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How Will Decreased Alewife Growth Rates and Salmonid Stocking Affect Sport Fish PCB Concentrations in Lake Ontario?

LELAND J. JACKSON*

Center for Limnology, University of Wisconsin, 680 North Park Street, Madison, Wisconsin 53706

Atmospheric deposition and resuspension from pelagic sediments are the two principal PCB sources to Great Lakes pelagic food webs today. The expansive nature of these sources makes their management and control impractical. Fisheries management, such as the numbers and species of salmonids stocked, represents a potential mechanism by which PCB concentrations in sport fish may be further reduced. I used a simulation model to examine the effect of alewife growth rates, alewife PCB concentrations, and stocking scenarios on sport fish PCB concentrations over the next decade. Eliminating lake trout is predicted to have little effect on growth rates and PCB concentrations of the remaining salmonids. However, eliminating chinook salmon will maximize growth rates of the remaining species and is predicted to lead to a 15% decline in lake trout PCB concentrations. If alewife growth rates decline, sport fish growth rates will also decline, and their PCB concentrations will increase. Reduced salmonid stocking carries the risk that alewife survival may increase, leading to a greater number of older and more contaminated alewife. If the average alewife consumed went from an age class 3+ to a 6+ fish, sport fish PCB concentrations are predicted to increase by 40% (lake trout) to 60% (chinook salmon and steelhead). Thus, prey PCB concentrations are likely to play a more important role than salmonid growth rates in determining salmonid PCB concentrations.

Introduction

Polychlorinated biphenyl (PCB) cleanup and control of their inputs are central to policies designed to restore the Great Lakes (*1*). There has been substantial progress made in reducing point source inputs, yet among Great Lakes contaminants PCBs rank second in risk (*2*) because they are abundant, persistent, and bioaccumulate. PCB concentrations in Great Lakes fishes have declined markedly since PCB manufacture and use was banned in the mid-1970s (*3*), and concentrations may be approaching constant levels (*4*). However, contaminants may interfere with reproduction and restoration of fish and wildlife (*5*). Contaminants therefore continue to raise concern for fish, wildlife, and indeed humans who consume Great Lakes fish (*6*−*8*).

The two principal sources of PCBs to the Great Lakes today are atmospheric deposition and resuspension from pelagic sediments (*9*, *10*). The expansive nature of these sources makes their management and control impractical. Current contaminant hot spots are scheduled for remedial action, but the largest point source reductions have likely been achieved. PCB loading to pelagic food webs might not experience further declines over the next few decades. The Great Lakes Sport Fish Consumption Advisory Task Force (*11*) has proposed an action level of 0.5 mg kg^{-1}. If adopted, public concern would heighten and pressure would be placed on managers to further reduce sport fish contaminant concentrations because many salmonids would exceed this consumption guideline.

Fisheries management (e.g., species and numbers of salmonids stocked) represents a mechanism by which sport fish PCB concentrations might be further reduced. Salmonid stocking affects forage fish contaminant dynamics because predation by stocked salmonids influences forage fish size structure and growth rates. Trophic transfer is the major pathway for organochlorine contaminant accumulation in fishes (*12*−*17*). Forage fish responses feedback to affect salmonid diets, growth rates, and their contaminant concentrations. Therefore, changes in the lake that alter forage fish growth rates or standing stocks, such as changes in phosphorus (P) loading, shunting of P cycling to the benthos by zebra mussels, etc., will also affect sport fish PCB concentrations.

Salmonid species composition is primarily determined by stocking because rates of successful natural reproduction are low (*18*). The heavy reliance of salmonid recruitment on hatchery plantings therefore represents a potential opportunity to affect predator−prey interactions in Great Lakes food webs and possibly even PCB concentrations in fishes. Stocking cuts have been implimented in Lake Ontario (*19*), and selective stocking of salmonids has been suggested as one mechanism by which sport fish PCB concentrations may be further reduced (*20*). Alewife growth rates may be further reduced by changes in land use practices, invasion by nonedible zooplankton, or shunting of nutrient cycling to the benthos by zebra mussels. In this paper, I use a simulation model to evaluate the changes in PCB concentrations of sport fish that might occur as the result of (1) discontinuation of stocking of selected salmonids assuming no change in the maximum age of alewife, (2) decreases in alewife growth rates that might arise from reductions in phosphorous loading or related factors, and (3) increases in alewife PCB concentrations if reduced stocking results in increased alewife age.

Model Description

The model is a six-species coupled ordinary differential equation model representing a simplified Lake Ontario pelagic food web. Model calibration was performed with data from 1971 to 1994. The forage species (alewife, *Alosa*

* Corresponding author telephone: (608) 262-3088; fax: (608) 265-2340; e-mail address: jackson@limnosun.limnology.wisc.edu.

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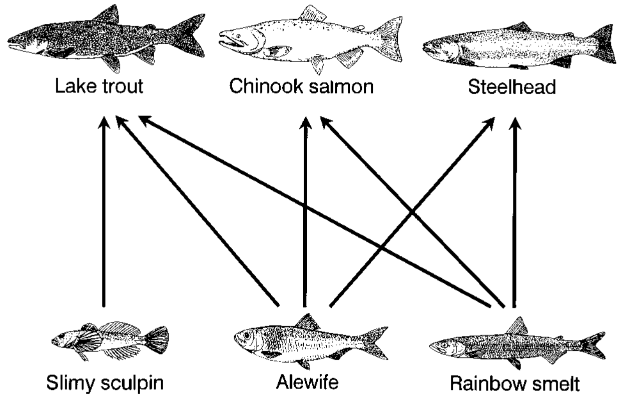

FIGURE 1. Conceptual model illustrating the trophic relationships of a simplified Lake Ontario pelagic food web. Arrows represent the flow of carbon and PCBs.

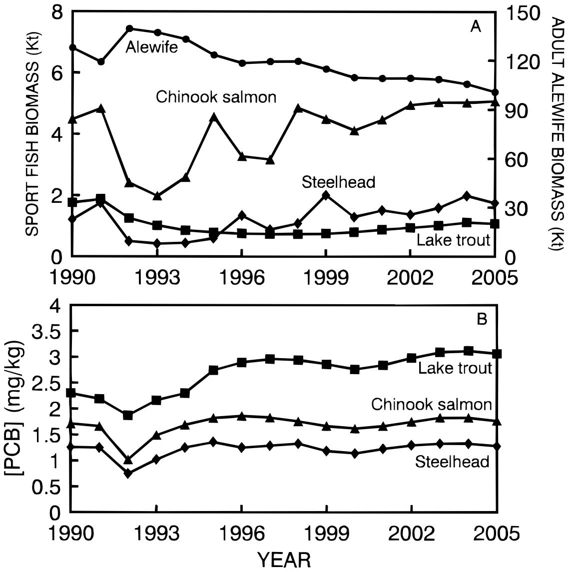

FIGURE 2. Baseline conditions of (A) biomass and (B) PCB concentrations for the average age class 4+ individual of three stocked sport fish and alewife, their principal forage. 1994 stocking rates and lake productivity have been assumed through the simulation.

psuedoharengus; rainbow smelt, *Osmerus mordax*; slimy sculpin, *Cottus cognatus*), stocked sport fish (chinook salmon, *Oncorhynchus tshawytscha*; steelhead, *O. mykiss*; lake trout, *Salvelinus namaycush*), and their trophic interactions are illustrated in Figure 1. Coho salmon (*O. kisutch*) and brown trout (*Salmo trutta*) predation on the forage fishes was included as their long-term averages. A detailed description of the model, including parameters and their values, calibration, and sensitivity analysis, is presented elsewhere (*21*). Below, I present a summarized description of the species dynamics.

The change in prey biomass was the net difference between growth and loss due to natural mortality and predation by stocked salmonids. Recruitment of alewife and smelt was described by a Shepherd (*22*) stock-recruitment function. Growth was made density dependent with a logistic formulation. Losses due to predation were described by a ratio-dependent functional response that allowed switching between alternative prey (*23*). Sculpins were included as fixed numbers and biomass because bottom trawls are not thought to provide reliable indices of their abundance due to low trawl efficiency (*18*).

The change in stocked sport fish biomass was the net difference between growth due to predation and loss terms due to natural mortality, attacks by sea lamprey (*Petromyzon marinus*), and harvest by anglers. Consumed prey was converted to predator biomass with growth efficiencies determined by bioenergetics (*24*). Natural mortality has been previously described (*18*), and lamprey attacks and harvest by anglers were consistent with estimates from creel surveys (*18*).

Dietary exposure of PCBs was considered to be the principal route of accumulation for the salmonids (*12–17*). PCB uptake was a function of the type and amount of prey consumed, prey PCB concentrations, and net dietary PCB assimilation efficiencies for each species. Smelt and sculpin PCB concentrations were taken from contaminant survey data (*25*). Empirical measures of alewife PCB concentrations were only available for the early 1970s (*13*) and early 1990s (average value 0.43 mg kg^{-1} fresh wt; D. M. Whittle, Fisheries and Oceans Canada, Burlington, Ontario, unpublished data). Alewife PCB concentrations between 1975 and 1990 were estimated by determining the concentrations necessary to lead to a time trend measured in lake trout (*15*).

Stocking cuts implemented between 1991 and 1994 may reduce salmonid predation and thereby increase survival of older age classes of alewife and their PCB concentrations too. In the Lake Ontario model, the oldest alewives were assumed to be about 3.5 years old. To examine the potential result of the forage base containing older, more contaminated alewives, I estimated PCB concentrations of age classes 4+, 5+, and 6+ fish with an alewife PCB accumulation model for Lake Michigan (*26*) calibrated to growth and PCB concentrations of Lake Ontario alewives.

The model was used to make projections of selected scenarios of PCB and biomass dynamics for the Lake Ontario pelagic food web. One scenario evaluated changes in growth rates of alewife, the principal forage species of all stocked salmonids in Lake Ontario. Additional scenarios considered the complete removal of either lake trout or chinook salmon and increases in alewife PCB concentrations that might arise from increased survival, given recent cuts in stocking.

Results

Baseline Conditions. Baseline conditions represent projections for the next decade (to year 2005) with the model calibrated to 1994, and it is these conditions to which the scenarios of change will be contrasted. Stocked sport fish biomass decreases between 1990 and 1995. This corresponds to cuts in stocking rates (*19*) that have already been implemented (28%, 12%, and 14% in 1992, 1993, and 1994, respectively). By 2005, sport fish biomass was ca. 5.07, 1.07, and 1.75 Kt for chinook salmon, lake trout, and steelhead, respectively (Figure 2A). Between 1992 and 2005, adult alewife biomass decreased from 140 to 100 Kt. PCB concentrations of age class 4+ sport fish are predicted to be 1.77, 3.06, and 1.28 mg kg^{-1} for chinook salmon, lake trout, and steelhead, respectively (Figure 2B).

Simulation Scenarios. Eliminating stocking of chinook salmon is predicted to increase the biomass of adult alewife by 25% by 2005 (Table 1, section A). Lake trout and steelhead biomass would also increase, albeit modestly, by 6–8%. There would be a slight decrease in lake trout and steelhead PCB concentrations as they experience dilution of their PCB concentrations due to increased growth rates.

TABLE 1

Lake Ontario Model Predictions (Year 2005) of Biomass and PCB Concentrations (mg kg^{-1}) for Sport Fish with (Section A) Stocking Cuts and (Section B) Reductions in Alewife Growth Rates

species	biomass (kt)	% change from baseline	PCB concn	% change from baseline
Section A: Species Eliminated from Stocking Program				
Chinook Salmon Not Stocked				
alewife	126.29	+25.3		
lake trout	1.16	+8.4	2.98	−2.6
steelhead	1.85	+5.7	1.27	−0.8
Lake Trout Not Stocked				
alewife	103.12	+2.3		
chinook salmon	5.13	+1.2	1.76	+0.6
steelhead	1.77	+1.1	1.28	0.0
Section B: Decreased Alewife Growth Rates				
10% Reduction in Alewife Growth Rates				
alewife	88.20	−12.5		
chinook salmon	4.85	−4.4	1.77	0.0
lake trout	1.02	−4.7	3.12	+0.2
steelhead	1.71	−2.3	1.28	0.0
20% Reduction in Alewife Growth Rates				
alewife	70.38	−30.2		
chinook salmon	4.46	−12.3	1.78	+0.6
lake trout	0.93	−13.1	3.22	+5.2
steelhead	1.62	−7.4	1.28	0.0
30% Reduction in Alewife Growth Rates				
alewife	43.13	−57.2		
chinook salmon	3.68	−27.4	1.81	+2.3
lake trout	0.76	−29.0	3.50	+14.4
steelhead	1.43	−18.3	1.29	+0.8

Eliminating lake trout would have a small effect on the remaining species. Alewife are predicted to increase their biomass by only 2%, and chinook salmon and lake trout would increase by less than 1% (Table 1, section A). Changes in sport fish PCB concentrations would not be detected.

Reductions in alewife growth rates are predicted to affect alewife and sport fish biomass. The predicted decrease in alewife biomass is not proportional to the reduction in their growth rate; for example, alewife biomass is about 5-fold more reduced at 30% than at 10% decreased growth rates (Table 1, section B). Lake trout biomass is strongly affected by decreasing alewife growth rates as lake trout biomass is reduced by ca. 5% with a 10% alewife growth rate reduction, but by almost 30% with a 30% alewife growth rate reduction. Chinook salmon and steelhead are also affected by the highest reduced alewife growth rate scenario, but to a lesser degree than lake trout. Lake trout PCB concentrations are predicted to increase substantially (Table 1, section B) as a result of their much reduced growth when alewife decline. Chinook salmon and steelhead PCB concentrations are also predicted to rise, but to a lesser degree than for the lake trout (Table 1, section B).

Sport fish PCB concentrations are predicted to increase if the recent cuts in salmonid stocking lead to increased survival of older age classes of alewife. For example, if the average alewife eaten changed from a 3+ to a 4+ individual, the model predicts that sport fish PCB concentrations would increase by 14% (lake trout) to 20% (chinook salmon and steelhead). If alewife survival increases and the average age class eaten was a 6+ fish, then the increases in PCB concentrations are predicted to range from 40% for lake trout to 60% for chinook salmon and steelhead (Table 2).

TABLE 2

PCB Concentrations of Alewives If Average Individual Eaten Changed from Age Class 3+ to 6+ and Resulting Sport Fish PCB Concentrations Corresponding to the Increase in Alewife Age Structure[a]

alewife		sport fish PCB (mg kg^{-1})		
age class	PCB (mg kg^{-1})	chinook salmon	lake trout	steelhead
3+	0.42	1.77	3.06	1.28
4+	0.55	2.12	3.49	1.54
5+	0.67	2.48	3.93	1.81
6+	0.79	2.84	4.36	2.07

[a] PCB concentrations of alewives were estimated with a Lake Michigan alewife PCB accumulation model (*26*) calibrated to Lake Ontario. Sport fish PCB concentrations are for age class 4+ individuals.

Discussion

Baseline Conditions. The baseline conditions illustrate that, for a given age class, lake trout are predicted to be the most contaminated and steelhead are predicted to be the least contaminated of the sport fish examined. This is consistent with their ratio of PCB assimilation efficiency to gross growth efficiency, i.e., lake trout have the highest ratios and steelhead have the lowest ratios. Lake trout age 4+ and older are predicted to exceed the current FDA consumption advisory of 2 mg kg^{-1} at 1994 target stocking rates and lake productivity.

Simulation Scenarios. Reductions in alewife growth rates are predicted to affect alewife and sport fish biomass. The larger effect on alewife biomass with decreasing alewife growth rates is the result of proportionately more predation by the salmonids with reduced alewife growth. The model therefore predicts that prey availability would have to drop to much lower levels than in the current simulations before prey availability would control the amount of predation. Lake trout biomass is strongly affected by decreasing alewife growth rates. For example, lake trout biomass is reduced by ca. 5% with a 10% alewife growth rate reduction, but by almost 30% with a 30% alewife growth rate reduction. Chinook salmon and steelhead are also affected by the highest reduced alewife growth rate scenario, but to a lesser degree than lake trout. Lake trout PCB concentrations are predicted to increase substantially (Table 1, section B) as a result of their much reduced growth when alewife decline coupled to some switching to the more contaminated alternative forage.

Alewife increased their biomass by 25% when chinook salmon were not stocked, indicating that the alewife are experiencing heavy predation by chinook salmon. In contrast, the weaker response of alewife (and chinook salmon and steelhead) to the removal of lake trout indicates that the lake trout demand on alewife is much lower than that of chinook salmon or steelhead. Although the total number of lake trout stocked at 1994 GLFC target levels exceeds 1 million, lake trout grow relatively slowly (10 years to reach 5.2 kg of body mass). The net result is that the Lake Ontario pelagic food web will most likely continue to be controlled primarily by the stocking of chinook salmon because their biomass accounts for most of the piscivory, and predator demand is completely controlled by the numbers and species of fish stocked. Regardless of whether chinook salmon or lake trout were eliminated from the stocking program, the small increases in PCB concentrations predicted in the remaining sport fish would be difficult to measure given the variability of PCB concentrations typically encountered in the Great Lakes' salmonid populations (*13, 27*).

Lower alewife growth rates are predicted to affect lake trout PCB concentrations more than concentrations in chinook salmon or steelhead. Continued reductions in P loading to Lake Ontario have been hypothesized to result in decreases in growth rates of fish at all levels of the pelagic food web (*28−30*). The greater effect on lake trout is consistent with their lower growth rate and higher PCB assimilation efficiency. It is also probable that with reductions in alewife productivity the alternative forage, smelt and sculpin, will experience heavier predation, thereby decreasing prey resources for fish that rely on these forage fish (e.g., young lake trout, *31*). As predator growth rates drop, the average size for a given age class will also drop. However, PCB concentrations are predicted to increase because respiratory costs become a larger component of the carbon budget, but PCB inputs continue to be directly related to consumption.

If the stocking cuts implemented between 1991 and 1994 lead to increased survival of alewife, then Lake Ontario's sport fish are predicted to experience increases in their PCB concentrations. Sport fish selectively seek the largest prey individuals (*32*). Increased survival of alewife resulting from decreased predation will likely increase the size and the age of the average forage fish consumed. Even a 2-year increase in the average age class consumed would lead to increases in sport fish concentrations of ca. 30−40%. This is a much larger change in sport fish concentrations than predicted for the changes in biomass where forage PCB concentrations were assumed to be static. It appears therefore that changes in prey PCB concentrations are likely to have a greater impact on sport fish PCB concentrations than sport fish growth rates. The smaller predicted change in lake trout PCB concentration results from their lower consumption of alewife compared to chinook salmon and steelhead.

Implications for Fisheries Management. Fisheries management could potentially alter PCB concentrations by affecting predator−prey interactions, carbon flow, and therefore PCB flow. In Lake Ontario differences in sport fish PCB concentrations are related to species physiology and behavior (PCB and carbon assimilation efficiencies, preferred temperatures, etc.). Diet PCB concentrations may play a smaller role in determining the average salmonid PCB concentration because all salmonids rely heavily on alewife as their primary forage and selectively seek the largest forage individuals (*32*). PCB concentrations have been shown to be nearly constant in smelt and sculpin (*25*), and this may also be true for Lake Ontario alewife, just as it is for Lake Michigan alewife (*4*). However, if salmonid predation is reduced to a level that allows alewife growth and survival to increase, then the alewife forage base should contain more older, larger, and more contaminated individuals than assumed in the simulations where only salmonid growth changed. If this happens, prey concentrations will play a greater role in the response of the salmonids. In fact, increased alewife growth and survival and consumption of those older individuals were hypothesized as a potential cause of the increase in age 4+ lake trout PCB concentrations between 1982 and 1984 (*15*).

The interaction between stocking, predation on the forage base, and alewife size and contaminant characteristics on one hand and the feedback of forage fish characteristics on salmonid growth and PCB concentrations on the other hand leads to an interesting management situation. Stocking fewer salmonids will likely lead to growth and sustainability of the alewife population. The population should contain greater numbers of older adults that can provide strong recruitment events, a good forage base for the salmonids, and therefore high salmonid growth rates. However, the average forage fish consumed will have higher PCB concentrations than under a poor forage fish growth scenario. Alternatively, stocking many salmonids generates high levels of predation that poses the risk of culling the alewife population to many pre-reproductive individuals. Low forage availability will decrease salmonid growth rates. The simulation I have performed indicates that prey PCB concentrations are more important than predator growth rates in determining predator PCB concentrations. Hence, it appears that managing the Lake Ontario pelagic fishery for salmonid growth and sustainability would not also manage the lake for minimal sport fish PCB concentrations. Clearly, reaching an optimum balance between salmonid growth rates and PCB concentrations would be a major challenge and would require the ability to accurately measure predator and prey biomass and to implement management options in a timely manner.

Preserving lake trout seems incompatible with managing the fishery for PCB concentrations because lake trout have unacceptably high PCB concentrations for human consumption. Under every scenario examined, age 4+ and older lake trout exceeded the FDA consumption guideline of 2 mg kg^{-1} total PCB. Thus, with the PCB concentrations of the lake trout's forage, it seems unlikely that any management action will reduce lake trout PCB concentrations (for 4+ and older fish) below the FDA consumption advisory. Managers therefore will have to weigh the costs of having lake trout that are considered unfit for human consumption, and presumably unfit for wildlife consumption too, with the benefits of having the lake trout contribute to the biodiversity of Lake Ontario.

Stocking steelhead presents a different set of considerations for lake managers. Steelhead PCB concentrations are consistently lower for a given size than for similar size chinook salmon or lake trout. The model predicts that the average steelhead should contain PCBs below the 2 mg kg^{-1} FDA action level under the range of scenarios explored. Steelhead exhibit the most natural recruitment per number stocked (but are not currently totally self-sustaining in the absence of hatchery plantings) and therefore might offer the best promise to become a self-sustaining species in Lake Ontario.

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Literature Cited

(1) National Research Council. *Restoration of Aquatic Ecosystems*; National Academy Press: Washington, DC, 1992.
(2) Bicknell, D. J. *Water Environ. Technol.* **1992**, *4*, 50−55.
(3) Hesselberg, R. J.; Hickey, J. P.; Nortrup, D. A.; Willford, W. A. *J. Great Lakes Res.* **1990**, *16*, 121−129.
(4) Stow, C. A.; Carpenter, S. R.; Eby, L. A.; Amrhein, J. F.; Hesselberg, R. J. *Ecol. Appl.* **1995**, *5*, 248−260.
(5) Kubiak, T. J.; Harris, H. J.; Smith, L. M.; Swartz, T. R.; Stalling, D. L.; Trick, J. A.; Sileo, L.; Doherty, D. E.; Erdman, T. C. *Arch. Environ. Contam. Toxicol.* **1989**, *18*, 706−727.
(6) Jacobson, J. L.; Fein, G. G.; Jacobson, J. L. Schwartz, P. M.; Dowler, J. K. *Child Dev.* **1985**, *56*, 853−860.
(7) Dar, E.; Kanarek, M. S.; Anderson, H. A.; Sonzogni, W. C. *Environ. Res.* **1992**, *59*, 189−201.
(8) Fiore, B. J.; Anderson, H. A.; Hanrahau, L. P.; Olsen, L. J.; Sonzogni, W. C. *Arch. Environ. Health* **1985**, *44*, 82−88.
(9) Sweet, C. W.; Murphy, T. J.; Bannasch, J. H.; Kelsey, C. A.; Hong, J. *J. Great Lakes Res.* **1993**, *19*, 109−128.
(10) Hermanson, M. H.; Christensen, E. R.; Buser, D. J.; Chen, L. M. *J. Great Lakes Res.* **1991**, *17*, 94−108.
(11) Anderson, H. A.; Amrhein, J. F.; Shubat, P.; Hesse, J. *Protocol for a uniform Great Lakes sport fish consumption advisory*; Great Lakes Sport Fish Advisory Task Force: 1993; 81 pp.
(12) Thomann, R. V.; Connolly, J. P. *Environ. Sci. Technol.* **1984**, *18*, 67−71.
(13) Rowan, D. J.; Rasmussen, J. B. *J. Great Lakes Res.* **1992**, *18*, 724−741.
(14) Rasmussen, J. B.; Rowan, D. J.; Lean, D. R. S.; Carey, J. H. *Can. J. Fish. Aquat. Sci.* **1990**, *47*, 2030−2038.
(15) Borgmann, U.; Whittle, D. M. *J. Great Lakes Res.* **1991**, *17*, 368−381.
(16) Gobas, F. A. P. C.; Zhang, X.; Wells, R. *Environ. Sci. Technol.* **1993**, *27*, 2855−2863.
(17) Madenjian, C. P.; Carpenter, S. R.; Eck, G. W.; Miller, M. A. *Can. J. Fish. Aquat. Sci.* **1993**, *50*, 97−109.
(18) Jones, M. L.; Koonce, J. F.; O'Gorman, R. *Trans. Am. Fish. Soc.* **1993**, *122*, 1002−1018.
(19) Great Lakes Fishery Commission. *Lake Ontario Fisheries Unit 1993 Annual Report*; 1994; 592 pp.
(20) Stow, C. A.; Carpenter, S. R., Madenjian, C. P.; Eby, L. A.; Jackson, L. J. *Bioscience* **1995**, *45*, 752−758.
(21) Jackson, L. J. *Ecol. Modell.*, in press.
(22) Shepherd, J. G. *J. Cons. Cons. Int. Explor. Mer* **1982**, *40*, 67−75.
(23) DeAngelis, D. L., Goldstein, R. A., O'Neill, R. V. *Ecology* **1975**, *56*, 881−892.
(24) Hewett, S. W.; Johnson, B. L. *Fish Bioenergetics Model 2*; UW Sea Grant Technical Report No. WIS-SG-92-250; 1992; 79 pp.
(25) Borgmann, U.; Whittle, D. M. *J. Great Lakes Res.* **1992**, *18*, 298−308.
(26) Jackson, L. J.; Carpenter, S. R. *J. Great Lakes Res.* **1995**, *21*, 112−120.
(27) Madenjian, C. P.; Carpenter, S. R.; Rand, P. S. *Can. J. Fish. Aquat. Sci.* **1994**, *51*, 800−807.
(28) Borgmann, U.; Whittle, D. M. *Can. J. Fish. Aquat. Sci.* **1993**, *51*, 693−700.
(29) Borgmann, U.; Shear, H.; Moore, J. *Can. J. Fish. Aquat. Sci.* **1984**, *41*, 1303−1309.
(30) Mills, E. L.; O'Gorman, R.; DeGisi, J.; Heberger, R. F.; House, R. A. *Can. J. Fish. Aquat. Sci.* **1992**, *49*, 2009−2019.
(31) Elrod, J. H.; O'Gorman, R. *Trans. Am. Fish. Soc.* **1991**, *120*, 290−302.
(32) Stewart, D. J.; Ibarra, M. *Can. J. Fish. Aquat. Sci.* **1991**, *48*, 909−922.

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