



Shifting trophic control of fishery–ecosystem dynamics following biological invasions

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Abstract. Increasing human population size and mobility have accelerated the translocation of nonnative species globally, which has become a major threat to conservation of biodiversity and ecosystem services. Introduced species can disrupt species interactions of the recipient ecosystem, triggering system-wide events, and amplify or dampen effects of existing pressures. We show how two pervasive intercontinental invasive consumers in North American lakes, dreissenids (filter-feeding mussels) and *Bythotrephes* (carnivorous zooplankton), nonlinearly modify consumer–resource dynamics and undermine management interventions to rebuild cold-water predatory fish biomass. Synthesizing 30 yr (1986–2015) of lake-wide monitoring data with a dynamic mass-balance food-web model (consisting of 61 species and trophic groups), we reconstructed historical food-web dynamics of Lake Simcoe, a large, temperate lake in Ontario, Canada that has shifted from a turbid to clear-water state. We then analyzed patterns of biomass fluctuations of three recreationally harvested, ecologically connected populations; lake trout (*Salvelinus namaycush*, a piscivore), lake whitefish (*Coregonus clupeaformis*, a benthivore), and cisco (*C. artedii*, a planktivore) before and after the invasions by testing hypotheses on their delayed recoveries under management interventions—predator manipulations (fishery removal and stocking) and nutrient (phosphorus) load reduction. Analyses suggest that fishery harvest primarily regulated early recovery trajectories of the piscivore and planktivore, weakening top-down control prior to the establishment of the invasive consumers. By contrast, the benthivore biomass patterns were shaped, in part, by the invasive mussels (via diet shift), independently of management actions. Although improved water quality (with reduced hypoxia in deeper water) and, in turn, higher macrophyte production are projected to expand the predation refuge for young fish, intensified planktivory (by *Bythotrephes*) and herbivory (by dreissenids) have triggered shifts in community composition (from pelagic to demersal dominance). These system-wide shifts, in turn, have substantially diminished ecosystem productivity, thereby shrinking fishery yields. Novel consumers can rewire food webs, disrupt energy flows, and suppress predator recoveries, underscoring the need to account for altered ecological reality when sustainably managing fishery resources in invaded ecosystems.

Key words: *depensation; Ecopath with Ecosim; ecosystem-based management; eutrophication; foraging arena; habitat structural complexity; process uncertainty; regime shift; resilience; transient dynamics; trophic cascade.*

INTRODUCTION

Humans have manipulated lake ecosystems for millennia by modifying species composition and interactions, reshaping food webs (Boivin et al. 2016, Bartley et al. 2019) through activities that promote socioeconomic

well-being, such as fisheries and agriculture (Balirwa et al. 2003, Bunnell et al. 2013). Since the late 20th century, owing to expansion of anthropogenic impacts in nature through increasing human population sizes and mobility, the rate of introduction of nonnative species to lakes has accelerated (Ricciardi and MacIsaac 2000, Strayer 2010, Havel et al. 2015), having devastating consequences in many systems with already weakened resilience from existing pressures (Olden et al. 2004). Successful invaders (and potential eradication attempts) can perturb species interactions in a recipient system horizontally (competition) and vertically (altered prey

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base or predation pressure), triggering cascades that can lead to loss of biodiversity and ecosystem services (Strayer et al. 2006). Some introductions have contributed to ecologically and socioeconomically catastrophic events such as the massive extinction of Lake Victoria cichlid fishes in the 1980s following Nile perch (*Lates niloticus*) introduction (Balirwa et al. 2003).

Two pervasive intercontinental invaders in North American lakes, *Dreissena* spp. (herein dreissenids) and *Bythotrephes longimanus* (herein *Bythotrephes*), have dramatically restructured food webs and triggered system-wide disruptions by modifying habitat complexity (Vanderploeg et al. 2002, Higgins and Vander Zanden 2010). Being a highly efficient filter feeder, dreissenids can trigger lake-wide processes (Hecky et al. 2004) that often increase water clarity and, in turn, promote light-limited production of submerged aquatic plants, macrophytes (Vanderploeg et al. 2002, Higgins and Vander Zanden 2010). These plants provide habitat that can serve as predation refuge for forage fishes and plankton, modulating consumer–resource dynamics (Vanderploeg et al. 2002, Higgins and Vander Zanden 2010). Dreissenids not only directly reroute energy pathways from pelagic to littoral areas (Higgins and Vander Zanden 2010) but can indirectly rewire species interactions (Jackson et al. 2017). By contrast, *Bythotrephes*, a large-bodied carnivorous cladoceran, often acts as a novel predator, depleting the prey base of native planktivores, thereby, in some cases, promoting algal blooms (Walsh et al. 2016). Predation pressure by *Bythotrephes* exerts top-down control of plankton (Lehman and Cáceres 1993), reducing plankton diversity (Yan et al. 2002) and even reversing cascades (Walsh et al. 2017). It remains unclear, however, how altered habitat complexity propagates through food webs to reshape recovery trajectories of depleted predatory fishes in invaded ecosystems.

We illustrate how invasive consumers that nonlinearly modify habitat complexity reshape food-web dynamics and influence the efficacy of management interventions to restore and conserve freshwater fishery resources. We follow a two-step procedure, (1) reconstructing and (2) analyzing historical food-web dynamics before and after invasions using a highly managed, well-studied lake in southern Ontario, Canada (Fig. 1a) as a case study. Our study system, Lake Simcoe, is a large, temperate lake (722 km² surface area; mean depth 14 m) that has experienced dramatic changes over recent decades (North et al. 2013). Owing to excessive point- and nonpoint-source input from human activities such as agriculture and residential development since the 1930s, the lake has been historically enriched with nutrients, particularly phosphorus, promoting massive algal blooms that depleted deep-water oxygen (waters below the thermocline; Evans et al. 1996). Cold-water populations that each require cold, well-oxygenated deep-water habitats, including lake trout (*Salvelinus namaycush*, an apex predator), lake whitefish (*Coregonus clupeaformis*, a benthivore), and cisco (*C. artedi*, a planktivore), have

experienced poor recruitment over the past half century (Evans et al. 1996). These exploited populations only recently started recovering (Fig. 1b): catches of lake trout and lake whitefish still largely consist of hatchery populations, whereas the cisco fishery was closed for 15 yr (2001–2015) after its collapse. Although phosphorus load reduction was initiated to restore deep-water habitats starting in 1984 (OMOE 2010), the initiatives were possibly confounded by the establishment of *Bythotrephes* and dreissenids in the mid-1990s (Fig. 1c–e).

To reconstruct the historical food-web dynamics, we first synthesize 30 yr (1986–2015) of extensive lake-wide monitoring data and time-varying diet information to build a dynamic mass-balance food-web model constrained by external forcing (fishing, stocking, phosphorus load, and limnological conditions). Then, we analyze how trophic disruption by the invasive consumers (*Bythotrephes* and dreissenids) interferes with restoration efforts and delays recoveries of the three ecologically connected, cold-water predators (lake trout, lake whitefish, and cisco). To do so, we stochastically simulate the food-web dynamics before and after the invasions under management scenarios of harvest control, stocking rate, and phosphorus load reduction. Specifically, we ask (1) how does fish biomass rebuilding respond to predator manipulations (fishery removal and stocking) following the invasions and (2) how do the invasive consumers modify fish biomass rebuilding in the lake while undergoing reductions to lake nutrient levels imposed by managers?

METHODS

Food-web model

Model structure.—We developed a food-web model for Lake Simcoe to estimate its historical dynamics using a mass-balance modeling framework, Ecopath with Ecosim (EwE) version 6.5.1 (available online).⁶ An EwE model integrates foraging, food consumption, growth, reproduction, and mortality of each species or trophic group in a food web (Christensen et al. 2008). The food-web model, covering the entire area of the lake, consists of 61 species and trophic groups including 40 fish species or groups, five zooplankton groups, 10 zoobenthos groups, two phytoplankton groups, one periphyton group, one macrophyte group, and two detritus groups. We selected 1986 as the baseline year because it is the earliest year for which data are available for the majority of modeled species or trophic groups and nearly a decade before the invasions of *Bythotrephes* and dreissenids (McNeice and Johanson 2004), allowing us to reconstruct the pre- and post-1995 (the establishment of the invasive consumers) food-web structures.

⁶<http://ecopath.org>

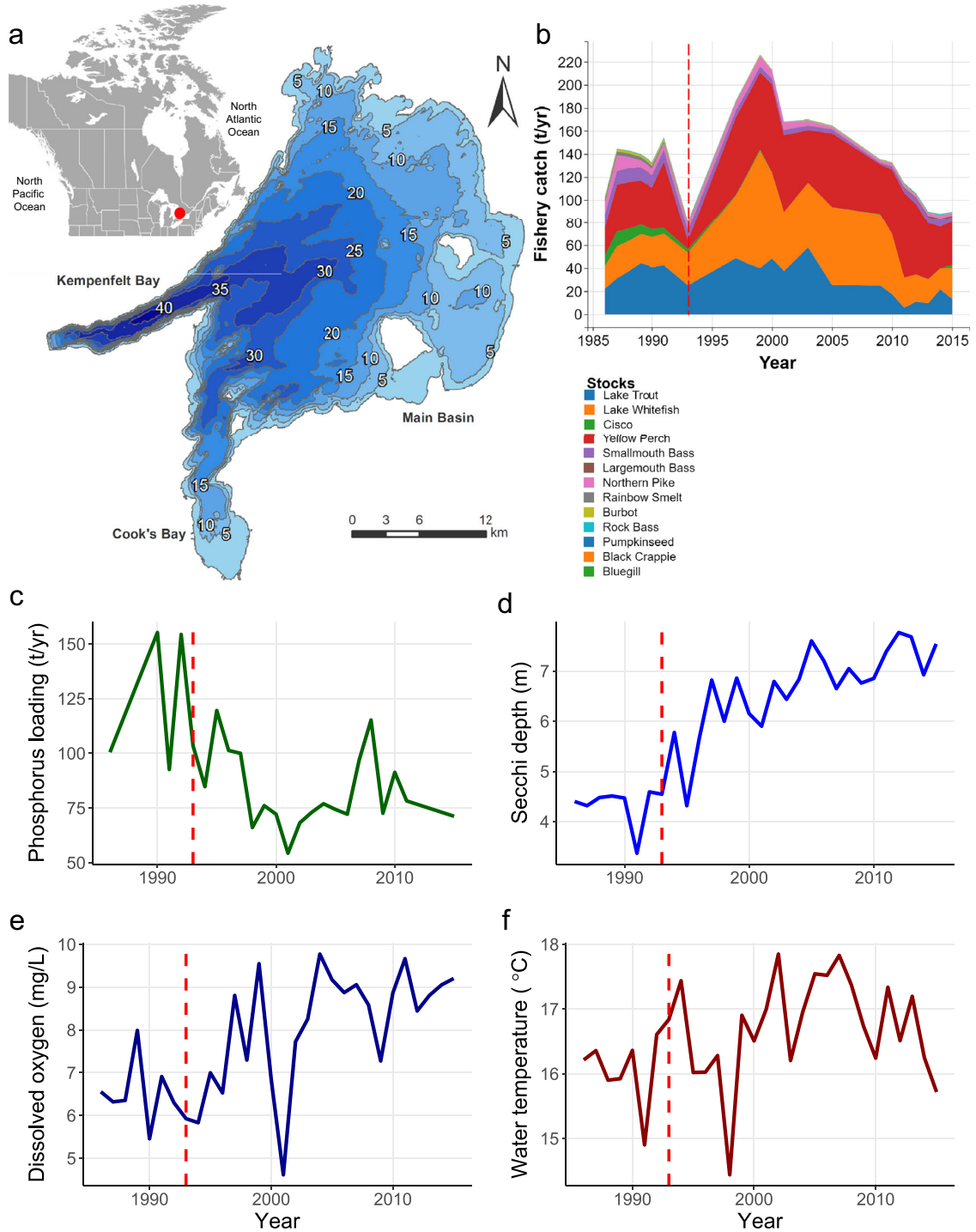


Fig. 1. Spatial and temporal summaries of a study system, Lake Simcoe (Ontario, Canada): (a) lake bathymetry; (b) reconstructed historical (1986–2015) catches (t/yr) of fished populations modeled in this study; time series (1986–2015) of (c) annual phosphorus loading (metric ton); (d) annual mean water clarity (Secchi depth, m), (e) annual mean hypolimnetic dissolved oxygen concentration (mg/L), and (f) annual mean surface-water (epilimnion) temperature (°C). In panel a, the red circle in the inset shows the location of the study system. In b–f, red dashed vertical lines show the year of dreissenid and *Bythotrephes* invasions (1993). In c–f, data points represent annual means of fortnightly measurements from sampling stations in the Main Basin.

Model parameterization.—We provide an overview of methods and data sources of the model, while detailed descriptions are given in Appendix S1. For each species or trophic group, we estimated seven core parameters of the food-web model: biomass (B); production to biomass ratio (P/B) or total mortality rate (Z); consumption to biomass ratio (Q/B); diet composition (DC); proportion of the unassimilated food to food consumed (U/Q); and fishery yield (Y , exploited fish species only) (Appendix S2: Table S1 and Data S1: diet composition). We set biomass accumulation (BA), a proportional production term (Christensen et al. 2008), to zero for all species and trophic groups, except for two fished populations supported by stocking (wild lake trout and wild lake whitefish) and one recently (2000) introduced species (bluegill *Lepomis macrochirus*).

Thirteen fish species are harvested by recreational fisheries (Appendix S2: Table S2). Six of these exploited species (lake trout, lake whitefish, cisco, yellow perch *Perca flavescens*, smallmouth bass *Micropterus dolomieu*, and northern pike *Esox lucius*) were represented by three or four life stages to simulate ontogenetic shifts in diet (Appendix S2: Table S3). We compiled time-series data on the fished species derived from 1986 to 2015 annual monitoring and creel surveys conducted by Lake Simcoe Fisheries Assessment Unit of the Ontario Ministry of Natural Resources and Forestry (MNRF) (Appendix S1: Table S1, Liddle and Moles 2012) and stomach-content data from 1975 to 2015 MNRF monitoring surveys (where available, Appendix S1: Table S1; Adkinson 2013).

For non-exploited forage fish species or groups (round goby *Neogobius melanostomus*, emerald shiner *Notropis atherinoides*, omnivorous forage fishes, and benthivorous forage fishes), we compiled data from the MNRF annual seine netting surveys (Appendix S1: Table S1). For zooplankton and phytoplankton groups, we compiled time-series data derived from annual monitoring surveys (1986–2015) conducted by Ontario Ministry of the Environment, Conservation and Parks (MECP; Appendix S1: Table S1, North et al. 2013). For data-limited trophic groups, we estimated the parameters using data derived from previous studies on Lake Simcoe; Rennie and Evans (2012) for zoobenthos, M. Rennie (*personal communication*) for mysids, Ozersky et al. (2012) for crayfishes (*Orconectes* spp.), Kanavillil and Kurissery (2013; with empirical models by Agusti et al. 1987) for periphyton, and Depew et al. (2011) for macrophytes.

To implement indirect, non-consumptive (mediation) effects of dreissenid grazing, which contribute to the shading effect of macrophytes on pelagic algae (resulting in higher water clarity), we adapted a two-step process combining two biomass-dependent forcing functions for macrophytes and algae (Okey et al. 2004, Christensen et al. 2008). The model first simulates a dreissenid biomass-dependent change in macrophyte production using a sigmoidal function (a multiplier scaled to the initial dreissenid biomass), and then, a macrophyte biomass-

dependent change in pelagic production (edible algae and cyanobacteria) that contributes to a shading effect using an exponential decay function (a multiplier scaled to the initial macrophyte biomass). The model further simulates an additional dreissenid-mediated effect, predation refuge by macrophytes, using a macrophyte biomass-dependent change in the trophic flow rate of biomass from prey to predator (Appendix S3: Eqs. S1, S2, Christensen et al. 2008).

Model fitting.—We fit the baseline model (the balanced Ecopath model with 1986 as the base year) to 37 time-series (1986–2015) of field observations using biomass indices of fished species (catch-per-unit-effort multiplied by mean body mass, t/km^2), fishery catches (t/km^2 ; Fig. 1b), and zooplankton and phytoplankton biomass (t/km^2 ; Appendix S3: Table S1 and Data S2: time series). We used a nonlinear search algorithm with vulnerability (vulnerability exchange rate, v_j) by consumer (the same v_i for all prey of a given consumer j) as a free, time-invariant parameter (the total number of parameters = 52) and a weighted sum of squared deviations as a criterion (a weight to each time series is based on data quality, Appendix S3: Table S1, Christensen et al. 2008). Prior to model fitting, this algorithm determines the number of parameters (consumer-specific v_j s) to be estimated by setting parameter blocks based on similarity in the parameter space (vulnerability search in EwE). Simulations of the baseline model were constrained by time series of estimated fishing mortality rates (Appendix S2: Fig. S1 and Data S2: time series) and reported hatchery-origin lake trout and lake whitefish yearling biomass (Fig. 2d, e; Data S2: time series). All input data were in annual time steps. We evaluated model performance in reproducing the historical biomass and catch dynamics of select species or trophic groups (Appendix S3: Table S1) using the Akaike information criterion (AIC).

In model fitting, we evaluated structural uncertainty in (1) mediation (non-consumptive) and (2) environmental functions implemented in the model. First, we tested if macrophytes influenced predator-prey interactions through (a) predator search rate, (b) prey exchange (from vulnerable to invulnerable) rate, (c) foraging area size, or (d) prey vulnerability by modifying how the mediation function affects v_j s in the model (Christensen et al. 2008). Second, we tested if model configurations that account for the time-varying habitat conditions, (a) phosphorus load reduction, (b) lake temperature effect on primary production, and (c) deep-water dissolved oxygen depletion on cold-water predators, have contributed to the historical dynamics of the food web. To implement dynamic phosphorus load forcing on primary production, we used the Michaelis-Menten function (Appendix S3: Eq. S3 and S4, Christensen et al. 2008) constrained by a time series of estimated annual lake-wide total phosphorus load during 1986–2015 derived from Evans et al. (1996) and LSRCA (2017) (Fig. 1c; Data S2: time series). To test time-varying temperature

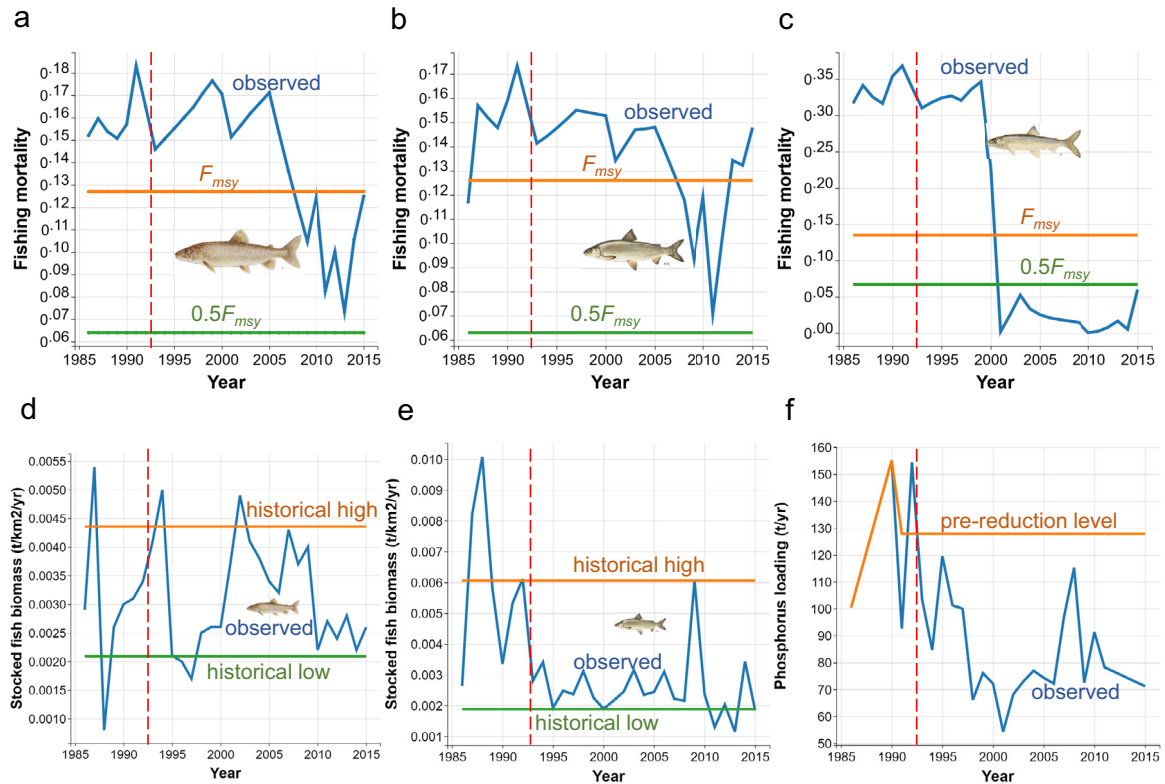


FIG. 2. Scenarios for the food-web model simulations: (a–c) observed and hypothesized fishing mortality rates of lake trout ($F_{MSY} = 0.127$ and $0.5F_{MSY}$), lake whitefish ($F_{MSY} = 0.126$ and $0.5F_{MSY}$), and cisco ($F_{MSY} = 0.135$ and $0.5F_{MSY}$) (fish images: New York State Department of Environmental Conservation [NYDEC]); (d, e) observed and hypothesized (historical high and low) stocking rates of hatchery-origin lake trout (0.00606 and 0.00209 t/km², respectively) and lake whitefish (0.00436 and 0.00189 t/km², respectively); (f) observed and hypothesized (pre-reduction in 1986–1990: 127.9 t/yr) phosphorus loading. Red dashed vertical lines show the year of dreissenid and *Bythotrephes* invasions (1993). In panel f, the scenario was based on observed phosphorus load (1986–1990) + the 1986–1990 mean observed load (1991–2015).

effects, benthic and pelagic primary productions were further forced by a nonlinear function parameterized with time series of depth- and area-averaged nearshore deep-water and offshore surface lake temperatures (respectively, Fig. 1f; Data S2: time series). To test adverse effects induced by deep-water oxygen depletion on the production of wild and hatchery-origin lake trout, wild and hatchery-origin lake whitefish, and cisco, simulations of the model were forced using a sigmoidal function parameterized with a time series of depth- and area-averaged deep-water dissolved oxygen concentration in Kempenfelt Bay and the Main Basin (Fig. 1e; Data S2: time series). Temperature and oxygen estimations were derived from 1986 to 2015 MECP annual survey data.

Hypothesis testing and scenario simulations

To evaluate the roles of *Bythotrephes* and dreissenids in the historical biomass dynamics of cold-water predators (lake trout, lake whitefish, and cisco) under time-varying harvest, stocking, and habitat conditions, we conducted virtual whole-ecosystem experiments using the best-

fitting food-web model with the mediation and environmental driver functions selected in the model fitting above. We developed “what if” management scenarios of predator manipulations (harvest and stocking) and nutrient-load reduction to test the following four hypotheses (*H*) that correspond to the questions examining the management efficacy on the post-invasion food web.

Ia: Predator harvest effects on the food web diminish following the invasions (post-1995)

We ran simulations by reducing harvest rates for the cold-water predators to harvesting at maximum sustainable yield (F_{MSY} , which was estimated using the Schaefer surplus production model, Appendix S1: Eq. S1), a commonly used management reference point, or 50% of F_{MSY} ($0.5F_{MSY}$) for each species (six scenarios in total, Fig 2a–c). These scenarios reduced harvest rates, on average, from observed for lake trout harvest rates by 11% at F_{MSY} or by 54% at $0.5F_{MSY}$ for the entire period, lake whitefish by 8.5% at F_{MSY} or by 53% at $0.5F_{MSY}$, and cisco by 58% at F_{MSY} or by 79% at $0.5F_{MSY}$ (before the fishery closure).

Ib: Predator stocking effects on the food web diminish following the invasions

We ran simulations by fixing stocking rates at historical low (10th percentile) and high (90th percentile) levels, and zero stocking for the entire period for lake trout and lake whitefish (six scenarios in total, Fig 2d, e). These scenarios increased stocking rates (from the observed) by, on average, 31% at the high level, and reduced by 21% at the low level for lake trout, and increased by 132% at the high level and reduced by 28% at the low level for lake whitefish.

2a: Phosphorus reduction (and reduced oxygen depletion) promotes fishery rebuilding

We ran simulations for a no phosphorus-reduction scenario by fixing phosphorus load with and without deep-water oxygen depletion at mean values prior to phosphorus load reduction (1986–1990) during the post-1991 period (Fig. 2f); these scenarios increased phosphorus load by, on average, 56% (from the observed) and reduced deep-water oxygen concentration by 15%. To further test for deep-water hypoxia effects on the cold-water predator (all life history stages) production, we also ran simulations without changing oxygen concentrations from the observed.

2b: Invasive consumers dampen fishery rebuilding under phosphorus reduction

We ran simulations for no-invasion scenarios by keeping biomass of (1) *Bythotrephes*, (2) dreissenids, and (3) both at a negligible level by applying artificial fishing mortality for the entire period.

To account for uncertainty in parameter estimation, we ran Monte Carlo (MC) simulations (N of trials = 1,000) for all scenarios, in which initial values of B , P/B , and Q/B were perturbed by a coefficient of variation (CV) based on data quality (Appendix S3: Table S2). The MC routine selects parameter values from a uniform distribution with its boundary set by $2 \times CV$ (Christensen et al. 2008). Prior to each MC run, the model based on a selected parameter set is checked for mass balance; if the model is not balanced, the parameter set is rejected, and the process is repeated (up to 10,000 times).

RESULTS

Model structural uncertainty and performance

We found that non-consumptive effects of dreissenids mediated through changes in primary producers and habitat complexity played a key role in regulating the post-invasion food-web dynamics when tested against the historical data. The model with both the dreissenid forcing function for primary producers and the macrophyte forcing function for consumers performed better than the models with either function alone or no mediation (Table 1). These indirect processes played a larger role in biomass dynamics of lake trout and lake whitefish than they did for cisco (Fig. 3). Further, the best-fitting model showed that macrophyte biomass dynamics influence consumer foraging by modulating both safe-

foraging-habitat size (foraging arena) and prey mixing rate (vulnerability exchange rate; Table 1 and Fig. 3).

The model with time-varying functions of phosphorus load, temperature, and dissolved oxygen performed better than models with any other combination of environmental drivers tested (Table 1). With no phosphorus-dependent function, the model underestimated lake trout and lake whitefish biomass (Fig. 3). With no dissolved oxygen-dependent function, the model did not capture lake trout biomass dynamics and underestimated lake whitefish biomass (Fig. 3). With no temperature-dependent function, the model did not capture lake trout and lake whitefish biomass dynamics and overestimated cisco biomass (Fig. 3). Overall, the best models showed lake trout and cisco had been strongly regulated by top-down forcing ($v_{js} > 100$), whereas lake whitefish had been regulated more by bottom-up forcing ($v_{js} = 1.0$, Appendix S3: Tables S3, S4).

The best-fitting model mostly captured the historical biomass and catch dynamics of fished species, zooplankton groups, and phytoplankton groups (Appendix S3: Figs. S1, S2). Adult wild lake trout biomass rose $22\times$ over 30 yr (Appendix S3: Fig. S1) primarily because of reduced (by 37%) fishing mortality (though catch rose $18\times$, Appendix S3: Fig. S2) since the mid-2000s and because survival of first-year fish improved (by 34%) following rainbow smelt collapse in the early 2000s. Total mortality of adult wild lake whitefish increased (by 18%) because of enhanced predation by recovering adult wild lake trout. However, lake whitefish biomass and catch rose $1.8\times$ and $13\times$ (respectively, Appendix S3: Figs. S1, S2) partly because of reduced predation on first-year fish by smelt and higher (by 48%) food consumption since the early 2000s when lake whitefish started consuming dreissenids (comprising, on average, 41% of the diet). Despite the 45% increased predation mortality by wild and hatchery-origin lake trout, adult cisco biomass rose $43\times$ (Appendix S3: Fig. S1) primarily because of reduced fishing mortality (by $>85\%$) after the cisco fishery closure.

The model also captured rising biomass and catch in other fished species including adult yellow perch and adult smallmouth bass biomass ($8\times$ and $29\times$ increase in biomass, and $5\times$ and $10\times$ increase in catch, respectively) in the 2000s and 2010s (Appendix S3: Figs. S1, S2); these species compete for food with or consume the young of the cold-water predators. Further, the model captured declining trends and shifts in biomass of the zooplankton and phytoplankton groups (on average, 56% and 53% decline, respectively, Appendix S3: Fig. S1) after the mid-1990s primarily because of *Bythotrephes* predation and dreissenid grazing (respectively).

Management interventions and species invasion scenarios

Harvest.—Reducing harvest rates throughout the study period increased wild adult lake trout biomass by, on average, 9% at F_{MSY} and 27% $0.5F_{MSY}$ in the first decade

TABLE 1. Results of model fitting and model selection for the food-web model to evaluate model structure of mediation and environmental driver functions (only wild lake trout, wild lake whitefish, and cisco shown).

Model	No. parameters	SS	Δ AIC	SS lake trout	SS lake whitefish	SS cisco
Mediation functions						
Vulnerability + foraging area	50	657.3	0.0	6.8	9.5	10.4
Foraging area	48	778.0	147.6	42.9	13.9	198.4
Predator search rate	50	675.9	25.1	10.9	20.0	163.8
Prey vulnerability	49	3,584.7	1,527.8	41.1	33.6	84.8
Consumers + producers	50	657.3	0.0	6.8	9.5	10.4
Producers only	49	678.2	26.0	11.6	8.2	189.0
Consumers only	48	778.2	147.8	51.6	56.1	94.6
No mediation	48	5,833.7	1,964.8	103.5	125.2	182.6
Environmental drivers						
Food web + phosphorus + temperature + DO	49	657.3	0.0	6.8	9.5	10.4
Food web + temperature + DO	50	2,110.3	1,052.1	18.5	17.3	254.1
Food web + phosphorus + DO	50	736.2	102.2	21.0	35.6	126.7
Food web + phosphorus + temperature	50	689.3	47.3	7.7	43.8	122.5
Food web + phosphorus	49	8,170.7	2,270.9	154.2	92.5	382.1
Food web + temperature	50	1,074.2	443.0	25.8	11.8	204.4
Food web + DO	50	5,350.5	1,891.3	110.0	89.2	393.9
Food web (no environmental driver)	49	1,011.5	386.5	22.03	12.33	188.6

Notes: No. parameters indicates the number of consumer-specific vulnerability parameters (v_{js}) estimated (Appendix S3: Tables S3, S4) during the model fitting, which was determined a priori by setting parameter blocks based on similarity in the parameter space (*Vulnerability search* in Ecopath with Ecosim [EwE] version 6.5.1). SS indicates minimum sum of squares. Δ AIC indicates deviation in Akaike information criterion from the base (no mediation) scenario. Model selection was performed using Δ AIC of each model.

(hereafter reported % are based on averages over years); lake trout biomass nearly tripled over the last two decades (Fig. 4a; Appendix S4: Table S1). Higher lake trout biomass reduced cisco biomass by 18% and wild lake whitefish biomass by 8%. By contrast, reducing lake whitefish harvest rates negligibly affected the biomass of the cold-water predators (Fig. 4a; Appendix S4: Table S1). Reducing cisco harvest rates increased cisco biomass by 18% (F_{MSY}) and 34% ($0.5F_{MSY}$) in the first decade, but cisco biomass continued to rise only at $0.5F_{MSY}$ (Fig. 4a and Appendix S4: Table S1), which, however, only negligibly affected the biomass of wild lake trout and wild lake whitefish (Fig. 4a; Appendix S4: Table S1).

Stocking.—Lowering lake trout stocking rates increased wild lake trout biomass by 26% and cisco biomass by 34% over the last two decades (Fig. 4b; Appendix S4: Table S1) primarily because of reduced predation by and competition with hatchery-origin fish. These findings were further supported by ceasing lake trout stocking altogether (Fig. 4b; Appendix S4: Table S1), whereas raising lake trout stocking rates negligibly affected their biomass. In further testing top-down control of the food web, the combination of lower lake trout harvest ($0.5F_{MSY}$) and cessation of lake trout stocking nearly doubled wild lake trout biomass and cisco biomass over the last two decades; however, wild lake whitefish biomass declined by 61% (Appendix S4: Fig. S1, Table S1).

This decline in wild lake whitefish biomass facilitated dreissenid biomass production and, in turn, macrophyte biomass production (Appendix S4: Table S2). Zooplankton biomass also increased because of reduced planktivory by young hatchery-origin fish (Appendix S4: Table S1). By contrast, when combined with higher lake trout harvest ($2.0F_{MSY}$), the benefit of ceasing lake trout stocking for wild lake trout disappeared, while cisco maintained high biomass (Appendix S4: Fig. S1, Table S1). Although modifying lake whitefish stocking rates negligibly affected wild lake whitefish biomass, maintaining these stocking rates increased wild lake trout biomass and cisco biomass (by ~31%, Fig. 4b). By contrast, ceasing stocking of lake whitefish ultimately halved wild lake trout biomass (Fig. 4b; Appendix S4: Fig. S1, Table S1) primarily because of reduced food supply.

Nutrient loading.—Effects of maintaining the phosphorus load from the 1980s emerged especially in the last two decades of simulations: high phosphorus load reduced wild lake trout biomass by 62% (with hypoxia) and by 21% (without hypoxia) (Fig. 5a; Appendix S4: Table S1). Likewise, high phosphorus load reduced cisco biomass by 40% (with hypoxia) and by 30% (without hypoxia) (Fig. 5a; Appendix S4: Table S1). By contrast, keeping high phosphorus load (with or without hypoxia) negligibly affected mean wild lake whitefish biomass but dampened its temporal oscillation (Fig. 5a; Appendix S4: Table S1).

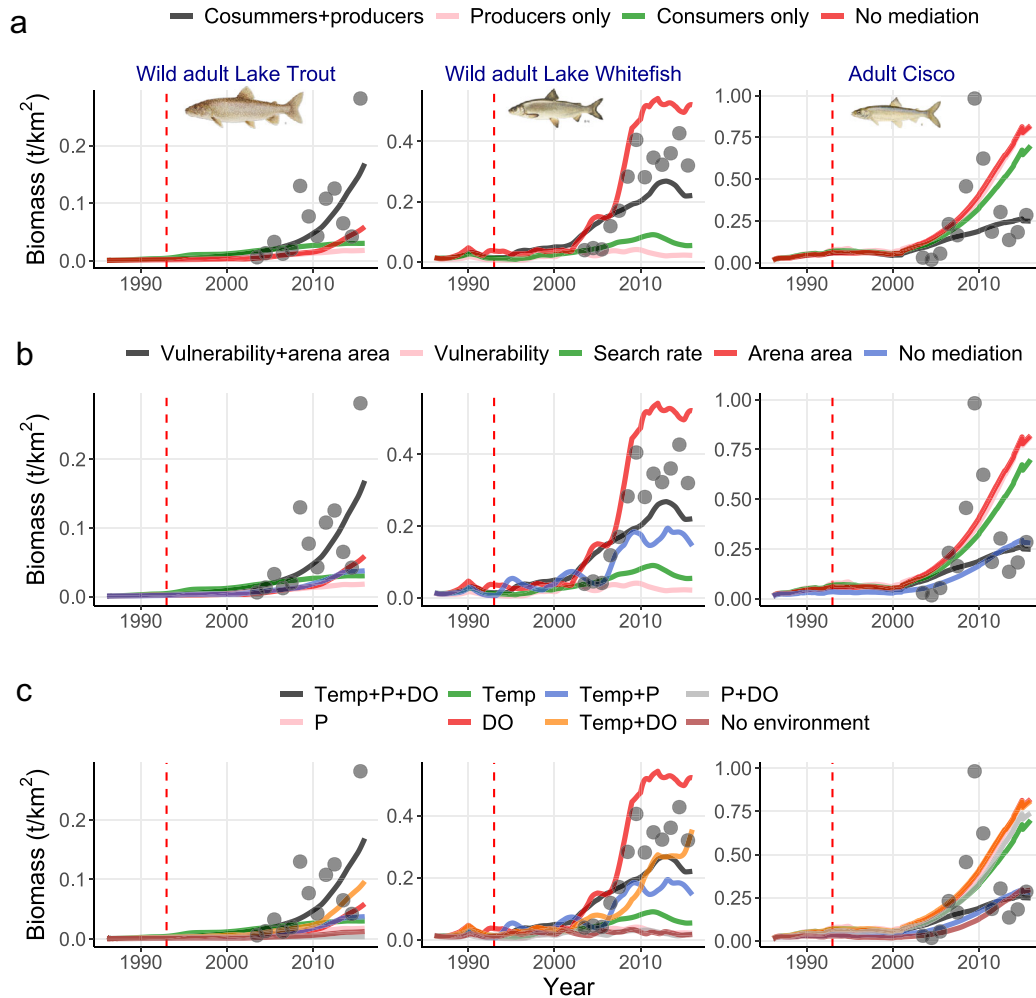


FIG. 3. Model-fitting results for wild adult lake trout, wild adult lake whitefish, and adult cisco (fish images: NYDEC) biomass using the food-web model with varying model structure for (a, b) consumer and producer mediations and (c) responses to limnological conditions. Solid lines indicate simulated biomass and gray circles indicate observed biomass. Red dashed vertical lines show the year of dreissenid and *Bythotrephes* invasions (1993).

Invasive consumers.—With no *Bythotrephes* invasion, wild lake trout and cisco biomass increased by 20% and 9% (respectively) because of greater pelagic prey biomass (a ~21% increase in herbivorous zooplankton biomass, Appendix S4: Table S2), whereas wild lake whitefish biomass changed little (Fig. 5b; Appendix S4: Table S1). With no dreissenid invasion, wild lake trout increased by 64% (Fig. 5b; Appendix S4: Table S1) because of greater trophic support (a ~58% increase in pelagic primary producer biomass, a ~64% increase zooplankton including *Bythotrephes* biomass, and a ~55% increase in forage fish biomass, Appendix S4: Table S2). By contrast, wild lake whitefish biomass declined by 40% because of reduced prey base; cisco biomass declined by 28% because of amplified lake trout predation (Fig. 5b; Appendix S4: Table S1). With no *Bythotrephes* or dreissenid invasion, wild lake trout biomass increased by 79%, resulting in a decline in cisco biomass of more than 50% despite

greater (by ~67%) plankton biomass (Fig. 5b; Appendix S4: Tables S1, S2).

DISCUSSION

Our study reveals that novel trophic links inserted by invasive consumers (*Bythotrephes* and dreissenids) can systematically modify how the food web of exploited lakes responds to time-varying, compounded, human perturbations under transient ecosystem dynamics. Emergent patterns show that these invasive consumers increase effects of harvest (which are often further mediated by trophic interactions) and confound effects of water quality control (nutrient-load reduction) on biological production of recovering predators, undermining efforts to restore ecosystems and depleted fishery resources. Although harvest control and nutrient-load reduction promote production of planktivores (cisco),

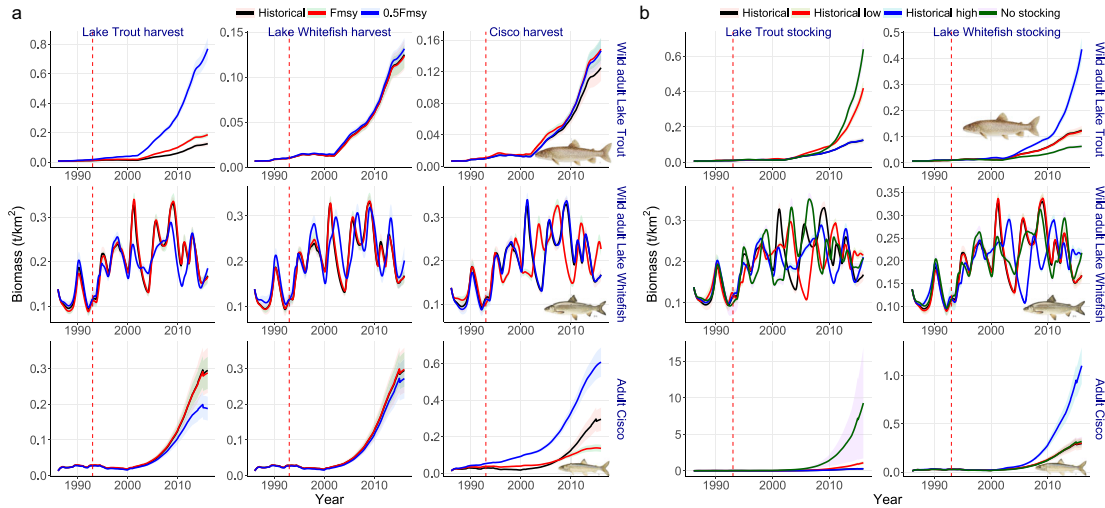


FIG. 4. Hindcasted (1986–2015) estimates of wild adult lake trout, wild adult lake whitefish, and adult cisco (fish images: NYDEC) biomass from the food-web model simulations under (a) harvest scenarios and (b) stocking scenarios. Solid lines indicate the mean projected biomass and ribbons indicate 95% confidence intervals computed from the Monte Carlo simulations ($N = 1,000$) by perturbing the initial parameter values (biomass B , production to biomass ratio P/B , and consumption to biomass ratio Q/B ; based on a coefficient of variation, Appendix S3: Table S2). Red dashed vertical lines show the year of dreissenid and *Bythotrephes* invasions (1993).

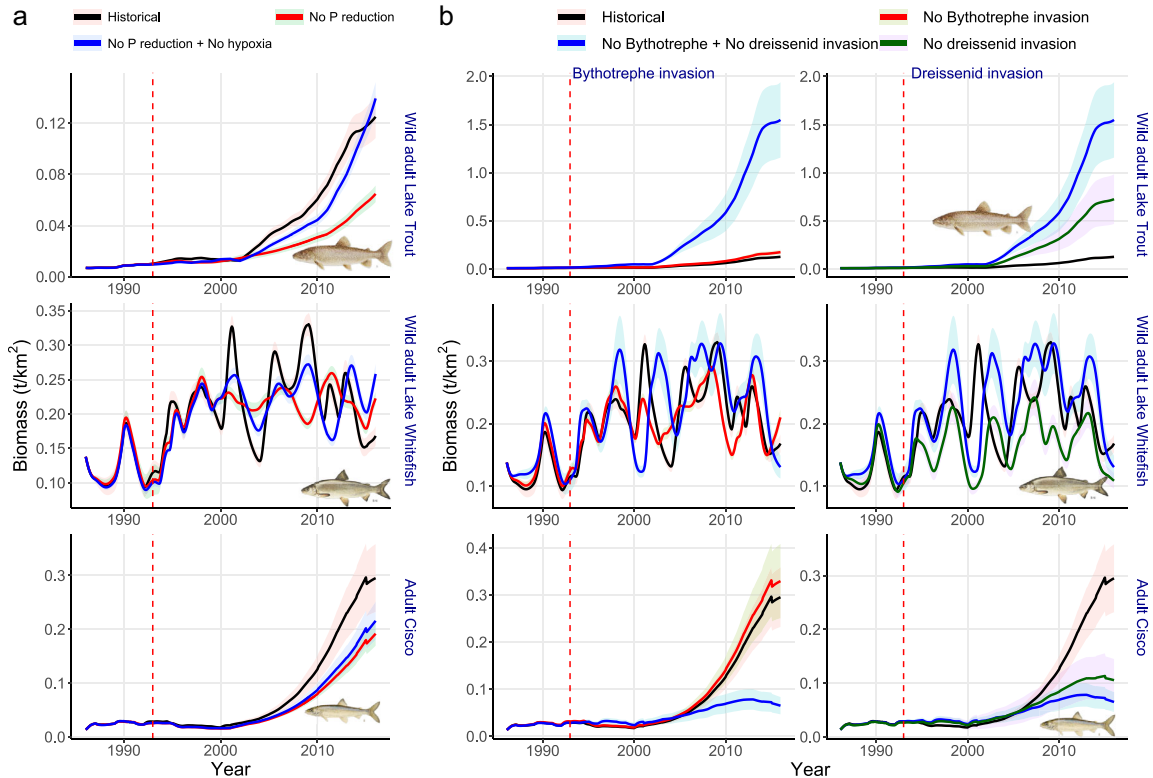


FIG. 5. Hindcasted (1986–2015) wild adult lake trout, wild adult lake whitefish, and adult cisco (fish images: NYDEC) biomass from the food-web model simulations under (a) phosphorus (P) reduction and hypoxia scenarios and (b) invasion scenarios. Solid lines indicate the mean projected biomass and ribbons indicate 95% confidence intervals computed from the Monte Carlo simulations ($N = 1,000$) by perturbing the initial parameter values (B , P/B , and Q/B) (based on a coefficient of variation, Appendix S3: Table S2). Red dashed vertical lines show the year of dreissenid and *Bythotrephes* invasions (1993).

their biomass dynamics are strongly regulated further by predation pressure before and after the invasions. Benthivores (lake whitefish), to a certain extent, benefit from enhanced food supply (dreissenids) that promotes their biomass production; however, owing partly to the newly formed trophic link, they become less responsive to management actions. By contrast, the nonnative herbivore diverts energy pathways and reduces trophic flow, limiting the capacity of the ecosystem to support production of apex predators (lake trout) and, in turn, slowing their recovery and diminishing fishery yields.

Weakened top-down control of the food web

Unsustainable harvest rates (here defined as biomass removal of more than the theoretical maximum sustainable yield) have severely depleted many freshwater predators, preventing them from successfully recruiting and rebuilding biomass (an emergent Allee effect; Walters and Kitchell 2001). In Lake Simcoe, historical commercial fishing (among other pressures) depleted apex predator populations including lake trout by the early 1950s (Dunlop et al. 2019), weakening top-down control and, in turn, likely facilitating the establishment of lower trophic-level invaders. However, our analyses suggest that the hatchery-origin population took over the trophic role as an apex predator, maintaining (albeit limited) top-down control on predators of young lake trout (the cultivation effect; Walters and Kitchell 2001). For example, predation by nonnative rainbow smelt is a major source of larval mortality of native fishes in North American lakes (Evans and Loftus 1987). Our work further suggests that the smelt collapse in the early 2000s promoted survival of young lake trout. Hatchery-origin lake trout predation on smelt, along with recent declines in lake trout harvest, likely contributed to the reemergence of lake trout natural recruitment after nearly four decades (Dolson 2012). However, simulations, complemented by field observation of stomach contents, also show that hatchery-origin populations compete with wild populations for food throughout all life stages (including via cannibalism), thereby limiting the capability of stocking alone as a management tool to rebuild depleted predator biomass.

Harvest alone, without accounting for ecological processes, such as predation or competition, may lead to collapse of mesopredators such as cisco (Stockwell et al. 2009). Time-varying consumer–resource dynamics contribute to cascade-strength variability in a food web (Piovia-Scott et al. 2017). Year-class failures and collapses of mesopredators can decouple trophic links and further weaken top-down regulation (Salomon et al. 2010). Our analyses suggest that unsustainable harvest rates prior to the 15-yr moratorium had contributed to the cisco fishery collapse (Fig. 6a, b). Continued predation by piscivores (including hatchery-origin and recovering wild lake trout) further delayed the planktivore's recovery. By contrast, wild lake whitefish (which had

been severely depleted prior to the study period) responded little or moderately to harvest control or stocking (Fig. 6a), thereby limiting recovery.

Trophic control reversal by species invasion

The dynamics of depleted fishery populations often become recruitment-dependent owing to selective removal of larger and older individuals (Rouyer et al. 2012) and increasingly more sensitive to environmental (bottom-up) fluctuations (Munch et al. 2005, Goto et al. 2018). The survival of early life-stage fishes is driven by a multitude of external forcing, including trophic control (Goto et al. 2015, Goto et al. 2020). Our analyses suggest that the lower trophic-level invaders can boost bottom-up control of the pelagic (by *Bythotrephes*) and benthic (by dreissenids) food-web dynamics and, in turn, upend trophic control of recruitment of predatory fishes, thereby slowing their recoveries. Field observation, for example, shows that survival rates of the stocked first-year lake trout abruptly declined by more than 50% in the mid-1990s (Dolson 2012). Simulations indicate that *Bythotrephes* predation on herbivorous cladocerans and cyclopoids reduces the food supply of and amplifies competition among planktivores (for example, cisco and young lake trout), thereby weakening food-web support for apex predators such as adult lake trout (Fig. 6b).

Simulated nonconsumptive processes mediated by dreissenids further reveal plausible scenarios for the modified food-web dynamics and recovery patterns of depleted predator populations. Our analyses suggest that gradually improving habitat quality (attenuating the direct hypoxia effect) through reduced phosphorus load promoted the survival of juvenile and adult lake trout and cisco. However, the establishment of dreissenids in the mid-1990s accelerated ecosystem changes and masked effects of phosphorus load reduction. With greater water clarity and, in turn, higher macrophyte production, expanded habitat size in littoral zones is projected to reduce the predation risk of small-bodied zooplankton and pelagic fishes (including cisco and young lake trout). High dreissenid production also enhances benthic food supply in invaded systems; an abrupt shift in food choice to and subsequent dependence on dreissenids (a “locked-in” predator–prey interaction) may have shaped the post-invasion biomass patterns of benthivores such as lake whitefish.

Analyses, however, suggest that a myriad of negative effects of dreissenid invasions far outweigh the positives. Their high grazing rates alone are projected to shrink the biomass of herbivorous zooplankton and zoobenthos by depleting shared food resources and reduce biomass of planktivores and piscivores as boosted bottom-up control reduces trophic efficiency. This dreissenid-driven “trophic squeeze” is also projected to reduce the apex predator fishery yield. Further, greater warm-water fish (for example, centrarchids) production resulting from enhanced nearshore benthic primary production

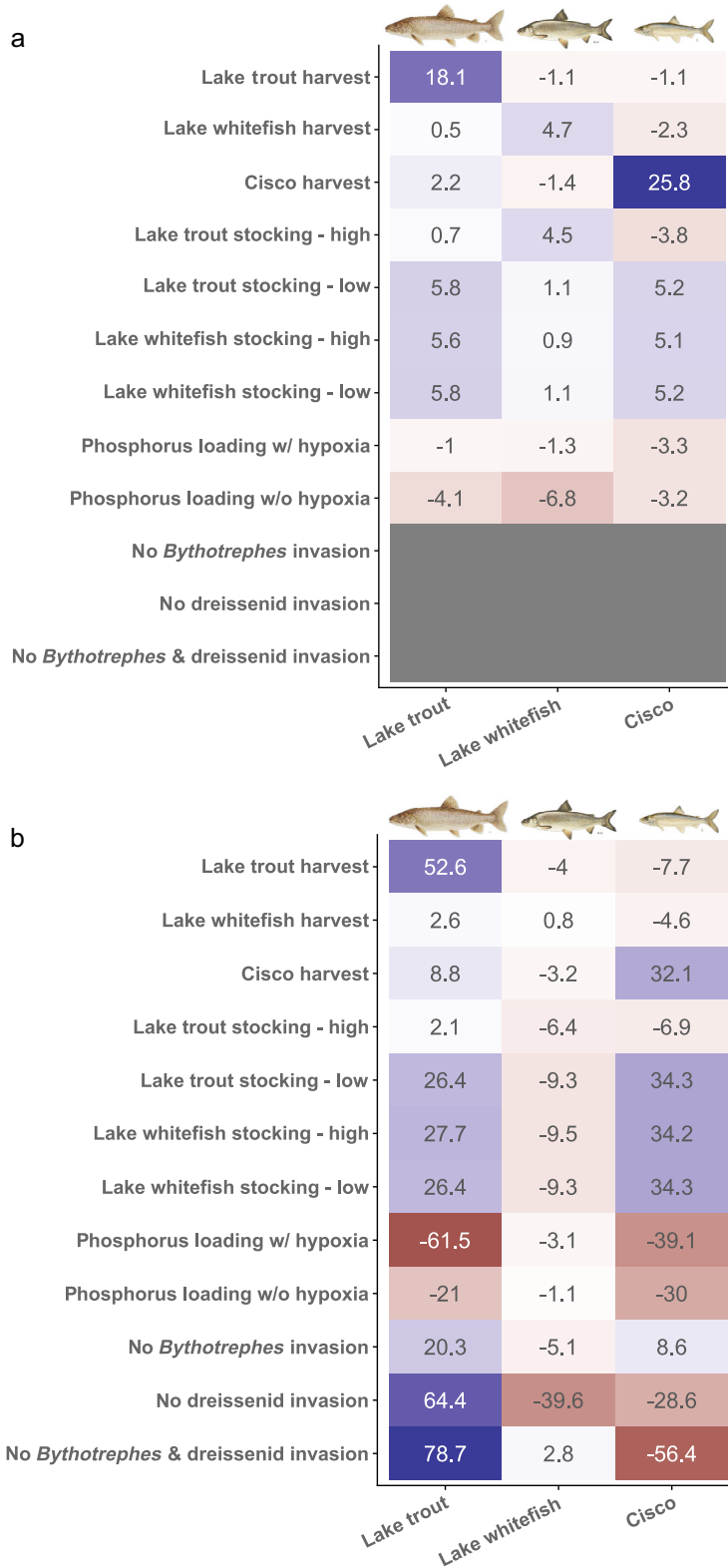


FIG. 6. Summary heat maps of results from the food-web model simulations under harvest, stocking, phosphorus load reduction, and species invasion (a) before 1995 and (b) after 1995. Values show relative differences (%) in biomass of adult wild lake trout, adult wild lake whitefish, and adult cisco (fish images: NYDEC) between the historical (observed) and the alternative scenarios (Figs. 4, 5). In panel a, gray cells show no change introduced before 1995 in the invasion scenarios.

intensifies (direct or apparent) resource competition with cold-water fishes in littoral zones (Vander Zanden et al. 1999, MacRae and Jackson 2001, Alofs and Jackson 2015). Although dreissenids can displace native species and provide an alternative food resource to benthivores, they can also trap a large amount of primary production as their production far exceeds consumption demand of their predators (Rutherford et al. 1999), bottlenecking energy flow (David et al. 2017), shortening the food chain, and shrinking fishery production.

Model uncertainty and limitations

Our model-guided analyses have some caveats. First, our current model does not simulate reproduction by hatchery-origin fish that contribute to wild populations (naturalization); modeled wild and hatchery-origin populations remain separate. In our study system, lake trout recruitment had been nearly absent until 2001, and, thus, the current wild population likely consists entirely or predominantly of offspring from hatchery-origin fish. However, we lack information on survival rates of offspring naturally reproduced by hatchery-origin lake trout and lake whitefish and on the extent of cross-fertilization between the wild and hatchery-origin populations. Future analyses will re-assess how these “naturalized” fishes have contributed to the recoveries as more survey data become available.

Second, this study focuses on interannual environmental variability on primary producers but does not account for spatial and intra-annual variability. These sources of uncertainty could regulate dynamic habitat use and life-history responses to seasonal changes by predators (Hrycik et al. 2019) potentially underestimating the role of environmental forcing in recruitment and production dynamics, while overestimating the roles of fishing and trophic control. Hypoxia of hypolimnetic water, for example, can vary greatly in its development over space and time (Nürnberg et al. 2013, Scavia et al. 2014). Future modeling efforts will benefit from reducing uncertainty in short-term biophysical dynamics (including early life-stage processes) in a spatially structured environment.

Managing fisheries in transitioning ecosystems

Human exploitation of ecosystem services has weakened the resilience of lakes (Dodds et al. 2013) and reduced their capacity to support predators (Stier et al. 2016, Rypel et al. 2018). With continued human population growth and ever-expanding global shipping traffic, a primary mode of nonnative species spread (Casas-Monroy et al. 2015, Sardain et al. 2019), increased invasion risk will remain a threat to freshwater predators, posing challenges to previously effective management strategies. Despite limitations in the approach used, our study sheds light on plausible mechanisms underlying recovery trajectories of predators aided by management

interventions under changing lake productivity and offers insights for rethinking future conservation efforts that are increasingly undermined by the introduction of nonnative species and their potentially irreversible ecological effects. We show that harvest management actions to rebuild exploited fish biomass, such as harvest control and stocking, can be ineffective and even inadvertently incur undesirable ecological side-effects (for example, a mortality increase in wild fish triggered by stocked fish) when implemented without accounting for changes in ecological stability and food-web processes. Real-world observation alone often poses challenges in deciphering how multiple, interacting pressures control food-web dynamics owing to process and measurement uncertainty (Jackson et al. 2017). Our work further indicates that when nonnative species act as “ecosystem engineers” such as dreissenids in a recipient system, the assessments of efforts to restore habitat complexity that supports fishery rebuilding (for example, nutrient control) can be obscured, owing partly to the slow, diffused processes, if not accounting for altered feedback mechanisms of the ecosystem (non-consumptive processes mediated by invaders). Lags in ecological responses to compounded (natural or human-mediated), local or global perturbations mask causal links, delaying management actions and obscuring evaluation of these actions (Rocha et al. 2018). We propose that resource management strategies in invaded systems be designed, implemented, and assessed by explicitly accounting for compounded, altered ecological responses to human exploitation and management interventions under known uncertainty.

More generally, with projected large-scale changes in climate and ecosystems including shifting ice phenology and thermal stratification timing (Blenckner et al. 2007), and, in turn, distribution (Goto et al. 2017), life-history events (Pedersen et al. 2018), and interactions of native and nonnative species (Strayer et al. 2006, Alofs et al. 2014), we expect that future invasion scenarios unfold in an increasingly uncertain and unpredictable manner, confounding efforts to restore biodiversity and ecosystem services to human well-being that lakes provide (Rahel and Olden 2008, Havel et al. 2015). Confronting process-based models with multiple sources of long-term observations, as demonstrated in this study, assists us in linking patterns of renewable resources to local trophic disruption (native vs. nonnative species) and, in turn, informing policy decisions to sustainably manage them in complex, dynamic ecosystems. Reconstruction of the past through process-based modeling allows us to not only understand such transient patterns but also reevaluate risks of management options through simulations in the context of alternative states of ecosystems in the face of irreducible uncertainty (Fulton et al. 2014). Redefining the “operating space,” management actions that set boundaries (such as nutrient and harvest control) for rebuilding and sustainable use of freshwater resources (Rockström et al. 2009), under likely future ecological

states will safeguard against rising ecosystem variability (Shelton et al. 2014).

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SUPPORTING INFORMATION

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