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Simulation of zebra mussels (*Dreissena polymorpha*) invasion and evaluation of impacts on Mille Lacs Lake, Minnesota: An ecosystem model

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ABSTRACT

In less than a decade after being first noticed in 2005, Zebra mussels (*Dreissena polymorpha*) became fully established in Mille Lacs Lake, Minnesota, USA. To explore the ecosystem-wide impact of this invasion in the premier walleye (*Sander vitreus*) lake, an ecosystem model with 51 functional groups was built using Ecopath and Ecosim (EwE) modelling suite. The model which represents the 1985 ecosystem condition of the lake was tuned to observed time series of fish abundance and fisheries catch data from 1985 to 2006. Zebra mussels were setup with a high initial biomass, and an adequate fishing pressure was applied on it with an aim to neutralize the effect on ecosystem caused by the inclusion of the mussels. At the onset of 2005 (the first year the mussels were observed in the lake), the fishing pressure was released with different trajectories so that we could mimic the non-nutritional challenges the species could have faced during its irruption in the lake. The fitted model was simulated to the year 2036 (30 years). To enhance the credibility of the model prediction, we compared the prediction with the available field data from 2007 to 2012: the model successfully forecasted most of the changes seen in the lake after the period of fitted-data. The simulation results indicated system-wide collapse of major predators including walleye due to the bottom-up trophic control as zebra mussels efficiently filter out the phytoplankton from the system. The result also indicated that the population of zebra mussels in the lake stabilized after attaining the maximum density within few years of the invasion. Furthermore, the model predicted a significant boost in smallmouth bass (*Micropterus dolomieui*) population when the mussels were incorporated in the diet of crayfish; remarkably, the predatory pressure did not cause a large impact on zebra mussels biomass. Our capability to predict the response of Mille Lacs Lake to zebra mussels invasion would largely depend on the dynamics of plankton groups, the response of juveniles of higher trophic fish species like walleye to the changing dynamics of plankton groups, and the response of yellow perch (*Perca flavescens*) population—a major prey in the system.

1. Introduction

Zebra Mussels (*Dreissena polymorpha*) are freshwater, sessile, filter-feeding mussels known for their tremendous reproductive potential (Mackie, 1991), high water-filtration rate (Kryger and Riisgård, 1988), and fast colonization on bottom substrates (Berkman et al., 1998; Ludyanskiy et al., 1993). After infestation, zebra mussels rapidly attain high densities: Lake Erie was reported to have a density of more than 3×10^5 individuals m^{-2} during 1990 (MacIsaac et al., 1991); average abundance of the mussels in Oneida Lake in 2001–2008 was 6000 individuals m^{-2} (Naddafi and Rudstam, 2013). Effective filtration of phytoplankton by zebra mussels has been observed to cause decreased productivity, improved water-clarity (Fahnenstiel et al., 2010) and changes to the plankton community (Allinger and Reavie, 2013; Fahnenstiel et al., 1995; Fishman et al., 2010). Their high level of planktivory affects the availability of nutrients and food for other species in the system. On account of their ability to modify benthic habitat structure and their effect on ecosystem function, invasive molluscs have often been referred to as 'ecosystem engineers' (Crooks, 2002; Gestoso et al., 2013; Gutiérrez et al., 2003). However, the species may also have some beneficial effects such as improving the water quality as observed in highly eutrophied Lake Erie (Allinger and Reavie, 2013).

Human-aided dispersal made possible the spread of this prolific species native to the Ponto-Caspian region (Black, Caspian, and

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Azov seas) through various regions of Europe—observed in England in 1824 (Karatayev et al., 1997)—and from Europe to North America (Karatayev et al., 1997; Ricciardi and MacIsaac, 2000). Lake St Clair was the first to witness the existence of zebra mussels in North America in 1988; later, it spread throughout the Great Lakes region (Mellina and Rasmussen, 1994) and eventually dispersed to lakes in Eastern USA and Canada (Benson, 2014). Many factors could be implicated in the swift proliferation of the mussels in North American waters (McMahon, 1996) such as: absence of effective predators like round goby (*Neogobius melatostomus*), a predator in their native waters (Naddafi and Rudstam, 2014); having high fecundity and growth rate; early maturity and short lifespan; and high temperature tolerance (Allen et al., 1999; McMahon, 1996). For these reasons, zebra mussels are considered "aggressive invaders" (Karatayev et al., 2007).

The complex food web of Mille Lacs Lake (MLL), Minnesota, USA includes around 50 fish species along with other vertebrates and invertebrates. Planktivory by zebra mussels affects the bottom of the food-web. Further, fisheries play an important role in determining the dynamics of food-web because the fished-species are integral component of the ecosystem in which they live. To assess the influence of zebra mussels invasion on the ecosystem of Mille Lacs Lake coupled with fishing pressure required an efficient ecosystem-wide modelling exercise. We built an ecosystem model using Ecopath with Ecosim (EwE) modelling suite (Christensen and Walters, 2004; Christensen et al., 2008) to examine the trophic impacts of zebra mussels invasion on Mille Lacs Lake ecosystem. There are some EwE-based explorations of ecosystem-wide impacts of zebra mussels invasion in Bay of Quinte, Canada, and Oneida Lake, USA (Miehls et al., 2009); Lake Huron and Lake Michigan (Langseth et al., 2012); and recently Saginaw Bay, Lake Huron (Kao et al., 2014). However, this is probably the first ecosystem modelling exercise on an important walleye lake ecosystem to assess the potential impacts on native species.

2. Materials and methods

2.1. Study area

Mille Lacs Lake is the second largest lake within Minnesota, located in east-central Minnesota (46.23° N, 93.64° W) (Fig. 1). The glacial lake covers an area approximately 537 km^2 with about 1080 km^2 of watershed area (Heiskary et al., 1994). The northern half of the lake has most of the lake's mud flats while the southern half of the lake has more gravel and rock bars. Maximum depth of the lake is 12.8 m while average depth is 8.8 m. The lake is one of the most productive large lakes for walleye fisheries (3.6 kg ha^{-1} year^{-1}) in the state (Radomski, 2003). Besides walleye, other principal game fish communities in the lake are yellow perch (*Perca flavescens*), northern pike (*Esox Lucius*), muskellunge (*Esox masquinongy*), and smallmouth bass (*Micropterus dolomieui*). In addition, at least 43 other fish species along with invertebrates and other vertebrates are part of the ecosystem. Yellow perch, cisco (*Coregonus artedi*), different species of shiners (*Notropis* spp.), darters (*Etheostoma* spp.), and minnows (*Pimephales* spp.) are the main forage species of the lake (MNDNR, 1997). A list of fish species used in the model with their scientific names is included as a supplementary information (Table A.1) provided with the manuscript. This lake has been infested with several invasive species such as: common carp (*Cyprinus carpio*), zebra mussels, Chinese mystery snails (*Bellamya chinensis*), banded mysterysnail (*Viviparus georgianus*), spiny water flea (*Bythotrephes longimanus*), Eurasian watermilfoil (*Myriophyllum spicatum*), and curly leaf pondweed (*Potamogeton crispus*) (MNDNR, 2012). Among those, zebra mussels have shown the most rapid spread in the lake: scuba divers first sighted them in 2005 at merely 3 sites (Fig. 2). The average density increased from just 5 individuals m^{-2} in 2008 to 11,540 individuals m^{-2} in 2013 (Tom Jones, MNDNR, Pers. Comm.). The species have spread across the eastern shore of the lake as well as along few sites on the western shore (Fig. 2).

2.2. Ecosystem model for Mille Lacs Lake, Minnesota

As mentioned before, an Ecopath and Ecosim (EwE version 6) ecosystem model was developed for Mille Lacs Lake with an aim to study the food-web dynamics of the lake, especially as a consequence of establishment of zebra mussels in the system. The Ecopath model characterized the ecosystem condition of the lake in the year 1985. Ecosystem drivers such as producers, consumers, and detritus were combined into 50-functional groups in the model: 21 groups of fish; 2 groups of birds; 8 groups of invertebrates; 1 group each for otters and minks, turtles, frogs, and zooplankton; 3 groups of producers; and 1 group for detritus. The functional groups and their dietary interactions in the model have been developed through an extensive process of consultation and interaction with Minnesota Department of Natural Resources (MNDNR), the chief collaborator in the research. Details of functional groups and other relevant materials about parameterization of the EwE model were precisely tabulated and included with this manuscript as a supplementary information (Table A.1). Age-structure in Ecopath is modelled using a multi-stanza setup: 6 species of fish were modelled with multi-stanza. The stanza feature allows a model to account for differences between juvenile and adult in the diet composition (many juveniles are planktivorous while adults are piscivorous), in the vulnerability to predation, and in the fishing mortality.

Each functional group in the static mass-balance model (Ecopath) was parameterized using life-history, production, consumption and diet matrix. The details of Ecopath and Ecosim can be explored in Christensen and Walters (2004); however, the following section presents the key aspects of the modelling routine. The mass-balance constraint ensures that the extraction of energy (by predation, fishing, etc.) from a functional group is replenished through consumption by the group; the two master equations of Ecopath explain those energy balance. The first equation ensures energy balance among a group as (Eq. (1)):

$$B_i * \left(\frac{P}{B}\right)_i = Y_i + \sum_j B_j * \left(\frac{Q}{B}\right)_j * DC_{ji} + E_i + BA_i + B_i * \left(\frac{P}{B}\right)_i * (1 - EE_i) \quad (1)$$

where subscript i and j indicates prey and predator group respectively; B stands for Biomass, P for production, Y for total fishery catch, Q for consumption, and E for net migration; DC_{ji} is the fraction of prey i in the diet of a predator j; BA accounts for biomass accumulation; and EE explains ecotrophic efficiency i.e. *the* fraction of a group mortality explained in the model.

The second equation explains the energy balance within a functional group as (Eq. (2)):

$$Consumption = Production + Respiration + Unassimilated\,food \quad (2)$$

The static mass-balance Ecopath model is then used to initiate a time-based dynamic simulation (Ecosim) for tracking changes in the biomass of species with temporal changes in catch patterns, food-web (predators-preys interaction), and environmental condition. The dynamic change is assessed using Eq. (3) derived from the first master equation of Ecopath:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i) * B_i \quad (3)$$