Evaluation of a Lake Whitefish Bioenergetics Model

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Abstract.—We evaluated the Wisconsin bioenergetics model for lake whitefish *Coregonus clu-peaformis* in the laboratory and in the field. For the laboratory evaluation, lake whitefish were fed rainbow smelt *Osmerus mordax* in four laboratory tanks during a 133-d experiment. Based on a comparison of bioenergetics model predictions of lake whitefish food consumption and growth with observed consumption and growth, we concluded that the bioenergetics model furnished significantly biased estimates of both food consumption and growth. On average, the model over-estimated consumption by 61% and underestimated growth by 16%. The source of the bias was probably an overestimation of the respiration rate. We therefore adjusted the respiration component of the bioenergetics model to obtain a good fit of the model to the observed consumption and growth in our laboratory tanks. Based on the adjusted model, predictions of food consumption over the 133-d period fell within 5% of observed consumption in three of the four tanks and within 9% of observed consumption in the remaining tank. We used polychlorinated biphenyls (PCBs) as a tracer to evaluate model performance in the field. Based on our laboratory experiment, the efficiency with which lake whitefish retained PCBs from their food (γ) was estimated at 0.45. We

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applied the bioenergetics model to Lake Michigan lake whitefish and then used PCB determinations of both lake whitefish and their prey from Lake Michigan to estimate γ in the field. Application of the original model to Lake Michigan lake whitefish yielded a field estimate of 0.28, implying that the original formulation of the model overestimated consumption in Lake Michigan by 61%. Application of the bioenergetics model with the adjusted respiration component resulted in a field γ estimate of 0.56, implying that this revised model underestimated consumption by 20%.

Populations of lake whitefish *Coregonus clupeaformis* have supported the most valuable commercial fishery in the upper Great Lakes since 1980 (S. Nelson, U.S. Geological Survey [USGS], Great Lakes Science Center, commercial catch [COMCAT] database, Ann Arbor, Michigan). Commercial harvest of lake whitefish in the Great Lakes increased more than 10-fold from 1959 to 1995, as the populations have shown a strong recovery since the 1960s (Ebener 1997). This remarkable recovery has been partially attributed to effective control of sea lampreys *Petromyzon marinus* beginning in the 1960s and continuing to the present time (Wells and McLain 1973; Ebener 1997; Madenjian et al. 2002a).

A bioenergetics model that could predict consumption and growth by lake whitefish with reasonable accuracy would not only serve as a valuable tool in understanding the feeding ecology and growth of lake whitefish in the Great Lakes but would also contribute to our understanding of Great Lakes food web dynamics. Bioenergetics modeling has already played a key role in our understanding of the trophic ecology and growth of fishes such as lake trout *Salvelinus namaycush* (Madenjian et al. 1998a) and yellow perch *Perca flavescens* (Hayward and Margraf 1987; Tyson and Knight 2001). Analogously, a reliable model for lake whitefish bioenergetics would allow us to better understand the changes in lake whitefish growth and condition associated with decreased abundance of amphipods *Diporeia* spp. (Pothoven et al. 2001; Madenjian et al. 2002a; Hoyle 2004; Owens et al. 2004). In addition, a proven bioenergetics model for lake whitefish could be applied to populations of lake whitefish in the Great Lakes to determine the annually consumed biomass of benthic invertebrates or fish. This type of application quantifies the flow of energy from one component of the food web to another and thereby facilitates the testing of hypotheses concerning food web dynamics. For example, Rudstam et al. (1994) applied bioenergetics models to populations of bloaters *Coregonus hoyi* and alewives *Alosa pseudoharengus* in Lake Michigan and estimated that annual consumption of *Diporeia* and shrimp *Mysis* spp. by bloaters and alewives more than doubled between 1974 and 1987.

Although a generalized coregonid bioenergetics model has been developed by Rudstam et al. (1994), this model has yet to be evaluated. Rudstam et al. (1994) developed and applied their model to bloaters, but they also suggested that their model could be used for other coregonine fishes as well. Their generalized coregonid model has been included in the latest version of Wisconsin fish bioenergetics model software (Hanson et al. 1997). Wisconsin bioenergetics models, a suite of fish bioenergetics models developed by researchers associated with the University of Wisconsin's Center for Limnology, have been widely applied in fisheries science (Hansen et al. 1993; Ney 1993).

The objectives of this study were to evaluate the generalized coregonid model (Rudstam et al. 1994), as applied to lake whitefish, in both the laboratory and in the field. We used the approach recommended by Madenjian et al. (2000) of first evaluating model performance in the laboratory and then evaluating model performance in the field using polychlorinated biphenyls (PCBs) as a tracer. If our evaluation showed that the model was performing poorly in the laboratory, we revised the model and then evaluated the revised model in the laboratory and in the field.

Methods

Laboratory experiment.—We conducted our laboratory experiment from 23 July through 5 December 2003. Lake whitefish were obtained from the Leech Lake Tribal Fish Hatchery (Cass Lake, Minnesota) during May 2001, when mean total length was approximately 100 mm and the fish were 4 months old. The fish were fed pelletized commercial food at the Great Lakes Science Center laboratory from May 2001 through April 2003. Beginning in May 2003, the lake whitefish were acclimated to a diet of rainbow smelt *Osmerus mordax*. We chose to use rainbow smelt during the experiment because (1) uneaten fish could be easily detected and monitored, whereas uneaten invertebrates could not be easily tracked within the tanks and (2) rainbow smelt were an important diet constituent for lake whitefish in certain waters of the Great Lakes (Devine 2002).

Lake whitefish were maintained in iron-filtered

well water at the Great Lakes Science Center in four 2,380-L circular tanks that had a water exchange rate of 15 L/min. Average (±95% confidence interval [CI] half-width) water velocities were 7.9 ± 0.3 cm/s in tank 1, 10.5 ± 0.2 cm/s in tank 2, 7.0 ± 0.5 cm/s in tank 3, and 8.9 ± 0.4 cm/s in tank 4, based on readings at 12 different locations in each tank. Water temperature was recorded daily in each of the four tanks. Water temperatures ranged from 11.0°C to 13.6°C and averaged 12.4°C over the course of the experiment. We chose to use the ambient well water temperature because its average approximated the average water temperature occupied by two lake whitefish equipped with archival tags for water temperature monitoring during late summer and early fall 2002–2003 in Lake Huron. Photoperiod duration was controlled with fluorescent lighting, which was adjusted seasonally to mimic the duration of daylight for the Great Lakes region.

Tanks 1, 3, and 4 were each stocked with 25 lake whitefish, and tank 2 was stocked with 29 lake whitefish. Each individual was weighed on 23 July 2003 at the start of the experiment and on 28 August, 2 October, 3 November, and 3 December 2003. Lake whitefish were fed thawed rainbow smelt that had been caught in Lake Erie during 2002, frozen, and stored at −30°C. Rainbow smelt were cut into approximately 1-cm-wide transverse sections before placement into the tanks. At the start of the experiment, we fed lake whitefish in all four tanks as much food as they would consume during one feeding each day. By the end of the first month, the feeding rate in tank 1 was nearly 1.0% of fish body weight per day (BW/d), whereas lake whitefish in tank 4 fed at a rate of only 0.5% BW/d. We also observed that fish in tank 1 grew at a rate faster than Lake Michigan lake whitefish during the first month, whereas the fish in tank 4 grew slower than Lake Michigan lake whitefish. Therefore, to ensure that the growth rate in our laboratory tanks bracketed the growth rate of lake whitefish in Lake Michigan (see Madenjian et al. 2004 for rationale), we fed the fish in tank 4 a restricted ration of 0.5% BW/d for the remainder of the experiment, and we continued to feed the fish in tank 1 ad libitum for the remainder of the experiment. After the first month of the experiment, fish in tanks 2 and 3 were fed a restricted ration of about 0.8% BW/d, the same rate at which they fed during the first month. All uneaten food was removed, air dried for 20 min, and weighed to the nearest 0.1 g. On average, over the duration of the entire 133-d experiment, lake whitefish in tank 4 consumed 0.5% BW/d, those in tank 1 consumed 0.9% BW/d, and those in tanks 2 and 3 consumed 0.8% BW/d.

At the start of the experiment, 10 fish each from tanks 1, 3, and 4 and 14 fish from tank 2 were sacrificed. At the conclusion of the experiment, all 15 of the remaining fish in each tank were frozen at −30°C until analysis. Additionally, ten 50-fish subsamples of rainbow smelt were stored at −30°C for later analysis. To determine energy density, lake whitefish were composited by stage (start or end) of experiment and tank number. Each lake whitefish composite or rainbow smelt composite was homogenized in a blender. We then dried 20–30 g of each homogenate at 70°C for 48 h, and approximately 1 g of each dried homogenate was combusted in a Parr 1261 isoperibol calorimeter.

Bioenergetics modeling of laboratory fish.—We applied the generalized coregonid bioenergetics model developed by Rudstam et al. (1994) to the data generated from our laboratory experiment. Inputs to the model included (1) water temperature regime experienced by lake whitefish in our laboratory tanks, (2) energy density of the rainbow smelt fed to the lake whitefish, and (3) energy density of the lake whitefish during the experiment. Thus, our application differed slightly from the Rudstam et al. (1994) application to Lake Michigan bloaters. Rather than estimating energy density of lake whitefish as a function of lake whitefish weight, as per Rudstam et al. (1994), we used our estimates of lake whitefish energy density at the start and end of the experiment and assumed a linear change over time. In addition, we assumed that the lake whitefish just maintained their position within the water flow of the tank; the same type of assumption has been made in laboratory evaluations of bioenergetics models for lake trout and Chinook salmon *Oncorhynchus tshawytscha* (Madenjian and O'Connor 1999; Madenjian et al. 2004). Based on limited daily observations of each tank, this assumption appeared to be reasonable. Thus, to model lake whitefish bioenergetics, we simulated a constant swimming speed equal to the average flow rate within the tank.

As per previous laboratory evaluations (Whitledge and Hayward 1997; Madenjian and O'Connor 1999; Madenjian et al. 2004), we used the bioenergetics model in two ways: (1) to predict consumption given the observed starting and ending average weights of lake whitefish over time *t* and (2) to predict growth given the starting average weight of lake whitefish and the observed average consumption over time. Predictions were gener-

ated for each test period (t = about 1 month) and for the entire duration of the experiment (t = 133 d). All predictions were generated on a tank-by-tank basis. The most recent version of the computer software written by Hanson et al. (1997) for the Wisconsin bioenergetics model was used for all bioenergetics modeling.

Laboratory evaluation of bioenergetics model predictions.—Predictions of the lake whitefish bioenergetics model were evaluated in a manner similar to that used by Madenjian and O'Connor (1999) and Madenjian et al. (2004) to evaluate lake trout and Chinook salmon bioenergetics models in the laboratory. For monthly predictions, a *t*-test for paired comparisons was used to determine whether the average difference between observed and predicted values was significantly different from zero. An average difference that was significantly different from zero would indicate significant bias in model predictions. In each case, the predicted value was subtracted from the observed value. In addition, a simple linear regression analysis was performed on the predicted values as a function of observed values. If the model predictions were unbiased, the slope of this regression line would not differ significantly from 1.0 and the intercept would not be significantly different from zero. Bonferroni 95% joint CIs were constructed to test the null hypothesis that the slope was equal to 1.0 and the intercept was equal to zero (Neter et al. 1983). We applied these statistical analyses to the sets of observations and model predictions for consumption and weight. Residuals from all statistical analyses were examined for significant autocorrelation (Madenjian and O'Connor 1999).

Owing to small sample sizes (N = 4), we did not perform formal statistical testing of the 133-d predictions of the bioenergetics model. To compare predicted with observed cumulative consumption, we simply formed the ratio of predicted to observed cumulative consumption. Similarly, predicted final weight over the entire 133-d period was compared with observed final weight by calculating the ratio of predicted to observed weights.

Revision of the bioenergetics model.—Revisions to the bioenergetics model were made if our laboratory evaluation revealed significant biases in model predictions of consumption and growth. We opted to modify the respiration component of the model because (1) in general, fish bioenergetics model predictions are especially dependent on values for the allometric parameters within the respiration component, whereas error in estimation of excretion and egestion parameters contributes lit-

tle to prediction error (Bartell et al. 1986), and (2) Trudel et al. (2001) suspected that the respiration measurements upon which the generalized coregonid bioenergetics model was developed (Rudstam et al. 1994) were inaccurate. To simplify the model calibration process, we only adjusted the intercept (RA) of the respiration model. We assigned RA values of 0.00050–0.00150 g $O_2 \cdot g^{-1} \cdot d^{-1}$ in 0.00005-g $O_2 \cdot g^{-1} \cdot d^{-1}$ increments and selected the RA value that yielded the lowest error sum of squares in predicting cumulative consumption (over the 133-d experiment) in each of the four tanks.

Laboratory estimation of net trophic transfer efficiency of PCBs.—The PCB concentrations in lake whitefish at the start and end of the laboratory experiment were determined from the same homogenates used for energy density determinations. Similarly, PCB concentrations were determined in the ten 50-fish composites of rainbow smelt fed to the lake whitefish, again with the same homogenates used to determine energy density. To determine concentrations of PCB congeners, we used negative chemical ionization mass spectrometry following the procedure outlined by Schmidt (1997). The method was modified to include a multi-layered anthropogenic column to remove oils and some interfering co-extractables (USEPA 1999). The instrument was calibrated with individual congener standards from AccuStandard (New Haven, Connecticut). A group of 70 congeners were individually quantified and then summed to yield total PCBs (Schmidt 1997). All samples were spiked with two non-Aroclor congeners (International Union of Pure and Applied Chemistry numbers 65 and 166). The calibration accuracy was checked for its ability to analyze Aroclor standards and obtain the predicted amounts and ratios obtained by Frame et al. (1996). Additional calibration verification was done by use of the West Coast Fish Studies standard supplied by AccuStandard. To ensure precision and accuracy, we analyzed appropriate quality control samples (blanks, matrix spikes, and duplicates). Spike recoveries ranged from 93% to 101%. For each of the four tanks, the net trophic transfer efficiency of total PCBs to lake whitefish from their prey (γ) was calculated by determining the increase in PCB body burden between the start and end of the experiment and dividing this increase by the amount of PCBs ingested by lake whitefish over the course of the experiment (see Madenjian et al. 2000, 2004 for more details).

Field sampling.—Lake whitefish were caught in

Lake Michigan near Muskegon, Michigan, by use of monofilament gill nets (mesh sizes ranging from 5.1 to 15.2 cm, stretch measure) and a 7.6-m semiballoon bottom trawl (13-mm stretch-mesh cod liner) during April–November 1998–2001. Gill nets and trawls were fished at depths ranging from 18 to 50 m. The total length (nearest mm) and weight (nearest g) of each lake whitefish were recorded. The stomach of each fish was removed and frozen.

During April–November 2002–2003, lake whitefish were caught with the above-mentioned gear in Lake Michigan near Muskegon, Michigan. Again, fishing depths ranged from 18 to 50 m. The length and weight of each lake whitefish were recorded. Additionally, scales for aging were removed from each fish. Each fish was then double wrapped in foil, bagged, and frozen. In the laboratory, fish were aged by counting annuli on the scales.

During spring, summer, and fall of 2002, *Mysis* were sampled from Lake Michigan near Muskegon, Michigan, by use of a 1-m-diameter plankton net (1,000-μm mesh) at night and then were separated from the rest of the catch, double wrapped in foil, bagged, and frozen. We used a Ponar grab and a benthic sled to capture *Diporeia* during daylight hours; *Diporeia* were then separated from the rest of the catch, double wrapped in foil, bagged, and frozen. Also, during summer 2002, dreissenid mussels were sampled with a 7.6-m bottom trawl. Mussels with shells that were within the 2–12-mm size range were separated from the rest of the catch, bagged, and frozen.

Laboratory processing of field samples.—In the laboratory, lake whitefish stomachs were thawed and then dissected. All identifiable contents were sorted by taxa and then weighed. Because diet composition was similar across various sizes of lake whitefish, we grouped the lake whitefish by season: spring (April–June), summer (July–August), and fall (September–November). Diet for each group was characterized by the percent total wet weight of all identifiable contents represented by each taxon.

After thawing, lake whitefish were grouped into five-fish composites based on 25.4-mm total length intervals. Each composite was homogenized in a blender, and both energy density and the total PCB concentration of each homogenate were determined on a wet-weight basis by use of the procedures described above.

After thawing, the invertebrates caught in Lake Michigan were grouped into composites based on

prey category and season. Each composite was then homogenized in a blender. For dreissenid mussels, both shells and soft tissue were included in the homogenate. For each homogenate, energy density and total PCB concentration were determined as outlined above.

To estimate the proportion of body weight lost via spawning, we used 20 ripe male and 16 ripe female lake whitefish caught during November 2003. The fish were placed on ice and were transported to the laboratory. In the laboratory, whole-fish weight was recorded for each of the 36 fish, and the gonads of each fish were removed and weighed. From these measurements, the mean proportion of total weight represented by the gonads was calculated for both sexes.

Characterization of temperature regime.—The temperature regime of lake whitefish reported on in this study represents preliminary data from an ongoing study of their annual temperature and depth distributions. The lake whitefish were obtained from commercial trap nets fished in Lake Huron between Hammond Bay and Alpena, Michigan, during 2002–2003. Tagging was as described in Bergstedt et al. (2003) at the site of the trap nets, and Lotek LTD 1110 archival tags were used instead of the Vemco archival tags. All tagged lake whitefish were released back into northern Lake Huron. Temperature data were summarized via biweekly averaging of data from 13 lake whitefish returned by commercial fishers; this same type of biweekly averaging was performed by Bergstedt et al. (2003) to characterize the lake trout temperature regime in northern Lake Huron. Lake whitefish ranged from 420 to 685 mm in total length at the time of recapture. We expected that water temperatures experienced by lake whitefish in Lake Huron would be similar to those experienced by Lake Michigan lake whitefish.

Bioenergetics modeling applied to the field.—We applied two different versions of the generalized coregonid bioenergetics model to Lake Michigan lake whitefish. For our first application, we used the original formulation by Rudstam et al. (1994) except that we replaced their predator energy density function with an energy density function based on our determinations of Lake Michigan lake whitefish energy density. In the second application, we used our energy density function and lowered the RA value from 0.00180 to 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$; this adjustment to the model was based on results from the laboratory evaluation.

For each of the two versions of the bioenergetics model, inputs to the model included (1) water tem-

perature regime based on preliminary results from the ongoing archival tag study in northern Lake Huron, (2) diet composition of Lake Michigan lake whitefish in the vicinity of Muskegon, Michigan, and (3) energy density of lake whitefish prey in Lake Michigan in the vicinity of Muskegon, Michigan. To summarize diet composition, we used the following six categories: *Diporeia*, *Mysis*, dreissenid mussels, chironomid midges, cladocerans *Bythotrephes* spp., and other. The other category consisted primarily of ostracods and snails (Gastropoda) during the spring and summer months and age-0 alewives during the fall. Energy densities of *Mysis*, *Diporeia*, and dreissenid mussels did not vary substantially with season; therefore, we assumed that the energy density of each prey category remained constant throughout the year. Energy densities of chironomids, *Bythotrephes*, and age-0 alewives were assigned values of 3,134 J/g (Cummins and Wuycheck 1971), 1,674 J/g (Lantry and Stewart 1993), and 4,435 J/g (Lantry and Stewart 1993), respectively; all energy densities are expressed on a wet-weight basis. We assumed that the energy densities of ostracods and snails were the same as for dreissenid mussels. Because winter diet was not investigated, we averaged spring and fall diet composition to obtain the winter diet composition; the same procedure was used to complete the diet schedules for coho salmon *O. kisutch* in Lake Michigan (Madenjian et al. 1998b).

Inspection of the plot of lake whitefish energy density as a function of weight revealed that energy density increased relatively rapidly as weight approached 800 g and then increased at a relatively slow rate as weight exceeded 800 g. Therefore, we fitted a regression line to energy densities corresponding to weights less than 800 g, and we fitted a second regression line to energy densities corresponding to larger weights. The same approach was used by Stewart et al. (1983) to characterize energy density in Lake Michigan lake trout.

For each version, we performed 15 bioenergetics model simulations corresponding to five different lake whitefish cohorts. Each simulation began on 1 June and ended on 31 May of the following year. The first simulated cohort began on 1 June 1997 and ended on 31 May 2002 (i.e., five simulations). The last simulated cohort began on 1 June 2001 and ended on 31 May 2002 (i.e., one simulation). The initial age for each cohort was 2 years. Thus, the final age attained by each cohort on 31 May 2002 ranged from 3 to 7 years. The same diet composition and prey energy density structure was used in each of the 15 simulations.

This range in ages was chosen based on the limitations of our diet and size-at-age data for lake whitefish. Using our spring 2002–2003 data, we calculated average weights for ages 2–7. Because most of the spring fish were caught in 2002, we chose 2002 as the final year for each cohort. Based on visual examination of the gonads of lake whitefish caught near Muskegon during November 2003, nearly all fish were mature by age 5 (S.A.P., unpublished data). Based on measurements of gonad weight and total body weight, we estimated that males and females lost 2.1% and 8.3%, respectively, of their body weight upon spawning. For Lake Michigan lake whitefish near Muskegon, the spawning peak typically occurs in mid-November (P. Jensen, Commercial Fish Company, Muskegon, personal communication). Therefore, for age-5 and older fish, lake whitefish lost 5.2% of their body weight (data averaged for both sexes) on 15 November in our bioenergetics model simulations.

Field estimation of γ.—For each model version, we used the same approach used by Madenjian et al. (1998a, 1998b, 2002b) to estimate the γ from prey to predator. Total PCB concentrations in Lake Michigan *Diporeia* and *Mysis* in 1994 were 80 and 40 ng/g, respectively (Madenjian et al. 1998b, 1998c). As mentioned above, we determined total PCB concentrations in *Diporeia*, *Mysis*, and dreissenid mussels during 2002 as part of our study. We assumed that PCB concentrations in *Diporeia* and *Mysis* declined exponentially between 1994 and 2002; we then calculated the rate of exponential decay (loss rate) for both taxa. In support of our assumption, Eby et al. (1997) concluded that PCB concentrations in Lake Michigan invertebrates have exhibited an exponential decline since 1970. Dreissenid mussel PCB concentration data were not available for 1994, so we assumed that the PCB concentration in dreissenid mussels decreased exponentially during 1994–2002 and that the loss rate was equal to the average loss rate (6.6% per year) calculated for *Diporeia* and *Mysis*. Chironomid PCB data were not available for Lake Michigan but were available for the Detroit River. Detroit River data indicated that the PCB concentration in chironomids was intermediate between those of dreissenid mussels and high-lipid burrowing mayflies *Hexagenia* spp. (K. Drouillard, University of Windsor, Windsor, Ontario, Canada, personal communication; Morrison et al. 1996). Therefore, we averaged the PCB concentrations in *Diporeia*, *Mysis*, and dreissenid mussels to estimate the PCB concentration in chironomids for

any given year. Age-0 alewife PCB concentration in 1994 was 178 ng/g (Madenjian et al. 1998b, 1998c), and we assumed that this concentration decreased exponentially over time at the same loss rate used for dreissenid mussels. Similarly, the PCB concentration in *Bythotrephes* in 1994 was 30 ng/g (Madenjian et al. 1998b), and we assumed that the same above-mentioned loss rate occurred during 1994–2002. The PCB concentration in snails and ostracods was assigned the same value as determined for dreissenid mussels for any given year.

Following the same procedure used in previous studies (Madenjian et al. 1998b, 1998c, 2002b), we fitted an exponential curve to PCB concentration in lake whitefish as a function of total length. To estimate PCB concentration for a given age of lake whitefish in 2002, we substituted the mean length of lake whitefish for that age in the fitted regression equation. Most of the lake whitefish PCB determinations for our study were based on fish caught during 2002 and supplemental catches obtained in 2003.

Based on the same approach as detailed in Madenjian et al. (1998b, 1998c, 2002b), bioenergetics modeling yielded estimates of food consumption by prey category, season, and year. Coupling of the food consumption estimates with PCB concentrations by prey category, season, and year allowed for calculation of the total amount of PCBs ingested by an average lake whitefish in a particular cohort. For our lake whitefish study, we made a slight modification to the previously used procedure because we were unable to estimate lake whitefish gross growth efficiency during the fish's first 2 years in the lake. Instead, we calculated the change in PCB body burden for each of the five lake whitefish cohorts and then divided the change in PCB body burden by the total amount of PCBs ingested by an average lake whitefish in the cohort to generate an estimate of γ. The change in PCB body burden was simply equal to the amount of PCBs in the lake whitefish of the appropriate age in 2002 minus the amount of PCBs in an age-2 lake whitefish during the year corresponding to the initiation of the cohort simulations. To estimate the PCB concentration of an age-2 lake whitefish in years prior to 2002, we used the above-mentioned PCB loss rate. In other words, we assumed that the PCB concentration in an age-2 lake whitefish from Lake Michigan declined exponentially at a loss rate of 6.6% per year during 1997–2002. This approach was reasonable because long-term changes in PCB concentrations of Lake Michigan

fishes generally follow an exponential decline (Madenjian et al. 1993, 1998c; De Vault et al. 1996).

Evaluation of bioenergetics model performance in Lake Michigan.—The performance of the two model versions was evaluated by use of the same procedure presented by Madenjian et al. (2000, 2004). First, we calculated mean estimates of γ for both the laboratory and the field. The inverse of the ratio of the mean field γ to the mean laboratory γ yielded an estimate of the ratio of model-predicted food consumption to actual food consumption by Lake Michigan lake whitefish. We calculated this ratio for each version of the bioenergetics model. Additionally, we applied a two-sample *t*-test to determine whether the mean field γ was significantly different from the mean laboratory γ.

Results

Laboratory Evaluation of the Model

The energy density of lake whitefish decreased in all four tanks during the course of the experiment. Initial lake whitefish energy densities (wet-weight basis) were 8,979 J/g in tank 1, 9,174 J/g in tank 2, 9,637 J/g in tank 3, and 9,479 J/g in tank 4. Final lake whitefish energy densities were 8,688 J/g in tank 1, 8,039 J/g in tank 2, 8,504 J/g in tank 3, and 8,310 J/g in tank 4. Energy densities of the 10 subsamples of rainbow smelt ranged from 5,086 to 5,574 J/g (mean = 5,382 J/g; SE = 54 J/g).

The generalized coregonid bioenergetics model consistently overestimated monthly consumption (Figure 1), and these predictions were significantly biased. Paired *t*-test results revealed that the mean difference between observed and predicted monthly consumption was significantly negative (mean difference = −122.5 g; $t = -14.13$; df = 15; $P < 0.0001$). Additionally, the slope of the regression line of predicted versus observed monthly consumption was significantly less than 1.0 (estimate of slope = 0.69; estimate of Bonferroni joint 95% CI half-width = 0.22), and the intercept was significantly greater than zero (estimate of intercept = 187.0 g; estimate of Bonferroni joint 95% CI half-width = 49.7 g) (Figure 1).

The generalized coregonid bioenergetics model consistently underestimated lake whitefish weight at the end of the test period (Figure 2), and these weight predictions were significantly biased. The observed final weight was significantly greater than the weight predicted by the bioenergetics
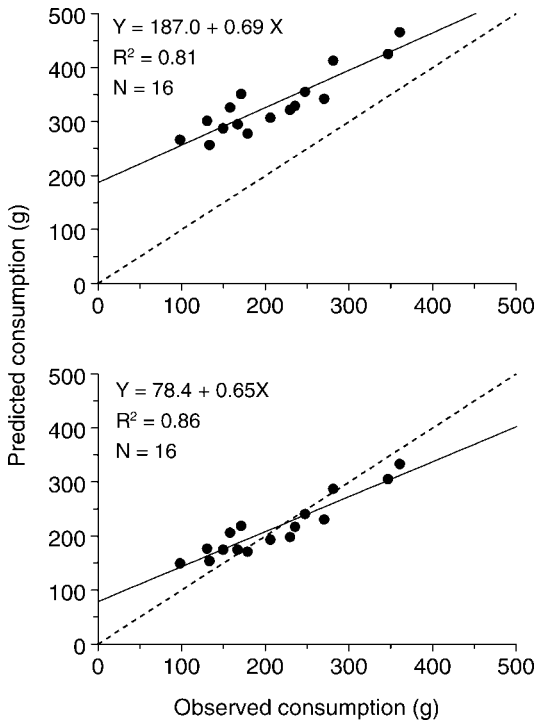
FIGURE 1.—Predicted consumption by an average lake whitefish in a test tank (four tanks) during a 1-month test period (four periods per tank) as a function of observed consumption. Predicted consumption is based on a generalized coregonid bioenergetics model (Rudstam et al. 1994; upper panel) and on our revision of that model (see equation 1; lower panel). In each panel, the solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.
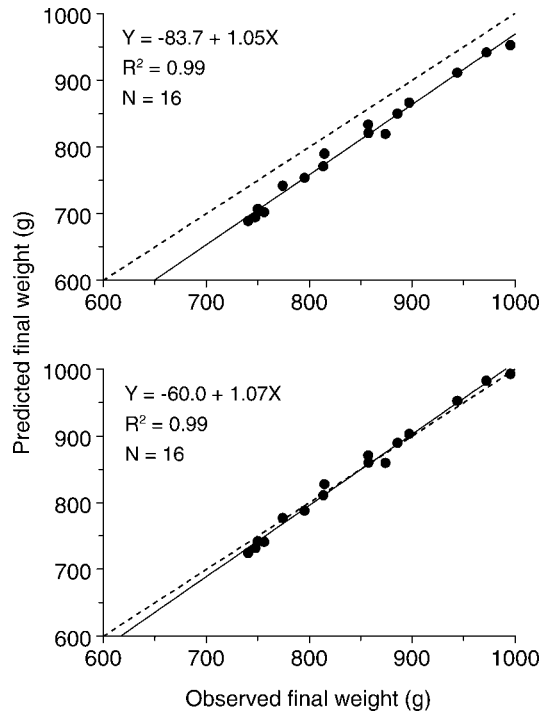
FIGURE 2.—Predicted final weight of an average lake whitefish in a test tank (four tanks) during a 1-month test period (four periods per tank) as a function of observed final weight. Predicted weight is based on a generalized coregonid bioenergetics model (Rudstam et al. 1994; upper panel) and our revision of that model (see equation 1; lower panel). In each panel, the solid line represents the regression line fitted to the points; the dashed line represents the line of 1:1 correspondence between predictions and observations.

model (mean difference = 39.4 g; t = 15.41; df = 15; $P < 0.0001$). Although the slope of the regression line of predicted versus observed final weight was not significantly different from 1.0 (estimate of slope = 1.05; estimate of Bonferroni joint 95% CI half-width = 0.08), the intercept was significantly less than zero (estimate of intercept = −83.7 g; estimate of Bonferroni joint 95% CI half-width = 64.2 g) (Figure 2).

Bioenergetics model predictions of cumulative consumption over the 133-d experiment were between 41% and 89% greater than observed cumulative consumption (Table 1). Bioenergetics model predictions of lake whitefish final weight were between 13% and 18% lower than observed final weights (Table 1).

Given the strong biases associated with the model, we adjusted the respiration component by sub-

stantially lowering RA from 0.00180 to 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$, that is,

$$R = 0.00085W^{0.12} \cdot e^{0.047T + 0.025U}, \quad (1)$$

where R = specific respiration rate (g $O_2 \cdot g^{-1} \cdot d^{-1}$), W = lake whitefish weight (g), T = water temperature (°C), and U = swimming speed (cm/s). This change provided more accurate predictions of consumption and growth in the laboratory tanks.

On average, our revised bioenergetics model based on equation (1) for the respiration component generated unbiased predictions of monthly consumption by lake whitefish in our laboratory tanks. Observed monthly consumption was not significantly different from predicted monthly consumption (mean difference = −4.3 g; t = −0.51; df = 15; $P = 0.6146$). However, the slope of the regression line of predicted versus observed

monthly consumption was significantly different from 1.0 (estimate of slope = 0.65; estimate of Bonferroni joint 95% CI half-width = 0.18), and the intercept was significantly different from zero (estimate of intercept = 78.4; estimate of Bonferroni joint 95% CI half-width = 39.3) (Figure 1). Hence, the regression analysis suggested that the model slightly overestimated consumption when the consumption rate was relatively low, and slightly underestimated consumption when the consumption rate was relatively high (Figure 1).

Our revised bioenergetics model furnished unbiased predictions of lake whitefish weight at the end of the test period. Observed and predicted final weights did not significantly differ (mean difference = 1.2 g; t = 0.43; df = 15; P = 0.6758). Furthermore, the slope of the regression line of observed versus predicted final weights was not significantly different from 1.0 (estimate of slope = 1.07; estimate of Bonferroni joint 95% CI half-width = 0.075), and the intercept was not significantly different from zero (estimate of intercept = −60.0 g; estimate of Bonferroni joint 95% CI half-width = 63.4) (Figure 2). Residuals from all statistical analyses were not significantly autocorrelated (P > 0.05); therefore, the assumption of independence was apparently met.

Predictions of consumption over the 133-d experiment by our revised bioenergetics model were within 9% of the observed cumulative consumption (Table 1). Further, the predicted cumulative consumption in tanks 2 and 3 was within 2.5% of observed cumulative consumption. Predictions of lake whitefish final weight were within 2% of the observed final weight (Table 1).

Laboratory Estimation of γ

Initial PCB concentrations of the lake whitefish composites ranged from 67 to 77 ng/g, whereas final PCB concentrations ranged from 86 to 93 ng/g (Table 1). Average PCB concentration in the 10 rainbow smelt composites was 67 ng/g (SE = 4 ng/g). Laboratory estimates of γ were 0.42 for tank 1, 0.39 for tank 2, 0.59 for tank 3, and 0.40 for tank 4 (Table 1). Thus, the mean laboratory estimate of γ was 0.45 (95% CI = 0.30–0.60).

Characterization of Temperature Regime

Based on averaged data from the 13 returns of archival tags, lake whitefish experienced a peak temperature of 11.1°C in early September (Figure 3). Mean temperature ranged from 7°C to 10°C for much of the summer. Mean temperature inhabited by lake whitefish declined rapidly during the fall

and early winter months. By early February, lake whitefish were situated in water colder than 1°C, where they remained until spring warming began in April (Figure 3).

Bioenergetics Modeling Applied to the Field

In Lake Michigan near Muskegon during 1998–2001, *Diporeia*, *Mysis*, and dreissenid mussels constituted the bulk of the lake whitefish diet (Table 2). Most of the remaining diet was composed of chironomids. The mean total length of the lake whitefish used in our diet analysis was 365 mm (range = 154–780 mm). Mean energy densities were 3,625 J/g for *Diporeia*, 3,924 J/g for *Mysis*, and 1,703 J/g for dreissenid mussels. These averages were based on one composite sample per season in the spring, summer, and fall.

The equation for the fitted regression line for lake whitefish weights less than 800 g was Y = 5,211 + 2.543W, where Y = energy density (J/g) of lake whitefish and W = lake whitefish weight (g). The equation for the fitted regression line for lake whitefish weights greater than or equal to 800 g was Y = 7,192 + 0.3078W. These two lines intersected at a weight of 886.3 g (Figure 4). In total, the caloric densities of 44 lake whitefish composites were determined.

Field Estimation of γ

The PCB concentration in Lake Michigan lake whitefish increased exponentially with increasing fish total length (Figure 5). Lake whitefish PCB concentrations ranged from 82 to 771 ng/g. The mean PCB concentrations in *Diporeia*, *Mysis*, and dreissenid mussels were 56, 15, and 16 ng/g, respectively.

Application of the original generalized coregonid bioenergetics model to Lake Michigan lake whitefish yielded a mean γ estimate of 0.28 (95% CI = 0.23–0.33; Table 3). Lowering the RA value from 0.00180 to 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$ resulted in a mean field γ estimate of 0.56 (95% CI = 0.46–0.66; Table 3). For each set of bioenergetics model applications, γ neither increased nor decreased with increasing age (Table 3).

Evaluation of Bioenergetics Model Performance in Lake Michigan

According to our analysis, the original formulation of the generalized coregonid bioenergetics model overestimated consumption by Lake Michigan lake whitefish by 61%. Lowering the value of RA from 0.00180 to 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$ led

TABLE 1.—Observed and predicted cumulative consumption and cumulative growth by lake whitefish held in laboratory tanks for 133 d. Predictions were based on a generalized coregonid bioenergetics model developed by Rudstam et al. (1994; original model) and on our revision (see equation 1) to that model (revised model). Lake whitefish were fed rainbow smelt. Observed consumption was equal to the total food eaten by all lake whitefish in a tank divided by the number of fish in the tank. Gross growth efficiency (GGE) was weight gain divided by the amount of food consumed. Also included are laboratory estimates of γ, the efficiency with which lake whitefish retained polychlorinated biphenyls (PCBs) from their food. The amount of PCBs ingested was equal to the total amount ingested by all fish in the tank divided by the number of fish in the tank.

	Observed average weight of lake whitefish (g)		Observed consumption (g)	Observed GGE	Original model			
Tank number	Initial	Final			Predicted consumption (g)	Predicted final weight (g)	Ratio of predicted to observed consumption	Ratio of predicted to observed final weight
1	713	897	1,010	0.183	1,426	777	1.411	0.866
2	736	886	865	0.174	1,383	734	1.599	0.829
3	841	996	928	0.166	1,430	853	1.541	0.857
4	726	796	559	0.124	1,057	654	1.889	0.822

to a revised bioenergetics model that underestimated consumption by 20%.

The mean field γ from application of the original model was significantly lower than the mean laboratory γ (*t*-test: $t = 3.73$, df $= 7$, $P = 0.0074$). The mean field γ from the revised model with the lower RA value did not significantly differ from the mean laboratory γ (*t*-test: $t = -1.89$, df $= 7$, $P = 0.1007$).

Discussion

Results from the laboratory and field evaluations corroborated one another in that both showed that the generalized coregonid bioenergetics model by Rudstam et al. (1994) substantially overestimated consumption by lake whitefish. Because the laboratory evaluation indicated an overestimation problem, we concluded that the generalized coregonid model as applied to lake whitefish was fundamentally flawed. This overestimation of consumption probably stemmed from overestimation of respiration rate. The generalized coregonid bioenergetics model by Rudstam et al. (1994) was based on lake whitefish respiration data presented by Bernatchez and Dodson (1985). Bernatchez and Dodson (1985) may have overestimated the respiration rate in their laboratory experiment, because (1) the lake whitefish were acclimated for only 30–60 min in the respirometer prior to measurement of oxygen consumption rate and (2) the measurement trial was only 30 min in duration. In contrast, lake trout were allowed to acclimate in the respirometer for 16 h prior to a 90-min measurement trial for a particular swimming speed in a study by Stewart et al. (1983). Consequently, we recommend that lake whitefish respirometry be re-

peated in the laboratory under a protocol similar to that followed by Stewart et al. (1983).

Until lake whitefish respirometry is repeated in the laboratory, we recommend application of our revised version of the bioenergetics model to lake whitefish. Lowering RA from 0.00180 to 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$ resulted in a substantial improvement in model performance in both the laboratory and the field. On average, the revised model predicted food consumption by lake whitefish in our laboratory tanks without any significant bias. Furthermore, revised-model predictions of cumulative consumption over the 133-d laboratory experiment in all four tanks were within 9% of observed values; the predicted cumulative consumption in tank 1, the tank with the highest feeding rate, was within 5% of observed cumulative consumption. According to regression analysis, the revised model tended to overestimate monthly consumption in the laboratory tanks at relatively low feeding rates and tended to underestimate monthly consumption at relatively high feeding rates. However, revised-model predictions of monthly consumption at the two highest observed feeding rates were still within 12% of observed values. On average, the revised model underestimated consumption by Lake Michigan lake whitefish by 20%. Whether the estimates of consumption in the field are ''corrected'' for this underestimation would be at the discretion of the user. One suggestion would be to generate estimates of consumption from the revised model, multiply those estimates by 1.2, and then determine whether this ''correction'' influences the overall conclusions from the modeling exercise.

Although both the laboratory and field evaluation results for the original model indicated a sub-

TABLE 1.—Extended.

Tank number	Revised model				Average PCB concentration (ng/g) of lake whitefish		Amount of PCBs ingested (ng)	γ
	Predicted consumption (g)	Predicted final weight (g)	Ratio of predicted to observed consumption	Ratio of predicted to observed final weight	Initial	Final		
1	964	911	0.954	1.016	72	89	67,242	0.424
2	883	880	1.021	0.993	73	86	57,559	0.391
3	926	996	0.998	1.001	67	93	61,758	0.587
4	609	780	1.088	0.981	77	89	37,228	0.400

stantial degree of overestimation of lake whitefish food consumption, these results were somewhat disparate with regard to performance of the revised bioenergetics model. Although the revised model, on average, generated unbiased predictions of consumption and growth in the laboratory tanks, it underestimated food consumption in the field by 20%. One possible explanation for this disparity could be that estimates of coefficients other than RA in the respiration component of the model were also biased. For example, perhaps the value of the slope coefficient for temperature (RQ) in the respiration component was overestimated in such a way that the revised model yielded reasonably accurate estimates of consumption in our laboratory tanks but underestimated consumption at water
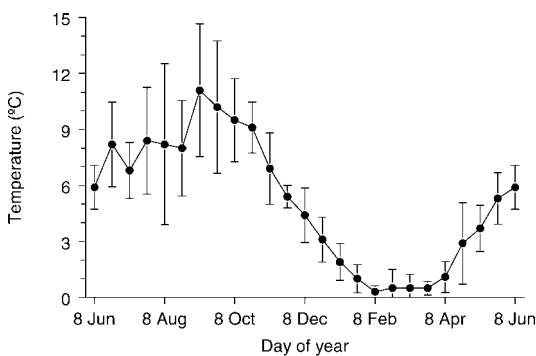

FIGURE 3.—Mean temperature recorded by archival tags implanted in lake whitefish that were released into northern Lake Huron during 2002–2003. Averages are based on the return of 13 tagged fish; the vertical bars indicate 95% confidence intervals. Temperatures recorded during the first or second half of each month were averaged and assigned to the midpoint day of the time period. See Bergstedt et al. (2003) for more details on the data summary procedure.

temperatures considerably lower than those observed in the tanks. Water temperature ranged from 11.6°C to 13.6°C in our laboratory tanks. However, according to the archival tag data, an average lake whitefish in northern Lake Huron remained in water colder than 10°C for much of the year. Of course, accurate measurements of lake whitefish respiration rates at various combinations of lake whitefish size, water temperature, and swimming speed would be needed to resolve this issue. Another factor that may partially explain the revised model's 20% underestimation of consumption in the field could be that lake whitefish in Lake Michigan near Muskegon experienced slightly warmer water temperatures than those in northern Lake Huron. Finally, the egestion component of the generalized coregonid model may be too simple for application to lake whitefish. One refinement of the egestion component would be to explicitly account for differences in digestibility among prey types, as was done by Stewart et al. (1983) in developing a lake trout bioenergetics model.

The value of γ has been shown to vary with food ration (Madenjian et al. 2000). However, we did not have to consider this effect in interpreting the results from our field evaluation because lake whitefish growth and food consumption observed in our laboratory tanks bracketed those observed in Lake Michigan. The growth rate in our laboratory tanks ranged from 0.5 to 1.4 g/d. In Lake Michigan, an average lake whitefish increased in weight from 520 to 1,180 g as age increased from 4 to 7 years (Table 3). Based on an assumed 7-month growing season (P.J.S., unpublished data), lake whitefish growth in Lake Michigan averaged 1.0 g/d, well within the bounds of growth observed in the laboratory. Consumption of food by lake

TABLE 2.—Percent seasonal diet compositions (wet-weight basis) for lake whitefish in Lake Michigan near Muskegon, Michigan, 1998–2001. Winter diet was estimated by averaging the diet compositions from the preceding fall and the following spring. The ''other'' category consisted primarily of snails in the spring, ostracods in the summer, and age-0 alewives in the fall; NA = not applicable.

Diet item and number of stomachs examined	Spring (Apr–Jun)	Summer (Jul–Aug)	Fall (Sep–Nov)	Winter (Dec–Mar)
Diet item				
Diporeia	22	32	32	27
Mysis	1	6	23	12
Dreissenid mussels	47	14	32	40
Chironomids	21	27	9	15
Bythotrephes			3	1
Other	9	21	1	5
Stomachs examined				
Nonempty stomachs	107	54	46	NA
Empty stomachs	37	1	38	NA

whitefish in our laboratory tanks ranged from 0.5% to 0.9% BW/d. If we adjust for 20% underestimation and assume that lake whitefish had a rainbow smelt diet, revised-model food consumption by lake whitefish during ages 4–7 in Lake Michigan would average 0.9% BW/d, which fell within the bounds of the feeding rate observed in the laboratory. In contrast, feeding rate had to be considered in evaluating a Chinook salmon bioenergetics model in the field, because growth and feeding rates were substantially higher in Lake Michigan than in the laboratory (Madenjian et al. 2004).

Our laboratory estimate of γ for lake whitefish was 0.45, whereas laboratory estimates of γ for lake trout and Chinook salmon ranged from 0.71 to 0.91 (Madenjian et al. 2000, 2004). The range in feeding rates from our lake whitefish laboratory study overlapped with the feeding rates adminis-tered in the two previous studies; therefore, differences in feeding rate were not responsible for γ being substantially lower for lake whitefish than for lake trout and Chinook salmon. Perhaps the gut uptake of PCBs is somehow enhanced in lake trout and Chinook salmon.

An implicit assumption in our field evaluation of the generalized coregonid bioenergetics models was that the γ from rainbow smelt to lake whitefish was equal to the γ from invertebrate prey to lake whitefish. To the best of our knowledge, no study has shown that γ varies substantially as prey is switched from fish to invertebrates. Moreover, good agreement between observed and predicted PCB concentrations in Lake Michigan bloaters was obtained when γ was assigned a value of 0.80 (Eby et al. 1997; L. Eby, University of Montana, Missoula, personal communication). Similarly, DeBoe
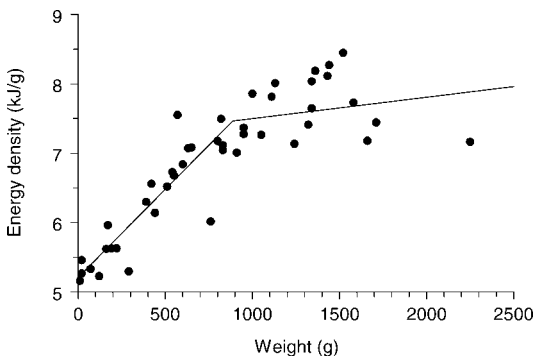

FIGURE 4.—Energy density on a wet-weight basis for five-fish composites of lake whitefish caught in Lake Michigan near Muskegon, Michigan, during 2002–2003 as related to the mean weight of the fish in the composite. Fitted regression lines are also shown; see text for more details.
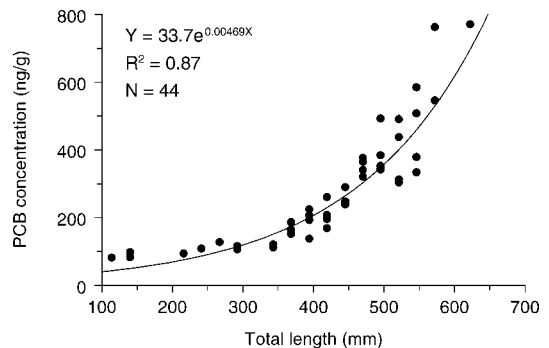

FIGURE 5.—Total PCB concentration on a wet-weight basis for five-fish composites of lake whitefish caught in Lake Michigan near Muskegon, Michigan, during 2002–2003 as related to the midpoint of the total length interval (25.4-mm intervals were used) for the composite sample. The fitted regression line is also shown.

TABLE 3.—Estimation of γ, the efficiency with which lake whitefish retained PCBs from their food, in Lake Michigan. Estimates were based on two versions of a generalized coregonid bioenergetics model: (1) original formulation by Rudstam et al. (1994; original model) and (2) revised formulation with respiration intercept (RA) = 0.00085 g $O_2 \cdot g^{-1} \cdot d^{-1}$, as shown in equation 1 (revised model). Gross growth efficiency (GGE) was the weight gain divided by the amount of food consumed. At age 2, lake whitefish averaged 290 mm in total length, 190 g in weight, and 132 ng/g in polychlorinated biphenyl (PCB) concentration.

Age (years)	Mean total length (mm)	Mean weight (g)	Lake whitefish PCB concentration (ng/g)	Original model			Revised model		
				GGE	PCBs ingested (ng)	γ	GGE	PCBs ingested (ng)	γ
3	322	320	153	0.041	99,604	0.223	0.082	50,416	0.441
4	392	520	212	0.039	274,845	0.298	0.077	138,946	0.589
5	449	800	277	0.036	565,172	0.339	0.071	284,936	0.672
6	471	930	307	0.027	937,231	0.270	0.055	460,469	0.550
7	503	1,180	357	0.024	1,441,166	0.268	0.049	702,146	0.551

(1994) was able to match model predictions with observed PCB concentrations of Lake Michigan deepwater sculpins *Myoxocephalus thompsonii* when γ was allowed to equal 0.75. In both of these modeling exercises, diets were assumed to consist entirely of invertebrates, primarily *Mysis* and *Diporeia*. As mentioned above, laboratory estimates of γ for lake trout and Chinook salmon feeding on fish ranged from 0.71 to 0.91 (Madenjian et al. 2000, 2004). This set of values suggests that γ would not significantly change when the prey is switched from fish to invertebrates.

Our evaluations of lake whitefish bioenergetics have led to substantial improvements in model performance in both the laboratory and the field. We envision refinement of the lake whitefish bioenergetics model to be an iterative process, and our data from laboratory and field evaluations should continue to be useful during the model refinement process. We believe that we have bettered model performance as much as presently possible. Future refinements would almost certainly require accurate measurements of lake whitefish respiration rates. Once a reliable respiration component of the model has been developed, then the new bioenergetics model can be applied to the data from our laboratory evaluation. Furthermore, the new model can also be applied to our Lake Michigan data for a field evaluation. Based on the outcomes of the laboratory and field evaluations, the new model can be appropriately revised and retested. The two-phase approach of a laboratory evaluation coupled with a field evaluation and the use of PCBs as a tracer offer an effective platform for examining and facilitating improvements in model performance.

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