Prey fish exploitation, salmonine production, and pelagic food web efficiency in Lake Ontario

Peter S. Rand and Donald J. Stewart

Abstract: Estimates of production and predation rates from bioenergetic models of chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*Oncorhynchus kisutch*), and lake trout (*Salvelinus namaycush*) suggest a long-term decline in their gross conversion efficiency (gross production/prey consumption) and the gross production to biomass ratio in Lake Ontario during 1978–1994. The former pattern was caused primarily by a declining trend in adult alewife (*Alosa pseudoharengus*) energy density during 1978–1985; the latter pattern resulted from reductions in growth rates (coho salmon) and a buildup of the older age-classes in the population (lake trout) over time. Model results suggest that over 100 and 25% of the annual production of adult alewife and rainbow smelt (*Osmerus mordax*), respectively, was consumed by salmonines during 1990 in Lake Ontario; hence, we claim that recent observations of reduced salmonine growth in Lake Ontario may be a result of prey limitation. Energy transfer from primary production to salmonines appeared to be more efficient in Lake Ontario than in Lake Michigan, probably due to higher stocking levels per unit area and higher densities of preferred prey fish in Lake Ontario. Through separate analyses, we arrived at conflicting conclusions concerning the sustainability of the food web configuration in Lake Ontario during 1990.

Résumé : D'après les estimations des taux de production et de prédation obtenues à partir de modèles bioénergétiques du saumon quinnat (*Oncorhynchus tshawytscha*), du saumon coho (*Oncorhynchus kisutch*) et du touladi (*Salvelinus namaycush*) entre 1978 et 1994, il y aurait eu une baisse à long terme de l'efficience alimentaire brute (production brute/consommation de proies) et du rapport entre la production brute et la biomasse dans le lac Ontario. Le premier profil correspondait surtout à une tendance à la baisse de la densité énergétique chez le gaspareau adulte (*Alosa pseudoharengus*) entre 1978 et 1985; le second découlait de baisses du taux de croissance (coho) et d'une accumulation des classes plus âgées dans la population (touladi) au cours des années. D'après les résultats du modèle, les salmoninés du lac Ontario auraient consommé, en 1990, respectivement plus de 100 et 25% de la production annuelle de gaspareaux et d'éperlans (*Osmerus mordax*) adultes; nous alléguons donc que la réduction de croissance observée récemment chez les salmoninés du lac Ontario peut s'expliquer par une limitation du nombre de proies. Le transfert d'énergie de la production primaire aux salmoninés semblait être plus efficace dans le lac Ontario que dans le lac Michigan, probablement à cause du taux d'ensemencement plus élevé par unité de surface et des densités plus élevées de proies de premier choix dans le lac Ontario. Des analyses séparées nous ont amenés à tirer des conclusions contradictoires sur la durabilité de la composition du réseau trophique dans le lac Ontario en 1990.
[Traduit par la Rédaction]

Introduction

The sustainability of Pacific salmon in the Great Lakes has received considerable attention since their successful introduction during the 1960s and 1970s. Initially intended to control a burgeoning population of alewife, the artificial propagation efforts within the Great Lakes basin have developed a recreational fishery that produces substantial economic revenue for many coastal communities (Talhelm 1988). The early optimism about the future of the sport fishery generated during the late 1970s and early 1980s was tempered by observed signs of ecological stress in the salmonine community in Lake Michigan, predicted initially by Stewart et al. (1981) and later recounted by Kitchell and Crowder (1986) and Stewart and Ibarra (1991). The hypotheses put forth by these investigators state that predatory salmonines have the potential to depress pelagic prey fish abundance, and hence, create conditions where prey fish become limiting, resulting in reductions in predator growth, condition, and survival.

Rand et al. (1994) noted declining size and condition of prey fishes in Lake Ontario during 1978–1990 and provided evidence from modeling exercises that chinook salmon (*Oncorhynchus tshawytscha*) would need to dramatically increase their food consumption rate to maintain observed growth rates over this period. In our companion paper (Rand and Stewart 1998), we report evidence to support this prediction based on analyses of a data set on salmonine diets collected in Lake Ontario. Lake Ontario has received relatively large numbers of salmonine hatchery plants per annum (Hartig et al. 1991), and prey fish in Lake Ontario have exhibited declines in growth and abundance since the early 1980s (O'Gorman et al. 1997). These trophic conditions can ultimately translate into increased stress on the predatory salmonines in the lake. Recent evidence from Lake Michigan of declines in salmonine growth and survival, shifts in diet to less preferred prey items, and the outbreak of diseases such as bacterial kidney disease

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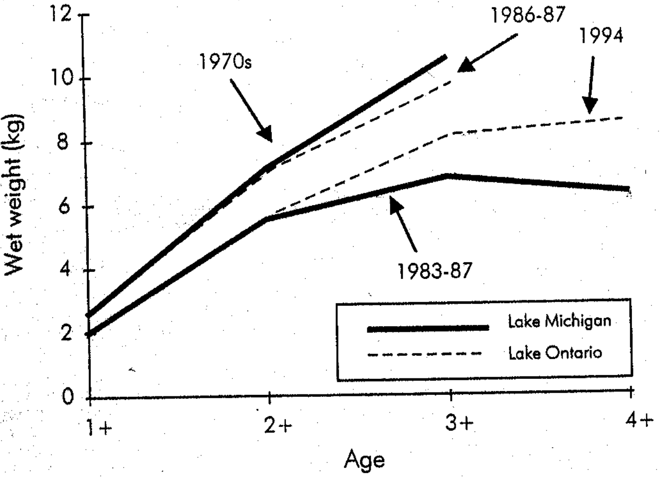
Fig. 1. Weight-at-age for sexually mature hatchery chinook salmon from Lake Michigan (Strawberry Creek, Wis.) and Lake Ontario (Salmon River, N.Y.). Years during which data were collected are included in the figure. Both reductions in size-at-age and delays in age-at-maturity have occurred in these populations over time.



(Stewart and Ibarra 1991) serves as a portent that we may be approaching the limits to salmonine production in these Great Lakes ecosystems.

A group of investigators have explicitly compared food web dynamics and trophic structure between lakes, particularly Lakes Michigan and Ontario (see Sprules et al. 1994 and accompanying papers in Can. J. Fish. Aquat. Sci. **51** and **52**), but a comprehensive comparison of trophic dynamics involving the salmonine populations in the two systems has not been undertaken. Little has been reported on dynamics of growth, survival, and production of salmonines during their pelagic residence in Lake Ontario. Some data on diets and thermal occupation have been reported (Brandt 1986; Olson et al. 1988; Rand and Stewart 1998), but few studies have explored longer term trends in bioenergetic processes exhibited by the populations. Jones et al. (1993) offered an approach to evaluate the dynamics of pelagic predator–prey dynamics in Lake Ontario. However, critical biological information on salmonines, such as trends in predator growth and survival rates, prey fish condition, and records of shifts in salmonine diets, was not available at the time the model was being developed.

To assess the level of predator stress within the Lake Ontario pelagic food web, we gathered and summarized critical biological information on the salmonine populations. We integrated these data into bioenergetic models to evaluate emergent properties of the population over time that serve as a measure of stress experienced by the populations. These measures included gross conversion efficiency and gross production to mean monthly biomass ratios (*P*:*B*). Lake-wide predation rates, along with independent estimates of prey fish biomass and production, provided measures of predator exploitation rates on the prey fish populations. In addition, biomass size spectra and biomass transfer efficiencies between trophic groups provided clues to constraints or "bottlenecks" within the food web structure that may place limits on production rates of apex predators in these ecosystems (Sprules et al. 1991; Sprules and Goyke 1994).

In this paper, we assess trends in production and predation of the dominant salmonines in Lake Ontario over nearly two decades. We test the null hypothesis that there exist no marked trends in higher order salmonine population processes in Lake Ontario that may provide evidence of ecological stress. We provide estimates during 1978–1994 of growth rates, survival, production, gross conversion efficiencies, and *P*:*B* for three of the dominant salmonines in Lake Ontario. We also estimate exploitation rates on alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) populations during 1990. Finally, we summarize expected production rates among and biomass transfer efficiencies between trophic groupings in Lakes Ontario and Michigan based on a particle-size model. These expected values are compared with estimates of production and biomass transfer efficiencies derived from this paper and from previous studies on the pelagic food webs of Lakes Ontario and Michigan (Sprules et al. 1994 and accompanying papers in Can. J. Fish. Aquat. Sci. **51** and **52**).

Methods

We developed species-specific bioenergetic models to estimate lake-wide predation and production by three of the dominant salmonine predators in Lake Ontario: chinook salmon, coho salmon (*Oncorhynchus kisutch*), and lake trout (*Salvelinus namaycush*). We used an energy balance approach and modeled daily growth and prey consumption by these species using algorithms from Hewett and Johnson (1992) implemented into a Visual Basic Macro in Microsoft Excel. In the interest of brevity, we do not include the detailed inputs to the model in the present paper. A description of the general modeling approach can be found in existing publications (Stewart et al. 1983; Stewart and Ibarra 1991; Hewett and Johnson 1992; Rand et al. 1993). Consumption and metabolic coefficients used in the model have been described elsewhere (chinook and coho salmon: Stewart and Ibarra 1991; lake trout: Stewart et al. 1983). Water temperature, energy density of predator and prey, and diet proportions (including invertebrates and prey fish) for the salmonines can be found in other publications (Elrod and O'Gorman 1991; Stewart and Ibarra 1991; Rand et al. 1993, 1994; Rand and Stewart 1998). We focus here on the description of data on growth and survival rates of Lake Ontario salmonines that have not been formalized into a publication.

Growth

Chinook salmon

We assumed that the wet weight of an average young of the year chinook salmon smolt on 1 May (first day of the model year) was 4 g (Stewart et al. 1981). We obtained weight-at-age data collected on returning, sexually mature adults from the Salmon River population monitored during egg-take operations at the Altmar Fish Hatchery in Altmar, New York (Fig. 1; Table 1; L. Wedge and D. Bishop, New York Department of Environmental Conservation (NYDEC), Cortland, N.Y., unpublished data). Individuals were aged based on scale analysis by NYDEC personnel. We modeled four separate age groups (1+ (jacks), 2+, 3+, and 4+). We applied mean weight-at-age measured during each year from data collected during 1986–1994. We computed mean weights by age during 1986–1994 and applied these over the years for which we had no data (1978–1985). For sexually mature cohorts, we terminated the simulations on day 240 (1 November).

Coho salmon

We assumed that the wet weight of an average yearling coho salmon smolt on 1 April (first day of the model year) was 50 g (Stewart et al. 1981). We modeled two separate life histories of coho salmon. Precocial males return to the river to spawn after one summer in the lake.

Table 1. Summary of weights, lake-wide abundance, prey consumption, production, and gross conversion efficiency for the three modeled salmonines by age group in Lake Ontario during 1990–1991.

Age	Weight (g)	Abundance (1000s)	PC (kt·year^{-1})	GP (kt·year^{-1})	*P:B*	GCE
			Chinook salmon			
0	4	3217	1.69	0.50	3.76	0.27
1	290	1731	4.46	1.29	1.45	0.29
2	1475	911	11.20	2.46	1.14	0.22
3	6159	374	5.18	6.89	0.36	0.12
4	8012	5	0.08	0.01	0.25	0.12
			Coho salmon			
1	50	330	0.03	0.01	1.93	0.20
2	1036	147	1.96	0.41	1.54	0.21
			Lake trout			
1	50	1842	1.49	0.17	1.37	0.12
2	231	1028	1.34	0.18	0.88	0.14
3	557	532	1.01	0.12	0.49	0.12
4	907	287	1.04	0.12	0.58	0.12
5	1756	142	0.71	0.09	0.49	0.13
6	2749	65	0.31	0.03	0.26	0.10
7	3384	31	0.17	0.01	0.21	0.08
8	3921	18	0.06	<0.01	0.06	0.03
9	3854	7	0.03	<0.01	0.17	0.07

Note: Mean weights and abundance are on 1 May, and model estimates of predation and production are cumulated during 1 May 1990 to 30 April 1991. PC, prey consumption; GP, gross production; *P:B*, gross production to mean monthly biomass ratio; GCE, gross conversion efficiency.

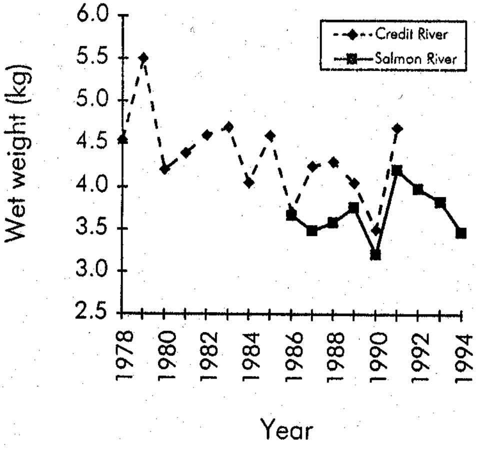
We applied final weights of jack salmon measured at the Altmar Fish Hatchery during 1986–1994 (Table 1; L. Wedge and D. Bishop, NYDEC, Cortland, N.Y., unpublished data). Because we lacked data prior to 1986, we computed mean weights for mature coho jacks during 1986–1994 and applied these over the years for which we had no data (1978–1985). We relied on a time series of weights of returning 2+ coho salmon to the Credit River, Ontario, during 1977–1991 (Fig. 2; J. Bowlby, Ontario Ministry of Natural Resources (OMNR), Picton, Ont., unpublished data) and data on final return weights of coho salmon collected at the Altmar Fish Hatchery on the Salmon River, N.Y., during 1986–1994 (Fig. 2; L. Wedge and D. Bishop, NYDEC, Cortland, N.Y., unpublished data). During years when the time series overlapped, we computed a mean final weight for the two populations. For sexually mature cohorts, we terminated the simulations on day 214 (1 November).

Lake trout

We used mean weight-at-age for lake trout sampled as part of a NYDEC monitoring program conducted in September during 1983–1994 (C. Schneider, NYDEC, Cape Vincent, N.Y., unpublished data). We derived mean weights by age during 1983–1994 and applied these over the years for which we had no data (1978–1982). We set the start day of the simulation on 1 July (stocked yearlings) and 1 September (all other age-classes) and modeled eight separate age groups (ages 1–8). We assumed that lake trout reach sexual maturity by age 5, as has been reported for similar Great Lakes populations (Stewart et al. 1983), and modeled the spawning event as a step function by decreasing wet weight of the average individual in each of the spawning age-classes by 10% on 1 November (Stewart et al. 1983; Stewart and Ibarra 1991).

Predator stocking and survival

Fig. 2. Weights at age 2+ for two populations (Credit River, Ont., and Salmon River, N.Y.) of sexually mature coho salmon in Lake Ontario during 1978–1994. Note the reduction in size-at-age occurring in the Credit River population over time.



Lake-wide abundance for each stocked salmonine was estimated from data on hatchery planting in New York State and the Province of Ontario (obtained from stocking records held by NYDEC and OMNR) and survival schedules. We present sources of data and methods for estimating survival rates applied to each of the modeled species below.

Chinook salmon

We estimated the survival rate from time of stocking to time of river return using data collected on the Salmon River population by NYDEC. The abundance and mortality sources for the 1989 and 1992 cohorts were tracked to derive lake survival rates. The original population consisted of 570 000 stocked spring smolts. Numbers returning were derived from Salmon River creel census data (lake and river) and estimated numbers reaching the hatchery for egg-take from the 1989 and 1992 year-classes (L. Wedge and D. Bishop, NYDEC, Cortland, N.Y., unpublished data). Ages were discriminated in the creel census based on length–frequency and in the hatchery using a scale-aged subsample. We calculated daily instantaneous mortality (Z, as in Ricker 1975) for each cohort. We assumed that (*i*) each life history stage exhibited the same survival rates, (*ii*) individuals spent 519 (1+, jacks), 914 (2+), 1279 (3+), or 1614 (4+) days in the lake prior to stream entry, and (*iii*) there was no immigration into or emigration from the population. We estimated survival to be 0.47 and 0.45·year^{-1} for the 1989 and 1992 cohorts, respectively. These values included both natural and lake harvest mortality. We computed a mean survival rate for the two cohorts and applied it over the entire time series in the model. We assumed that the average individual in the spawning population entered the stream on 1 November and that the computed annual instantaneous survival rates applied over the entire period of lake residence

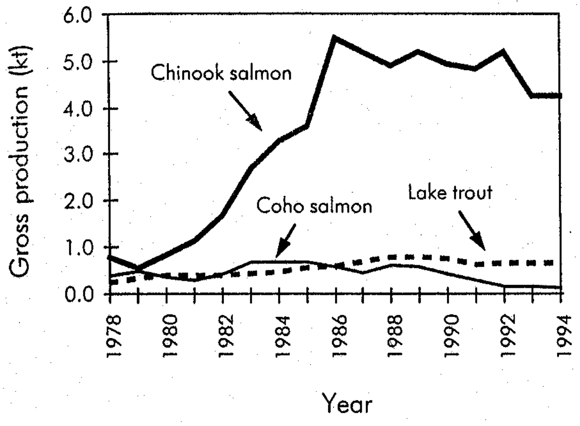
Coho salmon

In the absence of any natural mortality data for this species in Lake Ontario, we relied on rates derived for Lake Michigan coho salmon in Stewart et al. (1981) and Stewart and Ibarra (1991).

Lake trout

We developed a life table for Lake Ontario lake trout based on hatchery planting data and survival schedules. We applied the fingerling–yearling survival value of 41.7% that was reported for stocked lake trout in Lake Ontario (Elrod et al. 1988) to estimate yearling equivalents by year. For yearlings to age 4, we applied an annual survival rate of 52% estimated for Lake Michigan lake trout by Eck and Brown (1985). For ages greater than 4, we applied a value of 40% annual

Fig. 3. Model estimates of lake-wide production (wet weight·year^{-1}) by chinook salmon, coho salmon, and lake trout in Lake Ontario during 1978–1994.



survival based on catch-curve analysis of data collected on Lake Ontario lake trout by NYDEC (C. Schneider, NYDEC, Cape Vincent, N.Y., unpublished data).

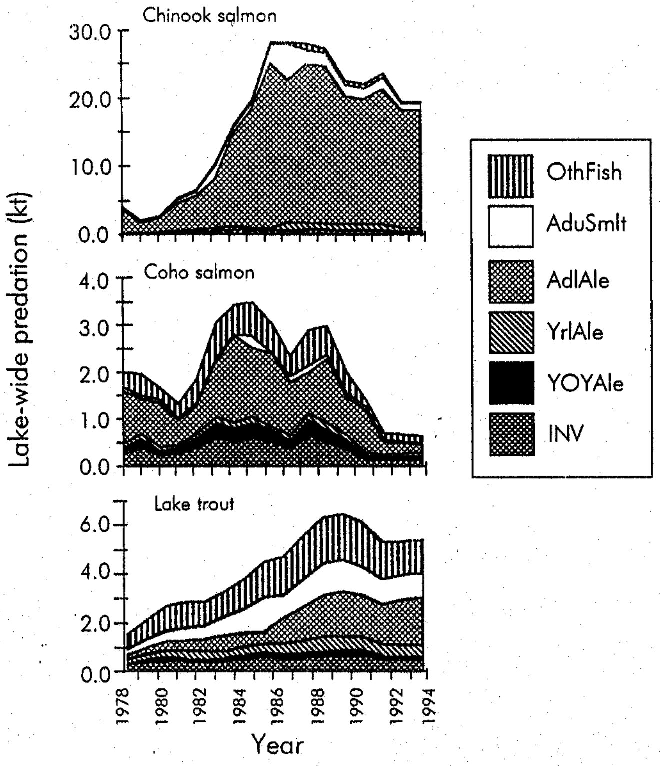
Predation rates, exploitation rates, and trophic efficiencies

From the bioenergetic model output, we estimated annual (over the interval 1 May 00 – 30 April 01) cumulative wet weight prey consumption, gross production, gross conversion efficiency (cumulative annual gross production/cumulative annual prey consumption, expressed as a proportion), and a gross production to mean monthly biomass (*P*:*B*) ratio for the three dominant salmonines during 1978–1994. We express wet weight predation and production rates in units of kilotonnes per year (lake-wide) and grams per square metre per year or kilograms per hectare per year.

We estimated prey fish exploitation rates (ER, expressed as a percentage) by dividing predation rates on alewife and rainbow smelt by the respective prey fish production estimates during 1990. To estimate predation by the entire salmonine community for our computation of ER, we summed values for the three modeled species with those reported for rainbow trout (*Oncorhynchus mykiss*) (Rand et al. 1993). We estimated predator demand by brown trout (*Salmo trutta*) by computing total predation for each diet type per stocked yearling equivalent for each of the above modeled salmonines. We then calculated mean consumption rate for each prey type across all predator species and multiplied the resulting values by the number of yearling equivalents of brown trout stocked during 1978–1994. These total predation estimates, along with values of prey fish production reported by Rand et al. (1995) for young-of-year (YOY) and older (yearlings and adults) age groups, enabled us to estimate ER on both the alewife and rainbow smelt populations during 1990.

We assembled data on pelagic production rates for four separate trophic groups in Lake Ontario during 1990 and Lake Michigan during 1987 to conduct an analysis on trophic efficiencies (TE) in both ecosystems (see Table 3 for sources of estimates of production rates). Here, we define TE (expressed as a percentage) as the cumulative annual production rate for a given trophic group (grams wet weight per square metre per year) divided by the same measure for the trophic level below it. We define food web efficiency (FWE, expressed as a percentage) as the cumulative annual production rate for the prey fish or the apex predators (grams wet weight per square metre per year) over the pelagic primary production rate in the same units. Using estimates of primary production rates in both lakes, we computed expected production rates within defined trophic groups using a range of published coefficients of particle-size conversion efficiencies (high: 0.18; low: 0.26) and a particle-size model (Sprules et al. 1991; Sprules and Goyke 1994). These expected values were contrasted with our estimates of production to gain insight into the structure of the pelagic food webs in both ecosystems.

Fig. 4. Model estimates of lake-wide predation (wet weight·year^{-1}) by chinook salmon, coho salmon, and lake trout in Lake Ontario during 1978–1994. Note the different *y*-axis scales for each plot. OthFish, other prey fish; AduSmlt, adult rainbow smelt (age ≥2); AdlAle, adult alewife (age ≥2); YrlAle, yearling alewife; YOYAle, young-of-year alewife; INV, invertebrates.



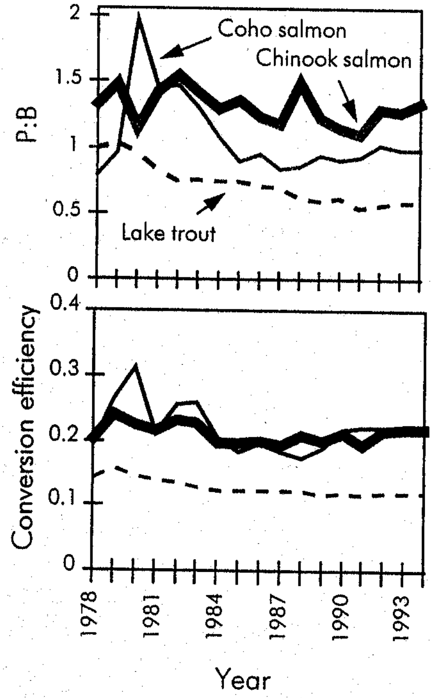
Results

Total lake-wide production of the three dominant salmonines increased over eightfold from 1978 to 1986 and then leveled off during 1987–1994 (Fig. 3). Lake-wide production rates leveled off during the late 1980s as a result of the lake-wide stocking limit imposed by Canada and the United States. Total gross production was dominated by chinook salmon, which accounted for over 70% of the annual production, reaching a peak of 5.5 kt (0.3 g·m^{-2}·year^{-1}) in 1986. Lake trout and coho salmon production ranged between 0.2 kt (0.01 g·m^{-2}·year^{-1}) and 0.8 kt (0.04 g·m^{-2}·year^{-1}) during the time series.

Model estimates of lake-wide prey consumption by the three salmonines varied by nearly an order of magnitude during 1978–1994 (4.6 kt or 0.3 g·m^{-2}·year^{-1} in 1979 to 38.5 kt or 2.1 g·m^{-2}·year^{-1} in 1988). Total predation has been declining somewhat in more recent years (27.0 kt or 1.5 g·m^{-2}·year^{-1} in 1994) largely due to reductions in stocking of coho salmon by the Province of Ontario (Fig. 4). Chinook salmon consumed the greatest amount of prey fish, and a large proportion of that predation (generally >75%) was directed toward adult alewife (age >2). Since 1986, chinook salmon predation accounted for approximately 80% of the total consumption by the three species.

There were marked downward trends in salmonine *P*:*B* and

Fig. 5. Trends in *P*:*B* and gross conversion efficiency in Lake Ontario salmonine populations during 1978–1994.



gross conversion efficiency from the late 1970s to the mid-1980s (Fig. 5). The high *P*:*B* (approximately 2.0) and gross conversion efficiency (approximately 0.30) in the early period for coho salmon resulted from both higher growth rates and greater energy density of their primary prey, adult alewife, in Lake Ontario. It is more difficult to infer trends for chinook salmon, given the absence of growth data prior to 1986. Lake trout *P*:*B* and conversion efficiency were generally low compared with the other modeled salmonines (*P*:*B* range 0.6–1.0, gross conversion efficiency range 0.11–0.15). The declining trend in these parameters for this species is also a reflection of increased recruitment of individuals into older, slower growing age-classes. We include a more detailed breakdown of predation and production values for all three salmonines during 1990 by predator age group (Table 1).

We estimated ER during 1990 in Lake Ontario at 13 and 11% on the alewife and rainbow smelt populations, respectively (Table 2). The predation rate, however, was weighted disproportionately toward the adults in the respective prey fish populations. The value for ER was within the range of 1–4% on the YOY and yearling ages groups of alewife and rainbow smelt. Predators consumed a much greater proportion of the available adult prey fish production during 1990 (ER > 100% on adult alewife, 25% on adult rainbow smelt).

TE varied from 5 to 15% and we detected a general pattern of decreasing efficiency with increasing trophic position in Lake Ontario during 1990 (Table 3). In Lake Ontario, TE from phytoplankton to zooplankton was 11.1%. The value for TE from zooplankton to prey fishes was intermediate (8.3%) and the lowest value for TE was computed from prey fishes to piscivores (4.6%) (Table 3), although a much higher TE (14.5%) was estimated when only production rates from the older prey fish age groups (i.e., those vulnerable as prey to salmonines) were included in the computation. Because no direct measures of zooplankton production have been published for Lake Michigan, it was only possible to compute TE from prey fishes to piscivores in this system during 1987. The TE estimate (3.2%) was lower than that estimated for Lake Ontario. If only older prey fish production were included, the resulting value for TE was still very low (4.8%) when compared with the Lake Ontario value.

Table 2. Summary of annual cumulative prey fish production and salmonine predation (wet weight) estimated in Lake Ontario during 1990–1991.

Prey fish age-class	Prey fish production (kt·year^{-1}) Alewife	Smelt	Salmonine predation (kt·year^{-1}) Alewife	Smelt	Prey fish ER Alewife	Smelt
YOY	207.0	10.5	1.5	na	1	na
Yearling	53.9	10.8	1.9	0.1	4	1
Adult	20.3	16.1	33.0	4.0	>100	25
Combined	281.2	37.4	36.4	4.1	13	11

Note: Values for prey fish production were derived using the model of Rand et al. (1995). Salmonine predation accounts for all five dominant species. ER, exploitation rate (salmonine consumption rate, expressed as a percentage of prey fish production rate).

In terms of absolute areal production rates, food web production in Lake Ontario during 1990 was in all cases equal to or greater than comparable trophic groups in Lake Michigan (Table 3). Phytoplankton production in Lake Ontario was 23% higher, YOY prey fish production was >400% higher, and piscivore production was >250% higher. Production rates of older prey fish were comparable in both ecosystems. The value for FWE was markedly higher in Lake Ontario than in Lake Michigan for both prey fish (67% higher) and piscivores (100% higher) (Table 3). However, if only yearling and adult prey fish were included in the FWE calculation, Lake Michigan was found to be more efficient (0.36%) than Lake Ontario (0.29%).

For Lake Ontario during 1990, estimates for zooplankton and prey fish production were higher than those predicted from a particle-size model using a range of literature values for particle-size conversion efficiencies (Table 3). The estimate for zooplankton production was about 3% higher than production predicted assuming a high particle-size conversion efficiency (0.18). Observed production levels for YOY and older prey fish were 32 and 14% higher, respectively, than those predicted using a high particle-size conversion efficiency. Only the value for piscivore production in Lake Ontario fell within the range of predictions from the particle-size model. For Lake Michigan, the estimates for YOY prey fish and piscivore production were within the range of production values predicted using the particle-size model. The estimates of production of older prey fishes exceeded the range predicted by the particle-size model using the high efficiency coefficient (0.18) by 40%, mirroring the results we found in Lake Ontario.

Discussion

Results from these analyses support the hypothesis that recent changes in the pelagic food web in Lake Ontario have caused trends in higher order population processes that indicate

Table 3. Individual sizes (wet), estimated and predicted production (wet), and wet weight biomass transfer efficiencies among and between trophic groups in Lakes Ontario and Michigan.

	Particle size (g)		Estimated production ($g \cdot m^{-2} \cdot year^{-1}$)		Predicted production ($g \cdot m^{-2} \cdot year^{-1}$)		Model accuracy	Efficiencies	
Trophic group	Minimum	Maximum		Source	Low PSCE	High PSCE	(%)	TE	FWE
				Lake Ontario					
Phytoplankton	3.70×10^{-13}	9.70×10^{-8}	1904.7	Sprules et al. 1991					
Zooplankton	9.70×10^{-8}	1.00×10^{-1}	212	Rand et al. 1995	75.2	206.8	2.5	11.1	
YOY prey fish	0.1	4	12	This study	1.3	9	32.4		
Older prey fish	4	208	5.6	This study	0.5	4.9	14.4	8.3	0.92, 0.29[a]
Salmonines	208	6667	0.8	This study	0.2	2.2	*	4.6, 14.5[a]	0.04
				Lake Michigan					
Phytoplankton	3.70×10^{-13}	9.70×10^{-8}	1547	Sprules and Goyke 1994					
Zooplankton	9.70×10^{-8}	1.00×10^{-1}	na		61.1	168	na	na	
YOY prey fish	0.1	4	2.9	Rand et al. 1995	1.1	7.3	*		
Older prey fish	4	208	5.6	Rand et al. 1995	0.4	4	40	na	0.55, 0.36[a]
Salmonines	208	6667	0.3	Stewart and Ibarra 1991	0.1	1.8	*	3.2, 4.8[a]	0.02

Note: In cases where estimated production exceeded the prediction from the particle-size model assuming high particle-size conversion efficiency, we computed a model accuracy rating by expressing the difference in the two values as a percentage. Asterisks were included in the table for cases where estimated production fell within the range of production values predicted using low and high particle-size conversion efficiencies. Efficiencies involving prey fish were calculated by combining YOY and older prey fish production unless otherwise noted. PSCE, particle-size conversion efficiency; TE, trophic efficiency; FWE, food web efficiency; Older, yearling and adult age-classes (see text for further description).

[a] Efficiency computed using only older prey fish production.

increased ecological stress among apex predators in this ecosystem. Both gross conversion efficiency and $P{:}B$ have declined steadily since the late 1970s and early 1980s. Furthermore, declines in prey fish abundance coincident with dramatic increases in salmonine populations appear to have created conditions where prey fish have become limiting to predators. Our results suggest that most production of adult prey fish in Lake Ontario in 1990 was consumed by predators. This suggests a tight coupling between predator and prey that may place salmonines at increased risk.

A number of signs in Lake Ontario indicate fundamental changes in the pelagic food web during recent years. Total phosphorus and algal biomass in the pelagia declined during 1981–1992 (Johengen et al. 1994). Growth and condition of alewife declined markedly during the same time period (Rand et al. 1994; O'Gorman et al. 1997). Observations at the Salmon River Hatchery since 1990 indicate increased age-at-maturity in chinook salmon (D. Bishop, NYDEC, Cortland, N.Y., personal communication). In 1994 in particular, a series of ecological measures indicated a marked change occurring within the food web. Mean size of *Daphnia* was shown to increase significantly during 1994 (Brandt et al. 1996), an indicator that was also observed in Lake Michigan following marked declines in alewife (Wells 1970; Scavia et al. 1986; Evans 1990). Estimates of prey fish biomass from acoustic surveys indicated that prey fish biomass during 1994 was lower than any of the other acoustic surveys conducted since 1991 (C. Schneider, NYDEC, Cape Vincent, N.Y., personal communication). Measures of weight-at-age for chinook and coho salmon in the Salmon River indicated a reduction in growth during 1994 (D. Bishop, NYDEC, Cortland, N.Y., personal communication). The pattern of reductions in growth and shifts in the spawning age distribution to older individuals appears to closely mimic observations made on a comparable hatchery population of chinook salmon in Lake Michigan (Strawberry Creek, Wis., Wisconsin Department of Natural Resources, unpublished data) during the mid-1980s following a decline in alewife lake-wide (see Fig. 1). Although growth appeared to rebound in 1995 in Lake Ontario (D. Bishop, NYDEC, Cortland, N.Y., personal communication), we anticipate conditions similar to those observed in 1994 to become more common in the future. These latter patterns observed in the lake may serve as an important sign that the limit to salmonine production in this ecosystem is being approached.

Trends in gross conversion efficiency and $P{:}B$ reported here for Lake Ontario salmonines closely mirror those observed for Lake Michigan salmonines (Stewart and Ibarra 1991). Chinook salmon in Lake Michigan and coho salmon in Lake Ontario have both experienced dramatic reductions in conversion efficiencies over a period of approximately a decade. The mechanisms, however, appear to be different. In Lake Michigan, chinook salmon exhibited a dramatic shift in prey from large alewife to small alewife and other fish during the mid-1980s (Stewart and Ibarra 1991). This switch in diet translated into reduced conversion efficiency based on an overall reduction of energy density of prey. In Lake Ontario, there is no compelling evidence of diet shifts to less preferred prey items (Rand and Stewart 1998) and the reductions in conversion efficiency reported here were due largely to declining trends in energy density observed in adult alewife (Rand et al. 1994). Values of $P{:}B$ for Lake Michigan salmonines during 1987 (Stewart and Ibarra 1991) were comparable with those estimated in Lake Ontario at the end of our modeled time series.

One potential problem in the bioenergetic model parameterization that may propagate error in our estimates of predation is uncertainty in field activity rates for salmonines. Rowan and Rasmussen (1996) recently reported results from a new technique of estimating in situ activity rates from measures of ^{137}Cs body burdens. These authors concluded that predictions of prey consumption by Lake Michigan salmonines derived by Stewart et al. (1981) and Stewart and Ibarra (1991) may be underestimated by approximately 33% due to greater activity costs for these fish in the field. We made no adjustments to the activity component of the model presented here due to the preliminary nature of these conclusions. Other field studies have shown that these bioenergetic models provide reasonable estimates of prey consumption by salmonines based on comparisons with field data (Beauchamp et al. 1989; Brodeur et al. 1992). We feel that much uncertainty still exists in certain parameters in the model of Rowan and Rasmussen (1996), particularly the assimilation rates, which may vary widely as a function of predator species, temperature, prey quality, or feeding rate. We encourage future researchers to try to reduce uncertainty in quantifying activity costs of salmon in the field. Recent advances in electromyogram telemetry may provide a more direct means for measuring this parameter for salmon in situ (e.g., Hinch et al. 1996).

Another critical uncertainty in this model analysis are the annual survival rates applied to predators in the model. We relied on data from only two cohorts to develop a population model for chinook salmon, and data were completely lacking for coho salmon. We encourage future efforts at reducing uncertainty in this model parameter, given its recognized sensitivity in these applications (see Rand et al. 1993). We did find that our estimated survival rates for hatchery chinook salmon in Lake Ontario (11–14% smolt – spawning adult survival) were similar to those reported for Lake Michigan chinook salmon (Stewart et al. 1981). These values for chinook salmon survival in the Great Lakes are approximately an order of magnitude larger than that reported for wild and hatchery chinook salmon in the Pacific Ocean (1–2% smolt – spawning adult survival: Cross et al. 1991; Bradford 1995). It is not clear what is the cause for this difference, but it may be due to depressed predation rates on juvenile chinook salmon in the Great Lakes relative to the Pacific coast. We presume that a Pacific predator community that has evolved sympatrically with salmon could impart a higher mortality on smolts than the existing predator community in the Great Lakes. The relatively high survival rates for chinook salmon in Lake Ontario have contributed greatly to the dramatic increases in predation and production rates that we report in this paper.

The comparison of TE between Lakes Michigan and Ontario indicated that energy is more efficiently translated through the food web to salmonines in Lake Ontario. Without reliable estimates of zooplankton production in Lake Michigan, it is difficult to ascertain efficiency of energy transfer between primary production and secondary production in that ecosystem. Although absolute rates of production of older prey fishes are similar between the two ecosystems, a much larger amount of energy is shunted to YOY prey fish production in Lake Ontario. Efficiency of energy transfer from phytoplankton to YOY and older prey fish was higher in Lake Ontario (0.92%) than in Lake Michigan (0.55%), largely due to the greater amount of YOY prey fish production occurring in Lake Ontario. This YOY production, however, is occurring in nearshore areas and embayments of Lake Ontario and perhaps should not be considered true pelagic production (Rand et al. 1995). Efficiency of energy transfer from phytoplankton to older prey fish was somewhat higher in Lake Michigan (0.36%) than in Lake Ontario (0.29%), perhaps due to relatively high growth rates and high gross conversion efficiencies for bloater (*Coregonus hoyi*) compared with alewife, as elucidated recently by Rudstam et al. (1994).

The rates of production and efficiency of energy transfer to salmonines appear to be markedly different between the two lake ecosystems. Production of salmonines per unit area in Lake Ontario is 250% greater and FWE (from phytoplankton to salmonines) is over 65% greater than in Lake Michigan. Higher stocking rates and more abundant preferred prey fish in Lake Ontario are likely responsible for higher production rates and trophic efficiencies in that ecosystem. Causes for lower efficiency in Lake Michigan's food web are likely due to the large amounts of energy consumed by deepwater coregonines. Presently, bloater in Lake Michigan form the majority of the prey fish biomass in that ecosystem (Rand et al. 1995). Bloater are generally not preferred as a prey item by salmonines (Stewart and Ibarra 1991) and thus contribute to lower FWE. Particularly striking is the difference between lakes in values of TE between older prey fish production and salmonines. The efficiency value in Lake Ontario (15%) was threefold higher than that estimated for Lake Michigan (5%). Values for TE reported here were generally lower than those reported in marine systems, where values approaching 15% are typical (Sheldon et al. 1977; Iverson 1990; Parsons and Chen 1994; Baumann 1995).

Mason et al. (1995) concluded that Lake Michigan habitat quality for salmonines was somewhat greater than in Lake Ontario, given thermal properties and the densities and spatial configuration of prey fishes. Results from this study suggest that Lake Ontario should exhibit higher salmonine habitat quality than Lake Michigan, given the greater abundance of preferred prey fish and the higher values for TE and FWE estimated in Lake Ontario. Mason et al. (1995) did not account for differences in diet preferences and relied on a simplified representation of salmonine foraging behavior. Precious little data are available to develop a more realistic foraging model that may help rectify this problem. We encourage continued efforts to quantify diet composition in both lakes and conduct studies to investigate adult salmonine foraging behavior under more controlled laboratory conditions (e.g., Savitz and Bardygula 1989). We feel that these efforts will provide a better understanding of foraging behavior and allow us to better predict the extent to which salmonines exploit different species of prey fish. Ultimately, these feeding behaviors need to be incorporated into the model framework of Mason et al. (1995) to provide a more realistic expression of differences in growth rate potentials between the two lake ecosystems.

Results from our comparison of predicted production rates from the particle-size model with production rates estimated from our study and from literature sources suggest that trophic transfer between phytoplankton and prey fish is relatively efficient in both lakes. For Lake Ontario, it appears that biomass transfer is very efficient from phytoplankton to prey fishes, with the best agreement resulting from using the highest particle-size conversion efficiencies found in the literature. We found similar results when trying to predict older prey fish production in Lake Michigan. However, if this high efficiency rating is appropriate between the prey fish and piscivore levels, the particle-size model results suggest that Lake Ontario could support over three times the level of salmonine production extant during 1990. Applying the same assumptions in Lake Michigan, we could claim that the system can support six times the level of salmonine production that was measured during 1987. We caution the reader of the dangers inherent in this application of the model. The approach assumes that the value for the particle-size conversion efficiency is constant over all trophic levels. We are aware of no independent measures of this particle-size conversion efficiency between predators and prey in the pelagic fish community in these ecosystems. In addition, we know from studies of Great Lakes prey fishes that the proportion of the prey fish community vulnerable to salmonine predation can be highly variable. Therefore, we caution the use of this type of model to help set salmon production targets in the Great Lakes, given the degree of uncertainty in model development.

So, what level of salmon production and predation can be sustained in Lake Ontario? To explore this issue of sustainable salmon production, we compare our results with results developed from other fish production studies. Downing and Plante (1993) summarized fish production and *P*:*B* for 38 lakes and 100 fish populations worldwide. These data provide us with an empirical foundation to compare with our results from Lake Ontario. The present study meets all Downing and Plante's (1993) criteria for acceptance except one. Those authors restricted their review to only lakes that did not receive artificial plants. This does provide us, however, with a unique opportunity to compare trophic conditions in Lake Ontario against a backdrop of data from "less managed" lakes.

We predicted 1990 production (kilograms per hectare) of prey fish and salmonines in Lake Ontario using Downing and Plante's (1993) multivariate regression equations assuming (*i*) total phosphorus in the epilimnion = 9 $\mu g \cdot L^{-1}$ (Johengen et al. 1994), (*ii*) mean annual air temperature = 10°C, (*iii*) maximum weight for prey fish = 30 g and maximum weight for a generalized salmonine = 4000 g, and (*iv*) standing crop biomass (during spring) for alewife = 1.88 $kg \cdot ha^{-1}$, rainbow smelt = 0.20 $kg \cdot ha^{-1}$, and salmonines (chinook, coho, and lake trout) = 0.18 $kg \cdot ha^{-1}$. Their model underestimated production rates for alewife (by a factor >20%) and salmonines (by a factor >30%), but appeared to more accurately predict production of rainbow smelt. This suggests that *P*:*B* observed for alewife and salmonines in Lake Ontario is relatively high when compared with other "natural" lakes worldwide. The alewife population in Lake Ontario can be considered exploited by stocked salmonines, and Downing and Plante (1993) speculated that exploited populations are generally more productive (by as much as 70%) when compared with comparable populations in unexploited lakes. This study suggests that intense piscivory by salmonines, on alewife in particular, creates conditions of relatively high *P*:*B* ratios for the alewife population. The rainbow smelt population is exploited to a lesser degree than alewife, which may help explain why Downing and Plante's (1993) model provided a more reasonable fit to the observed production rates for this population. Chinook and coho salmon in particular are responsible for the relatively high *P*:*B* exhibited by the salmonine community. Both species exhibit much higher *P*:*B* (after correcting for maximum body mass) than any fish population reviewed by Downing and Plante (1993).

Downing and Plante (1993) speculated that the sustainable yield of fish from lakes is approximately 10% of community fish production. We estimated "exploitation" rates (our ER) by salmonines in 1990 as 13 and 11% on all age-classes of alewife and rainbow smelt, respectively (Table 1). Although these rates of exploitation appear to approach this criterion of sustainable yield, we caution that all the sexually mature age groups of alewife and rainbow smelt are vulnerable to piscivory and strongly preferred by salmonine predators in the lake. Therefore, because a great majority of the total predation pressure is directed toward the reproductively mature age-classes, recruitment failures may occur in these prey fish populations. The situation appears to be even more extreme in Lake Michigan, where over 50% of the annual production of alewife (all age-classes combined) was estimated to be consumed by predators in 1987 (Brandt et al. 1991). This would help explain why alewife in Lake Michigan have been unable to recover from declines observed during the 1980s.

We must emphasize here that we are focusing on trophic conditions during only one year in each of these ecosystems. It remains unclear how prey fish and predators may respond over time to these trophic conditions. Eby et al. (1995) concluded that lake trout were able to maintain growth rates (and, by inference, feeding rates) across a 100-fold difference in prey densities. This study suggests that the rate of effective search (i.e., slope of feeding rate versus prey density at low prey density) for these predators may be very high. This allows salmonines to maintain relatively high feeding and growth rates, given a highly variable, and sometimes scarce, food supply. The reduction in growth observed for Lake Ontario salmonines during 1994 may provide us with a glimpse of exactly how low prey densities must become before we observe limitations in predator feeding and growth. Hindcasting and forecasting these trophic conditions in the pelagia over an extended time series, similar to the approach used by Jones et al. (1993), may provide a better indication of the extent to which the present food web configuration will persist.

Stocking policy in Lake Ontario has changed as a result of perceived risks of trophic imbalance between predator and prey (Jones et al. 1993). Stocking has been curtailed and predator demand has been reduced by 50% to help achieve a risk-averse strategy for managing the sport fishery (Brandt et al. 1996). We found conflicting results from the two approaches we applied here to assess sustainability of the salmonine community prior to these management actions. Results of the particle-size model suggest that we are underexploiting prey fish in both lakes, which leads to the conclusion that we could increase stocking levels above the lake-wide stocking limit enforced before the recent reduction in predator stocking (Brandt et al. 1996). Our production analysis suggests that during 1990, we may have been at the limit of sustainability or possibly overexploiting the prey base in Lake Ontario. It remains unclear to what extent the policy of reduced stocking of salmon and trout in Lake Ontario may alleviate this perceived imbalance in the trophic pelagic food web.

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