

Modeling Steelhead Population Energetics in Lakes Michigan and Ontario

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Abstract.—We developed a bioenergetics model for steelhead *Oncorhynchus mykiss* that simulates growth and consumption by separate life history forms in Lakes Michigan and Ontario. We estimated abundances of hatchery and wild smolts during 1975–1990 for both lakes based on stocking rates, survival schedules, and discrimination of the proportion of the lake population that was naturally recruited. Recruitment of wild steelhead varied as a function of presmolt winter severity in both lakes. Wild smolts accounted for 6–44% (during 1982–1989) and 18–33% (during 1978–1985) of total annual smolt production in Lakes Michigan and Ontario, respectively. We developed an age-structured population model with separate accounting for run timing (summer, fall, and spring) using the proportions of life history stages observed at weirs and estimated adult survival rates. We summarized data on growth, diet, water temperature, and energy contents of predator and prey to model lakewide prey consumption in both lakes during 1975–1990. Lakewide prey consumption by steelhead amounted to 9,500 tonnes·year⁻¹ in 1987 in Lake Michigan and 2,200 tonnes·year⁻¹ in 1990 in Lake Ontario. Because of their limited dietary reliance on alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax* and relatively low stocking density compared with other salmonines, steelhead consumed only 4% of available alewife production and 2% of total smelt production in 1987 in Lake Michigan. Although estimates of alewife production in Lake Ontario are presently unavailable, measures of alewife biomass in 1990 in Lake Ontario indicate that steelhead probably had a negligible effect on these prey fish. Steelhead consumed only 2% of total rainbow smelt production in Lake Ontario in 1990. Population biomass conversion efficiency (16.1%) and production-to-biomass ratio (mean, 1.18) for Lake Michigan steelhead are low compared with those of sympatric *Oncorhynchus* species. Sensitivity analysis of the population submodel indicated that the most sensitive parameters were lake survival and size at stocking.

Fishery managers throughout the Great Lakes basin have become increasingly concerned with the potential predator–prey imbalance that could result from overstocking of hatchery fish. The hypothesis that salmonine prey demand may exceed prey fish supply has been tested by various investigators with bioenergetics modeling (e.g., Stewart et al. 1981; Brandt et al. 1991; Stewart and Ibarra 1991). To derive more accurate estimates of total predation and production by the salmonine predators in the Great Lakes, a need exists to broaden the analysis to include steelhead *Oncorhynchus mykiss* and brown trout *Salmo trutta*. Due to lim-

ited data at the time, Stewart and Ibarra (1991) and Brandt et al. (1991) approximated steelhead and brown trout predation in Lake Michigan by first estimating yearling equivalents as 41.7% of the previous year's stocked fall fingerlings based on survival estimates for Lake Ontario lake trout *Salvelinus namaycush* (Elrod et al. 1988). They then assumed that predation by an individual yearling equivalent (including stocked yearlings and surviving stocked fall fingerlings) was approximately equal to the average consumption estimated for yearling lake trout, coho salmon *Oncorhynchus kisutch*, and chinook salmon *O.*

tshawytscha. This approach may be inaccurate given the differences in physiology, life history, and diet of steelhead and brown trout. The life history of Great Lakes brown trout remains poorly understood, but recent analyses of steelhead life history, energetics, and diet allow a more accurate assessment of steelhead predation and production in the Great Lakes.

Steelhead, first introduced into watersheds of the eastern United States in the late 1800s, now have become relatively abundant and contribute importantly to the highly valued sport fishery in all five of the Laurentian Great Lakes. Although extensively stocked throughout the Great Lakes, many wild populations have become established. Steelhead life history is complex, characterized by variable timing of spawning runs, repeat spawning, a diverse diet, and relatively broad habitat requirements (Biette et al. 1981).

There have been some attempts to simulate growth of rainbow trout (nonanadromous *O. mykiss*) with bioenergetic models. From and Rasmussen (1984) developed a growth model suitable for aquaculture based on aquarium experiments with juvenile rainbow trout fed pellet food. Serchuk et al. (1980) developed a general rainbow trout model based primarily on life history data from the Finger Lakes of New York (Hartman 1959) and a physiological growth model for sockeye salmon *Oncorhynchus nerka* (Brett et al. 1969). The model included growth from egg to adult and predicted annual recruitment based on a size-fecundity relationship and egg-to-adult survival schedules. Serchuk et al. (1980) used the model to solve an energy balance equation for growth of an average individual in an age- and sex-category matrix as a function of fish size, water temperature, and ration level. We feel the development of a new model of steelhead energetics is warranted given the recent advances in bioenergetics modeling techniques and our growing understanding of the energetics and life history of steelhead in the Great Lakes.

Our primary interest was to estimate whole-lake prey consumption by the steelhead population. Predicting ration level based on food density and water temperature (Serchuk et al. 1980) is fraught with uncertainty as a result of our limited understanding of salmonine foraging behavior and the difficulty of acquiring extensive data on available prey, although Goyke and Brandt (1993, this issue) are making progress in this area. Solving an energy balance equation for consumption allows ration levels to be constrained by observed growth

endpoints (Kitchell et al. 1977; Bartell et al. 1986). This modeling approach has been validated for several piscivores (e.g., Rice and Cochran 1984; Beauchamp et al. 1989; Brodeur et al. 1992) and is generally simpler than estimating daily ration from field studies due to the difficulty and expense of obtaining adequate sample sizes. In addition, steelhead feed intermittently throughout the day (e.g., Bisson 1978; Kelso and Kwain 1984) and consume large prey items that require long digestion times. This foraging behavior further complicates an empirical estimate of ration based on diel periodic sampling (Tyler 1970; Persson 1979; Cochran and Adelman 1982). Finally, with sufficient data on hatchery planting and wild smolt production into the Great Lakes, it was unnecessary to include the uncertainty of predicting egg-to-smolt survival rates as attempted by Serchuk et al. (1980).

Our primary objectives in this study were to develop a population energetics model of steelhead to estimate monthly prey consumption in Lake Michigan in 1987 and Lake Ontario in 1990 in comparison with available measures of prey fish biomass and production, and to compare steelhead predation with estimates of predation by sympatric salmonines. In addition, we estimated annual cumulative predation by steelhead in both lakes during 1975–1990. In this paper, we (1) summarize the available data on steelhead energetics and build an energy balance model for the average individual, (2) reconstruct the history of steelhead stocking in both lakes and estimate hatchery-smolt equivalents from 1975 to 1990 using a presmolt survival model, (3) estimate the yield of wild steelhead smolts from 1975 to 1990 in both lakes, (4) build a postsmolt, age-structured population model for the steelhead populations to estimate lake-wide abundances of adult fish, and (5) summarize appropriate lake-specific data used to implement the population energetics model.

Methods

We reviewed the pertinent literature on rainbow trout and steelhead physiology and energetics and integrated the information into an energy balance model for the average individual. Because several strains of steelhead have been introduced into the Great Lakes and the life history of steelhead is complex, we identified and explicitly modeled the most common life history forms. We use the term "life history form" to distinguish between individuals in a population that exhibit different eco-

logical characteristics such as run timing, spawning schedules, or growth patterns.

For the life history analysis, we relied principally on recent studies of wild steelhead biology in the Little Manistee River, Michigan (Seelbach 1993), and the Ganaraska River, Ontario (Karges 1987). The Little Manistee River is a low-gradient tributary with stable flow in central Michigan, and it typifies the highly productive steelhead rivers found in that region; it drains to Lake Michigan. The Ganaraska River, approximately 100 km east of Toronto, is a smaller river system in a watershed dominated by agriculture; it drains to Lake Ontario at Port Hope, and it is a good representative of the smolt-producing tributaries in that lake basin. We also drew from the comprehensive summary of Great Lakes steelhead life history by Biette et al. (1981 and references therein) and gained additional information through contacts with fishery managers throughout the two basins. Finally, to implement the population energetics model, we summarized data on lake-specific parameters to reflect the growth conditions for steelhead in the two lakes. These parameters include growth rate, diet, energy density of predator and prey, and water temperature.

Figure 1 shows the population energetics model diagrammatically. The major forcing functions of the model were hatchery and wild smolt inputs to a population model that accounted for numerical abundance based on three components of total mortality: poststocking, smolt-to-maiden spawning adult, and repeat spawning. Growth of and consumption by the average individual in each life history form (represented in Figure 1 by the consumer symbol of Odum 1983) were simulated with a bioenergetics model.

Energetics Model for the Average Individual

The model used in this analysis was based on the following energy balance equation solved on a daily time step for the average individual in the population (as in Kitchell 1983; Ney 1990):

$$G = C - (R_{\text{opt}} + R_{\text{sda}} + F + U);$$

G = growth, C = consumption, R_{opt} = optimal metabolism, including standard metabolism and an activity multiplier based on volitional swimming speed, R_{sda} = specific dynamic action, F = egestion, and U = excretion. Units were expressed in the model both in terms of wet weight (g) or energy equivalents (J). Details of the modeling approach were discussed by Stewart et al. (1983) and

Hewett and Johnson (1992). Our intent was to develop an energetics model that could be applied to all of the observed life history forms of steelhead. Consumption estimates for each life history form vary only with differences in diet, growth inputs, population abundance, and thermal history. Parameters used in the energetics model are listed in Table 1.

Consumption.—Because the bioenergetics model fits a growth trajectory between observed weights at age based on a constant proportion of maximum consumption (Hewett and Johnson 1992), we defined a mathematical relationship for weight and temperature dependences of food consumption. From and Rasmussen (1984) presented data on maximum consumption of rainbow trout at five water temperatures (5, 10, 15, 20, and 22°C). The highest rates of feeding in the study occurred at 20°C. We regressed maximum consumption against fish weight at 20°C from data that appear in their Appendix 1 and generated the following best-fit equation:

$$C_{\text{max}} = 0.184 \cdot W^{-0.30}, \quad (1)$$

C_{max} = maximum consumption ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) and W = fish wet weight (g) ($r^2 = 0.63$, $N = 8$). Use of equation (1) in preliminary simulations required steelhead to significantly exceed C_{max} to achieve the growth rates observed in Lake Michigan. Beauchamp et al. (1989) encountered this problem with sockeye salmon and concluded that either the intercept was too low or the slope coefficient was too large a negative value. Beauchamp et al. (1989) based their original analysis on a study by Brett (1971) who, like From and Rasmussen (1984), conducted feeding experiments in the laboratory using pellet food. Sensory cues for gut fullness may differ significantly between a diet of pellets and natural foods that fish encounter in the wild. We contend that fish fed meals of low-moisture, energy-rich pellets become satiated at lower levels of gut fullness than fish fed natural foods of higher water content and lower caloric density. To try to correct for this problem, we converted total calories consumed in the pellet diet (at 3,143 $\text{cal} \cdot \text{g}^{-1}$, wet weight, as reported in From and Rasmussen 1984) into a mass of some composite of natural prey (at 1,000 $\text{cal} \cdot \text{g}^{-1}$, wet weight) that provided an equivalent caloric intake. We multiplied the intercept in equation (1) by 3.143 to arrive at a corrected intercept value of 0.628. Although the computed slope value (-0.30) in equation (1) is comparable to other published values for salmonines (sockeye salmon, -0.35 ; Brett

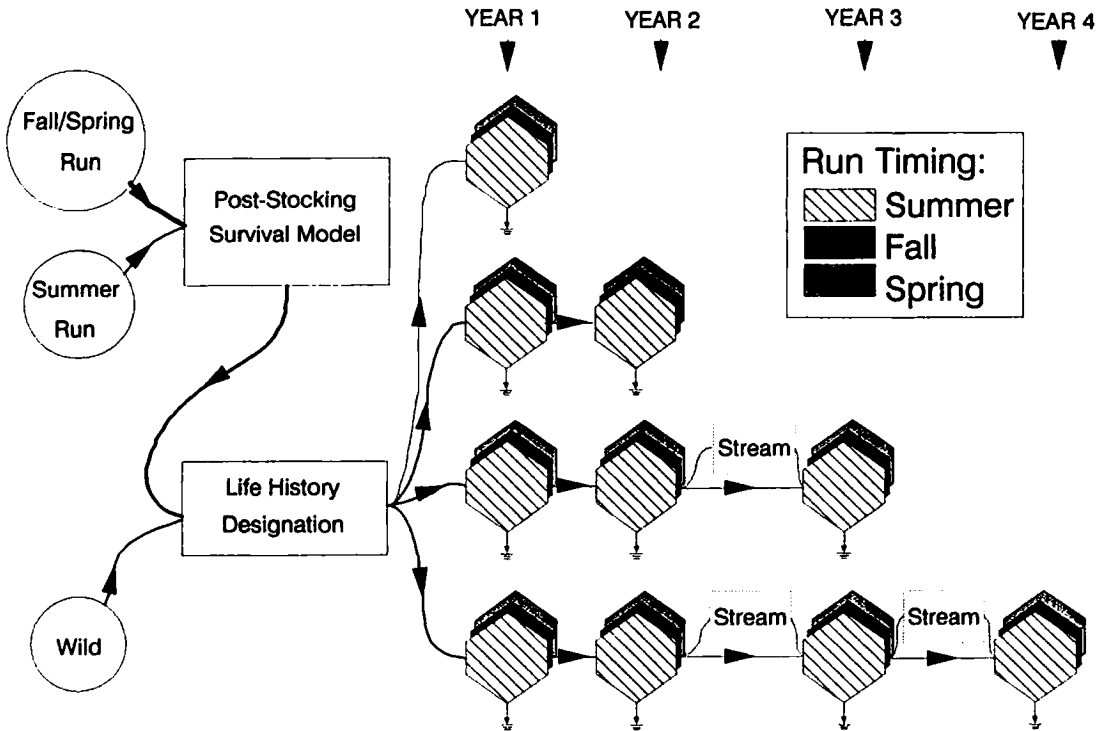


FIGURE 1.—Schematic diagram of the population energetics model formulated for steelhead in Lakes Michigan and Ontario. A poststocking survival model was applied to stocking records from both lakes to estimate hatchery smolt equivalents. These abundance estimates were multiplied by estimates of proportions of wild fish for each year-class to arrive at an estimate of whole-lake yield of wild smolts. The total population of smolts for each year was first partitioned into run-timing categories (summer, fall, or spring) and then further partitioned into each of seven life history forms characterized by time spent in lake and spawning schedule. These population estimates were then input into a bioenergetics model to estimate whole-lake prey consumption. Symbols used in diagram are from Odum (1983).

1971; brown trout, -0.24 ; Elliott 1976a; lake trout, -0.307 ; Stewart et al. 1983), the corrected intercept value exceeds values used in previous modeling studies (e.g., 0.303 ; Beauchamp et al. 1989; Stewart and Ibarra 1991). However, we assumed this corrected value better represented maximum consumption of fish feeding on natural foods.

We fitted the temperature dependence model of Thornton and Lessem (1978) to the consumption data of From and Rasmussen (1984). We scaled all consumption estimates to the measurements at 20°C and fitted the model by eye (Table 1). The resulting function took the common form of a physiological performance model, with a feeding optimum at 20°C and decreased performance on either side of this peak. The decline in feeding at temperatures greater than 20°C was precipitous, as has been observed for other fishes (e.g., Brett et al. 1969; Elliott 1976b; Stewart and Ibarra 1991, based on original data of Edsall et al. 1974).

Metabolism.—We modeled standard and active metabolism of steelhead using the model developed by Stewart et al. (1983):

$$R_{\text{opt}} = \alpha W^{\beta} \cdot e^{\rho T} \cdot e^{\nu S}; \quad (2)$$

R_{opt} = standard and active metabolism at volitional swimming speed, W = fish weight (g), T = water temperature ($^{\circ}\text{C}$), S = volitional swimming speed ($\text{cm} \cdot \text{s}^{-1}$) and α , β , ρ , ν = empirical constants.

Stewart (1980) conducted a literature review for weight and temperature dependences of standard metabolism in rainbow trout and concluded that the best available model for rainbow trout was that of Rao (1968, 1971):

$$R_{\text{std}} = 0.00264 \cdot W^{-0.217} \cdot e^{0.06818 \cdot T}; \quad (3)$$

R_{std} = standard metabolism (in $\text{g O}_2 \cdot \text{d}^{-1}$). Rao (1968, 1971) developed the model to predict standard metabolism by measuring metabolic rates at

TABLE 1.—Parameter values used to implement the bioenergetic model for steelhead trout. Model equations were described by Stewart et al. (1983) and Hewett and Johnson (1992).

Parameter description	Parameter value	Reference
Consumption (C)^a		
Intercept: C_{\max} at $(\theta_2 + \theta_3)/2$	0.628 g·g ⁻¹ ·d ⁻¹	From and Rasmussen (1984)
Coefficient: C_{\max} versus weight	-0.30	From and Rasmussen (1984)
Temperature for K_1	5°C	From and Rasmussen (1984)
Temperature for K_2	20°C	From and Rasmussen (1984)
Temperature for K_3	20°C	From and Rasmussen (1984)
Temperature for K_4	24°C	From and Rasmussen (1984)
K_1 : proportion of C_{\max} at θ_1	0.33	From and Rasmussen (1984)
K_2, K_3 : proportions of C_{\max} at θ_2, θ_3	0.98	From and Rasmussen (1984)
K_4 : proportion of C_{\max} at θ_4	0.20	From and Rasmussen (1984)
Metabolism (R)		
Intercept: R	0.00264 g·O ₂ ·d ⁻¹	Stewart (1980, from Rao 1968, 1971)
Coefficient: R versus weight	-0.217	Stewart (1980, from Rao 1968, 1971)
Coefficient: R versus temperature	0.06818	Stewart (1980, from Rao 1968, 1971)
Coefficient: R versus swimming speed	0.0234	Stewart (1980, from Rao 1968, 1971)
Swimming speed (S)		
Intercept: S	9.7 cm·s ⁻¹	Stewart (1980, from Weihs 1973)
Coefficient: S versus weight	0.13	Beauchamp et al. (1989)
Coefficient: S versus temperature	0.0405	Beauchamp et al. (1989, from Griffiths and Alderice 1972 and Glova and McInerney 1977)
Egestion (F)		
Intercept: proportion (P) egested versus temperature and ration	0.212	Elliott (1976a)
Coefficient: temperature versus egestion	-0.222	Elliott (1976a)
Coefficient: P versus egestion	0.631	Elliott (1976a)
Proportion of invertebrates indigestible: P_{inv}	0.10	Stewart et al. (1983)
Proportion of fish indigestible: P_{fish}	0.033	Stewart et al. (1983)
Excretion (U)		
Intercept: proportion (P) excreted versus temperature and ration	0.0314	Stewart et al. (1983, based on Elliott 1976a)
Coefficient: temperature versus excretion	0.58	Elliott (1976a)
Coefficient: P versus excretion	-0.299	Elliott (1976a)

^a C_{\max} is maximum consumption, θ_1 is lower threshold temperature, θ_2 and θ_3 are temperature bounds of C_{\max} ($\theta_2 = \theta_3$ if C_{\max} occurs at a single temperature), θ_4 is upper threshold temperature, and K_1 – K_4 are reaction rate multipliers (Thornton and Lessem 1978).

a range of activities and extrapolating back to zero activity. We used a coefficient of 13,560 J·g O₂⁻¹ to convert the intercept value in equation (3) (0.00264) to energy used (Elliott and Davidson 1975).

Swimming speed.—Empirical estimates of salmonine swimming speed (S in equation 2) in the field by Ruggerone et al. (1990) and Ogura and Ishida (1992) allowed us to test the validity of a previously developed swimming speed model based on optimal foraging theory and controlled laboratory experiments (Weihs 1973; Ware 1975; Stewart 1980; Beauchamp et al. 1989).

Ruggerone et al. (1990) tagged six prespawning steelhead adults with ultrasonic transmitters and tracked them along the central coast of British

Columbia during July. We inferred from the temperature curve in their paper (their Figure 3) and the swimming depth observations (at 15-min intervals) that the six fish occupied temperatures of 13–15°C.

Ogura and Ishida (1992) estimated swimming speeds of four coho salmon (511–571 mm fork length) in the central north Pacific Ocean using depth-sensing ultrasonic transmitters. We converted lengths of these fish to wet weights using a length–weight relationship developed for Lake Ontario coho salmon (Rand and Stewart, unpublished data). We inferred from the temperature profile figures in the paper and data on depth distributions that the tagged salmon occupied a temperature of 8.5°C. The reported ground speed es-

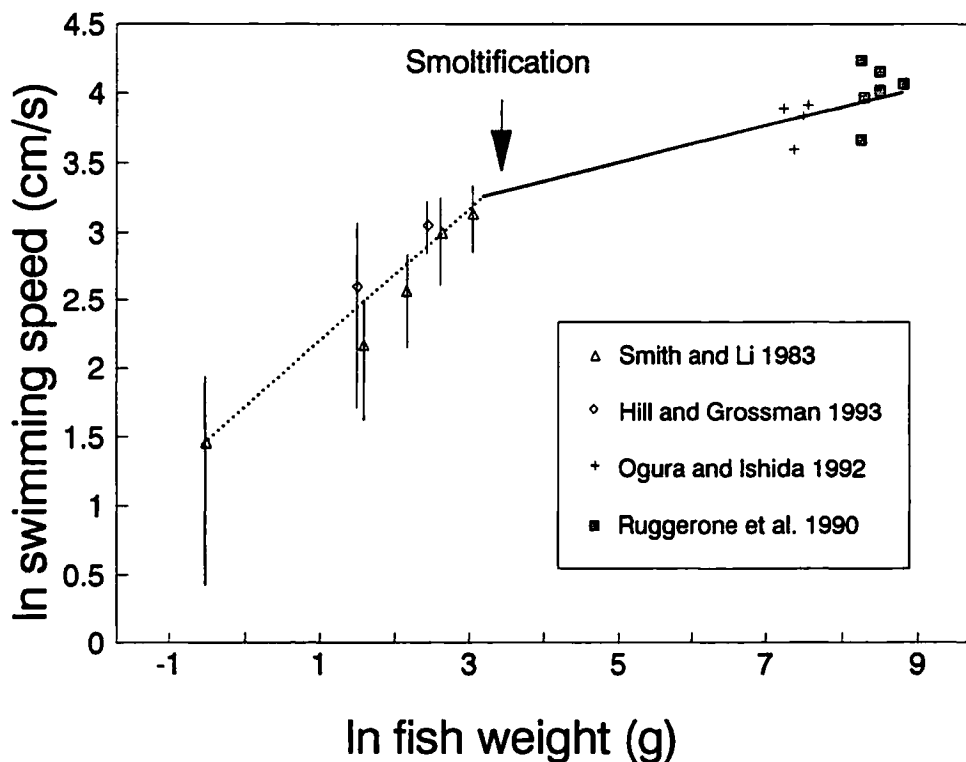


FIGURE 2.—A compilation of in situ measures of swimming speed ($\log_e[S]$) in relation to $\log_e(\text{weight}, W)$ for pre- and postsmolt rainbow trout, steelhead, and coho salmon. Predictions from the swimming speed model of Stewart (1980, solid line) agreed well with direct measures of swimming speed for steelhead (Ruggerone et al. 1990) and coho salmon (Ogura and Ishida 1992). A new model (dashed line) better fits data on presmolts ($S = 5.328 \cdot W^{0.485}$; $r^2 = 0.92$, $P = 0.002$). Data for presmolt rainbow trout and steelhead are from Smith and Li (1983; at 16°C) and Hill and Grossman (1993; at 15°C); vertical lines indicate 95% confidence intervals.

timates were temperature-corrected to 16°C based on the coefficient of swimming speed versus temperature (0.0405; Table 1).

The swimming speed model of Stewart (1980) accurately predicted speeds for the adult fish in these studies (Figure 2). The mean swimming speeds measured by Ruggerone et al. (1990) were on average 10% higher than the model predictions. Because the empirical data of Ruggerone et al. (1990) represented a time of more active migration, Stewart's model should predict lower activity because it was intended to simulate periods of foraging and cruising to locate food. The model fit the data of Ogura and Ishida (1992) within 1%. Stewart's (1980) model consistently overestimated swimming speed for stream-dwelling presmolts. An alternative linear least-squares regression fit the presmolt data well, but we chose Stewart's (1980) model to estimate S (equation 2) in our simulations because of the corroborating field data on adults (Table 1).

Egestion and excretion.—Although information on egestion and excretion is available for rainbow trout (Paulson 1980; From and Rasmussen 1984), the studies were based on fish fed artificial pellet food. Because the dynamics of gut assimilation and waste losses are likely to be quite different for wild fish feeding on invertebrates and fish, we chose to use the mixed-diet model formulation of Stewart et al. (1983) based in part on Elliott's (1976a) experiments on amphipod-fed brown trout (Table 1).

Population Model

Life history forms.—Both steelhead and domestic rainbow trout have had a long history in the Great Lakes basin (MacCrimmon and Gots 1972). Steelhead are distinguished from domestic rainbow trout by their parr-smolt transformations and subsequent migratory behavior. Pacific coast steelhead have been stocked in all five of the Laurentian Great Lakes. In the model, we separately

accounted for three subpopulations that differ in the timing of their spawning migrations. The populations that migrate in late fall or early spring (fall-spring-run steelhead) have had a longer history in the Great Lakes and presently represent the majority of steelhead in this region. These stocks generally spawn in the spring, although fall and winter spawnings have been recorded (Dodge and MacCrimmon 1970).

In 1975, Indiana introduced summer-run (or Skamania) steelhead into Lake Michigan. These fish originated in Washington, and are distinguished from the fall-spring-run steelhead by an earlier time of stream entry and a delayed age at maturity. These fish also spawn in the spring. We modeled summer-run steelhead as a separate group independent of the fall-spring-run steelhead in Lake Michigan. Relatively few summer-run steelhead have been stocked in Lake Ontario, so we did not include them in the Lake Ontario simulations.

Steelhead have successfully reproduced in the Great Lakes (Biette et al. 1981; Johnson and Ringler 1981; Seelbach 1993). There has been no evidence of successful reproduction by introduced summer-run fish, so we included all wild steelhead in the fall-spring-run category.

Domestic rainbow trout have been stocked extensively in Lakes Michigan and Ontario. Common strains included Shasta, McConoughy, White Sulfur, and Eagle Lake. We know very little about the domestic rainbow trout life history in the Great Lakes. Data on weight at age for domestic rainbow trout and steelhead in Lake Ontario demonstrate similar in-lake growth rates (Wedge 1983). Because of this similarity in growth rate, we included rainbow trout in the fall-spring-run category.

Hatchery smolts.—We estimated numerical abundance of hatchery smolt year-classes during 1975–1990 in Lakes Michigan and Ontario based on stocking data obtained from state and provincial agencies coupled with a poststocking survival model. Hatchery stocking has increased dramatically during this period, resulting in an expanding lake population of hatchery-reared individuals.

Seelbach (1987a) demonstrated the importance of size-biased instream survival of stocked steelhead in the Little Manistee River. In addition, Seelbach (1989) reported higher instream survival of fall fingerlings and small yearlings stocked in marginal-quality rivers, where competition between resident salmonines was presumably less intense. As a result of these observations, we applied differential presmolt survival to hatchery steelhead based on size and river stocking site (Ta-

TABLE 2.—Table of survival parameters applied to fall-spring-run and summer-run hatchery juveniles. Survival values represent the proportion of the original numbers of steelhead stocked that actually survive to smoltification and reach the lake proper. Fall fingerlings are aged approximately 6 months postfertilization and yearlings are aged approximately 14 months postfertilization and are stocked in the spring.

Age and size	Type of river stocked and time of smolting				
	Trout river		Marginal river		River mouth, year 1
	Year 1	Year 2	Year 1	Year 2	
Fingerlings (parr)	0.01	0.02	0.01	0.01	0.01
Small yearlings (< 150 mm)	0.01	0.01	0.03	0.07	0.20 ^a
Large yearlings (≥ 150 mm)	0.90	0.00	0.90	0.00	1.00
Yearlings ^b			0.15	0.00	

^a Based on partial survival from time of stocking to adult return of steelhead parr and age-2 smolts reported by T. M. Stauffer (Michigan Department of Natural Resources, unpublished, 1955) and Hassinger et al. (1974).

^b Applies to yearlings stocked in the St. Joseph River in Indiana and reflects increased mortality during emigration (P. W. Seelbach, unpublished data).

ble 2). We categorized tributary planting locations as either a trout river or a marginal river. We defined trout rivers as streams with coldwater fish communities including resident salmonines and marginal rivers as warmer streams with few or no resident salmonines. Seelbach (1987a) indicated a minimum size of a true smolt to be approximately 150 mm total length (TL). We assumed all fish stocked smaller than this size (small yearlings and fall fingerlings) were presmolts and consequently experienced lower survival than fish larger than 150 mm TL. Seelbach (unpublished data) found significantly lower survival of yearlings stocked in the upper reaches of the St. Joseph River in Indiana, possibly because of mortalities at three downstream hydroelectric dams. We applied a lower survival rate for plantings in this river system (Table 2).

Yearlings and fall fingerlings are commonly stocked in embayments and river mouths. We assumed all fall fingerlings stocked in the lake experience very low survival, based on results of survival of fall fingerlings stocked in tributaries (Table 2). We also assumed high survival (1.00) of large yearlings stocked at these locations based on the tributary studies. Results from two studies indicate that small yearlings stocked at river mouths as presmolts may experience lower survival than true smolts. Stauffer (unpublished data) found that survival to adult return was 68% lower

for spring emigrant wild parr in the Black River, Michigan, than for hatchery age-2 smolts stocked in the same river system. In a similar study, Hassinger et al. (1974) found survival of wild steelhead parr in Lake Superior to be 67% lower than age-2 smolt survival. If we assume a maximal survival rate to the lake of 0.90 for the age-2 smolts, survival for the parr would be approximately 0.29. We chose a conservative value of 0.20 to represent presmolt survival for parr stocked at river mouths (Table 2).

We extrapolated the presmolt survival model to all stocking in Lake Michigan tributaries and river mouths for 1975–1990. Detailed stocking information (numbers, size at stocking, and planting location) was obtained for Michigan (Michigan Fish Stocking Records, 1975–1990, Michigan Department of Natural Resources [MDNR], Lansing), Illinois (GLFC 1989), Indiana (G. Armstrong, Indiana Department of Natural Resources [IDNR], unpublished data), and Wisconsin (T. Schneider, Wisconsin Department of Natural Resources [WDNR], unpublished data; Hansen 1986). We characterized all rivers receiving steelhead plants in Michigan as either trout or marginal rivers based on extensive MDNR tributary surveys. We considered all tributaries in Indiana, Illinois, and Wisconsin to be marginal rivers based on available agency information (Avery 1974; T. Schneider and D. Brazo, personal communications).

Hatchery plants in Lake Ontario may also experience instream size-selective mortality. The number of yearlings stocked in Canada was relatively high during 1985–1990 (total, 1,098,000), but individual size at time of stocking was small (mean, 107 mm TL). Fewer (520,000) but larger (mean, 156 mm TL) yearlings were stocked in New York over the same period. The contribution of Canadian fish in the sport catch is smaller (3.2% of the 1991 harvest) than the contribution of New York fish (13.3% of the 1991 harvest; GLFC 1992a). In addition, Wedge (1983) noted better survival of a faster-growing hatchery strain of steelhead compared with a wild strain stocked at significantly smaller sizes.

We also characterized stocked Lake Ontario tributaries as either marginal or trout rivers. This classification was based on an extensive survey of New York tributaries for juvenile salmonids conducted by personnel of the New York Department of Environmental Conservation (NYDEC) in 1979 (Wedge 1983) and on information from the Ontario Ministry of Natural Resources, Picton. We

obtained the raw stocking numbers and mean size at stocking from state and provincial agency reports (GLFC 1992a) and personal communications with fishery and hatchery managers. We applied the poststocking survival model developed for Lake Michigan to these hatchery plantings for Lake Ontario.

To estimate survival values for stocked yearlings, it was necessary to partition the raw stocking numbers into small (presmolts) and large (true smolts) size categories. We estimated variability of yearling total length using data from five hatcheries that rear a majority of the steelhead stocked in both lakes (Platte River and Wolf Lake hatcheries in Michigan; Salmon River, Rome, and Caledonia hatcheries in New York). The mean standard deviation calculated from these data was approximately 20 mm TL. We applied this standard deviation to the average length at time of stocking to estimate the proportion of each yearling year-class that equaled or exceeded the 150-mm TL smolt threshold. Different survival values were then applied to the presmolts and smolts to calculate number of individuals entering the lake.

Wild smolts.—We estimated whole-lake yield of wild smolts based on the observed proportion of adult fish in the lake population that were naturally recruited. We discriminated between hatchery and wild Lake Michigan fish using the decision rule of Seelbach and Whelan (1988) based on circulus patterns on scales taken from adults caught in the sport fishery. Analysis of a small sample of scales from known wild and hatchery steelhead from Lake Ontario tributaries indicated this decision rule also applies to the Lake Ontario population (0.98 accuracy rate).

We obtained 880 scale samples from adult steelhead monitored in the summer MDNR boat survey conducted from ports along the Lake Michigan shoreline (Frankfort, Manistee, Ludington, South Haven, New Buffalo, and St. Joseph) during the summers of 1985–1991. We decided to analyze only fish caught in the open water in the summer (June–September), assuming that all stocks were evenly mixed and that open-water samples best represented the whole-lake population. This appears to be a valid assumption given the evidence of mixed fin clips in these samples and results of coded-wire tagging studies (Seelbach, unpublished data). We obtained a comparable collection of 1,792 archived scales taken during the spring Empire State Lake Ontario fishing derbies at ports along the New York border of Lake Ontario (Wilson, Oak Orchard, Rochester, Fair Ha-

TABLE 3.—Estimates of hatchery and wild steelhead smolt equivalents (in thousands) for Lakes Michigan and Ontario from 1975 to 1990. Estimates are provided for the proportion (with 95% confidence interval, CI) of each smolt year-class that was wild (P_W). These estimates were based on examinations of scales from adult fish taken in the sport fisheries in both lakes. Proportions were multiplied by the number (N) of hatchery smolt equivalents (FS = fall-spring run; SU = summer run) to estimate whole-lake yield of wild smolts (N_W).

Year	Lake Michigan					Lake Ontario			
	Number of scales	P_W (95% CI ^a)	N_{FS}	N_{SU}	N_W	Number of scales	P_W (95% CI ^b)	N_{FS}	N_W
1975			449	0	320 ^b			0	70 ^c
1976			609	125	283 ^b			67	60 ^c
1977			548	45	98 ^b	147	0.33 (0.15)	112	50
1978			359	104	98 ^b	319	0.20 (0.09)	113	29
1979			795	127	98 ^b	255	0.29 (0.11)	144	39
1980			856	3	98 ^b	285	0.18 (0.09)	231	39
1981			473	114	209 ^b	142	0.29 (0.15)	233	58
1982	26	0.21 (0.29)	311	123	93	202	0.24 (0.12)	210	49
1983	35	0.44 (0.34)	543	71	267	238	0.29 (0.11)	219	70
1984	54	0.41 (0.27)	877	177	434	128	0.34 (0.16)	163	58
1985	95	0.22 (0.16)	667	131	178	42	0.29 (0.27)	175	45
1986	105	0.06 (0.09)	782	350	65			206	57 ^c
1987	182	0.17 (0.10)	705	329	172			437	83 ^c
1988	116	0.12 (0.11)	392	252	80			411	60 ^c
1989	150	0.17 (0.11)	437	351	137			415	61 ^c
1990	117	0.13 (0.11)	475	351	111			480	78 ^c

^a Calculated as in Seelbach and Whelan (1988).

^b Estimate based on winter severity-wild smolt yield model for Lake Michigan.

^c Estimate based on winter severity, July flow-wild smolt yield model for Lake Ontario.

ven, Oswego, and Salmon River) from 1979 to 1986.

We processed the first 301 Lake Michigan scales blindly to assess the accuracy rate of identifying clipped fish as hatchery fish. Of 166 scales from clipped fish, only 5 were misidentified as wild, an accuracy rate of 0.97. We used the same approach on the first 428 scales analyzed from the Lake Ontario collection. Of 164 scales from clipped fish, only 8 were misidentified, an accuracy rate of 0.95. Because we did not determine classification error rate for identifying wild adult fish, we assumed the rate reported by Seelbach and Whelan (1988): 0.826.

We culled from the remaining envelopes those containing scales from fin-clipped fish and measured scales from the remaining unclipped fish in each lake collection. Agency personnel from the respective regions aged the fish. We estimated the proportion of wild fish by smolt year-class in both lakes using recorded ages and assuming that smolt-to-adult survival did not differ between wild and hatchery fish (Table 3). We did not distinguish between stream ages of smolts in this analysis. We calculated the 95% confidence interval for the estimated wild proportion using the formula from Seelbach and Whelan (1988) with the classification error rates presented above. By multiplying estimates of wild proportions by our numerical

estimates of hatchery smolt equivalents, we estimated absolute numbers of wild smolts produced lake-wide over the years of record in both lakes (Table 3).

After observing presmolt winter survival to vary from 13 to 90% in the Little Manistee River, Seelbach (1987b) hypothesized that smolt yield (Y) was related to an index of winter severity (ND, the number of days with air temperatures of -12°C or lower during January and February, measured at Cadillac, Michigan). We explored this hypothesis by regressing wild smolt yield against this winter severity index (Figure 3). After excluding the data set for the 1990 smolt year-class, which included only returns of 1- and 2-year-old fish, we fitted a least-squares linear regression to the data and found a clear pattern in the residuals. Smolt yield estimates from both temperature extremes were higher than the linear model predicted and yields at the intermediate temperatures were lower than the regression model prediction. We fitted a linear model to the 6 years of smolt yield estimates following the relatively mild winters ($\text{ND} \leq 30$) and found a significant negative relationship (Figure 3), which provides independent supporting evidence for Seelbach's (1987b) hypothesis. For winters with a severity index greater than 30, we assumed no effect on smolt yield (Figure 3) based on the pattern in the data. Little Manistee

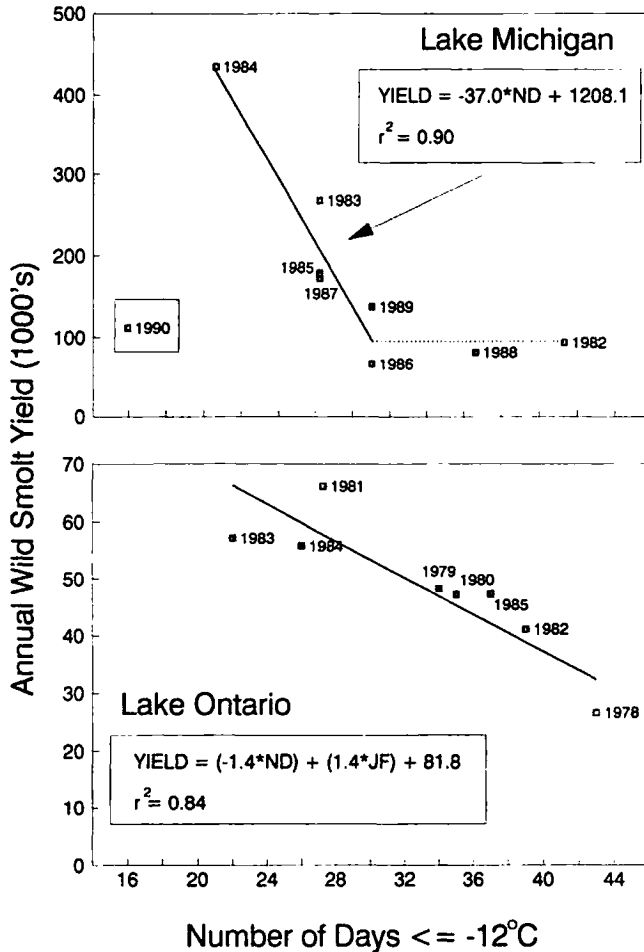


FIGURE 3.—Estimates of annual steelhead smolt yield in Lakes Michigan and Ontario based on an examination of scales taken from adults caught in the sport fishery. The data were regressed against a winter severity index (ND, number of days with air temperatures of -12°C or below). The estimate for the 1990 year-class was excluded from the Lake Michigan regression model because returns were incomplete for that cohort. Lake Ontario wild smolt yield varied as a function of winter severity and mean July stream flow (JF) in the year previous to smolting.

River steelhead smolts contributed approximately 13, 21, and 20% of the total lake-wide smolt yield in 1982, 1983, and 1984, respectively (data from Seelbach 1993). This proportion's relative consistency indicated that smolt yield was being regulated in similar ways over all steelhead-producing tributaries. We used this yield model to estimate whole-lake wild smolt production for 1975–1981 based on the record of air temperatures recorded at Cadillac, Michigan (Table 3).

We carried out a similar analysis of wild smolt yield in Lake Ontario. We found a significant relationship between wild smolt yield and the same winter severity index ($Y = -1.3 \cdot ND + 92.4$, $r^2 = 0.64$, $P < 0.022$) using climatological data re-

corded at a U.S. Geological Survey (USGS) station in Watertown, New York. Seelbach (unpublished data) noted that streams along the eastern border of Lake Ontario are hydrologically unstable and could affect instream survival and smolt yield. To explore the importance of stream discharge on annual smolt yield in Lake Ontario, we obtained a 15-year record (1975–1990) of daily mean discharge from Sandy Creek measured at a USGS gauge station in Adams, New York. This stream is hydrologically similar to two productive steelhead rivers in neighboring watersheds (Rand et al. 1992). We estimated mean monthly discharge and minimum daily flow during March–September of the year prior to smolting. With the

exclusion of the 1977 year-class, we found a significant positive relationship between residuals from the winter severity-smolt yield model and minimum daily flow in July ($R = 0.17 \cdot \text{JF} - 7.2$, $r^2 = 0.76$; R = residual and JF = mean July discharge in $\text{m}^3 \cdot \text{s}^{-1}$). The 1977 year-class experienced lower survival than would be predicted by the flow model, which may have been the result of a major flood in March 1977. The resulting multiple-regression equation explained more of the variability in annual smolt yield in Lake Ontario ($Y = -1.4 \cdot \text{ND} + 1.4 \cdot \text{JF} + 81.8$; $r^2 = 0.84$, $P = 0.003$). We applied this model to estimate wild smolt yield in Lake Ontario during 1975–1976 and 1987–1990 (Table 3).

Lake-phase life history.—As noted earlier, steelhead populations in the Great Lakes show a wide range of life history patterns (Biette et al. 1981). We shall show below that these different life history patterns are associated with different growth characteristics and therefore must be modeled separately if accurate population-level consumption estimates are to be obtained. Furthermore, the timing of the spawning run (summer, fall, or spring) influences the total time spent feeding in the lake and thus overall consumption, so separate accounts must be kept of subpopulations based on run timing. Finally, although data are available on life history (from scale interpretations) and run timing for adult fish, we require estimates of the proportion of fish by life history form at the time of smoltification. In this section we describe how we obtained these proportions.

Biette et al. (1981), in their synthesis of Great Lakes steelhead life history patterns, concluded that in most populations, over 97% of the returning adults spent 1–4 years in the lake, over 50% of the returning adults were virgin spawners, and very few fish spawned more than twice. Two more recent studies, one on a Lake Michigan tributary (Seelbach 1993) and the other on a Lake Ontario tributary (Karges 1987), obtained similar results. We elected to include only the seven most common life history forms observed in these studies (Table 4). We distinguish these life history forms using the convention of Seelbach (1993). The forms are defined by the number of years of stream residence prior to smoltification (we combined 1- and 2-year-old smolts—the two most commonly observed smolt ages), the number of years of lake residence prior to maiden spawning, and the number of subsequent spawning years.

We used data from the Little Manistee River weir (spring and fall runs: Seelbach 1993) and the

St. Joseph River (summer run: Seelbach, unpublished data) to describe the proportion of adults by life history form for Lake Michigan (Table 4). Fall-run steelhead in the Little Manistee River averaged 21% of the total annual run counted at the weir during 1979–1987. This is likely an underestimate of the true proportion because some fall-run steelhead remain below the weir in Manistee Lake over winter (Seelbach, personal observation). To account for these fish, we assumed (as a first approximation) that fall-run steelhead represent 33% of the total fall and spring runs. For adults in the summer, spring, and fall runs, we also used different proportions of life history form for the period prior to 1980 because the fall- and spring-run data indicate both delayed age at maturity and slower growth for the steelhead population as a whole during this earlier period (Seelbach 1993).

For Lake Ontario, we used data from the Ganaraska River weir in 1984 and 1985 (Karges 1987) to describe the proportion of spring-run adults by life history form. In the absence of data on fall-run proportions, we used the same fall : spring ratio as assumed for Lake Michigan. Growth (and presumably rates of maturation) of Lake Ontario steelhead appear to have been unaffected by colder lake conditions in the late 1970s, based on limited weight-at-age data for sport-caught steelhead during this period (L. Wedge, NYDEC, unpublished data).

We calculated annual survival in Lake Michigan from smolt to maiden adult based on estimates of smolt yield and returning adult abundance from cohorts in the Little Manistee River during 1982–1984 (Seelbach 1993). We calculated daily instantaneous mortality (Z , as in Ricker 1975) for the 3 years. We assumed (1) each life history form exhibited the same survival rates, (2) individuals spent either 730, 1,095 or 1,460 d in the lake prior to stream entry, and (3) there was no immigration into or emigration out of the population. We estimated mean annual survival over the 3 years of observations as $0.47 \cdot \text{year}^{-1}$ (SD, 0.18). This value includes both natural and harvest mortality.

For multiple-spawning life history forms, we used estimates of repeat-spawning survival derived from Seelbach (1993): $0.65 \cdot \text{year}^{-1}$ for 3-year-olds, $0.32 \cdot \text{year}^{-1}$ for 4-year-olds that had spawned once previously, and $0.44 \cdot \text{year}^{-1}$ for 4-year-olds that had spawned twice previously. These values represent averages over sexes and stream ages and were applied in place of the

TABLE 4.—Values used to estimate initial smolt life history proportions for each steelhead year-class in Lakes Michigan and Ontario. Life history proportions at time of spawning for Lake Michigan strains were taken from Seelbach (1993, and unpublished data). Spawning proportions for Lake Ontario spring-run fish were taken from Karges (1987). Survival to maiden spawn (SMS) and repeat-spawning survival (RSS) values were computed from data in Seelbach (1993).

Life history ^a	Spawner proportion			Survival			Smolt proportion		
	Summer run	Fall run	Spring run	SMS	RSS	Total ^b	Summer run	Fall run	Spring run
Lake Michigan 1975-1979									
1-2.1s0	0.02	0.10	0.00	0.47	1.00	0.47	0.00	0.02	0.00
1-2.2s0	0.05	0.20	0.19	0.22	1.00	0.22	0.01	0.10	0.07
1-2.3s0	0.31	0.55	0.51	0.10	1.00	0.10	0.17	0.62	0.40
1-2.2s1	0.08	0.09	0.08	0.22	0.65	0.14	0.03	0.07	0.04
1-2.4s0	0.23	0.01	0.04	0.05	1.00	0.05	0.25	0.02	0.06
1-2.3s1	0.30	0.04	0.16	0.10	0.32	0.03	0.51	0.14	0.40
1-2.2s1s1	0.03	0.01	0.02	0.22	0.29	0.06	0.03	0.02	0.02
Lake Michigan 1980-1990									
1-2.1s0	0.02	0.20	0.03	0.47	1.00	0.47	0.00	0.06	0.01
1-2.2s0	0.05	0.28	0.22	0.22	1.00	0.22	0.01	0.17	0.08
1-2.3s0	0.31	0.38	0.43	0.10	1.00	0.10	0.17	0.51	0.36
1-2.2s1	0.08	0.09	0.10	0.22	0.65	0.14	0.03	0.08	0.06
1-2.4s0	0.23	0.01	0.03	0.05	1.00	0.05	0.25	0.03	0.05
1-2.3s1	0.30	0.03	0.15	0.10	0.32	0.03	0.51	0.13	0.39
1-2.2s1s1	0.03	0.01	0.04	0.22	0.29	0.06	0.03	0.02	0.05
Lake Ontario 1975-1990									
1-2.1s0		0.20	0.07	0.47	1.00	0.47		0.06	0.01
1-2.2s0		0.28	0.09	0.22	1.00	0.22		0.17	0.03
1-2.3s0		0.38	0.37	0.10	1.00	0.10		0.51	0.26
1-2.2s1		0.09	0.05	0.22	0.65	0.14		0.08	0.02
1-2.4s0		0.01	0.25	0.05	1.00	0.05		0.03	0.35
1-2.3s1		0.03	0.13	0.10	0.32	0.03		0.13	0.28
1-2.2s1s1		0.01	0.04	0.22	0.29	0.06		0.02	0.04

^a Codes indicate number of stream years, number of lake years before first spawning and number of spawning years. For example, code 1-2.2s1s1 means fish lived 1 or 2 years in a stream (stream residency data were combined) and 2 years in the lake before spawning, then spawned in 2 subsequent years.

^b Total survival is SMS × RSS.

Z-value presented above during years following spawning. These survival values are comparable to estimates made by Kwain (1981) for a Lake Superior population ($0.59 \cdot \text{year}^{-1}$), and significantly higher than spawning survival for several rainbow trout populations in the Finger Lakes of New York (0.18 – $0.24 \cdot \text{year}^{-1}$; Hartman 1959).

Smolt-to-adult-spawning and repeat-spawning survival estimates were not available for either Lake Michigan summer-run or Lake Ontario steelhead. In the absence of these estimates, we assumed that the Lake Michigan estimates derived from the Little Manistee River data set (Seelbach 1993) are applicable.

We used the above survival estimates and observed proportions of each life history form observed at the weir to back-calculate the life history proportions for the smolts entering the lake. We multiplied observed life history proportions of adults by annual lake survival to arrive at an index which, when normalized, was used to estimate life history proportions of the smolt population (Table 4).

Lake-Specific Parameters

Lake growth rate.—We began simulations of all life history forms at 50 g wet weight on May 1 (day 1 of the simulation year), which represented the day the average hatchery and wild smolt entered the lake. Seelbach (1993) provided data on weight at stream return for each life history form of fall- and spring-run steelhead in Lake Michigan (Table 5). The slow-growth years were 1975–1979 and the faster-growth years were 1980–1990.

We derived estimates of spring weights during lake residence from a back-calculation technique based on a predictive equation relating scale radii to fish total length. We obtained scales from emigrant smolts and maiden spawning fish collected in the Little Manistee River ranging in size from 80 to 800 mm. Scales were magnified with a microprojector and measured from the center of formation to the outer edge of the scale along a radial line 20° from the longest axis. The regression of scale measurements against fish length was highly significant ($P < 0.001$) with a homogenous vari-

TABLE 5.—Weights at age for summer-, fall-, and spring-run steelhead in Lakes Michigan and Ontario. Seven life history forms were modeled for each steelhead population (forms are defined in Table 4). Two growth periods in Lake Michigan are represented, as described by Seelbach (1993). Growth data for Lake Ontario were taken from Karges (1987). Values are grams wet weight on May 1, except during years of spawning migration, when weights were recorded as summer weight (on August 1)—fall weight (on November 1)—spring weight (on April 1).

Life history	Smolt	Age on May 1			
		1	2	3	4
Lake Michigan, 1975-1979					
1-2.1s0	50	138 ^a -760 ^b -800			
1-2.2s0	50	448	1,434 ^a -2,325 ^b -2,503	1,723 ^a -2,180 ^b -2,294	3,045 ^a -3,855 ^b -4,058
1-2.2s1					
1-2.2s1s1					
1-2.3s0	50	392	2,153	2,535 ^a -3,406 ^b -3,452	3,717 ^a -3,651 ^b -3,900
1-2.3s1					
1-2.4s0	50	264	1,902	3,107	3,398 ^a -4,301 ^b -4,527
Lake Michigan, 1980-1990					
1-2.1s0	50	173 ^c -953-1,295			
1-2.2s0	50	732	1,658-2,688-2,894	2,782 ^d -3,521 ^c -3,706	3,366 ^d -4,261 ^c -4,485
1-2.2s1					
1-2.2s1s1					
1-2.3s0	50	637	2,493	2,945-3,957-4,011	4,289-4,213-4,501
1-2.3s1					
1-2.4s0	50	431	2,199	3,594	3,862 ^d -4,888 ^c -5,145
Lake Ontario, 1975-1990					
1-2.1s0	50	519-737			
1-2.2s0	50	416	1,081-1,123 ^f	1,657-1,649	3,315-2,971
1-2.2s1					
1-2.2s1s1					
1-2.3s0	50	363	967	2,493-2,481 ^f	3,185-2,855
1-2.3s1					
1-2.4s0	50	245	853	2,223	3,697-3,314 ^f

^a Based on ratio of summer weight : fall weight in corresponding category in growth period 1980–1990.

^b Based on ratio of fall weight : spring weight in corresponding category in growth period 1980–1990.

^c Based on model-simulated weight of fall-run fish on August 1.

^d Based on mean ratio of weights at age of summer-run fish caught in the open-water fishery in Lake Michigan in July–August 1989–1990 and weights at age of fall-run fish measured at the Little Manistee River weir in October–November 1979–1987.

^e From mean ratio of spring : fall weights at age measured on virgin growth forms (lake ages 1–3) and growth form 1-2.3s1 over the period 1979–1987 at the Little Manistee River weir.

^f Spring weight at age from Karges (1987).

ance about the regression line ($\log_e(TL) = 0.8716 \cdot \log_e(SR) + 5.4851$, $r^2 = 0.98$, $N = 263$; where TL = fish total length, mm, and SR = scale radius, μm).

We used the regression equation above to solve for fish length from measurements made on scales of returning fish of the 1982–1984 smolt cohorts from the Little Manistee River. Only scales from maiden spawners were used because scale resorption occurs at the time of spawning. We assumed the time of annulus formation corresponded to the first day of the simulation year (May 1). We converted back-calculated lengths to weights using the length–weight regression parameters of Seelbach (1993). Resulting spring weights were averaged over the three cohorts (Table 5) and used as growth points in our final simulations (Figure 4). We computed a matrix of conversion factors to apply to

observed weights at river return to generate a complete set of back-calculated growth data for all life history forms during the earlier growth period in Lake Michigan and for the whole 15-year record for Lake Ontario (Table 5).

We tested the assumption that Lake Michigan summer-run steelhead exhibited faster growth than fall–spring-running fish by comparing weight at age for both strains collected during the summer (July–September) both in the open lake (1989–1990) and in southern Michigan tributaries (1987–1989). Open-water samples indicated summer-run fish were on average 10% lower in weight at a particular age, but river samples indicated they averaged 6% heavier. Consequently, we assumed no significant growth rate differences between the two strains.

We set model time of entry into the spawning

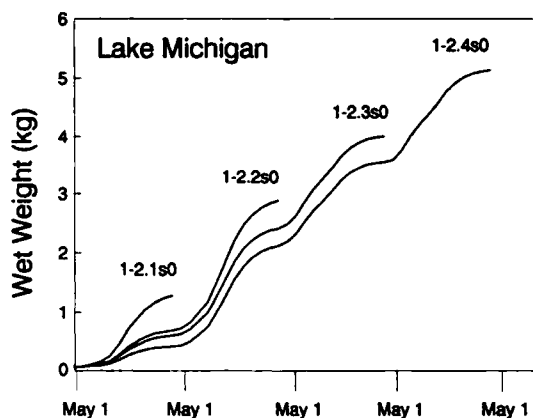


FIGURE 4.—Simulated growth of the four virgin life history forms of spring-run steelhead in Lake Michigan. Growth was fitted to empirical weight-at-age data based on measured size at the weir on the Little Manistee River (mean over period 1980–1987) and back-calculated spring weights during lake residence based on adult scale measurements. Life history notation is defined in Table 4.

streams at August 1 for summer-run fish, November 1 for fall-run fish, and April 1 for spring-run fish. We knew virtually nothing about the adult stream residence period, and because we were primarily interested in prey consumption in the lake, we did not model the stream phase of the adult steelhead life history. For repeat spawners, it was necessary to predict the weight of spent adults returning to the lake after spawning. Fall-run steelhead lose body weight during the stream residence period. Mottley (1938) found that spawning rainbow trout lost significant weight prior to spawning (9% and 14% wet-weight loss for females and males, respectively). We compared \log_{10} -transformed length–weight regressions of steelhead caught in a gill net in the Salmon River in November 1987 (sexually mature fish that had just entered the streams) with steelhead collected at the Salmon River Hatchery (5 km upstream) the following spring just prior to stripping (L. Wedge, NYDEC, unpublished data). Test for homogeneity of slopes was not significant ($P = 0.27$), which allowed us to use a pooled slope value. Intercepts were significant ($P < 0.001$). Adjusted least-squares means differed by 422 g (fall: 3,491 g; spring: 3,069 g), representing an overwinter drop in weight of the average individual of 12.1%. This value agrees well with Mottley's (1938) estimate. We multiplied this percentage by the weight on November 1 for fall-run and summer-run spawning fish that overwinter in the stream to estimate prespawning

weight the following spring (May 1). We reduced weight an additional 10% for all spawning fish (mean of males and females) that reentered the lake the following spring to account for gonadal losses during spawning (Stewart et al. 1983). We assumed in the model that spent spawners emigrated from the streams on May 1 (Seelbach 1993).

Diet.—Jude et al. (1987) examined diets of 79 juvenile steelhead caught with seines or gill nets near the Cook Power Plant on the eastern shore of Lake Michigan during 1973–1982. Total lengths of the juvenile fish ranged from 100 to 300 mm, corresponding to the first year of life in the lake. Diet composition was expressed in percentage wet weight. We constructed the juvenile diet schedule (simulation days 1–91) for both Lakes Michigan (Table 6) and Ontario (Table 7) using these data.

We summarized data from a diet survey of adult steelhead caught in the sport fishery between May and early September along the Wisconsin border of Lake Michigan from 1982 to 1988 (Table 6). Volunteers and University of Wisconsin personnel identified prey fish found in predator stomachs to species (if possible) and recorded total length. Prey fish categories used in the final diet table included rainbow smelt *Osmerus mordax*, small alewife *Alosa pseudoharengus* (< 8 g), large alewife (≥ 8 g), and other fish (including yellow perch *Perca flavescens*, slimy sculpin *Cottus cognatus*, and threespine stickleback *Gasterosteus aculeatus*). We used species-specific length–weight regression equations to convert prey total length to wet weight. The presence of invertebrates and zooplankton were noted in census years 1982–1987. During 1988, wet weights of these diet items were measured directly at the check stations. Because of the small sample size (143 stomachs with food), we chose to pool all the years and sort the data by month and predator size (according to weight-at-age estimates in Table 5). We applied the mean wet weights for invertebrates and zooplankton measured in 1988 to the corresponding size and month categories in the 1983–1987 data when these diet items were noted. We feel this was appropriate considering over 40% of the nonempty steelhead stomachs were from fish caught in 1988.

A diet survey of Lake Ontario steelhead was conducted from April to September along the New York shoreline during 1983–1988 (Table 7). State University of New York personnel and volunteers examined 225 nonempty steelhead stomachs (for results of the first two survey years, see Brandt 1986). We estimated wet-weight contributions of prey fish to the diet both seasonally and ontogenetically as described for the Lake Michigan sur-

TABLE 6.—Data on proportions of diet composition for Lake Michigan steelhead (P, by weight; subscripts are inv = macroinvertebrates, zoo = microcrustacean zooplankton, oth = other fish, rs = rainbow smelt, sma = small alewife (<8 g), and lga = large alewife (≥8 g). Estimates are based on data collected from a salmonine diet survey conducted along the Wisconsin border of Lake Michigan, 1983–1988. Because of relatively small annual samples, it was necessary to pool the annual samples. Data for juvenile steelhead were provided by D. J. Jude (University of Michigan) as unpublished data from the study of Jude et al. (1987). Simulation day 1 is May 1.

Simulation days	N	Food type					
		P _{inv}	P _{zoo}	P _{oth}	P _{rs}	P _{sma}	P _{lga}
Lake age 1							
1–60	51 ^a	0.83	0.05	0.12	0.00	0.00	0.00
61–91	^b	0.83	0.05	0.12	0.00	0.00	0.00
92–122	29 ^a	0.32	0.05	0.12	0.01	0.50	0.00
123–152	^c	0.06	0.06	0.64	0.10	0.08	0.06
153–183	^c	0.06	0.06	0.64	0.10	0.08	0.06
184–365 ^d	^e	0.31	0.07	0.00	0.08	0.38	0.16
Lake age 2							
1–60	27	0.31	0.07	0.00	0.08	0.38	0.16
61–91	16	0.08	0.31	0.00	0.08	0.37	0.16
92–122	18	0.06	0.06	0.64	0.10	0.08	0.06
123–152	^c	0.06	0.06	0.64	0.10	0.08	0.06
153–183	^c	0.06	0.06	0.64	0.10	0.08	0.06
184–365 ^d	^f	0.18	0.00	0.00	0.02	0.51	0.29
Lake age 3–4							
1–60	28	0.18	0.00	0.00	0.02	0.51	0.29
61–91	13	0.19	0.09	0.08	0.14	0.29	0.22
92–122	41	0.16	0.29	0.18	0.04	0.21	0.12
123–152	^g	0.16	0.29	0.18	0.04	0.21	0.12
153–183	^g	0.16	0.29	0.18	0.04	0.21	0.12
184–365 ^d	^h	0.18	0.00	0.00	0.02	0.51	0.29

^a Unpublished data from study of Jude et al. (1987).

^b Data from days 1–60 of lake age 1.

^c Data are from pooled sample of age-1 and age-2 fish caught from August and September.

^d Due to the absence of data during certain periods of the year, values for each day in this interval were estimated by linear interpolation between the tabled values for this interval and those preceding it.

^e Data from day 1 of lake age 2.

^f Data from day 1 of lake age 3.

^g Data are from pooled sample of age-3–4 fish caught in August and September.

^h Data from day 1 of lake age-3–4.

vey. Volunteers did not estimate contributions of invertebrates and zooplankton to the diet in the Lake Ontario survey, so we approximated these by applying values from corresponding Lake Michigan categories. We apportioned the remaining stomach contents among prey fish based on wet weights converted from prey lengths.

Predator and prey energy density.—We used data on ontogenetic and seasonal variability in Lake Michigan alewife energy density from Stewart and Binkowski (1986), based on original data of Flath and Diana (1985). Age-0 fish were put in the diet

TABLE 7.—Data on proportions of diet composition for Lake Ontario steelhead (P, by weight; subscripts are inv = macroinvertebrates, zoo = microcrustacean zooplankton, oth = other fish, rs = rainbow smelt, sma = small alewife (<8 g), and lga = large alewife (≥8 g). Estimates are based on data collected from a salmonine diet survey conducted along the New York shoreline of Lake Ontario, 1982–1988. Data for juvenile steelhead were taken from unpublished data from the study of Jude et al. (1987). Because no records were taken on invertebrate and zooplankton diet components in the survey, data for P_{inv} and P_{zoo} were taken directly from the Lake Michigan diet survey, and the remaining stomach contents were apportioned based on empirical wet weight proportions of observed prey fish. Simulation day 1 is May 1.

Simulation days	N	Food type					
		P _{inv} ^a	P _{zoo} ^a	P _{oth}	P _{rs}	P _{sma}	P _{lga}
Lake age 1							
1–60	51 ^b	0.83	0.05	0.12	0.00	0.00	0.00
61–91	^c	0.83	0.05	0.12	0.00	0.00	0.00
92–122	29 ^b	0.32	0.05	0.12	0.01	0.50	0.00
123–152	14	0.06	0.06	0.00	0.30	0.29	0.29
153–183	^d	0.06	0.06	0.00	0.30	0.29	0.29
184–333 ^e	^d	0.31	0.07	0.00	0.20	0.21	0.21
334–365	^d	0.31	0.07	0.00	0.20	0.21	0.21
Lake age 2							
1–60	53	0.31	0.07	0.00	0.09	0.10	0.43
61–91	27	0.08	0.31	0.00	0.15	0.10	0.36
92–122	^f	0.06	0.06	0.00	0.22	0.13	0.53
123–152	^f	0.06	0.06	0.00	0.22	0.13	0.53
153–183	^f	0.06	0.06	0.00	0.22	0.13	0.53
184–333 ^e	^g	0.18	0.00	0.00	0.38	0.10	0.34
334–365	17	0.18	0.00	0.00	0.38	0.10	0.34
Lake age 3–4							
1–60	73	0.18	0.00	0.00	0.13	0.16	0.53
61–91	21	0.20	0.08	0.00	0.00	0.04	0.68
92–122	20	0.18	0.31	0.00	0.31	0.07	0.13
123–152	^h	0.18	0.31	0.00	0.31	0.07	0.13
153–183	^h	0.18	0.31	0.00	0.31	0.07	0.13
184–333 ^e	ⁱ	0.18	0.00	0.00	0.13	0.16	0.53
334–365	ⁱ	0.18	0.00	0.00	0.13	0.16	0.53

^a Values in P_{inv} and P_{zoo} prey categories are taken directly from Lake Michigan diet survey (see Table 6).

^b Unpublished data from study of Jude et al. (1987).

^c Data from day 1 of lake age 1.

^d Data from days 123–152 of lake age 1; represents pooled sample from April to September.

^e Due to the absence of data during certain periods of the year, values for each day in this interval were estimated by linear interpolation between the tabled values for this interval and those preceding it.

^f Data on prey fish proportions taken from days 61–91 of lake age 2.

^g Data from days 334–365 of lake age 2.

^h Data from days 92–122 of lake age 3–4.

ⁱ Data from day 1 of lake age 3–4.

category of small alewife and yearling and older fish in the large alewife category. Seasonal energy densities of Lake Michigan rainbow smelt were those compiled by Lantry and Stewart (1993, this

issue). Ontogenetic and seasonal variability in energy densities of Lake Ontario alewives and rainbow smelt emerged from measurements of prey fish caught monthly in southeastern Lake Ontario during May–November 1989 and March 1990 (Rand et al., unpublished).

We assumed that energy densities of other prey fish remained constant over the annual cycle at $5,700 \text{ J} \cdot \text{g}^{-1}$, wet weight (Stewart et al. 1983). Stewart and Binkowski's (1986) value for cladocerans— $1,674 \text{ J} \cdot \text{g}^{-1}$, wet weight—was used for zooplankton. We approximated steelhead energy density using a relationship between energy (Q , $\text{J} \cdot \text{g}^{-1}$) and wet weight (W , g) developed for coho salmon in Lake Michigan: $Q = 5,763 + 0.986 \cdot W$ (Stewart and Ibarra 1991).

Water temperature.—We used the temperature data of Stewart et al. (1983) for the Lake Michigan simulations based on original measurements of Ayers (1962). For the Lake Ontario simulations, we used the temperature data collected at bioindex station 41 (midlake station) of the Canadian Center for Inland Waters (CCIW) monitoring program (O. Johanssen, CCIW, unpublished data). Weekly measurements of temperature were taken from the surface down to 10 m depth during 1981–1986. We assumed steelhead occupied the warmest water available up to but not exceeding the species' preferred temperature. Preferred temperatures were taken to be 19°C for the first summer in the lake and 15°C thereafter, based on laboratory studies by Kwain and McCauley (1978) and field determinations of occupied water temperatures in Lake Michigan (Spigarelli and Thommes 1979) and Lake Ontario (Haynes et al. 1986).

Sensitivity Analysis

Because a comprehensive sensitivity analysis has been conducted on a similar energetics model applied to lake trout (Stewart et al. 1983) and sockeye salmon (Beauchamp et al. 1989), we assessed the sensitivity of parameters used in the population submodel. We increased and decreased individual parameter values by 10% in the population model and compared model output to that of the nominal run. The sensitivity of eight parameters were assessed in the analysis: presmolt survival in trout rivers, presmolt survival in marginal rivers, presmolt survival in river mouths, annual lake survival, spawning survival, percent of fall–spring-run steelhead that run in the spring, smolt length at time of stocking, and occupied summer epilimnial temperature. We also ran a simulation of steelhead feeding only on inverte-

brates at 20°C from July 1 to September 1 to assess the bioenergetic responses of individuals occupying the thermal breaks characterized by higher concentrations of particles. The nominal simulation was of annual consumption by fall–spring-run steelhead in Lake Michigan in 1987.

Results

Seasonal Predation

We present modeling estimates of monthly cumulative consumption by steelhead in Lake Michigan in 1987 and in Lake Ontario in 1990 (Figure 5). Levels of predation in Lake Michigan closely followed the seasonal pattern of water temperature, reaching a low of 0.25 kilotonnes (kt) per month in March and a high of $1.3 \text{ kt} \cdot \text{month}^{-1}$ in September. Predation on large alewives ranged from 0.05 to $0.21 \text{ kt} \cdot \text{month}^{-1}$. Seasonal patterns of total prey consumption were similar in Lake Ontario. The lowest rate of predation occurred in April ($0.06 \text{ kt} \cdot \text{month}^{-1}$) and the greatest rate in September ($0.34 \text{ kt} \cdot \text{month}^{-1}$). Alewives composed a greater proportion of steelhead diets in Lake Ontario than in Lake Michigan, and rates of alewife consumption ranged from 0.02 to $0.13 \text{ kt} \cdot \text{month}^{-1}$. Stocking numbers per unit lake surface area and size at stocking were consistently higher in Lake Michigan than in Lake Ontario. In addition, wild smolt yield was significantly greater in Lake Michigan, due to more abundant and better-quality rearing streams. Steelhead growth was also significantly greater in Lake Michigan, which resulted in increased predation per individual stocked. These processes resulted in higher annual rates of steelhead predation in Lake Michigan in 1987 ($0.16 \text{ g} \cdot \text{m}^{-2}$) than in Lake Ontario in 1990 ($0.12 \text{ g} \cdot \text{m}^{-2}$).

Invertebrates represented an important component of total predation by the steelhead population in spring (34–36% by weight in June), and zooplankton (especially the exotic cladoceran *Bythotrephes cederstroemi*) made up a significant proportion of the diet in the fall (18% by weight in September). We calculated the proportion of available alewife production consumed by Lake Michigan steelhead in 1987 based on acoustic measures of biomass and model estimates of alewife production (Brandt et al. 1991). We estimated steelhead consumed 3.3 kt of alewives in 1987, which represented only 4% of the alewife production available to foraging salmonines in that year. This quantity of alewife removal is about half the 6.7 kt estimated for steelhead by Brandt et al.

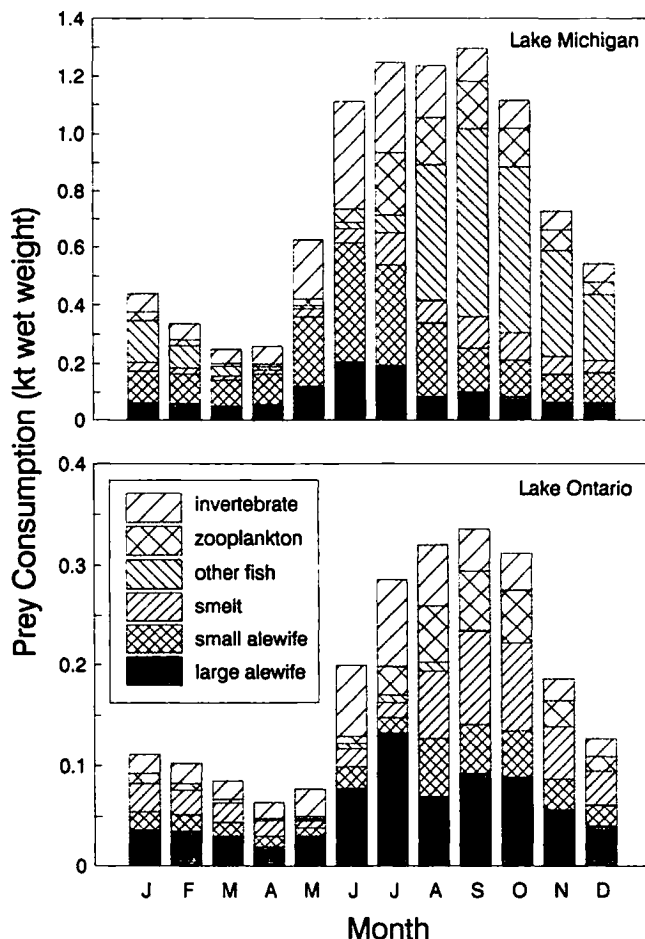


FIGURE 5.—Model estimates of consumption by diet type for Lake Michigan steelhead in 1987 and Lake Ontario steelhead in 1990. Bars represent cumulative predation (in kilotonnes [kt] wet weight) over the month.

(1991, Table 7, reported as 9.9 kt for rainbow trout and brown trout). Much of that discrepancy can be explained by differences in assumptions about diet composition (i.e., greater contribution of invertebrates in present analysis) and survival schedules. Steelhead consumed approximately 0.65 kt of rainbow smelt in 1987, which represented only 2% of total smelt production in Lake Michigan based on production estimates of Lantry and Stewart (1993). Although no estimates of alewife production are currently available for Lake Ontario, recent acoustic estimates (A. Goyke and S. Brandt, University of Maryland, personal communication) indicate that alewife biomass in Lake Ontario in 1990 exceeded that in Lake Michigan in 1987. Based on lower predation pressure by steelhead and higher alewife biomass in Lake Ontario, we concluded that steelhead had less impact

on available alewife production in Lake Ontario in 1990 than in Lake Michigan in 1987. Steelhead from Lake Ontario consumed 0.46 kt of rainbow smelt in 1990, which amounts to approximately 2% of total smelt production (Lantry and Stewart 1993).

Total Prey Consumption, 1975–1990

The magnitude of steelhead prey consumption in both lakes has increased dramatically since the mid 1970s (Figure 6). Predation in Lake Ontario increased fairly steadily to $2.2 \text{ kt} \cdot \text{year}^{-1}$ in 1990, whereas predation rates in Lake Michigan reached a peak of $9.5 \text{ kt} \cdot \text{year}^{-1}$ in 1986 and then dropped to $6.9 \text{ kt} \cdot \text{year}^{-1}$ in 1990. These trends in predation are driven largely by stocking. The drop in predation by Lake Michigan steelhead in the late 1980s was due primarily to reduced stocking of

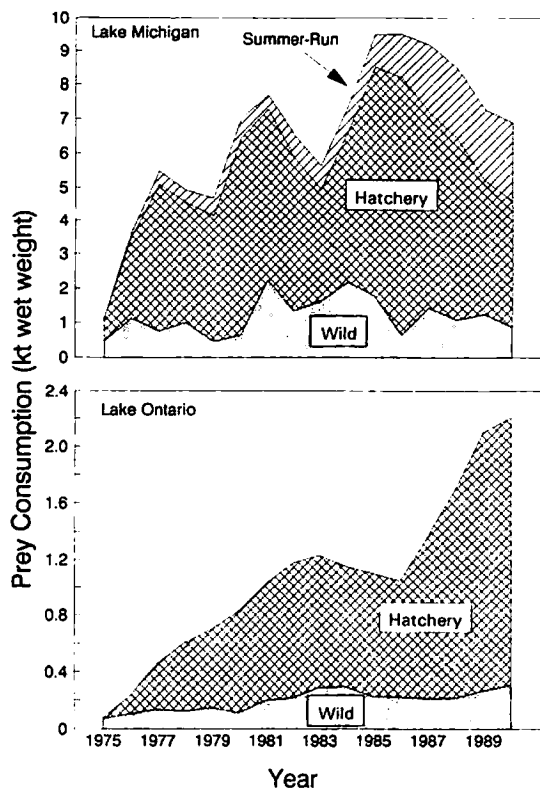


FIGURE 6.—Trends in total prey consumption (kilotonnes, kt) by steelhead in Lakes Michigan and Ontario over the period 1975–1990. Greater variability in Lake Michigan resulted from dynamics of natural recruitment and changes in year-to-year abundance and size of released hatchery fish.

the Shasta strain in Wisconsin. Year-to-year fluctuations in consumption were more pronounced in Lake Michigan, in part because wild smolts were both more abundant and more variable in recruitment (Figure 3). The hatchery year-classes also varied considerably in Lake Michigan. The predatory demand of summer-run steelhead in Lake Michigan has grown since the strain was introduced in 1976 (Figure 6). In 1990, summer-run steelhead accounted for 33% of total steelhead predation in Lake Michigan. Wild steelhead in 1990 accounted for 13 and 14% of total steelhead prey consumption in Lakes Michigan and Ontario, respectively.

Sympatric Salmonines in Lake Michigan

In comparison with previous modeling estimates for other salmonines (Stewart and Ibarra 1991), steelhead prey consumption represented 14% of the total predation by salmonines (brown

trout excluded) in Lake Michigan during 1987 (Figure 7). Chinook salmon were responsible for 63% of total predation, steelhead and coho salmon for 14% each, and lake trout for 9%. In terms of impact on alewife stocks, annual steelhead consumption (1.1 kt of large alewives and 2.2 kt of small alewives) was similar to that of coho salmon and lake trout but considerably lower than consumption by chinook salmon (11.5 kt of large and 19.3 kt of small alewives). Steelhead exhibited a lower population biomass conversion efficiency (16.1%; gross annual production/total annual consumption, in g wet weight) than the other *Onco-rhynchus* species, but it was similar to the conversion reported for lake trout (16.1%; Stewart and Ibarra 1991). This low value resulted from the larger invertebrate component in the diets of adult steelhead and slower growth rates compared with coho and chinook salmon. Steelhead production-to-biomass ratio (P:B) in 1987 was 1.18, which was lower than that of chinook salmon (1.6), similar to that of coho salmon (1.15), and higher than that of lake trout (0.6).

To better understand the differences in predation among species, we compared total predation per million fish stocked between the four common salmonines. We included estimates of consumption by chinook salmon, coho salmon, and lake trout originally reported by Stewart and Ibarra (1991). These values were compared to model estimates of consumption by 10^6 stocked fall fingerling steelhead and 10^6 stocked yearling steelhead (Figure 8). In the steelhead simulations, we assumed fingerlings and yearlings were stocked in equal proportions among marginal rivers, trout rivers, and river mouths. In addition, we estimated survival of yearlings based on a mean size of 150 mm TL and an SD of 20 mm. Because of high rates of fall fingerling mortality, total predation by 10^6 stocked fingerlings was only 0.43 kt. This estimate was an order of magnitude less than chinook salmon predation per million fingerlings stocked (5.9 kt), which can be attributed to higher survival and significantly greater growth rates of chinook salmon. Predation estimates for coho salmon (3.5 kt) and lake trout (2.5 kt) were calculated for yearling equivalents; the corresponding estimate for yearling steelhead (3.5 kt) matched that of coho salmon, although the steelhead ate more invertebrates (Figure 8).

Sensitivity Analysis

The most sensitive parameters affecting model output were annual lake survival and smolt length

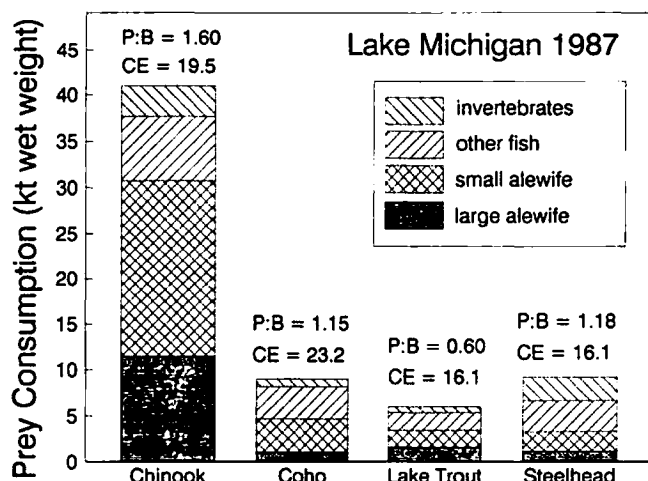


FIGURE 7.—Comparison of whole-lake predation estimates (kilotonnes, kt) for four common salmonines in Lake Michigan. Values for chinook salmon, coho salmon, and lake trout were taken from Stewart and Ibarra (1991). All predation estimates are based on conditions during 1987 in Lake Michigan. Chinook salmon accounted for 63% of the predation among these species and exhibited the highest production-to-biomass ratio (P:B). Steelhead had a relatively low conversion efficiency (CE, percent) and a moderate production-to-biomass ratio compared with the other salmonines.

(Figure 9). An increase of 10% from the nominal annual survival value resulted in nearly a 12% increase in annual consumption. Conversely, a decrease of 10% in the survival value resulted in a decrease in annual consumption by 11%. A 10% decrease in mean smolt length had a more pronounced effect on model output (−13.2%) than

did a 10% increase, which raised the estimate of consumption by 7.8%. Most smolts stocked are over the 150 mm TL threshold. A 10% decrease in mean size markedly increased the numbers of small yearlings, which have much lower survival (Table 2). Among the other model parameters, the presmolt survival parameter applied to marginal

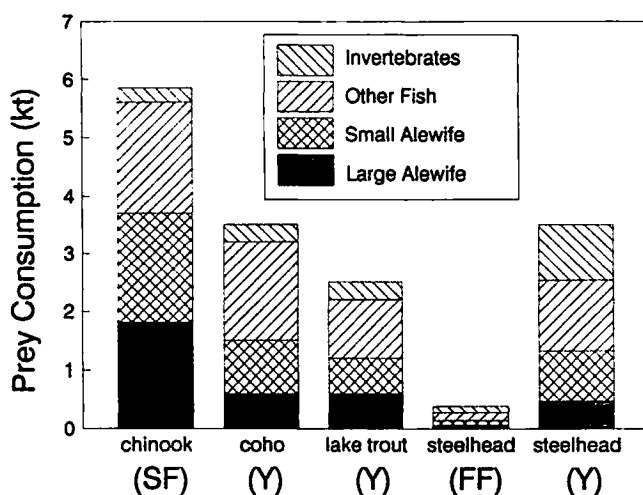


FIGURE 8.—Prey consumption (kilotonnes, kt) per million fish stocked for three previously modeled salmonines (Stewart and Ibarra 1991) and steelhead in Lake Michigan. Prey consumption estimates for yearlings (Y) were lowest for lake trout and similar for coho salmon and steelhead. Chinook salmon, stocked commonly as spring fingerlings (SF), exhibited the greatest predatory effect on prey. Diet of steelhead was more evenly distributed among the four diet categories. Predation by steelhead fall fingerlings (FF) was low due to high poststocking mortality.

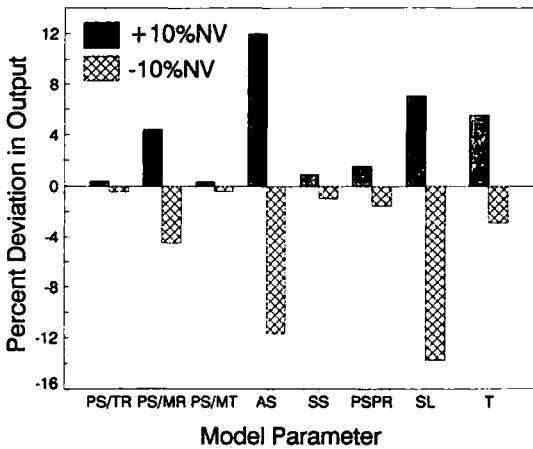


FIGURE 9.—Sensitivity of model output to parameter perturbations ($\pm 10\%$ of nominal value, NV) in the population submodel. Most sensitive parameters were lake survival (AS) and size of yearlings at stocking (SL). The other parameters, in order of sensitivity, are T (occupied summer epilimnial temperature), PS/MR (poststocking survival in marginal rivers), PSPR (proportion of population that migrates to streams in spring), SS (spawning survival), PS/TR (poststocking survival in trout rivers), and PS/MT (post-stocking survival in river mouths).

waters was more sensitive than the other presmolt survival values because marginal rivers were the most common receiving waters for stocked steelhead.

Our results from the hypothetical scenario of steelhead occupying warmer epilimnial waters and foraging exclusively on invertebrates for 2 months showed a significant drop in population conversion efficiency (0.16 to 0.11). To attain final size by the end of the simulation (based on weight-at-age values from the nominal run), individuals increased total consumption by 33% as a result of increased metabolic losses at warmer temperature but had lower energy content in their forage. A breakdown of the diet indicated that invertebrate consumption increased by 188% (by weight) from the nominal run, and fish consumption decreased by 30% (by weight).

Discussion

Steelhead appeared to have a limited predatory presence in the pelagic ecosystems of Lakes Michigan and Ontario. Lake Michigan steelhead consumed approximately 4% of the annual available alewife production and 2% of total rainbow smelt production, and accounted for approximately 14% of total salmonine predation (exclusive of brown

trout consumption) in 1987. Similarly, Lake Ontario steelhead consumed less than 2% of total rainbow smelt production and were likely to consume a very small proportion of available alewife production. Relatively low conversion efficiencies ($<17\%$) and P:B ratios (<1.2) of the steelhead populations in both lakes reflect their dietary use of energy-poor invertebrates and their moderate rates of growth in these lakes.

The steelhead's presumed preference for invertebrates may be related to their inefficiency at capturing prey fish in the pelagic environment. Savitz and Bardygula (1989) studied interactions between Lake Michigan salmonines and prey fishes in a large aquarium. They concluded that unlike more aggressive chinook and coho salmon, steelhead had trouble capturing fish in the open water and often relied on trapping prey in corners or along physical structures in the aquarium. Therefore, the evidence of steelhead foraging along the invertebrate-rich scum lines offshore (Haynes et al. 1986) may represent specialized foraging behavior, rather than competition for limited prey fish resources among the salmonine community.

Management Implications

With increased concern about the sustainability of the prey fish stocks in the Great Lakes, there is much interest in designing a stocking program that will effectively reduce the total demand for imperiled forage species by the stocked salmonines. One approach, discussed in some length by Stewart et al. (1981), is to adjust the species mix and increase the relative proportion of the species that have a lower reliance on alewife as a diet item. Steelhead have been recognized as fish that strongly supplement their diets with invertebrates and zooplankton, thus reducing overall impact on prey fish stocks. Steelhead also appear to consume a greater diversity of prey fish than chinook and coho salmon. Lake Michigan data indicate that yellow perch made up 58% (by weight) of prey consumed by 1- and 2-year-old steelhead and 17% of the diet of 3- and 4-year-olds in August and September. Threespine sticklebacks and slimy sculpin contributed much less to the diets. In the event of further declines in alewife abundance, it is possible that steelhead may more readily switch to alternative prey than the other sympatric *Onchorhynchus* spp.

The comparison of predation per million fish stocked allowed us to more equitably compare the predatory impact of each member of the salmonine community. Prey consumption per million

steelhead yearlings stocked is similar to that of coho salmon and greater than that of lake trout. Chinook salmon rely on small and large alewives much more than any of the other modeled salmonines. It is important to account for these differences when a new stocking management plan is designed.

We think steelhead exhibit certain other advantages with respect to future Great Lakes management directions. Because of the life history variability exhibited by steelhead in the Great Lakes, fishing pressure is effectively distributed more equitably in space and time. Successful lake and stream fisheries have developed for steelhead (Keller et al. 1990), and with the success of the summer-run strain in Lake Michigan and the dramatic recent rise in steelhead angling offshore in summer, the species supports fisheries in all seasons in both the lake and its tributaries. One of the objectives put forward by the Great Lakes Fishery Commission (GLFC 1992b) is to produce a naturally sustainable fishery. Although steelhead are exotics, they have been present in the Great Lakes for over 100 years and have developed productive wild populations. With further improvements in tributary water quality and fish habitat, this contribution is expected to grow in the future. Finally, contaminant body burden is significantly lower in steelhead than in other common stocked salmonines in the Great Lakes (Oliver and Niimi 1988; Madenjian et al., in press).

Further Research

Throughout the model-building process, several gaps in our knowledge of steelhead life history became evident. For example, our diet data may have underestimated the importance of invertebrates in the diets of adult steelhead. Many anecdotal observations from the summer boat fishery in Lakes Michigan and Ontario indicate steelhead diets consisting almost wholly of invertebrates. The period during which we conducted the diet surveys (1982–1988) was before the dramatic rise in the offshore steelhead fishery, so our samples may have underrepresented the fish foraging in these regions. Our modeled scenario of steelhead feeding in warmer epilimnial waters on invertebrates indicated that this behavior could significantly affect bioenergetics. This is an obvious subject for further research effort.

Our analysis indicated that more attention should be given to reducing uncertainty in the estimates of survival rates. We based our lake survival estimates in this study on the mean of 3

years of data on smolt-to-adult survival measured on a wild population in central Michigan (Seelbach 1993). Our presmolt survival values were obtained from several studies conducted by the MDNR (Seelbach 1987a, 1989, 1991). The resulting cohort life table for Lake Michigan is better than that for any previously studied population of steelhead in the Great Lakes, but similar studies are needed for the other lakes. As our sensitivity analysis revealed, more effort is needed in measuring annual variability of lake survival. The results of our sensitivity analysis of the presmolt survival estimates were misleading, because a 10% adjustment in a small value (0.01–0.10) has a smaller effect on the parameter than a 10% change in a larger value, such as our estimate of annual lake survival (0.47). Effort should be directed to measuring smolt yield through the use of smolt traps and closely monitoring adult returns from individual cohorts. Additional efforts should also be directed at more accurately quantifying hatchery smolt survival as a function of stocking size, location, and time of year.

Little is known of metabolic expenditures and diet of steelhead and other salmonines during the winter periods. No study to our knowledge has carried out detailed metabolic measures at very cold water temperatures (less than 4–5°C) and diet data are often lacking during this period. Cunjak et al. (1987) demonstrated loss of condition and insufficient energy intake during early winter for brook trout *Salvelinus fontinalis* in the Credit River, Ontario. They concluded that energy intake was limited due to a bottleneck in the digestion process rather than to ambient food limitations. Cunjak et al. estimated metabolic expenditures with Elliott's (1976b) experimentally derived relationship for brown trout at temperatures ranging from 3.8 to 19.5°C. It was necessary to extrapolate those results to as low as 0.7°C in Cunjak et al.'s (1987) study. We feel more work is necessary to understand the energetics of presmolt and adult fish at low water temperatures and attempts should be made to obtain diet data during cold periods. Such information might help elucidate mechanisms underlying the strong correlations between smolt survival and winter severity observed in this study. These studies are particularly critical for extending modeling analysis to the presmolt and adult stream phases in order to develop a more complete model over the entire life history of this species. This would serve as an important step in better managing wild steelhead populations throughout the Great Lakes.

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