

**Preliminary Evaluation of a Lake Whitefish
(*Coregonus clupeaformis*) Bioenergetics Model**

Charles P. Madenjian¹

U.S. Geological Survey
Great Lake Science Center
1451 Green Road
Ann Arbor, Michigan, U.S.A. 48105

Stephen A. Pothoven

National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
Muskegon Field Station
1431 Beach Street
Muskegon, Michigan, U.S.A. 49441

Philip J. Schneeberger

Michigan Department of Natural Resources
484 Cherry Creek Road
Marquette, Michigan, U.S.A. 49855

Daniel V. O'Connor

U.S. Geological Survey
Great Lake Science Center
1451 Green Road
Ann Arbor, Michigan, U.S.A. 48105

Stephen B. Brandt

National Oceanic and Atmospheric Administration
Great Lakes Environmental Research Laboratory
2205 Commonwealth Boulevard
Ann Arbor, Michigan, U.S.A. 48105

¹Corresponding author: cmadenjian@usgs.gov

Abstract

We conducted a preliminary evaluation of a lake whitefish (*Coregonus clupeaformis*) bioenergetics model by applying the model to size-at-age data for lake whitefish from northern Lake Michigan. We then compared estimates of gross growth efficiency (GGE) from our bioenergetics model with previously published estimates of GGE for bloater (*C. hoyi*) in Lake Michigan and for lake whitefish in Quebec. According to our model, the GGE of Lake Michigan lake whitefish decreased from 0.075 to 0.02 as age increased from 2 to 5 years. In contrast, the GGE of lake whitefish in Quebec inland waters decreased from 0.12 to 0.05 for the same ages. When our swimming-speed submodel was replaced with a submodel that had been used for lake trout (*Salvelinus namaycush*) in Lake Michigan and an observed predator energy density for Lake Michigan lake whitefish was employed, our model predicted that the GGE of Lake Michigan lake whitefish decreased from 0.12 to 0.04 as age increased from 2 to 5 years.

Introduction

Since 1980, the lake whitefish (*Coregonus clupeaformis*, hereafter, whitefish) has been the most commercially valuable fish in the upper Great Lakes (S. Nelson, United States Geological Survey, Great Lakes Science Center, COMCAT database, Ann Arbor, MI 48105, U.S.A.). Whitefish populations in the Great Lakes have shown a strong recovery since the 1960s with the commercial harvest increasing more than tenfold from 1959 to 1995 (Ebener 1997). This remarkable recovery has been attributed, in part, to effective control of sea lamprey (*Petromyzon marinus*), a program that began in the 1960s (Wells and McLain 1973; Ebener 1997; Madenjian et al. 2002). Sea lampreys invaded the upper Great Lakes during the 1940s and preyed heavily on whitefish during the 1950s.

The condition of whitefish at several locations in Lake Michigan has declined since 1995 (Pothoven et al. 2001; Madenjian et al. 2002). This decline has been partially attributed to a decrease in the abundance of *Diporeia* spp. (hereafter, diporeia as a common name) in nearshore waters and to the relatively high densities of whitefish in the lake. Diporeia has the highest lipid content of the major benthic macroinvertebrates in the lake and has been a favored prey item for Lake Michigan whitefish (Pothoven et al. 2001). The continued decrease in diporeia abundance during the 1990s has been associated with the zebra mussel (*Dreissena polymorpha*) invasion, but the specific mechanism by which zebra mussels could negatively affect diporeia remains unidentified (Nalepa et al. 2000; Madenjian et al. 2002).

Bioenergetics modeling has played a key role in the study of the feeding ecology and growth of fishes (Hayward and Margraf 1987; Madenjian et al. 1998). The Wisconsin bioenergetics models—a suite of fish bioenergetics models developed by researchers associated with the University of Wisconsin Center for Limnology—have been widely applied in fisheries science (Hansen et al. 1993; Ney 1993). Hanson et al. (1997) offered a generalized coregonine bioenergetics model (GCBM) in the latest versions of the Wisconsin bioenergetics models. This model was based largely on the bioenergetics model developed by Rudstam et al. (1994) for bloater (*C. hoyi*) in Lake Michigan. However, neither the GCBM nor the bloater model has been evaluated. A validated bioenergetics model for whitefish should be a useful tool to evaluate its energetic requirements and the impact of changing prey resources on its growth and condition.

The objective of this study was to conduct a preliminary evaluation of the GCBM proposed by Hanson et al. (1997) by applying the model to Lake Michigan whitefish. We then compared the model's predictions of gross growth efficiency (GGE) for whitefish with published estimates of GGE for Lake Michigan bloater and for whitefish from inland waters in Quebec. The GGE is equal to the increase in fish weight divided by the amount of food consumed by the fish to achieve its weight increase. Although whitefish typically attain much larger sizes than bloater, GGE estimates for Lake Michigan bloater were similar to GGE estimates for whitefish from Quebec's inland waters (Rudstam et al. 1994; Trudel et al. 2001). Therefore, a comparison of the model's predictions of GGE for Lake Michigan whitefish with previously published estimates for North American coregonines would serve as an initial check on the model's predictions.

We also determined the sensitivity of the generalized coregonine model predictions of food consumption for Lake Michigan whitefish to alterations in the submodel for fish activity. Activity can be an important contributor to the overall energy budget of a fish (Boisclair and Leggett 1989). To the best of our knowledge, direct measurements of swimming speeds of whitefish in lakes were not available. Therefore, an examination of the sensitivity of the model's predictions of GGE to changes in fish activity was warranted.

In addition, we investigated the sensitivity of the GCBM's predictions of food consumption for Lake Michigan whitefish to perturbations in predator energy density. Rudstam et al. (1994) developed a regression model for predicting coregonine energy density based on fish weight. We compared the energy density predicted by the regression equation with an actual measurement in 2000 of the energy density of Lake Michigan whitefish. We then compared estimates of food consumption by Lake Michigan whitefish from the Rudstam et al. (1994) regression equation with the actual measurements of energy density.

Methods

The Hanson et al. (1997) version of the Rudstam et al. bioenergetics model for bloater (1994) contained only one modification: the exponent for fish weight in the consumption submodel was changed from -0.538 to -0.32. This change was made to adapt the model to larger coregonine. Interestingly, the respiration component of the bloater bioenergetics model was based on laboratory observations of whitefish. The most-detailed respiration measurements on coregonines were performed by Bernatchez and Dodson (1985). They measured respiration rates of whitefish at three different water temperatures (5, 12, and 17°C) and at swimming speeds ranging from 20 $\text{cm}\cdot\text{s}^{-1}$ to 80 $\text{cm}\cdot\text{s}^{-1}$. These measurements were used to build the regression equations representing the respiration component of the bloater bioenergetics model (Rudstam et al. 1994). Direct observations of the swimming speeds of bloater in Lake Michigan were unavailable; however, volitional swimming speeds of bloaters were observed in large laboratory tanks (Rudstam et al. 1984). From these laboratory measurements, Rudstam et al. (1994) developed a regression equation relating swimming speed to bloater weight. According to this equation, a 300-g bloater would swim at 30 $\text{cm}\cdot\text{s}^{-1}$. Swimming speed was assumed to be independent of water temperature (Rudstam et al. 1994). The generalized coregonine

bioenergetics model's respiration and swimming-speed submodels are identical to those in the bloater bioenergetics model (Hanson et al. 1997).

Rudstam et al. (1994) described energy density of bloaters as a function of bloater weight. According to this function, bloater energy density was equal to $13\,050\text{ J}\cdot\text{g}^{-1}$ on a wet-weight basis for bloater weights $\geq 155\text{ g}$. The predator energy-density function used in the bloater bioenergetics model was identical to that used in the GCBM.

To estimate food consumption, we fitted the generalized coregonine model to observed weight-at-age data for Lake Michigan whitefish. Whitefish were captured in commercial trapnets in northern Lake Michigan during May 1991-2000. Fish were weighed to the nearest gram and aged by scales. Averaging mean weight-at-age across all years during 1991-2000, we obtained mean weights of 0.18 kg, 0.53 kg, 0.79 kg, 0.95 kg, and 1.16 kg for whitefish of ages 2, 3, 4, 5, and 6, respectively. The starting date for each model simulation was 1 May and the ending date was 30 April of the following year. For each simulation run, the appropriate starting and ending weights were chosen from the mean weights presented above, and consumption during the simulation year was estimated from the model.

According to Christie and Regier (1988), the optimal temperature range for subadult and adult whitefish is 10 to 14°C. To bound the effect of water temperature on consumption estimates, we performed simulations under four summer maximum water temperatures: 8, 10, 12, and 15°C. For the 10°C summer-maximum-water-temperature regime, we used the temperature schedule used by Stewart et al. (1983) for modeling Lake Michigan lake trout (*Salvelinus namaycush*). Stewart et al. (1983), using an annual cycle of water temperature for the surface waters of Lake Michigan in the middle of the lake, assumed that lake trout would occupy 10°C water for as long as that water temperature was available. We used this same annual cycle of water temperature to develop temperature regimes under the 8, 12, and 15°C summer-maximum scenarios. In each scenario, we assumed that whitefish would occupy waters of the summer-maximum temperature for as long as that temperature was available.

We performed a set of simulations for each of the four water-temperature scenarios outlined above. Each set of simulations consisted of four runs—

one run for each of the four age groups bounded between ages 2 and 6. Because the diet of whitefish in Lake Michigan is similar to that of adult bloater (Rudstam et al. 1994; Pothoven et al. 2001), we used the diet schedule for adult bloater in our whitefish bioenergetics simulations. Rudstam et al. (1994) assumed that adult bloater fed exclusively on benthic prey—primarily *Mysis* and diporeia—and that their caloric density was 4000 J·g⁻¹ on a wet-weight basis. We used the predator energy-density function developed of Rudstam et al. (1994) in these four sets of simulations.

To explore the sensitivity of the model predictions to swimming speed, we conducted an additional set of simulations in which the swimming-speed submodel by Rudstam et al. (1994) was replaced with the swimming-speed submodel used for Lake Michigan lake trout by Stewart et al. (1983). The swimming-speed submodel developed by Rudstam et al. (1994) yielded a swimming-speed estimate of 45 cm·s⁻¹ for a 1.5-kg whitefish. This speed appeared to be excessively high because it substantially exceeded swimming speeds predicted by Stewart and Ibarra (1991) for similarly sized coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon in Lake Michigan. Underwater observations of both whitefish and lake trout swimming in trapnets in Hammond Bay, Lake Huron, by PJS suggested that whitefish are no more active than lake trout. Furthermore, Stewart et al. (1983) predicted that lake trout were less active than salmon in Lake Michigan. Therefore, we replaced the Rudstam et al. (1994) swimming-speed submodel with the submodel developed by Stewart et al. (1983) for Lake Michigan lake trout, and we performed a set of four—one simulation for each of the four whitefish age groups—simulations with a summer-maximum water temperature of 10°C.

To explore the sensitivity of model predictions to predator energy density, we conducted a final set of simulations in which the Rudstam et al. (1994) predator energy-density function was replaced with a mean energy density based on a recent determination of energy density of Lake Michigan whitefish.

Using bomb calorimetry, we determined that the mean energy density of five whitefish from Lake Michigan, captured near Muskegon, Michigan, in 2000 was $6531 \text{ J}\cdot\text{g}^{-1}$ on a wet-weight basis. In contrast, the Rudstam et al. (1994) predator energy-density function yielded an estimate of $13\,050 \text{ J}\cdot\text{g}^{-1}$ on a wet-weight basis for fish with weights $\geq 155 \text{ g}$. Therefore, we replaced the Rudstam et al. (1994) predator energy-density function with the mean energy-density value of $6531 \text{ J}\cdot\text{g}^{-1}$ and performed a set of four—one simulation for each of the four whitefish age groups—simulations using the lake trout swimming-speed submodel and a summer-maximum water temperature of 10°C .

Results

According to our bioenergetics-model simulations, the GGE of whitefish decreased slightly as the summer-maximum water temperature increased from 8 to 15°C (Fig. 1). Averaging across all four water-temperature regimes, the GGE of whitefish during their third year in the lake was 0.075 , and the GGE of whitefish during their fifth year was 0.02 .

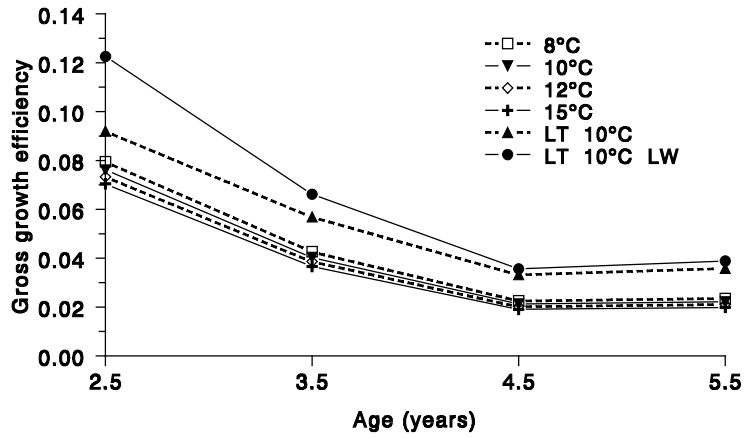


Fig. 1. The GGE of lake whitefish in northern Lake Michigan during 1991-2000 was estimated as follows: four lower curves—unmodified generalized coregonine bioenergetics model of Hanson et al. (1997) using summer-maximum water temperatures of 8, 10, 12, and 15°C; second curve from top—as above with original swimming-speed submodel replaced with the swimming-speed submodel of Stewart et al. (1983) for Lake Michigan lake trout and a summer-maximum water temperature of 10°C; and top curve—as above with the lake trout swimming-speed submodel, the predator energy-density function replaced by a value of $6531 \text{ J}\cdot\text{g}^{-1}$ (wet-weight basis), and a summer-maximum water temperature of 10°C.

Replacing the Rudstam et al. (1994) swimming-speed submodel with the Stewart et al. (1983) swimming-speed submodel for lake trout led to a substantial increase in the GGE at all ages (Fig. 1). Whitefish GGEs during their third and fifth years in the lake were 0.09 and 0.035, respectively.

Using the lake trout swimming-speed submodel and replacing the Rudstam et al. (1994) predator energy-density function with an actual caloric density for Lake Michigan whitefish led to a considerable increase in GGE for younger fish but only a slight increase for older fish (Fig. 1). Whitefish GGEs during their third and fifth years in the lake were 0.12 and 0.04, respectively.

Discussion

Estimates of the GGE from the unmodified version of the generalized coregonine bioenergetics model applied to Lake Michigan whitefish were relatively low compared with published estimates for Lake Michigan bloater by Rudstam et al. (1994) or with published estimates for whitefish from inland waters in northern Quebec (Trudel et al. 2001; M. Trudel, Department of Fisheries and Oceans, Nanaimo, British Columbia, V9R 5K6, Canada, personal communication). Rudstam et al. (1994) generated estimates of bloater GGE of 0.10 and 0.05 for their third and fifth years in Lake Michigan, respectively. Trudel et al. (2001) developed their own bioenergetics model using mercury as a tracer for whitefish in Quebec. Their model predicted that whitefish GGEs during their third and fifth years in inland waters of northern Quebec were 0.12 and 0.05, respectively. In contrast, the unmodified version of the GCBM by Hanson et al. (1997) predicted that whitefish GGEs during their third and fifth years in Lake Michigan would be 0.075 and 0.02, respectively.

The Rudstam et al. (1994) swimming-speed submodel may have overestimated swimming speeds of whitefish in Lake Michigan. As mentioned above, the estimated swimming speed of $45 \text{ cm}\cdot\text{s}^{-1}$ appeared to be too high. Stewart and Ibarra (1991) commented that Pacific salmon would be expected to exhibit relatively high swimming speeds because they evolved to swim long distances searching for active, pelagic prey. Yet, the average annual swimming speed predicted by the submodel developed by Stewart and Ibarra (1991) for 1.5-kg chinook and coho salmon in Lake Michigan was $35 \text{ cm}\cdot\text{s}^{-1}$.

The predator energy-density function developed by Rudstam et al. (1994) substantially overestimated the energy density of Lake Michigan whitefish. Energy density estimated by the unmodified GCBM was $13\,050\text{ J}\cdot\text{g}^{-1}$, whereas the actual energy density for Lake Michigan whitefish was measured at $6531\text{ J}\cdot\text{g}^{-1}$. Interestingly, when the lake trout swimming-speed submodel was incorporated into the generalized coregonine bioenergetics model and a more realistic value of energy density of whitefish in Lake Michigan was used, the modified bioenergetics model yielded estimates of GGE for Lake Michigan whitefish that were in accord with previously published estimates of GGE for Lake Michigan bloater and for whitefish in inland waters of northern Quebec.

Our study did not show that the unmodified version of the GCBM was providing inaccurate estimates of food consumption by whitefish in Lake Michigan. Nevertheless, the disagreement between the predictions of GGE for Lake Michigan whitefish and the estimates of GGE for Lake Michigan bloater and whitefish in northern Quebec suggested that the unmodified version of the GCBM was substantially overestimating food consumption by whitefish in Lake Michigan. Clearly, the GCBM needs to be thoroughly evaluated. The approach recommended by Madenjian et al. (2000) would not only provide a plan for a reasonably thorough evaluation of the generalized coregonine bioenergetics model but would also serve as a framework to improve the model performance should the evaluation indicate model deficiencies. In the Madenjian et al. (2000) approach, consumption and growth of whitefish in laboratory tanks would be compared to model predictions of consumption and growth.

A comparison of field and laboratory estimates of PCB net-trophic-transfer efficiency would also serve as a field evaluation of the GCBM. In the laboratory, the efficiency of the net trophic transfer of PCBs to whitefish could be measured by determining PCB concentrations in the whitefish at the start and end of the experiment and by determining PCB concentrations in their food. A field estimate of PCB net-trophic-transfer efficiency to whitefish from their prey could be generated by applying the GCBM to Lake Michigan whitefish to estimate food consumption and by determining PCB concentrations in both whitefish and their prey. Because the respiration component of the bioenergetics model is based on detailed respiration measurements over a range of swimming speeds and water temperatures, we suspect that the model performance in the laboratory would be reasonably

good. Because the swimming speeds predicted in the field by the model appear to be unrealistically high and the model estimate of predator energy density is biased high, we suspect that the model substantially overestimates food consumption. Should a thorough evaluation of the model confirm our suspicions, the swimming-speed submodel and the predator energy-density function of the GCBM should be modified, and the modified model should be applied to several Lake Michigan whitefish data sets to test the accuracy of its predictions.

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