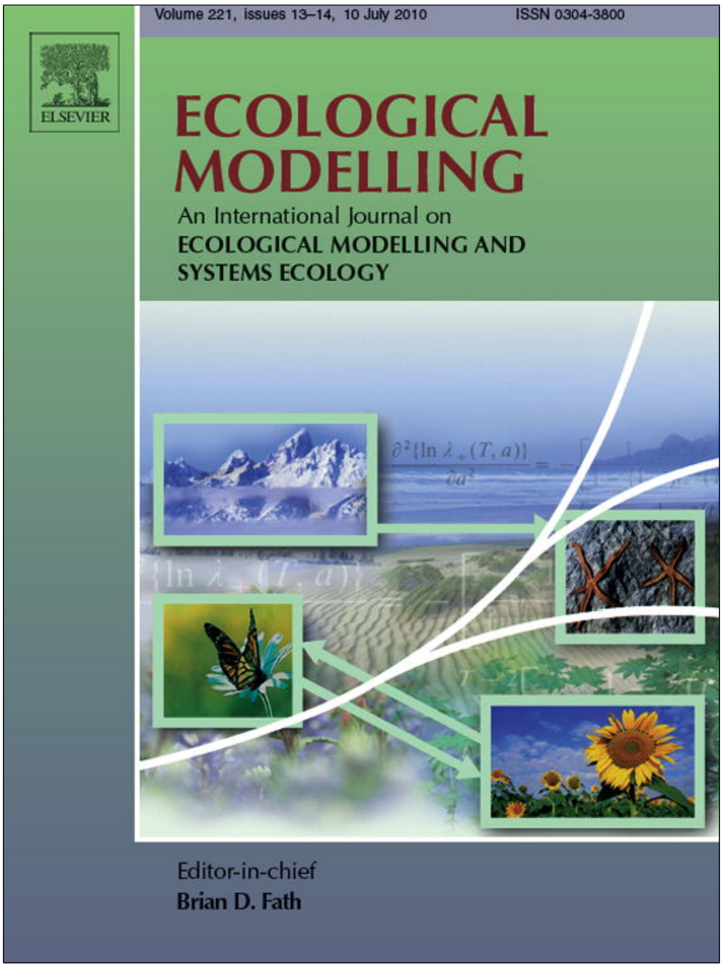
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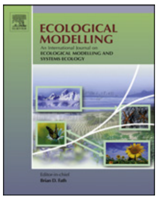

Elucidation of ecosystem attributes of an oligotrophic lake in Hokkaido, Japan, using Ecopath with Ecosim (*EwE*)

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ABSTRACT

The fishing practices in the oligotrophic Lake Toya, Hokkaido, Japan, have profound implications in the ecosystem sustainability. The status of the sockeye salmon (*Oncorhynchus nerka*) population has become a serious concern among the lake managers and policy makers during the last decades. While the decline of the sockeye salmon population has been well documented in Lake Toya, there is considerable uncertainty with regards to the impact on the broader system dynamics. In this study, our objective is to address this knowledge gap by undertaking a synthesis of the Lake Toya food web using the mass-balance modeling software Ecopath with Ecosim (*EwE*). Our primary research question is to examine the repercussions of the declining sockeye salmon population on the trophic dynamics of the lake. Namely, we assess if there are any competing species that might have benefited from the decrease of sockeye salmon standing biomass and to what extent do these changes propagate through the Lake Toya food web? Our analysis pinpoints the critical role of the Japanese smelt (*Hypomesus transpacificus nipponensis*) in the system, which demonstrates a wide range of effects on several functional groups at both higher and lower trophic levels in Lake Toya. In particular, being a substantial portion of the masu salmon (*Oncorhynchus masou*) and adult sockeye salmon diets, the Japanese smelt has a positive impact on the top predators of the system. Amphipods, insects, and shrimp strongly benefit from the autochthonous and allochthonous organic matter in the system, while the tight coupling between phytoplankton and zooplankton seems to be particularly critical for the integrity of the Lake Toya food web. Whereas the values of the different ecosystem attributes (e.g., primary production/biomass, biomass/total throughput, system omnivory index, amount of recycled throughput, Finn's cycling index) provide evidence that Lake Toya is an immature system, we note that the internal redundancy and the system overhead estimates suggest that the lake possesses substantial reserves to overcome external perturbations. We also examined the effects of a variety of fishing policies on the biomass of masu salmon and adult sockeye salmon, which verify the belief that the adult sockeye population is quite fragile with high likelihood to collapse. Our analysis also predicts that sockeye will not rebound unless the fishing pressure exerted is substantially reduced (>50% of the reference levels used). Masu salmon seems to benefit under all the scenarios examined indicating that the intensity of the current fishing activities is significantly lower than its biomass accumulation rate in the system.

> "...the benefits of a model, even if its intended use is to provide predictions, are not necessarily related to the precision of those predictions..Relatively imprecise models, coupled with a thoughtful exploration of uncertainty, can advise and inform policy decisions..." Essington (2007)

1. Introduction

More than 20% of the global freshwater fish species are being threatened or have become extinct during the last 3–4 decades (Jackson et al., 2001). In particular, according to a recent Food and Agriculture Organization (2009) report, an approximate 80% of 523 world fish stocks have been identified as fully exploited or overexploited, while estimated fish stocks of several million tonnes at the beginning of the 1960s have undergone a dramatic decrease worldwide (Hilborn et al., 2003). Compared to marine fisheries, the pressure exerted on fish populations in inland waters is more intense because the problem is accentuated by an increasing range of anthropogenic disturbances unrelated to recreational

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and/or commercial fishing, such as eutrophication, contaminant pollution, and habitat destruction (Schindler, 2001). In developed countries, the exploitation of fisheries is largely driven by continuous technological innovation and increasing capacity to target stocks of commercially valued species. As a result, historical trends of fish populations in lakes and rivers in developed countries provide overwhelming evidence of significant decline over the 20th century (Jackson et al., 2001). For instance, 33% of the fish stocks in the United States have been classified as "overfished or depleted" (Hilborn et al., 2003). The overexploitation of fisheries resources is equally dramatic in developing countries, despite the limited access to all the technological advancements. Namely, 95% of the fishers worldwide are located in developing countries and account for approximately 58% of the 98 million tonnes of annual fish catch (FAO, 2005). Generally, there is little doubt among the scientific community about the threats to the integrity of the contemporary fish populations and the profound undermining exerted by the climbing fishing rates.

The existing patterns of fishing significantly alter the structure, productivity, and resilience of biotic communities (Pauly et al., 1998; Quero, 1998; Jukic-Peladic et al., 2001; Scheffer et al., 2001; Allan et al., 2005; Otto et al., 2008), and can induce a range of complex food web modifications usually involving several interacting species at different trophic levels (Larkin, 1996; Pauly et al., 2002; Ormerod, 2003; Rocklin et al., 2009). The modern fishing practices selectively target large fish and ultimately lead to species extinction and biodiversity reduction (Conover and Munch, 2002; Allan et al., 2005; Frank et al., 2005). Furthermore, one of the most worrisome consequences of selectively fishing commercially valued species is the progressive shrinkage of the food web size due to sequential loss of apex predators (Pauly et al., 2002; Pace et al., 1999; Myers et al., 2007; Casini et al., 2008), which in turn leads to the so-called "fishing down the food web" effect (Pauly et al., 1998). These practices are associated with a substantial reduction of the number and length of the pathways that link fish populations with the rest biotic compartments of the aquatic food webs. Consequently, the formerly diversified food web structures are being significantly simplified, which has a profound impact on the trophic relationships and feeding patterns, e.g., predators have limited options to switching among different preys when their abundance fluctuates. Size-based fishing practices can also bring genetic alterations in fish species (Heino et al., 2002; Conover and Munch, 2002; Olsen et al., 2004), while other indirect consequences include the endangerment of aquatic mammals, turtles, and aquatic birds (Cook et al., 1997; Pauly et al., 2002). Fishing pressure also gradually undermines the system resilience and creates the potential for dramatic switches to the prevailing dynamic regimes; also known as shifts to "alternative stable states" (Scheffer et al., 2001).

A characteristic example of fishing practices that have profound implications in the ecosystem sustainability is the Lake Toya in Japan, where the status of the sockeye salmon population has become a serious concern among the lake managers and policy makers during the last decades (Matsuishi et al., 2002; Matsuishi and Ueda, 2004). Historically, the lake supports two salmon species: sockeye salmon (*Oncorhynchus nerka*) and masu salmon (*Oncorhynchus masou*). The sockeye salmon is highly preferred by the local people of Hokkaido due to its special use as "sashimi"; a type of delicious raw fish dish in Japan. In addition, many anglers join in recreational fishing during their leisure time from nearby areas and intensify the pressure exerted on this species. Thus, both commercial and recreational fishers are equally important threats to the integrity of sockeye salmon population in the lake. Despite the well-coordinated management guidelines along with the attempts to release hatchery-produced larvae, the sockeye salmon stock continues to decline (Matsuishi and Ueda, 2004). The annual commercial catch of sockeye salmon in Lake Toya was 143 t in 1963 but dramatically decreased to 0.5–1.5 t in the 1990s and, in spite of a slight increase in 1992, the catches have remained quite low since then. The situation is further aggravated by the following facts: (i) both recreational and commercial fishermen still have no harvest quota; (ii) the catch figures exclude fish harvest by recreational fishermen, which may be higher than the commercial one (Matsuishi et al., 2002; Matsuishi and Ueda, 2004); and (iii) the actual stock depletion rate may be much higher than what is manifested by the documented harvest declines. These trends in Lake Toya's fisheries raise serious concerns among the Japanese fish ecologists that if the present practices do not alter the stock may suddenly collapse.

While there is little doubt about the sockeye salmon population decline in Lake Toya, there is also considerable uncertainty with regards to its implications on the broader system dynamics. Several independent investigations have mainly focused on individual aspects of the food web, without accounting for the tight biotic inter-relationships (e.g., species competition, prey-predator interactions) that underlie the lake phenology (Makino et al., 1996; Makino and Ban, 1998; Shoji et al., 2000; Matsuishi et al., 2002, 2004; Makino et al., 2003). Nonetheless, the multi-species perspective is increasingly recognized as an integral part of any fisheries' management decision, and can offer insights into the interactions among lake productivity, community structure, and system resilience to external perturbations (Link, 2002; Rochet and Trenkel, 2003). In this study, our objective is to address this knowledge gap by undertaking a synthesis of the Lake Toya food web using the mass-balance modeling software Ecopath with Ecosim (*EwE*) (Christensen et al., 2000). Our primary research question is to examine the repercussions of the declining sockeye salmon population on the current trophic dynamics of the lake. Namely, we assess if there are any competing species that may have benefited from the decrease of sockeye salmon standing biomass. How do these changes propagate through the Lake Toya food web? Our study also presents the results of a network analysis (flow indices, cycles and pathways) and elucidates the different attributes (e.g., primary production/biomass, biomass/total throughput, system omnivory index) of the lake in its current state. Finally, we conclude by examining the potential implications of allochthonous matter on the interplay among the physical, chemical, and biological components of the lake.

2. Materials and methods

2.1. Study site

The Lake Toya is located at the western part of Shikotsu-Toya National Park in southern Hokkaido (lat. 42°36′N, long. 140°51′E), Japan (Fig. 1). The Toya Hot Springs and the Usu Volcano group are located at the southern shore of the lake. Lake Toya is an oligotrophic system of volcanic origin with pyroclastic sediments. The lake has an almost circular shape with a surface area of 70 km^2 and a shoreline length of 36 km. The lake volume is 8.19 km^3 with maximum depth of 179 m and mean depth of 116 m. The 173 km^2 catchment area of the lake is drained by 30 streams, although their discharge rates are relatively small. The Horobetsu and the Sibetsu rivers are the main natural outflows from the lake, while the Oru River has become a new outlet through water diversion for hydroelectric power generation and flood control. The lake water is also used for agricultural irrigation and drinking water supply. Since 1937, the lake was receiving sulfur mining wastewater from the Osaru River, containing strong acid water that gradually decreased water alkalinity. The lake water ultimately reached its lowest pH level in 1970 (pH = 5), which resulted in the gradual killing of several fish species (Goto et al., 1978). The lake acid-

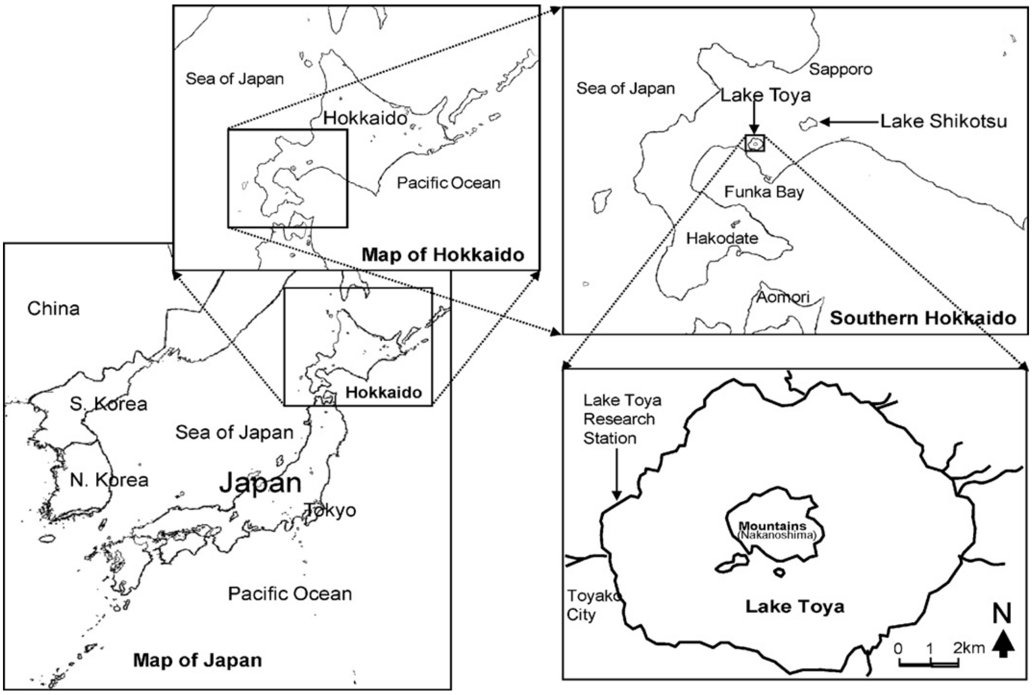

Fig. 1. Maps and location of Lake Toya in southern Hokkaido, Japan.

ity has significantly improved since then (pH = 6.8–7.0) due to a neutralization treatment coupled by the closure of the upstream sulfur mine in 1972 (Hokkaido Institute of Environmental Science, 2005), Lake Toya can be currently characterized as an oligotrophic monomictic system with an annual average total phosphorus concentration of 3 μg L^{-1}, total nitrogen of 150 μg L^{-1}, a chlorophyll *a* concentration of 0.3 μg L^{-1}, and 600 μg L^{-1} of chemical oxygen demand (Nakano and Ban, 2003). A fairly regular spring phytoplankton bloom occurs in Lake Toya, mainly dominated by colonial or filamentous species, e.g., *Dinobryon* (Chrysophytes) and *Aulacoseira* (Bacillariophytes), while the genus *Bosmina* is the dominant resident of the zooplankton community (Hokkaido Institute of Environmental Science, 2005).

The lake was characterized by a diverse array of aquatic fauna before the acidification in 1970, which has not reappeared yet since the recent system restoration. The majority of present fish species have been introduced from nearby lakes. Currently, the fish species in Lake Toya includes sockeye salmon (*Oncorhynchus nerka*), masu salmon (*Oncorhynchus masou*), Japanese pond smelt (*Hypomesus transpacificus nipponensis*), rosyface dace (*Tribolodon ezoe*), white spotted charr (*Salvelinus leucomaenis*), rainbow trout (*Oncorhynchus mykiss*), Japanese loach (*Misgurnus anguillicaudatus*), Japanese sculpin (*Cottus amblystomopsis*), common carp (*Cyprinus carpio*), common freshwater goby (*Gymnogobius urotaenia*), and floating goby (*Rhinogobius* sp.). Freshwater shrimp (e.g. *Palaemon paucidens*) and amphipoda (e.g. *Jesogammarus jesoensis*) can also be found in the lake. A few alien species, such as brown trout (*Salmo trutta*), and signal crayfish (*Pacifastacus leniusculus*) have recently been discovered in Lake Toya. Based on the relatively low frequency of occurrence of these alien species, it is hypothesized that their effect on the sockeye salmon population may be negligible. However, severe ecosystem disturbances induced by alien species have been recently reported for several Japanese lakes (Azuma and Motomura, 1998; Matsuishi et al., 2002), and therefore their effect on the sockeye salmon population as well as on the ecosystem dynamics as a whole invites further investigation.

Sockeye salmon and masu salmon are the only fish species commercially exploited in Lake Toya, whereas the remaining species have little commercial importance. For recreational fishing, anglers are obligated to buy a fishing license that can be either a seasonal-permit (approximately US$ 130) or a day-permit (approximately US$ 8). These permits allow a minimum total length limit of 150 mm for sockeye salmon, a maximum of three rods and three hooks for each rod, and are based on authorized recreational fishing regulations. On the contrary, the commercial fishery is exclusively operated by the Lake Toya Fishery Cooperative Association (LTFCA) using gillnets. Commercial fishery catches both sockeye salmon and masu salmon, while anglers are highly biased for sockeye salmon.

2.2. Software

Ecopath with Ecosim (*EwE*) has been extensively used to quantify ecosystem attributes and to examine the relative role of various ecological processes or stressors (Christensen and Pauly, 1992; Walters et al., 1997, 1999; Pauly et al., 2000; Okey et al., 2004; Christensen and Walters, 2004). In this study, we used the EwE software (version 5.1) to evaluate trophic interactions and energy fluxes within the Lake Toya food web. Ecopath is expressed by a set of equations as follows:

$$B_i \times \left(\frac{P_i}{B_i}\right) \times EE_i = Y_i + \sum_{j=1}^{n} B_j \times \left(\frac{Q}{B}\right)_j \times DC_{ji} \qquad (1)$$

where B_i is the biomass of the group i during the study period, $i = 1, \ldots, n$ functional groups, $(P/B)_i$ is the production/biomass of group i (equal to total mortality under the equilibrium assumption), EE_i is the ecotrophic efficiency (fraction of production consumed within the system or exported from it, including harvesting), Y_i is the fishing yield of the group i ($Y_i = F_i B_i$ where F_i is the fishing mortality rate), B_j is the biomass of the consumer j, $(Q/B)_j$ is the consumption/biomass of j and DC_{ji} is the fraction of i in the diet of j. Eq. (1) expresses the steady-state model for each ecosystem component that guides the trophic flow analysis. The Ecosim routine used in *EwE* is a dynamic simulation platform that uses the linear equations of steady-state Ecopath model (Walters et al., 1997), isolating the biomass accumulation term and setting up differential equations

Table 1
Functional groups of the Lake Toya ecosystem model, Hokkaido, Japan.

No.	Group name	Description
1	Masu salmon	Masu salmon (*Oncorhynchus masou masou)* (all ages)
2	Adult sockeye salmon	Lacustrine sockeye salmon (*Oncorhynchus nerka)* (>18 cm)
3	Juvenile sockeye salmon	Lacustrine sockeye salmon (*Oncorhynchus nerka)* (<18 cm)
4	Japanese smelt	Japanese smelt (*Hypomesus transpacificus nipponensis*)
5	Other fishes	White spotted charr (*Salvelinus leucomaenis*), rainbow trout (*Oncorhynchus mykiss*), rosyface dace (*Tribolodon ezoe*), common freshwater goby (*Gymnogobius urotaenia*), floating goby (*Rhinogobius* sp.), common carp (*Cyprinus carpio*)
6	Freshwater shrimp	Sujiebi shrimp (*Palaemon paucidens*)
7	Amphipods	Freshwater amphipod (*Jesogammarus jesoensis*)
8	Aquatic insects	Chironomids, such as: *Stictochironomus* sp. , *Sergentia* sp., *Polypedilum* sp., *Cryptochironomus* sp., *Paratendipes* sp., *Tanytarsini* sp., *Procladius* sp. and other insects of the lake
9	Zooplankton	The zooplankton community of the lake
10	Phytoplankton	The phytoplankton community of the lake
11	Organic matter	Exogenous organic matter delivered in the lake from the subsequent streams
12	Detritus	Endogenous (biogenic) matter of the lake

of the form:

$$\frac{dB_i}{dt} = g_i \sum_j C_{ji} - \sum_j C_{ij} + I_i - (M_i + F_i + e_i)B_i \tag{2}$$

where dB_i/dt represents the biomass growth rate, g_i is the net growth efficiency (production/consumption ratio), $\sum_j C_{ji}$ is the total consumption rate of group i, $\sum_j C_{ij}$ is the predation of all predators on group i, M_i the non-predation natural mortality rate, F_i is the fishing mortality rate, e_i is emigration rate and I_i is immigration rate. This general equation supports predictions of how biomass develops over time as a consequence of changes in fishing patterns or in other ecosystem forcing functions, e.g., gear effort (Christensen et al., 2000).

2.3. Model design and parameter estimation

We used the similarity of the habitat, diet and life history characteristics to formulate a total of 11 functional groups (Table 1). The biomass estimates of sockeye salmon were derived from the virtual population analysis (VPA), based upon: (i) catch-at-age data of samplings routinely carried out from 1992 to 2004 by the Lake Toya Research Station, Field Science Centre (FSC) for Northern Biosphere, Hokkaido University, and (ii) the DeLury method using catch-per-unit-effort (CPUE) data of angling surveys carried out from 1998 to 2004, except from 2000 when the lake fishery was closed due to a volcanic eruption of a nearby mountain (Matsuishi et al., submitted for publication). The masu salmon biomass was calculated using the ratio (=0.5) of masu to sockeye salmon in the angling surveys. Because of the lack of reliable data regarding the biomass of the remaining groups, the majority of the missing parameters were estimated by specifying reasonable ecotrophic efficiency (*EE*) values to solve the Ecopath master equation. For sockeye and masu salmon, *EE* values were assigned the highest (0.98) values due to their high contribution to the total catches from the lake. Relatively high values (0.96) were also considered for Japanese smelt and zooplankton due to their expected importance as food source for several fish populations. For the group that lumps all the rest benthopelagic fish species together (see following description), *EE* value was fixed at the rather low value of 0.80 due to their expected limited exploitation and predation. For the remaining functional groups (freshwater shrimp, amphipods, aquatic insects, zooplankton, and phytoplankton), the ecotrophic efficiencies were set at a value of 0.95, i.e., 95% of the production is used in the system due to predation/food utilization (Moreau et al., 1993).

The production/biomass (*P*/*B*) estimates for masu salmon, adult sockeye, juvenile sockeye salmon, and Japanese smelt were based on the following equation (Beverton and Holt, 1957):

$$\frac{P}{B} = \frac{K(L_\infty - \bar{L})}{\bar{L} - L_c} \tag{3}$$

where L_∞ (i.e., the asymptotic average maximum body size) and K (i.e., the growth rate coefficient that determines how quickly the maximum is attained) are parameters of the von Bertalanffy growth model: $L_t = L_\infty(1 - e^{-K(t-t_0)})$ with t_0 being the hypothetical age at which the species has zero length, L_c is the minimum body length in the catch, and $\bar{L}$ is the average body length of catch. The parameters of the von Bertalanffy growth function were estimated using non-linear optimization to fit the growth curve to the observed length composition data from the FSC samples.

Consumption rates (*Q*/*B*) for masu salmon, adult sockeye, juvenile sockeye salmon and Japanese smelt were estimated by the following empirical relationship (Palomares and Pauly, 1998):

$$\log(Q/B) = 7.964 - 0.204 \log W_\infty - 1.965T' + 0.083A + 0.532h + 0.398d \tag{4}$$

where W_∞ is a parameter of the von Bertalanffy weight growth function; T is an expression for the mean annual temperature of the water body, expressed using $T' = 1000/\text{Kelvin}$ ($\text{Kelvin} = {}^\circ\text{C} + 273.15$); A is the aspect ratio of the caudal fin which is closely related to the average level of activity and is calculated from $A = l^2/s$, where l is the height of the caudal fin and s is the surface area; h and d are dummy parameters, where $h = 1$ for herbivorous group and $d = 1$ for detritus feeder; otherwise h and d were set equal to zero. The mean water temperature of the Lake Toya was set equal to 11.1 °C, the aspect ratio was assumed to be $A = 3.3325$ for masu salmon; $A = 3.2780$ for both groups of sockeye salmon; $A = 3.2320$ for Japanese smelt, and $h = d = 0$ (Sakano, 1999). It has also been assumed that the asymptotic weight (W_∞) is equal to the weight at L_∞, and therefore the length-weight relationship was estimated as follows:

$$W_\infty = aL^b \tag{5}$$

where a and b are the parameters of the allometric relationship obtained from nonlinear fitting to length and weight data from Lake Toya.

The group labelled as "other fish" consists of species like Japanese charr, rainbow trout, rosyface dace, common freshwater goby, floating goby, and common carp, which were grouped together because of their low biomass values observed in the lake. The goby may contribute half of this group's total biomass, although there is lack of precise information about the abundance levels of the above species in Lake Toya. Thus, *P/B* and *Q/B* ratios have been set equal to the values assigned to goby; a realistic assumption, given that the majority of this group's species are small and fast growing (Christensen et al., 2005). The *P/B* and *Q/B* ratios of shrimp were obtained from Liu et al. (2007). The production to biomass

Table 2
Diet compositions of the biotic compartments included in the Lake Toya ecosystem model.

Group number	Prey	Predator								
		1	2	3	4	5	6	7	8	9
1	Masu salmon									
2	Adult sockeye salmon									
3	Juvenile sockeye salmon	0.100	0.070							
4	Japanese smelt	0.840	0.500	0.040	0.050					
5	Other fishes	0.020	0.020							
6	Shrimp					0.150				
7	Amphipods	0.010	0.110	0.180	0.210	0.100				
8	Insects	0.020	0.190	0.300	0.050	0.200	0.050		0.050	
9	Zooplankton	0.010	0.110	0.480	0.690	0.500	0.200	0.300	0.050	0.050
10	Phytoplankton					0.010	0.100	0.050	0.050	0.750
11	Organic matter							0.150	0.350	0.100
12	Detritus					0.040	0.650	0.500	0.500	0.100
	Sum	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

ratio of amphipods was obtained from the Ishikawa and Urabe (2002) study for Lake Biwa in Japan, while the consumption to biomass ratio (*Q*/*B*) was adapted from Lin et al. (2006). The production (*P*/*B*) and consumption to biomass (*Q*/*B*) ratios for insects were based on Gamito and Erzini (2005). The *P*/*B* and *Q*/*B* values for phytoplankton and detritus were adapted from Moreau et al. (1993). Diet composition of masu salmon, sockeye salmon and Japanese smelt was obtained from the stomach contents of samples collected from 1999 to 2003 (Table 2). Fish species included in the “other fish” group were considered to be primarily zooplaktivorous and detrivorous based on the information available in FishBase (Froese and Pauly, 2006). The diet content of amphipods was adapted from Lin et al. (2006), while the diet contents for shrimp, insects, and zooplankton were specified following the Matsuishi et al. (2006) study for Lake Victoria.

Trophic levels were calculated as the biomass weighted average of food items plus 1, and the omnivory index was used to gain insights into the variance of the trophic levels of a consumer's prey groups (Pauly et al., 1993). Network analysis routines of *EwE* (Ulanowicz, 1986; Ulanowicz and Kay, 1991), were used to calculate system properties and flow indicators based on theoretical concepts of Odum (1969) and Ulanowicz (1986). A routine proposed by Ulanowicz (1995) was used to aggregate the food web on discrete trophic levels (sensu Lindeman, 1942), which then were used to assess the flow distributions and trophic transfer efficiency (TTE) in the system. The mixed trophic index was used to determine direct and indirect trophic impacts among groups (Ulanowicz and Puccia, 1990). The potential implications of allochthonous matter on the food web dynamics of the lake were examined by introducing a second “detritus-like” compartment that contributes to the diets of zooplankton, insects, and amphipods. Our configuration postulated that this compartment does not receive any biogenic material from the rest functional groups, while the present analysis is based on a ratio of autochthonous to allochthonous organic matter equal to 0.5 combined with a 5 t km^{-2} yr^{-1} import rate in the system. The effects of the latter assumptions were found to be negligible on the final outputs, although the model did not achieve balance with import rates lower than 4.2 t km^{-2} yr^{-1}. Finally, we used the sensitivity analysis routine to explore the influence of the input parameters on the model outputs by varying the original parameter estimates in 10% increments from −50% to 50% (default in *EwE*). The overall quality of the model was also examined using the pedigree index routine (Christensen et al., 2005).

3. Results

A preliminary exploratory analysis showed that the inclusion of allochthonous organic matter in the model did not alter significantly the estimates of the trophic levels (*TLs*), biomass (*B*), ecotrophic efficiency (*EE*), production per consumption ratio (*P*/*Q*), net efficiencies (*NE*), omnivory index (*OI*), flow to detritus (*FD*), ratio of respiration to assimilation (R/A), and the ratio of production to respiration (P/R) (Table 3). The Ecopath outputs presented herein are also based on the average estimates of the fishing (commercial and recreational) mortality rates for masu (2.64 kg km^{-2} yr^{-1}) and sockeye salmon (24.45 kg km^{-2} yr^{-1}) catches from the mid-90s until 2005 (Matsuishi et al., 2002). According to the model outputs, the trophic levels (*TLs*) assigned to the functional groups were varying between 1.0 and 4.12 (Table 3). Top predators were the masu salmon (*TL* = 4.12) followed by the adult sockeye salmon (*TL* = 3.75). Among the other groups, juvenile sockeye salmon, Japanese smelt and the “other fish” group were associated with *TL* values higher

Table 3
Ecopath outputs for the Lake Toya ecosystem model.

Group name	TL	B	P/B	Q/B	EE	P/Q	R/A	P/R	FD	NE	OI
Masu salmon	4.12	22.7	0.54	3.84	0.98	0.14	0.82	0.21	0.02	0.18	0.04
Adult sockeye salmon	3.75	45.5	0.33	4.73	0.98	0.07	0.91	0.10	0.04	0.09	0.25
Juvenile sockeye salmon	3.16	14.1	1.72	10.12	0.95	0.17	0.79	0.27	0.03	0.21	0.05
Japanese smelt	3.17	303	1.24	11.26	0.96	0.11	0.86	0.16	0.70	0.14	0.06
Other fishes	3.07	5.8	1.50	10.00	0.80	0.15	0.81	0.23	0.01	0.19	0.07
Shrimp	2.27	5.9	1.83	24.40	0.80	0.08	0.91	0.10	0.03	0.09	0.21
Amphipods	2.32	136	6.00	33.00	0.95	0.18	0.77	0.29	0.94	0.23	0.23
Insects	2.11	110	4.20	30.00	0.95	0.14	0.83	0.21	0.69	0.18	0.11
Zooplankton	2.05	162	33.50	140.00	0.95	0.24	0.70	0.43	4.80	0.30	0.05
Phytoplankton	1.00	50.2	365.00	–	0.95	–	–	–	0.92	–	0.00
Organic Materials	1.00	2000	–	–	0.819	–	–	–	0.90	–	0.00
Detritus	1.00	1000	–	–	0.689	–	–	–	0.00	–	0.35

Note: TL is the trophic level, *B* is biomass (kg km^{-2}), *P*/*B* is the production rate (yr^{-1}), Q/B is the consumption rate (yr^{-1}), *EE* is the ecotrophic efficiency, *P*/*Q* is the production/consumption ratio, *R*/*A* is the ratio of respiration to assimilation, *P*/*R* is the ratio of production to respiration, *FD* is the flow to detritus (t km^{-2} yr^{-1}), *NE* is the net efficiency, and *OI* is the omnivory index.

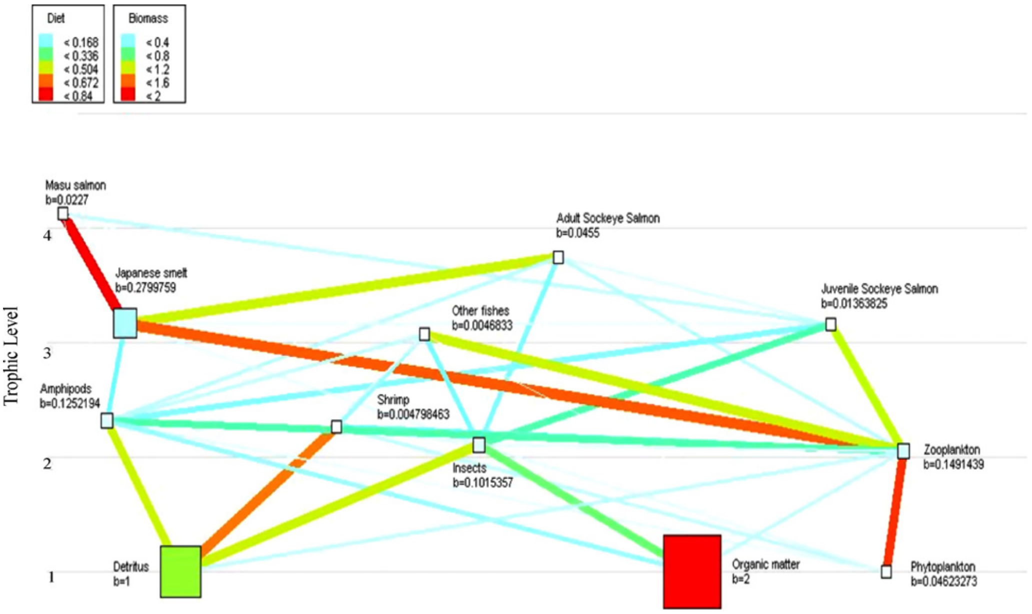

Fig. 2. The Ecopath outputs based on the Lake Toya food web conceptualization. Thickness and colour of the lines illustrate the magnitude of the flow rates. The vertical line demonstrates the functional TL of each biotic compartment. The estimated abundance values of the modelled groups are also displayed.

than 3. Other non-fish groups, including zooplankton, were classified to *TL*s between 2.0 and 2.4. The total fish biomass density obtained from the Lake Toya ecosystem model was 0.3911 t km^{-2}, which is very close to the more recent empirical estimates for Lake Toya. In terms of biomass, the ecosystem is overwhelmingly dominated by the Japanese smelt (303 kg km^{-2}), followed by sockeye salmon (45.5 kg km^{-2}) and masu salmon (≈22.7 kg km^{-2}). The biomass of zooplankton, amphipods, and insects in the system varies within the 110–165 kg km^{-2} range, whereas the phytoplankton biomass was estimated to be approximately 50.2 kg km^{-2}. Notably, the *EE* value for detritus (i.e., the ratio between the flows in and out of the detritus box) was slightly decreased from 0.79 to 0.69 when the role of exogenous organic matter was accounted for by the model. Among the relatively wide range (0.08–0.24) of *P*/*Q* (or gross food conversion efficiency) ratios, the lowest values were found for sockeye salmon (0.07) and shrimp (0.08), whereas the highest values were assigned to zooplankton (0.24), amphipods (0.18), and juveline sockeye salmon (0.17). The *OI* values pro-

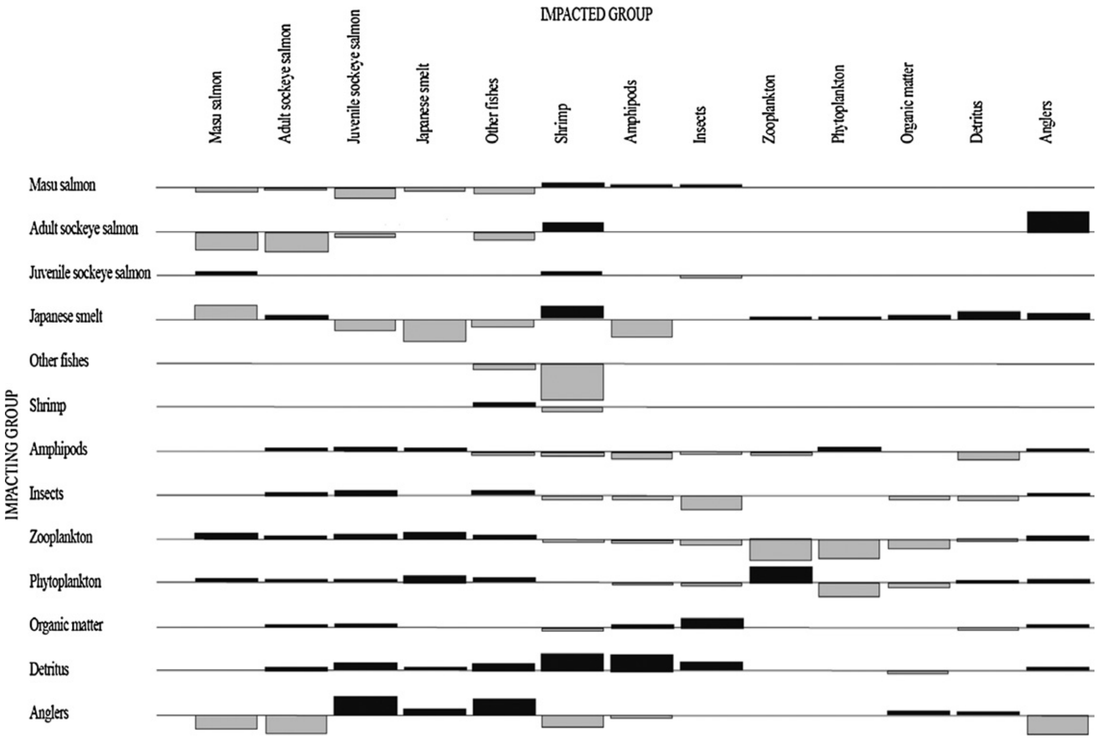

Fig. 3. The mixed trophic impact analysis of the Lake Toya ecosystem model. Impacting and impacted groups are placed along the vertical and horizontal axis, respectively. Grey and black bars represent direct and indirect impact. The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts. The bars should not be interpreted in an absolute sense: the impacts are relative and comparable among groups.

Table 4
Trophic transfer matrix of Lake Toya ecosystem model showing the distribution of flows (t km^{-2} yr^{-1}) by groups and trophic levels.

Group	Trophic level				
	I	II	III	IV	V
Masu salmon	0.00	0.00	0.00	0.07	0.01
Adult sockeye salmon	0.00	0.00	0.08	0.13	0.01
Juvenile sockeye salmon	0.00	0.00	0.13	0.02	0.00
Japanese smelt	0.00	0.00	3.18	0.24	0.00
Other fishes	0.00	0.00	0.05	0.00	0.00
Shrimp	0.00	0.11	0.04	0.00	0.00
Amphipods	0.00	3.13	1.34	0.00	0.00
Insects	0.00	3.14	0.17	0.00	0.00
Zooplankton	0.00	22.65	0.00	0.00	0.00
Phytoplankton	18.31	0.00	0.00	0.00	0.00
Organic matter	5.00	0.00	0.00	0.00	0.00
Detritus	9.08	0.00	0.00	0.00	0.00
Total	32.38	29.03	5.00	0.46	0.02

vide evidence of high specialization for the masu salmon (0.04), the juvenile sockeye salmon (0.05), and the Japanese smelt (0.06), whereas amphipods (0.23) and shrimp (0.21) appear to be more flexible with regards to their feeding patterns. According to the model outputs, the detritus pool is being replenished by the egested food, the fecal material or the non-living particulate matter from zooplankton (4.80 t km^{-2} yr^{-1}) and amphipods (0.94 t km^{-2} yr^{-1}), followed by phytoplankton (0.92 t km^{-2} yr^{-1}) and the Japanese smelt (0.70 t km^{-2} yr^{-1}). The values of the respiration to assimilation (*R/A*) and production to respiration (*P/R*) ratios for all groups were less than 1, which was one of the criteria used to accept the present Ecopath solution.

Among the trophic relationships considered by the Lake Toya ecosystem model, our analysis highlights the central role of the Japanese smelt which demonstrates a wide range of effects on several functional groups at both higher and lower trophic levels in Lake Toya (Figs. 2 and 3). In particular, being a substantial portion of the masu salmon diet, the Japanese smelt has a direct positive impact on the top predator of the system. It also indirectly favours the increase of the shrimp biomass probably through the competition with the "other fish" group, which in turn strongly rely on shrimp for their production and growth. The results also showed that the juvenile sockeye salmon has negligible impact on the abundance and the composition of the fish community. Masu and adult sockeye salmon dominate and negatively control the populations of all the smaller fish species of the lake. They also positively impact the invertebrate community of the lake possibly due to the alleviation from the pressure exerted by the Japanese smelt and the other small fish species. Amphipods, insects, and shrimp strongly benefit from the autochthonous and/or allochthonous organic matter of the system. We also emphasize the relatively tight coupling between phytoplankton and zooplankton that seems to be critical for the integrity of the Lake Toya food web. Finally, the anglers exert significant control on the masu and sockeye salmon populations, which then cascades as an indirect positive effect on the smaller fish populations (juvenile sockeye salmon, Japanese smelt, other fish) and as a negative impact on their prey (shrimp, amphipods).

When aggregating the system into discrete trophic levels, the breakdown of the trophic flows by groups and trophic levels stresses the importance of phytoplankton on the ecosystem functioning (Table 4). In particular, our model predicts that 56.5% of the total flows from the first trophic level originate from phytoplankton, and assigns a secondary role to the biogenic (28%) and exogenous (15.5%) organic matter. Zooplankton overwhelmingly dominates the flows (78%) at the herbivore/detritivore level (II), followed by the insects (10.8%) and the amphipods (10.7%). Japanese smelt and amphipods dominate the first order carnivore level (III).

Table 5
Transfer efficiency at various *TL*s showing the contribution of detritus and primary production to the Lake Toya trophic network.

Sources	TL			
	II	III	IV	V
Producer	22.6	15	11.7	10.5
Detritus	18.5	13.3	11	10.3
All flows	21	14.5	11.5	10.5

Note: Proportion of total flow originating from detritus: 0.44 Transfer efficiencies (calc. as geometric mean for TL II–IV): Primary producers: 15.8%.
Detritus: 13.9%.
Total: 15.2%.

The higher trophic levels (IV and V) primarily comprise the flows associated with the Japanese smelt and secondarily those with masu and the adult sockeye salmon. The geometric means of the transfer efficiencies of the flows originating from detritus and the primary producers through the trophic levels II-IV, calculated as the ratio between the sum of the exports from a given trophic level, plus the flow that is transferred from the trophic level to the next, and the throughput on that trophic level, were approximately 14% and 16%, respectively (Table 5).

To characterize the structure and system size of the ecosystem, we examined the key lake attributes derived from the model (Table 6). The sum of all consumption and all respiratory flows in the system were estimated to be 34.50 and 20.46 t km^{-2} yr^{-1}, respectively. Notably, relative to a simpler model configuration without allochthonous organic matter (not presented here), the total exports from the system (2.85 t km^{-2} yr^{-1}), the sum of all flows into detritus (14.08 t km^{-2} yr^{-1}) and the total system throughput (72.00 t km^{-2} yr^{-1}) were all higher when accounting for its role into the system. The estimate of the production to respiration ratio (0.90) as well as the negative value (−2.15 t km^{-2} yr^{-1}) of the net system production (i.e., the difference between total primary production and total respiration) are plausible and primarily reflect the role of the subsidies of organic matter from the watershed. The relatively high values of the primary production/biomass $\geq$21.40 yr^{-1} (i.e., accumulation of biomass over time) and the total biomass/total throughput <0.01 (low available energy flow used to support the total system biomass) are indicative of a system that undergoes its early developmental stages. The low values of the connectance (0.43) and the system omnivory (0.12) indices also suggest a linear rather than a "web-like" food chain structure. Finally, both the plausibly low value of the fishery efficiency index (0.001455) and the mean trophic level of the catch (3.78) stem from the fact that the fishery is mainly concentrated on the apex predators of Lake Toya (i.e., masu and sockeye salmon).

Table 6
Ecosystem indicators describing the Lake Toya ecosystem structure.

Parameter	Values	Units
Sum of all consumption	34.50	t km^{-2} yr^{-1}
Sum of all exports	2.85	t km^{-2} yr^{-1}
Sum of all respiratory flows	20.46	t km^{-2} yr^{-1}
Sum of all flows into detritus	14.08	t km^{-2} yr^{-1}
Total system throughput	72.00	t km^{-2} yr^{-1}
Sum of all production	24.00	t km^{-2} yr^{-1}
Calculated total net primary production	18.31	t km^{-2} yr^{-1}
Total primary production/total respiration	0.90	
Net system production	−2.15	t km^{-2} yr^{-1}
Total primary production/total biomass	21.40	yr^{-1}
Total biomass/total throughput	0.012	yr^{-1}
Total biomass (excluding detritus)	0.86	t km^{-2}
Gross efficiency (catch/net p.p.)	0.001455	
Total catches	0.027	t km^{-2} yr^{-1}
Mean trophic level of the catch	3.78	
Connectance Index	0.43	
System Omnivory Index	0.12	

Table 7
Totals of flux indices for the Lake Toya ecosystem model.

Source	Ascendency		Overhead		Capacity	
	Flowbits	%	Flowbits	%	Flowbits	%
Imports	19.2	6.7	0	0	19.2	6.7
Internal flow	43.5	15.1	139.9	48.6	183.4	63.7
Export	8.4	2.9	5.1	1.8	13.5	4.7
Respiration	21.8	7.6	49.9	17.3	71.6	24.9
Totals	93	32.3	194.9	67.7	287.8	100

Table 8
Cycling and path lengths for the Lake Toya ecosystem model.

Cycles and pathways	Values	Units
Throughput cycled (excluding detritus)	1.47	$\mathrm{t\,km^{-2}\,yr^{-1}}$
Predatory cycling index	3.29	% of throughput without detritus
Throughput cycled (including detritus)	5.21	$\mathrm{t\,km^{-2}\,yr^{-1}}$
Finn's cycling index	7.24	% of total throughput
Finn's mean path length	3.08	
Finn's straight-through path length	2.11	without detritus
Finn's straight-through path length	2.86	with detritus

The total ascendency of the system (93 flow bits) primarily consists of the internal flows (43.5 flow bits or 15.1% of the total fluxes in the lake), followed by the respiration (7.6%), the imports (6.7%), and the exports (2.9%) (Table 7). Importantly, the internal redundancy (i.e., the overhead on the internal flow) and the system overhead are fairly high (≈68% of the development capacity) indicating that Lake Toya possesses substantial reserves to overcome unanticipated external disturbances. Relative to the values typically reported in the literature (Fayram et al., 2006; Liu et al., 2007; Villanueva et al., 2008; Yunkai-Li et al., 2008), the amount of recycled throughput, the Finn's cycling index, and the values of Finn's mean and straight-through path length also suggest that Lake Toya is probably an immature and fairly simple system (Table 8). Finally, we note that the ecotrophic efficiency and the production/biomass values assigned to Japanese smelt, other fish, and juvenile sockeye salmon appear to be particularly influential on the model outputs. The measure of the model quality obtained through the pedigree index routine of *EwE* was 0.413, indicating that our model is founded upon inputs that lie close to the dichotomy between local and literature-based information.

3.1. Analysis of scenarios

We also examined the effects of a variety of fishing policies on the biomass of masu salmon and adult sockeye salmon. Given the high uncertainty about the current levels of fishing pressure, we designed a wide range of scenarios using as reference existing estimates for masu ($2.64\,\mathrm{kg\,km^{-2}\,yr^{-1}}$) and sockeye salmon ($24.45\,\mathrm{kg\,km^{-2}\,yr^{-1}}$) catches from the mid-90s (Table 9). Using a vulnerability setting that postulates a balanced bottom-up and top-down control, our results show that the adult sockeye is quite fragile with high likelihood to collapse (Figs. 4–5; panels b–c), while its population will not rebound unless the fishing pressure exerted is reduced by at least 50% of the reference levels (Figs. 4–5a). By contrast, masu salmon seems to benefit under all the scenarios examined and its biomass increases by 250–500% relative to the present standing stock (Table 10). The predominance of masu salmon over the rest residents of the Lake Toya fish community provides evidence that the intensity of the current fishing activities is significantly lower than the masu salmon biomass accumulation rate in the system (≈$9.37\,\mathrm{kg\,km^{-2}\,yr^{-1}}$). Our modeling experiments also suggest that the efforts to restore the adult sockeye salmon population (e.g., by reducing the fishing pressure) may result in a moderate wane of the populations of the smaller fish species (Scenarios 1 and 4). Finally, to put these projections into perspective, we ran the same scenarios with two (somewhat extreme) vulnerability matrices assuming strong top-down (Matrix B) and bottom-up (Matrix C) control. Our results showed that the sensitivity of the projected trends to the vulnerability settings was overwhelming. We also note the strong cascade effects induced by the second matrix, which seems to magnify the trophic inter-relationships identified with the mixed trophic impact analysis (Fig. 3). For example, the increased masu and sockeye salmon populations control the Japanese smelt biomass which then provides competitive advantage to the smaller fish species (juvenile sockeye salmon, other fish) of the lake. The latter pattern results in a selective elimination of the shrimp population and a dramatic increase of the rest invertebrate community (amphipods, insects) due to the alleviation of the pressure exerted from the Japanese smelt and/or the competition with the shrimp for the organic matter of the system.

4. Discussion

Ecopath with Ecosim (EwE) has provided the foundation for several ecosystem-based approaches to fisheries management in the recent limnological literature (e.g., Kitchell et al., 2000; Fayram et al., 2006; Matsuishi et al., 2006; Liu et al., 2007; Villanueva et al., 2008; Yunkai-Li et al., 2008). Depending on the intended use, Essington (2007) classified the EwE studies in two main categories: (i) heuristic applications, where the model was used to illuminate trophic inter-relationships and to pinpoint unexpected implications of management actions; and (ii) predictive uses aiming to offer a formal examination of policy-relevant responses of the fish community (e.g., stock biomass, maximum sustainable yield). The type of questions being addressed from the latter category raises the issue of model credibility, and usually invites a rigorous assessment of the uncertainties associated with the EwE predictions. In this regard, the Essington (2007) paper used nine published Ecopath models to reach the plausible (but oftentimes overlooked) conclusion that the derived estimates are as reliable as the input data used. Even for the exploratory-type of applications, however,

Table 9
Scenarios of alternative fishing policies for Lake Toya. The examined policies are expressed as fishing mortality rates ($\mathrm{t\,km^{-2}\,yr^{-1}}$) and as percentage changes relative to existing estimates for masu and sockeye salmon catches over a 10-yr period (1995–2005).

Simulation	Fishing mortality rates		Percentage	
	Masu salmon	Adult sockeye salmon	Masu salmon	Adult sockeye salmon
Scenario 1	0.0026	0.013	100%	50%
Scenario 2	0.0026	0.024	100%	100%
Scenario 3	0.0026	0.036	100%	150%
Scenario 4	0.0053	0.013	200%	50%
Scenario 5	0.0053	0.024	200%	100%
Scenario 6	0.0053	0.036	200%	150%

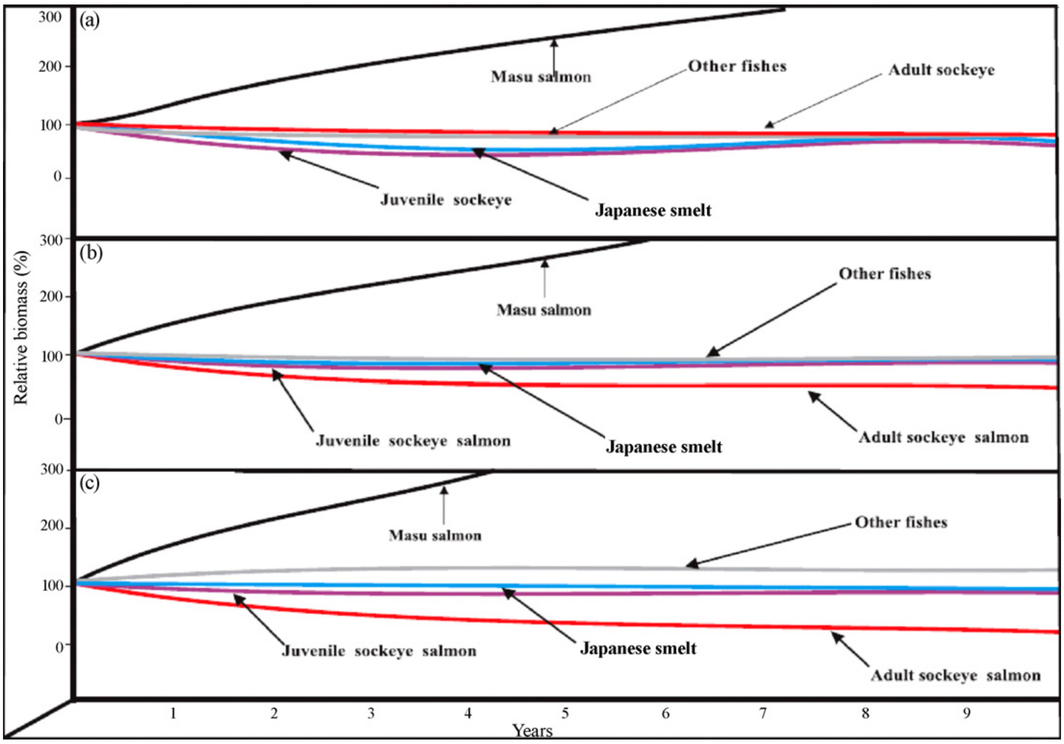

Fig. 4. Predicted relative changes in biomass resulting from fishing mortality rates of: (*upper panel*) 0.002643 t km^{-2} yr^{-1} for masu salmon and 0.013 t km^{-2} yr^{-1} for sockeye salmon (Scenario 1, Table 9); (*middle panel*) 0.002643 t km^{-2} yr^{-1} for masu salmon and 0.024 t km^{-2} yr^{-1} for sockeye salmon (Scenario 2, Table 9); (*lower panel*) 0.002643 t km^{-2} yr^{-1} for masu salmon and 0.036 t km^{-2} yr^{-1} for sockeye salmon (Scenario 3, Table 9). The projections are based on the mixed-control predatory mechanism.

the same study stressed that "*because these models have a large number of input parameters (typically far more input parameters than output parameters), there may be multiple ways to balance a model that lead to multiple predictions based on the same initial data*". Acknowledging the deficiency of the available information from the system as well as the uncertainties associated with any modeling endeavour (Arhonditsis and Brett, 2004; Arhonditsis et al., 2006), the present analysis primarily focused on the characterization of

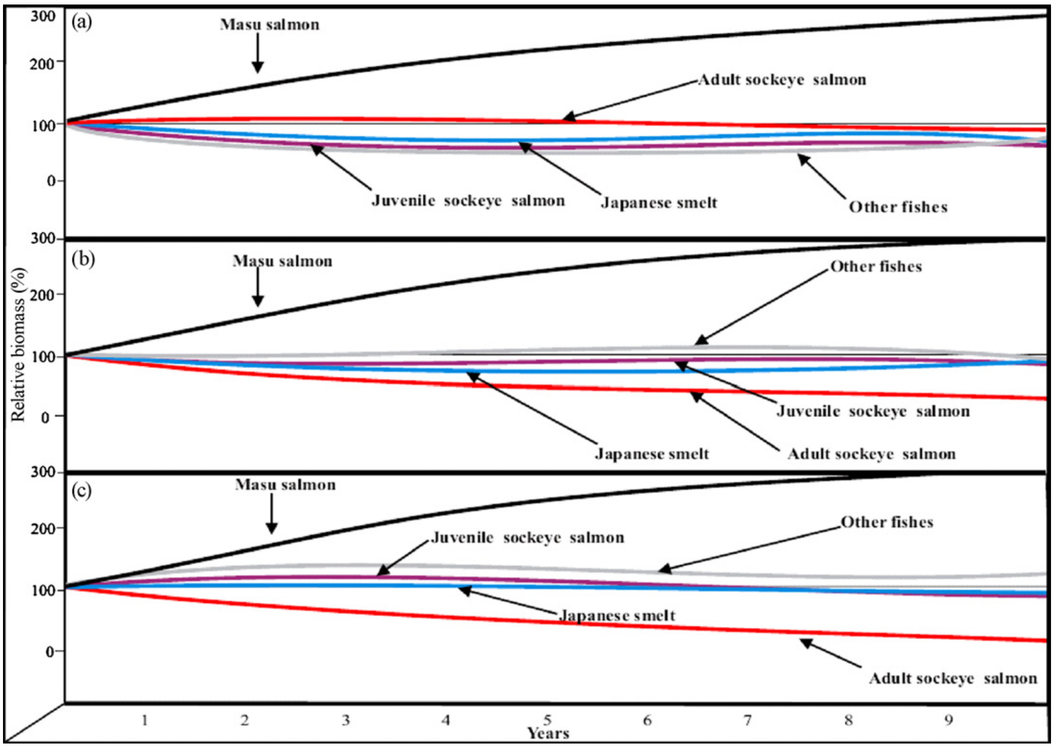

Fig. 5. Predicted relative changes in biomass resulting from fishing mortality rates of: (*upper panel*) 0.005286 t km^{-2} yr^{-1} for masu salmon and 0.013 t km^{-2} yr^{-1} for sockeye salmon (Scenario 4, Table 9); (*middle panel*) 0.005286 t km^{-2} yr^{-1} for masu salmon and 0.024 t km^{-2} yr^{-1} for sockeye salmon (Scenario 5, Table 9); (*lower panel*) 0.005286 t km^{-2} yr^{-1} for masu salmon and 0.036 t km^{-2} yr^{-1} for sockeye salmon (Scenario 6, Table 9). The projections are based on the mixed-control predatory mechanism.

Table 10
Relative changes between the baseline levels (*Ecopath* output) and the biomass values projected at the end of the tenth year after the implementation of different fishing policies in Lake Toya, Hokkaido, Japan. The three matrices postulate different predatory-control mechanisms (vulnerability values): Matrix A (mixed control), Matrix B (top-down control), and Matrix C (bottom-up).

Matrix A						
Prey/Predator	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6
Masu salmon	418%	459%	485%	282%	313%	367%
Adult sockeye salmon	90%	50%	34%	91%	51%	34%
Juvenile sockeye salmon	88%	96%	101%	88%	97%	101%
Japanese smelt	91%	96%	99%	91%	97%	100%
Other fishes	89%	105%	112%	90%	105%	113%
Shrimp	124%	89%	71%	123%	88%	70%
Amphipods	121%	110%	104%	120%	109%	103%
Insects	103%	105%	105%	103%	104%	105%
Zooplankton	99%	99%	99%	99%	99%	99%
Phytoplankton	101%	101%	100%	101%	101%	100%
Organic materials	96%	97%	98%	96%	98%	98%
Detritus	94%	97%	98%	94%	97%	99%
Matrix B						
Masu salmon	579%	615%	633%	422%	441%	451%
Adult sockeye salmon	164%	97%	68%	190%	88%	63%
Juvenile sockeye salmon	137%	146%	151%	132%	141%	147%
Japanese smelt	25%	28%	29%	30%	36%	37%
Other fishes	535%	604%	647%	487%	509%	552%
Shrimp	1%	0%	0%	0%	1%	0%
Amphipods	1192%	1184%	1182%	1100%	1014%	1007%
Insects	130%	132%	132%	127%	129%	129%
Zooplankton	63%	63%	63%	63%	63%	63%
Phytoplankton	192%	193%	193%	191%	191%	192%
Organic matter	73%	73%	73%	74%	74%	74%
Detritus	45%	45%	45%	45%	45%	45%
Matrix C						
Masu salmon	281%	281%	281%	197%	188%	188%
Adult sockeye salmon	108%	58%	37%	108%	58%	37%
Juvenile sockeye salmon	100%	100%	100%	100%	100%	100%
Japanese smelt	100%	100%	100%	100%	100%	100%
Other fishes	100%	100%	100%	100%	100%	100%
Shrimp	100%	100%	100%	100%	100%	100%
Amphipods	100%	100%	100%	100%	100%	100%
Insects	100%	100%	100%	100%	100%	100%
Zooplankton	100%	100%	100%	100%	100%	100%
Phytoplankton	100%	100%	100%	100%	100%	100%
Organic matter	100%	100%	100%	100%	100%	100%
Detritus	100%	100%	100%	100%	100%	100%

the basic ecosystem attributes, and the identification of the most important causal connections in the Lake Toya food web. These objectives were examined under the prism of a declining sockeye salmon population that appears to have important implications on the trophic dynamics of the lake. Moreover, the Ecosim-derived projections did not intend to offer numerical guidance for decision making support, but rather to unravel the structural alterations that may arise in the Lake Toya food web if the contemporary fishing practices do not change.

4.1. Ecosystem attributes

Following Odum's (1969) principles of ecological succession, the majority of the EwE applications have attempted to quantify the effects of different management actions and/or external perturbations (nutrient loading, fishing pressure) through the relative values of metrics that characterize community energetics and structure, life histories, nutrient cycling, selection pressure, and overall homeostasis. The underlying premise is to characterize the stage of ecosystem development (mature or immature) which in turn may offer insights into the system stability (Fayram et al., 2006). Although the relationship between maturity and stability has been a controversial issue (Christensen, 1995; Tilman, 1996; Ulanowicz, 1997; Perez-Espana and Arreguin-Sanchez, 2001), it is generally believed that mature ecosystems demonstrate greater stability and therefore greater resilience, resistance, or persistence to overcome external disturbances (sensu Ulanowicz, 1997). In our study, all the ecosystem bioenergetics such as the primary production/biomass, the biomass/total throughput, the connectance and system omnivory provided evidence that Lake Toya is an immature system with a linear food chain structure. Notably, according to Odum's (1969) interpretation, production to respiration ratios lower than unity also reflect systems in their early development stages that may suffer from organic pollution. Because Lake Toya in its current state does not experience any organic pollution problems, we hypothesize that this result primarily stems from the lake's oligotrophic character and its consequent reliance upon allochthonous (non-point) organic subsidies. In particular, our model predicts that an approximate 15.5% of the total flows from the first trophic level originate from the exogenous organic matter, which renders support to its explicit consideration (instead of a single detritus compartment) in the Lake Toya ecosystem model (Allesina et al., 2006).

Another important trend in ecosystem successional development is the increase of the amount of nutrients and energy recycled (or entrapped) within the ecosystem (Vasconcellos et al., 1997). Likewise, the effective number of pathways that a unit of (energy or nutrient) flow will be passing through on its way from inflow to outflow is also expected to increase in mature systems. In this study, our estimates fall within the area delineated by the Finn's cycling index *vs* mean path length relationship in Christensen and Pauly (1993; see their Fig. 9, p. 345). However, our analysis also predicts a relatively high system overhead (68%) suggesting the lake possesses substantial reserves to overcome external disturbances. While the latter finding may seem counterintuitive, given the aforementioned preconception of a positive correlation between system maturity and stability, our study is not the first one to report such result. For example, Yunkai-Li et al. (2008) recently reported a similarly high system overhead ratio (74.1%) for Lake Taihu, which negated the general evidence of an immature and relatively simple system provided by their Ecopath analysis. Moreover, our predictions for the system overhead-Finn's cycling index pair are not incongruous with the Christensen and Pauly's (1993) parabolic relationship (Fig. 6, p. 343) derived from 41 ecosystems; in particular, Lake Toya falls within its steepest segment where the system overhead increases rapidly with the cycling until it levels off at an approximate cycling value of 15%. Our results are also in agreement with the Vasconcellos et al.'s (1997) assertions that recycling is critical in modulating the ecosystem stability, and thus systems with high capacity to recycle detritus are better equipped to recover from external perturbations. Similar arguments were made by the Perez-Espana and Arreguin-Sanchez (2001) study advocating that ecosystem maturity and stability are related but in an inverse way of what has been traditionally hypothesized, i.e., immature systems are more stable and the stability decreases as systems become more complex and mature.

4.2. The role of microbial communities

Because our models predicts that approximately 3.75 t km^{-2} yr^{-1} of the detrital material is being recycled within the system, the elucidation of the potentially important nutrient regeneration mechanisms emerges as a pivotal issue in the Lake Toya functioning. In oligotrophic environments, the microbial loop is usually expected to be a significant pathway from primary production to higher trophic levels, underscoring the qualitative and quantitative role of microbial communities on aquatic biogeochemical processes (Cotner and Biddanda, 2002; Arhonditsis et al., 2004). In this regard, Nakano and Ban (2003) examined the spatiotemporal patterns of planktonic bacteria, chroococcoid cyanobacteria, and heterotrophic nanoflagellates in the system. While the Nakano and Ban (2003) study reported fairly low bacterial abundances relative to other oligotrophic systems, it also revealed a tight coupling between the thermal stratification and the vertical distributions of both bacteria and cyanobacteria. Interestingly, it was shown that cyanobacterial abundance declined toward the surface, although the same zone was typically associated with higher frequency of dividing cells due to the most favourable light conditions (Nakano and Ban, 2003). This pattern was attributed to the increased grazing by the heterotrophic nanoflagellates, which also appear to shape the bacterial vertical profiles. Moreover, aside from the grazing pressure exerted from the flagellates, the same study surmised that the bacteria variability may also be driven by the nutrient availability. The assertion of nutrient-limited bacterial growth is not necessarily supportive of the substantial nutrient regeneration predicted from our modeling exercise, but may also shift the focus on the role of heterotrophic flagellates and microzooplankton as remineralizers in the water column; an idea that was also advocated by the classical Azam et al. (1983) study.

4.3. Plankton dynamics

Our analysis also highlights the relatively tight coupling between phytoplankton and zooplankton that seems to be critical for the integrity of the Lake Toya food web, although existing evidence from the system does not unequivocally address the strength of that relationship. For example, earlier work by Makino et al. (1996) examined the diel vertical migration and diel feeding rhythms of two cladocerans, *Daphnia longispina* and *Bosmina coregoni*, and reported two interesting phenomena: (i) the two species did not feed during the daylight period even though they resided in the chlorophyll maximum layer; and (ii) they paradoxically ascended out of the chlorophyll-rich deep zone, their daytime habitat, to the chlorophyll-poor surface layer at night. The former pattern was interpreted as a strategy to reduce their mortality due to fish predation, through a minimization of their motion as well as through a reduction of their gut content in algal pigments (Mourelatos et al., 1989), while the nocturnal ascent was deemed as a preference for warmer temperatures even if they have to sacrifice the better food conditions (Williamson et al., 1996). In contrast, Makino et al. (2003) reported a "better dead than unfed" type of behaviour for the cyclopoid copepod *Cyclops cf. sibiricus*, arising from the dilemma to stay in its typical habitat (the shallow part of hypolimnion) where the risk for fish predation is high or to migrate down to deeper water where it will be experiencing adverse food conditions. Regarding the same species, Makino and Ban (2000) also asserted that it has developed a remarkable adaptation to Lake Toya's oligotrophic environment and can successfully complete its life cycle on algal diet alone. In this study, our Ecopath model suggests that 56.5% of the total flows from the first trophic level originate from phytoplankton, and that the associated transfer efficiency to the second trophic level (II) was 22.6%. On the other hand, according to our model outputs, the biogenic and exogenous organic matter may seem to play a secondary role but still accounts for a substantial proportion (43.5%) of the flow transferred across the primary producer/herbivore interface. Given that zooplankton overwhelmingly dominates the flows (78%) at the herbivore/detrivore level, we believe that these predictions are very critical about the ecosystem functioning and invite further investigation of two compelling questions: (i) To what extent the abundance and nutritional value (fatty acid content, stoichiometric nutrient ratios) of phytoplankton can meet the requirements of the zooplankton community in the oligotrophic Lake Toya? (ii) Is the quality of the allochthonous organic matter sufficient to sustain herbivorous production?

4.4. Allochthonous versus autochthonous production

The importance of the actual role of the exogenous particulate organic material has received considerable attention in freshwater ecology, and it has been shown that the impact of terrestrial subsidies depends on characteristics of the allochthonous material, the pathway of entry into the food web, the zooplankton community structure, and the system productivity (Carpenter et al., 2005; Cole et al., 2006; Pace et al., 2007). Generally, allochthony seems to be low in both eutrophic lakes and oligotrophic, clear-water lakes, whereas the terrestrial subsidy to consumers is considered significant in relatively small systems with greater humic content, i.e., higher color and dissolved organic carbon (Pace et al., 2007). Earlier studies pointed out that cladocerans are less dependent relative to copepods on autochthonous sources, and can obtain their carbon through direct feeding on terrestrially derived particulate organic carbon (Cole et al., 2006). Nonetheless, this hypothesis was not verified from Pace et al. (2007), who suggested that cladocerans are mainly supported from autochthonous carbon (even if they have to vertically migrate below the mixed layer) and selectively from some allochthonous sources, such as Gram-negative bacteria. More recently, Brett et al. (2009) challenged the traditional notion that terrestrial carbon inputs dominate the carbon flux of nutrient poor lakes with vegetated watersheds. Namely, this study provided evidence that the terrestrial carbon of higher plant origin likely has small contribution to zooplankton and fish production than the autochthonous production by phytoplankton rich in essential fatty acids. It was also hypothesized that the lower quality terrestrial carbon may be used for the catabolism to meet the metabolic energy demands, whereas the autochthonous material is directly utilized for new somatic growth (Brett et al., 2009). In Lake Toya, the pronounced diel vertical migrations and the diet contents in the zooplankton guts probably render support to the latter views and reiterate the dependence of the food web on the phytoplankton production (Makino and Ban, 1998; Makino et al., 2003).

4.5. Trends of the fish community

Predictive modeling (Ecosim) also demonstrated trends that are on a par with other evidence from the system that the adult sockeye population is quite fragile with high likelihood to collapse. We also note the moderate decrease of the juvenile sockeye salmon abundance under the present fishing levels (Scenarios 2 and 4), possibly reflecting the depensation effects on juvenile survival and recruitment as a result of the adult abundance decrease (Walters and Kitchell, 2001). Recently, Matsuishi et al. (2002) carried out mail and access point surveys to estimate the catch numbers and angling efforts of recreational angling, and the estimated exploitation rates were ranging from 62% to 78%. These numbers are worrisome and unless concerted action is taken, the potential for degradation of the fisheries resources is prevalent. In particular, based on a "moderate" vulnerability setting that postulates a balanced bottom-up and top-down control, our projections are that the sockeye salmon population will not rebound unless the fishing pressure exerted is reduced by at least 50% of the reference extraction levels ($\approx$25 kg km^{-2} yr^{-1}). It should also be noted that the present analysis of scenarios reflects the average stocking rates that have resulted in the Ecopath base biomass (40,000 individuals) along with a relatively favourable recruitment power (<0.1). Future improvements of the present predictive exercise should be sought in two main directions: (i) in view of the model sensitivity to the vulnerability parameters, one plausible next step is the search for vulnerability estimates that give better 'fit' to the recently derived time series of sockeye salmon abundance (Matshuishi, unpublished data), and possibly represent more realistically the predatory control mechanisms in the system; and (ii) an explicit examination of the interplay between the stocking rates and the angling efforts should offer more objective insights into the stability domain of the lake. In particular, Fayram et al. (2006) argued that angler behaviour can easily counteract the benefits from stocking and may end up having dire repercussions on system stability. The same study also pointed out that these effects may be more pronounced in oligotrophic systems because of their relatively immature character. Assuming that this hypothesis holds true, then the local fisheries managers should carefully consider angler effort responses to stocking, if they want to maintain the integrity of the Lake Toya food web.

Masu salmon's life history has received considerable attention in Lake Toya, because of a unique lacustrine ("puerile") life form of the mature males which, after migrating to the lake, returns to the natal creeks while maintaining the parr marks (Yamamoto et al., 2000). Our analysis supports prospect of a thriving masu salmon population which seems to be the primary species benefiting from the sockeye salmon decline. The predominance of masu salmon provides evidence that the current fishing intensity (2.64 kg km^{-2} yr^{-1}) is significantly lower than the predicted masu salmon biomass accumulation rate in the system ($\approx$9.37 kg km^{-2} yr^{-1}). Finally, our study also highlighted the critical role of the Japanese smelt in the system, which appears to be a key player in the majority of the trophic relationships considered in our model. To further underscore its importance in the Lake Toya trophic dynamics, we designed a "fishing down the food web" type of scenario that will increase by 25% the present mortality levels of the Japanese smelt (not presented here). Our simulations showed that the decrease of the Japanese smelt stock will negatively affect the populations of the top predators; in particular, the increase rates of the masu salmon biomass was 60–80% lower than those reported under the second and fifth fishing scenarios (Table 9). The same hypothetical scenario also favours a substantial increase of the biomass of the other smaller-sized residents of the Lake Toya fish community (i.e., juvenile sockeye salmon, "other fish" group).

In an attempt to integrate the trophic dynamic with the energy flow views of the lake food webs, Vander Zanden et al. (2005) argued that the benthic habitats can offer substantial energetic subsidies that strengthen the prey–predator relationships and the top-down control. The same study promoted the adoption of holistic depictions of lake food webs in which benthic and pelagic communities are tightly intertwined. Likewise, the absence of the spatial dimension from our modeling analysis implicitly postulates a stronger benthic–pelagic linkage, which in turn may have bolstered the projected trophic interactions in the system. While the close coupling between the benthic and pelagic habitats in Lake Toya is not an unrealistic assumption, we believe that the explicit consideration of space should allow the evaluation of the robustness of some of our predictions.

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