn, Rice and Scugog Lakes there has been a decline in abundance of walleye which corresponded with an increase in small and largemouth bass (Ontario Ministry of Natural Resources 2008). While walleye targeted effort has decreased, overall effort has remained fairly constant (Ontario Ministry of

Natural Resources 2008), implying that anglers have switched from targeting walleye to other species, specifically bass. Reduction in targeted fishing effort could reduce yield via density dependent mechanisms or bottlenecks (Shuter 1990), which in this case implies increasing walleye population density leading to fewer resources being partitioned among individuals which decreases growth rate and condition of walleye (Van Den Avyle 1993).

The Bay of Quinte was the most obvious outlier result compared with all our other data, in that it is the only system where the Lester et al. (2004) model underestimated current (post-dreissenid establishment) walleye production. The Bay of Quinte has been described as being an "open system" where walleye (and other species) have the potential to migrate in and out of the Bay into Lake Ontario (J. Hoyle, Ontario Ministry of Natural Resources and Forestry, Picton, Ontario, personal communication, 2014). Yield estimates for the Bay may therefore actually represent supplementation from fishes migrating from Lake Ontario proper, which may influence the degree to which the limnology of the Bay is actually driving walleye production in this system. This potential subsidization may in part have contributed to the greater-than-predicted production following dreissenid establishment.

Though Oneida Lake had an overall decrease in angling effort from the late 1950's, there has actually been an increase in percent of anglers targeting walleye in recent years (VanDeValk et al., in press). There are additional factors that could contribute to the decline in walleye seen that are unique to this system. It has been suggested that yield declines are linked to decreases in abundance of gizzard shad (Idrisi et al. 2001) which are a major prey species for walleye in this lake. Rudstam et al. (2004)

argued that cormorant predation played a large role in the decline of sub-adult walleye in Oneida Lake.

As another key input to the Lester et al. (2004) model, GDD is also subject to change during the period which dreissenid mussels established on the lakes evaluated in this study. Climate change trends have been hypothesized to decrease production of cool water fish species like the walleye due to direct changes in thermal habitat and growth rates (Ontario Ministry of Natural Resources 2008). However, over the time period being modeled, GDD in this region of Southern Ontario has not increased significantly (Rennie et al. 2010), suggesting the impact of any measured change would be minimal. Additionally, in the Lester et al. (2004) model, GDD is multiplicative. Therefore, an increase in GDD would result in an even greater over-prediction of walleye yield, further exacerbating the difference between observed yield and those predicted by the model reported here.

Additional changes in ecosystem dynamics due to filter feeding dreissenids may have also impacted walleye habitat and production. For instance, in the Bay of Quinte aquatic vegetation distribution was limited by turbid water conditions prior to dreissenid establishment (Hoyle et al. 2008). Dreissenid-induced water column clearing provides more light and expands macrophyte coverage which increases foraging habitat for predatory competitors of walleye (Bowlby et al. 1991) and further reduces walleye habitat in both quality and quantity (Bowlby et al. 2010). In the Kawartha Lakes, the increase in abundance of bass species coincident with declines in walleye (Ontario Ministry of Natural Resources 2008) is hypothesized to cause reduced composition and

abundance of phytoplankton and zooplankton (Nate et al. 2011), and increased predation and competition (Robillard and Fox 2006).

The establishment of large populations of dreissenids has also been linked to effects on phosphorus recycling and transport due to the mussels filtering ability. Dreissenids are the basis for the conceptual "nearshore phosphorus shunt" (Hecky et al. 2004). Under the nearshore phosphorus shunt, dreissenids redirect phosphorus from the offshore to the nearshore, where it becomes sequestered and returns in only small concentrations to the water column. Thus while offshore nutrient concentrations decline with dreissenid establishment, the nearshore is transformed into a nutrient rich zone characterized by increases littoral benthic invertebrate biomass (Higgins and Vander Zanden 2010). Though walleye integrate both benthic and pelagic food webs (Vander Zanden and Vadeboncoeur 2002) evidence suggests that they grow more efficiently when consuming large pelagic prey (Henderson et al. 2004, Kaufman et al. 2006). As offshore production declines in the face of dreissenid establishment, walleye may become more reliant on nearshore resources, resulting in poorer growth which has other life history implications such as delayed maturity (Venturelli et al. 2010).

In conclusion, our results show significant increases in lake water clarity and significant decreases in walleye yield (both observed, and predicted on the basis of water clarity alone) following invasion of dreissenid mussels. However, while a portion of that decline in yield is attributed to water clarity increases, our study indicates that the underestimation of walleye yield declines by the walleye production model I used is likely due to concurrent changes in both phosphorus loading and walleye-targeted effort

in the lakes analyzed. Our study suggests that expectations of declines in walleye yield with dreissenid invasion may be exacerbated in lakes undergoing TP reduction efforts and/or changes in either the fishery or management practices.

References

Ali, M.A., and Anctil, M. 1977. Retinal structure and function in the walleye (*Stizostedion vitreum vitreum*) and sauger (*Stizostedion canadense*). J. Fish. Res. Board Can. **34**(10): 1467-1474.

Bowlby, J. N., Mathers, A., Hurley, D. A., Eckert, T. H., 1991. The resurgence of walleye in Lake Ontario. *In* Status of Walleye in the Great Lakes: Case Studies Prepared for the 1989 Workshop. *Edited by* P.J. Colby, C.A. Lewis and R.L. Eshenroder. Great Lakes Fish. Comm. Spec. Publ. 91. pp 169–205.

Bowlby, J. N., J.A. Hoyle, J.R. Lantry and B.J. Morrison. 2010. The status of walleye in Lake Ontario, 1988–2006. *In* Status of walleye in the Great Lakes: Proceedings of the 2006 Symposium. *Edited by* E. Roseman, P. Kocovsky and C. Vandergoot. Great Lakes Fish. Comm. Tech. Rep. 69. pp. 165–188.

Chow-Fraser, P. 1991. Use of the morphoedaphic index to predict nutrient status and algal biomass in some Canadian lakes. Can. J. Fish. Aquat. Sci. **48**: 1909-1918.

Chu, C., C.K. Minns, J.E. Moore and E.S. Millard. 2004. Impact of Oligiotrophication, Temperature, and Water Levels on Walleye Habitat in the Bay of Quinte, Lake Ontario. Trans. Am. Fish. Soc. **133**: 868-879.

Fisheries and Oceans Canada. 2007. Canadian Fisheries Statistics 2002-2004 [online]. Available from http://www.dfo-mpo.gc.ca/stats/commercial/cfs/2004/section7-3-14-eng.htm#ta3.2.1 [accessed 10 November 2014].

Fisheries and Oceans Canada. 2010. 2010 Survey of recreational fishing in Canada [online]. Available from http://www.dfo-mpo.gc.ca/stats/rec/canada-rec-eng.htm [accessed 10 November 2014].

Frie, R.V., J.K. Anderson and M.J. Larson. 1989. Age Verification of Walleyes from Lake of the Woods, Minnesota. J. Great Lakes Res. **15**(2): 298-305.

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton and T. Howell. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**: 1285-1293.

Henderson, B.A., G.E. Morgan and A. Vaillancourt. 2004. Growth, ingestion rates and metabolic activity of walleye in lakes with and without lake herring. J. Fish Biol. **65**: 1270-1282.

Higgins, S.N. and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. **80:** 179-196.

Hoyle, J.A., J. N. Bowlby and B. J. Morrison. 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosyst. Health **11**(4): 403-411.

Hoyle, J.A., Bowlby, J.N., Brousseau, C.M., Johnson, T.B., Morrison, B.J., and Randall, R.G. 2012. Fish community structure in the Bay of Quinte, Lake Ontario: The influence of nutrient levels and invasive species. Aquat. Ecosyst. Health. **15**(4): 370-384.

Idrisi, N., E.L. Mills, L.G. Rudstam and D.J. Stewart. 2001. Impacts of zebra mussels (*Dreissena polymorpha*) on the pelagic lower trophic levels of Oneida Lake, New York. Can. J. Fish. Aquat. Sci. **58**: 1430-1441.

Jackson, J.R., L.G. Rudstam, T.E. Brooking, S.D. Krueger, K.T. Holeck, C. Hotaling and J.L. Forney. 2012. The fisheries and limnology of Oneida Lake 2000-2011. New York Federal Aid in Sport Fish Restoration, Study 2, F-61-R.

Kaufman, S.D., J.M. Gunn, G.E. Morgan and P. Couture. 2006. Muscle enzymes reveal walleye (*Sander vitreus*) are less active when larger prey (cisco, *Coregonus artedi*) are present. Can. J. Fish. Aquat. Sci. **63**: 970-979.

Lester, N.P., Dextrase, A.J., Kushneriuk, R.S., Rawson, M.R., and Ryan, P.A. 2004. Light and temperature: key factors affecting walleye abundance and production. T. Am. Fish. Soc. **133**(3): 588-605.

Moore, G.A. 1944. The retinae of two North American teleosts with special reference to their tapeta lucida. J. Comp. Neurol., **80**(3): 369-379.

Nate, N. A., M. J. Hansen, L. G. Rudstam, R.L. Knight and S.P. Newman. 2011. Population and community dynamics of walleye. *In* Biology, management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries Society, Bethesda, Maryland, pp. 321-374.

Nicholls, K.H., J.A. Hoyle, O.E. Johannsson and R. Dermott. 2011. A biological regime shift in the Bay of Quinte ecosystem (Lake Ontario) associated with the establishment of invasive dreissenid mussels. J. Great Lakes Res. **37**: 310-317.

Ontario Ministry of Natural Resources. 2008. Background information to fisheries management plan for fisheries management Zone 17. Ontario Ministry of Natural Resources, Peterborough District, Kawartha Lakes Fisheries Assessment Unit.

Phosphorus Management Strategies Task Force. 1980. Phosphorus management for the Great Lakes. Final Report to the Great Lakes Water Quality Board and the Great Lakes Science Advisory Board. International Joint Commission, Windsor.

Rennie, M.D., W.G. Sprules and A. Vaillancourt. 2010. Changes in fish condition and mercury vary by region, not *Bythotrephes* invasion: a result of climate change? Ecography **33**: 471-482.

Robillard, M.M. and M.G. Fox. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Can. J. Fish. Aquat. Sci. **63**: 798-809.

Rudstam, L.G., A. J. VanDeValk, C.M. Adams, J.T.H. Coleman, J.L. Forney and M.E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecol. Appl. **14**(1): 149-163.

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. **34**(10): 1481-1491.

Shuter, B.J. 1990. Population-level indicators of stress. American Fisheries Society Symposium **8**: 145-166.

Stevens, R.J.J., and Neilson, M.A. 1987. Response of Lake Ontario to reductions in phosphorous load, 1967–82. Can. J. Fish. Aquat. Sci. **44**: 2059–2069.

Vander Zanden, M.J. and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology **83**(8): 2151-2161.

VanDeValk, A.J., Rudstam, L.G. Jackson, J.R., and S.D. Krueger. In press. The Oneida Lake fishery: interactions between fishing and fish. *In* Oneida Lake: longterm dynamics of a managed ecosystem and its fisheries. *Edited by* L.G. Rudstam, E.L. Mills, J.R. Jackson, and D.J. Stewart. American Fisheries Society, Bethesda, Maryland.

Van Den Avyle, M.J. 1993. Dynamics of Exploited Fish Populations. *In* Inland Fisheries Management in North America. *Edited by* W. Hubert and C. Kohler. American Fisheries Society, Bethesda, MD. pp. 105-135.

Venturelli, P.A., N.P. Lester, T.R. Marshall and B.J. Shuter. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. Can. J. Fish. Aquat. Sci. **67**: 1057-1067.

White, M. 2006. Phosphorus and the Kawartha Lakes (land use, lake morphology and phosphorus loading) [online]. Available from http://www.lakefieldherald.com/KLSA/ MikeWhitereport.pdf [accessed 20 October 2014].

Table 3-1. Morphology and climate of lakes included in model analysis.

Lake	Area (ha)	Max. depth (m)	Mean depth (m)	Mixing status	Growing degree days (>5°C)
Balsam, ON	4 665	14.9	5.0	Stratified	1867
Bay of Quinte, ON	25 740	37.8	14.5	Stratified	2236
Buckhorn, ON	3 191	9.4	2.1	Stratified	1885
Chemong, ON	2 280	6.7	2.4	Stratified	1920
Oneida, NY	20 670	16.8	6.8	Mixed	2821
Pigeon, ON	5 349	17.4	3.0	Stratified	1885
Rice, ON	10 018	7.9	2.6	Mixed	1959
Scugog, ON	6 374	7.0	1.8	Mixed	1920

Table 3-2. Observed and predicted post-invasion water clarity changes. Predicted values based on water clarity model averaging outlined in Chapter 2.

Lake	Year Invaded	Pre-invasion Secchi depth (m)	Post-invasion Secchi depth (m)	Observed Δ Secchi depth (m)	Predicted post-invasion Secchi depth (m)	Predicted Δ Secchi depth (m)
Balsam	1998	4.23	4.24	0.01	4.60	0.37
Bay of Quinte	1994	1.80	2.91	1.11	2.46	0.66
Buckhorn	1996	2.63	3.14	0.51	2.94	0.31
Chemong	1997	2.12	3.02	0.90	2.47	0.35
Oneida	1995	2.61	3.45	0.84	3.17	0.56
Pigeon	1994	2.92	3.24	0.32	3.29	0.37
Rice	2003	1.73	2.03	0.30	2.12	0.39
Scugog	1991	0.87	1.11	0.24	1.17	0.30

Table 3-3. Observed and predicted post-invasion walleye yield changes. Predicted values based on Lester et al. (2004) model.

Lake	Year Invaded	Observed pre-invasion walleye yield (kg/ha/yr)	Observed post-invasion walleye yield (kg/ha/yr)	Observed Δ yield (kg/ha/yr)	Predicted post-invasion walleye yield (kg/ha/yr)	Predicted Δ yield (kg/ha/yr)
Balsam, ON	1998	1.17	0.18	-0.99	1.44	0.27
Bay of Quinte, ON	1994	2.67	1.37	-1.30	0.35	-2.32
Buckhorn, ON	1996	1.99	0.87	-1.12	1.77	-0.22
Chemong, ON	1997	2.02	1.11	-0.92	1.84	-0.18
Oneida, NY	1995	9.92	1.80	-8.11	4.19	-5.73
Pigeon, ON	1994	2.18	0.89	-1.29	1.89	-0.29
Rice, ON	2003	3.74	2.14	-1.60	2.58	-1.16
Scugog, ON	1991	1.86	1.92	0.06	2.76	0.90

Table 3-4. Linear slope regression of year on fishing effort in 6 lakes for both the entire time period with data available and constrained to include only those years with data after invasion of dreissenid mussels. * indicates Pigeon, Buckhorn and Chemong Lakes consolidated into one sample.

Lake	Year Invaded	Slope (1955-2010)	Slope (Post-invasion)
Balsam	1998	-0.468	-1.328
Bay of Quinte	1994	0.198	-1.819
Oneida	1995	-0.633	0.429
Rice	2003	-0.940	n/a
Scugog	1991	-0.139	-0.496
Tri*	1996	-1.084	-1.212

Figure 3-1. Map showing location of studied ecosystems around the Lake Ontario region.
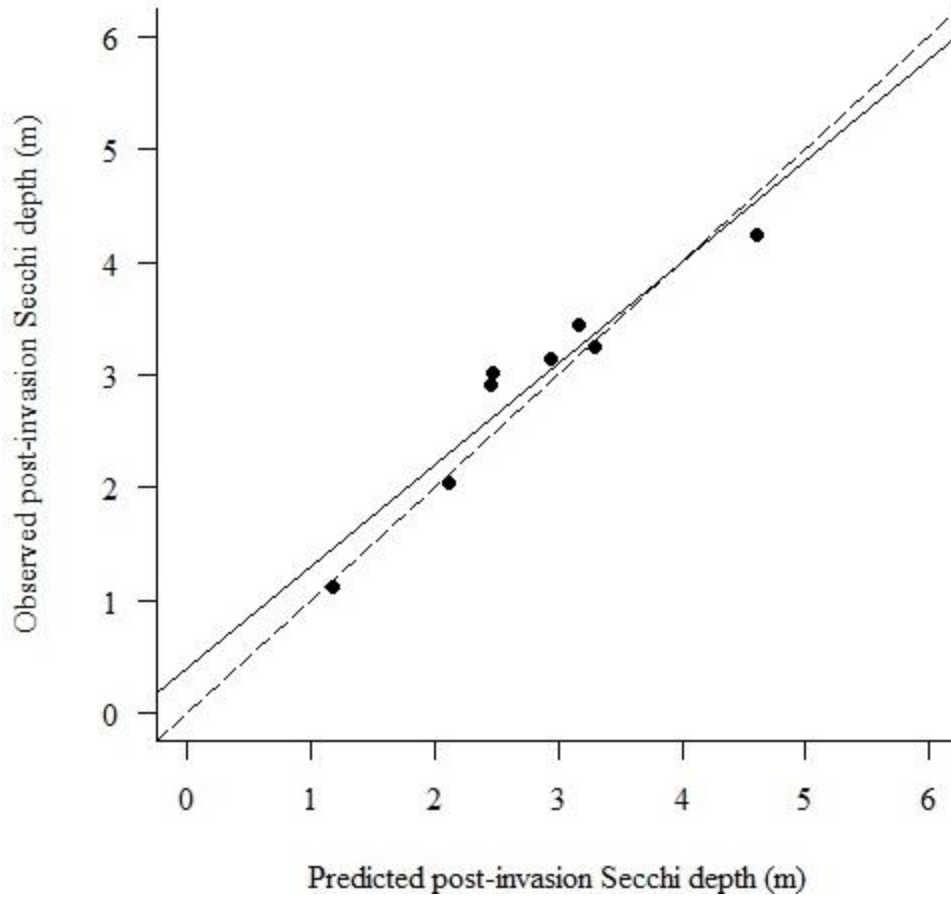
Figure 3-2. Predicted vs. observed post-dreissenid invasion Secchi depth (m) in 8 small lakes in the Great Lakes region of North America based on model averaging AIC models discussed in Chapter 2. Dashed line 1:1, Solid line R^2=0.9042 (slope=0.899, p=0.215).
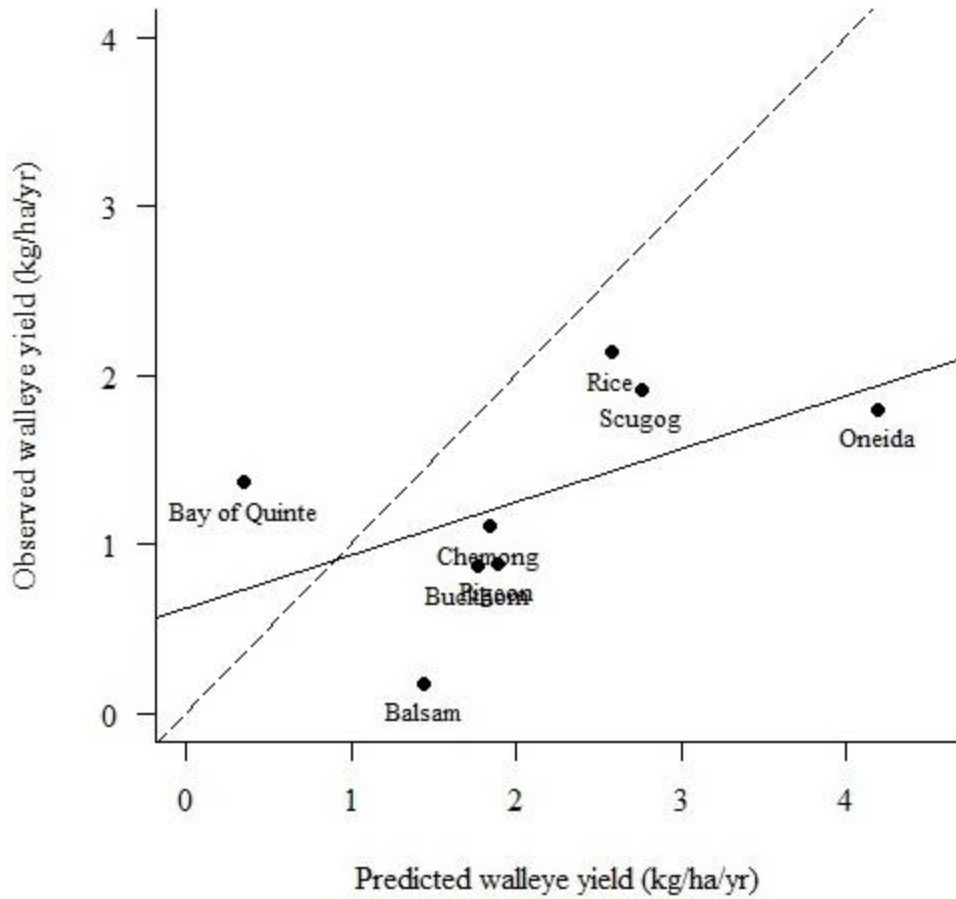
Figure 3-3. Predicted vs. observed estimates of post-dreissenid invasion walleye yield. Lakes to the right of the 1:1 line have overpredicted walleye yield values when compared to observed values, generated with the model incorporating dreissenid-induced water clarity changes. Dashed line 1:1, Solid line $R^2=0.2899$ (slope=0.314, p<0.01).
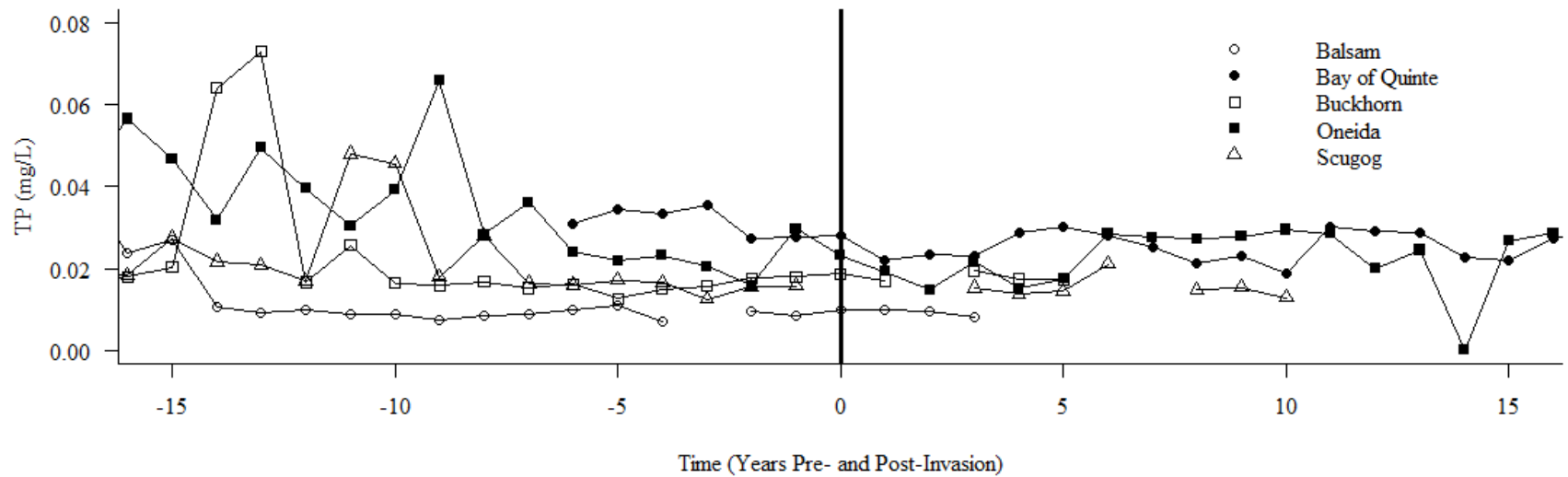
Figure 3-4. Time series of total phosphorus concentration (TP, mg/L) in pre- and post-dreissenid invasion in 5 lake ecosystems. Solid vertical line represents year of invasion.
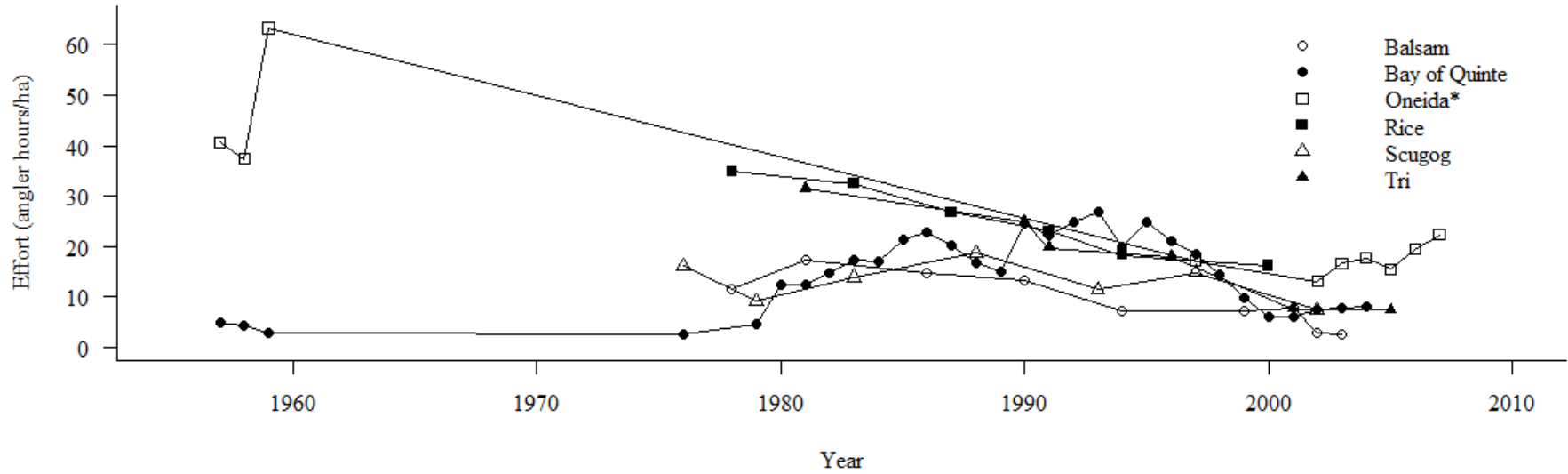
Figure 3-5. Fishing effort (number of rod hours per hectare) in 5 lakes included in this analysis. Effort data based on creel surveys conducted by the Kawartha Lakes Fisheries Assessment Unit, OMNR (data from Hoyle et al. 2008) and Oneida Lake creel assessment (VanDeValk, in press). * represents lakes with total effort data, all others are walleye-targeted effort.

Chapter 4: Extension of a walleye (*Sander vitreus*) production model to Manitoban Boreal Shield/Plains lakes and predicted consequences of dreissenid establishment

Abstract

Walleye (*Sander vitreus*) constitute an important natural resource in Canadian inland lakes, both on and off the Boreal Shield. In the province of Manitoba a large and valuable commercial walleye fishery is supported by lakes predominantly on the Boreal Plains which contributes approximately 60% to the national average annual harvest value. In North America, walleye have a range which overlaps that of the invasive dreissenid mussel. With the recent invasion of zebra mussels (*Dreissena polymorpha*) into Lake Winnipeg, a major producer of walleye, concern is rising in regards to the potential effect of these filter feeding mussels on walleye production. Using the Akaike information criterion model selection approach I determined the best predictive models of walleye yield for Boreal Shield and Boreal Plains lakes. I adapt and assess the predictive capacity of a previously published model applied to Shield lakes, and develop a new model to describe lakes from Boreal Plains ecozones. I combined these walleye production models with a model predicting dreissenid-induced water clarity increase to forecast how increase water clarity resulting from dreissenid invasion will affect walleye production. Dreissenid establishment is predicted to increase Secchi depths across all Manitoban lakes by an average of 0.4 m. By contrast, predicted walleye yield from lakes in both ecozones responded variably to simulated dreissenid-induced water clarity change ranging from a decrease of 2.4 kg/ha/yr to an increase of 0.9 kg/ha/yr.

84

Introduction

Since their introduction to the Great Lakes area in the late 1980s, dreissenid mussels (the zebra mussel (*Dreissenia polymorpha*) and quagga mussel (*Dreissenia rostriformis bugensis*)) have rapidly spread across waterways in North America and now are present in over 744 freshwater lakes in the United States alone (United States Geological Survey 2015). Until recently, the presence of dreissenids in Canada was limited to the province of Ontario. In the fall of 2013, zebra mussels were detected in Manitoba with specimens discovered in Lake Winnipeg harbours at the end of the fishing season (Government of Manitoba 2013). The watershed of Lake Winnipeg encompasses an area of nearly one million square kilometers and is home to 5.5 million Canadians and 1.1 million Americans (Environment Canada and Manitoba Water Stewardship 2011). The ecological risk of the zebra mussel to sub-drainages (Therriault et al. 2012) was reported as being high in Manitoba and into the western provinces, thus there is now significant concern regarding the spread of this invasive species throughout the watershed.

Specific concerns exist for the potential effects of dreissenids on fish populations. There is evidence that dreissenid mussels have contributed to growth declines and changes in foraging of Great Lakes whitefish (Rennie et al. 2013), but their effects on other fish species are not well understood. Recent work demonstrated that projected dreissenid-induced changes in walleye yield on Ontarian Shield lakes was variable, and was estimated to decline by approximately 5% on average (see Chapter 2). In lakes where dreissenids have invaded, walleye production fell by approximately 50% following

dreissenid establishment, though other factors likely contributed to this dramatic decline (see Chapter 3).

Walleye are an important commercial and recreational fish species throughout North America and are the most lucrative in terms of commercial value and tourist dollars generated from anglers in most freshwater lakes in the northern latitudes (Frie et al. 1989). Commercially, Manitoba produces on average 67% of the volume of walleye from Canadian lakes (Fisheries and Oceans Canada 2007), averaging well over ~4.5×10^6 kg in recent years (Lumb et al. 2011). This Manitoban commercial walleye fishery has contributed $29.4 million to the average landed value of walleye nation-wide (Fisheries and Oceans Canada 2007).

As one of the most productive inland lakes for commercial walleye in North America, second only to Lake Erie (Lemm 2002) and the largest lake in Canada outside of the Great Lakes (Environment Canada and Manitoba Water Stewardship 2011), the sustainability of the Lake Winnipeg walleye fishery is of high importance. This lake produces 47% of the total fish production from all commercial lakes in Manitoba and 67% of the landed value of the harvest (Manitoba Water Stewardship 2010), with a value of approximately $20 million annually (Manitoba Water Stewardship 2010). With zebra mussels found in Lake Winnipeg in 2013 and slowly becoming established in the lake, fishers are becoming increasingly concerned with their potential effect on the valuable walleye fishery.

Due to their filtration abilities, dreissenid mussels increase water clarity which could result in a decrease in habitat for light-sensitive fish species like the walleye. Declines in walleye harvest coincident with establishment of dreissenid mussels have

been reported in lakes near the Great Lakes region, including the Bay of Quinte (Hoyle et al. 2008) and some Kawartha Lakes (Robillard and Fox 2006). Walleye yield has been projected to decrease in these types of systems due to a decrease in suitable walleye habitat (see Chapter 2, 3). Lester et al. (2004) hypothesized that this is due to increased water clarity which decreases thermal-optical habitat area (TOHA) following the establishment of filter feeding dreissenid mussels. However, responses of walleye yield to dreissenid establishment appear to be variable (see Chapter 2, 3).

A walleye production model (Lester et al. 2004) was developed and evaluated for Boreal Shield lakes in Ontario, but may not be representative of lakes in other ecozones in North America. A large portion of walleye distribution in North America (Zhao et al. 2008) extends into the Boreal Plains and Prairie region west and south of the Shield. The three western Canadian prairie provinces (Manitoba, Saskatchewan and Alberta) have important walleye fisheries which contribute 63% to the average annual value of the commercial walleye fishery in North America (Fisheries and Oceans Canada 2007). With a large portion of the landed value for this species originating from non-Shield lakes there is a need for the evaluation of the Shield-based Lester et al. (2004) model to lakes beyond the Shield and, if necessary, the development of a model that better describes walleye production from lakes on the Boreal Plains and Prairies.

Given that the inland walleye fishery in North America is so economically important, the potential impact of invasive dreissenid mussels on walleye fisheries could be immense. Our specific objectives in this study were to (i) evaluate models which predict the production of walleye in Boreal Plains and Prairie lakes, representative of the most productive and economically important lake types for this species in North

87

America, and (ii) estimate how changes in water clarity associated with invasive dreissenids would affect walleye production in lakes from the Boreal Plains and Prairie ecozones.

Methods

Study site

The Canadian province of Manitoba is well situated for this study, containing lakes supporting walleye in all three ecozones under investigation (Figure 4-1). Lakes are representative of the general range of walleye-producing lakes found throughout North America. Twenty-three Manitoban lakes with sufficient data were included in analyses and were distributed across the three southernmost ecozones in the province: Boreal Shield, Boreal Plains and Prairies (Appendix C).

Data compilation

Lake morphometry was provided by Manitoba Conservation and Water Stewardship for all for routinely sampled Manitoban lakes. Those lakes with no reported surface area or mean depth were calculated from contour maps (Canada Map Sales 2014). Manitoba commercial fishery data was provided by the Freshwater Fish Marketing Corporation, which is the single desk marketing agency for Manitoba's commercial fishers (Manitoba Water Stewardship 2010). Recreational fishery data for lakes in Manitoba's Whiteshell region was from Hagenson and O'Connor (1979). Growing degree days (GDD) above 5°C, which is the base temperature for walleye growth (Chezik et al. 2014), for lakes included in this analysis were provided by Manitoba Conservation and Water Stewardship where available and otherwise estimated from a map of GDD gradients in Manitoba provided by University of Winnipeg (R.Smith, University of

Winnipeg, Winnipeg, Manitoba, personal communication, 2014). Water quality data for routinely sampled Manitoban lakes was provided by Manitoba Conservation and Water Stewardship. In lakes where total dissolved solids (TDS) data was unavailable it was estimated from conductivity (Gale and Goodchild 1982). The remaining lakes were sampled in summer 2013 and water samples were analyzed at the Freshwater Institute in Winnipeg, Manitoba.

In this study, yield is defined as the maximum sustainable yield (MSY) that, as described by Ricker (1975), is "the largest average harvest that can be continuously taken under existing environmental conditions". In order to ensure accurate estimates of yield, lakes were limited to those that met the criteria outlined in Lester et al. (2004). These criteria included lakes where: (1) the fishing effort was moderate to high; (2) multiple years of harvest data were available; and (3) the annual variability of harvest was low (Lester et al. 2004). A full list of lakes with data is provided in Appendix C.

The North and South Basins of Lake Winnipeg were considered as two independent lakes to account for differences in morphometry, water quality and fishing effort (Environment Canada and Manitoba Water Stewardship 2011). The lake was divided at the northern end of the "narrows" of the lake, as per previous analyses (Johnston et al. 2012; Sheppard 2013) with the narrows of the lake being included in the south basin calculation (Figure 4-2). Lake Winnipeg walleye yield values were taken from a period of relative stability (2005-present) as determined by the 95% confidence intervals of a thin-plate regression spline (Figure 4-3) from a generalized additive model (GAM) with a gamma error distribution and a log-link function applied to walleye yield across years in Lake Winnipeg.

Data analysis

A principal components analysis (PCA) was used to identify those physical lake variables that accounted for the most of the variation in our dataset. All continuous lake variables were log transformed to ensure assumptions of normality were met. Comparisons between mean parameter values of lakes from different ecozones were made to investigate similarities using two-sample *t* tests with a Welch correction on degrees of freedom to account for differences in variation between groups. Comparisons of variables pre- and post-invasion of dreissenids were assessed using paired Student's *t* test.

Model development and evaluation

An information-theoretic approach was taken to provide quantitative evidence for the performance of each model developed. I categorized lakes based on ecozone and analyzed the fit of six models that provide an estimate of walleye yield based lake morphometry and ecosystem productivity. These models include adaptations of: 1) the traditional characterization of the morphoedaphic index (MEI) that estimates fish yield based on mean depth and TDS (Ryder 1965, Table 4-3, Equation 5); 2) a model that uses area as a substitute for mean depth, assuming that area predicts walleye yield better than mean depth (Christie and Regier 1988, Table 4-3, Equation 3); and 3) a model that incorporates both temperature and light as indicators of walleye habitat area, and TDS as an estimate of food availability (Lester et al. 2004, Table 4-3, Equation 1). Another three models I developed were included that incorporated a combination of TOHA and total phosphorus (TP). These six models were compared using AIC_c model evaluation for both Shield and Plains lakes.

Water clarity parameter values ("k") included in the calculation of TOHA (see Appendix B for equation formulation) were estimated based on ecozone lake type as per Koenings and Edmundson (1991) and Lester et al. (2004). The parameter k relates light extinction to Secchi depths across a variety of lake types depending on the turbidity and color of the water. In Shield lakes k=2.12, as per Lester et al. (2004), and for Plains and Prairie lakes k=1.00 which is more representative of lakes with high turbidity. Owing to their small sample size (n=2), Prairie lakes were excluded from model development.

Models were evaluated to determine the best predictors of walleye yield in Manitoban lakes. Generalized linear models (GLM) using log-link functions with the gamma error distribution were used to fit the model. As in Chapter 2, the model that produced the smallest AIC_c value ($AIC_{c\ min}$) was determined to be the "best" among the models (Akaike 1973), strength of evidence for each model (ΔAIC_c and $wAIC_c$, Burnham and Anderson 2002) formed the basis of model selection and the null model was included as an indicator of relative model performance.

Estimating dreissenid impacts on walleye yield

The walleye production model that estimated a best fit for each ecozone was used in conjunction with a water clarity model that estimates change in Secchi depth associated with the establishment of invasive dreissenids (see Chapter 2). I used this method to predict the expected change in walleye production post-dreissenid establishment. Predicted changes in walleye yield in lakes across the three ecozones (Boreal Shield, Boreal Plains and Prairies) were compared via prediction intervals of a representative lake from each ecozone, where model input parameters for these "lakes" were the median across all lakes of that ecozone.

In order to determine the variable(s) that influence magnitude and direction of change in walleye yield, GLM with identity-link functions and the Gaussian distribution were developed and compared. To remove issues associated with multicollinearity between explanatory variables, variance inflation factors (VIF) were calculated. In order to make comparisons across categorical and continuous variables, the output VIF^(1/(2df) (where df is the number of coefficients) was used in order to reduce the VIF to a linear measure (Fox and Monette 1990). Those variables with VIF > 10 were excluded to remove their linear relationship with other independent variables in the dataset (Quinn and Keough 2002, Hair et al. 2009).

Results

Lakes analyzed in this study were from three different ecozones in the province of Manitoba (Boreal Shield, Boreal Plains and Prairies) and spanned a wide range of size, depth and trophic status (Table 4-1). Water clarity ranges in these lakes from 0.44 m to 3.9 m (Secchi depth) with no significant relationship to walleye yield (Pearson's product-moment correlation, t_{22} = -0.09, p = 0.932), which ranged from 0.078 kg/ha/yr in South Indian Lake to 5.74 kg/ha/yr in Caddy Lake.

The PCA illustrated the variation among different lake types (Figure 4-4) and revealed the importance of ecozone (Table 4-2) which influenced the groupings of the data points along the first two axes. Together, the first two principal components explained 65% of the variation across lakes. Lake ecozones were separated for further analyses with lakes from the Boreal Plains and Prairies combined where necessary due to low sample size of Prairie lakes (n=2).

Lakes were found to differ between ecozones in a number of variables.

Commercial walleye production was greater in Boreal Plains and Prairie lakes

contributing 96% and Boreal Shield lakes 4% of total landed production in the province

of Manitoba. There were no statistically significant differences found in any parameters

between ecozones except mean TDS which was over four times greater in lakes from the

Boreal Plains and Prairies (mean $\pm$ SD , 426.47 mg/L $\pm$ 271.11 mg/L) than Boreal Shield

lakes (94.10 mg/L $\pm$ 43.63 mg/L, two-sample t test, $t_{9.334} = 3.84$, $p < 0.005$). The

maximum TDS value in the Lester et al. (2004) dataset was 156 mg/L, in the Manitoban

Shield data set was 199 mg/L and in the Manitoban Boreal Plains and Prairies data set

was 799 mg/L, a four-fold difference between the maximum values observed between

Shield and Plains/Prairies.

AIC$_c$ model evaluation for Manitoban Shield Lakes indicated the adapted Lester

et al. (2004) model was the highest performing (Table 4-3, Equation 1). The predictions

of Manitoban Shield lake walleye yield generated by the Lester et al. (2004) model were

found to be not statistically different from observed values (paired t test, $t_{13} = 0.54$, $p =$

0.599) (Figure 4-5). There was no significant difference found in mean lake area between

the dataset from Lester et al. (2004) and the Manitoba Shield lakes (two-sample t test,

$t_{14.762} = $ -1.01, $p = 0.328$). There was, however, a statistically significant difference

between datasets when comparing mean depth (two-sample t test, $t_{30.164} = 2.18$, $p < 0.05$)

with Ontarian Shield lakes deeper on average (mean $\pm$ SD , 7.27 m $\pm$ 4.32 m) than

Manitoban Shield lakes (5.07 m $\pm$ 2.30 m). TDS was also found to be significantly

different between the two (two-sample t test, $t_{18.639} = $ -2.62, $p < 0.05$); Manitoban Shield

lakes had higher mean TDS values (mean ± SD, 94.10 mg/L ± 43.63 mg/L) than Ontarian

Shield lakes (60.61 mg/L ± 36.88 mg/L).

AIC_c model evaluation for Boreal Plains lakes resulted in 94% support for the

model that included TOHA and TP (Table 4-4, Model 1). The predictions from this

model were also found to be not statistically different from observed values (paired t test,

$t_7 = 0.07$, $p = 0.943$).

The Prairie lake walleye yields were estimated from the model generated for

Boreal Plains lakes (Table 4-4, Model 1) where it did not predict as accurately for Prairie

lakes as it did for those from the Boreal Plains (Figure 4-6). Because of the small sample

size of Prairie lakes they were unable to be analyzed or modelled on their own, and thus

were not used to generate the model but are presented here simply for examination and

are provided for comparison only. Predictions of walleye yield from Prairie lakes

generated with the Boreal Plains model were found to be not statistically different from

observed values (paired t test, $t_1 = -4.45$, $p = 0.143$).

A recently developed water clarity model (see Chapter 2) was applied to the

Manitoban lakes in this analysis to determine the magnitude of change in Secchi depth

(m) predicted for these lakes based on pre-invasion Secchi depth and lake morphometric

characteristics were dreissenids to establish. Secchi depth was predicted to increase in all

analyzed lakes (Table 4-5; paired t test, $t_{23} = -21.78$, $p < 0.001$), with the highest

predicted increase in the north basin of Lake Winnipeg at 0.60 m, and the smallest,

0.25m, in Dauphin Lake.

This predicted increase in water clarity was subsequently input into the walleye

production models for Boreal Shield and Boreal Plains and Prairies to predict potential

change in walleye yield based on dreissenid-induced water clarity increases. Change in

predicted walleye yield ranged from a decline by 2.36 kg/ha/yr in Caddy Lake to an

increase by 2.63 kg/ha/yr in Dauphin Lake (Figure 4-7). Increases in walleye yield were

predicted for 16 of the 24 systems analyzed. Lakes with predicted walleye yield increases

tended to have lower pre-invasion Secchi depth (mean ± SD, 1.24 m ± 0.57 m) and

predicted post-invasion Secchi depth (1.65 m ± 0.63 m). Lakes with predicted walleye

yield decreases had Secchi depth values observed to be 1.88 m ± 0.89 m and were

predicted to surpass 2 m post-invasion (2.34 m ± 0.89 m).

Mean estimated change in walleye yield following dreissenid establishment for

Manitoban Shield lakes was -0.08 ± 0.85 kg/ha/yr (mean ± SD), for Manitoban Plains

lakes was -0.02 ± 0.26 kg/ha/yr and for Manitoban Prairie lakes was 2.30 ± 0.46 kg/ha/yr.

Ecozone was shown to have an effect on change in yield as determined by the non-

overlap of prediction intervals ($\alpha = 0.95$) for representative lakes between the Prairies

and the two other ecozones; indicating differences in the predicted outcome of dreissenid

establishment on walleye yield between Boreal Shield (0.76 ± 0.12 kg/ha/yr) and Plains

lakes (0.73 ± 0.25 kg/ha/yr) versus Prairie lakes (5.69 ± 3.81 kg/ha/yr). However,

changes in walleye yield were found to be not statistically different from zero in all of

Manitoban Shield lakes (paired t test, $t_{13} = 0.37$, $p = 0.716$), Manitoban Boreal Plains

lakes (paired t test, $t_7 = 0.17$, $p = 0.868$) and Manitoban Prairies lakes (paired t test, $t_1 = -$

7.04, $p = 0.090$).

VIF calculations highlighted collinearity between maximum and mean depth so

for subsequent model analysis maximum depth was removed as a predictor variable. All

other variables were free of issues of multicollinearity. Predicted change in yield was

consistently predicted best by ecozone regardless of the combinations of parameters input. When predicting change in walleye yield based on individual parameters, ecozone and Secchi depth contributed to a 0.98 wAIC$_c$ value indicating the strength of the combination of these two variables in the model evaluation (Table 4-6).

Discussion

This research highlights the importance of ecozone in estimating walleye production. The adaptation of a previously published walleye model (Lester et al. 2004) which was developed on Ontarian Shield lakes accurately described Shield lakes in Manitoba, indicating the application of the parameters in this model outside of the region it was developed but only among lakes of the same ecozone; the adapted Lester et al. (2004) model did not perform well applied to lakes of the Boreal Plains or Prairie region. As a result, I generated a new model for lakes on the Boreal Plains based on TP as an indicator of primary productivity, which was found to perform best among all other candidate models. Lakes tend to differ by ecozone based on size and productivity, which likely influences the relationship with nutrients related to fish production. Our study emphasizes the need for ecozone specific fisheries production models as applied to walleye.

I present evidence that ecozones may also dictate the potential response of walleye to dreissenid invasion. Prairie lakes responded differently (and positively, on average) compared to both Boreal Shield and Plains lakes. This variation in our estimated outcomes, as well as a limited amount of available data, likely contributed to our inability to predict significant changes in walleye yield resulting from dreissenid invasion across the Manitoban lakes evaluated in this study. In contrast, lakes reported in Nigel et al.

(2004) lake dataset were predicted to generate a statistically significant 5% decline in walleye production (though the sample size was more than twice as large as the Manitoban dataset; see Chapter 2), as well as findings that 7 of 8 lakes on or near the Ontarian Boreal Shield responded negatively to dreissenid invasion (see Chapter 3).

On average, lakes in this analysis that had a predicted increase in walleye yield also had a shallower pre-invasion mean Secchi depth (~1.24 m) than those which predicted walleye yield declines (~1.65 m). The direction of change in walleye yield post-invasion is hypothesized to be influenced by optimum Secchi depth, which in Lester et al. (2004) is defined as the water clarity that produces the greatest amount of walleye TOHA. This was found in the Lester et al. (2004) lake dataset to be a mean of 2 m with a narrow range that approximated a bell curve. Thus, lakes with a deeper pre-invasion Secchi depth that exceeds 2m after clearing by invasive dreissenids would move on the downward part of the curve indicating a decreasing walleye TOHA and ultimately production. Those lakes with a shallower pre-invasion Secchi depth (<2 m) would be predicted to have walleye yield increases with increasing water clarity, as they move closer towards the optimum Secchi depth which supports greater walleye production.

The exact mechanisms by which increased water clarity might translate into a decrease in walleye yield are not exactly known. The idea behind this suite of predictions is based on the hypothesis that with an increase in water clarity caused by invasive dreissenid mussels, optimal habitat area for walleye will change which will cause changes in their production levels. It is hypothesized to include reduced foraging efficiency in the clearer water, increased predation/competition, reduced food

supply/availability (Nate et al., 2011) or a change in walleye distribution to deeper, cooler waters (Bowlby et al., 2010).

It is important to investigate the potential changes in walleye yield for lakes on the Boreal Plains and Prairies as they contribute to a large portion of the national freshwater commercial walleye catch. Manitoba alone makes up well over half of Canada's landed walleye volume (Fisheries and Oceans Canada 2007) and within Manitoba, 96% of commercially caught walleye are from lakes on the Boreal Plains and Prairies. Following the recent invasion of zebra mussels into Lake Winnipeg, the potential exists for spread of these non-native mussels over a large geographic region as the Lake Winnipeg watershed extends into the western prairie provinces (Manitoba, Saskatchewan and Alberta). This could have serious implications for the commercial fishery which, in these three provinces, is worth over $20 million dollars annually.

The model developed by Lester et al. (2004) was a more sophisticated development of the MEI as described by Ryder (1965) which related the morphology of a system to its primary production to provide an estimate of that system's ability to produce fish. TDS was used in both of these models as an indicator of primary productivity because it was, and still remains, a readily available ecosystem parameter. Though some have reported relationships between TDS and TP (Chow-Fraser 1991), Downing et al. (1990) showed that fish production was more strongly related to TP than with MEI (which relies on both TDS and lake area) from a wide range of lake types. The importance of TP in estimating rates of fish production as demonstrated by Downing et al. (1990) is supported by the importance of this parameter in our model selection for Boreal Plains lakes.

Due to the small sample size of Prairie lakes in this dataset (n=2), I was unable to model them separately. Instead, predictions for Prairie lakes were based on the equation generated for Boreal Plains lakes. This resulted in less accurate predictions (Figure 4-6), though they were not statistically different from observed values. Due to this, the post-invasion predictions of walleye yield for the Prairie lakes are much higher than those seen in the other ecozones but this can be partially accounted for by the inaccuracy of the predictions. An extension to the research presented here should be focused on better characterizing the factors influencing walleye production in Prairie lakes by surveying additional systems with available data.

Lake Winnipeg

Lake Winnipeg specifically had small predicted increases in walleye yield post-invasion (Table 4-5) though this trend was not shared by all lakes in the Plains ecozone. Predicted post-invasion Secchi depths in both basins of Lake Winnipeg do not surpass the 2 m "optimum Secchi depth" threshold, indicating an increase in walleye TOHA over the invasion period. Across all lakes of this ecozone in Manitoba, mean change in yield was -0.02 ± 0.26 kg/ha/yr, suggesting that an increase in water clarity induced by dreissenids may not have a large effect on walleye yield in these lake types.

However, TP along with TOHA was identified as a driver of walleye yield in Boreal Plains lakes as demonstrated by AIC_c model selection (Table 4-4, Equation 1). It has been hypothesized that increased phosphorus loading into Lake Winnipeg since the early 2000s has been partly responsible for the increased lake-wide harvest rates observed since that time (Figure 4-3). Recently Environment Canada, in response to increased prevalence of algal blooms on Lake Winnipeg, pledged to decrease phosphorus loadings

into the lake by 50% (to pre-1990 levels) by 2017 (Environment Canada 2013). When inputting this hypothetical 50% TP decrease into the model, walleye yield in Lake Winnipeg is predicted to decrease by 0.04 kg/ha/yr in the North Basin (a 1% decrease compared to current yield estimates) and 0.88 kg/ha/yr in the South Basin (a nearly 32% decrease). These yield levels are reminiscent of 1990's walleye harvest on Lake Winnipeg (see Figure 4-3), before the surge of high walleye landings after the year 2000. This large of a decrease in yield in the South Basin, which is the cornerstone of the walleye fishery in the lake currently, could result in substantial economic consequences for the commercial walleye fishery on Lake Winnipeg.

 Fisheries management applications

This research has implications for fisheries managers in the prairie provinces and Midwestern United States, by providing a model with which to estimate walleye production in lakes of different ecozones. I propose an alternate walleye production model that accurately predicts walleye yield in lakes from the Boreal Plains ecozone which represents a large part of walleye habitat in North America. Predictive models of walleye yield that incorporated TP were found to be a more accurate indicator of walleye production in shallow, well-mixed lakes compared with TDS. Our study further shows that using a water clarity model (developed in Chapter 2) to predict increased Secchi depth caused by invasive dreissenids, lakes from different ecozones may respond differently to dreissenid invasion, with Prairie lakes potentially increasing in production relative to Boreal Shield or Plains lakes. Future research based on the work presented in this study should focus on development of a Prairie ecozone model and generating data

for a broader range of lake types to better understand what drives variation in the predicted response of walleye populations to increases in water clarity.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B.N. Petrov & F. Ckaski (editors), Proceedings of the Second International Symposium on Information Theory, Akademiai Kiado.

Bowlby, J.N., J.A. Hoyle, J.R. Lantry and B.J. Morrison. 2010. The status of walleye in Lake Ontario 1988-2006. Pages 165-188 *In* E. Roseman, P. Kocovsky and C. Vandergoot (editors). Status of walleye in the Great Lakes: proceedings of the 2006 Symposium. Great Lakes Fisheries Commission Technical Report 69.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach (2nd edition). Springer-Verlag, New York.

Canada Map Sales. 2014. Manitoba listing: Manitoba lakes angling maps. Available from http://www.canadamapsales.com/en/catalogue/AnglingMaps/ManitobaLakes/Manitoba Listing/inind.html. [accessed 11 June 2013].

Chezik, K.A., N.P. Lester and P.A. Venturelli. 2014. Fish growth and degree-days I: selecting a base temperature for a within-population study. Can. J. Fish. Aquat. Sci. **71**:47-55.

Chow-Fraser, P. 1991. Use of the morphoedaphic index to predict nutrient status and algal biomass in some Canadian lakes. Can. J. Fish. Aquat. Sci. **48**:1909-1918.

Christie, G. C. and H. A. Wegier. 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. **45**:301-314.

Downing, J,A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. **47**: 1929-1936.

Environment Canada 2013. Planning for a Sustainable Future: A Federal Sustainable Development Strategy for Canada 2013-2016. Theme II. Maintaining Water Quality and Availability. Target 3.7: Lake Winnipeg Basin. Available from https://www.ec.gc.ca/dd-sd/default.asp?lang=en&n=AD293762-1/#t3.7. [accessed 17 December 2014].

Environment Canada and Manitoba Water Stewardship. 2011. State of Lake Winnipeg: 1999-2007. Available: http://www.gov.mb.ca/waterstewardship/water_quality/state_lk_winnipeg_ report/pdf/state_of_lake_winnipeg_rpt_technical_low_resolution.pdf. [accessed 20 November 2012].

Fisheries and Oceans Canada. 2007. Canadian Fisheries Statistics 2002-2004. Available: http://www.dfo-mpo.gc.ca/stats/commercial/cfs/2004/section7-3-14-eng.htm#ta3.2.1. [accessed 11 July 2014].

Fox, J. and G. Monette. 1990. Generalized collinearity diagnostics. J. Am. Statist. Assoc. **87**(417): 178-183.

Frie, R.V., J.K. Anderson and M.J. Larson. 1989. Age Verification of Walleyes from Lake of the Woods, Minnesota. J. Great Lakes Res. **15**:298-305.

Gale, G.E. and G.A. Goodchild. 1982. Review and reformulation of the relationship between standard conductance and total dissolved solids. Environmental Dynamics Section, Fisheries Branch, Ontario Ministry of Natural Resources, May 1982.

Government of Manitoba. 2013. Adult zebra mussels found in Lake Winnipeg. Available from http://news.gov.mb.ca/news/?item=19256. [accessed 31 October 2013].

Hagenson, I. and J.F. O'Connor. 1979. A fisheries inventory of Obukowin and Aikens Lakes, 1978. Manitoba Deptartment of Natural Resources. Fisheries MS Report No. 79-75.

Hair, J.F. Jr., R.E. Anderson, R.L. Tatham and W.C. Black. 2009. Multivariate data analysis, 7th Ed. Pearson Prentice Hall, New York, New York.

Hoyle, J.A. , J. N. Bowlby & B. J. Morrison. 2008. Lake whitefish and walleye population responses to dreissenid mussel invasion in eastern Lake Ontario. Aquat. Ecosys. Health Manage. **11**:403-411.

Johnston, T.A., W. Lysack and W.C. Leggett. 2012. Abundance, growth, and life history characteristics of sympatric walleye (*Sander vitreus*) and sauger (*Sander Canadensis*) in Lake Winnipeg, Manitoba. J. Great Lakes Res. **38**:35-46.

Koenings, J.P. and J.A. Edmundson. 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effects of yellow color and turbidity. Limnol. Oceanogr. **36**: 91-105.

Lemm, L.P. 2002. Characterization of the Canadian commercial walleye fishery. M.Sc. Thesis, Department of Agribusiness and Applied Economics, North Dakota State University, Fargo, ND.

Lester, N.P., A.J. Dextrase, R.S. Kushneriuk, M.R. Rawson and P.A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. Trans. Am. Fish. Soc. **133**:588-605.

Lumb, C.E., Franzin, W.G. and Watkinson, D.A. 2011. Pages 123-127 *in* Environment Canada and Manitoba Water Stewardship (editors). State of Lake Winnipeg 1999 to 2007: Fish.

Manitoba Water Stewardship. 2010. A Profile of Manitoba's Commercial Fishery. Available from http://www.gov.mb.ca/waterstewardship/fisheries/commercial/history.pdf [accessed 22 November 2012].

Nate, N. A., M. J. Hansen, L. G. Rudstam, R. L. Knight, and S. P. Newman. 2011. Population and community dynamics of walleye. Pages 321-374 *in* B. Barton, editor. Biology, management and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland.

Quinn, G.P. and M.J. Keough. 2002. Multiple and complex regression. Pages 111-154. Experimental design and data analysis for biologists. Cambridge University Press, New York, New York.

Rennie, M.D. 2013. Context-dependent changes in lake whitefish populations associated with dreissenid invasion. Pages 661-680 *in* T. Nalepa & D. Schloesser, editors. Quagga and Zebra Mussels: Biology, Impacts, and Control (2nd edition). CRC Press, Boca Raton, Florida.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Robillard, M.M. and M.G. Fox. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Can. J. Fish. Aquat. Sci. **63**:798-809.

Ryder, R.A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. **94**:214-218.

Sheppard, K. 2013. Spatial and seasonal variation in diet, growth and condition of walleye (*Sander vitreus*), sauger (*Sander canadensis*) and dwarf walleye (*Sander vitreus*) in Lake Winnipeg, Manitoba. M.Sc. thesis, Department of Biological Sciences, University of Manitoba, Winnipeg, MB.

Therriault, T.W., A.M. Weisse, S.N. Higgins, Y. Guo, and J. Duhaime. 2013. Risk Assessment for Three Dreissenid Mussels (*Dreissena polymorpha*, *Dreissena rostriformis bugensis*, and *Mytilopsis leucophaeta*) in Canadian Freshwater Ecosystems. Canadian Science Advisory Secretariat Research Document 2012/174.

United States Geological Survey. 2015. Zebra mussel distribution [online]. Available

from http://fl.biology.usgs.gov/Nonindigenous_Species/Zebra_mussel_distribution/

zebra_mussel_distribution.html [accessed 10 March 2015].

Zhao, Y., B.J. Shuter and D.A. Jackson. 2008. Life history variation parallels

phylogeographical patterns in North American walleye (*Sander vitreus*) populations.

Can. J. Fish. Aquat. Sci. **65**:198-211.

Table 4-1. Range of parameter values in 23 Manitoban commercially and recreationally fished lakes used in this analysis. z_{max}, maximum depth; z_{mean}, mean depth; TP, total phosphorus; TDS, total dissolved solids.

Parameter	Units	Range	Mean	Median
Area	ha	318 – 1 923 750	166 329.2	24262.0
GDD	C	1088.2 – 1746.0	1522.8	1532.3
z_{max}	m	3.0 – 32.3	15.11	16.0
z_{mean}	m	1.8 – 13.3	5.42	4.5
Secchi	m	0.44 – 3.9	1.45	1.5
TDS	mg/L	30.82 – 799.96	232.59	143.7
TP	mg/L	0.01 – 0.11	0.035	0.03
Yield	kg/ha/yr	0.078 – 5.74	1.267	0.631

Table 4-2. Principal Component Analysis (PCA) loadings of lake variables on

components 1 and 2. Bold indicates variables heavily loaded on that axis. * indicates

variables which are categorical, all others are continuous.

Variable	PC1	PC2
Ecozone*	**-0.5079**	0.2074
Area (ha)	**0.5064**	0.1941
GDD (°C)	-0.0602	**-0.4766**
TDS (mg/L)	**0.4910**	-0.0773
TP (mg/L)	0.1594	-0.3641
z_{max} (m)	-0.0716	**0.5499**
z_{mean} (m)	0.0834	0.3891
Secchi depth (m)	-0.2560	0.1114
Yield (kg/ha/yr)	-0.3712	-0.2956

Table 4-3. Model selection for Manitoban Boreal Shield Lakes. AIC_c, ΔAIC_c and $wAIC_c$ values for the seven AIC_c models. TOHA, Thermal-Optical Habitat Area (ha); TP, total phosphorus (mg/L); TDS, total dissolved solids (mg/L); Area, lake surface area (ha), z_{mean}, mean depth (m), * indicates the null model.

Model	AIC_c	ΔAIC_c	$wAIC_c$
(1) log (Harvest) = -0.933 + 0.520 (TOHA) + 0.867 (TDS)	264.91	0.00	0.582
(2) log (Harvest) = 1.937 + 0.619 (TOHA)	266.68	1.77	0.239
(3) log (Harvest) = 0.902 + 0.428 (area) + 0.502 (TDS)	268.61	3.71	0.091
(4) log (Harvest) = 3.537 + 0.632 (TOHA) + 0.502 (TP)	268.69	3.79	0.088
(5) log (Harvest) = -0.843 + 1.030 (z_{mean}) + 1.799 (TDS)	280.53	15.63	0.000
(6)* log (Harvest) = 9.128	286.84	21.94	0.000
(7) log (Harvest) = 9.694 + 0.163 (TP)	289.44	24.54	0.000

Table 4-4. Model selection for Manitoban Boreal Plains Lakes. AIC_c, ΔAIC_c and $wAIC_c$ values for the seven AIC_c models. TOHA, Thermal-Optical Habitat Area (ha); TP, total phosphorus (mg/L); TDS, total dissolved solids (mg/L); Area, lake surface area (ha), z_{mean}, mean depth (m), * indicates the null model.

Model	AIC_c	ΔAIC_c	$wAIC_c$
(1) log (Harvest) = 8.256 + 0.606 (TOHA) + 1.472 (TP)	194.34	0.00	0.935
(2) log (Harvest) = 19.947 + 2.421 (TP)	201.61	7.27	0.025
(3) log (Harvest) = 2.028 + 1.066 (area) – 0.544 (TDS)	202.08	7.74	0.019
(4) log (Harvest) = -2.340+ 1.038 (TOHA)	202.36	8.02	0.017
(5) log (Harvest) = 0.446 + 0.961 (TOHA) – 0.308 (TDS)	205.12	10.78	0.004
(6) log (Harvest) = 9.867 + 2.252 (z_{mean}) – 0.353 (TDS)	211.96	17.62	0.000
(7)* log (Harvest) = 12.601	212.74	16.88	0.000

Table 4-5. Predicted change in Secchi depth (m) and walleye yield (kg/ha/yr) post-dreissenid establishment in 23 Manitoban lakes.

Lake	Ecozone	Pre-z_{sec} (m)	Predicted post-z_{sec} (m)	Δz_{sec} (m)	Pre-yield (kg/ha/yr)	Predicted post-yield (kg/ha/yr)	Δ yield (kg/ha/yr)
Assean	Shield	0.84	1.17	0.33	0.10	0.96	0.86
Betula	Shield	1.52	1.82	0.30	3.04	3.96	0.65
Brereton	Shield	2.35	2.76	0.41	0.94	1.10	0.16
Caddy	Shield	1.55	1.90	0.35	5.74	3.38	-2.36
Cedar	Plains	1.98	2.48	0.50	0.93	0.48	-0.44
Cormorant	Plains	3.90	4.49	0.59	0.31	0.19	-0.12
Dauphin	Prairie	0.50	0.75	0.25	0.09	2.72	2.63
Eleanor	Shield	1.10	1.54	0.44	1.57	2.11	0.54
Gauer	Shield	1.94	2.43	0.49	0.30	0.43	0.13
Jessica	Shield	1.10	1.41	0.31	1.60	2.07	0.47
Little Limestone	Plains	1.50	1.97	0.47	0.43	0.49	0.06
Manitoba	Prairie	0.71	1.09	0.38	0.51	2.48	1.97
Nutimik	Shield	1.41	1.93	0.52	4.21	2.96	-1.25
Playgreen	Shield	1.64	2.11	0.47	0.93	0.64	-0.29
Setting	Shield	1.77	2.27	0.50	0.30	0.76	0.46
Sisipuk	Shield	1.50	1.97	0.47	0.76	0.52	-0.23
South Indian	Shield	0.88	1.34	0.46	0.08	0.08	0.01
Split	Shield	0.44	0.72	0.28	0.34	0.44	0.10
St. Martin	Plains	1.18	1.60	0.42	0.10	0.50	0.41
Waterhen	Plains	1.50	1.88	0.38	0.89	0.62	-0.27
White	Shield	1.59	1.92	0.33	3.85	3.41	-0.44
Winnipeg (North Basin)	Plains	1.23	1.83	0.60	0.47	0.61	0.14
Winnipeg (South Basin)	Plains	0.70	1.11	0.42	2.76	2.84	0.08
Winnipegosis	Plains	2.07	2.60	0.53	0.16	0.18	0.02

Table 4-6. Model selection for change in walleye yield (Δ yield). AIC_c, ΔAIC_c and $wAIC_c$ values for the seven AIC_c models. Secchi depth (m); TP, total phosphorus (mg/L); Area, lake surface area (ha), TDS, total dissolved solids (mg/L); z_{mean}, mean depth (m); GDD, growing degree days above 5°C, * indicates the null model.

Model	AIC_c	ΔAIC_c	$wAIC_c$
(1) Δ yield = -0.0159 + 2.317 (Ecozone[Prairie]) − 0.068 (Ecozone[Shield])	57.14	0.00	0.965
(2) Δ yield = 0.373 - 0.900 (Secchi)	65.00	7.86	0.019
(3) Δ yield = 2.128 + 0.568 (TP)	68.13	10.98	0.004
(4) Δ yield = -1.021 + 0.120 (area)	68.51	11.37	0.003
(5) Δ yield = -1.580 + 0.341 (TDS)	68.52	11.38	0.003
(6)* Δ yield = 0.654	68.56	11.42	0.003
(7) Δ yield = 0.654 - 0.337 (z_{mean})	70.12	12.98	0.001
(8) Δ yield = 0.714 - 0.079 (GDD)	71.18	14.04	0.001
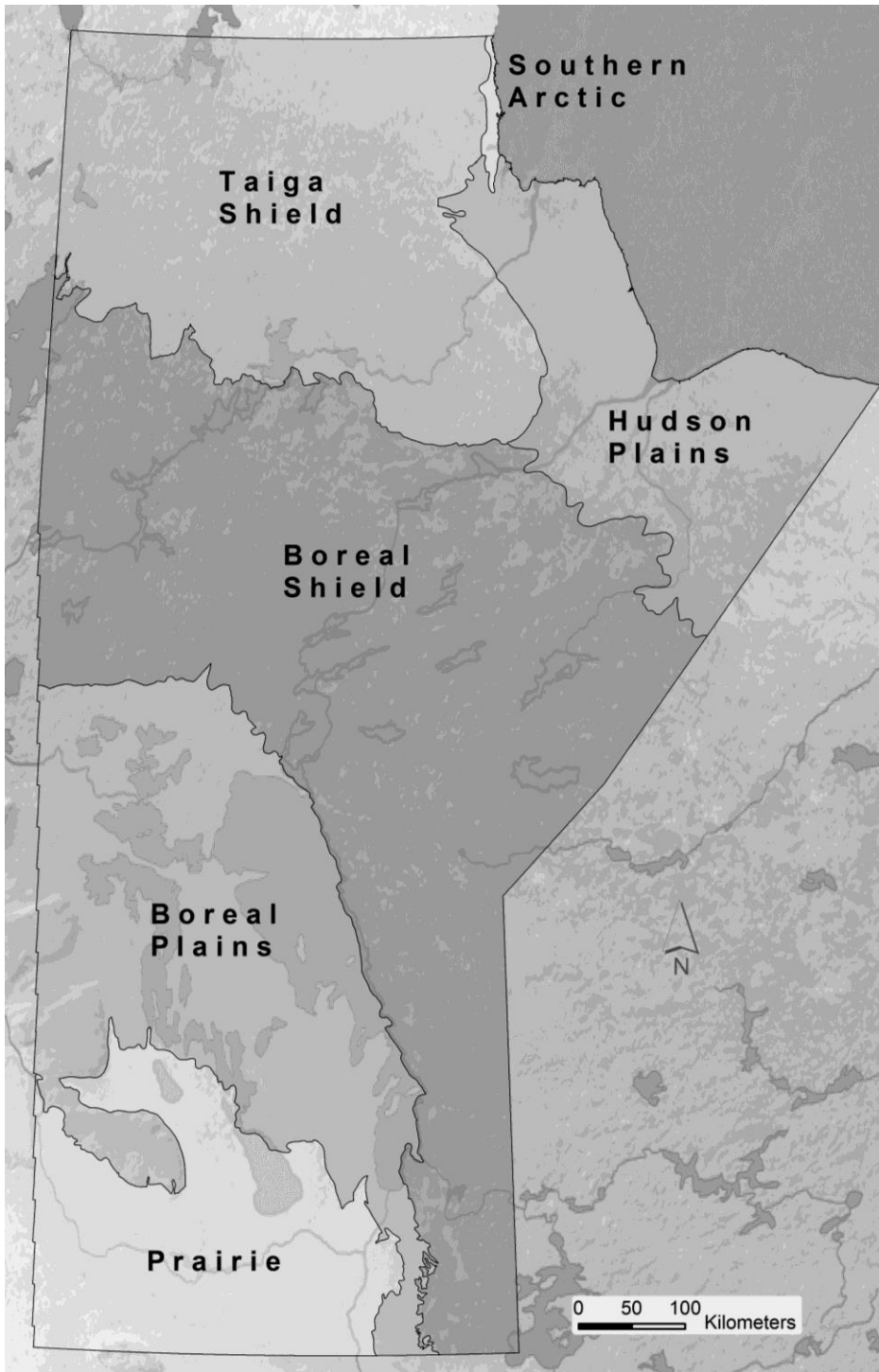
Figure 4-1. Ecozones of Manitoba.

Figure 4-2. Division of Lake Winnipeg, Manitoba into three separate zones (the "Narrows" is incorporated into the South Basin for analysis purposes).
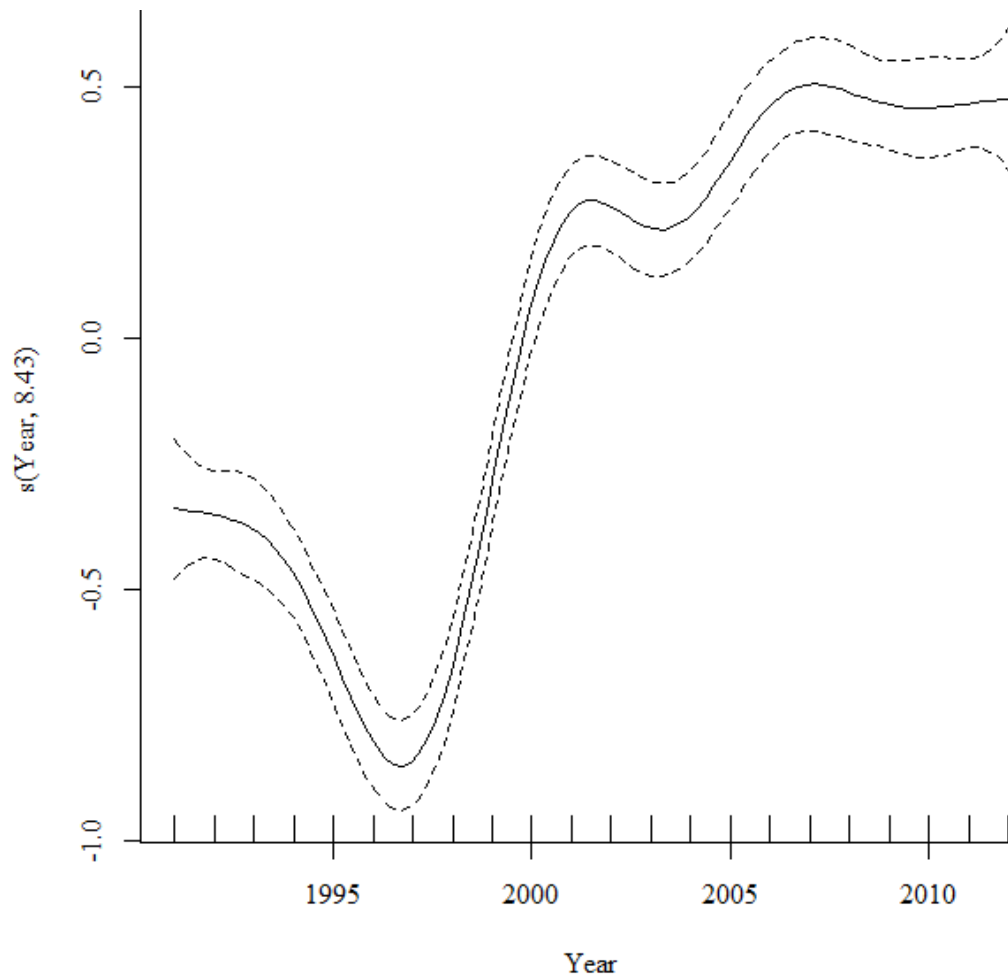
Figure 4-3. Generalized additive model (GAM) of Lake Winnipeg walleye yield from 1991-2012 with a thin-plate regression spline and 95% confidence intervals where y-axis equals *s(covariate, estimated degrees of freedom)*.
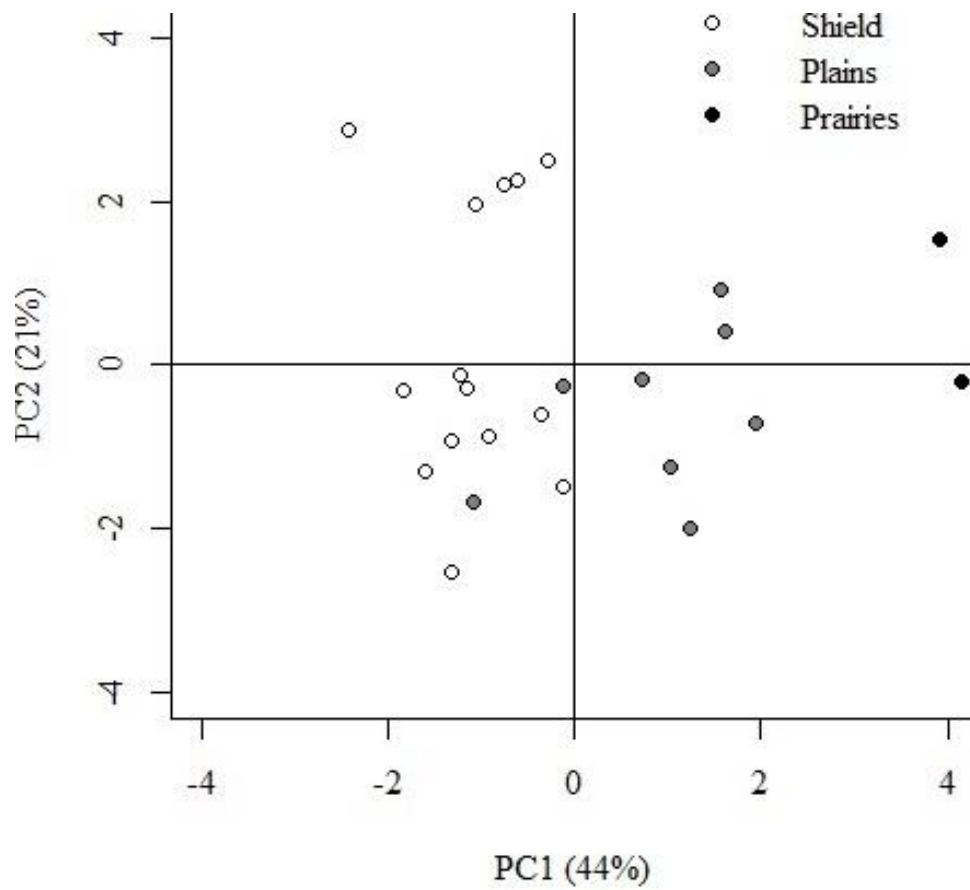
Figure 4-4. Principal Component Analysis (PCA) biplot showing variation in Manitoban

lakes separated by ecozone. Variation explained in each axis is indicated.
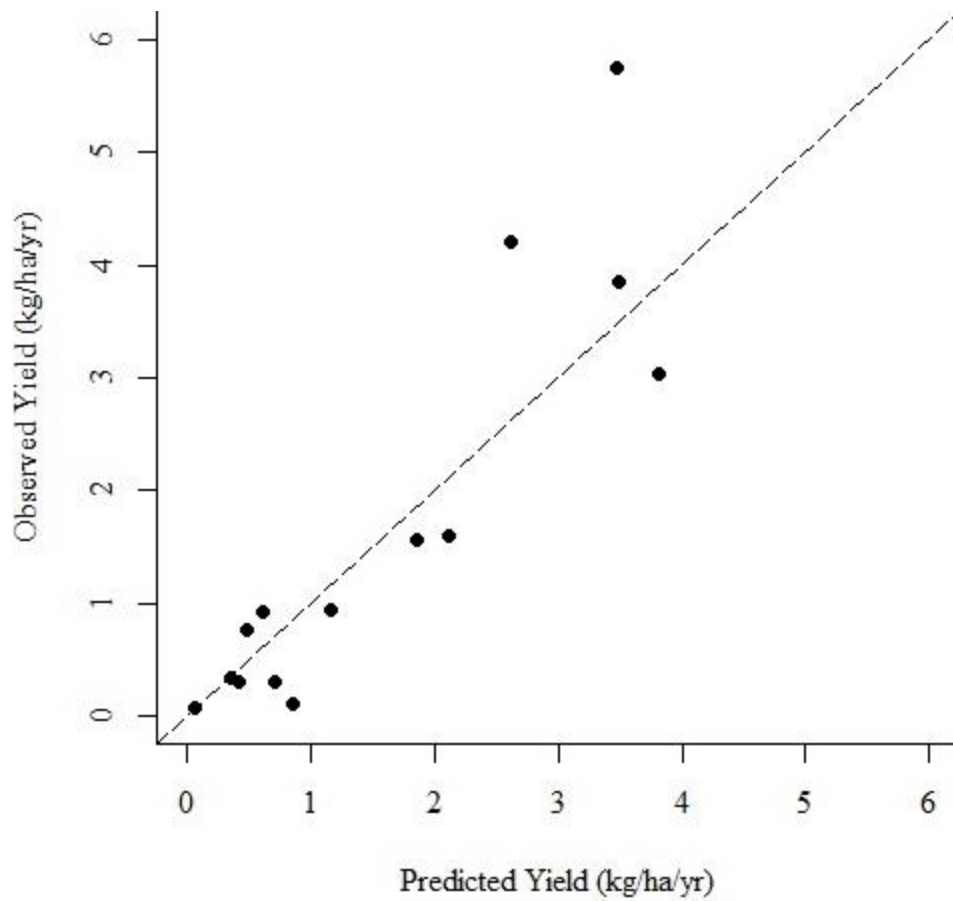
Figure 4-5. Predictions of walleye yield (kg/ha/yr) for Manitoban Boreal Shield lakes based on model using total dissolved solids (TDS, mg/L) and thermal-optical habitat area (TOHA, ha). Table 4-3, Equation 1. Dashed line, 1:1 line.
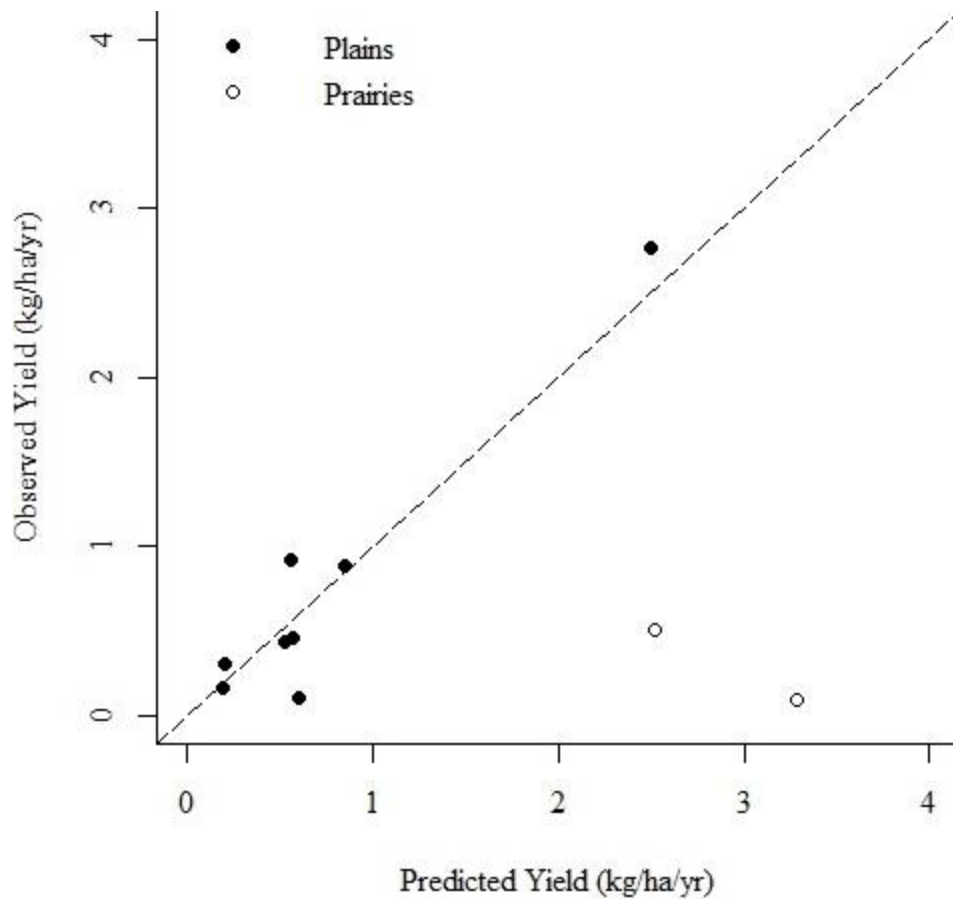
Figure 4-6. Predictions of walleye yield (kg/ha/yr) for Manitoban Boreal Plains and Prairies lakes based on model using total phosphorus (TP, mg/L) and thermal-optical habitat area (TOHA, ha). Table 4-4, Equation 1. Dashed line, 1:1 line.
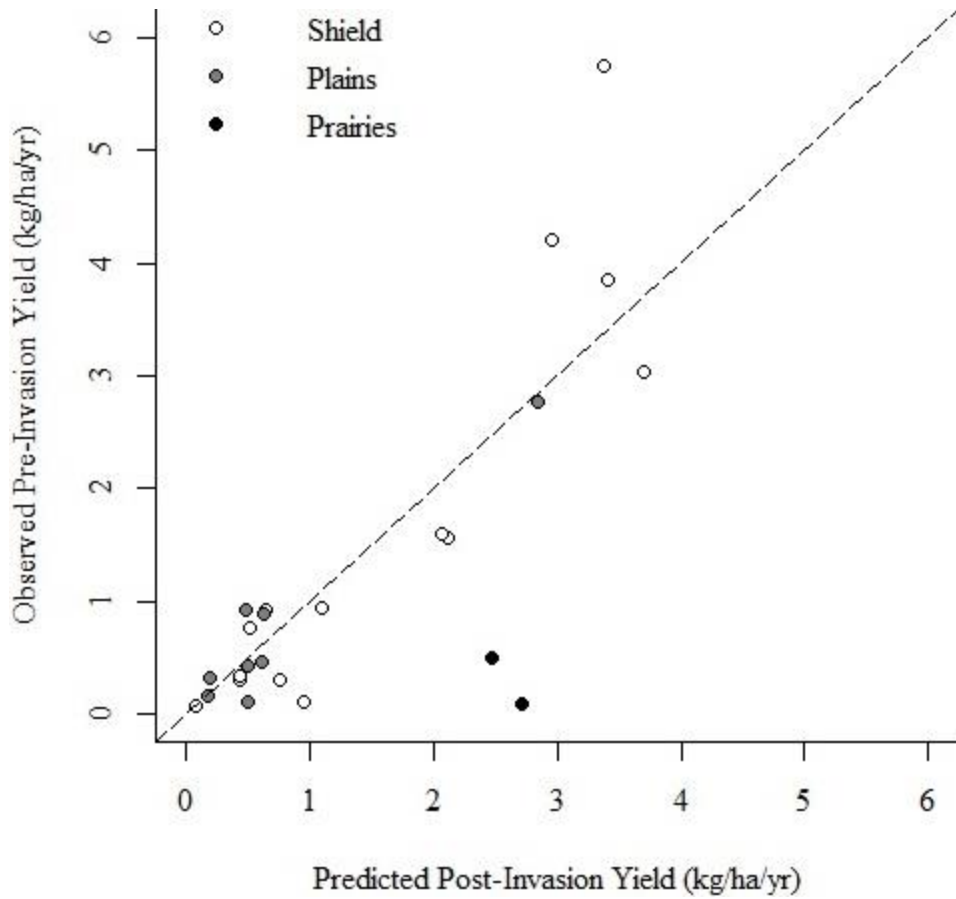
Figure 4-7. Predicted walleye yield (kg/ha/yr) in all Manitoban lake types based on increased Secchi depth (m) due to invasive dreissenid mussels using ecozone-specific model formulations. Dashed line is a 1:1 and represents no change; values below the line show an increase in walleye yield due to increased water clarity.

Chapter 5: Conclusions and Recommendations

In this thesis, I have demonstrated the major impacts that dreissenids can have on lake water clarity and, in turn, the major effects that they may have on walleye populations, an economic driver of commercial and recreational fisheries in North America. This was achieved using a statistical modelling approach beginning with a longitudinal study examining a number of lakes invaded with dreissenids to determine the observed changes in water clarity seen in these systems to inform a predictive model. This model was extended to systems where an observed decline in walleye yield was seen following dreissenid invasion and was found to account for a portion of the decline, while total phosphorus (TP) reductions and angler effort may have also contributed. Application of walleye production models to lakes in Manitoba highlighted the importance of ecozone in models predicting walleye yield and forecasting these effects in lakes. However, projected effects of dreissenid invasion on the basis of water clarity improvements alone are predicted to have variable effects on walleye yield in these systems.

Previous research has shown the effects of dreissenids on lake water clarity (Higgins and Vander Zanden 2010) but to date none have looked at extending that into a predictive model of the changes in Secchi depth seen with dreissenid invasion. In Chapter 2, I utilized lake characteristics shown to have an effect on magnitude of water clarity changes to develop a model which predicts change in Secchi depth in uninvaded lakes. Secchi depth is a readily available indicator of ecosystem condition and results of Chapter 2, as well as other published meta-analyses (Higgins and Vander Zanden 2010), suggest that the effects of dreissenids on water clarity are long-term, with no sign of

diminishing within 15-20 years post-invasion. This model provides a tool for mangers who wish to explore the potential impacts of dreissenid establishment on systems at risk to understand effects on light dynamics and can be extended to understand impacts on other ecosystem processes and biota, including macrophyte growth, benthic production and fisheries.

Synergistic effects due to this long-term change in water clarity can be drastic and effect many aspects of lake ecology. Mixing depth, also known as the depth of thermal stratification, is an important part of lake productivity as it affects distribution of plankton and fish (Yu and Culver 2000) and is affected by increased water clarity by altering the depth to which sunlight penetrates and heats the water column. The water clarity model can be extended to mixing depth via percent light transmission (Fee et al. 1996) and has predicted a significant effect on mixing depth with dreissenid-induced water clarity increases.

Fish populations are not immune to the effects of water clarity, specifically for the light-sensitive walleye species. Increased water clarity is hypothesized to affect walleye production by constricting walleye into sub-optimal optical habitat (Lester et al. 2004) due to their propensity for dim-light habitat (Ryder et al. 1977). This could affect metabolism and reproductive success, along with prey interactions and increased competition with predators (Bowlby et al. 1991; Leisti et al. 2006; Nate et al. 2011; Robillard and Fox 2006). Using a walleye production model from Lester et al. (2004) in combination with the water clarity model, walleye yield was estimated to decline by 5% in a set of Ontarian lakes in a post-invasion scenario with increase clarity. Combined with

considerations regarding thermocline depth, walleye could be further constricted into smaller optimal thermal habitat zones (Lester et al. 2004).

Investigation into freshwater lakes in the Great Lakes region which have seen declines in walleye yield following the invasion of dreissenid mussels suggested the decline observed accompanying increases in water clarity were likely exacerbated by other factors. Though clarity explained one third of the observed decline in walleye yield, concurrent declines in both walleye-targeted angler effort and TP contributed as well. Data from Ontario Ministry of Natural Resources (2008) indicates that while total fishing effort has remained constant, bass-targeted effort has increased causing a decrease in walleye-targeted effort thereby decreasing harvest of this species. TP declined over this time period as a result of both legislative impositions of phosphorus reduction strategies as well as the sequestering of phosphorus in the nearshore via the nearshore phosphorus shunt (Hecky et al. 2004). The importance of TP in estimating walleye production featured prominently in Chapter 4, where TP played a role in estimating walleye yield from Boreal Plains lakes, though lake type seems to modulate the importance of this parameter as a driver of fish production.

Combination of the walleye production models with the water clarity model provided a prediction of change in walleye yield under an invasion scenario in these non-invaded Manitoban lakes. While change in walleye yield post-dreissenid invasion was found to be non-significant, this response has been shown to be best predicted by both ecozone and water clarity. Predicted outcomes varied greatly in contrast to observed declines in walleye yield in some Ontarian lakes (see Chapter 3). This is hypothesized to

arise from synergistic effects of dreissenids on thermal habitat and mixing depth (see Chapter 2) and TP (Hecky et al. 2004), suggesting changes in water clarity alone may underestimate the impacts of invasive dreissenids on walleye populations.

The potential applications of these results are not limited to lakes within the province of Manitoba. The province of Manitoba was chosen as a study site for this research because of the presence of the three ecozones (Boreal Shield, Boreal Plains and Prairies) that generate the majority of walleye production across North America (Fisheries and Oceans Canada 2007) and the overlap of these ecozones with the distribution of this species. Other aquatic ecosystems which are at threat of invasion by dreissenids can apply the models developed here to inform the potential effects caused by dreissenid mussels on lake water clarity, mixing depth and walleye production rates. There could be value into conducting further research into American lakes which have walleye production estimates, like those in Minnesota, to see if lakes in Boreal Shield and Plains ecozones similar to those in Manitoba respond in the same way as predictions for Manitoban lakes.

Directed future research and monitoring should be expanded to potentially seek to develop a model for Prairie lakes as they were not well estimated by the model produced for Boreal Plains lakes. Research and monitoring should collect data from additional systems in order to provide a greater sample size for lakes of this ecozone in order to apply a model with higher accuracy. The highlighted importance of TP in Boreal Shield lakes indicates that more research needs to be done on the role of TP on walleye yield before phosphorus input into Lake Winnipeg is drastically reduced.

Much research has focused on the effects of invasive dreissenid mussels on water quality and nutrient dynamics while little has addressed the effect on fish communities. Previous research has shown the importance of the link of fish production to productivity at the base of the food chain (Ryder 1965, Downing et al. 1990). The work reported here supports these links, and highlights the potential role for invasive dreissenids in modifying these linkages. In order to determine the exact mechanisms of these invasions which cause changes in walleye populations, more research needs to be done in this field.

References

Bowlby, J. N., Mathers, A., Hurley, D. A., Eckert, T. H., 1991. The resurgence of walleye in Lake Ontario. *In* Status of Walleye in the Great Lakes: Case Studies Prepared for the 1989 Workshop. *Edited by* P.J. Colby, C.A. Lewis and R.L. Eshenroder. Great Lakes Fish. Comm. Spec. Publ. 91. pp 169–205.

Downing, J,A., C. Plante, and S. Lalonde. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. **47**: 1929-1936.

Fee, E.J., R.E. Hecky, S.E.M. Kasian and D.R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. Limnol. Oceanogr. **41:** 912-920.

Fisheries and Oceans Canada. 2007. Canadian Fisheries Statistics 2002-2004. Available from http://www.dfo-mpo.gc.ca/stats/commercial/cfs/2004/section7-3-14-eng.htm#ta3.2.1. [accessed 11 July 2014].

Hecky, R.E., R.E.H. Smith, D.R. Barton, S.J. Guildford, W.D. Taylor, M.N. Charlton, and T. Howell. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Can. J. Fish. Aquat. Sci. **61**: 1285-1293.

Higgins, S.N. and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. **80:** 179-196.

Leisti, K. E., E.S. Millard and C.K. Minns. 2006. Assessment of submergent macrophytes in the Bay of Quinte, Lake Ontario, August 2004, including historical context. Can. MS Rpt. Fish. Aquat. Sci. 2762.

Lester, N.P., A.J. Dextrase, R.S. Kushneriuk, M.R. Rawson and P.A. Ryan. 2004. Light and temperature: key factors affecting walleye abundance and production. T. Am. Fish. Soc., **133:** 588-605.

Nate, N. A., M. J. Hansen, L. G. Rudstam, R.L. Knight and S.P. Newman. 2011. Population and community dynamics of walleye. *In* Biology, management, and culture of walleye and sauger. *Edited by* B.A. Barton. American Fisheries Society, Bethesda, Maryland, pp. 321-374.

Robillard, M.M. and M.G. Fox. 2006. Historical changes in abundance and community structure of warmwater piscivore communities associated with changes in water clarity, nutrients, and temperature. Can. J. Fish. Aquat. Sci. **63**: 798-809. doi: 10.1139/f05-259.

Ryder, R.A. 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. **94**:214-218.

Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board. Can. **34**(10): 1481-1491. doi: 10.1139/f77-213.

Yu, N. And D.A. Culver. 2000. Can zebra mussels change stratification patterns in a small reservoir? Hydrobiologia **431:** 175-184.

Appendix A. List of freshwater lakes (n = 53) included in analysis of dreissenid effects. Z indicates presence of zebra mussels only, B indicates both zebra and quagga mussels. * indicates pre-calculated grand Secchi depth (m) means and not raw annual data. ↓[P] indicates known phosphorus reduction efforts.

Lake	Data Source	Location	Mixing Status	Year Invaded	Area (ha)	Max. Depth (m)	Mean Depth (m)	Species Present	↓[P]
Beulah	EPA Storet[1]	WI, USA	Stratified	1999	337.5	17.7	5.2	Z	N
Big Cedar	EPA Storet	WI, USA	Stratified	2002	377.2	32	10.4	Z	N
Carlos	EPA Storet	MN, USA	Stratified	2009	1051.6	49.7	14	Z	N
Cedar	Higgins[2]	WI, USA	Mixed	2001	57.46	6.4	2.74	Z	N
Champlain	EPA Storet	NY/VT, USA	Stratified	1993	112664.5	121.9	19.5	Z	N
Clear	EPA Storet	IA, USA	Mixed	2005	1500	9.1	3	Z	N
Cowdrey	EPA Storet	MN, USA	Stratified	2009	98.2	15.9	6.7	Z	N
Crystal	EPA Storet	WI, USA	Stratified	2001	52.2	18.6	6.1	Z	N
Darling	EPA Storet	MN, USA	Stratified	2009	424.9	18.9	5.8	Z	N
Dunmore	EPA Storet	VT, USA	Stratified	1999	419.7	32	33.5	Z	N
Erie (central)	Higgins *	CAN/USA	Stratified	1989	1618400	29	18.3	B	Y
Erie (east)	Higgins *	CAN/USA	Stratified	1990	615600	64	24	B	Y
Geneva	EPA Storet	WI, USA	Stratified	1995	2117	41.2	18.6	Z	N
Golden	Higgins	WI, USA	Stratified	2003	101.1	14.02	6.4	Z	N
Green	Higgins	WI, USA	Stratified	2001	2972.8	71.9	31.7	Z	N
Gull	MPCA[3]	MN, USA	Stratified	2010	4025.4	24.4	8.8	Z	N
Hunters	EPA Storet	WI, USA	Mixed	2002	54	11	1.5	Z	N
Huron	Higgins *	CAN/USA	Stratified	1990	5959600	229	59	B	Y
Lac La Belle	EPA Storet	WI, USA	Stratified	1999	471	13.7	3.4	Z	N
Leelanau	Higgins *	MI, USA	Stratified	1997	3483	36.9	13.1	Z	N
Little Muskego	EPA Storet	WI, USA	Stratified	1999	204.7	19.8	4.3	Z	N
Long	Higgins	WI, USA	Stratified	2002	170	14.3	6.7	Z	N
Machinakee	Higgins	WI, USA	Mixed	2002	180	6.4	1.8	Z	N

Margaret	MPCA	MN, USA	Mixed	2008	89.8	7.9	3.2	Z	N
Mary	EPA Storet	WI, USA	Stratified	2002	120	10.1	2.7	Z	N
Metonga	EPA Storet	WI, USA	Stratified	2001	824.8	24.1	7.6	Z	N
Mille Lacs	EPA Storet	MN, USA	Mixed	2005	51891.3	12.8	6.4	Z	N
Minnetonka	MPCA	MN, USA	Stratified	2010	5960.8	34.4	8.5	Z	N
Nagawicka	EPA Storet	WI, USA	Stratified	1998	397	27.4	11	Z	N
North	EPA Storet	WI, USA	Stratified	2002	178	23.8	11.3	Z	N
Oconomowoc	EPA Storet	WI, USA	Stratified	1999	331	18.3	9.8	Z	N
Oneida	KNB[4]	NY, USA	Mixed	1991	20670	16.8	6.8	B	Y
Onondaga	Higgins *	NY, USA	Stratified	1992	1200	19.5	10.9	B	N
Ontario	Higgins *	CAN/USA	Stratified	1989	1896000	244	86	B	Y
Ossawinnamakee	MPCA	MN, USA	Stratified	2003	279.5	19.2	6.4	Z	N
Pawaukee	EPA Storet	WI, USA	Stratified	2001	1009	13.7	4.6	Z	N
Pelican	MPCA	MN, USA	Stratified	2009	3386.1	31.7	6.4	Z	N
Pike	Higgins	WI, USA	Mixed	2003	211.2	13.7	4.1	Z	N
Poygan	EPA Storet	WI, USA	Mixed	2000	5675.3	3.4	1.8	Z	N
Rice	EPA Storet *	MN, USA	Mixed	2005	130.5	7.6	3	Z	N
Rice	OMNRF [5]*	ON, CAN	Mixed	1994	9183.5	13.4	2.6	Z	N
Seneca	J.D. Halfman[6]	NY, USA	Stratified	1992	17320.6	198.4	88.6	B	N
Shawano	EPA Storet	WI, USA	Mixed	2001	2500	12	2.7	Z	N
Silver	Higgins *	WI, USA	Stratified	1994	190	13.1	4.8	Z	N
Simcoe	OMOE[7]	ON, CAN	Stratified	1994	72200	44	14	B	Y
St Clair	Higgins *	CAN/USA	Mixed	1988	110000	6.4	3	Z	N
Upper Nemahbin	EPA Storet	WI, USA	Stratified	1998	112.1	18.3	9	Z	N
Upper Phantom	Higgins	WI, USA	Mixed	2002	43.3	8.8	3.4	Z	N
Upper Prior	EPA Storet	MN, USA	Stratified	2007	136.4	13.7	3.4	Z	N
Victoria	EPA Storet	MN, USA	Stratified	2009	168.8	18.3	10.7	Z	N
Wabusee	Higgins	WI, USA	Mixed	1999	52.2	22.86	5.79	Z	N

| Wind | EPA Storet * | WI, USA | Mixed | 2002 | 372 | 14.3 | 3.1 | Z | N |
| Winnebago | EPA Storet | WI, USA | Mixed | 1999 | 53393.8 | 6.4 | 4.6 | Z | N |

[1] = EPA Storet database, available at: http://www.epa.gov/storet/, [2] = Higgins and Vander Zanden 2010, [3] = MPCA, 520 Lafayette Road N, St. Paul, MN 55155-4194, [4] = KNB database, available at: https://knb.ecoinformatics.org/, [5] = OMNRF, 300 Water Street, Peterborough, ON K9J 8M5, [6] = OMOE, 125 Resources Road, Etobicoke, ON M9P 3V6

Appendix B. Predictive equations of thermal-optical habitat area and walleye yield based on Lester et al. 2004.

This appendix describes the formulae developed by Lester et al. (2004) to estimate walleye thermal-optical habitat area (TOHA, ha) and yield (kg/ha/yr).

Walleye thermal-optical habitat area

TOHA was approximated as

$$\text{TOHA} = (\text{GDD}-623)^{0.73}\,\text{Area}\,P_T z_{rel} e^{-z_{rel}/0.12k} \tag{B1}$$

where GDD = growing degree days (°C), Area = lake surface area (ha), P_T = proportion of lake area above the thermocline, z_{rel} = relative Secchi depth (m) and k = water clarity parameter.

Relative Secchi depth (z_{rel}) is calculated as

$$z_{rel} = \frac{z_{sec}}{z_{max}\,(1-e^{-s})} \tag{B2}$$

where z_{sec} = Secchi depth (m), z_{max} = maximum depth (m) and s = basin shape parameter.

Basin shape (s) is calculated as

$$s = \frac{3r+(r^2+8r)^{0.5}}{4(1-r)} \tag{B3}$$

where $r = \dfrac{z_{mean}}{z_{max}}$, where z_{mean} = mean depth (m).

Walleye yield

Yield was approximated as

$$\text{Yield} = 0.011\,\frac{\text{TOHA}}{\text{Area}}\,\text{TDS}^{0.534} \tag{B4}$$

Appendix C. List of Manitoban lakes with data available. * denotes lake met criteria to be included in analysis. Comm. indicates lakes fished commercially, Rec. indicates lakes fished recreationally only.

Lake	Prov.	Type	Ecozone	Area (ha)	z_{max} (m)	z_{mean} (m)	GDD (°C)	z_T (m)	z_{sec} (m)	TDS (mg/L)	TP (mg/L)	Yield (kg/ha/yr)
Assean*	MB	Comm.	Shield	7630	19.8	3.0	1088	0	0.8	131.06	0.020	0.099
Beresford	MB	Rec.	Shield	295	6.0	3.0	1744	0	1.6	46.70	0.020	n/a
Betula*	MB	Rec.	Shield	521	6.7	1.8	1744	0	1.5	85.00	0.030	3.040
Big Whiteshell	MB	Rec.	Shield	1773	10.4	2.8	1689	4.1	1.8	77.63	0.050	n/a
Bird	MB	Rec.	Shield	683	13.8	9.9	1744	0	1.6	23.98	0.020	n/a
Black	MB	Rec.	Shield	632	7.0	3.3	1744	0	1.5	33.00	0.025	n/a
Booster	MB	Rec.	Shield	616	18.0	5.6	1744	6	6.0	37.30	0.020	n/a
Brereton*	MB	Rec.	Shield	882	6.4	4.1	1689	0	2.4	30.82	0.073	0.940
Caddy*	MB	Rec.	Shield	318	5.8	2.9	1689	0	1.6	59.14	0.030	5.740
Cedar*	MB	Comm.	Plains	124600	10.0	4.2	1517	0	2.0	223.00	0.019	0.925
Cormorant*	MB	Comm.	Plains	33300	27.5	8.5	1444	0	3.9	185.96	0.012	0.312
Dauphin*	MB	Comm.	Prairie	51830	3.0	1.9	1645	0	0.5	293.71	0.074	0.091
Echo	MB	Rec.	Shield	1390	21.0	8.3	1744	11.1	3.0	55.00	0.020	n/a
Eleanor*	MB	Rec.	Shield	934	26.8	7.9	1744	0	1.1	79.97	0.030	1.570
Gauer*	MB	Comm.	Shield	26300	20.0	4.8	1088	0	1.9	90.96	0.020	0.297
Gem	MB	Rec.	Shield	839	12.0	5.7	1744	7.6	2.1	57.00	n/a	n/a
Jessica*	MB	Rec.	Shield	815	4.9	2.0	1689	0	1.1	55.65	0.050	1.600
Little Limestone*	MB	Comm.	Plains	3524	10.9	6.0	1517	0	1.5	241.76	0.014	0.434
Manitoba*	MB	Comm.	Prairie	462400	7.0	5.0	1738	0	0.7	673.99	0.101	0.505
Nutimik*	MB	Rec.	Shield	637	32.3	11.9	1744	0	1.4	97.63	0.033	4.210
Playgreen*	MB	Comm.	Shield	67500	18.6	4.0	1340	0	1.6	194.67	0.041	0.927
Setting*	MB	Comm.	Shield	13468	23.3	5.8	1369	0	1.8	103.19	0.029	0.296

Sisipuk*	MB	Comm.	Shield	22224	18.0	5.1	1547	0	1.5	79.92	0.023	0.757
South Indian*	MB	Comm.	Shield	201500	30.0	9.8	1088	0	0.9	62.83	0.022	0.078
Split*	MB	Comm.	Shield	26900	23.0	5.6	1088	0	0.4	184.33	0.041	0.340
St. Martin*	MB	Comm.	Plains	33631	6.0	3.9	1738	0	0.1	658.00	0.022	0.102
Waterhen*	MB	Comm.	Plains	17550	4.6	2.4	1515	0	1.5	626.71	0.028	0.893
White*	MB	Rec.	Shield	637	7.0	2.3	1744	0	1.6	85.00	0.040	3.850
Winnipeg (NB)*	MB	Comm.	Plains	1923750	19.0	13.3	1517	0	1.2	186.76	0.061	0.467
Winnipeg (SB)*	MB	Comm.	Plains	451250	14.0	9.7	1746	0	0.7	189.45	0.107	2.764
Winnipegosis*	MB	Comm.	Plains	519800	18.0	4.2	1517	0	2.1	670.66	0.021	0.162
Andy	ON	Rec.	Shield	163	14.6	6.0	1398	7	4.5	61.29	0.008	n/a
Atikwa	ON	Rec.	Shield	5388	59.5	13.2	1499	9	4.7	26.58	0.002	n/a
Dogtooth	ON	Rec.	Shield	2728	42.0	10.8	1500	8.5	3.7	29.98	0.013	n/a
Dryberry	ON	Rec.	Shield	10905	105.5	22.1	1500	10	6.3	20.08	0.005	n/a
Hawk	ON	Rec.	Shield	892	102.7	27.5	1467	10	7.0	27.36	0.008	n/a
Populus	ON	Rec.	Shield	666	39.0	8.2	1500	7	3.8	51.19	0.007	n/a
Windermere	ON	Rec.	Shield	96	49.1	11.6	1430	8	6.8	28.11	0.012	n/a
Winnange	ON	Rec.	Shield	2388	112.8	27.4	1500	0	6.6	23.31	0.006	n/a