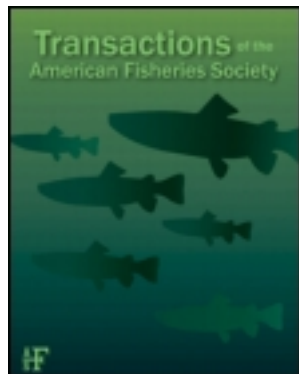


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Dynamics of Consumption and Food Conversion by Lake Michigan Alewives: An Energetics-Modeling Synthesis

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Abstract.—We developed an energetics model for the alewife *Alosa pseudoharengus* to evaluate consumption and conversion efficiency processes. We estimated alewife standard metabolism (R) as a function of wet body weight (W , g) and water temperature (T , °C): R ($\text{g}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) = $0.0073W^{-0.215}e^{0.0548T}$. We estimated maximum daily ration for 15-g, yearling alewives at 20°C to be as much as 37% of their body weight in experiments of 24 h. Modeling simulations based on observed growth in Lake Michigan indicated that yearling alewives may attain close to 70% of their estimated maximum consumption rate during September and October. Simulation results indicated wide seasonal variations in consumption rates; almost 50% of the yearly consumption by an individual adult alewife (age \geq II) occurs in September and October, suggesting abundant food and possibly relaxed competition during that season. In contrast, adult alewives lose weight during the summer when stratification of Lake Michigan would permit orientation to water temperatures optimal for growth, suggesting that serious food limitations during that period may heighten competitive interactions. Over an annual cycle, adults converted only 1.3–2.8% of food consumed (wet weight) to body biomass; young of the year converted 5%. Conversion of energy consumed to body energy was higher than biomass conversion, but still relatively low for older age-classes—2.3–5.2% for adults and 12.7% for young of the year. Total annual consumption and conversion efficiency estimates were relatively insensitive to assumptions about seasonal dynamics of body energy density ($\text{J}\cdot\text{g}^{-1}$ wet weight) but within seasons when energy density was changing rapidly, an assumption of constant energy density yielded errors of –45% to 104% for those variables.

The alewife *Alosa pseudoharengus* has been one of the dominant fish species in lakes Michigan and Huron since about 1960, and in Lake Ontario since before 1900 (Smith 1970). Intense competition from, and perhaps predation on early life stages of other forage fishes by, the alewife may have contributed to the drastic declines and extinctions of native planktivorous fishes that have occurred in these lakes (Smith 1970; Crowder 1980, 1986). The almost explosive recoveries of bloater *Core-*

gonus hoyi, yellow perch *Perca flavescens*, and, to a lesser extent, rainbow smelt *Osmerus mordax* and deepwater sculpin *Myoxocephalus thompsoni* following a recent decline of alewives in Lake Michigan provide further evidence for strong interactions between alewives and other fishes (Jude and Tesar 1985; Wells 1985). Quantifying ecological processes such as predation rates and competitive interactions in systems as large as the Great Lakes is a difficult task. Models like the one de-

veloped here are powerful tools for estimating fluxes of materials and energy, such as consumption rates (Stewart et al. 1983; Rice and Cochran 1984; Bartell et al. 1986), and such estimates can enhance our understanding of temporal and spatial patterns of interactions between species (Longhurst 1984).

Millions of salmonine predators have been stocked annually into the Great Lakes to maintain an extremely valuable sport fishery. Those salmonines have relied heavily on alewives as forage (Stewart et al. 1981; Eck and Brown 1985). Recent sharp declines in alewife abundance in lakes Huron and Michigan (Eck and Brown 1985; Jude and Tesar 1985; Wells 1985; R. L. Argyle, U.S. Fish and Wildlife Service, Ann Arbor, Michigan, personal communication) suggest that forage needs of the salmonine assemblages may have exceeded the sustainable production capacities of the alewife stocks. Alewife populations may have been depressed initially by a series of cold winters (Eck and Brown 1985), allowing heavy predation inertia from salmonines (Stewart et al. 1981) to further reduce the populations. We clearly need a better understanding of seasonal and longer-term production dynamics for each of the major forage fishes in the Great Lakes if we desire sustained fishery productivity (Kitchell 1985). Our alewife model is a step towards that realization.

Our specific objective in this paper is to evaluate seasonal and ontogenetic dynamics of consumption and food conversion processes of the alewife in Lake Michigan, thereby improving our concepts of when and how alewives affect pelagic ecosystems of the Great Lakes. To this end, we developed a bioenergetics model for the individual alewife in Lake Michigan through laboratory studies of metabolism, volitional swimming speeds, and maximum daily consumption rates, and combined these data with a synthesis of available information on ecological energetics of the alewife and related taxa. We also evaluated the model to determine the sensitivity of consumption and conversion efficiency estimates to alternative assumptions about seasonal dynamics of body weight and energy density.

Model Development

Our energetics model for the alewife is based on a mass-balance equation in which growth equals consumption minus metabolism and waste losses (e.g., Winberg 1956; Kitchell et al. 1977; Kitchell 1983). The set of functions used here are most similar to those developed for the lake trout *Sal-*

velinus namaycush (Stewart et al. 1983), but differ in four respects. (1) A seasonal cycle of body energy density (joules per gram wet weight) was modeled according to the observations of Flath and Diana (1985). Newly developed theory for modeling growth of a fish with a seasonal energy cycle (Stewart et al. 1983) is applied and evaluated for the first time. (2) Growth patterns for cohorts 2–8 (ages I–VIII) were modeled by dividing each simulation year into four growth seasons; consumption rate was varied between seasons (e.g., Rice and Cochran 1984) as needed to closely approximate the complicated seasonal growth dynamics reported by Flath and Diana (1985). Our model thus provides the first detailed growth simulation covering the entire life of a clupeoid fish. (3) Temperature dependence of maximum consumption rate was modeled with the function of Thornton and Lessem (1978). (4) Egestion and excretion were modeled, respectively, as constant proportions of consumption and assimilated food, simplifications suggested by Bartell et al. (1986).

Physiological Parameters for the Alewife

Parameter values for physiological processes (Table 1) were estimated from our own laboratory studies (see Appendix for methods) or were used directly from or developed from the literature.

Metabolism

The least-squares solution for the standard metabolism model, linearized by \log_e transformation, was (regression $R^2 = 0.71$)

$$\begin{aligned} \log_e R \text{ (mL O}_2 \cdot \text{kg}^{-1} \cdot \text{h}^{-1}) \\ = 4.894 - 0.215 \log_e W + 0.0548T; \end{aligned}$$

W is wet body weight (g) and T is temperature ($^{\circ}\text{C}$). With the weight-dependence coefficient, $\beta = -0.215$, all data were corrected to a 15-g fish and plotted against temperature to assess variation due to possible spontaneous activity in the respirometer (Figure 1). The wide variation in data suggested that the derived relationship could be higher than standard metabolism. To obtain a closer approximation to standard metabolism (by definition the lowest possible for an alert fish), the intercept was adjusted downward in order that the regression line passed through the mean value for metabolism at 5°C ; at 5°C , the alewives were extremely sluggish. This new line passed through the lower edge of the scatter of data (Figure 1). For modeling estimates of consumption, either intercept value would be sufficiently accurate because consumption estimates are relatively insensitive

TABLE 1.—Symbols and estimated physiological parameter values used to implement an energetics model for the alewife. Parameters are for equations in Stewart et al. (1983) and Thornton and Lessem (1978).

Sym- bol	Parameter description	Parameter value(s)
Consumption, C_{max}		
a	Intercept: C_{max} at $(\theta_2 + \theta_3)/2$	0.846
b	Coefficient: C_{max} versus weight	$(g \cdot g^{-1} \cdot d^{-1})$ -0.30
θ_1	Temperature for K_1 (Thornton and Lessem)	5, 4, 3 ^a
θ_2	Temperature for K_2 (Thornton and Lessem)	24, 20, 16 ^a
θ_3	Temperature for K_3 (Thornton and Lessem)	26, 22, 18 ^a
θ_4	Temperature for K_4 (Thornton and Lessem)	29, 27, 25 ^a
K_1	Proportion C_{max} at θ_1	0.17
K_2, K_3	Proportion C_{max} at θ_2, θ_3	0.98
K_4	Proportion C_{max} at θ_4	0.01
Metabolism, R		
α	Intercept: R	0.00367
β	Coefficient: R versus weight	$(g \ O_2 \cdot d^{-1})$ -0.215
ρ	Coefficient: R versus temperature	0.0548
ν	Coefficient: R versus swimming speed	0.03
SDA	Coefficient: specific dynamic action	0.175
Swimming speed, U		
ω	Intercept: U ($<9^\circ C$)	5.78
ω	Intercept: U ($\geq 9^\circ C$)	22.08
δ	Coefficient: U versus weight	$(cm \cdot s^{-1})$ -0.045
ϕ	Coefficient: U versus temperature ($<9^\circ C$)	0.149
ϕ	Coefficient: U versus temperature ($\geq 9^\circ C$)	0.0
Egestion, F		
f	Proportion of consumed food egested	0.16
Excretion, E		
ϵ	Proportion of assimilated food excreted	0.10

^a Values for young of the year, yearling, adult.

to errors in estimating that parameter (Bartell et al. 1986). The final model for a first approximation of standard metabolism (Figure 2), based on an example of $6,826 \text{ J} \cdot \text{g}^{-1}$ wet weight of alewife, was

$$R \text{ (g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}\text{)} = 0.0073W^{-0.215}e^{0.0548T}$$

The intercept value, $\alpha = 0.0073$, must be in terms of $\text{g } O_2 \cdot \text{d}^{-1}$ for input to the model; for $13,560 \text{ J} \cdot \text{g}^{-1} O_2$ (Elliott and Davison 1975), this parameter is 0.00367. In the context of the growth model, the intercept value was corrected on each simulation day for the average energy density of the various foods being eaten to give metabolism in

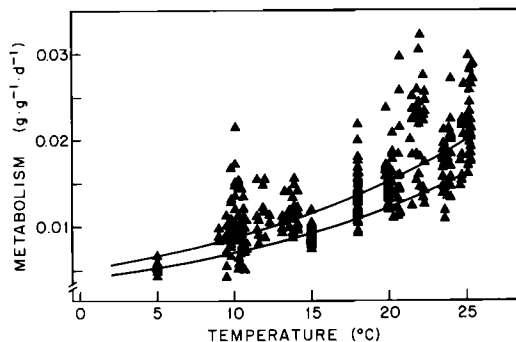


FIGURE 1.—Relationship of daily specific metabolism of alewives to temperature. All data were standardized to a 15-g fish. The upper line is a least-squares regression estimate of metabolism, including that due to spontaneous activity in the respirometer chambers. The lower line has the same slope but was adjusted downward to fit the mean metabolism at $5^\circ C$, which is considered a first approximation of standard metabolism.

gram equivalents of the day's forage. Daily specific growth rate of an average individual alewife was computed in terms of gram food equivalents per gram body weight per day, then corrected for relative energy densities of the alewife (which vary with age and season: Figure 3) and its food on that particular day (Stewart et al. 1983).

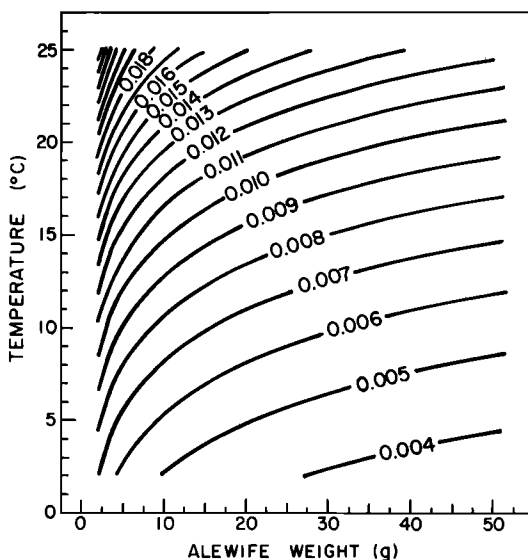


FIGURE 2.—Contour plot of daily specific standard metabolism ($\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$) of alewives versus temperature and fish weight.

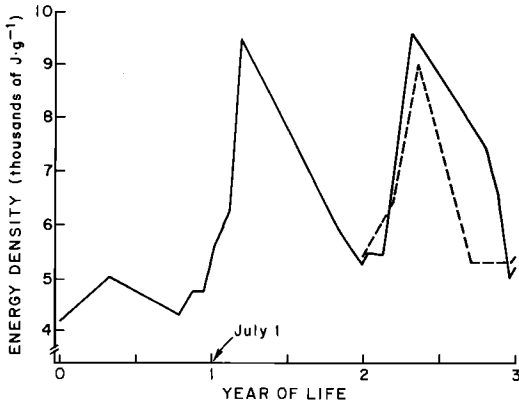


FIGURE 3.—Seasonal changes in energy density per gram wet weight for the alewife during its first 3 years of life in Lake Michigan (solid line; based largely on data provided by J. Diana, University of Michigan, Ann Arbor, personal communication, and presented in Flath and Diana 1985). Values calculated by Stewart et al. (1983) from data in Yeo (1978) are plotted for comparison (dashed line).

Swimming Speed

Colby (1973), observing approximately 7-g alewives in a large laboratory pool, reported that swimming speed, U ($\text{cm}\cdot\text{s}^{-1}$), increased rapidly between 3 and 9°C ($Q_{10} = 4.34$; coefficient for temperature dependence of swimming speed, $\phi = 0.149$) but appeared to level off at temperatures between 9 and 13°C. Volitional swimming speeds (U) estimated by us for three sets of 30 observations of small fish were 14.6, 20.6, and 26.9 $\text{cm}\cdot\text{s}^{-1}$; the overall average was 20.7 $\text{cm}\cdot\text{s}^{-1}$. Estimates for four sets of 30 observations of large fish were 16.2, 18.1, 18.8, and 24.3 $\text{cm}\cdot\text{s}^{-1}$; the overall average was 19.4 $\text{cm}\cdot\text{s}^{-1}$. To account for metabolism due to swimming activity (Stewart et al. 1983), the function for standard metabolism is multiplied by $e^{\nu U}$, ν being the coefficient for swimming-speed dependence of metabolism. We set ν at 0.03, the measured value for the aholehole *Kuhlia sandvicencis* (Muir and Niimi 1972). The aholehole is a modest-sized (up to 20 cm), euryhaline fish with a body form not radically different from a herring's. Swimming speeds for the small alewives yielded estimates for the metabolic increment above standard metabolism due to swimming activity ($e^{\nu U}$) of 1.55, 1.86, and 2.24; for the average swimming speed, the value was 1.86. Corresponding values for the large fish were 1.63, 1.72, 1.75, and 2.07, and 1.79 for the average speed. If weight dependence of swimming speed is assumed to be a power function of body weight (Ware 1978;

Stewart et al. 1983) and relatively independent of temperature at higher temperatures (Colby 1973), our results yield the following model:

$$U (\text{cm}\cdot\text{s}^{-1}; T \geq 9^\circ\text{C}) = 22.08 W^{-0.045}$$

Incorporation of Colby's (1973) results for the temperature dependence of swimming speed at lower temperatures yields

$$U (\text{cm}\cdot\text{s}^{-1}; T < 9^\circ\text{C}) = 5.78 W^{-0.045} e^{0.149T}$$

These two equations were used in the alewife bioenergetics model to estimate daily volitional swimming speeds for the alewife in Lake Michigan (Stewart et al. 1983).

Maximum Consumption

Eight replicate feeding experiments were completed at 20°C. Mean weights for fish in the eight groups only ranged from 11.7 to 16.1 g, too small a range for the weight dependence of C_{max} to be estimated. We postulated that the relationship of C_{max} to weight is a power function with a weight-dependence coefficient of 0.7 (-0.3 for daily specific rate), a value similar to 0.744 estimated for young Atlantic herring *Clupea harengus* (DeSilva and Balbontin 1974) and other fishes (e.g., Brett 1971). Using the value of 0.7, we normalized results from the 20°C experiments to a standard 15-g fish. We thus estimated that a 15-g alewife at 20°C can consume 37.6% (range, 33.2–42.7%) of its body weight per day in brine shrimp. The C_{max} was about 23.5% of body weight per day on a dry-weight basis. Back-extrapolation yields a C_{max} estimate of 85% on a wet-weight basis or 53% as dry weight for a 1-g alewife.

Maximum daily ration for many fishes increases with increasing temperature to a maximum near the fishes' preferred temperature, then declines to near zero just below maximum lethal temperature (e.g., Elliott 1976b; Kitchell et al. 1977; Brett 1983; Bevelhimer et al. 1985). We assumed this to be true for the alewife. Temperature dependence of maximum ration was modeled with the algorithm of Thornton and Lessem (1978; see Table 1 for parameter estimates). Preferred temperatures were 16°C for adult and 24–25°C for young-of-the-year alewives; lethal temperatures were 28°C for adults and 32°C for young-of-the-year alewives (Otto et al. 1976). We assumed that yearling alewives were intermediate in their physiology and behavior, 20°C being their preferred and 30°C their lethal temperatures. The offshore, epilimnetic thermal environment of yearling alewives is consistent with this assumption. Preferred temperatures for rain-

bow trout *Salmo gairdneri* decrease in a continuous manner from about 19 to 13°C during their first year of life (Kwain and McCauley 1978). Alewives well adapted to laboratory conditions can survive at temperatures higher than those observed by Otto et al. (1976; see McCauley and Binkowski 1982). Results from Otto et al., however, may be appropriate for modeling alewives in Lake Michigan, where they may be variously stressed by low winter temperatures and poor nutrition (Colby 1973).

Specific Dynamic Action (SDA)

The metabolic cost of processing ingested food was modeled as a constant proportion of assimilated food, $SDA(C - F)$, which may be reasonable given the relatively low sensitivity of such models to errors in estimating SDA (Kitchell et al. 1977; Stewart et al. 1983; Bartell et al. 1986). Specific dynamic action has not been measured for the alewife. Alewives were assumed to be similar to aholehole, whose estimated SDA ranges between 0.16 and 0.19 (Muir and Niimi 1972). We chose the midpoint of that range, 0.175, as a first approximation for the alewife. That is similar to values reported for various other fishes (e.g., Beamish 1974) and should be sufficiently accurate.

Egestion and Excretion

As a first approximation, we modeled egestion as a constant proportion of food consumed, $F = 0.16C$, and excretion as a constant proportion of assimilated food, $E = 0.10(C - F)$. Error analyses of an earlier version of this model which included Elliott's (1976a) equations for egestion and excretion as functions of temperature and ration indicated that treating F and E as constant proportions of consumption would not produce noticeable errors in model estimates of consumption (Bartell et al. 1986). The values for these two parameters are approximately those that would be obtained from Elliott's (1976a) functions for these processes averaged over the year. Total waste losses thus estimated are similar to those implemented by Kitchell et al. (1974) for a model of the bluegill *Lepomis macrochirus* feeding on zooplankton (i.e., 25% of consumption).

Evaluation of Physiological Parameters

Metabolism.—The weight dependence coefficient, -0.215 , is not noticeably different from values for nonsalmonid fishes reported by Winberg (1956), and is in close agreement with the value of -0.227 estimated for Atlantic herring (DeSilva

and Balbontin 1974). It is also within the range of values (-0.18 to -0.28) reported for juvenile Atlantic menhaden *Brevoortia tyrannus* at temperatures of 10–25°C (Hettler 1976). The temperature dependence coefficient is identical to that ($\rho = 0.0548$; $Q_{10} = 1.73$) estimated for young-of-the-year blueback herring *Alosa aestivalis* (Burbidge 1974). Burbidge, however, allowed only 1–3 h for his fish to acclimate after placing them in the respirometer chamber, which may not be enough time. When we solved our relationship for the size of fish studied by Burbidge (about 2.2 g), and converted Burbidge's results to measurement units identical to ours, his intercept value was almost double that estimated by us for the alewife.

Swimming speed.—Katz (1978) estimated volitional swimming speeds for a school of young-of-the-year American shad *Alosa sapidissima* (average total length 110 mm) in a large laboratory tank (water temperature, 23.6–28.3°C; photoperiod, 14 h 25 min light, 9 h 35 min darkness). Hourly observations were made over 4 d. The American shad formed schools and swam relatively fast during the day then slowed down, dispersed, and swam as individuals at night. Averaging the 97 observations in Katz's Figure 1, we estimated a daily volitional swimming speed of $16.1 \text{ cm} \cdot \text{s}^{-1}$ (which yields $e^{0.03(16.1)} = 1.62$). Given the variation in Katz's data, this speed is reasonably close to values estimated for the alewife. These two species of *Alosa* appear to swim much slower on the average than the phytoplanktivorous Atlantic menhaden studied by Durbin and Durbin (1983). Colby's (1973) observation that alewife swimming speeds increased rapidly as temperatures rose from low values, then leveled off above 9°C, is in general agreement with the temperature response pattern for volitional swimming speeds of chub mackerel *Scomber japonicus* (Schaefer 1986).

Maximum consumption.—We chose maximum daily ration (C_{\max}) for study because this determines the ultimate upper bound on the growth potential of a fish. Together with estimates of standard metabolism and other energetics parameters, it permits evaluation of scope for growth of the alewife, and this can, in turn, provide useful insights into the species' distributional and behavioral ecology (Warren and Davis 1967; Kitchell et al. 1977; Webb 1978; Rice et al. 1983).

Our maximum ration estimate of 37.6% body weight per day appears to be relatively high for a 15-g (yearling) alewife but, as DeSilva and Balbontin (1974) noted, perception of what fishes

should be able to consume may be biased by a historical research emphasis on predatory temperate-zone fishes such as the salmonines. The daily consumption capacities of the various highly active pelagic fishes that have been studied seem to be consistently higher than those of less active fishes (e.g., Hatanaka et al. 1957; Leong and O'Connell 1969; Magnuson 1969; DeSilva and Balbontin 1974; Enderlein 1981). Many tropical fishes also have high daily rations (Pandian and Vivekanandan 1985) similar to our estimate of C_{\max} for the alewife. Planktivores also may be able to process ingested food at a faster rate than many other fishes because of the relatively large surface area of the small food particles they consume (Enderlein 1981). The alewife's ability to feed both day and night (Janssen and Brandt 1980) may also facilitate relatively high daily rations.

For the northern anchovy *Engraulis mordax* feeding in the laboratory on brine shrimp, Leong and O'Connell (1969) related consumption rate to foraging time and body weight with a linear model. By that relationship, a 15-g fish feeding for 1 h consumes 1.72 g or 11.4% of fish wet weight. Leong and O'Connell also found that gut evacuation rate was high enough to permit several such feeding bouts per day. Although they did not try to estimate maximum daily ration for the northern anchovy, their results clearly are consistent with our findings for the alewife.

DeSilva and Balbontin (1974) observed that Atlantic herring fed to satiation twice daily (thus, probably not given a maximum ration) would consume food equal to 17–21% of body wet weight per day on some days. Such days of high ration, however, were generally followed by one to a few days of lower ration. This suggests that our estimates for the alewife would likely be lower if our experiments had continued for several days. Our simulations indicate, nonetheless, that yearling alewives must consume at almost 70% of the maximum rate we estimated in the laboratory to attain their observed fall growth rates (Table 2). If the intercept of our C_{\max} equation were adjusted downward, all of the estimated proportions of maximum ration would increase (Table 2), but none of our inferences would change. We conclude that our estimates of maximum consumption are reasonable and offer the foregoing model as a provocative and fully testable hypothesis. If supported by further studies, it might provide a partial explanation for the alewife's well-known capacity to rapidly and dramatically restructure zooplankton populations (e.g., Wells 1970; Warshaw 1972),

a process with possible attendant effects on phytoplankton communities and nutrient-cycling processes (Carpenter and Kitchell 1984; Scavia et al. 1986).

Application of the Alewife Model to the Lake Michigan System

Site-Specific Variables

Growth and length-weight relationship. — Lengths (L) and weights (W) of alewives at the end of each year of life (1 July) in Lake Michigan (Table 3, after Brown 1972) support a generalized relationship for juveniles and adults for combined male and female data:

$$\log_e W \text{ (g)} = -4.72 + 2.96 \log_e L \text{ (cm)}.$$

Larval and small juvenile alewives are much more slender for a given length than would be predicted by backwards extrapolation of an adult length-weight relationship. Analysis of data provided by P. Rago (University of Michigan, Ann Arbor, unpublished) for formalin-preserved alewives 5 to 25 mm long, combined with our own data for 25- to 43-mm fresh-frozen specimens, yielded ($R^2 = 0.99$; $N = 56$)

$$\log_e W \text{ (g)} = -6.7091 + 4.3157 \log_e L \text{ (cm)}.$$

This intersects the generalized adult relationship at 43.4 mm and 0.68 g. For our simulations, we used a starting weight of 0.25 g (31–35 mm), about the size at which gut and gill raker morphology first approximate that of adults (Norden 1968).

We simulated growth of the average individual alewife in Lake Michigan by iteratively adjusting consumption to a proportion (P) of maximum consumption until the desired weight end point for a particular time interval was attained within 0.002 g (Kitchell et al. 1977; Stewart et al. 1983). Model years consisted of 365 daily time steps. We simulated growth of the first cohort by fitting the model to the annual end point of weight (Table 3). To accurately simulate the growth dynamics reported by Flath and Diana (1985) for older fishes, we divided the year into four growth seasons and adjusted P separately for each season, a procedure used by Rice and Cochran (1984) for modeling largemouth bass *Micropterus salmoides*. To model growth of the alewife over its second through eighth year of life in Lake Michigan, we used the annual end points of growth from Brown (1972) for weight on 1 July of each simulation year (Table 3), and data for age-classes I–IV from Flath and Diana (1985, but we worked from their original data provided by J. Diana, University of Michi-

TABLE 2.—Comparison of annual weight gain, spawning losses, food consumption, and gross conversion efficiency for various age-classes of Lake Michigan alewives based on a simulation for an average individual alewife. Conversion efficiency calculations included gametes shed.

Model cohort (age-class)	Weight gain (g)	Gametes shed (g)	Proportion of maximum consumption, <i>P</i> , by growth season (simulation days)				Total annual consumption		Gross conversion efficiency (%)	
			Summer (1–50)	Fall (51–119)	Winter (120–351)	Spring (352–365)	Grams	Kilo-joules	Wet-weight basis	Energy basis
1 (0–I)	7.41	0.0	0.47	0.47	0.47	0.47	148	310	5.0	12.7
2 (I–II)	16.26	0.0	0.45	0.67 ^a	0.15 ^b	0.32 ^c	342	876	4.6	9.6
3 (II–III)	9.72	2.38	0.19	0.41	0.10	0.26	426	1,206	2.8	5.2
4 (III–IV)	6.92	2.89	0.19	0.42	0.08	0.26	511	1,439	1.9	3.5
5 (IV–V)	5.84	3.30	0.19	0.44	0.08	0.26	574	1,612	1.6	2.9
6 (V–VI)	6.42	3.76	0.19	0.45	0.07	0.27	636	1,786	1.6	2.9
7 (VI–VII)	5.21	4.13	0.19	0.46	0.07	0.27	690	1,933	1.4	2.4
8 (VII–VIII)	5.25	4.50	0.19	0.46	0.06	0.27	741	2,072	1.3	2.3

^a Simulation days 51–76. ^b Days 77–323. ^c Days 324–365.

gan, Ann Arbor) for estimating the seasonal pattern of weight change. We calculated proportional deviations of Flath and Diana’s observed weights from a straight-line fit between their annual end points of weight. Those deviations then were used to approximate weights (\hat{W}_i) on the same days between Brown’s (1972) observed annual end points for each cohort:

$$W_i = \hat{W}_i [1 + (W_j - \hat{W}_j) / W_j];$$

\hat{W} = weight on any given day of the year as calculated by linear interpolation between observed annual end points of body weight, subscript *i* denoting Brown’s (1972) data and *j* denoting Flath and Diana’s (1985) data;

W_j = observed weight from Flath and Diana (1985) for the same day.

Values for the proportional deviations [($W_j -$

\hat{W}_j)/ W_j] for model cohort 2 were: day 50 = 0.319, day 76 = 0.607, and day 324 = -0.409; values for cohorts 3–8 were: day 50 = -0.094, day 119 = 0.229, day 351 = 0.036. The resulting weights and corresponding *P* values estimated for the final day of each simulation interval (or growth season) for cohorts 2–8 are listed in Tables 4 and 2, respectively. Flath and Diana (1985) had more than four observations within each year, but we found that four intervals were sufficient to simulate the seasonal dynamics.

Flath and Diana (1985) implied that declines in alewife weight between late fall and early spring were relatively linear, but they had no midwinter data to substantiate that assumption. To approximate that assumed winter growth pattern, we implemented a routine that computed maintenance ration (i.e., an iterative fit for zero growth) for each day during the coldest part of the winter (below 4°C). As the model was formulated, this constraint was needed to prevent a more drastic weight loss during winter when alewife energy density was declining sharply.

Energy density of alewives.—Alewives in Lake Michigan go through a rather dramatic seasonal cycle of energy density (Yeo 1978; Flath and Diana 1985), the modeling of which is very important both for evaluating conversion of invertebrate forage to alewife biomass (see below) and for estimating conversion of alewives to salmonid predator biomass (Stewart et al. 1981, 1983). The seasonal cycles of energy density used in simulations presented here are based on the observations of Flath and Diana (1985). Working from sample dates, energy densities, and percentage water data generously provided by J. Diana, we calculated energy density per gram wet weight for each of

TABLE 3.—Lengths and weights of alewives at the end of each year of life in Lake Michigan. Data are based on $\log_{10} W$ (g) = -4.9 + 2.91 $\log_{10} L$ (mm) for males, and $\log_{10} W$ (g) = -5.12 + 3.01 $\log_{10} L$ (mm) for females (Brown 1972).

End of year of life	Males		Females		Average weight (g)
	Centimeters	Grams	Centimeters	Grams	
1	9.8	7.84	9.8	7.47	7.66
2	14.4	24.03	14.4	23.81	23.92
3	15.9	32.07	16.4	35.21	33.64
4	16.9	38.30	17.5	42.81	40.56
5	17.7	43.81	18.3	48.98	46.40
6	18.4	49.05	19.2	56.59	52.82
7	18.9	53.03	19.9	63.03	58.03
8	19.7	59.83	20.3	66.92	63.38

TABLE 4.—Simulated average body weights for model cohorts 2–8 of the alewife in Lake Michigan. Simulations were forced to match the given final weights for each interval by iterative adjustment of ration during that interval. Day 1 is 1 July.

Simulation interval (d)	Alewife cohort						
	2	3	4	5	6	7	8
1–50	13.05	22.86	31.31	37.44	42.80	48.46	53.20
51–119(76 ^a)	17.75	33.30	44.12	52.20	59.61	67.01	73.47
120(77 ^a)–351(324 ^a)	13.05	34.48	41.76	47.86	54.49	59.93	65.47
352(325 ^a)–365	23.92	33.64	40.56	46.40	52.82	58.03	63.38

^a Day for cohort 2 only.

their sample dates and estimated values for all intervening days of the year by linear interpolation (Figure 3).

A value of $4,185 \text{ J} \cdot \text{g}^{-1}$ was assumed for young-of-the-year alewives on the first day of the simulation (1 July), although energy densities of such small alewives have never been measured. Flath and Diana's (1985) only observations on young-of-the-year fishes ($5,020 \text{ J} \cdot \text{g}^{-1}$) were made in October. Their estimate of $4,310 \text{ J} \cdot \text{g}^{-1}$ for yearling alewives in mid-April (Figure 3) is only slightly higher than our assumed starting value for young of the year. The seasonal pattern of changes in energy density for the third year of life (Figure 3) represents a composite of Flath and Diana's data for age-classes III and IV with values averaged for the two sexes. Energy values for years 4–8 were assumed identical to those of year 3. Growth calculated at each daily time step was corrected for the seasonally varying energy density of the alewife and the weighted average energy density of its diet on that day (Stewart et al. 1983).

Analysis of the energy-density data revealed a precise relationship between energy density of the alewife and percentage dry matter, including ash ($R^2 = 0.99$; $N = 22$; range of observations = 20–35% dry matter):

$$\begin{aligned} \text{J} \cdot \text{g}^{-1} \text{ (wet weight)} \\ = -4,102 + 387 \times \% \text{ dry matter.} \end{aligned}$$

Application of this equation might greatly reduce the time and cost of future studies of alewife energy cycling because it obviates or greatly reduces the need for bomb calorimetry. This, in turn, would permit larger or more frequent samples. Flath and Diana (1985) indicated that percent lipid was an excellent indicator of body energy in alewives, but lipid content is more expensive to measure and generally not quite as good as percent dry weight for predicting energy density. The same is true for salmonines (Stewart 1980) and perhaps other fishes.

Reproduction.—A few larger individuals of Lake Michigan alewives may spawn in their second year, but the majority spawn for the first time in their third or fourth year (Norden 1967). We modeled reproduction starting with age-class III (during the fourth summer in the lake: Table 2; Figure 4) and with all gametes shed as a step-function weight loss in mid-June (simulation day 352). Energy density of the ripe gonads was similar to that of the whole fish at that time of the year (Flath and Diana 1985), so no corrections for relative energy densities were needed. Gonad weights for Lake Michigan alewives were about 5.1% total body weight for males and 10.3% for females (Norden 1967); average for the two sexes was 7.67%. Average reduction in gonad weight between ripe and spent individuals for males and females of age-classes III and IV was about 90% (J. Diana, personal communication). The average weight of

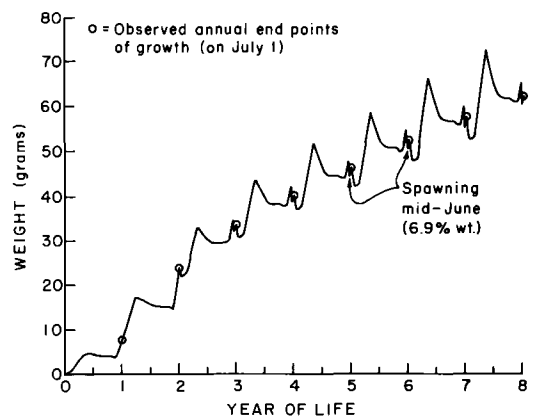


FIGURE 4.—Simulated growth of alewives in Lake Michigan based on a model using the parameters in Table 1, site-specific data summarized in the text, size-at-age data from Brown (1972, shown in Table 3), and data on seasonal growth dynamics from Flath and Diana (1985) for approximations of weights on various days within each year (Table 4).

gametes shed by all mature individuals in the population would, therefore, be about 6.9% of body weight. We made the simplifying assumption that this value was a reasonable approximation for age-classes III and older.

Diet composition.—Seasonal and age-dependent changes in diet composition of Lake Michigan alewives were determined from the literature (Morsell and Norden 1968; Webb and McComish 1974; Rhodes and McComish 1975; Brandt 1980; Janssen and Brandt 1980; Wells 1980; Crowder et al. 1981). Three matrices of percentage diet composition for four food types—cladocerans, copepods, the amphipod *Pontoporeia hoyi*, and opossum shrimp *Mysis relicta*—were developed for young of the year, yearlings, and all older age-classes (S. Hewett, University of Wisconsin–Madison, unpublished data). The percentage contribution of a food item to the diet on days of the year between times reported in the literature was linearly interpolated. This procedure differs from that used by Stewart et al. (1983) in which percentage diet composition was modeled as constant within each of various time periods during the year. On each simulation day, diet composition was input from the appropriate diet matrix and used to compute average energy density of food consumed on that day.

Alewives consumed a mixture of cladocerans and copepods until the middle of their second summer in the lake. At about that time, they began eating *Pontoporeia hoyi*, which gradually increased in the diet to about 25% by the end of the second year. During their second winter in the lake, *Mysis relicta* was added to the diet and persisted at a level of 10–15% of the diet for all older age-classes. For the first two age-classes, copepods were the dominant food item during winter, spring, and summer, and cladocerans dominated in the fall. For all older age-classes, copepods and *P. hoyi* were most important during winter, spring, and summer, and cladocerans again dominated the fall diet.

Wet-weight energy densities for zooplankters were estimated from data in Cummins and Wuycheck (1971); constant values of 1,674 J·g⁻¹ for cladocerans and 2,300 J·g⁻¹ for copepods were assumed. Cummins and Wuycheck (1971) reported 3,382 J·g⁻¹ for gammarid amphipods and 3,908–4,434 for other amphipods. As an approximation, we used constant values of 4,185 J·g⁻¹ for *Pontoporeia hoyi* and 4,604 J·g⁻¹ for *Mysis relicta*.

Water temperatures.—We assumed that young-

of-the-year and yearling alewives will orient to the warmest water available up to, but not exceeding, their preferred temperature. Alewives are spawned in the littoral zone of Lake Michigan and young of the year may encounter temperatures up to 25°C in midsummer, at least along the southeastern shore (Jude et al. 1975). Yearlings are in the epilimnion in midlake, where they may encounter temperatures up to 20°C (Figure 5).

Adult alewives prefer 16°C but may occupy water that exceeds this temperature during the spawning season in some parts of the lake. After spawning, they typically move offshore below the thermocline, where they undergo a daily vertical migration (Janssen and Brandt 1980). We assumed that adult alewives migrate from 6°C to 16°C each day. The average daily temperature is then 11°C. Growth of a rainbow trout undergoing a daily temperature cycle will be similar to one held at a constant temperature slightly higher than the average temperature of the cycle (Hokanson et al. 1977). We thus assumed that the alewife's daily cycle could be represented by a single water temperature of 12°C during the period that the lake was stratified (Figure 5).

Results and Discussion of Simulations

Growth.—The set of physiological parameters (Table 1) and site-specific variables (Figures 3, 5; Tables 2–4) were used to simulate growth of the average individual alewife in Lake Michigan (Figure 4). Growth in body weight and energy occurs

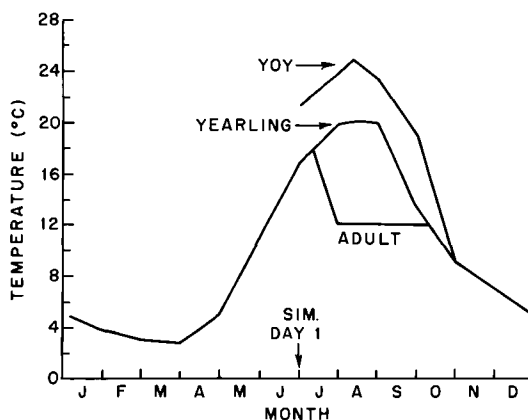


FIGURE 5.—Typical seasonal cycles of water temperatures assumed to be occupied by various age-classes of alewives in Lake Michigan, based on a composite of information from Otto et al. (1976), Jude et al. (1975), and Ayers (1962). Simulation day 1 is 1 July; YOY is young of year.

predominately in late summer and fall, and adults may suffer weight and energy losses during both midsummer and winter (Flath and Diana 1985). Relatively rapid growth rates in the first 2 years of life and during the fall in subsequent years indicate the high growth potential of the alewife, a potential perhaps more fully realized in the north Atlantic Ocean, where alewives attain a much larger size than in Lake Michigan (Brown 1972). The saw-toothed growth pattern of the alewife in Lake Michigan (Figure 4) resembles that of Atlantic herring from the North Sea (Ursin 1979), although a larger proportion of annual weight losses from Atlantic herring is due to gametes shed.

The alewife model is the first to simulate weight and energy dynamics over the entire life of a clupeoid fish. Previous clupeoid energetics models have treated only one size or age-class (Durbin and Durbin 1983; Kerr and Dickie 1985) or have failed to account for dynamics of energy density (Andersen and Ursin 1977; Kerr and Dickie 1985). Because the dynamics of energy density and energy differences between Atlantic herring and their prey were not fully accounted for, Andersen and Ursin's (1977:Table 25) consumption estimates probably are too low and their conversion efficiency estimates too high by a factor of 2 to 4. Modeling of clupeoids poses special problems because most species have extended periods of negative growth which are often associated with relatively high reproductive effort (e.g., Leggett and Carscadden 1978; Ursin 1979; Hunter and Leong 1981), and over the annual cycle, variations in body wet weight and energy density may not closely parallel each other as depletion of body lipids is compensated by water intake (Lasker 1970; Flath and Diana 1985). The alewife model accounts for all of these processes and perhaps could be applied to any clupeoid, given the appropriate species and site-specific data. Application of this modeling approach to other clupeoids, which together compose about a third of all fish catches in the world (Whitehead 1985), could greatly enhance our understanding of the production dynamics and ecological interactions of these species on a global basis.

Consumption rates.—Our modeling estimates of consumption expressed as a proportion of maximum consumption (Table 2) may be viewed as relative indices of consumption rates for comparison between seasons and age-classes. Ontogenetic changes appear to involve a general decline in consumption rates between cohorts 1 and 3, perhaps reflecting food limitations in older cohorts (see

below). Consumption potential changes seasonally in all cohorts as a function of temperature, but the proportion of maximum consumption that is realized becomes more seasonally variable after the first cohort.

Seasonal changes in consumption rates for cohort 3 (Figure 6) are perhaps typical for adult alewives. We estimated that about 50% of total annual consumption by an adult alewife may occur in a 2-month period in the fall (Table 5). This implies that annual production dynamics of alewives may be strongly linked to production dynamics of the zooplankton community during September and October. That time period may represent an especially sensitive or critical interval that warrants further study. The early onset of winter by 1 month, for example, may greatly reduce annual growth (production), overwinter survival, and levels of competition between alewives and other planktivores. Another implication of high fall consumption rates for all age-classes of alewives is that production of invertebrate forage is very high during that season. Competition with other fishes thus might be relatively lower in the fall than in other seasons.

During more than half the year in Lake Michigan, adult alewives are apparently at or below maintenance rations, clearly indicating that they may be seriously food-limited at times. This is especially evident in mid-summer when the lake is stratified and adults can orient to their preferred temperature which, for most fishes, appears to be close to the optimum temperature for growth (Jobling 1981; McCauley and Casselman 1981). Poor summer growth by alewives appears to be a paradox, and further research on the ecological mechanisms involved is warranted. If alewives are food-limited in midsummer, this season could be one of intense competitive interactions perhaps promoting niche shifts and complementarity (e.g., Crowder et al. 1981; Crowder 1986).

Weight and energy losses over the winter may indicate food limitations and possible competitive interactions during that season as well (Flath and Diana 1985), but low-temperature stress may be an added complication (Colby 1973; Eck and Brown 1985). Our modeling results indicate nonetheless that alewives must be feeding during the winter or they would lose more weight and energy than has been observed (Figure 6a). Comparison of Yeo's (1978) data on alewife energy density in 1973–1974 with those of Flath and Diana (1985) for 1979–1981 indicates that there can be marked year-to-year differences in the rate at which Lake

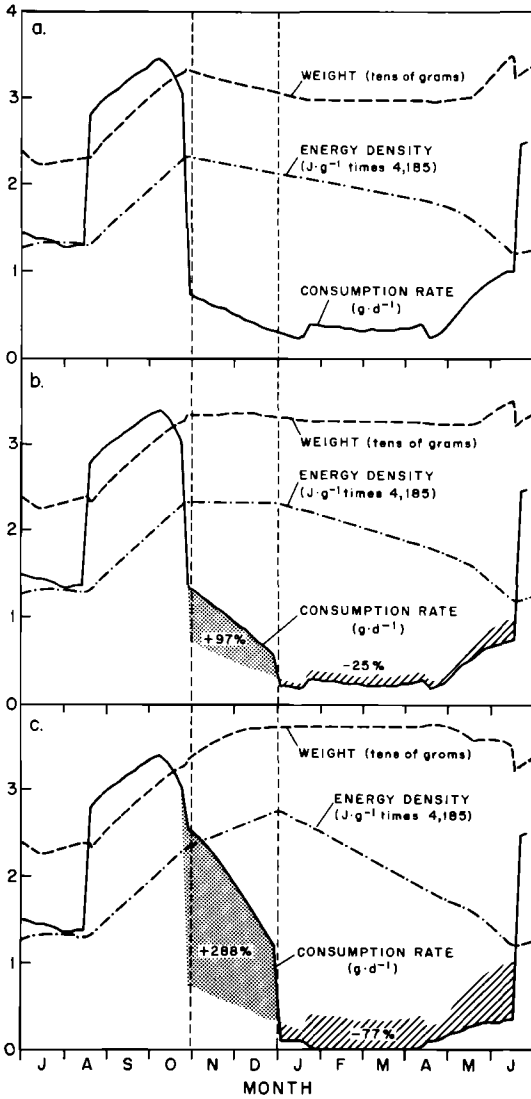


FIGURE 6.—Comparison of consumption rate ($g \cdot d^{-1}$) for cohort 3 of the alewife in Lake Michigan with changes in body weight and energy density during November and December under three assumptions: (a) weight and energy density decline slightly during November and December according to a standard simulation based on inferences of Flath and Diana (1985); (b) weight and energy density remain constant during this interval; (c) weight and energy density increase at half the rate of the preceding 2 months.

Michigan alewives deplete their energy stores over the winter (Figure 3). A sample of 42 yearling and adult alewives taken off Two Rivers, Wisconsin, on 30 January 1986 had an average energy density of 6,209 (SD = 1,491) $J \cdot g^{-1}$ wet weight (based on

the dry weight–energy relationship given above) which falls on the line connecting Yeo’s estimates (Figure 3). Comparison of these observations on winter energy density to temperature conditions and abundances of alewives and their competitors, however, does not yield a pattern that would explain such variation (Table 6), suggesting that a long time series of such data may be needed to resolve possible complex interactions between the variables.

Crowder’s (1986) hypothesis of intense competition between alewives and other planktivores in Lake Michigan might be evaluated by comparing estimates of invertebrate forage production to modeling estimates of consumption by alewives and their presumed competitors. Such an exercise might demonstrate at least that food resources are (or are not) scarce enough to be limiting at certain times and places. Such a modeling synthesis, however, is not yet possible because various components needed to model pelagic systems in the Great Lakes are still under development. As a minimum, we still need energetics models for the bloater and rainbow smelt and production estimates for certain key invertebrate taxa.

Conversion efficiency.—Gross conversion efficiencies (percentages of consumed food, or energy, that are converted to body weight, or body energy, and gametes) were calculated for each cohort in Lake Michigan from a simulation of the average individual (Table 2). Conversion efficiencies declined steadily with increasing age, a pattern typical of many other fishes (e.g., Webb 1978; Ursin 1979; Majkowski and Waiwood 1981; Adams et al. 1982). Conversion of energy was about double that of weight because energy density of the typical alewife was generally much higher than the average energy density of its diet, a situation similar to that found for lake trout (Stewart et al. 1983) and probably true for many other fishes (e.g., Elliott 1976b). The relatively lower efficiencies of cohorts 3–8 were undoubtedly due to their weight losses during summer and winter.

Biomass conversion efficiencies of 10–30% or more have been reported for many fishes (e.g., Ursin 1979). Our estimate of biomass conversion for young-of-the-year alewives is only about half the 9.3% reported for young-of-the-year blueback herring (Burbidge 1974). Alewives in Lake Michigan thus appear to be extremely inefficient (adults) or at best average (juveniles) at converting available food to growth when the complete annual cycle is considered. Much of the secondary production channeled into Lake Michigan alewives is

TABLE 5.—Comparison of consumption estimates for Lake Michigan alewives based on modeling simulations of cohort 3 for decreasing, constant, or increasing body weights and energy densities during November and December (corresponding to plots in Figure 6). Simulation day 1 is 1 July.

Growth season (d)	Assumption for weight and energy changes					
	Decreasing		Constant		Increasing	
	Grams	%	Grams	%	Grams	%
Summer (1–50)	67	15.7	67	15.3	67	14.6
Early fall (51–119)	218	51.2	218	49.7	218	47.4
Late fall (120–184)	32	7.6	63	14.4	124	27.0
Winter (185–351)	75	17.5	56	12.8	17	3.7
Spring (352–365)	34	8.0	34	7.8	34	7.4
Annual total	426	100	438	100	460	100
Net change (%)	0		+2.8		+8.0	

apparently dissipated as metabolic heat. We hypothesize that where alewives overlap in diet, time, and space with native Great Lakes fishes such as the bloater, the latter might make more efficient use of the same invertebrate forage. Alewives nonetheless have the potential for high conversion efficiencies if food is sufficiently abundant. We estimated that alewives at or near maximum rations may have conversion efficiencies over 30%, which is similar to estimates for Atlantic menhaden on high rations (Durbin and Durbin 1983).

An extremely interesting and still not fully explained observation is that the total fishery yield from Lake Michigan increased noticeably in the mid-1960s over yields during the previous 45 years as the fish community and catch became dominated by alewives (Smith 1968; Eck and Brown 1985). That pattern is even more surprising when one considers the extremely poor conversion efficiency of alewives. Alewives are very proficient, versatile feeders (Wells 1970; Janssen 1978), but that alone may not explain the apparently enhanced fishery productivity of the Lake Michigan system. It may be possible that alewives actually enhance productivity of lower trophic levels by altering the size structure of the zooplankton com-

munity (Carpenter and Kitchell 1984), thereby generating their own production feed-back loop involving food particles too small for the native fishes. A framework for investigating the latter hypothesis might be obtained by interfacing the alewife model with that of Carpenter and Kitchell (1984).

Model Evaluation

It is now well established that the modeling approach used here, in which consumption is estimated by fits of a model to observed growth, is a robust procedure in that consumption estimates have relatively low sensitivities to uncertainties in estimation of most physiological parameters (Kitchell et al. 1977; Majkowski and Waiwood 1981; Rice et al. 1983; Stewart et al. 1983; Bartell et al. 1986). Bartell et al. (1986) clearly demonstrated how fitting such models to observed growth constrains errors in model predictions. It follows logically from those results that use of shorter time intervals between the growth observations to which the model is forced to fit with zero bias would further constrain errors (e.g., Rice and Cochran 1984 and the present work). Given the extensive error analyses published previously, we have cho-

TABLE 6.—Qualitative comparison of estimated midwinter energy density of adult alewives in 3 years with differing winter temperature conditions, alewife abundances, and competitor fish abundances (based on Yeo 1978; Eck and Brown 1985; Flath and Diana 1985; Wells 1985; personal observations).

Year(s)	Midwinter energy density of alewives	Winter conditions	Alewife abundance	Competitor fish abundances
1974	Low	Average	Moderate to high; increasing	Low
1979–1981	High	Cold	Moderate; decreasing	Moderate; increasing
1986	Low	Cold	Very low	Very high

sen to restrict our sensitivity analyses to evaluations of errors in consumption and conversion estimates that might result from uncertainties about seasonal dynamics of body wet weight and energy density.

Late Fall Growth Assumptions

Our standard simulation involves an extrapolation of growth and energy from Flath and Diana's (1985) last fall data (about 27 October) to their first spring data (in April). Because there are no data for November and December, we can not rule out the possibility that weight and energy remain constant or actually continue to increase during that period. Water temperatures in those months are still high enough for alewives to feed (Colby 1973). We ran two additional simulations for cohort 3 with weight and energy constant (Figure 6b) and increasing (Figure 6c) to evaluate effects on consumption estimates of alternative hypotheses about growth in late fall.

Results indicate that for estimates of total annual consumption, the alternative hypotheses make at most an 8% difference in estimates (Table 5). Because our growth simulations were constrained to a fixed annual end point, higher consumption in late fall was compensated in part by lower consumption over the winter (i.e., faster weight loss over winter). If one is especially concerned about interactions of alewives with their forage base and competitors during the late fall, having better data on growth and energy dynamics during that period could be very important. The assumption of increasing weight and energy yields almost a 300% increase in consumption estimates for November and December (Figure 6c; Table 5).

Seasonal Energy Cycles

Winberg (1956) suggested that the energy density of many fishes could be considered constant for the purpose of bioenergetics computations and this approach has been widely used (e.g., Kitchell et al. 1977; Ursin 1979; Majkowski and Waiwood 1981; Rice et al. 1983; Kerr and Dickie 1985). Strong seasonal cycles of energy storage and depletion, however, are typical of clupeoid fishes (e.g., Lasker 1970; Leggett and Carscadden 1978; Ursin 1979; Pierce et al. 1980; Hunter and Leong 1981; Flath and Diana 1985) and less extreme cycles occur in many other fishes (e.g., Newsome and Leduc 1975; Foltz and Norden 1977; Basimi and Grove 1985; Booth and Keast 1986). Such cycles may be more prevalent in temperate climates, but some tropical fishes could have similar energy

cycles related to spawning, seasonal migrations, and flooding cycles of rivers.

Stewart et al. (1983) developed a model for growth of fishes with ontogenetic and seasonal changes of energy density. Implementation of that model for lake trout, which had ontogenetic increases but not a seasonal cycle of energy density, revealed that failure to account for the ontogenetic changes would yield a substantial underestimation of energy conversion efficiency (Kitchell 1983; Stewart et al. 1983). The alewife model represents the first application of that same growth theory to a fish with a strong seasonal cycle of energy density, thereby providing a framework for estimating sensitivity of consumption and conversion efficiency estimates to alternative assumptions about seasonal dynamics of energy density.

The alewife in Lake Michigan is ideal for such an evaluation because its annual energy cycle (Figure 3) is among the most extreme yet reported, a worst-case example. To evaluate the importance of precisely modeling a strong seasonal energy density cycle, we made three additional simulations of alewife cohort 3 using the Winberg paradigm of constant energy density (Table 7). The three constant-energy values chosen were the minimum, average, and maximum values observed for adult alewives in Lake Michigan (Flath and Diana 1985). Those values encompassed the possible errors that could result from making a single energy density estimate and assuming that it was constant throughout the year.

Results of those simulations indicated that, when integrated over the entire year, errors in estimating conversion of wet weight and consumption of both wet weight and energy were relatively small (4–10%; Table 7). Conversion efficiency of energy, however, was overestimated by 71% in the simulation at constant high $9.7 \text{ kJ} \cdot \text{g}^{-1}$. All three of the constant-energy simulations underestimated consumption during seasons with rapid gains in weight and energy (especially fall), and overestimated consumption during periods of losses (especially winter). Errors in estimating wet-weight conversion efficiencies were similar in magnitude but opposite in direction from errors in estimating energy conversions and consumption of both wet weight and energy.

The most important effect of assuming constant energy density was to strongly dampen the predicted seasonal dynamics of consumption and conversion. That, in turn, could greatly distort perceptions of temporal and spatial patterns of interactions between a fish, its forage, and its competi-

TABLE 7.—Comparison of consumption and percentage gross conversion efficiency by alewife cohort 3 (age-class II–III) during different growth seasons based on simulations of the average individual in Lake Michigan under four assumptions: (1) an annual cycle of energy density occurs from 5.0 to 9.7 kJ·g⁻¹ alewife wet weight (Figure 3), our standard simulation; (2) energy density remains constant at the lowest observed value, 5.0 kJ·g⁻¹; (3) energy density remains constant at 7.5 kJ·g⁻¹, the average of 365 daily values from the cycle in (1); and (4) energy density remains constant at the highest observed value, 9.7 kJ·g⁻¹. Assuming our standard simulation with cyclical energy is correct, we estimated the maximum errors associated with the three constant energy simulations; the greatest deviations are marked by asterisks (*). Simulation days for the growth seasons were summer 1–50, fall 51–119, winter 120–351, and spring 352–365; day 1 was 1 July.

Energy assumption, kJ·g ⁻¹	Wet weight (g) by growth season					Energy (kJ) by growth season				
	Summer	Fall	Winter	Spring	Total	Summer	Fall	Winter	Spring	Total
Consumption										
Cycle, 5.0–9.7	67	218	107	34	426	186	582	337	101	1,206
Constant, 5.0	64	128*	196	30*	418	178	341*	615	88*	1,222
Constant, 7.5	63	144	199	32	438	175	384	625	94	1,278
Constant, 9.7	61*	158	201*	34	454*	172*	422	632*	100	1,326*
Maximum error (%)	-9	-41	88	-12	7	-8	-41	88	-13	10
% conversion										
Cycle, 5.0–9.7	-1.6	4.8	1.1	4.5	2.8	-0.7	34.0	-44.6	15.9	5.2
Constant, 5.0	-1.7	8.2*	0.6	5.2*	2.9*	-3.0	15.3*	1.0	8.8*	5.0
Constant, 7.5	-1.7*	7.3	0.6*	4.8	2.8	-4.5	20.4	1.4	12.3	7.1
Constant, 9.7	-1.7	6.6	0.6	4.5	2.7*	-6.0*	24.0	1.8*	15.0	8.9*
Maximum error (%)	6	71	-45	16	±4	-757	-55	104	-45	71

itors, and perhaps lead to misdirection of research efforts. The desirability or necessity of closely modeling a seasonal energy cycle depends on the amplitude of the cycle and on the ultimate objective of the study. If the cycle is not very pronounced or total annual consumption estimates are all that are needed, the constant-energy assumption should be adequate. The constant-energy value that gave total annual consumption estimates closest to those from the standard simulation was 5.0 kJ·g⁻¹, which was similar to the beginning and ending values for the observed annual cycle (Table 7; Figure 3). For more incisive ecological applications designed to analyze dynamic interactions among key components of an ecosystem such as Lake Michigan, a detailed accounting of seasonal energy cycles in fishes like the alewife is imperative.

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Appendix: Methods for Estimating Physiological Parameters of Alewives

Alewives for studies of metabolism, swimming speed, and consumption were collected by lift net or beach seine from Lake Michigan, mostly near Milwaukee, Wisconsin, and acclimated at their test temperature ($\pm 1^\circ\text{C}$) for at least 4 months. Fish were starved for 48 h before metabolism and consumption experiments.

Metabolism.—Respirometer chambers were clear plexiglass cylinders 45 cm in diameter and 11.5 cm deep (volume = 18 L) with a small inflow hole on one side and an outflow siphon attached to the other side. Water flowed through the chamber at a known rate (adjusted for the fish biomass in the chamber), and oxygen consumption was measured as the differential between inflow and outflow with a YSI Model 54 oxygen meter with polarographic probe. Fish were lightly anesthetized with tricaine (MS-222) to reduce handling stress while they were placed in the respirometer chambers. Two or more fish were placed in each chamber; relatively more fish were used in experiments with smaller individuals in order to provide a measurable oxygen differential between inflow and outflow. For fish less than about 5 g, it was necessary to use smaller chambers (3.7-L glass jars). All chambers were submerged in the same large insulated water tank to provide uniform temperature and background oxygen concentrations. Temperature was controlled to within $\pm 0.5^\circ\text{C}$ for experiments done in 1977–1979 and within $\pm 1^\circ\text{C}$ for experiments during 1970 and 1972 (Binkowski 1975).

For 10–14 d, two readings were taken each day at approximately 0900 and 1600 hours and averaged to obtain daily mean values. Results indicated that fish required 1–2 d to calm down after being placed in a chamber. Beamish (1964) observed a similar pattern in experiments with two other species of fishes. The first 48 h thus were eliminated from the analysis. After day 6, some of the smaller fishes died, especially at high temperatures. For this reason, analysis was further restricted to days 3, 4, 5, and 6. When a fish died in a chamber, it was removed and data taken from that chamber during the preceding 24 h were discarded. Finally, we discarded data from chambers having only one fish because alewives tended to be excitable when alone; other species show lower metabolism when in groups (Parker 1973; Hettler 1976). This severe restriction of the data eliminated subjective decisions about whether or not a given day's observations were representative or

elevated due to excitement of the fish. For analysis, each daily mean was considered an independent observation (Table A1). The metabolism data were analyzed by multiple linear regression to estimate the parameters α , β , and ρ (Table 1; Stewart et al. 1983).

Swimming speed.—We estimated volitional swimming speeds of two size classes of alewives in 1.2-m-diameter tanks at 15°C . The smaller alewives averaged 4.20 g (SD = 1.69) and 78 mm (SD = 11), and the larger fish averaged 18.5 g (SD = 5.53) and 125 mm (SD = 11); each size class was about equally divided between two tanks and there were several dozen fish in each tank. We estimated the time taken by fish to swim between marks 1 m apart on the perimeter of a tank using a stopwatch and following individual fish among a large school circling the perimeter of the tank. Thirty estimates were made for fishes in each tank in the morning (1000–1100 hours) and for fishes in three of the four tanks in the afternoon (1400–1500 hours). The fourth tank contained smaller individuals that assumed an elliptical swimming pattern in the afternoon and did not follow the perimeter of the tank. We therefore obtained 120 observations for the larger fish and 90 for the smaller fish, all taken on 25 April 1985. After we measured swimming speeds, six or seven fish were taken from each tank, blotted, weighed (to 0.01 g), and measured (total length, mm).

Maximum consumption.—We conducted consumption experiments either in 1.2-m-diameter tanks (900 L) or in 0.5-m \times 1.1-m oval tanks (200 L) with continuous flow-through and aeration. The outflow was covered with a nitex mesh to prevent loss of uneaten food. Groups of about 20 fish were transferred to experimental tanks 60 d prior to an

TABLE A1.—Number of observations of alewife metabolism at various temperatures and fish wet weights; each observation represents the mean of two daily measurements.

Weight range (g)	Temperature range ($^\circ\text{C}$)					Total
	4–7	8–12	13–17	18–22	23–26	
1–9	0	30	49	66	12	157
10–19	6	24	13	72	75	190
20–29	0	24	5	2	0	31
30–39	0	16	0	0	0	16
40+	0	4	0	0	0	4
Total	6	98	67	140	87	398

experiment and maintained with a temperature ($\pm 1^\circ\text{C}$) and diet (frozen brine shrimp, *Artemia* sp.) identical to that used for each experiment. Brine shrimp were thawed 24 h before an experiment, placed in a fine-mesh net in a refrigerator at 5°C , and allowed to drop for 24 h to remove excess water. At the start of each experiment, four 1–4-g aliquots of the food being used were weighed in tared dishes, then dried to a constant weight at 60°C to determine percent water. Values of 83 to 85% water were typical.

The alewives fed ad libitum at the start, end, and every 4 h over a 24-h period (seven feedings). The final feeding was at 23.5 h from the start. The

photoperiod during each experiment was approximately 10 h light and 14 h darkness. A large proportion of all food was eaten in some experiments, indicating that the alewives fed both day and night. After the last feeding, uneaten food was recovered, placed in a fine-mesh net, allowed to drip under refrigeration for 24 h, weighed, and dried to a constant weight at 60°C . Experimental fish were starved for 48 h to clear the gut, weighed, and then killed and dried to a constant weight at 60°C to determine percent water. This procedure allowed evaluation of C_{max} in terms of both wet and dry weights.