An Energetics Model for Lake Trout, *Salvelinus namaycush*: Application to the Lake Michigan Population[1]

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An energetics model is implemented for lake trout, *Salvelinus namaycush*, and applied to the Lake Michigan population. It includes an egestion function allowing any proportional mix of fish and invertebrates in the diet, a growth model accounting for both ontogenetic and seasonal changes in energy-density of predator and prey, a model for typical in situ swimming speed, and reproductive energy losses due to gametes shed. Gross conversion efficiency of energy by lake trout over their life (21.8%) is about twice the efficiency of converting biomass to growth because they store large amounts of high-energy fats. Highest conversion efficiencies are obtained by relatively fast-growing individuals, and over half the annual energy assimilated by older age-classes may be shed as gametes. Sensitivity analysis indicates a general robustness of the model, especially for estimating consumption by fitting a known growth curve. Largest sensitivities were for the intercept and weight dependence coefficients of metabolism. Population biomass and associated predatory impact of a given cohort increase steadily for about 3.5 yr then decline steadily after fishing mortality becomes important in the fourth year in the lake. This slow response time precludes manipulation of lake trout stocking densities as a means to control short-term prey fluctuations. Predation by lake trout on alewife, *Alosa pseudoharengus*, has been increasing steadily since 1965 to about 8 400 $t \cdot yr^{-1}$, and is projected to rise to almost 12 000 $t \cdot yr^{-1}$ by 1990.

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On a élaboré un modèle de l'énergétique à l'intention du touladi, *Salvelinus namaycush*, que l'on a appliqué à la population du lac Michigan. Le modèle inclut une fonction d'égestion permettant d'introduire dans le régime alimentaire un mélange proportionnel de poissons et d'invertébrés, un modèle de croissance qui tient compte des changements à la fois ontogéniques et saisonniers de l'énergie et de la densité du prédateur et de la proie, un modèle de vitesse de nage in situ typique et, enfin, la perte d'énergie reproductrice par suite de la mise en liberté de gamètes. Comme le touladi emmagasine de grandes quantités de graisse de haute énergie, le rendement nutritif brut durant toute la vie du touladi (21,8 %) est environ le double de celui de conversion de la biomasse en croissance. On obtient des rendements maxima avec des individus à croissance relativement rapide, et plus de la moitié de l'énergie accumulée par les poissons plus âgés peut être libérée sous forme de gamètes. D'après une analyse de sensibilité, le modèle est généralement solide, surtout lorsqu'il s'agit d'estimer la consommation en adaptant une courbe de croissance connue. Les sensibilités les plus importantes touchent l'ordonnée à l'origine et les coefficients de métabolisme dépendant du poids. La biomasse de la population et l'impact de prédation qui lui est associée d'une cohorte

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donnée augmente régulièrement pendant environ 3,5 ans, pour ensuite diminuer de même une fois que la mortalité par pêche est devenue importante dans le lac pendant la quatrième année. À cause de cette lente réponse, on ne peut manipuler la densité des peuplements de touladis d'un lac comme moyen de contrôle à court terme des fluctuations des proies. La prédation du touladi sur le gaspareau, *Alosa pseudoharengus*, a augmenté régulièrement depuis 1965 pour atteindre environ 8 400 $\mathrm{tm \cdot an^{-1}}$ et on prévoit qu'en 1990, elle aura atteint presque 12 000 $\mathrm{tm \cdot an^{-1}}$.

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THE lake trout (or charr), *Salvelinus namaycush*, has historically been a dominant top predator as well as an important component of the commercial catch in Lake Michigan. Extinction of wild populations in the mid-1950s and reestablishment of a hatchery-dependent (nonreproducing) lake trout population by the early 1970s is well-known (Smith 1968; Wells and McLain 1973; Rybicki and Keller 1978). The existing population supports an important sport fishery. Managers are being pressed by public enthusiasm to increase salmonid stocking densities, but increases cannot continue indefinitely because salmonid production in Lake Michigan must necessarily be limited by available production of forage organisms.

This study uses bioenergetics modeling to address a fundamental management question: "What are the forage requirements of existing and projected future lake trout populations in Lake Michigan?" It brings together subsets of data from studies conducted at the Great Lakes Fishery Laboratory (GLFL, USFWS) (D. Rottiers and associates, unpublished data summarized in Research Completion Reports; G. Eck, personal communication, GLFL, Ann Arbor, MI), available literature, and newly developed energetics theory. The approach begins with a mass-balance equation (Winberg 1956; Warren and Davis 1967; Kitchell et al. 1977; Webb 1978), and is the latest in a series (e.g. Kitchell et al. 1974; Kitchell et al. 1977; Weininger 1978; Breck and Kitchell 1979; Kitchell and Breck 1980). New functions are developed for egestion, swimming speed and growth with ontogenetic and seasonal changes in energy density of predator and prey.

Our objective is to reconstruct food consumption from observed growth rather than to predict growth. Observed growth in Lake Michigan results from consumption integrated over time. The summation of daily growth, metabolism, and waste losses provides an estimate of daily consumption for the average individual lake trout. Given the existing data base on the energetics of lake trout, we believe the energetics approach may be the most cost-effective and perhaps the most accurate of available methods (Mann 1978) for estimating annual forage needs of the trout. Forage requirements of the average individual are extended to the entire population using a population model with mortality rate estimates from Rybicki and Keller (1978). Absence of natural reproduction in the Lake Michigan population simplifies population biomass estimates, since known recruitments come from hatcheries.

Components of the Energetics Model

ENERGETICS BALANCE AND MAXIMUM CONSUMPTION

Our energetics model is based on the assumption that the sole energy source for an animal is its food (C, consumption), and that all energy taken in must be used (R, metabolism; SDA, specific dynamic action), lost (F, egestion; E, excretion), or accumulated (ΔB, growth). These components form the energetics balance:

$$C = R + SDA + F + E + \Delta B$$

All components can be converted between mass and energy units. In the remainder of this section the relationship of these components to their controlling variables are developed.

Growth must necessarily be less than or equal to that attainable at maximum consumption. In modeling simulations, laboratory estimates of maximum consumption are adjusted downward until the model fits observed growth (see below). Ad libitum weight-specific consumption $C_{\max}$ ($\mathrm{g \cdot g^{-1} \cdot d^{-1}}$), increases exponentially with increasing temperature at low temperatures, reaches a maximum level at some optimum temperature, and decreases at temperatures greater than optimum (Brett et al. 1969; Edsall et al. 1974; Elliott 1975a, b). For low temperatures, $C_{\max}$ can be represented as a negative power function of weight (Brett 1971a; Kerr 1971; Elliott 1976b), and an exponential function of temperature (Elliott 1976b):

$$(1) \qquad C_{\max} = a\, W^{b} \cdot e^{qT}$$

where, W = fish weight, g
T = temperature, °C
and a, b, q = empirical constants.

This simple model differs from our previous work (Kitchell et al. 1977) but may be appropriate for the temperature range which a lake trout typically occupies of its own volition.

The parameters of eq. (1) can be estimated from a series of laboratory studies conducted in 1970 and 1972 at the Great Lakes Fishery Laboratory (GLFL), Ann Arbor (D. Rottiers, D. O'Conner, and T. Edsall, unpublished data), using lake trout obtained as fingerlings from the Jordan River National Fish Hatchery. Fish of three initial size-classes (about 40, 250, and 1200 g) were held in tanks at 12°C, and fish of the smallest size-class were held at eight temperatures (3.5, 5.0, 7.0, 10.0, 12.0, 15.0, 18.0, and 20.0°C). All fish for a particular experimental condition were grouped in a single tank. All fish were fed excess rations of freshly thawed pieces of alewife (*Alosa pseudoharengus*) twice daily throughout the 12-wk experiment, with the exception of one 2-wk period. During this 2-wk period, insufficient supplies of alewife made it necessary to feed some groups of fish (at 5, 7, 10, 15, and 18°C in 1970) with dry fish pellets. All data from this exceptional 2-wk interval were omitted. Uneaten food was recovered and its weight subtracted from the original amount fed to determine the daily food consumption.

Weight dependence of C_{max} was evaluated using the three size-groups studied at 12°C. In these tanks, consumption and growth of the fish declined noticeably in the latter part of the experiment, suggesting that the fish were stressed in some way. Estimates of maximum consumption were made using the four highest values for each group. This approach is comparable to that used by Brett (1971a) for estimating C_{max} of sockeye salmon, *Oncorhynchus nerka*.

The natural logarithm of the weekly average of daily observations for C_{max} ($g \cdot g^{-1} \cdot d^{-1}$) for each tank of fish was regressed against the natural logarithm of average individual fish weight for the tank. The resulting regression equation for fish at 12°C:

$$(2) \qquad \log_e C_{max} = -1.503 - 0.307 \log_e W,$$

fit the data closely ($r^2 = 0.99$). The weight dependence coefficient, $b = -0.307$, falls between Elliott's (1976b) estimates of -0.241 for brown trout, *Salmo trutta*, at 12°C and the value -0.35 which was estimated for sockeye salmon at 15°C (analysis of data in Brett 1971a). It is within the range (-0.302 to -0.335) found by Niimi and Beamish (1973) for largemouth bass, *Micropterus salmoides*.

The temperature dependence of C_{max} was evaluated for temperatures up to and including 10°C, because this is the range of temperatures typically occupied by lake trout in Lake Michigan. The weekly average of daily C_{max} observations for each tank was adjusted to equivalent consumption for a 50-g fish using the weight dependence exponent, -0.307. The natural logarithms of these values were regressed on average weekly temperature for each tank. The following regression equation provided a good fit ($r^2 = 0.78$, $P < 0.001$, $n = 75$, 50-g fish).

$$(3) \qquad \log_e C_{max} = -4.033 + 0.123T$$

Residuals from this regression and the previous one were evenly scattered about the regression lines, indicating homogeneous variance for both regressions.

Solving each of the two regression equations given above for C_{max} at 12°C and 50 g revealed that the equation for temperature dependence (3) gives an estimate 15% higher than that from the weight dependence equation (2). Because the weight dependence relationship was derived from a relatively small data set ($n = 12$), we chose to use the weight dependence slope in combination with the intercept and slope from the temperature dependence function. The intercept in $g \cdot g^{-1} \cdot d^{-1}$ for the combined functions will be:

$$a = (e^{-4.033}/50^{-0.307}) = 0.059.$$

The complete model for C_{max} in $g \cdot g^{-1} \cdot d^{-1}$ is therefore:

$$(4) \qquad C_{max} = 0.059\, W^{-0.307} \cdot e^{0.123T}.$$

The intercept should be considered a conservative first approximation because the twice-per-day feeding schedule may not have been sufficient for the trout to attain their absolute upper limit. We chose not to use multiple regression for analysis of the consumption data because the experimental design was not fully crossed.

STANDARD AND ACTIVE METABOLISM

That part of a fish's consumed energy that is used to assimilate the remainder is called the heat increment (Niimi and Beamish 1973) or the specific dynamic action, *SDA*. Beamish (1974) found *SDA* to be 17% of assimilated or usable consumption ($C-F$) for fish on a piscivorous diet, and this proportion was relatively independent of temperature and ration size. Kitchell et al. (1977) modeled *SDA* as a (smaller) proportion of total consumption; this may lead to small errors when diet shifts from invertebrates to fish or a mixture. Here we assume *SDA* is a constant proportion of $C-F$:

$$SDA = 0.17 \cdot (C-F).$$

A general model for total daily metabolism, R_U in $g\ O_2 \cdot d^{-1}$ (5), of a salmonid (excluding *SDA*) was obtained by merging functions for weight and temperature dependence of standard metabolism with that for swimming speed dependence of metabolism (Stewart 1980):

$$(5) \qquad R_U = \alpha W^{\beta} \cdot e^{\rho T} \cdot e^{\nu U}$$

where, U = swimming speed, $cm \cdot s^{-1}$
and, α, β, ρ, ν = empirical constants.

An extensive study of lake trout metabolism as a function of weight, temperature, and swimming speed has been conducted at the GLFL using a flow-through tunnel respirometer (D. V. Rottiers, unpublished data; Bell and Terhume 1970). Fingerlings from the Jordan River National Fish Hatchery were reared to appropriate sizes at GLFL. A total of 578 observations (Table 1) were available for lake trout ranging from 20 to 1800 g, and at temperatures of 3.5, 5, 7, 10, and 15°C. The metabolic rates of fish were measured at swimming speeds of 0.6 to 3.0 body lengths $(bl) \cdot s^{-1}$. Individual fish were used in most experiments although small fish were run in groups of three and very small fish in groups of 20, to provide measurable metabolic rates. Additional observations at 18°C were omitted because they appeared to be above the range of constant exponential increase of metabolism with temperature.

Lake trout were fasted and exercised (10–15 $cm \cdot s^{-1}$) for 48 h then weighed and moved to the respirometer where they were forced to swim. Oxygen consumption was measured continuously during the 24 h the fish were in the respirometer. During the last 8 h of each test the swimming speed was increased in stepwise fashion (10 $cm \cdot s^{-1}$ at 90-min intervals) from the initial speed of 10 or 20 $cm \cdot s^{-1}$ to the final speed of 50 or 60 $cm \cdot s^{-1}$. The O_2 level in the respirometer was maintained above 70% saturation (by regulating exchange rate) so that rate of consumption by the fish was reasonably independent of oxygen level (based on analysis of data in Gibson and Fry 1954).

Oxygen was measured using a YSI model 54 oxygen meter that was calibrated daily using the Alsterberg modification of

TABLE 1. Number of observations for metabolism of lake trout, *Salvelinus namaycush* (at various fish weights, swimming speeds and temperatures), that were used for multiple regression analysis (D. V. Rottiers, unpublished data).

Weight range (g)	Swimming speed ($\mathrm{cm \cdot s^{-1}}$)	Temperature (°C)					
		3.5	5	7	10	15	Totals
1–200							
	10	0	0	0	0	1	1
	20	7	0	6	13	13	39
	30	7	0	6	13	14	40
	40	7	0	6	9	14	36
	50	7	0	6	3	13	29
	60	0	0	4	3	8	15
201–400							
	20	2	0	5	8	3	18
	30	3	0	9	8	5	25
	40	3	0	9	8	5	25
	50	3	0	9	8	4	24
	60	2	0	5	5	2	14
401–600							
	30	5	1	3	9	11	29
	40	5	1	3	9	11	29
	50	5	1	3	9	11	29
	60	3	0	3	8	7	21
601–800							
	30	7	4	3	4	8	26
	40	7	4	3	4	8	26
	50	7	4	3	4	6	24
	60	6	4	3	3	5	21
801–1000							
	30	4	2	2	8	3	19
	40	4	2	2	8	3	19
	50	4	2	2	8	3	19
	60	3	1	2	8	2	16
1001–2000							
	30	0	2	0	1	3	6
	40	0	3	0	3	4	10
	50	0	3	0	3	4	10
	60	0	2	0	2	4	8
Totals		101	36	97	169	175	578

the Winkler method. Background oxygen consumption rarely exceeded 0.1 $\mathrm{mg \cdot L^{-1}}$ and was checked weekly by running the apparatus without fish. Data were corrected whenever background level exceeded 0.1 $\mathrm{mg \cdot L^{-1}}$. Flow rates were controlled by varying pump speed.

The metabolism data were analyzed using multiple linear regression to estimate the parameters α, β, ρ, and ν. The least squares solution for the general model presented above (R_U in $\mathrm{g\ O_2 \cdot d^{-1}}$, linearized by $\log_e$ transformation) was:

$$(6)\quad \log_e R_U = \log_e 0.00463 + 0.705 \log_e W + 0.059T + 0.0232U.$$

This model fit the data very well ($R^2 = 0.94$, $P < 0.001$). Examination of residual plots indicated homogeneous variance for each of the predictor variables.

The value 13560 $\mathrm{J \cdot g^{-1}\ O_2}$ (3240 $\mathrm{cal \cdot g^{-1}\ O_2}$ or 4.63 $\mathrm{cal \cdot mL^{-1}\ O_2}$) is an appropriate oxycalorific coefficient for converting oxygen respired to energy utilized for a salmonid (Elliott and Davidson 1975; Elliott 1976b). For lake trout with 6280 $\mathrm{J \cdot g^{-1}}$ (1500 $\mathrm{cal \cdot g^{-1}}$) wet weight, the model for metabolism, R_U (6), can be converted to weight-specific metabolism by changing β to $\beta - 1$ and correcting the intercept, $\alpha = 0.00463$, for relative energy density of oxygen and fish. Thus,

$$\alpha = 0.00463\ (13560/6280) = 0.0100,$$

and the complete model for R_U in terms of gram equivalents (or $\mathrm{g \cdot g^{-1} \cdot d^{-1}}$) becomes:

$$R_U = 0.0100\ W^{-0.295} \cdot e^{0.059T} \cdot e^{0.0232U}.$$

In the context of the growth model developed below, energy density, Q, of both the predator and its principal forage may vary seasonally and ontogenetically; α is therefore variable. We begin each simulation with $\alpha = 0.00463$. This value is corrected each day for the relative Q's of oxygen and the food being eaten. Daily specific metabolism is then computed in terms of gram equivalents of the day's forage and can be entered into the mass-balance equation along with daily specific consumption and other components of the energy budget (all expressed in food equivalents per gram fish weight per day). Daily specific growth rate for the average individual fish is therefore computed initially in terms of gram food equivalents per gram body weight per day. To estimate the total growth increment for a given time step, we corrected the growth estimate in food terms for relative Q's of food and fish (see Model Development).

Smith et al. (1978) estimated temperature dependence of routine metabolism of juvenile lake trout (1–4 g) by direct calorimetry. The fish were placed in groups in the metabolic chamber, a modified bomb calorimeter, and changes in water temperature were measured. Results from experiments done at 6, 10, 15, and 18°C indicate exponentially increasing metabolism between 6 and 15°C with a leveling off of the rate of increase between 15 and 18°C. This pattern is in good agreement with our results, suggesting that perhaps Smith et al. were wrong to include the 18°C data in their regression. Assuming a mean weight of 2 g and a weight dependence coefficient of $\beta = 0.705$, least-squares regression estimate of daily metabolism (g $O_2 \cdot d^{-1}$) for a 1-g fish versus temperature over the range 6–15°C was $0.0053\ e^{0.0635T}$ ($r^2 = 0.99$, $n = 3$, our analysis of data in Smith et al.). Values for both intercept, $\alpha = 0.0053$, and temperature dependence coefficient, $\rho = 0.063$, are higher than estimates derived above, but not markedly so. Since activity was not controlled or measured in experiments by Smith et al., a relatively high value for α was to be expected. It is to some extent reassuring that results from the two studies are as close as they are, considering the radically different approaches used.

SWIMMING SPEED

To complete the model for metabolism, we needed an estimate of in situ typical daily swimming speed. Optimum swimming speed, U_{OPT} in $cm \cdot s^{-1}$ (7), for salmonids may vary as a positive power function of weight, and temperature dependence of U_{OPT} over low temperatures might be represented as an exponential function for a first approximation (Ware 1978; Stewart 1980).

$$(7) \qquad U_{OPT} = \omega W^{\delta} \cdot e^{\phi T}$$

where, ω, δ, ϕ = empirical constants.

There are no lake trout data available from which to estimate the temperature dependence coefficient, ϕ. As a working hypothesis, this parameter is set to 0.0405 ($Q_{10} = 1.5$), the value estimated by Stewart (1980) from published laboratory observations on temperature dependence of maximum swimming capacity in coho, *Oncorhynchus kisutch* (e.g. Griffiths and Alderdice 1972).

Ware (1978) used hydrodynamics theory combined with considerations of visual acuity, food size, and concentration to estimate optimum foraging and cruising speeds for sockeye salmon. Weight dependence of swimming speed was about 0.13 for both optima. Given the probable marked difference between the typical daily swimming behavior of planktivorous sockeye and epibenthic, piscivorous lake trout, we assumed that lake trout would have a lower weight dependence coefficient. We used $\delta = 0.05$ as a first hypothesis. (If Ware's value of 0.13 is used with a corresponding appropriate value for ω, consumption estimates for the average individual would be about 2% lower over 9 yr of life in the lake.)

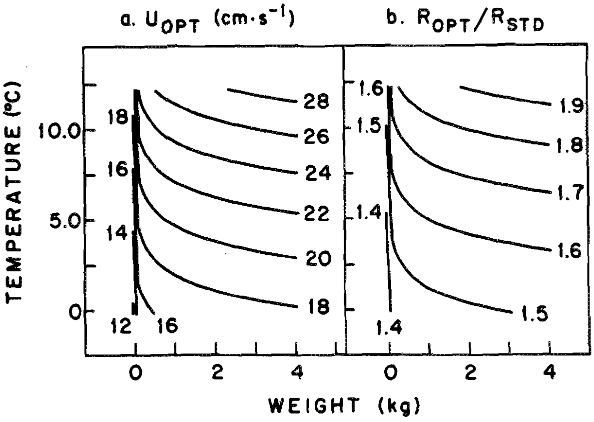

FIG. 1. Contour plots for (a) relationship for theoretical speed (U_{OPT}, $cm \cdot s^{-1}$) of lake trout to weight and temperature; and (b) relationship of the ratio R_{OPT}/R_{STD} to weight and temperature for lake trout.

Large lake trout have been tracked using ultrasonic tags in Lake Superior during the spawning season (R. Horrall, Laboratory of Limnology, University of Wisconsin, Madison, WI, personal communication). Six of the tagged fish were observed to swim; little or no movement was observed for others after tagging, indicating that either the tags fell off or the fish remained stationary. Analysis of tracks showing movement yielded an estimate of 0.46 $bl \cdot s^{-1}$ or 36 $cm \cdot s^{-1}$ for fish averaging 77.5 cm total length. Fish of 77.5 cm should weigh 5220 g based on a length-weight equation for lake trout from central Lake Michigan (Rybicki and Keller 1978). The tracked fish had been displaced from their spawning reef, and thus may have moved faster than would be the case at other times of the year. As a working hypothesis, the swimming speed estimate was arbitrarily reduced 25% to 27 $cm \cdot s^{-1}$ to compensate for this possible bias.

Using 27 $cm \cdot s^{-1}$ at 5220 g with $\delta = 0.05$ gives:

$$U_{OPT} = 17.6 W^{0.05}$$

Adding the temperature dependence term and correcting 17.6 $cm \cdot s^{-1}$ to 11.7 at 0°C gives the following completed model for typical in situ swimming speed of lake trout in $cm \cdot s^{-1}$:

$$(8) \qquad U_{OPT} = 11.7\ W^{0.05} \cdot e^{0.0405T}.$$

Total metabolism at typical in situ swimming speed is defined as:

$$R_{OPT} = \alpha W^{\beta} \cdot e^{\rho T} \cdot e^{\nu U_{OPT}}.$$

Equation (8) indicates swimming speeds will range from 11.7 $cm \cdot s^{-1}$ for 1-g fish at 0°C to about 28 $cm \cdot s^{-1}$ at 12°C for the largest lake trout found in Lake Michigan (Fig. 1a).

The increment in metabolism above standard metabolism (R_{STD}) due to activity, $R_{\mathrm{OPT}}/R_{\mathrm{STD}}$ or $e^{\nu U_{\mathrm{OPT}}}$, ranges from 1.4 at low temperature and small size to 1.9 at high temperature and large size (Fig. 1b). $R_{\mathrm{OPT}}/R_{\mathrm{STD}}$ may be two times higher for large rainbow than for lake trout; large sockeye may be up to three times higher than lake trout (Stewart 1980). This may be reasonable considering the relatively pelagic lifestyle of large rainbow and sockeye (Brett 1971b); lake trout on the other hand are more typically found on or near the bottom.

EXCRETION

Proportion of consumption excreted, E/C, may vary as a function of temperature and ration (Elliott 1976a):

$$E/C = \epsilon_1 T^{\epsilon_2} \cdot e^{\epsilon_3 P}$$

where, P = ration, $C_{\max}/C$,
and $\epsilon_1, \epsilon_2, \epsilon_3$ = empirical constants.
Parameter values reported by Elliott for brown trout eating amphipods were $\epsilon_1 = 0.0252$, $\epsilon_2 = 0.58$, and $\epsilon_3 = -0.299$. Proportion excreted therefore increases with increasing temperature and decreases with increasing ration. Since egested calories cannot be excreted, we modified the value for ϵ_1 to give an expression for egestion that was independent of fraction of ingested food that is indigestible. At the average values of 10°C and a ration of $P = 0.5$, $F/C = 0.174$ from Elliott's equation, and proportion of food assimilated is $(C-F)/C = 0.826$. An approximate corrected value for ϵ_1 is $0.0259/0.826 = 0.0314$, and the revised equation for excretion of assimilated food is

$$(9) \quad E/(C-F) = 0.0314T^{0.58} \cdot e^{-0.299P}.$$

Daily specific excretion in grams food per gram body weight per day is obtained by multiplying both sides of the equation by $C-F$.

EGESTION: A GENERAL MODEL FOR MIXED DIETS

Proportion of consumption egested, F/C, may also vary as a function of temperature and ration (Brockson and Bugge 1974; Elliott 1976a; Caulton 1978). Elliott proposed

$$(10) \quad F/C = f_1 T^{f_2} \cdot e^{f_3 P}$$

where, f_1, f_2, f_3 = empirical constants.
Elliott's parameter estimates for an invertebrate diet were $f_1 = 0.212$, $f_2 = -0.222$, and $f_3 = 0.631$. In contrast to excretion, proportion of consumption egested decreases (or assimilation efficiency increases) with increasing temperature, and F/C increases with increasing ration. Unfortunately, a study comparable to that of Elliott (1976a) has never been done for a piscivorous fish or for one on a mixed fish−invertebrate diet.

Weininger (1978) adjusted Elliott's parameter values to obtain a first approximation of a model for egestion when eating only fish. This was done by lowering the value of the intercept, f_1, by a proportion assumed to be indigestible chitin, then increasing the ration dependence coefficient, f_3. These adjustments retain the general shape of the response surface defined by Elliott's model. Weininger's modification gave precise estimates of proportion egested at $P = 0$ and at $P = 1$ (the points used to revise f_3), but gave progressively larger errors as P approaches 0.5. Rather than develop this model for the general case of a mixed fish−invertebrate diet, it was abandoned and the following model implemented. This new model retains the essence of Elliott's model (10, 11) as well as Weininger's modification of it.

The new model starts with F/C for an all invertebrate diet as computed directly from Elliott's (1976a) model and parameter estimates:

$$(11) \quad F/C = 0.212T^{-0.222} \cdot e^{0.631P}.$$

This estimate is then adjusted for proportion of fish in the diet. In the case of an all invertebrate diet, the adjustments all cancel out and leave Elliott's model.

It is assumed that for any food type there is some minimal proportion that will not be assimilated even under the extremes of very low ration and high temperature. From Elliott's model, a brown trout at 25°C and on near-zero ration of amphipods will still egest just over 10% of the food consumed. The absolutely indigestible proportion of an invertebrate diet, K_{INV}, is therefore assumed to be 0.10. Among the lowest estimates for egestion of a piscivorous diet are Kelso's (1972) estimates for walleye (*Stizostedion v. vitreum*) of 3.1% on a yellow perch (*Perca flavescens*) diet, and 2.1% on an emerald shiner (*Notropis atherinoides*) diet. Values of 5−10% are not unusual, but may not be minimal; the indigestible proportion of a fish diet was arbitrarily set at $K_{\mathrm{FISH}} = 0.033$.

The first step in adjusting F/C for fish in the diet is to compute the proportion of the diet that is indigestible, K_1:

$$K_1 = (P_{\mathrm{INV}} \cdot K_{\mathrm{INV}}) + [(1 - P_{\mathrm{INV}}) \cdot K_{\mathrm{FISH}}]$$

where P_{INV} = proportion of the day's diet composed of invertebrates: P_{INV} values were read from an input array of diet composition.

The second step is to subtract the indigestible proportion (~chitin) of an all invertebrate diet from the initial F/C estimate; $(F/C) - K_{\mathrm{INV}}$ gives an estimate of the proportion of consumption scheduled for egestion that is composed of flesh or other potentially assimilatable materials. When fish are eaten, Elliott's model for F/C will underestimate the value of $(F/C) - K_{\mathrm{INV}}$. This must be increased in proportion to the ratio of actual proportion of the diet available for assimilation $(1 - K_1)$ and that proportion potentially assimilatable from an all invertebrate diet $(1 - K_{\mathrm{INV}})$. Finally, this adjusted value for potentially assimilatable materials that are scheduled for egestion is added to the proportion of the diet that is indigestible, K_1, to yield an estimate of proportion of consumption to be egested for the particular mix of fish and invertebrates in the diet, F_{ADJ}/C. The complete general model for mixed diets is therefore:

$$F/C = f_1 T^{f_2} \cdot e^{f_3 P}$$

$$(12) \quad K_1 = (P_{\mathrm{INV}} \cdot K_{\mathrm{INV}}) + [(1 - P_{\mathrm{INV}}) \cdot K_{\mathrm{FISH}}]$$

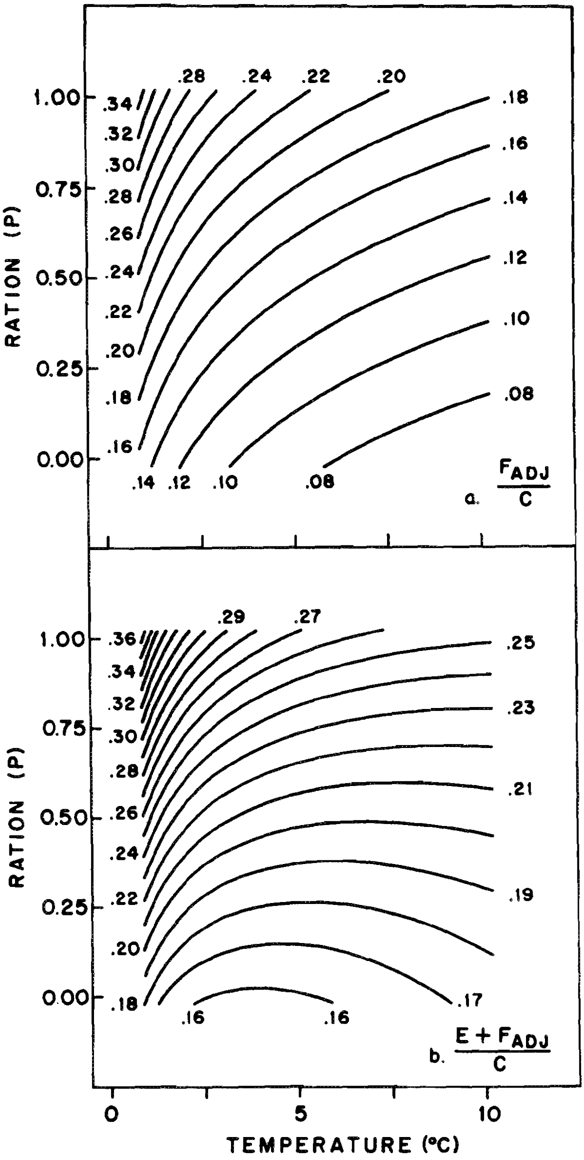

FIG. 2. (a) Contour plot (200-g lake trout eating all fish) for relationship of proportion of consumed food that is egested (F_{ADJ}/C) to temperature and ration ($P = C/C_{MAX}$); and (b) contour plot (for a similar lake trout) for relationship of total waste loss, $(E + F_{ADJ})/C$, to temperature and ration.

$$F_{ADJ}/C = \left[\left(\frac{F}{C} - K_{INV}\right) \cdot \frac{1 - K_I}{1 - K_{INV}}\right] + K_I.$$

Daily specific egestion in grams food per gram body weight per day is then obtained by multiplying F_{ADJ}/C by C. It can be easily demonstrated that this model reduces to the original F/C when $P_{INV} = 1$, in which case $K_I = K_{INV}$.

Equation (12) estimates egestion for lake trout on an all fish diet ranging from about 0.08 at 10°C and low rations to 0.34 at low temperatures and maximum ration (Fig. 2a). At midsummer conditions (10°C and $P = 0.5$), 12% of consumption is egested. Adding F_{ADJ}/C (12) to $E/(C - F)$ (9) gives estimates of total proportion of consumption going to waste losses of 0.16–0.36 (Fig. 2b).

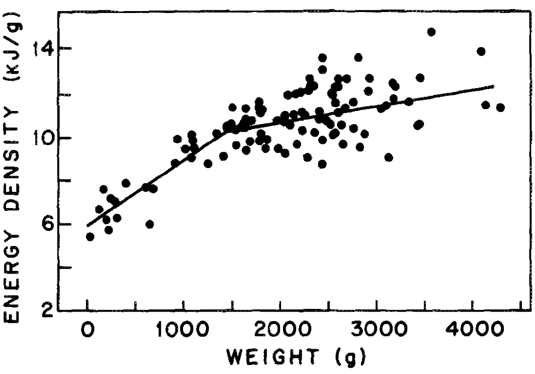

FIG. 3. Weight dependence of energy density ($J \cdot g^{-1}$ wet weight) for lake trout from Lake Michigan (based on Rottiers and Tucker 1982).

ENERGY DENSITY

Knowing the relative energy density or Q's of a predator and its prey is essential if an accurate estimate of predatory consumption is to be made from observed growth rate of the predator. Energy density of 113 individual lake trout from Lake Michigan (collected 1969–71) was determined by bomb calorimetry (Rottiers and Tucker 1982). The Q of lake trout increased with weight, especially for smaller fish (Fig. 3). Attempts to find a simple transformation that would linearize this relationship were unsuccessful. Rather than develop a nonlinear regression model to fit these data, two separate linear regressions were done for fish above and below 1500 g. Using linear equations here makes the growth model developed below mathematically tractable. The regression equations intersect at 1472 g; this is taken as the point to change from one regression line to the next. The model for Q of lake trout in $J \cdot g^{-1}$ wet weight is:

(13) $Q\ (\leq 1472\ g) = 5700 + 3.08W;$

(14) $Q\ (>1472\ g) = 9090 + 0.778W.$

It is obvious that Q can more than double over the life span of a lake trout (Fig. 3). The smallest observed lake trout have a Q of about 5256 $J \cdot g^{-1}$ (1256 $cal \cdot g^{-1}$) which is higher than the value of 4185 $J \cdot g^{-1}$ (1000 $cal \cdot g^{-1}$) suggested by Winberg (1956) as typical for fishes. The importance of accounting for changes in Q is clear; large, old trout must accumulate twice as much energy as young trout to gain the same amount of weight. Energy density of lake trout may also have a seasonal cycle, but available data were too variable to resolve this with certainty. A seasonal cycle of Q was thus not modeled for the trout.

A Growth Model with Ontogenetic and Seasonal Changes in Energy per Unit Weight

MODEL DEVELOPMENT

Earlier studies have assumed that consumers and their food have the same Q (e.g. Kitchell et al. 1974, 1977; Weininger 1978). The previous section shows that this simple assumption might yield substantial errors when working with salmonids which store large quantities of fat and thereby double their Q over their life. There are also marked differences in Q of invertebrate and fish forage (Cummins and Wuycheck 1971). Furthermore, certain fishes such as the alewife may go through rather dramatic seasonal cycles of Q (Yeo 1978). Consideration of changes in Q should provide a more rigorous estimate of true food needs or predatory impact by lake trout. Solving the energy balance for growth (15) gives an initial estimate for growth of the average individual, ΔB_{IND}, in grams food per gram body weight per day:

$$(15)\quad \Delta B_{IND} = C - (R_{OPT} + SDA + F_{ADJ} + E).$$

In previous studies, growth was added to weight at a given time step (t) to get weight at the next time step ($t + 1$):

$$W_{t+1} = W_t + (\Delta B_{IND} \cdot W_t).$$

If a predator and its prey differ in energy density, then correction for relative energy value of the predator Q_α, and average energy value of all items in its diet, Q_{FOOD}, had to be made:

$$(16)\quad W_{t+1} = [(W_t \cdot Q_\alpha) + (\Delta B_{IND} \cdot W_t \cdot Q_{FOOD})]/Q_\alpha.$$

For the simulations presented below, an array of diet composition for each cohort was input to the model. This included estimates of proportion by weight of four different forage types: invertebrates, (P_{INV}), young-of-the-year alewife, (P_{YOY}), adult alewife, (P_{ADU}), and other fish, (P_{OTH}). Since these proportions may change seasonally, diet composition is reevaluated at each time step (see following section, Food Habits of Lake Trout). Energy density of invertebrates, Q_{INV}, and other fish, Q_{OTH}, were treated as constants. Energy density of alewife is known to follow a seasonal cycle. Observed values at four different times of the year were used to compute a value for energy density of alewife, Q_{ALE}, on each day of the year by linear interpolation. From proportional diet composition and observed Q's of forage, the average energy density of the predator's diet, Q_{FOOD}, can be calculated.

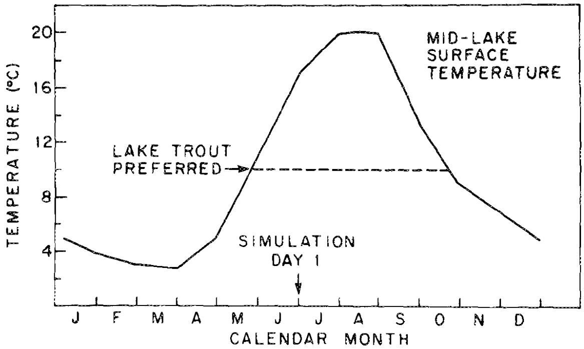

FIG. 4. Seasonal cycle of midlake surface water temperature in Lake Michigan based on Ayers (1962), and temperature (10°C, dashed line) assumed to be occupied by lake trout when surface water gets warmer than 10°C during summer months.

$$Q_{FOOD} = (P_{INV} \cdot Q_{INV}) + (P_{OTH} \cdot Q_{OTH}) + [(P_{YOY} + P_{ADU}) \cdot Q_{ALE}].$$

To simulate weight change in a fish exhibiting seasonal cycles in energy (but not ontogenetic changes), we found the energy value of the consumer for the next time step, $Q_{\alpha 2}$, using the interpolation scheme. The weight change equation is as eq. (16), with the divisor replaced by $Q_{\alpha 2}$.

Calculation of growth for a fish with marked ontogenetic changes in energy density is readily resolvable for the case when energy density is a linear function of body weight. Replacing Q_α in eq. (16) with $Q_\alpha + Q_\beta \cdot W$ gives:

$$(17)\quad W_{t+1} = [W_t \cdot (Q_\alpha + Q_\beta \cdot W_t) + (\Delta B_{IND} \cdot W_t \cdot Q_{FOOD})]/(Q_\alpha + Q_\beta \cdot W_{t+1}).$$

This can be solved for W_{t+1} using the quadratic formula.

$$(18)\quad W_{t+1} = \frac{-Q_\alpha + \sqrt{Q_\alpha^2 + [4 \cdot Q_\beta \cdot (W_t \cdot (Q_\alpha + Q_\beta \cdot W_t) + (\Delta B_{IND} \cdot W_t \cdot Q_{FOOD}))]}}{2 \cdot Q_\beta}.$$

Finally, growth of a predator with both a seasonal cycle and an ontogenetic change of energy density can be computed. In this case, the value of Q_α at time t will be changing to $Q_{\alpha 2}$ at $t + 1$; $Q_{\alpha 2}$ comes from the interpolation scheme described above. W_{t+1} is found by solving:

$$(19)\quad Q_\beta \cdot W^2_{t+1} + Q_{\alpha 2} \cdot W_{t+1} - [W_t \cdot (Q_\alpha + Q_\beta \cdot W_t) + (\Delta B_{IND} \cdot W_t \cdot Q_{FOOD})] = 0.$$

When growth of an individual, ΔB_{IND} (15), has been adjusted for changes in Q using eq. 16, 17, 18, or 19, it will be referred to as adjusted growth, ΔB_{ADJ}.

The Lake Michigan Lake Trout Population: Site Specific Variables

WATER TEMPERATURE AND PREFERRED TEMPERATURE

Actual temperature occupied by the typical individual of a fish population appears to be an interaction of available temperature, preferred temperature, and to some extent, recent temperature experience or acclimation (Neill and Magnuson 1974). It is believed that water temperature of a lake changes at a rate which permits nearly continuous acclimation to whatever temperature the fish occupies, except for the special case of vertical migration through a sharp temperature gradient. For lake trout, we hypothesized that they will occupy the warmest available temperature up to but not exceeding their preferred temperature (Beitinger and Magnuson 1975).

The final temperature preferred by yearling lake trout in laboratory studies was 11.7°C, independent of starting acclimation temperature (McCauley and Tait 1970). Field observations on lake trout suggest they normally occupy a temperature about 2°C lower than the laboratory determined preferendum (Ferguson 1958; Spangler and Berst 1976). Factors such as relative food availability, predator avoidance, interference competition, etc., will modify orientation to the preferred temperature (Magnuson et al. 1979). An observed thermal history is thus more appropriate when known. For the simulations presented herein, the preferred or maximum summer temperature occupied in Lake Michigan is assumed to be 10°C. The annual temperature cycle (Fig. 4) was estimated from midlake data from Ayers (1962), and this agrees with observations of Carr et al. (1973).

FOOD HABITS OF LAKE TROUT

Actual food habits of lake trout (expressed as proportional, wet-weight diet composition) are critical site-specific data needed for quantitative evaluation of predatory impact upon various forage organisms. Gary Eck (GLFL, U.S.F.W.S., Ann Arbor, MI, personal communication) has in progress an extensive study of seasonal food habitats of lake trout in Lake Michigan, and has provided us with preliminary data expressed in percentage occurrence of various food types. We converted these data to approximate proportions by weight using the following assumed typical live weights (g): sculpin adults = 20, juveniles = 2; smelt adults = 32, juveniles = 4; alewife (spring/summer/fall) adults = 34/29/33, juveniles = 3.9/10/3.7. These data were based on values for fish caught in experimental trawls in Lake Michigan (L. Moffett, Michigan Department of Natural Resources, personal communication), and for alewife, based on average lengths of those in the trout stomachs (G. Eck, GLFL, U.S.F.W.S., Ann Arbor, MI, personal communication). Data were combined with observations of Dryer et al. (1965) on food habits of small lake trout in Lake Superior, since Eck caught relatively few small juveniles in Lake Michigan. Dryer et al. indicated that benthic invertebrates may be an important component of the diet in juvenile lake trout. The proportions of invertebrates in the diet of lake trout of various size-classes were estimated from Dryer et al. to be 0.75 (100−200 mm fish length), 0.30 (200−300 mm), 0.10 (300−400 mm), 0.0 (> 400 mm).

The above information was combined as model input (Table 2) of diet composition by weight for various size-classes of lake trout in each of three different seasons — winter and spring (Dec.−May), summer (June−Oct.), and fall (Nov.). The one month fall season is the period when Eck noted that juvenile alewife were moving into deeper water and were preyed upon heavily by lake trout. Data for smelt and sculpin were merged to form a single food class termed "other fish." This gives proportions of four food types for the lake trout: invertebrates (P_{INV}), young-of-the-year alewife (P_{YOY}), adult alewife (P_{ADU}), and other fish (P_{OTH}).

Diet composition of Lake Michigan lake trout changes noticeably with size (Table 2). Small trout feed on invertebrates and small fishes. As size increases to about 1500 g, smelt and sculpin are increasingly important diet components. Trout larger than about 2000 g eat almost entirely adult alewife, except during the fall. The observations of Eck on summer food habits of lake trout are in very close agreement with those of Rybicki and Keller (1978).

The model developed above also requires estimates of Q for the various food types in the diet, both to convert metabolism to grams food equivalent and to convert growth in grams food equivalent to growth in body weight, ΔB_{ADJ}. In the Great Lakes, *Mysis relicta* and *Pontoporeia hoyi* are important components of the invertebrate forage of young lake trout (Dryer et al. 1965). Estimates of wet weight Q for these two invertebrates could not be located; it was assumed that they are typical Malacostraca with 4310 $J \cdot g^{-1}$ wet weight (Cummins and Wuycheck 1971).

Smelt have been studied by Foltz (1974) and data in an appendix of his thesis provide a basis for estimating wet weight Q. Foltz and Norden (1977) only gave dry weight data. Foltz presented seasonal data for both sexes of 3- and 4-yr-old smelt. A seasonal cycle of Q was evident, but not nearly as pronounced as that for alewife (Yeo 1978). The overall average value was estimated to be 5700 $J \cdot g^{-1}$ wet weight based on the 20 mean values (five dates, two sexes, two age-classes) presented by Foltz. This value was used as a constant for "other fish," Q_{OTH}, in the lake trout diet. Brockson et al. (1968) estimated 5210 $J \cdot g^{-1}$ wet weight for *Cottus perplexus*, which is reasonably close to the smelt estimate. Estimates of Q for slimy sculpin (*Cottus cognatus*, 5740 $J \cdot g^{-1}$) and deepwater sculpin (*Myoxocephalus thompsoni*, 5420 $J \cdot g^{-1}$) from Lake Michigan are also closely similar (Rottiers and Tucker 1982).

Alewife show a pronounced seasonal cycle of energy density, Q_{ALE}, and this was modeled using energy estimates for four different times of the year with linear interpolation between the observations. The values for Q_{ALE} (calculated from data presented in Yeo 1978) were 5330 (June), 6450 (Sept.), 9080 (Nov.), and 5270 (March) $J \cdot g^{-1}$. There may also be an ontogenetic change during the first 1 or 2 yr of life but Yeo did not have enough data on small fish to draw definite conclusions. If there is an ontogenetic change for older age-classes, it is obscured by the seasonal cycle. If YOY alewife have relatively lower Q, then simulation estimates of YOY alewife consumption by lake trout will be conservative.

GROWTH

Growth of lake trout is faster in the southern part of Lake

TABLE 2. Proportional composition by weight of four food categories in the diet of Lake Michigan lake trout (*Salvelinus namaycush*) at various times of the year. Day 1 of a modeling simulation is July 1. Based on data from Eck (GLFL, Ann Arbor, personal communication) and Dryer et al. (1965).

Cohort	Simulation days		Food type			
	Start	End	P_{INV}	P_{OTH}	P_{YOY}	P_{ADU}
1	1	120	0.75	0.21	0.04	0.0
	121	150	0.30	0.66	0.04	0.0
	151	330	0.30	0.54	0.16	0.0
	331	360	0.30	0.13	0.57	0.0
2	1	120	0.10	0.53	0.0	0.37
	121	150	0.10	0.31	0.59	0.0
	151	330	0.10	0.72	0.0	0.18
	331	360	0.10	0.53	0.0	0.39
3	1	120	0.0	0.53	0.0	0.47
	121	150	0.0	0.35	0.65	0.0
	151	330	0.0	0.57	0.0	0.43
	331	360	0.0	0.53	0.0	0.47
4	1	120	0.0	0.17	0.0	0.83
	121	150	0.0	0.16	0.84	0.0
	151	330	0.0	0.43	0.0	0.57
	331	360	0.0	0.17	0.0	0.83
5	1	120	0.0	0.17	0.0	0.83
	121	150	0.0	0.03	0.97	0.0
	151	330	0.0	0.23	0.0	0.77
	331	360	0.0	0.06	0.0	0.94
6	1	120	0.0	0.06	0.0	0.94
	121	150	0.0	0.03	0.97	0.0
	151	330	0.0	0.23	0.0	0.77
	331	360	0.0	0.06	0.0	0.94
7–9	1	120	0.0	0.02	0.0	0.98
	121	150	0.0	0.03	0.97	0.0
	151	330	0.0	0.14	0.0	0.86
	331	360	0.0	0.02	0.0	0.98

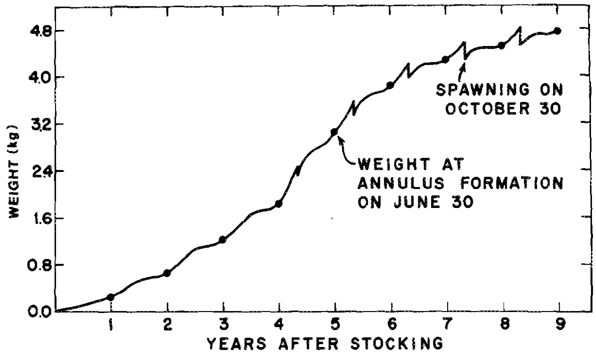

FIG. 5. Simulated growth of the average individual lake trout in Lake Michigan as fit to the annual end points of growth (●) based on the average of values estimated for three different parts of Lake Michigan — south, mid, north — by Rybicki and Keller (1978).

Michigan than in the northern part (Rybicki and Keller 1978). Our modeling simulations are fit to the annual end points of growth. We used the average southern, midlake, and northern observations given by Rybicki and Keller (1978: p. 41). Their mean size estimate for age-class 8 in the southern region was actually lower than for age 7, perhaps due to the small sample size. We therefore used average size of midlake and northern fish for age-classes 8 and 9 (i.e. growth end points for model cohorts 7 and 8). The model was extended to the end of 9 yr in the lake by assuming the weight gain between cohorts 7 and 8, 239 g, was the same as that between 8 and 9. Final weight for age-class 2 (cohort 1) is taken from Weininger (1978) and based on a subset of Rybicki and Keller's original data. The growth curve thus derived was assumed to be representative of a lake-wide average (Fig. 5). The starting weight was set at 20 g on June 30 (age-class 1+), and weight in grams at 1-yr intervals thereafter were: 1 = 260, 2 = 659, 3 = 1216, 4 = 1828, 5 = 3044, 6 = 3842, 7 = 4281, 8 = 4520, 9 = 4760. June 30 corresponds approximately to the time lake trout are stocked as well as the typical time for formation of scale annuli.

Growth depends on P (ration or C/C_{max} defined above) as well as C_{max}. Since P is unknown, it must be estimated by simulation. For a given cohort, P is given an arbitrary intermediate starting value such as 0.5. A growth simulation is then run and the simulated annual end point of growth is compared to the desired (or observed) annual end point. P is then adjusted up or down depending on whether the simulation was too high or too low, and additional iterations are done until observed final weight is obtained with the desired degree of accuracy (e.g. ± 0.2%). The iteration routine used was that developed by Weininger (1978). The actual value of P may vary seasonally with food availability, but this possibility cannot be tested because we only have annual estimates of weight.

REPRODUCTION

Lake trout in Lake Michigan apparently spawn each fall,

TABLE 3. Symbols and estimated (or postulated) parameter values used to implement an energetics model for Lake Michigan lake trout (*Salvelinus namaycush*).

Process	Symbol	Parameter description	Parameter value
Consumption	a	Intercept for maximum consumption (C_{max}), @ 0°C	0.059 ($g \cdot g^{-1} \cdot d^{-1}$)
	b	Weight dependence coefficient for C_{max}	−0.307
	q	Temperature dependence coefficient for C_{max}	0.123
	T_{PREF}	Preferred temperature (upper bound on C_{max})	10.0°C
Metabolism	α	Intercept for metabolism	0.00463 ($g\ O_2 \cdot d^{-1}$)
	β	Coefficient for metabolism vs. weight	−0.295
	ρ	Coefficient for metabolism vs. temperature	0.059
	ν	Coefficient for metabolism vs. swimming speed	0.0232
Swimming speed	ω	Intercept for optimum swimming speed	11.7 ($cm \cdot s^{-1}$)
	δ	Coefficient for optimum swimming speed vs. weight	0.05
	ϕ	Coefficient for optimum swimming speed vs. temperature	0.0405
	SDA	Specific dynamic action coefficient	0.17
Egestion	f_1	Intercept for proportion of consumed food egested	0.212
	f_2	Coefficient for egestion vs. temperature	−0.222
	f_3	Coefficient for egestion vs. feeding level	0.631
	K_{INV}	Indigestible fraction of invertebrate diet	0.10
	K_{FISH}	Indigestible fraction of fish diet	0.033
Excretion	ϵ_1	Intercept for proportion of consumed food excreted	0.0314
	ϵ_2	Coefficient for excretion vs. temperature	0.58
	ϵ_3	Coefficient for excretion vs. feeding level	−0.299

but for some unknown reason, there has been virtually no recruitment of naturally spawned young. Reproductive products lost each year are nonetheless weight gained through additional consumption and should be considered when evaluating predation and conversion efficiency. Female lake trout weighing less than 5 kg lay an estimated 12.1% body weight as eggs (Eschmeyer 1955: p. 66, assuming 0.1 $g \cdot egg^{-1}$). Male gonads change from an average maximum of 3.1% body weight to 1.7% at end of the spawning season for a loss of 1.4%; thus, average loss for both sexes is 6.8% (Eschmeyer 1955). For simulations presented below, this average constant proportion of body weight was lost as a step function on day 120 (October 30) of cohorts 5–9 (Fig. 5).

NUMBERS, BIOMASS, MORTALITY, AND PRODUCTION

Model components and site specific variables presented above are sufficient to simulate the average individual lake trout in Lake Michigan. Extension to the entire Lake Michigan population requires estimates of numbers stocked and mortality rates. Past, present, and projected future stocking rates for lake trout in Lake Michigan, 1965–90, were summarized in Stewart (1980). To simulate the population in any given year, we estimated numbers starting in each age-class or cohort from actual numbers stocked in that year and up to 8 previous years. Mortality rates presented below were used for determining numbers in all but the first cohort.

Rybicki and Keller (1978) estimated instantaneous total mortality rate for lake trout vulnerable to the sport fishery in Lake Michigan (i.e. after 4 yr in the lake) as a function of fishing effort in various statistical districts. They extrapolated this relationship to zero fishing effort to get an estimate of 24.7% average annual natural mortality, or 0.284 for the average instantaneous natural mortality rate. From the difference between total mortality and natural mortality, Rybicki and Keller estimated the average lake-wide annual fishing mortality to be 30%. The average annual instantaneous harvest rate was therefore $0.3567 \cdot yr^{-1}$, but fishing is mostly concentrated in the 6-mo period May through October (Rybicki and Keller 1978). The annual instantaneous harvest rate is therefore $0.7134 \cdot yr^{-1}$ during May–October and zero for the remaining 6 mo.

For lake trout during their first 4 yr in the lake, we used Rybicki and Keller's (1978) estimate of 37% annual natural mortality rate. This was based on an estimate for age-class 2 from trawling catch-per-unit-effort in only one area of the lake. Given that rate estimates can vary somewhat for different areas of the lake, their estimate for young age-classes needs to be substantiated by further studies. The model presented herein is relatively sensitive to errors in mortality rate estimates.

Total annual survival rates used to determine numbers starting each cohort were derived from the above natural and harvest mortality rates. During the first 4 yr, there was relatively little fishing mortality; the primary fishing method, trolling, seems to select strongly for large fish. Fishing was assumed to become an important source of mortality in the fifth summer (i.e. at start of eleventh month, May, of the fourth cohort).

Rybicki and Keller (1978) assumed population decreases were continuously exponential with natural mortality evenly distributed over the entire year, and fishing evenly spread over May–October. The same model was used herein. Daily instantaneous natural mortality was estimated to be $0.284/360 = 7.889 \times 10^{-4}$; daily instantaneous fishing mortality was $0.7134/360 = 19.817 \times 10^{-4}$ during the 6-mo fishing season. Gross and net production for the time step can be estimated as:

$$PR_{GROSS} = (W_{t+1} - W_t) \cdot N_t,$$

and

$$PR_{\mathrm{NET}} = PR_{\mathrm{GROSS}} - (Z \cdot W_t),$$

where Z is total loss of numbers to mortality during the time step. This completes the equation series for the energetics model, as well as derivation of the various parameters for the Lake Michigan lake trout population. Parameters for the primary energetics functions are summarized in Table 3.

Energetics of the Average Individual Lake Trout

IMPLEMENTATION OF NEW MODEL FEATURES

The above energetics equations extend Weininger's (1978) original development for lake trout. Changes include: (1) a slightly different growth curve with higher first-year growth and one more year in the lake; (2) a new egestion function for mixed diets to replace Weininger's fish-diet modification of Elliott's (1976a) egestion model; (3) a growth model with ontogenetic changes of Q in trout and seasonal cycle of Q in its prey to replace assumed Q food = Q trout = 4440 $\mathrm{J \cdot g^{-1}}$ as a constant throughout; (4) reproductive energy losses for mature fish compared to none in the earlier version; and (5) a model for size and temperature dependence of swimming speed in place of previously assumed 0.46 $\mathrm{bl \cdot s^{-1}}$ swimming speed constant at $T > 5°\mathrm{C}$, and 0.33 $\mathrm{bl \cdot s^{-1}}$ at $T \leq 5°\mathrm{C}$.

Implementation of these new features revealed that the original version underestimated assimilation efficiency. Gross conversion efficiency of energy (21.8%) over the life of a lake trout, including energy released as gametes, is about twice the conversion efficiency of mass (12.2% herein, or 12.8% estimated by Weininger 1978) because lake trout store large amounts of high-energy fats. Another important conclusion from comparison of results from the two versions is that the model as originally formulated was relatively robust in its estimates of accumulative consumption with an overall increase of only 3.4% between the old and new versions at the end of 8 yr in the lake. The ninth cohort of the new version adds another 18% to the total estimate for the average individual, but relatively few trout survive to this age. This robustness gives added confidence in the model estimate for predatory impact of lake trout on their forage, which was the ultimate objective of this modeling exercise.

The fact that implementation of these model features does not seriously alter the overall consumption estimates obscures the finer-scale changes that have been induced. Consumption, conversion efficiency, and their seasonality have been altered differentially within the different age-classes providing what should be a more realistic model for the life history of lake trout. The new egestion function was not expected to greatly alter either Elliott's model or Weininger's modification for a fish diet, but rather to allow realistic simulation of egestion with mixed diets. The model for linear increase in lake trout energy density implies that large trout consume twice as much food as small trout per unit gain in weight. If Q of the prey has a seasonal cycle, trout will have a parallel seasonal cycle of conversion efficiency. If Q of the prey were lowered a certain percentage, the total consumption estimate would increase by a greater percentage. This emphasizes the importance of modeling energy density of both predator and prey with reasonable accuracy. The assumption that a planktivorous fish has the same Q as zooplankton (e.g. Kitchell et al. 1977, YOY yellow perch), may give a 2- to 3-fold underestimate of zooplankton consumed, since zooplankton typically have 1/2 to 1/3 the Q of a fish. Implementation of the mixed diet means small fish eating invertebrates will have a relatively lower conversion efficiency and need to eat more per unit weight gain than in the original version. Finally, the new swimming speed model increases metabolism for small fish and lowers it for large fish; these two effects compensate each other when integrated over the life of a lake trout.

TABLE 4. Normalized sensitivities of accumulative consumption estimates for Lake Michigan lake trout to deviations of various input parameters (see text for explanation of procedures and normalization).

	Parameter input error			Parameter input error	
Parameter	+10%	−10%	Parameter	+10%	−10%
Consumption			Egestion		
a	−0.05	+0.07	f_1	+0.25	−0.24
b	−0.11	+0.17	f_2	+0.11	−0.10
q	−0.04	+0.05	f_3	+0.08	−0.07
T_{PREF}	+0.28	−0.28	K_{INV}	−0.12	+0.11
Metabolism			K_{FISH}	−0.04	+0.04
α	+0.72	−0.71	Excretion		
β	+1.91	−1.47	ϵ_1	+0.13	−0.12
ρ	+0.32	−0.30	ϵ_2	+0.16	−0.14
ν	+0.40	−0.38	ϵ_3	+0.02	−0.02
Swimming speed			Energy density		
ω	+0.40	−0.38	< 1472 g Q_α	+0.05	−0.05
δ	+0.16	−0.15	< 1472 g Q_β	+0.04	−0.04
ϕ	+0.12	−0.12	> 1472 g Q_α	+0.17	−0.17
SDA	+0.25	−0.24	> 1472 g Q_β	+0.09	−0.09
			Q_{INV}	−0.02	+0.02
			Q_{OTH}	−0.17	+0.18

TABLE 5. Normalized sensitivities of accumulative metabolism (g O_2, $R + SDA$) estimates for Lake Michigan lake trout to deviation of various input parameters (see text for explanation of procedures and normalization).

	Parameter input error			Parameter input error	
Parameter	+10%	−10%	Parameter	+10%	−10%
Consumption			Egestion		
a	0.0	−0.01	f_1	0.0	−0.01
b	0.0	−0.01	f_2	−0.01	0.1
q	+0.02	−0.03	f_3	0.0	−0.01
T_{PREF}	+0.35	−0.38	K_{INV}	0.0	−0.01
Metabolism			K_{FISH}	−0.01	0.0
α	+0.92	−0.92	Excretion		
β	2.45	−1.93	ϵ_1	+0.02	−0.03
ρ	+0.40	−0.39	ϵ_2	+0.03	−0.03
ν	+0.51	−0.50	ϵ_3	0.0	−0.01
Swimming speed			Energy density		
ω	+0.51	−0.50	< 1472 g Q_α	0.0	−0.01
δ	+0.20	−0.20	< 1472 g Q_β	0.0	−0.01
ϕ	+0.15	−0.15	> 1472 g Q_α	+0.03	−0.04
SDA	+0.32	−0.31	> 1472 g Q_β	+0.02	−0.02
			Q_{INV}	−0.01	0.0
			Q_{OTH}	−0.01	0.0

SENSITIVITY ANALYSIS FOR CONSUMPTION AND METABOLISM

A sensitivity analysis was done on the complete energetics model for the average individual lake trout in Lake Michigan using the 9-yr growth curve developed from Rybicki and Keller (1978). The objective was to determine to what extent errors in estimating various model parameters influence estimates of accumulative consumption and metabolism over the life of a lake trout. Each of 26 input parameters was separately varied +10% then −10% and resultant changes in consumption and metabolism were compared to nominal estimates from the standard simulation which used best available parameter estimates derived in preceding sections.

Sensitivity of a computed output value to deviation of an input parameter was calculated using the method presented by Kitchell et al. (1977);

$$S_x(p) = (p \cdot \Delta x)/(x \cdot \Delta p)$$

where, $S_x(p)$ = sensitivity of output parameter x to deviations of input parameter p,
p = nominal value of input parameter p,
Δp = input deviation of input parameter p,
x = nominal value of output parameter x from standard simulation,
and Δx = deviation of output parameter x due to Δp.

A sensitivity of 1.0 indicates that a 10% error in an input parameter will yield a 10% error in estimates of output such as consumption or metabolism. The higher the absolute sensitivity value ($|S_x(p)|$), the greater the potential for error.

Sensitivities to consumption, egestion, excretion, and energy parameters were all quite low (Table 4). Sensitivity to an energy density parameter, however, may be close to 1.0 when the predator is eating only that particular food type. Sensitivity of the consumption estimate to errors in estimating energy content of alewife may be close to 1.0 because it forms a large component of the lake trout's diet. Sensitivity of consumption and metabolism estimates to errors in determining the annual cycle of energy content in alewife were not explicitly evaluated. Highest sensitivities were to the metabolism parameters, α and β, with moderate sensitivities to ρ and ν. Since the swimming speed parameter ω is multiplied by ν, its sensitivity is identical to that of ν; sensitivity is low to other swimming speed parameters. Relative sensitivity of metabolism estimates to input errors of various model parameters (Table 5) follows a pattern almost identical to that of consumption estimates.

Relatively high sensitivity of the various metabolism parameters points to the need for good laboratory studies on metabolism of fishes. In the present model, high sensitivities are offset by good confidence in our parameter estimates which are based on a large data set. More observations of in situ swimming speed would be useful, considering the moderate sensitivity of the parameter ω.

Results of the sensitivity analysis indicate a general robustness of the model, especially for estimating consumption by fitting a known growth curve. This supports conclusions from comparison of old and new versions of this model which were discussed in the previous section. Sensitivities of various parameters appear to be lower for consumption and metabolism estimates than for estimates of growth as presented by Kitchell et al. (1977). The ±10% input errors used here may be reasonable approximations of our confidence in many of the parameters, suggesting that estimates of consumption for the average individual lake trout may be within 20% or less of actual value. Far greater uncertainties are involved in estimates of mortality rates for the entire population and this should be a subject for continuing research. Substantial

TABLE 6. Comparison of weight gain, ration, total consumption, and gross conversion efficiency of biomass for the average individuals of the nine lake trout cohorts in Lake Michigan. Based on an energetics modeling simulation with starting weight of 20 g for the first cohort. Growth curve (Fig. 5) is from Rybicki and Keller (1978). Also given are total weight and energy gained, consumed, and % conversion over 9 yr of life. It was assumed that 6.8% body weight was lost as reproductive products on day 120 (cohorts 5–9 only). Gametes lost were added to weight gained to calculate efficiency; gametes were assumed to have 6240 $J \cdot g^{-1}$ wet weight (Cummins and Wuycheck 1971).

Cohort	Weight (g)	Weight gain (g)	Gametes lost (g)	Ration (C/C_{max})	Food consumed (g)	% Gross conversion efficiency
1	260	240	0	0.749	983	24.4
2	659	399	0	0.562	2062	19.4
3	1216	557	0	0.575	3487	16.0
4	1828	612	0	0.522	4408	13.9
5	3044	1216	167	0.684	8010	17.3
6	3842	798	242	0.546	8160	12.7
7	4281	439	287	0.459	7690	9.4
8	4520	239	311	0.417	7380	7.5
9	4760	240	328	0.420	7710	7.4
Total grams		4740	1335		49890	12.2
Total joules		60.9×10^6	8.3×10^6		317.9×10^6	21.8

deviation from the smooth exponential mortality assumed has obvious important consequences. For example, Kitchell and Breck (1980) demonstrated that lamprey-induced mortality can be strongly pulsed in late summer or early autumn.

CONVERSION EFFICIENCY

Gross conversion efficiency ($\Delta B_{ADJ}/C$) can provide a useful index of the general well-being of a fish under a given set of diet and environmental conditions. Evaluation of conversion over the range of temperatures normally occupied in the field and at growth rates possible at various ration levels can also yield useful information about optimum conditions for a particular species (Webb 1978; Brett and Groves 1979). To evaluate relative well-being of the various cohorts of lake trout in Lake Michigan, we summarized results from the standard simulation for the average individual by cohort to get estimates of overall gross conversion efficiency for each cohort.

Results of this analysis (Table 6) indicated relatively high conversion efficiency for the first cohort and lowest conversion for the oldest two cohorts. Conversion estimates for the older cohorts would appear to be much lower if gamete losses were ignored. Efficiency for the first cohort was unexpectedly high, considering the large invertebrate component in the diet. Cohorts 2–7 show substantial variation, apparently related to the amount of growth occurring in a given year. Fish growing faster are on higher rations and tend to have better conversion.

Higher conversion efficiency at relatively higher rations is displayed in a contour plot of $\Delta B_{ADJ}/C$ versus temperature and daily specific growth rate (Fig. 6). These results with maximum conversion at maximum ration are similar to those of Elliott (1976b) and modeling simulations for yellow perch (Kitchell et al. 1977), but differ from Brett et al.'s (1969) observed maximum conversion at rations slightly below maximum. The model as presently developed consistently

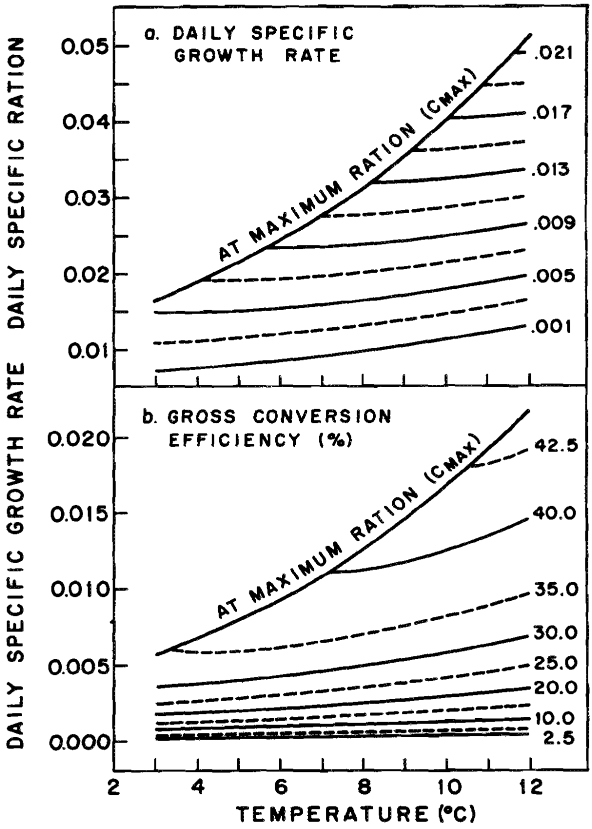

FIG. 6. (a) Contour plot of daily specific growth rate ($g \cdot g^{-1} \cdot d^{-1}$, ΔB_{ADJ}) for a 200-g lake trout eating alewife versus daily specific ration ($g \cdot g^{-1} \cdot d^{-1}$) and temperature, and (b) contour plot of gross conversion efficiency (%) for a similar lake trout at various daily specific growth rates (ΔB_{ADJ}) and temperatures.

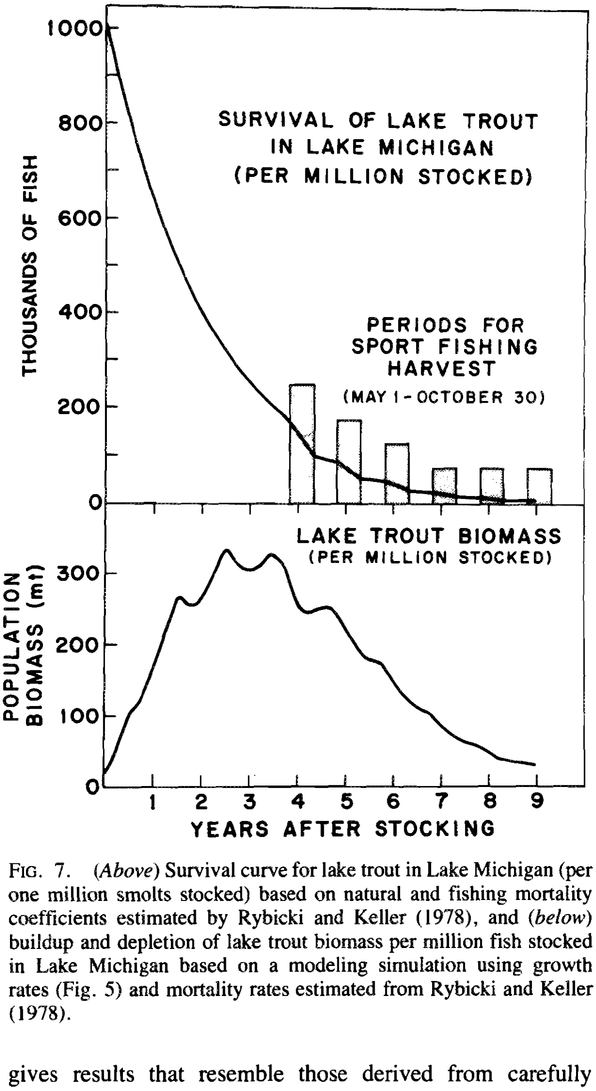

FIG. 7. (*Above*) Survival curve for lake trout in Lake Michigan (per one million smolts stocked) based on natural and fishing mortality coefficients estimated by Rybicki and Keller (1978), and (*below*) buildup and depletion of lake trout biomass per million fish stocked in Lake Michigan based on a modeling simulation using growth rates (Fig. 5) and mortality rates estimated from Rybicki and Keller (1978).

gives results that resemble those derived from carefully controlled experiments by Elliott (1976b).

Predatory Impact of the Lake Trout Population

POPULATION SIMULATION FOR ONE MILLION FISH

Results of the foregoing analyses relate to the average individual lake trout. The full numbers–biomass capabilities of the model were implemented to evaluate (1) build-up of population biomass and consumption over time from stocking to the end of 9 yr, (2) relative importance of different trout cohorts in preying on various forage types, and (3) total predatory impact on alewife by lake trout since they were planted in 1965, with projections of alewife consumption by lake trout to 1990. The mortality coefficients were those derived above from data presented in Rybicki and Keller (1978).

The first two objectives in this section were addressed using modeling simulations for one million lake trout stocked once and followed over 9 yr. This differs from the following simulations of actual populations in the lake in various years since actual numbers in a given cohort of a given year are dependent on the variable numbers stocked in previous years. The population simulation for a million fish indicates a steady build-up of population biomass over the first 3.5 yr to 330 $t \cdot million^{-1}$ stocked (Fig. 7). Biomass may have risen slightly higher, but sport fishing (Fig. 7) becomes important in the fifth summer after stocking (Rybicki and Keller 1978) and this harvesting sharply curtails further increment of total population biomass. As might be expected, total consumption also rises to a peak in the third cohort then declines steadily with older cohorts (Table 7). Because of these time-lags in the system, manipulation of stocking densities for lake trout is not an effective means of moderating fluctuations in prey densities (Stewart et al. 1981). It seems possible, however, that lake trout could partially dampen prey fluctuations by short-term changes in consumption rates, and this would show up as annual variation in growth rate.

A comparison of relative predatory impact of various cohorts on different forage types (Table 7) indicates that invertebrates are most important for the first cohort, while YOY alewife, other fish (smelt and sculpin), and invertebrates are all relatively important in the second and third years in the lake. Older cohorts eat predominately adult alewife as noted earlier (Table 2). A comparison of percent composition of the total diet integrated over all cohorts, indicates a relatively higher importance of invertebrates and other fish in the population simulation compared to the average individual (Table 7, bottom). This of course is related to the large numbers of young trout that do not survive to attack adult alewife in the simulation for the entire population.

POPULATION SIMULATIONS FOR 1965–90

The general concensus over the past 15 yr has been that there is an abundance of forage fishes in Lake Michigan and substantial increases in stocking densities of predatory salmonids are still possible (e.g. Borgeson 1977). This lake trout modeling study was part of a larger effort to evaluate the null hypothesis that salmonids in Lake Michigan are not seriously impacting their forage base (Stewart et al. 1981). As noted above, the model appears to be robust and reasonable confidence can be put in consumption estimates, at least for the average individual. The numbers in each cohort during each year for the period 1965–90 were estimated from actual or projected numbers stocked as summarized in Stewart (1980) and mortality coefficients derived from Rybicki and Keller (1978).

Predation of lake trout on alewife has been building up steadily since 1965 to about 8.4 million $kg \cdot yr^{-1}$ (8400 $t \cdot yr^{-1}$), and is projected to rise to almost 12 000 $t \cdot yr^{-1}$ by 1990 (Fig. 8). This amount of consumption by itself might represent only a small fraction of the alewife biomass in Lake Michigan in a given year as estimated by Hatch et al. (1981). Lake trout, however, represent only about 20% of the predatory salmonids stocked in the lake, and together, the various salmonids could be eating as much as 20–33% of the annual alewife production in some years (Stewart et al. 1981).

Additional simulations were done for 1980–90 with

TABLE 7. Comparison of predatory impact of various lake trout cohorts upon different forage types in Lake Michigan. Based on energetics modeling simulations using the growth curve (Fig. 5) from Rybicki and Keller (1978), and food data from Table 2. All values are for a 360-d simulation year.

	Consumption by average individual[a]				Consumption per million stocked[b]				
Cohort	Invert. (g)	Other fish (g)	YOY alewife (g)	Adult alewife (g)	Invert. (t)	Other fish (t)	YOY alewife (t)	Adult alewife (t)	All foods (t)
1	410	377	197	0	332	289	137	0	758
2	206	1205	111	539	104	602	59	277	1042
3	0	1845	204	1438	0	590	68	462	1120
4	0	1166	332	2907	0	227	70	589	886
5	0	1328	683	6006	0	136	68	608	812
6	0	960	695	6500	0	48	36	354	438
7	0	480	653	6560	0	13	18	188	219
8	0	459	626	6290	0	6	9	96	111
9	0	479	655	6580	0	4	5	52	61
Totals	616	8299	4156	36820	436	1915	470	2626	5447
% of diet	1.2	16.6	8.3	73.8	8.0	35.2	8.6	48.2	100.0

[a] Based on a simulation for a single fish (no mortality).

[b] Based on a simulation for the entire population with mortality functions implemented.

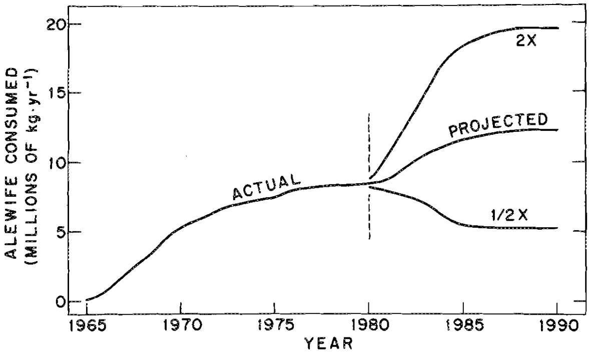

FIG. 8. Estimated actual annual consumption of alewife by lake trout in Lake Michigan during various years based on modeling simulations for the entire trout populations, with projections to 1990. Upper and lower curves between 1980 and 1990 are based on the assumptions that the stocking rate was either held constant at 2× or ½× the 1980 rate.

double and half the number of lake trout stocked in 1980 to determine how rapidly a change in stocking density might be reflected in altered predation rates (Fig. 8). These results emphasize the point made earlier that about 4 yr may be needed to effect a marked change. Reductions in lake trout population biomass can perhaps be effected more rapidly through increased fishing effort. It could be desirable to do this in the event of a collapse of the forage fish populations, but changes of stocking densities for the various salmon would yield quicker responses (Stewart et al. 1981).

The simulation results presented herein were intended to provide first indications of the forage requirements of past, present, and projected future lake trout populations in Lake Michigan. We believe that our overall estimates are reasonable but recognize that a number of refinements should be possible, including evaluation of year-to-year and regional variation of feeding rates and diet composition. As our knowledge of the Great Lakes increases, we anticipate that the modeling approach developed herein will become a progressively more powerful research and management tool.

Summary

1) Analyses indicate that the model developed herein is especially well suited for providing estimates of consumption by fitting a known growth curve. The energetics modeling approach can provide estimates of predation rates of utility for evaluating predator−prey interactions.

2) Conversion efficiency of energy (21.8%) by lake trout over their 9-yr life in Lake Michigan is about twice that of converting mass to growth (12.2%) due to high-energy fat storage. Failure to consider both ontogenetic increases and seasonal cycles of energy density in both predator and prey can give 2- to 3-fold errors in energy intake estimates based on energetic modeling simulations.

3) Greatest sensitivities of the model to errors of parameter estimation were for parameters relating metabolism to weight, indicating the need for good laboratory studies on metabolism.

4) Highest mass conversion efficiencies are obtained by relatively fast-growing individuals, and a major proportion of energy assimilated annually by older cohorts may be shed as gametes.

5) Peak predatory impact of lake trout occurs 3.5 yr after stocking; peak impact on alewife occurs in the 4th and 5th year, precluding manipulations of stocking densities as a means to control short-term prey fluctuations.

6) Predation by lake trout on alewife has increased steadily since 1965 and further increases are projected for the near future. The model can provide managers with initial indications of possible impacts from these planned increases and various alternative stocking policies.

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