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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 (Maclsaac 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)):

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

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)):

$$\textit{Consumption} = \textit{Production} + \textit{Respiration} + \textit{Unassimilated food} \tag{2}$$

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:

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

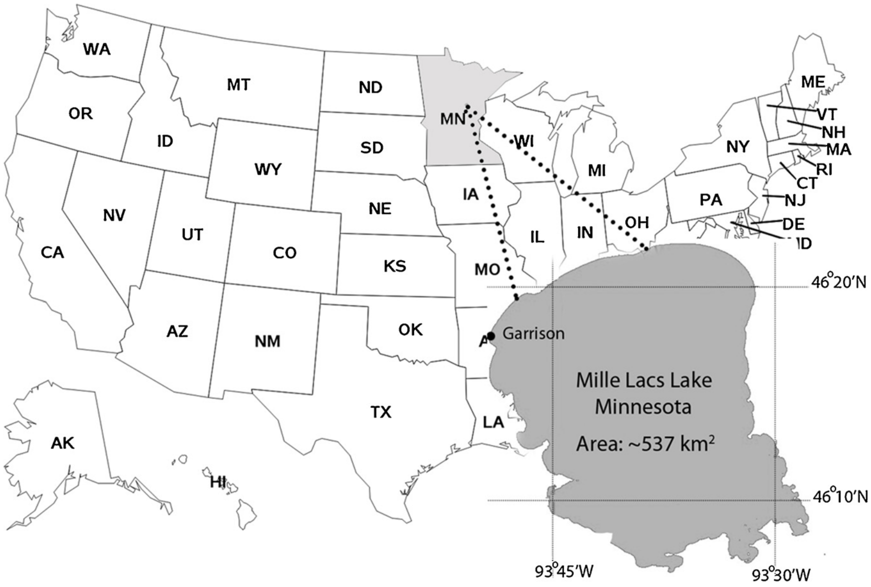

Fig. 1. Mille Lacs Lake, Minnesota, USA. Inset lake map also shows the location of the city of Garrison on the north-west side.
Source: Background US map-generated using SAS/GRAPH map datasets; the inset for Mille Lacs Lake was obtained from Minnesota Department of Natural Resources.

Fig. 2. Spreading of zebra mussels in Mille Lacs Lake, Minnesota. The species was first noticed in 2005 at 3 sites, and by 2013, it spread into large regions of the lake.

where dB_i/dt is the biomass growth rate of group i in time-interval dt; g_i denotes net growth efficiency (production/consumption) of group i; Q_{ji} is the consumption by group i (group i is a predator) while Q_{ij} is for group i consumed by predators (group i is a prey; I_i is the immigration; MO_i explains other mortality rate excluding fishing and predation and F_i is the fishing mortality rate.

Consumption (predation) by a group depends on available biomass of its prey and their exchange rate between unavailable and available states (foraging arena theory: Walters et al., 1997). The dynamic simulation was tuned with historic time series data of catch and abundance in order to reconstruct the past pattern of the important species from 1985 through 2006.

2.2.1. Parametrization of zebra mussels in 1985 EwE model

An EwE modelling approach requires that all functional groups be included in the model from the start of simulations; hence, zebra mussels were included as an additional functional group (51st). A summary of steps taken in order to model zebra mussels' invasion using EwE was shown in the conceptual diagram (Fig. 3). The filter-feeders obtain their food by filtering water—an adult zebra mussel can filter around a litre/day, and phytoplankton constitutes most of their diet (Benson et al., 2012; Snyder et al., 1997). Langseth et al. (2012) used (80%) phytoplankton in the diet of zebra mussels in Lake Huron model; however, Jaeger (2006) indicated higher proportion of detritus in their diet. Based on the literatures, diet of the mussels was adjusted as 70% phytoplankton and 30% detritus. The consumption per unit biomass (Q/B), 4.1 year^{-1}, was obtained from an energetics-based estimate (Schneider, 1992). Production over biomass (P/B) value was obtained from the study of Jaeger (2006) as 1.35 year^{-1}.

The biomass of zebra mussels were estimated from the annual monitoring data obtained by scuba diving at 250 sites in the Lake. In 2013, zebra mussels were observed in 88 out of the 250 sites monitored (Fig. 2), indicating that the mussels had spread to about 34% of the lake locations (Tom Jones, MNDNR, pers. comm.). The density at the various sites ranged from 538 to 32,292 individuals m^{-2} with an

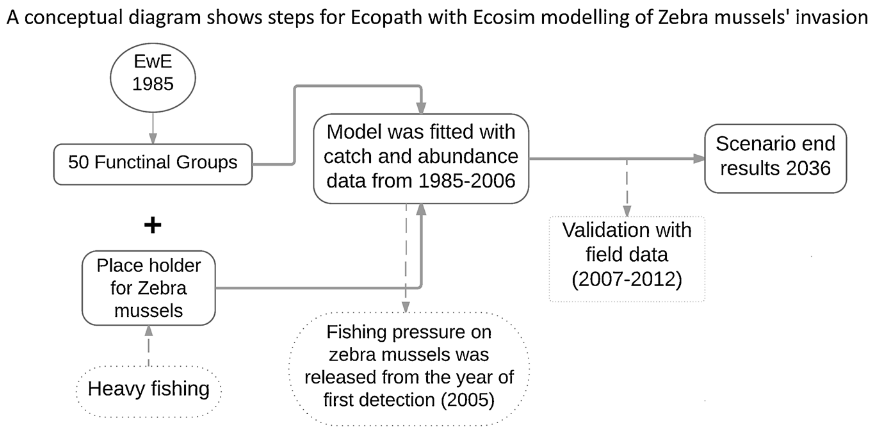

Fig. 3. A summary of key steps for the modelling of zebra mussels' invasion in Ecopath with Ecosim (EwE).

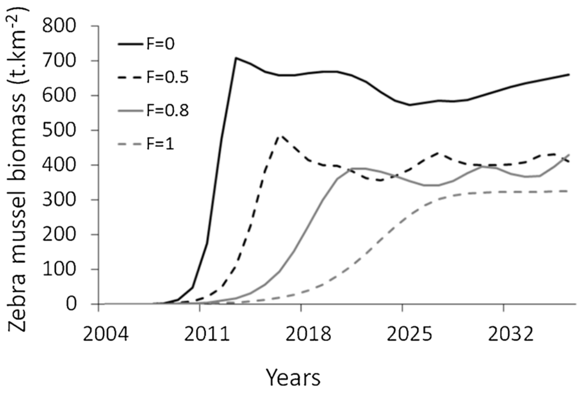

Fig. 4. Zebra mussels trajectories at different fishing mortalities. The solid black line shows the simulation of invasion when there is no fishing pressure on the zebra mussels, and the other lines show the projection when there are some fishing pressures on them.

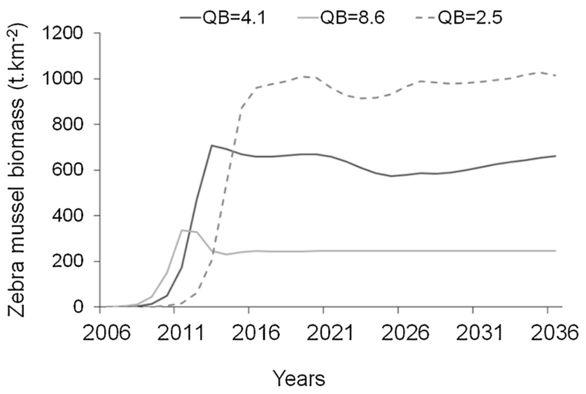

Fig. 5. Sensitivity test on zebra mussels trajectories to their Q/B parameter. $Q/B = 4.1$ represents the base value chosen for the Ecopath model.

average of 11,540 individuals m^{-2}. Based on the samples obtained at two sites (Spider Island and Deep Cove) in the lake, on an average, zebra mussel weighs 0.28 g. By multiplying the weight and density, the current biomass was estimated as 1100 tons km^{-2}, and 95% confidence limit for the estimate were 600 to 1600 tons km^{-2}.

2.2.2. Simulation of the invasion

The newly added functional group (zebra mussels) was set up with a high initial biomass (1100 tons km^{-2}) in 1985. The biomass was constrained to be very low until 2005 by applying high fishing pressure on it. The fitted model (fitted from 1985 to 2006) was simulated for 30 years (till the year 2036). At the onset of 2005, the fishing pressure was gradually released allowing the mussels biomass to increase; the rate of relaxation was calibrated in such a way that the dynamics of observed density matched with the trend of predicted density during the initial period of invasion. To satisfy the ecopath mass-balance principle, a negative biomass accumulation of the magnitude equal to the amount of phytoplankton consumed by zebra mussels was applied onto the phytoplankton group (Langseth et al., 2012).

Based on a comparison across multiple lakes infested with zebra mussels, Burlakova et al. (2006) suggested that availability of suitable substrate limited zebra mussels population size. In addition, extended periods of high temperature (29–30 °C) in summer affected growth and tissue condition and caused mortality of zebra mussels in Lower Mississippi River (Allen et al., 1999). Mille Lacs Lake also experienced higher temperature in few years after the invasion of zebra mussels, so there were possibilities that these changes could stress zebra mussels to some extent. In an effort to mimic these sort of non-nutrional challenges the mussels could have faced in invading and colonising in the lake, we used different trajectories for releasing fishing pressure from zebra mussels. The non-nutritional challenges may include: substrate limitation, high summer temperatures, and others for which we do not have much information such as presence of predators that were not accounted for in the model or calcium levels in water.

2.2.3. Effects on zebra mussel predators

Analysis of stomach contents of major fish predators in Mille Lacs Lake provided evidence of very low predation on zebra mussels: 118 smallmouth bass, 115 northern pike, and 677 walleye diets were analysed, and the quantities of zebra mussels in their diets were 0.0616%, 0.0048%, and 1.030% respectively (Tyler Ahrenstorff, MNDNR, pers. comm.). We incorporated these diet estimates in the model and explored the impact on zebra mussels and its predators. Though not observed in Mille Lacs Lake, several field-experiment based studies reported that crayfish feed on zebra mussels (Goote and Bergman, 2012; Love and Savino, 1993; Macisaac, 1994); therefore, we also explored scenarios with zebra mussels constituting (i) 20%, (ii) 30% and, (iii) 50% of crayfish diet.

3. Results

3.1. Zebra mussels biomass

The model was able to reproduce the explosion of zebra mussels reasonably well in the lake. When fishing pressure was completely released and zebra mussels were allowed to grow freely, their biomass increased rapidly and plateaued at ~700 tons km^{-2}. The predicted biomass was lower than the observed biomass, but the

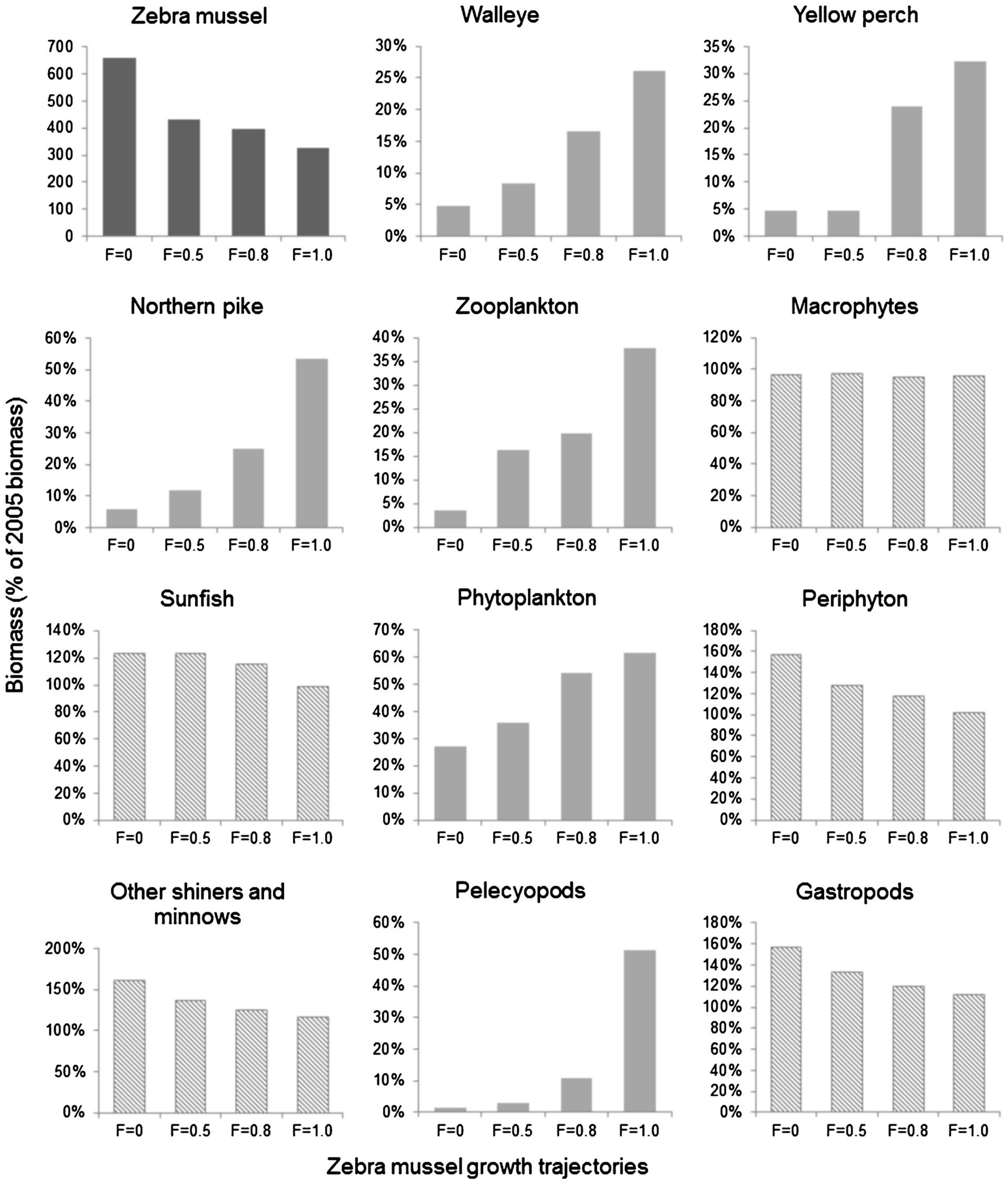

Fig. 6. Biomass of various species at the end of the simulation. The end biomasses are expressed as a percentage of their corresponding 2005 biomasses (except zebra mussels for which the absolute biomass is shown). *F* values indicate the level of fishing pressure applied on zebra mussels from the year of invasion 2005 onwards. The grey bars represent species which are negatively impacted by zebra mussels; the shaded bars show species that are either positively affected or unaffected by zebra mussels.

estimate was within confidence interval (CI) of observed biomass (95% CI, 600–1600). In the model, the biomass at which zebra mussels levelled-off depended on the amount of fishing pressure released. By applying different trajectories of fishing mortality, we simulated non-nutritional challenges for spread of zebra mussels in the system, and the lowest value at which the biomass stabilized was ~300 tons km^{-2} (Fig. 4).

Further, we also conducted a simple test of the sensitivity of zebra mussels' biomass trajectory in response to their consumption to biomass ratio (Q/B). We found that the level to which zebra mussels would increase was sensitive to their consumption rate (Q/B) (Fig. 5). At the higher Q/B levels, biomass plateaued at a lower level; this was because at higher Q/B more phytoplankton was consumed to achieve the same level of production.

3.2. *Effects on food chain: bottom-up trophic control*

It was found that increases in zebra mussels caused phytoplankton to decline drastically (Fig. 6: phytoplankton) which resulted in a decline in zooplankton. Since these plankton groups also

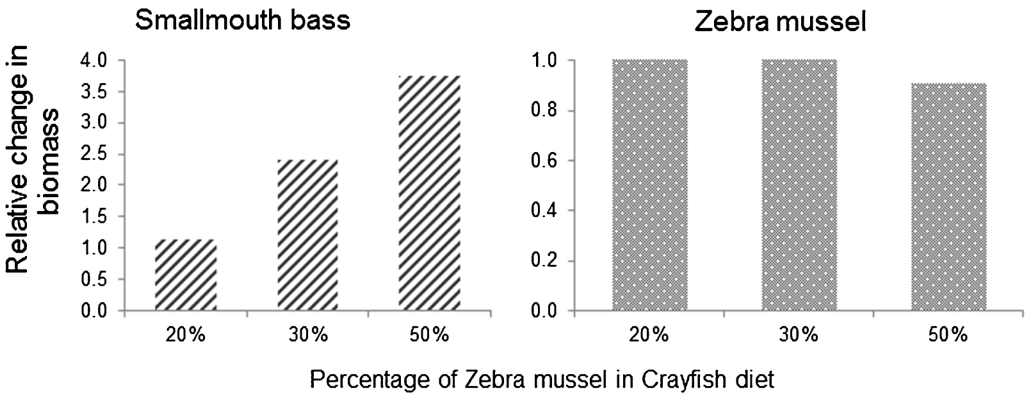

Fig. 7. Zebra mussels-crayfish-smallmouth bass interactions. The graph shows biomass levels for smallmouth bass and zebra mussels at the end of simulation year when zebra mussels were included in the diet of crayfish by 20%, 30%, and 50%. The changes are shown relative to not including zebra mussels in diet of crayfish.

constitute a bulk of diets of numerous insect species; their abundance also declined in response to the decline in plankton. Zooplankton and insects together form a large proportion of young yellow perch diet; hence, a decline in yellow perch was observed. Zooplankton is also a major food item for many juvenile fish. Therefore, a reduction in juvenile fish especially yellow perch which is the most important prey in Mille Lacs Lake badly affected the apex predators such as walleye and northern pike. In summary, the simulation results showed that invasion of zebra mussels caused the decline of the primary and secondary producers in the lake, and this effect moved up the food chain and major fish species declined (Fig. 6).

On the other hand, some species showed increases in biomass (Fig. 6). The model predicted an increase in periphyton which led to an increase in sunfish (*Lepomis* spp.), other shiners and minnows (the functional group comprised a number of tiny forage species (Table A.1). Macrophytes remained at their base levels in the models, and gastropods which consume macrophytes increased because their main predators declined while food remained continuously available.

3.3. *Effects on zebra mussel predators*

The effects of adding small amounts of zebra mussels (∼1%) to the diets of walleye, northern pike, and smallmouth bass made no observable difference in the dynamics of zebra mussels or other species in the lake. On the other hand, adding zebra mussels to crayfish diets led to increase in crayfish biomass. Since smallmouth bass mostly consumes crayfish, increase in the latter also led to increase in biomass of smallmouth bass. As the proportion of zebra mussels in crayfish diet was increased, crayfish biomass continued to increase and smallmouth bass also steadily increased. Noticeably, the increased predation had a very small impact on zebra mussels (Fig. 7).

4. Confronting model prediction with field data

As mentioned the EwE model was fitted to the historical catch and abundance data from 1985 to 2006, and the fitted model was driven for another 30 years (till 2036). The model predictions were compared to the available field data of zebra mussels' biomass, water clarity in the form of Secchi disk readings, zooplankton density, and the abundance of many fish functional groups from 2007 to 2012. In most cases, model predictions were consistent with the trends in observed data as shown in the following sections.

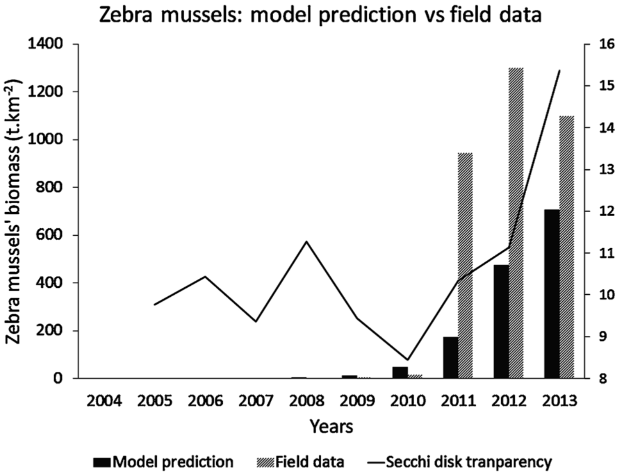

Fig. 8. Zebra mussels observed biomass vs predicted biomass from the invasion (2005) to 2013. Water transparency in the form of Secchi disk readings range during the same time period was also overlaid on the graph (line graph with axis on right).

4.1. *Zebra mussels biomass vs water clarity*

Both observed and predicted biomass trend of zebra mussels included rapid population growth, though field estimates were higher than the model's prediction (Fig. 8). That zebra mussels attained maximum density within few years of invasion was observed in several lakes in North America (Burlakova et al., 2006), and the present findings from Mille Lacs Lake further support the typical rapid growth pattern. Zebra mussels are filter-feeding species well-known for their capacity to clarify water by filtering phytoplankton out of a system. Mille Lacs Lake transparency trend (Secchi disk readings) has also increased rapidly with the mussels (Fig. 8): the transparency trend which was almost stable around 12 feet historically, increased after 2010 and reached to as high as 15 feet. 3 feet increment in transparency of the lake in merely 3 years reflects their tremendous presence in the lake as well as their filtration rate.

4.2. *Zooplankton: model prediction vs observed density*

In the ecosystem model, zooplankton entirely feeds on phytoplankton; thus a reduction in phytoplankton biomass caused zooplankton to decline substantially. Total observed zooplankton density declined from nearly 70 l^{-1} in the beginning of invasion to nearly 25 l^{-1} by the year 2013. The model predicts the similar declining trend (Fig. 9). However, with regards to the proportion of different types of zooplankton, the observed data indicate that

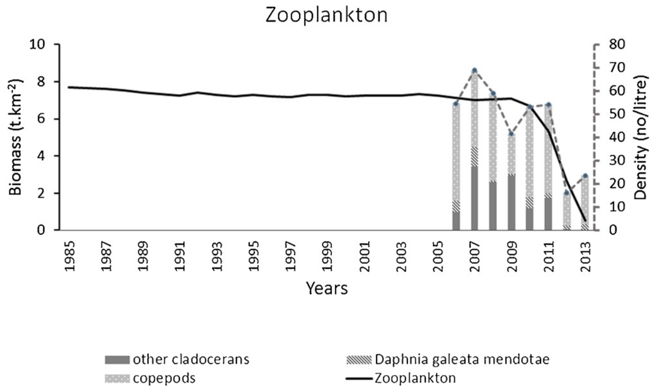

Fig. 9. Zooplankton biomass prediction vs observed density. The line graph represents zooplankton biomass predicted by model while bars (axis on right) represent observed density. Each bar also shows the relative proportion of different species of zooplankton.

copepods were least affected compared to cladocerans. Since the model included a single group for entire zooplankton communities, it was unable to capture the differences to the species level. Changes in zooplankton community structure indicate that different community of zooplankton interact differently with phytoplankton community, and that there may be some phytoplankton components that were less affected by zebra mussels' irruption and supported zooplankton like copepods from declining. This is perhaps a major limitation of the present model with single phytoplankton and zooplankton group, especially with regards to using the model for future prediction. This suggests that any future work for studying ecosystem-wide impacts of zebra mussels' invasion should include a higher resolution of plankton at the lower trophic levels.

4.3. *Fish species: model prediction vs observed CPUE*

To keep track of changes in the abundance of fish, Mille Lacs Lake is monitored by test-netting at 32 locations across the lake. The pattern of average CPUE time-series observed from these nets was compared from the model predictions for a number of species given below (Fig. 10). Model prediction was in quite good agreement with the observed trend in most of the cases.

5. Discussion

5.1. *Zebra mussel biomass*

The rapid increase in zebra mussels followed by levelling-off of the population is a response that has been recorded across several instances of zebra mussel infestation. In a study across multiple lakes infested with zebra mussels, it was observed that populations of the mussels increased rapidly and then stabilized; it took approximately 3 years to reach maximum density from the detection of their presence and about 7–12 years from the first date of invasion (Burlakova et al., 2006). In Saginaw Bay in Lake Huron and Long Point Bay in Lake Erie, zebra mussels reached their maximum levels within two years of being detected (reviewed in: Burlakova et al., 2006). In Mille Lacs Lake, as stated earlier, the presence of zebra mussels was recorded at 3 sites in 2005, and by 2012, the population achieved a very high-density and since then the population has been remaining relatively stable

The model predicted similar trends across all the scenarios explored using the different fishing pressure trajectories. The sensitivity analysis indicated that the biomass at which zebra mussel population stabilised could vary depending on their Q/B parameter: a lower Q/B (than used in the model) predicted much higher biomass. The sensitivity of the model prediction to the Q/B parameter and stabilization at a biomass level lower than the field estimate indicates towards a nutrient limitation for zebra mussels in Mille Lacs Lake. If the model prediction of stable biomass was reached at a level higher than the field estimate, we would have had more confidence in a non-nutrient limitation.

Yet another approach to model the invasion in EwE is to introduce zebra mussels with negligible biomass (merely a place holder) in year 1985. The low biomass level be then maintained till the year before the invasion and the biomass be forced to increase from the year of invasion using the external time-series data. The approach of forcing the biomass appears simpler, but we observed two major challenges in the approach. The biomass of zebra mussels increased rapidly and when the forcing mechanism was used till the years of available field-data, the model was not stable to respond to changes from the current year (2013) onwards for which the zebra mussel field estimates of biomass were not available. The main advantage of using the method adopted here was that it was possible to compare the zebra mussels response predicted by the model against the observed biomass. It was also possible to tune the model to respond to observed changes and in 2013 the behaviour of the zebra mussels functional group was stable such that it could be used for future projections unlike the other scenario where users needed to depend on the forcing mechanism to maintain the invasive species biomass within a model.

5.2. *Effects on food web*

Studies across various lakes established a consistent decline in chlorophyll level after the invasion of zebra mussels (Cha et al., 2013; Higgins et al., 2011; Mida et al., 2010). Huge declines in various phytoplankton species, especially diatoms in Lake Michigan were recorded following invasion by mussels (Fahnenstiel et al., 2010; Vanderploeg et al., 2010). Reduction in phytoplankton negatively affected zooplankton (Watkins et al., 2013), and this was linked to decline of lake whitefish (*Coregonus clupeaformis*) in the Great Lakes (Herbst et al., 2013).

The model prediction about the system-wide collapse of forage and predatory fish species at the end of simulation (2036) may be an overestimation of zebra mussels' influence. Some weaknesses in the model could have created a simple pathway for the predicted declines—the model was constrained by a single aggregate group for phytoplankton and zooplankton each, and therefore it was not able to explore the shift in phytoplankton composition as observed in some other lakes: shift from larger to smaller diatoms in Lake Erie (Barbiero et al., 2009) and sometimes to less desirable groups like cyanobacteria and *Mi*crocystis (Fishman et al., 2010). Different phytoplankton groups might be differently vulnerable to zebra mussels, thus not totally limiting the availability for all zooplankton. This is reflected in the sampling data (Fig. 9) where total zooplankton in the lake declined after the invasion, but the copepods were less affected compared to that of daphnia and other cladocerans. Similarly the model cannot capture changes in zooplankton communities such as observed in Lake Huron: amphipod diporeia and cladocerans were replaced by copepods (Barbiero et al., 2009). Plankton community shifts would affect different fish groups differently based on their dependence on specific phytoplankton and zooplankton groups. The limitations of the model are further complicated by the invasion of spiny water fleas in Mille Lacs Lake (first recorded in 2009) because this species is also capable of changing the zooplankton community structure (Yan et al., 2001) thereby affecting the food availability for the juvenile fish communities.

The response of Mille Lacs Lake food web to zebra mussels invasion is governed by at least three factors: (1) How do the juveniles

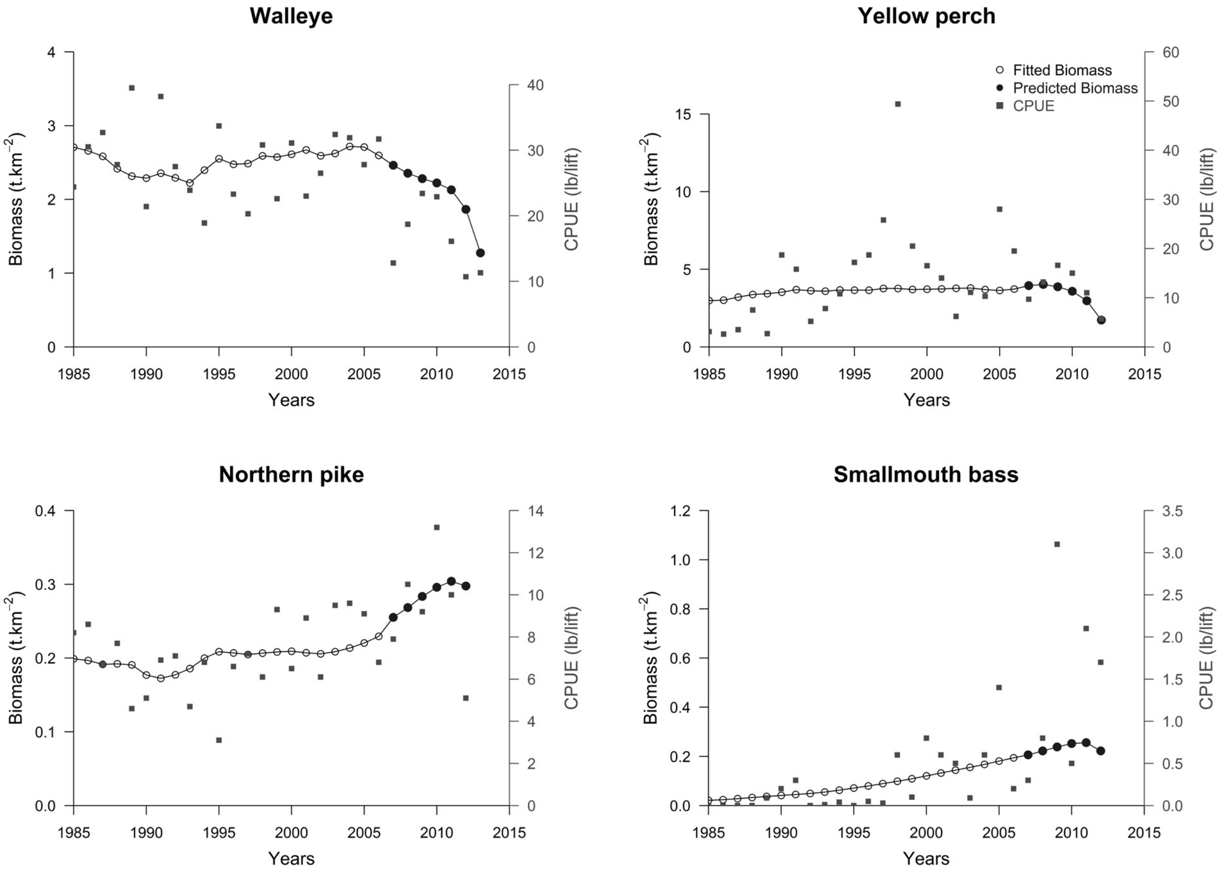

Fig. 10. Model prediction of biomass against assessment gill net CPUE. Squares represent observed CPUE trend (axis on right). Empty circles are from the ecosystem model fitted to CPUE data (1985–2006) while filled-circles are the model predictions starting from year 2007. The trend of the predicted lines is in close agreement with the observed data.

of different fish groups respond to shifts in plankton community; (2) How does the invertebrate community respond to zebra mussels; and lastly but perhaps most importantly from Mille Lacs Lake perspective (3) Is yellow perch able to use alternate pathways for obtaining energy (i.e. an altered plankton community or an altered invertebrate community). But, this would not be a trivial exercise. Even if we split the different phytoplankton and zooplankton groups, the model will not be strengthened unless these new groups are parameterized differently.

5.3. Effects on zebra mussel predators

Crayfish densities and smallmouth bass densities have reportedly increased in the last few years in Mille Lacs Lake. The analysis suggests that a possible cause for this could be an increase in crayfish owing to zebra mussels consumption. Crayfish foraging on other invertebrates is not affected negatively by zebra mussels because of their ability to “burrow under zebra mussel colonies” (Beekey et al., 2004). It is probably worth mentioning the potential of invasion by round goby (predator of zebra mussels in its native waters) in Mille Lacs Lake ecosystem. Round gobies have been observed in the Great Lakes and have been spotted in the Duluth/Superior Harbour, it cannot be ruled out that the species could potentially enter into Mille Lacs Lake. In Lake Erie round gobies invasion occurred in 1990; its population increased, and it became an important prey for smallmouth bass (Hogan et al., 2007) and introduced-salmon; however, round gobies in Lake Erie also heavily consume smallmouth bass eggs (nests) and therefore affect smallmouth bass recruitment (Steinhart et al., 2004). Thus a potential round goby invasion could have mixed impacts on the Mille Lacs Lake ecosystem.

From a management perspective in Mille Lacs Lake, it is important to carefully monitor the responses of species especially yellow perch and walleye over the next few years. If yellow perch population remains relatively stable, walleye and many other top predators would probably not face prey shortage. However, in Lake Ontario, zebra mussels affected walleye recruitment causing the fisheries to be less productive (Hoyle et al., 2008) due to decreased survival of early life stages. The decreased survival could be from an increased foraging risk under clearer water or lack of suitable prey; however, it is not possible to predict similar life-history bottlenecks based on the current model resolution. A key task for management would be to carefully monitor the abundance trends of the life history stages of yellow perch and walleye till it is clear whether there are issues related to decline in walleye recruitment or prey shortage. The model suggests that there is a possibility to increase recreational fishing on smallmouth bass. Allocations for fishing walleye have consistently decreased over the last few years. Smallmouth bass might offer options to diversify recreational fishing opportunities on Mille Lacs Lake and thereby support local industries dependent on recreational fisheries.

6. Conclusion

The model was the first attempt at predicting ecosystem-wide impacts of zebra mussel invasion in Mille Lacs Lake. Model predictions were in close-agreement with the field-data for many species when compared from year 2006 to 2012. It predicted severe declines in phytoplankton and zooplankton densities followed by a system-wide collapse of forage fish and top predators including walleye. The model predicted increases in species such as shiners and minnows and sunfish which depend on periphyton. Model predictions of system-wide collapses by the end of simulation year might be overestimated owing to a limited resolution of the model at the level of primary and first-order secondary consumers. The work predicted a steady increase in smallmouth bass population subsequent to a possible crayfish-zebra mussels interaction in the lake. Finally we conclude that zebra mussels populations would probably stabilize after the initial population boom already recorded based on the different scenarios explored in the model.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.01.019.

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