

Lake Michigan offshore ecosystem structure and food web changes from 1987 to 2008

Mark W. Rogers, David B. Bunnell, Charles P. Madenjian, and David M. Warner

Abstract: Ecosystems undergo dynamic changes owing to species invasions, fisheries management decisions, landscape modifications, and nutrient inputs. At Lake Michigan, new invaders (e.g., dreissenid mussels (*Dreissena* spp.), spiny water flea (*Bythotrephes longimanus*), round goby (*Neogobius melanostomus*)) have proliferated and altered energy transfer pathways, while nutrient concentrations and stocking rates to support fisheries have changed. We developed an ecosystem model to describe food web structure in 1987 and ran simulations through 2008 to evaluate changes in biomass of functional groups, predator consumption, and effects of recently invading species. Keystone functional groups from 1987 were identified as *Mysis*, burbot (*Lota lota*), phytoplankton, alewife (*Alosa pseudoharengus*), nonpredatory cladocerans, and Chinook salmon (*Oncorhynchus tshawytscha*). Simulations predicted biomass reductions across all trophic levels and predicted biomasses fit observed trends for most functional groups. The effects of invasive species (e.g., dreissenid grazing) increased across simulation years, but were difficult to disentangle from other changes (e.g., declining offshore nutrient concentrations). In total, our model effectively represented recent changes to the Lake Michigan ecosystem and provides an ecosystem-based tool for exploring future resource management scenarios.

Résumé : Les écosystèmes subissent des changements dynamiques découlant de l'invasion d'espèces, de décisions touchant à la gestion des pêches, de modifications du paysage et d'apports de nutriments. Au lac Michigan, de nouveaux envahisseurs (p. ex. dreissenés (*Dreissena* spp.), cladocère épineux (*Bythotrephes longimanus*), gobie à taches noires (*Neogobius melanostomus*)) ont proliféré et modifié les voies de transfert d'énergie, alors que les concentrations de nutriments et les taux d'empoisonnement visant à appuyer les pêches ont changé. Nous avons élaboré un modèle d'écosystème pour décrire la structure du réseau trophique en 1987 et effectué des simulations jusqu'en 2008 pour évaluer les variations de la biomasse des groupes fonctionnels, la consommation des prédateurs et les effets d'espèces envahissantes récentes. Les groupes fonctionnels clés en 1987 étaient les mysis (*Mysis*), la lotte (*Lota lota*), le gaspareau (*Alosa pseudoharengus*), les cladocères non prédateurs et le saumon quinnat (*Oncorhynchus tshawytscha*). Les simulations ont prédit des réductions de la biomasse à tous les niveaux trophiques et les prédictions de la biomasse concordaient avec les tendances observées pour la plupart des groupes fonctionnels. Si les effets des espèces envahissantes (p. ex. broutage des dreissenés) augmentent au fil des années simulées, il est difficile de les départager d'autres changements (p. ex. diminution des concentrations de nutriments au large). Globalement, notre modèle représente adéquatement les changements récents à l'écosystème du lac Michigan et constitue un outil écosystémique permettant d'explorer des scénarios de gestion future des ressources. [Traduit par la Rédaction]

Introduction

Worldwide, freshwater ecosystems are challenged from multiple, sometimes simultaneous, stressors including invasive species, climate change, changing nutrient inputs, overfishing, and competing water resource demands (i.e., irrigation, hydroelectric power; see overview by Ormerod et al. 2010). The Laurentian Great Lakes are illustrative of several of these stressors, as multiple lakes have experienced periods of ecosystem disturbance over the past century. For example, in Lakes Huron and Michigan, the 1930s–1950s period coincided with invasions of sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseudoharengus*), and rainbow smelt (*Osmerus mordax*). These invasions, coupled with overfishing, led to the extirpation of several native Coregonidae planktivorous fish species and severe declines in native lake trout (*Salvelinus namaycush*), the apex predator. The second period (mid-1960s–1970s) was highlighted by limits on nutrient inputs, control of sea lamprey, and the establishment of Pacific salmonines and lake trout through stocking to create sport fisheries throughout all of the Great

Lakes. The third period (1980s–2000s) has been largely shaped by new invaders at intermediate trophic levels, primarily zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*, respectively; hereafter collectively referred to as dreissenids), spiny water flea (*Bythotrephes longimanus*), and round goby (*Neogobius melanostomus*).

The extent to which each stressor and, in particular, invasive species have proliferated varied by lake (Bunnell et al. 2014), yet a growing body of knowledge has described how these species interact within their trophic niches when they become abundant. Dreissenid mussels modify benthic habitats (Vanderploeg et al. 2002), and their filter feeding can exceed primary production during spring isothermal periods when they can access phytoplankton from the entire water column (Fahnenstiel et al. 2010; Vanderploeg et al. 2010). They likely sequester nutrients that otherwise would have been transferred to offshore pelagic zones (see Hecky et al. 2004; Vanderploeg et al. 2010), and this is believed to underlie declines in phytoplankton production even during summer stratification (Pothoven and Fahnenstiel 2013). The effects of

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Bythotrephes are primarily limited to their zooplankton prey, both through direct planktivory and through indirect means whereby the presence of *Bythotrephes* induces zooplankters to migrate to cooler, less productive waters. *Bythotrephes* have the capacity to consume even the largest of daphnid species (Schulz and Yurista 1999), and thus, *Bythotrephes* has been implicated in the dramatic decline of cladoceran species richness across the Great Lakes (Barbiero and Tuchman 2004). *Bythotrephes* specific consumption rates can exceed 100% of their body mass (Yurista et al. 2010), and Bunnell et al. (2011) reported that planktivory by *Bythotrephes* in Lake Huron can exceed that of fish planktivores and *Mysis* spp. Round goby are believed to have outcompeted several native fishes (Janssen and Jude 2001) through its aggressive behavior and also may negatively influence native sportfish reproduction via consumption of incubating eggs (Steinhart et al. 2004). At the same time, adult round gobies have a positive ecosystem effect by consuming dreissenid mussels, thereby returning energy that otherwise could be sequestered in dreissenid mussel tissue to the food web. Furthermore, round gobies are becoming increasingly important to the diets of native species such as burbot (*Lota lota*) and lake trout (Jacobs et al. 2010). The establishment of multiple mid-trophic-level invaders coupled with the oligotrophication of several Great Lakes has been implicated as a major disruption to historical Great Lakes energy transfer pathways (Barbiero et al. 2012).

Identifying drivers of ecosystem dynamics is particularly difficult when multiple stressors are simultaneously occurring, potentially even confounding one another. The extent to which ecosystem changes were influenced by these new invaders, long-term declines in nutrient inputs, or the accumulation of piscivore biomass in the Great Lakes remains unclear. A more complete understanding of the potentially interacting effects requires an ecosystem modeling approach that can illuminate how the structure of the food web has changed in recent decades and, in turn, effectively guide management of water quality or fisheries. Food-web-based ecosystem models allow evaluation of trophic relationship networks, species interactions, and ecosystem structure and function (Dunne et al. 2002a).

We sought to develop a mass-balance ecosystem model, with a time-dynamic component, to explore recent changes in ecosystem biomass and food web structure within Lake Michigan's offshore habitat. Our motivation was to understand how Lake Michigan's food web has changed during recent decades so that managers can begin to address the concern that invaders have reduced the capacity of Lake Michigan to support pelagic fish biomass. Specifically, we developed an Ecopath model balanced for 1987, just prior to the invasion of dreissenid mussels and round gobies. We then used Ecosim to incorporate time-dynamic influences on the ecosystem (e.g., piscivores stocking, fisheries, and nutrients) and to validate our model by fitting to time series amassed across multiple trophic levels from 1988 to 2008. Our Ecopath with Ecosim model allowed us to address several ecological questions: (i) What are the keystone species groups that have had disproportionate impact on food web interactions? (ii) How do measures of Lake Michigan food web structure (i.e., trophic transfer efficiency, food web connectance) compare with other ecosystems? (iii) Can food web interactions explain biomass changes for ecosystem functional groups between 1987 and 2008? (iv) What food web interactions and ecosystem-level effects of recent invaders (i.e., dreissenid mussels, round gobies) can be detected?

Methods

Overview of Ecopath mass-balance and Ecosim time-dynamic simulations

We parameterized our Lake Michigan ecosystem model using Ecopath with Ecosim (EwE; available at <http://www.Ecopath.org>). EwE is a mass-balance approach that uses specified trophic linkages among biomass groups where food web interactions are a

function of productivity, consumption, and predation defined by input parameters for each functional group, which include biomass (B), production (P), consumption (Q), diet composition (i.e., proportion by mass), and ecotrophic efficiency (EE, the proportion of P/B explained by additive fishing and predation mortalities within the model; Christensen and Walters 2004). For unfished species, EE provides an index of the importance of predation as a driver of the dynamics for a given group (i.e., high EE indicative of "top-down" control). A second equation regulates that each group's consumption is equal to the sum of production, respiration, and unassimilated loss in accordance with bioenergetics theory. Biomass groups can be modeled as (i) an aggregation of trophically similar species (i.e., a functional group), (ii) individual species with no explicit age structure, or (iii) a "multistanza" group that accommodates age structure for individual species. Required inputs for each Ecopath group include four of the following five data for each model group: B ($\text{kg}\cdot\text{ha}^{-1}$), P/B (year^{-1}), Q/B (year^{-1}), P/Q (i.e., gross conversion efficiency, GCE in bioenergetics models; year^{-1}), and (or) EE. Diet composition of each prey to each predator and fishery removals ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) by individual fleets are also required inputs. Thus, Ecopath results in a biomass-based mass-balance representation of the food web where group interconnections are modeled with a series of linear equations.

Ecosim inherits food web relationships and population dynamics parameters from Ecopath for carrying out time-dynamic simulations. In Ecosim, Ecopath relationships are expressed as coupled differential equations where additions to population biomass result from consumption times growth efficiency and losses occur to fishing and predation mortalities. Ecosim is founded in Foraging Arena Theory (see Walters and Martell 2004; Ahrens et al. 2012), where consumption is limited by prey dynamics that determine their vulnerability to predators. In Ecosim, vulnerability parameters determine how much the predation mortality of a prey can increase with increased predator biomass as a result of fast or slow exchange to the vulnerable prey pool. When a vulnerability is low (i.e., close to one), that prey group's predation mortality is largely independent of predator biomass, as for prey species with highly risk-sensitive foraging. In contrast, predators will exhibit strong top-down control when a vulnerability value is high. The default vulnerability in Ecosim is two, which assumes that if a predator group's biomass increased to carrying capacity it would at most double the predation mortality on a prey group. Vulnerabilities are estimated within Ecosim by fitting to functional group time series data (see Christensen and Walters 2004; Ahrens et al. 2012), such that modeled group dynamics in the ecosystem model follow observed biomass trends through time. Ahrens et al. (2012) reported that estimated vulnerabilities reflect the difference between a predator's biomass and their carrying capacity in the ecosystem where higher vulnerabilities indicate low biomass relative to potential biomass. A statistical goodness of fit is generated as a weighted sum of squares of log biomasses from log-predicted biomasses, where users can individually weight time series (Christensen and Walters 2004). Useful time series for driving Ecosim time-dynamics include fishing effort by fishery, fishing and (or) total mortality rates, fishery catches, and primary production rate multipliers (e.g., relative nutrient levels).

Specified Lake Michigan model

Our model was developed to describe Lake Michigan's offshore ecosystem food web (i.e., depths >30 m, excluding Green Bay and Grand Traverse Bay). We parameterized Ecopath to reflect the 1987 state, which was prior to the invasion of round goby and dreissenids. Our ecosystem model focused on groups that we considered critical to Lake Michigan's fisheries sustainability and that have been highlighted as important to offshore food web dynamics (Table 1). In some cases, we combined species into functional groups based on diet composition and the ability to discriminate among them in diet composition analyses. Age structure was

Table 1. Lake Michigan Ecopath model input parameters.

Group No.	Group name (age)	B (kg·ha ⁻¹)	P/B (year ⁻¹)	Q/B (year ⁻¹)	EE	P/Q (year ⁻¹)	U/Q (year ⁻¹)	Detritus import (g·m ⁻² ·year ⁻¹)
1	Lake trout (6+)*	0.420	0.47	3.6			0.2	0
2	Lake trout (1–6)*	0.469	0.32	5.1			0.2	0
3	Lake trout stocked*	0.006	0.00	15.0			0.2	0
4	Burbot*	0.850	0.40	3.3			0.2	0
5	Brown trout*	0.290	0.24	5.5			0.2	0
6	Brown trout stocked*	0.001	0.00	23.1			0.2	0
7	Chinook wild (6+)	0.014	4.00	3.4			0.2	0
8	Chinook wild*	0.469	0.60	4.9			0.2	0
9	Chinook stocked (6+)	0.051	4.00	3.5			0.2	0
10	Chinook stocked*	1.767	0.60	5.0			0.2	0
11	Chinook stocked (0)*	0.003	0.00	25.2			0.2	0
12	Steelhead (6+)	0.105	2.00	1.8			0.2	0
13	Steelhead*	0.980	0.38	2.4			0.2	0
14	Steelhead stocked (0)*	0.011	0.00	7.4			0.2	0
15	Coho (3+)	0.045	3.00	1.2			0.2	0
16	Coho*	0.139	0.35	1.6			0.2	0
17	Coho stocked (0)*	0.001	0.00	5.0			0.2	0
18	Lake whitefish*	5.600	0.58	8.0			0.2	0
19	Rainbow smelt*		1.04	7.0	0.90		0.2	0
20	Alewife (1+)*	8.400	1.40	12.0			0.2	0
21	Alewife (0)	2.109	2.40	26.9			0.2	0
22	Bloater (1+)*	39.000	0.70	4.0			0.2	0
23	Bloater (0)	1.395	1.30	11.7			0.2	0
24	Slimy sculpin*		1.00	12.0	0.95		0.2	0
25	Deepwater sculpin*	19.700	0.60	10.0			0.2	0
26	Round goby*	0.003	1.75	11.4			0.2	0
27	Ninespine stickleback*	0.090	2.39	14.0			0.2	0
28	Dreissenid*	0.044	1.00	17.0			0.6	0
29	Fingernail clam*	8.800	1.40	11.9			0.2	0
30	<i>Diporeia</i> *	148.000	2.02	5.8			0.2	0
31	<i>Mysis</i> *		2.90	16.0	0.95		0.2	0
32	Calanoid copepod*	28.100	10.30			0.27	0.2	0
33	Nonpredatory cladoceran*	18.300	21.00			0.27	0.2	0
34	<i>Bythotrephes</i> *	0.500	40.00	85.0			0.4	0
35	Cyclopoid copepod*	8.100	19.80			0.26	0.2	0
36	Rotifer*	12.000	44.90			0.24	0.4	0
37	Oligochaete–chironomid*	158.000	1.76	8.0			0.2	0
38	Diatom*	13.400	350.00				0.0	0
39	Plankton*	67.400	250.00				0.0	0
40	Diatomdetritus	5.000					0.0	0
41	Detritus	50.000					0.0	0

Note: B, biomass; P, production; Q, consumption; EE, ecotrophic efficiency; and U, unassimilated. An asterisk (*) denotes groups with time series in Ecosim.

incorporated for salmonines to allow modeling of hatchery stockings where the first age stanza represented the hatchery period and presmolt phases spent in tributaries for anadromous species. Age structure was also incorporated for bloater (*Coregonus hoyi*) and alewife because of ontogenetic diet and habitat shifts. In general, our Ecopath model provided a mass-balanced snapshot of Lake Michigan's food web integrated across seasons. Our Ecopath model should be considered as a plausible reconstruction (i.e., hypothesis) of Lake Michigan's ecosystem structure and inter-group interactions. Below we describe group-specific inputs and data sources used in the model.

Mass-balance group inputs

Salmonines

Salmonid group states and rate parameters were primarily from age-structured stock assessment model estimates provided by the Lake Michigan Technical Committee Modeling Subcommittee of the Great Lakes Fishery Commission. Lake trout B, Z, and fishery-specific catches were derived from estimated 1987 age-weighted means for Lake Michigan lake trout fishery management units excluding Grand Traverse Bay and Green Bay. For lake trout, we

included an age-0 stanza, an age-1+ to age-6 stanza, and an age-6+ stanza. Lake trout recruitment in Lake Michigan was completely supported by hatchery stockings during our modeled time period (C. Madenjian, US Geological Survey, personal communication, 2010), and thus, we did not model a naturally reproducing lake trout group. The age-0 stanza represented time in the hatchery and diet was imported (i.e., they did not feed on model prey groups). Lake trout diet composition for other stanzas was estimated from data collected at Lake Michigan in 1994–1995 (see Madenjian et al. 1998 for methods).

Chinook salmon (*Oncorhynchus tshawytscha*) were divided into wild-reproduced and hatchery groups. Chinook salmon were successfully introduced into Lake Michigan in the late 1960s (Hansen and Holey 2002). By 1987, natural recruitment was estimated at 23% of total Chinook salmon recruitment, and natural contributions have increased to around 50% in some recent years (Claramunt et al. 2008). Ecopath biomass for wild and hatchery Chinook groups were estimated using 1987 predicted lakewide biomass from an age-structured model (I. Tsehay, Michigan State University, unpublished data), multiplying by year-specific estimates of the proportion wild-at-age for each age group and dividing by

lakewide surface area (excluding Green Bay and Grand Traverse Bay). Production/biomass was input as the 1987 total instantaneous mortality estimate from an age-structured population model and assumed equal for hatchery and wild groups (R. Claramunt, Lake Michigan Technical Committee Salmonid Working Group, personal communication, 2010). Consumption/biomass for age-1+ age groups (i.e., wild and hatchery) was derived using the GCE of 0.12 for ages 3–4 reported by [Rand and Stewart \(1998\)](#) and were assumed equal for hatchery and wild groups. Chinook salmon have semelparous life histories, where adults return to rivers for spawning and age-5 is the maximum age in Lake Michigan stock assessment models for this species. To capture this life-history trait within Ecopath, we established an age-6+ stanza and created an artificial fishery that removed this portion of the Chinook salmon population at an exploitation rate of one. Diet composition was from data collected by the Michigan Department of Natural Resources (R. Claramunt, MDNR, unpublished data). The age-6+ and age-0 groups were modeled with 100% imported diet to prevent them from feeding within the modeled ecosystem.

Coho salmon (*Oncorhynchus kisutch*), steelhead (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) biomasses were input using the 1987 lakewide estimate from an age-structured model (I. Tsehay, Michigan State University, personal communication, 2011) divided by lakewide surface area (excluding Green Bay and Grand Traverse Bay). We included an age-0 stanza for the hatchery period and an age stanza to represent semelparous spawners that we removed by modeling an artificial fishery, as described for Chinook salmon. Total instantaneous mortalities and fishing mortalities were also from the age-structured model weighted by biomass-at-age (I. Tsehay, Michigan State University, personal communication, 2011). Coho salmon Q/B was derived from an assumed GCE of 0.2 ([Rand and Stewart 1998](#)), and diet composition inputs were from data collected by the Michigan Department of Natural Resources in 2009. Steelhead Q/B was also derived from an assumed GCE of 0.16 ([Rand and Stewart 1998](#)), and diet composition inputs were from data reported by [Rand et al. \(1993\)](#). Brown trout Q/B was derived assuming a GCE of 0.04, and diet composition was derived from data reported by [Jude et al. \(1987\)](#).

Other predatory fishes

Burbot biomass was averaged across 1986 to 1988 US Geological Survey (USGS) bottom trawl density estimates. Mortality and consumption values were not available for burbot from offshore Lake Michigan, and thus we used a P/B of 0.4 as reported by [Stapanian and Madenjian \(2007\)](#) for Lake Erie and Q/B was derived based on a GCE of 0.12 reported by [Rudstam et al. \(1995\)](#) for Green Bay. Burbot diet composition was based on Lake Michigan data from >39 m depth reported by [Fratt \(1991\)](#) and modified to include round goby (see methods below). We did not model fishing mortality for burbot because the extensiveness of fishing mortality in offshore waters (i.e., not within Green Bay or Grand Traverse Bay) is unknown.

Lake whitefish (*Coregonus clupeaformis*) biomass was estimated using 1987 estimates from age-structured models developed for Lake Michigan Management Units (data provided by D. Caroffino, Lake Michigan Technical Committee Modeling Subcommittee Co-chair, December 2010). We included estimates from multiple lake whitefish management unit (WFM) models and calculated a mean biomass and mean P/B weighted by WFM area. Consumption to biomass was derived assuming a GCE of 0.07 based on the range reported by [Pothoven and Madenjian \(2008\)](#). Diet composition was from postinvasion data ([Pothoven and Madenjian 2008](#)) to ensure that lake whitefish would utilize dreissenids as prey in our time-dynamic simulations. Diet composition inputs were modified for invasive contributions as described below.

Prey fish

Prey fish groups included rainbow smelt, alewife, bloater, slimy sculpin (*Cottus cognatus*), deepwater sculpin (*Myoxocephalus thompsonii*), round goby, and ninespine stickleback (*Pungitius pungitius*). Prey fish biomass inputs were from the 1987 USGS bottom trawl survey except for rainbow smelt and age-0 groups (e.g., age-0 alewife). Survey methods have been described previously by [Madenjian et al. \(2003\)](#) and [Bunnell et al. \(2006\)](#). We chose to estimate rainbow smelt biomass in Ecopath because rainbow smelt catchability to bottom trawls is low. For example, 1992 hydroacoustics density estimates were nearly three times higher than bottom trawl density estimates in that year. Diet composition for most prey fish (except ninespine stickleback and round goby) were collected in 1994 and 1995 (see [Davis et al. 2005](#)). Round goby were not detected in USGS Lake Michigan bottom trawls until 2003, and thus, we relied on diet composition data from 2009–2010 sampling (J. French and J. Londer, USGS Great Lakes Science Center, unpublished data).

Prey fish population rate parameters were from multiple sources. Production to biomass for adult alewife and adult bloater were estimated from catch curve analysis using trawl catches and estimated ages (USGS Great Lakes Science Center, unpublished data). Consumption to biomass for alewives was derived assuming GCE = 0.09 for age-0 alewife and was estimated by Ecopath for age-1+ alewife as described above for salmonine age stanzas. Bloater Q/B was derived by using a GCE of 0.08 reported for age-1+ bloater during 1986–1987 ([Rudstam et al. 1994](#)). Rainbow smelt P/B , Q/B , and P/Q inputs were averaged across age-0 through age-5 values reported for Lake Michigan ([Lantry and Stewart 1993](#)). We could not find Lake Michigan total mortality estimates for slimy sculpin and deepwater sculpin, and thus, we assumed a P/B of 1.0 for slimy sculpin and 0.60 for deepwater sculpin, each within the range reported for other systems ([Petrosky and Waters 1975](#); [Kitchell et al. 2000](#)). Production to consumption was also difficult to find for slimy sculpin and deepwater sculpin. For slimy sculpin and deepwater sculpin Q/B , we assumed that P/Q values were similar to those reported for a Lake Superior Ecopath model ([Kitchell et al. 2000](#)). Round goby P/B was assumed to be 1.75 and was within the range reported for Lake Erie round goby ([Bunnell et al. 2005](#)). Round goby Q/B was derived based on a GCE of 0.175 ([Lee and Johnson 2005](#)). Ninespine stickleback P/B was estimated from a length-based empirical equation ([Lorenzen 2000](#)) using adult natural mortality (1.0) and length infinity (9.6 cm) values from Fish-Base ([Froese and Pauly 2011](#)). Ninespine stickleback Q/B was derived assuming a GCE of 0.25.

Benthic invertebrates

Four benthic invertebrate groups were modeled: sphaeriids, *Diporeia*, oligochaete-chironomids, and dreissenids. Chironomidae were found at low abundance in Lake Michigan relative to our other benthic invertebrates ([Nalepa et al. 1998](#)), and thus, we combined them with oligochaetes (hereafter collectively referred to as oligochaete). We initialized the model biomasses for sphaeriids, *Diporeia*, and oligochaetes using 1987 southern Lake Michigan densities reported in [Nalepa et al. \(1998\)](#) weighted by depth areas (excluding data from 16–30 m). Dreissenid biomass was modeled as shell-free wet mass. Other population dynamics and diet input values for benthic invertebrates are shown in [Tables 1 and 2](#).

Benthipelagic invertebrates

Our Mysis input biomass was derived using data reported in [Lehman et al. \(1990\)](#). For biomass, we used the estimate from 1988 because sampling did not occur at sites >100 m in 1987, which likely underestimated Mysis abundance. We assumed a mean length of 10 mm and used the length–mass relationship of [Johannsson \(1992\)](#), assuming a 16% dry mass to wet mass ratio ([Hewett and Johnson 1992](#)), to convert density per area to biomass per area. Our Mysis P/B of 2.9 was based on previous Great Lakes

Table 2. Lake Michigan Ecopath model diet composition inputs.

Group No.	Prey group name (age)	Predator group No.																																							
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37			
1	Lake trout (6+)																																								
2	Lake trout (1–6)		0.00																																						
3	Lake trout stocked																																								
4	Burbot																																								
5	Brown trout																																								
6	Brown trout stocked																																								
7	Chinook wild (6+)																																								
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9	Chinook stocked (6+)																																								
10	Chinook stocked																																								
11	Chinook stocked (0)																																								
12	Steelhead (6+)																																								
13	Steelhead																																								
14	Steelhead stocked (0)																																								
15	Coho (3+)																																								
16	Coho																																								
17	Coho stocked (0)																																								
18	Lake whitefish																																								
19	Rainbow smelt	0.05	0.10		0.10	0.14			0.01		0.01			0.06																											
20	Alewife (1+)	0.62	0.25		0.12	0.45			0.71		0.71			0.21		0.67																									
21	Alewife (0)	0.12	0.25		0.03	0.10			0.25		0.25			0.27		0.33		0.01																							
22	Bloater (1+)	0.13	0.06		0.22				0.02		0.02																														
23	Bloater (0)	0.01	0.02		0.06																																				
24	Slimy sculpin	0.03	0.06		0.16	0.07								0.01																											
25	Deepwater sculpin	0.02	0.02		0.20																																				
26	Round goby	0.00	0.00		0.00											0.00		0.00																							
27	Ninespine stickleback				0.00				0.01		0.01																														
28	Dreissenid																	0.00							0.00																
29	Fingernail clam																	0.16						0.02																	
30	<i>Diporeia</i>		0.01		0.01													0.47	0.06	0.14	0.12	0.51	0.40	0.20	0.66	0.03	0.02						0.04								
31	<i>Mysis</i>	0.01	0.12		0.09													0.32	0.57	0.10	0.02	0.30	0.26	0.03	0.34	0.78	0.63														
32	Calanoid copepod		0.08																0.23	0.30	0.43	0.10	0.20			0.17	0.11						0.12				0.10				
33	Nonpredatory cladoceran		0.02											0.02					0.14	0.30	0.19	0.04	0.07	0.76	0.00		0.19					0.26			0.80						
34	<i>Bythotrephes</i>	0.00	0.00						0.00		0.00								0.00	0.02	0.00	0.01	0.03																		
35	Cyclopoid copepod													0.02					0.01	0.15	0.24	0.03	0.01				0.01					0.12			0.10						
36	Rotifers																			0.00									0.00												
37	Oligochaete–chironomid		0.00			0.09												0.04							0.01	0.00	0.02	0.04													
38	Diatom																														0.25	0.20			0.40	0.10					
39	Plankton																													0.65	0.80			0.21	0.60	0.90		1.00			
40	Diatom detritus																													0.05			0.90	0.13							
41	Detritus																													0.05		0.10	0.13						1.00	1.00	
	Import	0.00	0.00	1.00	0.00	0.15	1.00	1.00	0.00	1.00	0.00	1.00	1.00	0.40	1.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
	Sum	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	

studies as reported by Sell (1982), and we assumed a GCE = 0.15 (Johannsson et al. 1994). Mysis were modeled as omnivores (Sierszen et al. 2011), and diet composition inputs were derived from Lake Ontario data averaged across seasons (Johannsson et al. 2003).

Zooplankton

Zooplankton groups were divided into calanoid copepod, cyclopoid copepod, nonpredatory cladoceran, *Bythotrephes*, and rotifers. We excluded the predatory zooplanktons *Leptodora* spp. and *Cercopagis* spp. because they were found at much lower densities than *Bythotrephes* during our modeled time period (R. Barbiero, CSC, unpublished data). Zooplankton group biomass inputs were from the EPA Great Lakes National Program Office (GLNPO) surveys (R. Barbiero, CSC, unpublished data). Production/biomass ratios for copepods, cladocerans, and rotifers were estimated using empirical temperature-dependent relationships from Shuter and Ing (1997) assuming a mean temperature at 20 m of 11 °C (T. Croley, NOAA – Great Lakes Environmental Research Laboratory (GLERL), unpublished data). *Bythotrephes* P/B was based on temperature-dependent mean daily values reported by Foster and Sprules (2009) multiplied by 90 days (i.e., the span of their study). *Bythotrephes* Q/B equaled 85 (assuming that 40% of consumption was unassimilated), which resulted in a P/Q equal to 0.47. Other zooplankton group Q/B values were derived using GCE estimated for rotifers, copepods, and cladocerans (0.24, 0.26, and 0.27, respectively; Straile 1997). Diet composition for zooplankton (except *Bythotrephes*) was assumed to be 100% phytoplankton. *Bythotrephes* diet composition was assumed to be 10% calanoid copepod, 10% cyclopoid copepod, and 80% nonpredatory cladoceran to reflect selectivity for cladocerans (Vanderploeg et al. 1993; Schulz and Yurista 1999).

Primary producers

Primary producers were divided into diatoms and other phytoplankton (hereafter referred to as plankton). Diatoms were included as an individual group because they have been noted as a key contributor to ecosystem productivity that has been negatively affected by dreissenid establishment (Fahnenstiel et al. 2010). Our plankton group included all other edible and nonedible species. Primary producer biomass inputs were calculated by averaging across 1986–1988 biomasses reported in Makarewicz et al. (1998) and assuming a euphotic depth of 20 m (i.e., the maximum depth they sampled).

Detritus

We modeled two detritus groups. The first was a generalized detritus pool, to which all groups flowed, with the exception of diatoms. Our other detritus group was “diatom detritus”, which emulated a specific pool used by *Diporeia* for foraging, thus determining their productivity. We only allowed foraging on our diatom detritus pool by *Diporeia* and dreissenids to incorporate a hypothesized interaction between these two that has been proposed as a mechanism resulting in *Diporeia* biomass declines.

Modeled fisheries

Our model included commercial fisheries for lake trout and lake whitefish and recreational fisheries for salmonines. We also modeled sea lamprey as a fishery, rather than a functional group, because they can be ecologically viewed as a mortality source owing to their parasitic life history. Fishery-specific fishing mortality rates from stock assessments (Lake Michigan Technical Committee Modeling Subcommittee; I. Tsehaye, Michigan State University, personal communication, 2011) were used to derive landings using Baranov's catch equation (Ricker 1975). Lake trout and lake whitefish fishery-specific catches and mortalities were averaged across management units weighted by abundance within management units. Chinook recreational fishery catches were partitioned between wild and hatchery fish by multiplying

annual fishing mortality-at-age by estimated biomass-at-age for each group, thus assuming equal vulnerability to harvest. We modeled several artificial fisheries as additional mortality sources. For example, artificial fisheries were modeled to remove semelparous species (e.g., coho salmon) from the ecosystem at ages exceeding their maximum ages used in stock assessment models.

Modeling invasive species

For the time-dynamic ecosystem component that spanned 1988 through 2008, we needed to include two invasive species groups (dreissenid mussels, round gobies) in the 1987 Ecopath mass-balance model even though they had not yet invaded Lake Michigan. We included invasive species in Ecopath at a biomass near zero, and then we used biomass time series as forcing functions to drive their abundances through time (see Langseth et al. 2012). For predators that preyed on these invasive species, we used postinvasion contributions of their diet and down-scaled them based on the ratio of present day biomass to our input biomass that was close to zero. Other diet items were downscaled proportionately such that the total diet summed to one.

Ecopath indices of trophic structure and networks

We used several measures of food web connectivity and predator-prey associations to describe the structure of the Lake Michigan food web. Food web connectivity metrics included (i) the number of links among functional groups, (ii) directed connectance, calculated as (L/S^2) , where L is the number of realized links and S is the number of model species, (iii) characteristic path length, which equals the mean length of the shortest path between species pairs and was used as an index of separation among groups within our food web, and (iv) transfer efficiency among trophic levels, which was estimated. We also used keystone species, those with disproportionate impacts on communities (Power et al. 1996), which were identified within Ecopath according to methods in Christensen and Walters (2004) and Libralato et al. (2006). Finally, influential network interactions involving the highest ranked keystone species were evaluated using modified input-output analysis (i.e., mixed trophic impact analysis; Ulanowicz and Puccia 1990) to indicate how changes in the biomass of an influential group would affect (i.e., direction and relative impact) other groups in the ecosystem.

Time-dynamic simulations (Ecosim)

Model balancing, fitting, and selection

Time-dynamic simulations were carried out from our mass-balance year (i.e., 1987) through 2008. Our simulations were driven by time series of fish stockings and fishery harvests. For fish stockings, we input annual stocking rates from 1988 to 2008 for lake trout, Chinook salmon, coho salmon, steelhead, and brown trout relative to 1987 stocking rates (US Fish and Wildlife Service and Great Lakes Fishery Commission 2010). For fisheries harvest, salmonine and lake whitefish biomass and mortality (i.e., by fishing fleet and total mortality) time series were from age-structured model estimates (D. Caroffino, Lake Michigan Technical Committee Modeling Subcommittee, personal communication, 2010).

Model balance occurred when EEs for all groups were less than one, which indicated that biomass and production terms exceeded losses. We constructed time series that represented all trophic levels for model fitting and performance evaluations (Table 1). Time series allowed us to estimate vulnerabilities that minimized sums of squares between observed and predicted biomasses. To estimate vulnerability values, we focused only on those consumers with available biomass time series (i.e., one value for each predator applied to all of its prey, totaling 27 estimates), rather than the 144 possible vulnerability values for each predator-prey combination. For the remaining vulnerability values, except round goby and dreissenids, we used the default value

of two. For round goby and dreissenids, vulnerabilities were set at a high number (100 and 1000, respectively). Setting high vulnerabilities for invaders prevented their Q/B values from declining as their biomasses increased, which would have resulted in limited population growth when their observed population biomasses were rapidly increasing.

Beyond fishing mortalities, stocking rates, and species invasions as ecosystem drivers, we also explored whether inclusion of year-specific primary production information in Ecosim improved overall model fit. Production anomalies can be input as a forcing function, where the primary producer's production rate is multiplied by a value relative to its baseline Ecopath P/B . We compared the fit among four different models. For the first two models, we used two different time series of total phosphorus concentrations as indices of annual productivity anomalies: one from the EPA–GLNPO annual lakewide surveys during April and the other from the NOAA–GLERL annual surveys offshore of Muskegon, Michigan, during midstratification (i.e., late summer). Thus, simulations with the first two models that included year-specific primary production anomalies caused the productivity rates of primary producer groups to vary with observed data relative to 1987 values. For the third model, annual production anomalies were estimated within Ecosim (see Christensen et al. 2008). Lastly, we fit a model that did not include year-specific primary production anomalies; this assumed no temporal pattern in primary productivity and attributed all system dynamics to predator–prey interactions, fishing effects, or stocking. We selected our most parsimonious model using Akaike's information criterion (AIC) (see <http://sources.ecopath.org/trac/Ecopath/ticket/904>).

Results

Ecopath model balance and fitting

Our Ecopath model did not initially balance and problematic groups were slimy sculpin, *Mysis*, *Diporeia*, and age-0 alewife. We manually adjusted initial model inputs to achieve model balance (reflected in Table 1). Consumption of slimy sculpin by burbot was estimated to exceed sculpin biomass density. Slimy sculpin catchability to daytime bottom trawls is biased low relative to trawling at night (Yule et al. 2007); thus, we input an EE of 0.95 and estimated biomass needed to support modeled consumption given our other inputs. *Mysis* and *Diporeia* biomass inputs also were not initially supportive of modeled consumption, primarily owing to bloater predation. Thus, we allowed Ecopath to estimate *Mysis* biomass assuming an EE = 0.95, rather than using the 1988 survey value, and decreased our bloater Q/B from 8.8 to 4 (i.e., a GCE from 0.08 to 0.17); this reduction was justified because recent sampling of adult bloater has indicated adult bloater do not occupy temperatures warmer than 5 °C (see TeWinkel and Fleischer 1999; Bunnell et al. 2011), yet Rudstam et al. (1994) assumed adult bloater would occupy 10 °C water when available. The decrease in bloater consumption rate allowed *Diporeia* production to exceed losses. Age-0 alewife production was also too low to support salmonine predation. To achieve balance for age-0 alewives, we increased their P/B value to 2.4 using Lorenzen's (1996) allometric relationship between body size and natural mortality.

Ecopath indices of trophic structure and networks

Our Ecopath mass-balance model revealed estimates of food web connectivity, keystone species, influential interactions, and trophic transfer for the 1987 ecosystem. Our diet composition inputs (Table 2) resulted in 149 food chain links and an average of 3.92 links per functional group. Total directed connectance equaled 0.097, which was the ratio between the number of realized links and the number of functional groups. Characteristic path length, which was the mean shortest path length among all predator–prey combinations and an index of separation among

groups within the food web, equaled 1.79. Trophic transfer efficiencies averaged 10.1% across trophic levels and were highest for trophic level 2 (TE = 12.7%) and lowest for trophic level 4 (TE = 6.6%).

The highest ranked keystone functional groups in descending order were as follows: *Mysis*, burbot, plankton, alewives, nonpredatory cladocerans, and Chinook salmon. Input–output analysis revealed which functional groups were most highly influenced by the keystone groups (Table 3). Some network interactions were not surprising (e.g., bivalves benefitting from phytoplankton), whereas others were more difficult to interpret (e.g., positive effect of Chinook salmon on rotifers). *Mysis* had mixed effects across fish groups and the strongest negative impact on nonpredatory cladocerans, one of their primary prey. Nonpredatory cladocerans had positive impacts on *Bythotrephes*. Phytoplankton had positive impacts on all functional groups except diatoms, *Diporeia*, deepwater sculpin, oligochaetes, and itself. Burbot were indicated to have negative impacts on almost all species (including itself), with the strongest effects on benthic prey fish; surprisingly, there was a weak positive effect on ninespine stickleback. Adult alewives were predicted by the model to benefit not only salmonines, as had been expected, but also phytoplankton, dreissenid mussels, and some herbivorous zooplankton. Chinook salmon had high potential for intraspecific competition and also strong negative impacts on alewives.

Ecosim model balancing, fitting, and selection

We used time series data from multiple sources and across multiple trophic levels to estimate vulnerability parameters that determined prey flow rates from invulnerable to vulnerable states. Our best-fitting model, as determined using AIC values, resulted from allowing Ecosim to estimate both vulnerability and annual production anomalies. Models that did not include estimated annual production anomalies, or used empirical total phosphorus concentrations as an index of production anomalies (i.e., EPA–GLNPO and NOAA–GLERL time series), all had ΔAIC values >11 relative to our best model. Hence, including both predator–prey dynamics and allowing primary production to vary across years provided the best fits to time series to validate our model. In general, the model was able to predict the pattern for most functional group biomass trends, although some exceptions were evident (see Fig. 1 and details below).

Ecosim time-dynamic outputs

Overall trends

Ecosim predicted a fivefold increase in offshore ecosystem total biomass from 1987 to 2008, but this was driven by the proliferation of dreissenid mussels (there was a 61% total biomass decrease if dreissenid biomass was removed). Biomass reductions were predicted for groups at all trophic levels (Fig. 2). Lake whitefish was the only native group with higher predicted biomass in 2008 than in 1987. All salmonine groups, except non-native brown trout, had lower predicted biomasses in 2008 than in 1987. These declines, in part, were driven by trends in salmonine stocking rates. For example, Chinook salmon stocking decreased by approximately 50% over the course of our modeled time period. Total prey fish biomass estimates declined by 80% during our 22-year time period despite the invasion of a new forage fish (i.e., round goby), which was estimated to comprise 6% of total prey fish biomass in our final simulation year. *Mysis* biomass was predicted to decrease by 75%; however, we had high uncertainty in our 1987 biomass estimate and relatively few years of data to evaluate our predictions between 1988 and 2008. The benthic amphipod *Diporeia* biomass was predicted to decline by 87% in our simulations. All zooplankton groups were predicted to have declined between our initial and final simulation years, and rotifers were predicted to have declined by nearly 100%. Declining rotifer biomass was driven by increased predation mortality. Even though rotifers contributed

Table 3. Input–output analysis results for Lake Michigan ecosystem model keystone species and selected invasive species.

Impacted group	Impacting group								Impacting invasive group		
	Mysis	Burbot	Plankton	Alewife (1+)	Alewife (0)	Nonpredatory cladoceran	Chinook wild	Chinook stocked	Round goby	Dreissenid	Bythotrephes
Lake trout (6+)	−0.064	−0.025	0.048	0.320	−0.018	0.054	−0.022	−0.086	−0.00001	0.00034	−0.00057
Lake trout (1–6)	0.014	−0.032	0.068	0.010	0.120	0.042	−0.008	−0.032	−0.00003	0.00048	−0.00659
Burbot	0.062	−0.206	0.087	0.075	−0.007	0.106	−0.006	−0.024	0.00078	0.00062	−0.00840
Brown trout	−0.032	−0.033	0.046	0.162	0.015	0.050	−0.013	−0.052	−0.00004	0.00032	−0.00354
Chinook wild	−0.069	−0.017	0.055	0.261	0.072	0.046	−0.128	−0.485	−0.00001	0.00039	−0.00225
Chinook stocked	−0.069	−0.017	0.055	0.261	0.072	0.046	−0.128	−0.485	−0.00001	0.00039	−0.00225
Steelhead	−0.044	−0.017	0.034	0.064	0.104	0.025	−0.011	−0.042	−0.00001	0.00024	−0.00323
Coho	−0.080	−0.018	0.054	0.241	0.112	0.041	−0.023	−0.091	0.00002	0.00038	−0.00247
Lake whitefish	0.088	0.056	0.060	0.019	0.002	0.013	−0.001	−0.005	0.00006	0.00065	−0.00146
Rainbow smelt	0.318	−0.092	0.146	−0.069	−0.078	0.088	−0.004	−0.015	−0.00015	0.00104	−0.01470
Alewife (1+)	−0.130	−0.030	0.120	−0.203	−0.100	0.126	−0.051	−0.199	−0.00002	0.00084	−0.00201
Alewife (0)	−0.223	−0.049	0.087	−0.159	−0.120	−0.004	−0.038	−0.149	−0.00002	0.00058	−0.01090
Bloater (1+)	0.053	0.043	0.041	0.005	−0.009	0.024	0.000	−0.001	0.00003	0.00028	0.00106
Bloater (0)	0.013	−0.519	0.036	−0.067	−0.036	−0.024	0.008	0.030	−0.00053	0.00024	0.02870
Slimy sculpin	−0.340	−0.488	0.189	−0.002	−0.041	0.491	0.003	0.013	−0.00044	0.00136	−0.04720
Deepwater sculpin	0.118	−0.548	−0.030	−0.063	−0.010	−0.057	0.006	0.024	−0.00056	−0.00022	0.00323
Round goby	0.466	−0.317	0.123	−0.005	−0.021	0.020	0.003	0.010	−0.00042	0.00296	−0.00814
Ninespine stickleback	0.430	0.094	0.165	−0.199	−0.091	0.165	−0.079	−0.310	0.00001	0.00117	−0.02250
Dreissenid	0.015	−0.035	0.311	0.129	0.001	−0.061	−0.009	−0.036	−0.00339	0.00197	0.01280
Fingernail clam	0.012	−0.006	0.413	0.164	−0.003	−0.072	−0.012	−0.045	−0.00004	0.00272	0.01290
<i>Diporeia</i>	−0.132	0.110	−0.034	−0.008	−0.003	−0.012	0.000	0.002	0.00014	−0.00027	0.00134
Mysis	−0.249	0.192	0.223	0.064	−0.013	0.142	−0.003	−0.013	0.00006	0.00158	−0.01760
Calanoid copepod	−0.226	−0.053	0.149	−0.007	−0.081	−0.156	0.005	0.020	−0.00004	0.00103	0.00169
Nonpredatory cladoceran	−0.400	−0.099	0.348	0.118	−0.023	−0.249	−0.007	−0.028	−0.00004	0.00250	−0.07410
<i>Bythotrephes</i>	−0.337	−0.015	0.221	−0.276	0.025	0.501	0.018	0.071	0.00004	0.00159	−0.06210
Cyclopoid copepod	−0.344	−0.092	0.046	−0.001	−0.044	−0.166	0.002	0.009	−0.00003	0.00027	−0.00114
Rotifer	0.176	0.043	0.505	−0.559	0.081	−0.202	0.035	0.137	0.00006	−0.01170	0.01500
Oligochaete–chironomid	−0.042	−0.014	−0.050	−0.092	0.012	−0.038	0.007	0.027	−0.00015	−0.00045	0.00295
Diatom	0.288	0.072	−0.151	−0.019	0.057	0.014	−0.002	−0.007	0.00004	−0.00125	0.01100
Plankton	0.049	0.012	−0.372	0.228	−0.018	−0.079	−0.015	−0.059	−0.00001	0.00451	0.01320
Diatom detritus	0.019	−0.121	0.001	−0.001	0.004	−0.008	0.000	0.000	−0.00013	−0.00001	0.00109
Detritus	−0.014	−0.009	0.028	0.075	−0.009	0.023	−0.006	−0.023	0.00012	0.00026	−0.00126

Note: Bold values indicate maximum and minimum for each impacting group.

only 2% to the diets of dreissenids, dreissenid predation was predicted to increase rotifer mortality 30-fold. Total phytoplankton biomass (i.e., diatoms plus other phytoplankton) was predicted to decline by approximately 60% across our modeled time period owing to both increased predation and production anomaly effects. Calanoid copepods, nonpredatory cladocerans, and rotifers were dominant phytoplankton grazers in early simulation years (accounting for 90% of total predation), whereas calanoid copepods became the dominant grazer in latter simulation years. Dreissenids accounted for about 60% of total phytoplankton grazing between 2006 and 2008.

Interactions between piscivores and their prey

Predicted total prey fish consumed ($\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) by piscivores showed a declining trend between 1987 and 2008. Total predicted prey fish consumed was 35% lower in our final simulation year relative to our first simulation year, and total predicted prey fish biomass decreased by 79% over this time (Fig. 2). Chinook salmon consumed the largest proportion of prey fish (range = 45%–66%), followed by lake trout (range = 12%–21%). Prey fish consumption by burbot declined through time, and prey fish consumed by predators other than Chinook salmon and lake trout always accounted for at least 25% of total predicted prey fish consumed.

Interactions between planktivores–benthivores and their prey

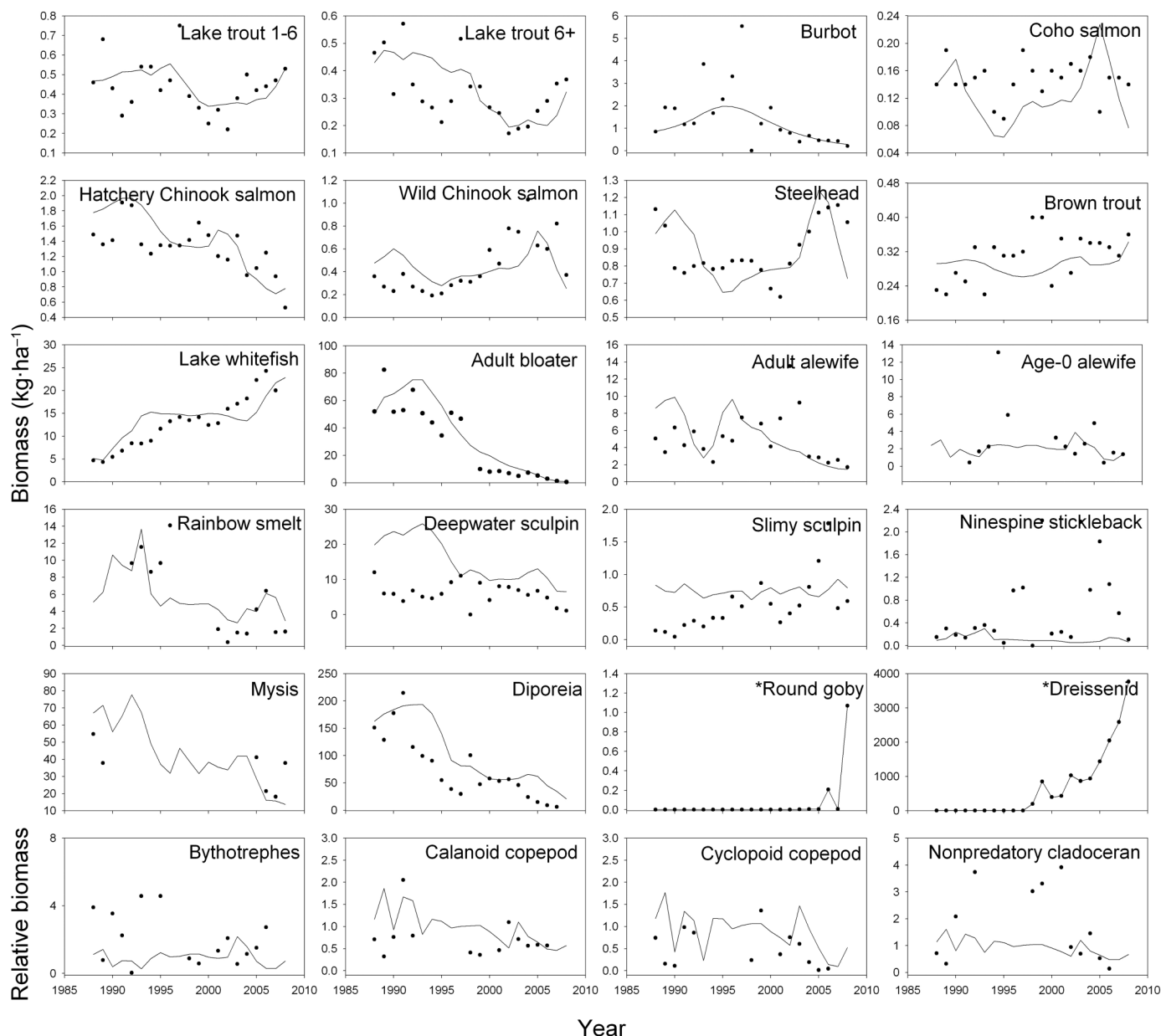
Total Mysis consumed by prey fishes varied between 36 and 206 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ across simulation years and exhibited a decreasing trend between the early 1990s and 2008 (Fig. 2). Bloaters were a dominant Mysis predator in our initial simulation years, whereas deepwater sculpin was the dominant predator in our

later simulation years. Mysis were predicted to become a common diet component for lake whitefish as the *Diporeia* population crashed and dreissenid biomass accumulated. Total zooplankton consumed varied through time and largely tracked Mysis biomass trends (Fig. 2). Invertebrate planktivores (i.e., Mysis and *Bythotrephes*) consumed the largest proportion of zooplankton across all years (range = 0.70–0.83), followed by bloater and alewife (combined range = 0.16–0.28). Consumption of *Diporeia* increased between 1987 and 1993 and then generally declined to very low levels as *Diporeia* biomass plummeted. The primary consumers of *Diporeia* were bloater and deepwater sculpin through the early 2000s, whereafter deepwater sculpin was the dominant consumer in late simulation years. Consumption of *Bythotrephes* was variable but appeared to decline between 1996 and 2008 largely owing to the decrease in lakewide bloater biomass (even though it comprised only 0.03 of bloater diets). *Bythotrephes* consumed by alewife did not decrease proportionately to alewife biomass declines, and *Bythotrephes* were never predicted to contribute more than 8% to alewife diets. Total phytoplankton (i.e., diatoms plus other phytoplankton) consumed varied through time as a function of predator biomasses, but showed a peak in the early 2000s that coincided with invasion and proliferation of dreissenid mussels (Fig. 2).

Impact of invasive species

Our time-dynamic food web model allowed us to evaluate effects of recent invasive species (i.e., round goby, dreissenids, and *Bythotrephes*) on other functional groups at our mass-balance state. We used the highest and lowest values of input–output analysis for each recent invader as an index of which groups are most

Fig. 1. Observed (points) and predicted (line) biomasses for selected Lake Michigan ecosystem model functional groups; relative biomasses relate to Ecopath inputs for 1987 (an asterisk (*) indicates invasive groups with forced biomasses).



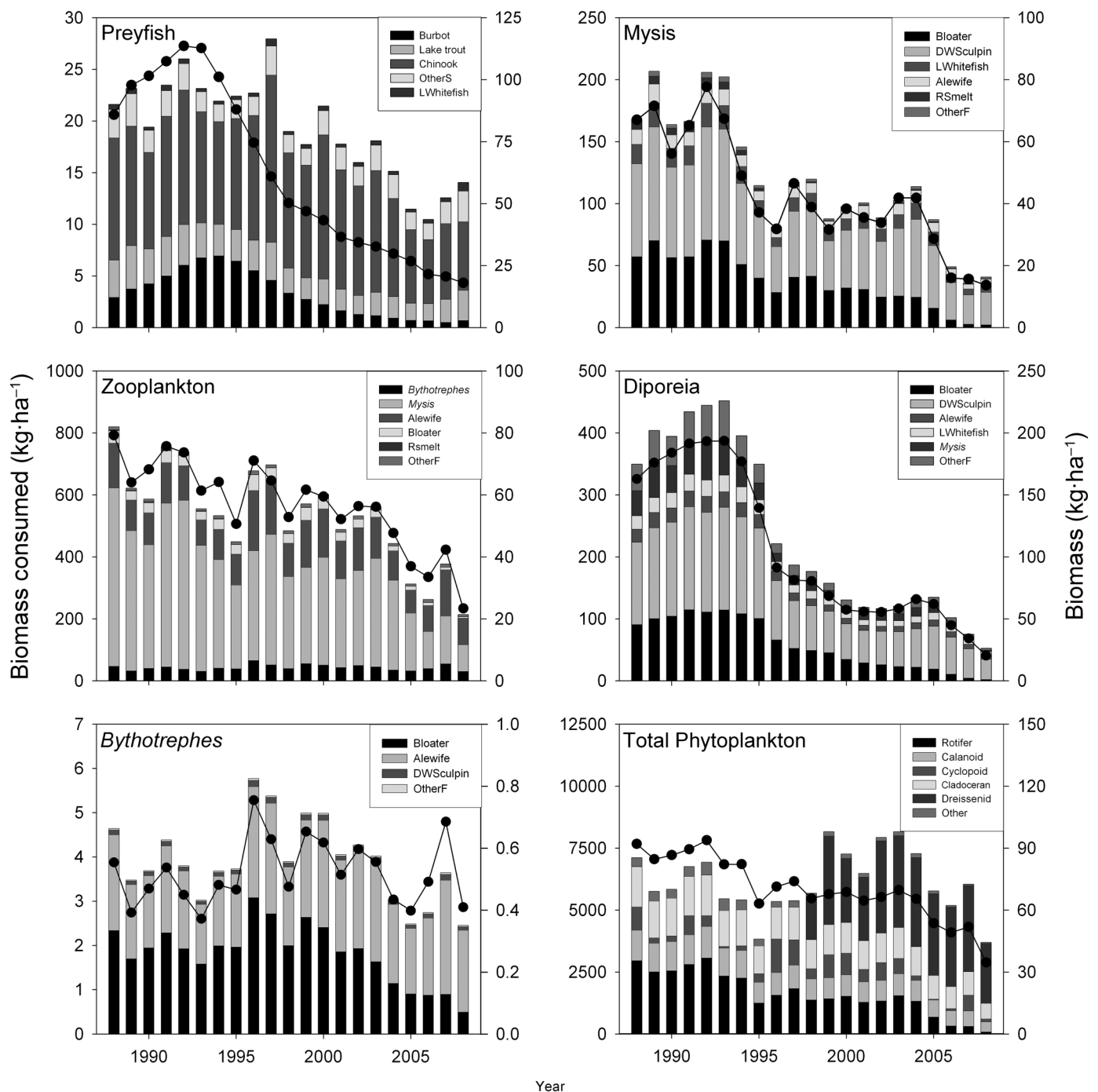
positively and negatively affected by invasive species (Table 3). Although our input biomass for round gobies and dreissenids were very low (because inputs were for before the invasion time period), which resulted in low absolute magnitudes, results from input-output analysis still provided an indication of direction and relative magnitude of their interactions with other groups. In general, round goby had the most positive input-output value for burbot and negative impacts for most other fish groups and dreissenids. Dreissenids had the strongest negative impact on rotifers, whereas round goby and *Bythotrephes* had positive impacts on rotifers. Dreissenids had positive effects on round goby. Unexpectedly, input-output analysis indicated a positive effect of dreissenids on plankton, which we believe was an indication of competition among primary producers in an oligotrophic system whereby negative dreissenid effects on diatoms could allow for increased phytoplankton production. *Bythotrephes* negatively affected nonpredatory cladocerans, as expected. *Bythotrephes* also negatively affected all prey fish excluding bloater and deepwater

sculpin, as *Bythotrephes* was competing with prey fish for zooplankton.

Discussion

Quantifying the complexity of aquatic ecosystems, changes through time, and stressors that perturb ecosystem function is a challenge, even in rigorously studied systems, but also a requirement for moving forward with ecosystem-based management. The Lake Michigan ecosystem experienced multiple perturbations in the 1980s, and thereafter, that resulted in two decades of food-web-related science investigations. Our ecosystem model was able to capture functional group biomass trends, decreased ecosystem production by non-dreissenids, and diet composition changes across multiple trophic levels during this transitional time period. For example, predicted contributions of dreissenids to lake whitefish diets were ~35% and predicted contributions of round goby to burbot diets were ~50%, which agreed with recent

Fig. 2. Estimated annual consumption (bars, y axis) of prey groups and estimated prey group biomass (line, z axis) through time. OtherS = other salmonids; OtherF = other fish.



field observations (Pothoven and Madenjian 2008; Jacobs et al. 2010, respectively). Thus, our development of an offshore Lake Michigan ecosystem model provided a heuristic tool for understanding potential drivers to ecosystem function and in future applications will (i) provide a tool for exploring alternative ecosystem-based management scenarios (i.e., changes in stocking, changes in productivity) and (ii) create a “stepping stone” model for exploring alternative hypotheses regarding ecosystem structure, function, and interspecies relationships.

Model balancing and fitting procedures revealed data limitations as well as uncertainty in model structure and performance. Although relatively data-rich, Lake Michigan still has many gaps

in biomass, production, consumption, and diet estimates for several species. As a result, to achieve model balance we resorted to estimating some parameters rather than using empirically derived estimates from Lake Michigan. For example, putatively low catchability of slimy sculpin and rainbow smelt to bottom trawls caused us to assume an EE for those groups (rather than allowing Ecopath to estimate EE based on production and mortality) to derive their biomasses. Because slimy sculpin and rainbow smelt contribute to the diets of juvenile and intermediate-sized lake trout (Madenjian et al. 2002), our assumed EE had implications for the model’s ability to fit lake trout biomass dynamics, and this likely cascaded to other groups that lake trout influenced (e.g.,

alewife, bloater). Another large data gap was diet composition of invertebrate planktivores, including *Bythotrephes* and *Mysis*, which caused us to use information from other lakes (e.g., Lake Ontario; [Johannsson et al. 2001](#)). Given that *Bythotrephes* and *Mysis* were primary zooplankton consumers in our model, developing quantitative methods for empirical diet estimation of *Bythotrephes* should be a top research priority. Similarly, some calanoid and cyclopoid copepods have been described as either omnivorous or even predatory ([Balcer et al. 1984](#)), yet we were unaware of any quantitative data that could have allowed for us to characterize the proportion of their diets that were non-phytoplankton. Finally, the lack of time series data and high interannual variation within some time series affected our ability to evaluate model performance and, thus, highlighted the importance of long-term monitoring programs at all trophic levels for developing and evaluating time-dynamic ecosystem models. For example, *Mysis* were our highest ranked keystone species, yet it also was one of our most incomplete biomass time series available to evaluate model performance. How data gaps may have limited our model's performance or caused unexpected model results is unknown.

There is growing scientific research regarding the relative importance of top-down and bottom-up regulation in Great Lakes food webs (see overview by [Bunnell et al. 2014](#)); our model provided evidence that both drivers were important in Lake Michigan. From the bottom-up perspective, we found that inclusion of annual variability in primary production between 1987 and 2008 (a period of overall declining productivity) improved our model fits in Ecosim. Furthermore, Ecopath-derived EEs (i.e., for the 1987 snapshot) were lower than expected for some zooplankton groups (e.g., calanoid copepod = 0.68, *Bythotrephes* = 0.21), which suggested that predation pressure was not an extremely controlling factor for those groups. Finally, the declines in standing stock biomass predicted by Ecosim between 1987 and 2008 for the majority of groups across trophic levels was consistent with the coincident decline in primary production; although increased biomass of lake whitefish illustrated that not all production at higher trophic levels was inhibited. Conversely, there was evidence for strong top-down regulation acting on several species groups during the 1987 Ecopath mass balance. For example, EEs were initially estimated to exceed one for slimy sculpin, *Mysis*, *Diporeia*, rainbow smelt, and age-0 alewife. Although some of these anomalies could have been the result of biased inputs for other parameters (i.e., low catchability for some fish species to bottom trawling), we believe predation pressure to have been extremely high for each of these species groups. Derived EEs for most other groups were relatively high (e.g., >0.80) at Ecopath mass balance (e.g., age-1+ alewife = 0.95). Previous research has concluded that predation is a common regulating factor within Lake Michigan's offshore food web (e.g., [Madenjian et al. 2002](#)). Determining influences of top-down versus bottom-up drivers is further complicated by annual variation in the interactions between functional groups. For example, [Warner et al. \(2008\)](#) concluded that strong alewife year classes have a positive bottom-up effect on Chinook salmon abundance in Lake Michigan, and [Madenjian et al. \(2005\)](#) concluded salmonines are a controlling factor on alewife recruitment in Lake Michigan because alewife year classes that experience high predation produce fewer recruits. In total, we concur with [Stewart and Sprules \(2011\)](#) that trying to infer the relative importance of these drivers with these ecosystem models is complicated, and interpretations can be overly simplistic. Ultimately, we believe that specific drivers can be important to specific groups and that our model cannot elucidate one driver to be universally more important than another in driving the Lake Michigan ecosystem.

Keystone species in Lake Michigan

Our highest ranked keystone functional groups for the 1987 food web included species from all trophic levels. The highest ranked keystone functional group was *Mysis*. Surprisingly, input-

output analysis revealed *Mysis* to have strong positive impacts on rainbow smelt, ninespine stickleback, and round goby, rather than three other species that historically have had diets much more dominated by *Mysis* — bloater, deepwater sculpin, and slimy sculpins. *Mysis* was predicted to have the strongest negative impacts on its prey (nonpredatory cladocerans, cyclopoid and calanoid copepods) as well as a possible competitor (*Bythotrephes*) and also was apparently vulnerable to intraspecific competition.

Two piscivore functional groups (burbot and Chinook salmon) also were among the top six keystone groups identified in the model. In general, EwE models have been referred to as "predator hungry", where strong top-down influences are common ([Plaganyi and Butterworth 2004](#)). Given the relatively little management focus on burbot relative to other Lake Michigan piscivores, it was somewhat surprising that burbot was the second-highest keystone group. We suspect that burbot was identified as a keystone group because its diet is much more diverse than the other salmonines, which explains why input-output analyses revealed burbot to have the strongest negative effect on deepwater sculpin, age-0 bloater, slimy sculpin, and round goby. A trophic cascade was also revealed with burbot having the strongest positive impact on *Mysis*, as burbot consume many *Mysis* predators. Given that salmonid predation on alewives has been considered one of the strongest Lake Michigan food web linkages ([Madenjian et al. 2002](#); [Warner et al. 2008](#)) and that the control of alewife was believed to have community-level consequences on the food web, including facilitating the establishment of *Bythotrephes* (see [Bunnell et al. 2006](#); [Pothoven et al. 2007](#); [Madenjian et al. 2008](#)), we were somewhat surprised that Chinook salmon ranked sixth, and not higher, among keystone functional groups.

The third-highest keystone functional group was plankton (i.e., phytoplankton other than diatoms). [Libralato et al. \(2006\)](#) conducted a meta-analysis of keystone species outputs from 41 Ecopath and Ecosim models and found that phytoplankton rarely occurred as a top keystone group except in oceanic upwelling systems. Input-output analyses revealed plankton to have strong positive effects on both primary (e.g., rotifers, nonpredatory cladocerans, *Mysis*, fingernail clams, dreissenids) and secondary (e.g., *Bythotrephes*, slimy sculpin, adult alewife, rainbow smelt) consumers. The other functional groups identified among the top six keystone groups were alewives and nonpredatory cladocerans. Alewives were predicted to have beneficial impacts to salmonines, as expected, but they were also predicted to have positive effects on plankton, dreissenid mussels, and some herbivorous zooplankton. These latter results can likely be attributed to indirect pathways where rotifer consumption by alewife (despite them contributing less than 1% to alewife diet composition) released phytoplankton from predation mortality, which, in turn, benefited herbivorous zooplankton groups and dreissenids. We note that the ecosystem model was not designed to account for the negative impacts of alewife (via thiamine deficiency) to salmonine reproduction (see [Fitzsimmons et al. 1999](#)). The final keystone group, nonpredatory cladocerans, were predicted to have positive impacts on *Bythotrephes* and slimy sculpin (even though they comprised only 7% of their diet) and indicated vulnerability for intraspecific competition.

Measures of food web structure

In addition to determining influential functional groups, our model estimated trophic transfer efficiency and food web linkages to better understand food web structure. Ecopath-estimated trophic transfer efficiency across all trophic levels equaled 10.2%, very similar to the often assumed 10% trophic transfer between trophic levels ([Lindeman 1942](#)). Our trophic transfer efficiency was higher than those reported for Lake Ontario (e.g., approximately 5% in [Christensen and Pauly 1993](#)). For example, [Stewart and Sprules \(2011\)](#) reported trophic transfer efficiency from trophic level 3 to level 4 at about 4%, whereas our value was 8.5%.

Stewart and Sprules' (2011) estimate of trophic transfer efficiency from prey fish to Chinook salmon for the 2001–2005 time period was similar to our Lake Michigan estimates. Consumer trophic transfer efficiency decreased with increasing trophic level. A similar pattern was reported for Lake Ontario (Stewart 2010) and the Puget Sound (Harvey et al. 2010), which was attributed to increased respiration and lower predation pressure for high-level consumers relative to lower trophic-level groups. We also reported 3.92 links/consumer, which can be placed in a broader context by comparison with a meta-analysis for marine and estuarine systems (Dunne et al. 2004). Our estimate was more similar to measures from estuarine systems (range = 2.2 to 4.7) than marine systems (range = 7.0 to 17.8) reported by Dunne et al. (2004). Our characteristic path length was 1.79, which was within the range (1.3–2.7, median = 1.9) reported for multiple aquatic food webs that included freshwater, estuarine, and marine systems (Dunne et al. 2004). Path lengths near two are more likely to exhibit trophic cascades than in systems with longer average paths where species are more widely separated. Our directed connectance value was close to 0.1, which indicated a sparsity of realized links relative to potential links. Dunne et al. (2002b) concluded that connectance values of 0.1 are common, yet those that are most highly connected are more robust to species losses. Baiser et al. (2010) concluded that connectance was the best predictor of invasion success, although the relationships differed among trophic levels. For the lowest trophic levels (i.e., nonconsumers) and top predators, invasion success was predicted to increase with connectance. Conversely, for herbivores, invasion success was predicted to decrease with increased connectance. Thus, mean connectance value did not suggest that Lake Michigan's food web structure was highly vulnerable to one particular trophic level over another, but our characteristic path length suggested successful invasive species would likely have the ability to influence adjacent trophic levels through trophic cascades.

Exploring mechanisms underlying changes in biomass within trophic levels

Piscivores (salmonines and burbot)

Biomass trends for total salmonines showed a 35% decrease between 1987 and 2008; however, numbers of total salmonids stocked only decreased by 15% over this same period (US Fish and Wildlife and Great Lakes Fishery Commission 2010). Although our model accounted for increasing wild production of non-native salmonines in Lake Michigan, we could still be underestimating biomass of Chinook salmon if high levels of immigration from Lake Huron have been occurring since the early 2000s. Preliminary analyses indicated that Chinook salmon stocked into Lake Huron in the 1990s and 2000s, and were later recovered, had about a 20% chance of being recovered in Lake Michigan (R. Clark, Michigan State University, personal communication, 2013). Burbot showed an overall 77% decrease in biomass during the 22-year time period with a biomass peak in the mid-1990s. The decrease in burbot annual biomass was coupled with decreased annual Q/B , which was predicted to decline by approximately 48% from 1987 to 2006. However, the model predicted a 60% increase in burbot Q/B for our last simulation years following the invasion of round goby and their becoming a prominent diet item for burbot.

Lake whitefish

Lake whitefish showed substantial biomass increases through time in our model, similar to trends that have been observed across most of the Great Lakes (Ebener 1997). Lake whitefish biomass increases have been hypothesized to occur for multiple reasons (e.g., reduced predation on juveniles by invasive species; see Ebener et al. 2008 and references therein), and our model indicated that a plausible mechanism was simply a reduction in total mortality through time. Because our model did not include predation on larval lake whitefish, lake whitefish mortality was pri-

marily driven by fishing mortality through time and enabled the model to capture stock assessment model estimates of abundance. We could not explicitly account for observed declining lake whitefish growth and condition within our model, but Q/B estimates were predicted to decrease by 65% from 1987 to 2008. Despite declines in Q/B , the increased population biomass resulted in a more than doubling in lake whitefish total consumption from 70 to 156 kg·ha⁻¹·year⁻¹. Our model did not suggest a reduction in lake whitefish carrying capacity owing to recent food web changes as proposed by Kratzer et al. (2007) and Wright and Ebener (2007).

Prey fish

Predicted prey fish biomass decreased between 1987 and 2008. The largest prey fish group change during 1987 to 2008, excluding round goby, was bloater. Our model was not able to explain the dramatic decline in bloater biomass despite decreasing population exploitation (Bunnell et al. 2006). Our initial simulation contradicted monitoring data because it predicted a fivefold increase in bloater biomass, likely owing to the decline in salmonine biomass over the time period. Therefore, we imposed an artificial fishery to tune the model's bloater predictions to match field-observed biomasses through time. Our artificial fishery resulted in a 98% decrease in bloater biomass from 1987 to 2008. The reason for the steep decline in bloater abundance since the early 1990s is not clear, but several hypotheses, including changes in the stock–recruitment relationship (Bunnell et al. 2006) and reduced fecundity (Bunnell et al. 2012), have been explored.

Adult alewife biomass declined through time and predicted total mortality varied between 0.7 and 2.0, which was within the range of cohort-based catch curve analyses estimated from bottom trawl data (C.P. Madenjian, personal communication, 2011). Chinook salmon accounted for 50%–74% of total alewife predation mortality across all simulation years. Slimy sculpin biomass estimates varied through time and did not show a strong trend, whereas deepwater sculpin biomass was predicted to decline through time. Declining deepwater sculpin densities have been observed in recent bottom trawl surveys (Madenjian et al. 2012), although one potential explanation is that their population has moved to deeper water than is currently surveyed. Ninespine stickleback biomass remained low and relatively invariable across simulation years. Madenjian et al. (2010) reported an increase in ninespine stickleback at Lake Michigan and hypothesized that dreissenid-induced *Cladophora* spp. expansion could improve stickleback spawning habitat and that salmonid predation was unimportant because of low contributions of stickleback to salmonid diets. Further exploration of this hypothesis could be possible with our EwE model by employing time-varying vulnerabilities to simulate *Cladophora* spp. influences on predation mortality for ninespine stickleback following Foraging Arena Theory.

Invertebrates

Our *Mysis* predictions followed the observed declining biomass trend, with the caveat that several gaps existed. Pothoven et al. (2010) reported decreased *Mysis* production from the mid-1990s to the late 2000s. This decline fits with the hypothesis of Pothoven et al. (2000) that declines in *Diporeia* would increase predation pressure by bloater and deepwater sculpin on *Mysis*. In more recent work, Pothoven et al. (2010) suggested that *Mysis* production may still be suppressed in the future despite low prey fish biomasses. Our model also suggested that consumption of *Mysis* by lake whitefish could compensate for declining consumption by bloater to constrain *Mysis* population increases.

Predicted biomass for *Bythotrephes* between 1987 and 2008 revealed no measurable trend. Our model poorly explained variation in *Bythotrephes* abundance through time and thus did not capture relatively high biomass levels in the early and late part of

the time series. Primary *Bythotrephes* predators in descending order were age-1+ alewife, bloater, and deepwater sculpin. Using *Bythotrephes* production rates, age-1+ alewife consumption rates, and predicted diet composition from 1987 to 2008 from our model indicated that *Bythotrephes* would have to on average comprise at least 25% of age-1+ alewife diet for alewife consumption to exceed *Bythotrephes* production (range across years = 15% to 55%). Pothoven et al. (2007) reported that alewife consumption could exceed *Bythotrephes* production in nearshore Lake Michigan waters during August. Our model results supported Pothoven et al.'s (2007) conclusion that alewife could potentially control *Bythotrephes*; however, diet content analysis from offshore Lake Michigan in 2010 did not indicate that *Bythotrephes* contributed substantially to alewife diets (USGS Great Lakes Science Center, unpublished data).

Our model predicted the drastic decline in *Diporeia* biomass. Previous research has indicated that *Diporeia* densities were regulated by prey fish consumption prior to the proliferation of dreissenids (McDonald et al. 1990), but thereafter the precipitous drop was associated with dreissenids inhibiting *Diporeia* foraging ability (reviewed in Nalepa et al. 2005). A proposed mechanism is dreissenid filtering of the spring diatom bloom, which is critical to *Diporeia* production. An untested hypothesis is that consumption by benthivores, such as bloater (that reached record high levels of abundance about the time of dreissenid establishment), contributed to the *Diporeia* decline. Our model revealed no support for this hypothesis because although *Diporeia* predation mortality varied across our modeled time period, it did not show an increasing trend following dreissenid invasion. Rather, our model predicted a more than twofold increase in *Diporeia* feeding time between 1987 and 2008. Hence, our model was consistent with the hypothesis that *Diporeia* foraging was inhibited by dreissenids.

Zooplankton functional groups biomasses were predicted to decline, but among-year variability was more dynamic than that exhibited by prey fish. Our predicted biomasses had poor fits to observed data in some cases, but observed data were also quite variable among years. Predation effects were evident and the major zooplankton predators through time were *Mysis*, *Bythotrephes*, and alewives. Bottom-up effects were also evident because simulations that did not include production anomalies drastically underestimated variation in annual biomass. Our model did not capture high *Bythotrephes* biomasses reported for 2007 and 2008 (Vanderploeg et al. 2012), and because our model did not separate omnivorous or predatory species out of the zooplankton groups (such as *Limnocalanus macrurus* from calanoid copepods or *Diacyclops thomasi* from cyclopoid copepods), our model may have underrepresented planktivory and potential top-down control. Vanderploeg et al. (2012) argued that increased predaceous zooplankton biomass, despite a decrease in total zooplankton biomass, would have required increased primary production during a time of declining total phosphorus.

Impacts and predatory control of recent invasive species: dreissenid mussels and round gobies

The roles of dreissenid mussels and round gobies as predators and prey resources in Lake Michigan's food web were evident as they proliferated in our later model years. Dreissenid grazing on phytoplankton from our model was lower than expected (i.e., <20% of total phytoplankton mortality) based on other studies of dreissenid effects in Lake Michigan. For example, recent studies have indicated that dreissenids are reducing phytoplankton biomass during both spring and summer seasons (Fahnenstiel et al. 2010; Vanderploeg et al. 2010; Pothoven and Fahnenstiel 2013). Unfortunately, our model could not isolate the effects of dreissenid mussels and the underlying reduction in offshore nutrient concentrations (which could also be indirectly related to dreissenid mussels) because inclusion of both was important to our model's performance. Our model did show that reduced zooplankton biomasses in later model years resulted in reduced

zooplankton grazing effects and partially compensated for the increased grazing by dreissenids. As dreissenid biomass increased, Q/B was predicted to decrease by approximately 50% and suggested that producer resources could become limiting, but this value was sensitive to our assumed vulnerability parameter of 1000. Given the biomass of dreissenids and round gobies were forced in our model, we were unable to explore their own vulnerability to top-down control by predation; however, lakewide biomass of both were still increasing in our last simulation year.

Our time-dynamic ecosystem model incorporated multiple, simultaneous stressors that can affect aquatic ecosystem function and captured many of the changes that occurred in Lake Michigan during a transitional period. Our model used food web interactions to predict one of the most dramatic Lake Michigan ecosystem changes of declining *Diporeia* biomass, but could not explain the dramatic decline of bloater. Ultimately, we cannot discern the relative importance of recent invasive species and lake productivity on Lake Michigan's food web changes because both were occurring at the same time and required inclusion to produce the most parsimonious time-dynamic model. We found top-down factors to be important as illustrated by high ecotrophic efficiencies for many prey groups, which was similar to many other EwE models (see Plaganyi and Butterworth 2004), but also found improved model performance by including primary production anomalies that indicated an importance of bottom-up forces on Lake Michigan food web function. Thus, our ecosystem-based exploration highlighted the complexity of Lake Michigan's offshore food web structure and ecological changes that occurred following species invasions and a changing nutrient regime. In conclusion, our model represents a step towards exploring scenarios of nutrient concentrations, population trajectories of invasive species, and alternative stocking scenarios to help inform management decisions from an ecosystem perspective.

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