

Sustainability of the Lake Superior Fish Community: Interactions in a Food Web Context

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ABSTRACT

The restoration and rehabilitation of the native fish communities is a long-term goal for the Laurentian Great Lakes. In Lake Superior, the ongoing restoration of the native lake trout populations is now regarded as one of the major success stories in fisheries management. However, populations of the deepwater morphotype (siscowet lake trout) have increased much more substantially than those of the nearshore morphotype (lean lake trout), and the ecosystem now contains an assemblage of exotic species such as sea lamprey, rainbow smelt, and Pacific salmon (chinook, coho, and steelhead). Those species play an important role in defining the constraints and opportunities for ecosystem management. We combined an equilibrium mass balance model (Ecopath) with a dynamic food web model (Ecosim) to evaluate the ecological consequences of future alternative management strategies and the interaction of two different sets of life history characteristics for fishes at the top of the food web. Relatively rapid turnover rates occur among the exotic forage fish, rainbow smelt, and its primary predators, exotic Pacific salmonids. Slower turnover rates occur among the native lake trout and burbot and their primary prey—lake herring,

smelt, deepwater cisco, and sculpins. The abundance of forage fish is a key constraint for all salmonids in Lake Superior. Smelt and *Mysis* play a prominent role in sustaining the current trophic structure. Competition between the native lake trout and the exotic salmonids is asymmetric. Reductions in the salmon population yield only a modest benefit for the stocks of lake trout, whereas increased fishing of lake trout produces substantial potential increases in the yields of Pacific salmon to recreational fisheries. The deepwater or siscowet morphotype of lake trout has become very abundant. Although it plays a major role in the structure of the food web it offers little potential for the restoration of a valuable commercial or recreational fishery. Even if a combination of strong management actions is implemented, the populations of lean (nearshore) lake trout cannot be restored to pre-fishery and pre-lamprey levels. Thus, management strategy must accept the ecological constraints due in part to the presence of exotics and choose alternatives that sustain public interest in the resources while continuing the gradual progress toward restoration.

Key words: fishes; fisheries; ecosystem; food web; Lake Superior; Great Lakes; modeling; Ecosim; Eco-path; trophic interactions.

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INTRODUCTION

A new ecosystem perspective is emerging based on the growing recognition that fishery exploitation is a major force in the structure of aquatic systems (NRC 1998; NMFS 1999). In fact, the ecosystem approach has a long and substantial history in the Laurentian Great Lakes. The restoration, rehabilitation, and sustainability of native fish communities has been the primary focus of Great Lakes fisheries managers (Burkett and others 1995). The goal is to establish fish communities based on levels of self-sustaining stocks similar to those that existed prior to the major declines in fish populations due to overexploitation, habitat loss, and invasion of the sea lamprey. Following the implementation of the sea lamprey control program in the 1950s (Smith and others 1974) and close regulation of commercial fisheries, the downward trends reversed and the principal species began to recover (Dryer and King 1968; MacCallum and Selgeby 1987; Hansen and others 1995a). Achieving these goals requires the recognition that the Lake Superior system now includes exotic species and that public interests are now very different from those in the past. These factors represent major constraints on the rehabilitation and full restoration of native species. In addition, some of these new exotics (for example, Pacific salmon) are also valuable renewable resources and thus represent new opportunities. Attaining an understanding of the balance between such constraints and opportunities is the key prerequisite to establishing realistic, sustainable management strategies. Negus (1995) summarized the problem succinctly:

Because of limited forage biomass, enhancement of lake trout may come at the expense of other salmonine stocks. Such constraints will undoubtedly raise opposition from anglers who have become accustomed to thinking of Lake Superior as an unlimited resource.

Of all the Laurentian Great Lakes, Lake Superior is the only one to retain significant native stocks representative of its ancestral state (Burkett and others 1995). Recent reports of the Great Lakes Fisheries Commission indicate that the Lake Superior fish community continues to change in ways that reflect the general goals of restoration and rehabilitation (Hansen 1994). For example, lake trout (*Salmonidae*) have established self-sustaining populations (Hansen 1995a, 1995b). As a result, resource managers have decided to eliminate stocking of lake trout from the Apostle Islands, Wisconsin, eastward to Grand Marais, Michigan (Anony-

Table 1. Common and Scientific Names of Fishes and Invertebrates

Common Name	Scientific Name
Lake trout	<i>Salvelinus namaycush</i>
Brook trout (coaster)	<i>Salvelinus fontinalis</i>
Sea lamprey	<i>Petromyzon marinus</i>
Coho salmon	<i>Oncorhynchus kisutch</i>
Chinook salmon	<i>Oncorhynchus tshawytscha</i>
Rainbow (steelhead) trout	<i>Oncorhynchus mykiss</i>
Pink salmon	<i>Oncorhynchus gorbuscha</i>
Brown trout	<i>Salmo trutta</i>
Burbot	<i>Lota lota</i>
Deepwater cisco (bloater chub)	<i>Coregonus hoyi</i>
Lake herring	<i>Coregonus artedii</i>
Lake whitefish	<i>Coregonus clupeaformis</i>
Eurasian ruffe	<i>Gymnocephalus cernuus</i>
Round goby	<i>Neogobius melanostomus</i>
Rainbow smelt	<i>Osmerus mordax</i>
Slimy sculpin	<i>Cottus cognatus</i>
Deepwater sculpin	<i>Myoxocephalus quadricornus</i>
Suckers	<i>Catostomus</i> spp.
Lake sturgeon	<i>Acipenser fulvescens</i>
Walleye	<i>Stizostedion vitreum</i>
Mysids	<i>Mysis relicta</i>

mous 1996). In addition, members of the native *Coregonus* group (whitefish, lake herring, and deepwater cisco or chub, family *Salmonidae*) have recovered from their formerly low levels. Nevertheless, the system is and will remain different from that of the ancestral state.

The fish community now contains many exotic species (Table 1). Sea lamprey, rainbow smelt, Eurasian ruffe, round goby, and naturalized, self-sustaining populations of exotic Pacific salmon (pink, coho, chinook, and steelhead) plus European brown trout are major additions to an assemblage formerly dominated by lake trout, ciscoes, whitefish, sculpins (*Cottidae*), suckers (*Catostomidae*), and burbot (*Gadidae*). In addition, this system now supports a variety of commercial and treaty rights fishery activities and a substantial tenor of interests in recreational fisheries. The food web of Lake Superior includes a diversity of interactions unknown a century ago. Thus, there are significant and continuing challenges to the effective definition of sustainable resource management goals (Kitchell 1991; Koonce and Jones 1994).

A general review of the current conditions in Lake Superior reveals that food web interactions are strongly expressed by trends in fish populations. A

25-year record of stock assessment by the United States Geological Survey, Great Lakes Science Center (formerly the National Biological Service) indicates that the stock of lake herring—formerly the dominant prey of lake trout—is now 10 times that observed in the early 1980s and that their biomass is five to six times that of the dominant forage species, rainbow smelt (MacCallum and Selgeby 1987; Conner 1991, Selgeby and others 1994; Bronte and Hoff 1999). Smelt biomass is now 25% of that observed 2 decades ago, and the age structure has changed to strong dominance by juveniles (MacCallum and Selgeby 1987). As in Lake Michigan, these changes can be attributed largely to predation effects (Stewart and Ibarra 1991). The decline in stocks of deepwater cisco follows much the same pattern observed for smelt. This decline can be attributed to increased predation by the expanding population of siscowet (deepwater form) lake trout (Selgeby and others 1994). As in Lake Michigan, commercial fisheries for whitefish have seen continued increases or sustained levels in total yield. Lake trout comprise 90% of total salmonine yields in the recreational fishery (Peck and others 1994). In the most recent estimates (1990–92), lake trout harvests were at about 33% of fish community goals. Siscowet stocks began to recover after the implementation of lamprey control and continued to increase through the early 1980s. Stocks of near-shore lake trout (leans) have also increased, but less dramatically so. The proportion of large mature fish increased during the early 1980s but remains unchanged today. Wild (naturally reproduced) stocks dominate in the eastern regions and are generally increasing throughout the lake, although planted fish continue to be more abundant than wild fish in Minnesota waters. Lamprey-induced mortality remains at about 15% per year for the preferred hosts, large lake trout. The growth rates of lake trout show no consistent lakewide trend over the past 15 years; however, growth rates appear to be declining in the eastern regions of the lake, where native stocks are best established. The size and age structure of the lake trout stocks suggest that mortality due to fishery harvests and lamprey predation has yielded mortality rates at or near the target total.

Historically, lake trout preyed upon the abundant coregonines (*Coregonus* spp.) (Dryer and others 1965), but they switched to rainbow smelt after severe declines in the population of both the lake trout and coregonines and the exponential increase in rainbow smelt during the mid 1950s (Lawrie and Rahrer 1972; Selgeby 1982). The diets of lake trout and the introduced salmonids contained up to 90%

rainbow smelt through the 1980s and early 1990s, even though the stocks of rainbow smelt declined dramatically during that period (Conner 1991; Conner and others 1993; Bronte and others 1994). Recent evidence suggests a shift in the diet of lake trout to a larger complement of *Coregonus* spp. and an increase in the occurrence of *Mysis* in the diets of fish from the eastern waters of the lake (Bronte and others 1994). A latitudinal gradient in diet composition is also likely (Bronte and others 1994), similar to the north–south trend in Lake Michigan (Miller and Holey 1992) and Lake Huron (Diana 1990).

The remaining 10% of the recreational fishery harvest derives largely from populations of steelhead, brown trout, coho, and chinook salmon. Although initially established by hatchery plantings, each of these anadromous species has since established some naturalized reproducing populations. The extent of their recruitment success and contribution to the fishery varies with time and differs among regions of the lake (Peck and others 1999). This is a subject of substantial concern because attempts to restore lake trout stocks and the anadromous form of brook trout ('coaster' brook trout) may be impeded if natal stream habitats are densely populated by other salmonids and/or if the forage resources available to the native stocks are also heavily preyed upon by exotic salmonids.

In this paper, we develop and apply a modeling approach as one way to clarify the opportunities and constraints that must be addressed in developing realistic plans for sustainable fishery management in Lake Superior. A second set of questions addressed herein relates to the variations in the life history characteristics of exotic and native species as a factor in forecasting the outcome of restoration practices in an ecological setting that is fundamentally different from that of the original condition. A confounding component of the latter issue is that each of the exotic species has life history characteristics that make it apparently more r-selected than its ecologically equivalent native species. For example, Pacific salmon grow more rapidly than lake trout, then typically mature and reproduce at ages of 2–4 years whereas native lake trout grow slowly and mature at 6–7 years of age. Among the prey fishes, the exotic rainbow smelt matures at age 2 or 3, whereas the native *Coregonus* spp. mature at ages 3–5. Those characteristics make the exotics more likely to respond quickly to perturbations—their life histories are among the 'fast' variables in this food web. That response capacity is in contrast to the 'slow' variables expressed in the life histories of the native apex predators, lake trout and burbot, and the native prey, sculpins and *Coregonus* spp. Under

ceteris paribus conditions, any increase in the abundance of limited prey resources would be first expressed in the growth and survival rates for exotic salmonids. Any management practice that increased the stocking rate of exotic salmonids would reduce the availability of food resources for the nearshore (lean) stocks of lake trout. Any management practice that altered mortality rates due to fisheries for salmonids would be expressed in predation rates imposed on both exotic and native prey fishes.

In other words, this paper attempts to address two of the most difficult problems faced by resource managers and applied ecologists—the restoration of ecological systems and dealing with the perturbations caused by exotics. The structures of both the food web and the management systems must account for the fast variable responses that favor exotics and enhance the slow variable responses that encourage the restoration of native species.

METHODS

Our analyses are based on the Ecosim model that derives from the initial conditions estimated in our development of an Ecopath model for the system under study. The Ecopath model was initially developed by Polovina (1984) and subsequently modified (Christensen and Pauly 1992) in applications to scores of ecosystems (Christensen and Pauly 1993). At this writing, Ecopath models have been developed for approximately 90 different systems (D. Pauly personal communication). Recent applications include analyses of the linkage between primary production and fish production for the world's oceans (Pauly and Christensen 1995) and estimates of changes in trophic structure due to fishery exploitation in both marine and freshwater systems (Pauly and others 1998).

The derivation of the Ecopath models and their application are detailed in Pauly and others (1993) and will be only briefly summarized herein. The pertinent software and documentation are available without cost at <http://www.fisheries.com>. The core component of an Ecopath model is the balance of production and losses for each component of an ecosystem. It is expressed in the following equation:

$$\begin{aligned} &\text{Production} + \text{Immigration} - \\ &\quad \text{Predatory losses} - \text{Nonpredatory mortality} - \\ &\quad \quad \quad \text{Harvest} - \text{Emigration} = 0 \quad (1) \end{aligned}$$

In other words, the system is set to steady state based on estimates of rates for each of the terms in

Eq. (1). This equilibrium condition allows analyses of flows between trophic levels and a means for estimating the relative importance of individual state variables (for instance, species) or processes (for example, detritivory, selective predation, targeted fisheries, and so on). An important aspect of this process is that the ratio of production to biomass (P/B) is equal to the sum of all sources of mortality—those due to predation, exploitation, and other causes. Thus, the system is set to equilibrium based on the current levels of mortality, biomass, and production. Those parameters are based on empirical estimates that include both the scale and the context of the ecosystem under consideration. Thus, an Ecopath model represents a very strongly data-based estimate of the current state of the system based on the principles of thermodynamics and a balanced budget at the ecosystem scale. Any change in inputs, exports, or exploitation rates will therefore be reflected in the development of a new steady-state condition.

Walters and others (1997) developed the Ecosim model to allow for dynamic simulation of the effects of changes in the initial steady-state condition for an Ecopath model. User inputs to Ecosim can alter the initial conditions for exploitation rates, predator-prey interactions, and/or external changes in the environment as applied to any of the state variables in the Ecopath model. Ecosim then calculates the time course for consequent change in all other state variables for the ecosystem and the new equilibrium condition. Derivation of the Ecosim model is detailed in Walters and others (1997), and an example of applications is presented in Kitchell and others (1999). The software is available at <http://www.fisheries.com>, and a version with density-dependent or compensatory responses in individual fish growth rates is now available (Walters and others 2000).

The master equation for Ecosim allows changes in the balanced budget for any state variable (B):

$$\begin{aligned} dB/dt = &\text{Production} - \text{Predatory losses} - \\ &\quad \quad \quad \text{Nonpredatory losses} - \text{Harvest} \quad (2) \end{aligned}$$

Because all Ecopath variables are embedded in a food web, the effects of changes in one variable may be expressed in any and all others. Their dynamics depend on the linkages stated in the trophic flow matrix and in the parameters that are used to define each. For example, organisms with large P/B values (for example, phytoplankton, zooplankton, or Pacific salmon species) respond rapidly to perturbation and achieve new steady-state values quickly. Those with low P/B values (for instance, lake trout),

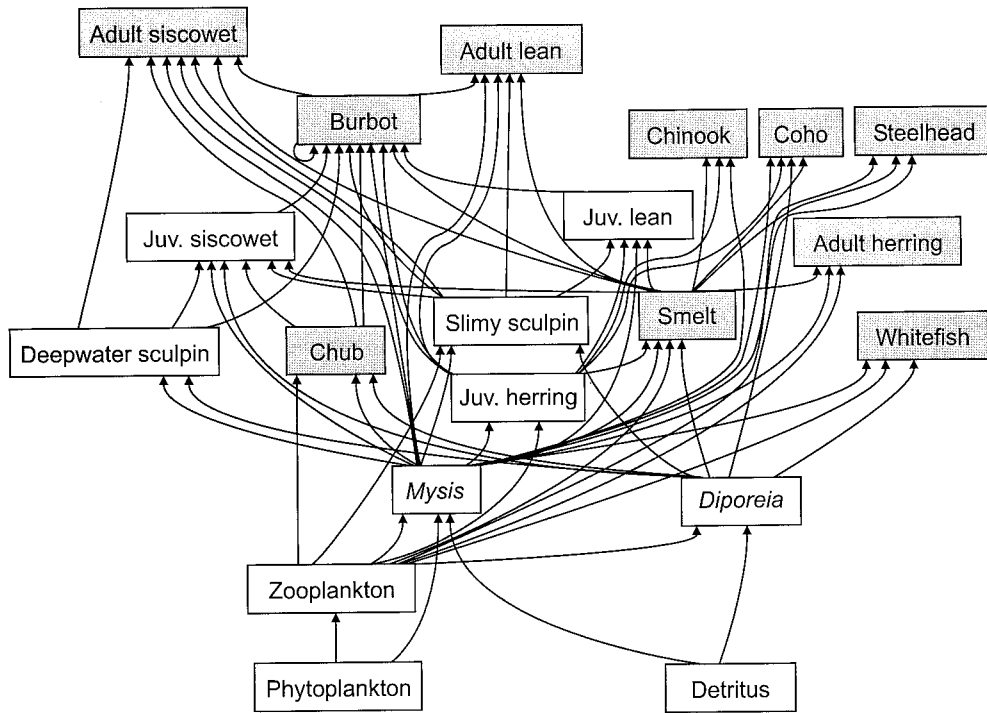


Fig. 1. The food web for Lake Superior. Vertical position approximates trophic levels. Shaded boxes represent species subject to fishery exploitation.

which are indicative of K-strategy life histories or low turnover rates, respond slowly and with substantial lags.

Both Ecopath and Ecosim have a diversity of options and alternative functions that are available to the user. In both cases, we employed the initial or default conditions provided with the software.

The trophic structure developed for the Lake Superior model is presented in Figure 1. Common names of key food web components are used in the text; their scientific names are given in Table 1. As state variables, we distinguished those species for which sufficient abundance, life history, and ecological information were available to estimate parameters for the Ecopath model. Those with minor roles in the diet matrix were aggregated in a category of 'other' fishes/invertebrates. Thus, the food web depicted in Figure 1 differs somewhat from the species list presented in Table 1. Resolution is high at the top of the food web, but aggregation is required for lower trophic levels, where hundreds of species may be represented by one state variable (for example, phytoplankton).

The basic inputs for an Ecopath include estimates of biomass turnover rates (production/biomass, P/B), total annual consumption/biomass (Q/B), the proportion of total mortality (Z) due to fishery exploitation (F), and ecotrophic efficiency (EE), which is defined as the proportion of the total annual production that stays within the boundaries of

the defined system (Table 2). If one of those parameters is unknown, the Ecopath software balances the ecosystem budget and provides an estimate for that value.

A second set of inputs to Ecopath represents the trophic interactions. For each predator, the relative components (percentage of biomass) of the diet for each type of prey are entered in the matrix. Our diet matrix is summarized in Table 3. Sources for these inputs were derived from studies of the food habits of the major species (for example, Conner and others 1993; Johnson and others 1998). The process is outlined in the Modeling Protocol.

Ecosim allows the user to split species into adult and juvenile pools, each with distinct parameter sets, to account for ontogenetic changes. Thus, food web components that experience major shifts in physiological rates, diet, predators, and/or vulnerability to fishing behave more realistically in Ecosim. The adult and juvenile pools are linked using a delay-difference model, in which juvenile biomass gradually recruits into the adult pool following a time lag for maturation, and adult biomass contributes to the juvenile pool according to a stock-recruitment relationship. The conceptual framework and derivations of this method are described in Walters and others (1997). In our study, three types of fish were split into juvenile and adult subgroups: lake herring, lean lake trout, and siscowet. Parameters required by Ecosim to link the juvenile and

Table 2. Biomass, Total Production (P/B), Consumption (Q/B), and Ecotrophic Efficiency Values for the Lake Superior Food Web Model

Group	Code	Trophic Level	Biomass (g/100/m ²)	P/B (y ⁻¹)	Q/B (y ⁻¹)	Ecotrophic Efficiency	Harvest (g/100/m ² /y)
Phytoplankton	Phyt	1.0	359.43	442.02	—	0.75	—
Zooplankton	Zoop	2.0	323.29	12.90	365.00	0.90	—
<i>Mysis</i>	Mys	2.5	184.94	2.00	25.00	0.85	—
<i>Diporeia</i>	Dip	2.1	193.67	2.00	25.00	0.85	—
Rainbow smelt	Rsm	3.4	6.13	2.20	10.30	0.90	0.06
Juvenile herring	JHer	3.0	9.42	2.00	15.00	0.90	0.00
Adult herring	Her	3.2	9.00	0.70	5.00	0.14	0.09
Chubs	Chub	3.2	23.55	0.80	15.16	0.95	0.05
Whitefish	Wht	3.3	13.47	0.60	15.00	0.15	1.21
Slimy sculpin	Sls	3.1	7.00	0.85	12.00	0.62	0.00
Deepwater sculpin	Dws	3.3	27.20	0.60	10.00	0.45	0.00
Juvenile lean trout	JLlt	4.1	0.64	0.80	6.39	0.18	0.00
Adult lean trout	Llt	4.1	3.36	0.41	2.59	0.29	0.40
Juvenile siscowet	JSis	3.7	7.40	0.76	3.90	0.03	0.00
Adult siscowet	Sis	4.2	15.60	0.25	1.81	0.03	0.12
Burbot	Bur	4.0	8.60	0.45	2.10	0.98	0.00
Chinook	Chin	4.1	0.02	1.22	7.10	0.90	0.02
Coho	Coho	3.9	0.03	1.25	6.70	0.90	0.03
Steelhead	Stl	3.7	0.00	0.83	7.70	0.90	0.00
Other fish/invert ^a	Other	2.5	52.93	2.50	20.00	0.90	—
Detritus	Det	1.0	300.00	—	—	0.09	—

Values that appear in bold type indicate Ecopath estimates. All other values were specified from independent analyses.
^a“Other fish/invert” group includes aquatic invertebrates, terrestrial insects, and small forage fishes.

adult groups (von Bertalanffy K, age at recruitment, mass at recruitment, and average adult mass) were derived from studies by Ebener (1995) and Bronte (unpublished) and are shown in Table 4. Recruitment was assumed to be knife-edge.

Modeling Protocol

Parameter estimates for the Ecopath model were derived by a three-step process. First, a subgroup of the coauthors (those based in Madison, Wisconsin) consulted the available literature to develop the initial estimates for P/B, Q/B, Z, F, and EE. Shortly thereafter, we convened a workshop that included the coauthors who represented the Lake Superior Technical Committee and the full spectrum of represented institutions. This meeting produced a second iteration of the parameter estimates and a consensus about the kinds of simulation studies that might be most instructive. The third step was a gradual process of incorporating the workshop suggestions and subsequent improvements, such as greater detail and updated results, as inputs to the diet matrix used to characterize the Ecopath model.

The first version of the model emphasized the use

of EE as the Ecopath unknown because the workshop participants had some confidence in their estimates of the other inputs. In its strict definition, EE represents the amount of biomass accounted for through the combination of within-system processes (for example, mortality due to predation or harvest). In most Ecopath applications, the value of EE is assumed to be about 0.9. In this case, our EE values are highly variable. Some of that variability is due to uncertainty; some is probably due to error. We cannot distinguish between the two sources at this stage. We can, however, accommodate that uncertainty by setting generous margins in our interpretation of modeling results. For example, if a state variable changes less than about 25% in response to a manipulation, then we view it as generally unresponsive and interpret the change conservatively.

We focused our simulations on the actions most likely to be taken through fishery agencies—that is, the constraint or enhancement of exploitation processes. We also addressed the question of how a major environmental forcing function such as the interannual variability in climate conditions—for

Table 3. Diet composition estimates for Lake Superior Ecopath

Prey	Predator																			
	Zoop	Mys	Dip	Rsm	JHer	Her	Chub	Wht	Sls	Dws	JLlt	Llt	JSis	Sis	Bur	Chin	Coho	Stl	Other	
Phyt	—	0.25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Zoop	—	0.5	0.1	0.15	0.95	0.7	0.65	0.1	0.01	—	—	—	—	—	—	—	—	—	—	—
Mys	—	—	—	0.65	0.05	0.25	0.3	0.1	0.06	0.4	0.15	0.02	0.42	0.03	0.01	0.1	0.05	0.01	—	—
Dip	—	—	—	0.15	—	—	0.05	0.3	0.9	0.6	—	—	0.09	—	—	—	0.05	—	—	—
Rsm	—	—	—	—	—	0.05	—	—	—	—	0.35	0.32	0.04	0.06	0.14	0.55	0.45	0.25	—	—
JHer	—	—	—	0.05	—	—	—	—	—	—	0.35	0.45	—	0.1	0.3	0.25	0.05	—	—	—
Her	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chub	—	—	—	—	—	—	—	—	—	—	—	—	0.01	0.49	0.2	—	—	—	—	—
Wht	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sls	—	—	—	—	—	—	—	—	—	—	0.12	0.05	0.07	0.02	0.01	—	—	—	—	—
Dws	—	—	—	—	—	—	—	—	—	—	—	—	0.15	0.1	0.01	—	—	—	—	—
JLlt	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	0.01	—	—	—	—	—
Lt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.01	—	—	—	—	—
JSis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Sis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bur	—	—	—	—	—	—	—	—	—	—	—	0.06	—	0.1	0.03	—	—	—	—	—
Chin	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coho	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stl	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Other	—	—	—	—	—	—	—	0.5	0.03	—	0.03	0.1	0.22	0.1	0.29	0.1	0.4	0.64	—	—
Det	—	0.25	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.5

Values indicate proportions of the total diet of predator group j (row header) that consists of prey group i (column header). Group codes are given in Table 2.

Table 4. Parameters Used to Link Juvenile and Adult Pools in the Ecosim Delay-Difference Function

Species	von Bertalanffy K	Age at <i>R</i> (y)	Mass at <i>R</i> (g)	Avg. Adult Mass (g)
Herring	0.167	4	200	315
Lean lake trout	0.142	5	590	1250
Siscowet	0.053	8	590	1250

instance, those due to El Niño–La Niña oscillations—might alter the ecological processes represented in this model of trophic interactions. We simulated the interannual variance in primary production based on estimated temperature dependence for algal growth rates and long-term records for surface water temperatures (Watson and others 1996). We coupled that with a stochastic effect on the food web by simulating a major decade-long decline in smelt abundance. Lastly, we created a scenario based on the invasion of another exotic (the quagga mussel) and its possible effects on native species.

When the responses of a group of species are similar (for example, chinook, coho, and steelhead salmon) or highly correlated (for instance, phytoplankton and zooplankton), only one of those groups may be included as representative. In some cases, we simulated a 10-year period of some management action followed by its removal. This allows evidence of the rate of response to a change and the rate of recovery or evidence of hysteresis when the change is removed. We confined our simulations to a 50-year interval. Forecasts beyond that horizon seem overly optimistic.

The real test of adequacy for this type of modeling approach is in its ability to present logical consequences that would not be apparent unless one could reason through the complexity of a large connected set of food web interactions. In other words, the model should teach us something we didn't know. In addition, the result should make sense after we have seen it and after we have developed an understanding of how the interactions caused the result.

RESULTS

Modeling Scenarios

Each scenario, its background rationale, and its interpretation is detailed here. Figures are scaled so that biomass is normalized to the initial estimates (Table 2) as a value of 1, then depicted as relative departures from the initial condition in response to the simulated manipulation. Manipulations are ini-

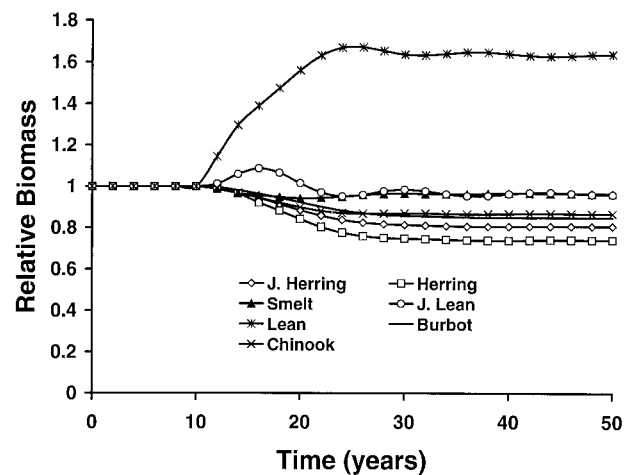


Fig. 2. Simulated responses of selected food web components to sustained closure of current fisheries for lean lake trout after year 10.

tiated at about year 10. In each case, state variables represented in the accompanying graphic are those that exhibited important responses, including those that showed an unanticipated absence of change.

Scenario 1: Close all fisheries for lean lake trout Rationale: The recovery of lean lake trout stocks seems to be impeded by the continuing high levels of mortality. The closure of fisheries that target adult lean lake trout would allow us to evaluate the potential for restoration of the leans to their former abundance and a greater sustainable yield for future fisheries when they are allowed to reopen.

Simulation Results (Figure 2): Lean lake trout biomass increased about 50% during the 10-year period after fishery closure and leveled off at about 60% of former abundance within 15 years. The biomass of its major prey (herring) declined. Pacific salmon (coho, chinook, and steelhead) and burbot all declined as lake trout increased. Rates of decline were approximately in proportion to the P/B estimate of turnover rates for each.

Unexpected Results: Juvenile lean trout biomass rose and then declined, indicating an ecological constraint to recruitment. Smelt responded very little to increased lean lake trout, and siscowet (not

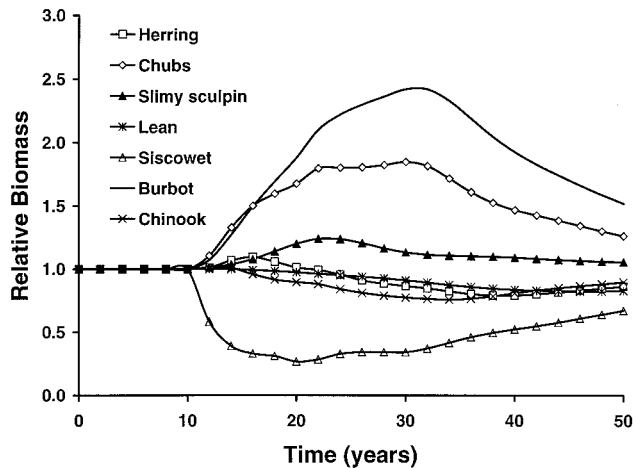


Fig. 3. Simulated responses to a 10-y period of intensive fishing for siscowet lake trout.

shown) was unaffected. A 10-year closure would reveal much of the potential recovery for lean lake trout and its ecological consequences.

Scenario 2: Encourage fisheries for siscowet lake trout
Rationale: Targeted removal of the undesirable deepwater siscowet (a 10-fold increase in F for 10 years) would release forage resources that can enhance the lean lake trout stocks, while allowing continued exploitation of lean trout and herring at the present rates. This strategy would appease existing fishery interests (both commercial and recreational) and address issues raised by treaty rights fisheries.

Simulation Results (Figure 3): Siscowet biomass declines sharply and lean lake trout biomass decreases, but by only about 20%. Chubs and burbot exhibit large increases.

Unexpected Results: Herring show little response. Salmon (for instance, chinook) decline only slightly. Chubs and burbot continue to increase even after siscowet mortality is reduced and do not peak until about 10 years later. This long lag in responses delays the recovery of siscowet and salmon.

Scenario 3: Close fisheries for lean lake trout and their native prey, lake herring, while continuing targeted removal of siscowets for a 10-year period
Rationale: Fishery closures protect adult lean trout, but continued fishing for their primary native prey, lake herring, limits the potential for recovery. Cessation of herring fishing would allow greater recruitment and increased prey availability. The increased mortality of siscowets would accelerate the recovery of stocks of lean lake trout and lake herring.

Simulation Results (Figure 4): Siscowets decline sharply. Herring biomass increases by about 25%; then it declines as lean lake trout biomass increases

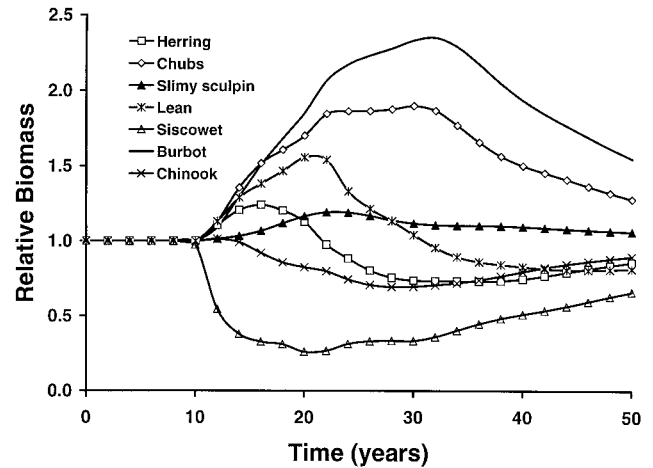


Fig. 4. Simulated responses to a combination of 10-year closure of fisheries for lean lake trout and lake herring coupled with an intensive fishery for siscowet lake trout.

over that of scenario 2 in a lagged predator-prey response. Burbot and chubs increase dramatically. Lags in recovery after the 10-year period of fishing are similar to those seen in scenario 2. Lean lake trout decline when their fisheries are resumed and continue to do so due to the increased burbot biomass.

Unexpected Results: The protection of native forage fishes does not enhance recovery of a sustainable population of lean lake trout. Smelt are little affected. Again, strong responses by burbot and chubs create substantial lags in response to management actions.

Scenario 4: Nature's variability and uncontrollable events overwhelm management-actions
Rationale: Due to variable climate (for instance, El Niño), unpredictable recruitment events, and/or mass mortalities caused by the outbreak of disease or density-independent recruitment failures, the Lake Superior ecosystem is beyond the controls of fisheries management. There is no reason to pretend otherwise. Opponents of sustainable fishery management often invoke this argument because it is difficult to reject and because it leads to the conclusion that fishers should behave opportunistically and without constraint.

To evaluate the role of variability in nature, we set up a simulation that contained the variance in primary production (up to $\pm 25\%$ based on estimated temperature dependence for algal growth rates), which is known to accompany interannual differences in the long-term records for surface temperature. We then added a simulated stochastic event that had a direct strong effect on a key forage fish population. We caused smelt to decline to very

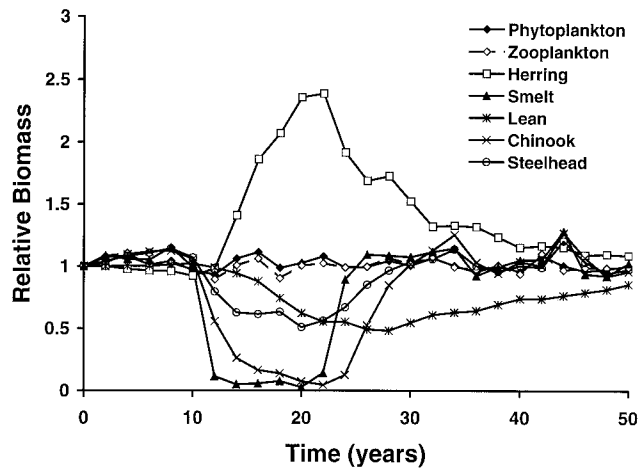


Fig. 5. Simulation of a collapse of smelt populations during years 10–20 of a 50-year period that includes stochastic variability owing to climate effects on primary production rates.

low levels for 10 years, then allowed their recovery. This set of model results includes both environmental forcing due to climate variability and the equivalent of a large-scale stochastic perturbation to the middle of the food web. It serves as a challenge to sustainable management efforts derived from the Ecosim modeling approach.

Simulation Results (Figure 5): Phytoplankton and zooplankton biomasses show positively correlated synchronous responses to variable primary production rates. Trophic cascade effects are not apparent within the natural variability at these levels or in response to the smelt collapse. As smelt decline to very low levels, the stocks of Pacific salmon and lean lake trout follow in kind. Herring increase very strongly. Recovery of the smelt population after 10 years is rapid. It is followed by a modest lag in the recovery of salmon and a gradual decline of herring. Long lags develop in the recovery of lean lake trout.

Unexpected Results: Siscowets and most other components of the food web seem unaffected by the smelt collapse. Extremely long lags develop in the recovery of lean lake trout. Responses in excess of about $\pm 25\%$ can be discerned if seen as trends against the variability owing to interannual climate fluctuation.

Scenario 5: Invasion by exotics destabilizes food web interactions *Rationale:* The Great Lakes are infamous for a continuing parade of exotic species. Some, such as the sea lamprey, alewife, and smelt, have had profound long-lasting effects. Others, such as the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*), have had strong effects that were evident soon after invasion, but

their long-term impact is unknown. Among the current concerns about the ecological effects of exotics are reports that the population of *Diporeia affinis*, the native amphipod, has decreased dramatically according to recent records from Lake Michigan (Nalepa and others 1998) and Lake Ontario (Hoyle and others 1999). In the latter case, the decline in amphipods is associated with declining numbers of lake whitefish and an increased abundance of exotic mussels.

Zebra mussels are known to inhabit some of the warm productive bays of Lake Superior, but the open water habitat appears to have lower levels of productivity and water temperature than are required by the epilimnetic *D. polymorpha*. However, the deepwater quagga mussel, *D. bugensis*, is tolerant of cold temperatures and occurs in the lower lakes, so it may be expected to invade Lake Superior. If so, we reasoned that it would compete with *Diporeia* for food resources. Accordingly, we conducted a simulation that reduced *Diporeia* to approximately 20% of its initial abundance and used that model to evaluate the potential direct and indirect effects of adding yet another exotic to the food web.

Simulation Results: As expected, the reduction in *Diporeia* caused declines in its major predators—slimy sculpin, deepwater sculpin, and lake whitefish (Figure 6).

Unexpected Results: When *Diporeia* was reduced to 20% of its previous population, slimy sculpin decreased to virtual extirpation. This outcome is probably due to the combination of a decrease in primary prey (90% of the slimy sculpin diet is *Diporeia*) and modest increases (less than 20%) in the number of sculpin predators (lake trout and burbot). Herring also declined somewhat due to increases in both its primary zooplanktivorous competitors (smelt and *Mysis*).

The most striking result in this simulation is the enhancement of steelhead, chinook, coho (not shown) and smelt. This result is due to increases in *Mysis* as a consequence of the decline in both sculpin species and their predation effect on *Mysis*. The increase in the *Mysis* population provides more prey for the salmonids and smelt, which are also a primary prey of the salmonids.

Thus, the invasion by the exotic *Dreissena* produces a set of indirect interactions that enhance the populations of other exotics—all three Pacific salmon and smelt. If the decline of *Diporeia* in Lake Michigan and Lake Ontario has an alternative explanation other than mussel invasion, the simulated outcome in Lake Superior would probably be much the same.

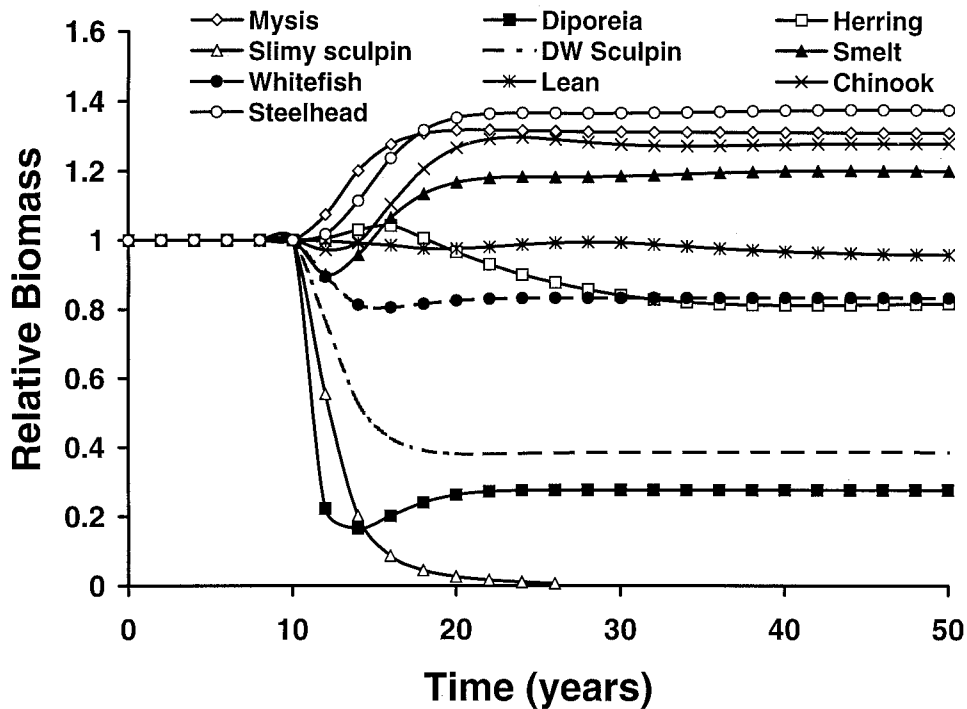


Fig. 6. Simulation of ecological effects derived from reduction in abundance of the benthic amphipod, *Diporeia affinis*.

DISCUSSION

Our five scenarios focus on the restoration objectives that dominate contemporary fishery management for the Great Lakes. The progression of those scenarios approximates the sequence of fishery management actions most likely to be followed to support of the current restoration goals. One important conclusion is immediately obvious—the enhancement of stocks of lean lake trout is a goal that is not easy to accomplish. To the extent that this model portrays a reasonable picture of the current state of system productivity and food web interactions, substantial increases in native fish populations may not be possible because they are constrained by the existing structure of the system and/or by the prospect that the system is at or near carrying capacity. In other words, it seems possible that the current state of Lake Superior is as close as we can get to the restored state.

We have not presented a simulation of the outcome of an obvious management alternative—enhancement of the Pacific salmon through intensified hatchery production and stocking. That result is surprisingly dull in that the biomass of Pacific salmon is a very small part of the biomass at the apex of this food web. Actions that would increase salmon by two- or threefold are of little consequence to the dynamics of native fishes. That conclusion must be regarded with caution, because there is a substantial and unexplored spatial dimen-

sion to the interactions between salmon, the near-shore lean lake trout stocks, and the forage fish populations that support them. The next generation of this type of modeling effort should include a spatial context that distinguishes between the littoral community and that of the offshore zone. It should also recognize the habitat heterogeneity represented in this, the largest of the world's lakes. Spatially explicit analyses should also explore the utility of providing zones where fishing is prohibited, as an experimental approach that could establish a better understanding of the outcome of real-world management actions. A recent analysis of stable isotope distribution in the western arm of Lake Superior showed that some fishes are highly mobile, whereas others are relatively sedentary (Harvey and Kitchell 2000). Therefore, management actions aimed at the geographic restriction of fish exploitation would have complex spatial effects.

Of greater immediate consequence is the hitherto unrecognized effect of an enormous biomass of siscowet lake trout. The recovery of siscowet populations is an important achievement for fishery managers because they are indeed the evidence of restoration through natural reproduction. On the other hand, their ecological inertia (resistance to change) creates a major constraint for fishery managers because the nearshore lean lake trout are much more highly desired. Even the very stringent

measures of targeted fisheries aimed at removing the siscowets seem to offer only limited hope for the full recovery of the lean lake trout stocks. Our model suggests that burbot would be the primary beneficiary of such management actions. Note, however, that the practical application of a fishery that targets siscowet (for example, deepwater gill nets) would also produce a significant bycatch of burbot. Our model does not include that prospect, nor does it include the effect of other bycatches in any of the simulated fishery applications. That refinement must wait for subsequent modeling efforts.

A surprising set of consequences developed when we simulated invasion by the exotic *Dreissena*. That scenario produced a set of indirect interactions that enhanced the populations of other exotics—specifically, Pacific salmon and rainbow smelt. We caution, however, that our model does not include the exotic mussels, nor the effects they would bring to an Ecopath built around trophic interactions in a system where such mussels were abundant. Obviously, this result points up the need for vigilance to the invasion of *D. bugensis* and awareness of its ecological consequences to Lake Superior. Such an invasion would probably take some time, so its effects would not develop as quickly as those represented in our simulation. When set against the background variability owing to climate effects, the ecological changes derived from this invasion might not be apparent for 2 or more decades. In order to accelerate our learning about this prospect, we might consider developing Ecopath models for those areas of the Great Lakes where exotic mussels have become or are becoming very abundant (for example, the littoral zones of all of the lower lakes, western Lake Erie, Saginaw Bay, Green Bay, and the Bay of Quinte). Thus, a combination of modeling and field studies could delineate the mechanisms and the rates of ecological change related to this exotic and any others that might follow it.

In keeping with the theme of slow–fast dynamics in this special section of the Journal, we have revealed two subsets of predator–prey interactions at the top of the Lake Superior food web. One is a ‘fast’ set dominated by such exotic fishes as the Pacific salmon and rainbow smelt. Both species have much more rapid growth and maturation schedules (that is, life history characteristics as represented by P/B for each) than their ecological equivalents, the ‘slow’ native lake trout and coregonines (lake herring and deepwater cisco or chub). Other papers in this section deal with thresholds, surprises, and nonlinearities in ecosystems. Our version of an Ecosim model for Lake

Superior is developed from an Ecopath approach, which creates an equilibrium as the initial condition. This modeling approach is less likely to demonstrate dramatic nonlinearities in its responses (McClanahan 1995). Nevertheless, our modeling results include a number of unexpected outcomes, including virtual extirpation, because of the situation that arises when management actions are portrayed in a food web context where the combination of feedback pathways creates outcomes that are more complex than would be imagined by a simple linear extrapolation.

Simple expectations based on *r*-selected (= fast) vs *K*-selected (= slow) characteristics would have the salmon–smelt interactions easily able to overwhelm the lake trout–coregonine interactions if the competitive equilibrium required to create a balanced Ecopath model were disturbed by some increased mortality to lake trout, such as that due to fisheries. In fact, a more complex result emerged. In simulations where lean lake trout were enhanced, salmon suffered. In each of the simulations where siscowet lake trout were diminished, salmon also suffered. The mechanism for this result appears to be that the reduction of siscowet allows chubs to flourish, which increases predation on *Mysis*, and that burbot increase in response to the greater abundance of chubs. As a result, the stocks of preferred forage fish for salmon (smelt) are reduced and salmon therefore decline. This sequence of events is best represented in Figure 4. Logically, one would wonder how many of these complexities are embedded in the diet matrix used to fuel the Ecopath model and how those interactions might be altered by indirect effects not immediately evident in the structure of the food web.

As a simple, direct test of these interactions, we conducted an analysis of the predator–prey matrix. We set up a simple procedure that used the model as a context to increase the mortality rate on each predator by 10-fold and established a simple basis for significance—net increase or decrease of greater than 50% after a 50-year period. This procedure is designed to allow the transient responses to develop and a new equilibrium to be established. The outcome of that sequence of tests is summarized in Table 5. Empty matrix cells mean that the response was a change of less than 50%. Cells with +1 reflect an increase of at least 50% in the biomass of a prey if the predator is removed; those with –1 represent a decrease of at least 50%. Cells with +2 represent severalfold increase, whereas those with –2 reflect virtual elimination.

The general conclusions of this exercise reinforce those derived from our series of management sce-

Table 5. Equilibrium Biomass Changes in Response to Removal of Predators

Consumer Removed	Biomass Response																				
	Phyt	Zoop	Mys	Dip	Rsm	JHer	Her	Chub	Wht	Sls	Dws	JLlt	Llt	JSis	Sis	Bur	Chin	Coho	Stl	Other	
Mys	-	-	■	-	-1	+1	+1	+1	-	-	-1	-	-	-1	-	+1	-1	-1	-	-	-
Dip	-	-	-	■	-	-	-	-	-	-2	-1	-	-	-	-	-	-	-	-	+1	-
Rsm	-	-	-	-	■	-	+1	-	-	-	-	-1	-	-	-	-	-2	-1	-	-	-
JHer	-	-	-	-	+1	■	-2	-	-	-	-	-	-	-	-	-	-	+1	+1	-	-
Her	-	-	-	-	+1	-	■	-	-	-	-	-	-	-	-	-	-	+1	+1	-	-
Chub	-	-	+1	-	+1	-	-	■	-	-	+1	-	-	-1	-1	-	+1	+1	+1	-	-
Wht	-	-	-	-	-	-1	-	-	■	-	-	-	-	+1	-	+1	+1	+1	+1	+1	+1
Sls	-	-	-	-	-	-	-	-	-	■	-	-	-	-	-	-	-	-	-	-	-
Dws	-	-	+1	+1	+1	-	-1	-	-	+1	■	-	-	-	-	-	+1	+1	+1	-	-
JLlt	-	-	-	-	+1	-	+1	-	-	-	-	■	-2	-	-	-	+1	+1	+1	-	-
Llt	-	-	-	-	+1	-	+1	-	-	-	-	-	■	-	-	-	+1	+1	+1	-	-
JSis	-	-	-	-	-	-	-	+1	-	+1	-	-	-	■	-2	+1	-	-	-	-	-
Sis	-	-	-	-	-	-	-	+1	-	+1	-	-	-	-	■	+1	-	-	-	-	-
Bur	-	-	-	-	-	-	-	+1	-	-	-	-	-	-	-	■	-	-	-	-	-
Chin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-	-
Coho	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-	-
Stl	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	■	-	-
Other	-	-	-	-	-	-	-	-	-1	-	-	-	-	-	-	-	-	-	-	■	-2

Values of +1 or -1 indicate >50% change in response to removal of the individual consumer group; values of +2 represent severalfold increases whereas those of -2 indicate virtual elimination. Codes are given in Table 2.

narios. First, the removal of lean lake trout has few negative effects. The positive effects are simple and expected—an increase in smelt, herring, and some other apex predators (coho and chinook salmon) but little effect on siscowet and burbot. Other effects are also as expected; the removal of smelt has negative effects on the number of juvenile and adult lean lake trout and on each of the salmon, particularly chinook. On the other hand, the removal of siscowet has positive effects on native fishes such as chubs, sculpins, and burbot. The exotic salmon have little impact—positive or negative—on any of their prey or competitors, probably due to their relatively small biomass in our current estimates for the entire Lake Superior system. In addition, the diets of some of the salmon (for example, steelhead) include a very large proportion of terrestrial insects. In our diet matrix, these insects are external to the system, in that they are represented as ‘other’ prey. Even so, it is interesting to note that reductions in many of these species are reflected in positive or negative responses by salmon. In a general sense, anything that enhances smelt (such as the removal of their predators or competitors) will have a positive effect on salmon. Any interpretation of these results should include the caution that Ecopath predator–prey interactions are represented by a static diet composition. In other words, predators do not switch to alternate prey when one or more of their primary prey are reduced due to changes in the dynamics of the food web.

For managers, this modeling analysis offers some simple but instructive lessons:

1. To increase the abundance of lean lake trout, both their stocks and that of their primary prey (herring) must be protected from exploitation. This increase will occur more rapidly if siscowets are the focus of an aggressive targeted fishery that is sustained for many years. The failure to protect leans and herring in the presence of a targeted siscowet fishery or a fishery of short duration will allow burbot to flourish, and salmon will decline. The matrix test indicates that there is no scheme for competitor or predator removal that will allow leans to increase on a sustainable basis. All of the responses of lean lake trout to reductions in other species are neutral or negative, except for removal of burbot. However, a fishery that targets burbot is unlikely because of its associated bycatch of lake trout. Alternatively, the current and perhaps increasing abundance of

the native self-sustaining siscowet lake trout and burbot may represent evidence of success in the restoration effort.

2. Management strategy for increasing stocks of Pacific salmon requires special attention to the food web interactions that have adverse effects on smelt. Smelt have declined in Lake Superior. Thus, the trade-offs associated with a limited forage base must always be taken into account in terms of their critical linkages with other ecosystem responses to future management actions.
3. Our analyses suggest that Lake Superior offers less opportunity for the enhancement of native fish stocks than had been assumed in the most recent statement of restoration goals. This important conclusion must be tempered by certain caveats due to the limitations of the Ecopath/Ecosim modeling approach. First, the modeling process starts with the components of a balanced budget based on our estimates of current biomasses and trophic interactions. The general goal of increased biomass for each of the native species may not be well represented in the current model structure. A second notable limitation to this model is its lack of spatial resolution. There is strong evidence from a variety of sources that regional and local variability has a significant influence on ecosystem dynamics. A spatially explicit approach is now needed to evaluate the significance of that variability to the overall production of the Lake Superior ecosystem.

Models such as this one are abstractions and simplifications. They should be viewed as learning tools, not prescriptive or empirical devices. Our simulation of invasion by another exotic (*D. bugensis*) resulted in profound and unanticipated ecological effects that would provide a positive feedback and favor the existing exotics. In this case, the modeled process and its ecological expression is wholly inferred. Clearly, a comparative approach based on field studies and models built for systems that do or do not contain the exotic(s) of interest offers greater potential for understanding and anticipating the ecological consequences of yet another exotic. The current and growing interest in reestablishing coaster brook trout in Lake Superior offers an analogous challenge. We believe that Ecopath/Ecosim modeling offers an excellent standardized approach to those kinds of analyses, and we encourage the development of similar models for other Great Lakes ecosystems.

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