Appendix D. Bioenergetics Modeling of Chinook Salmon and Lake Trout in Lake Huron: Methods and Results.

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1.0 Overview of the bioenergetics modeling

The Wisconsin bioenergetics model (e.g., Stewart et al. 1983, Hanson et al. 1997) was used as a basis for estimating consumption given information on increments in growth and other inputs including, environmental temperature regimes, diets, and predator and prey energy density. The fundamental bioenergetics model is an energy balance equation that allocates consumed energy to various processes including accumulation in terms of growth:

\[
\frac{dB}{dt} = C - (R + F + U)
\]

Where \( dB/dt \) is growth rate, and C, R, F, and U are consumption, respiration, egestion and excretion rates. Typically these rates are expressed as per unit energy or “specific” rates, and these rates are modeled as depending upon body mass and temperature. When used with observed information on growth (as is the case here) a tuning parameter (\( p \), the proportion of maximum consumption) is adjusted to set consumption at a level that produces the observed growth. Because growth data are typically units of mass, diets are in terms of proportions of mass consumed, and maximum consumption rates are in units of mass, the model requires inputs on the energy density of different types of prey and sizes of predators.

2.0 Methods

2.1 Smoothed proportions of maximum consumption

The \( p \) that produced a perfect match with growth are not the \( p \) we used in our final calculations producing results reported here for gross conversion efficiency, consumption, and other quantities of interest. Instead, in a second stage we fit a polynomial model (depending on year and predator total length (TL)) to these “observed \( p \)”, and then passed the predicted \( p \) from that model through the bioenergetics calculations to obtain final results. Our approach here essentially assumes that the proportion of maximum consumption will change gradually or at least smoothly as a function of time and fish size, and that variation that cannot be captured by a relatively low degree polynomial is due to observation error. We note that the observed \( p \) can be viewed as a transformation of the data on predator growth and other assumed inputs, and hence fitting a polynomial to the observed \( p \) is equivalent to fitting a statistical model to the growth data. This procedure allows for uncertainty estimates on the predicted \( p \) and anything that can be calculated from them. Given the large number of results reported here and fairly evident patterns we do not report uncertainty on most calculated quantities. We do calculate predicted \( p \) for fish of specified TL and provide asymptotic standard errors for these estimates to provide a sense of how well estimated the predicted \( p \) values are.

More specifically, we fit the statistical model:

\[
p_{ay} = a_0(y) + a_1(y)\overline{L}_{ay} + a_2(y)\overline{L}_{ay}^2 + a_3(y)\overline{L}_{ay}^3 + \varepsilon_{ay}
\]
where $\tilde{L}_{av} = (TL_{av} - 500)/500$ , $a_i(y) = b_{0i} + b_{1i}\tilde{y} + b_{2i}\tilde{y}^2 + b_{3i}\tilde{y}^3 + b_{4i}\tilde{y}^4$ , $\tilde{y} = (y - 1988)/1988$ , and $\varepsilon \sim N(0,\sigma^2)$ . We recognize that there is likely high frequency variation that is real that this procedure treats as “noise”, however we suspect much of the high frequency variation does in fact represent sampling variation in diets, size-at-age, and other inputs. In addition, we compared patterns suggested by calculations using the observed and predicted $p$ to evaluate robustness, and largely confine our conclusions to trends and not year specific results.

### 2.2 Methods specific to lake trout

#### 2.2.1 Modeling structure for lake trout

Bioenergetics calculations were done starting in either 1976 (northern region) or 1984 (north-central and southern region) through to 2008, with separate calculations by region. The northern region represented conditions in the MH1 statistical district and adjacent Ontario waters. The north-central region represented conditions in the MH2 statistical district and adjacent Ontario waters. The southern region represented conditions in the MH3 and further south statistical districts and adjacent Ontario waters. As is usual with Wisconsin bioenergetics models, calculations were done in daily time steps. For lake trout, day one corresponded to May 1, so that initiation of calculations would correspond with the timing of annual spring gill net surveys, the source of information on lake trout size-at-age. Energy losses due to reproduction are assumed to occur on day 184.

#### 2.2.2 Size-at-age information for lake trout

Length-at-age estimates assumed to correspond to day 1 of bioenergetics calculations were obtained for MH1 and MH2 combined and for MH3, MH4, MH5, and MH6 combined based on fits of a time-varying von Bertalanffy model to biological data from spring survey data (Appendix A). The estimates based on MH1 and MH2 combined data were assumed to apply to both the northern and north-central regions, and estimates from MH3 and further south statistical districts were used for the southern region. Mass-at-age values were obtained based on these length-at-age estimates and power functions relating mass to length, which were fit separately for MH1 (northern region), MH2 (north-central region), and MH3-MH6 (southern region), and had coefficients that varied over years (Appendix A). The fundamental bioenergetics calculations were done in terms of mass of fish, which was initiated at day one based on these mass-at-age estimates, and updated daily based on the bioenergetics calculations, which took into account the “tuning parameter” $p$, so as to match (or approximate) the mass-at-age for the next year and next older age. Although bioenergetics processes are based on fish mass, fish diets were based on the length of a predator. Hence length was calculated from mass during each day of bioenergetics calculations, using the year specific mass-length relationship for that region.

#### 2.2.3 Energy density of lake trout

Energy density of lake trout was assumed to follow a piece-wise linear function specified as a linear function of body mass with separate slopes and intercepts for body mass below and above 1.5kg (figure D.1). Different relationships were specified for three different year ranges for each of the three regions.
modeled. The early period extended until 1990. The middle period extended from 1991 to 2000. The late period included 2001 and later. The energy density relationship for the early period was based on assumed relationships used in earlier bioenergetics applications for lake trout (Stewart et al. 1983, Stewart and Ibarra 1991). The energy density relationship for the middle period was based on energy density data reported by Dobiesz (2003). The energy density relationship for the late period was calculated based on statistical models fit as part of this study (Appendix C, table D.1). More specifically, a statistical model that related muscle water content to lake trout length, allowing for separate intercepts for lake (Lake Michigan or Lake Huron) was used to generate predicted muscle water content as a function of fish length for Lake Huron. Although the lowest AIC model included maturity as well as these variables, the simpler model used here was highly competitive (within 0.4 in AIC of best model). Whole body energy density was obtained based on a quadratic function of muscle water content. Although a number of substantially more complex models allowing for random year effects, and fixed effects of sex, season, and length had much lower AIC values, most of the variation in predicted values was captured by water content and water content squared. Mass-length relationship using region and year specific coefficients were used to generate mass versus length relationships for each region for 2006 and 2007, and these six sets of predicted mass at length were averaged. These years were used because they are the years that provided energy density data. A single mass-at-length prediction was desired given that the energetic models did not allow for regional variation. Finally the predicted relationship between energy density and mass was plotted, and then this was examined and a piecewise function was determined that approximated the relationship in this plot.

Energy density of gametes that were lost during reproduction were set to constant value used in other bioenergetics applications for lake trout (Stewart et al. 1983, Stewart and Ibarra 1991).

2.2.4 Diet for lake trout

Data on the fish portion of the diet was based on sampling data collected by Michigan DNR (all regions) and CORA (from MH1 statistical district). 1996 and earlier diets were recorded in numbers and proportions of different fish categories calculated directly from these, which assumes different prey fish had equal mass. Starting in 1997 the standard protocol was to assess stomach contents in terms of mass. Within a year, all diet samples from the growing season (May through October) were pooled for a fish size category for each region, then proportions by prey fish type were calculated. Diets of prey fish were calculated for three size-categories of lake trout, total length \( \leq 400 \) mm, \( 400 \) mm \( < \) total length \( \leq 600 \) mm, and total length \( > 600 \) mm. Recognized prey fish categories included alewife, rainbow smelt, stickleback, corigonines, round gobies, and other fish. These categories, however, were further summarized into the categories: alewife, round gobies, and rainbow smelt plus other fish. The bioenergetics model used these proportions as the relative proportions of prey fish during the “growth season” (through day 184 of the bioenergetics year that started on May 1). In the bioenergetics model lake trout with total length less than or equal to 260 mm were assumed to have a proportion of fish in their diet linearly related to their total length (TL) in mm by

\[
P_{\text{fish}} = -0.391 + 0.00433 \text{ TL}
\]
Fish greater than 260 mm TL but less than or equal to 400 mm TL were assumed to have a proportion fish in their diet given by

\[ P_{\text{fish}} = -0.785 + 0.00447 \text{TL} \] for all regions and years.

Lake trout greater than 400 mm were assumed to only eat fish. These assumptions and regression equations were based on analysis of data reported by Dryer et al. (1965).

During the winter, lake trout diets were modified by changing the relative proportions of alewife and rainbow smelt to one another, while retaining their total proportional contribution to the diet. During winter the proportion alewife of the alewife plus rainbow smelt total were 0.35, 0.26, and 0.29 for small (TL less than or equal to 400 mm), medium (TL greater than 400 mm and less than 600 mm), and large (TL greater than 600 mm) lake trout. These same adjustments applied in all regions and years, based on all available data collected during November through April.

The proportion of the diet that was alewife was allocated between small (age-0, < =120 mm TL) and large (age 1 and above, > 120 mm TL) fish, a necessary distinction because of different energy densities associated with the different size categories. The proportions of alewife assumed to be in the small category during an early period (1990 and earlier) were 0.9, 0.4, and 0.1, for small, medium, and large lake trout respectively. During a middle period (1991 through 2000) these proportions were set to 0.95, 0.7, 0.4, and during a late period (2001 and later) they were set to 0.99, 0.95, and 0.9.

2.2.5 Temperatures occupied by Lake Trout

Temperatures vary seasonally on a daily basis in the bioenergetics model. Input temperatures are based on Bergstedt (2003, 2008), who collected temperature occupancy data continuously based on lake trout carrying temperature recording tags. The temperature regimes were assumed to be the same for all three modeled regions.

2.2.6 Mortality and abundance-at-age for lake trout

Calculations of actual consumption per lake trout present at the start of the year and expanding this to population level consumption requires information on abundance-at-age and mortality-rates-at-age. These estimates were obtained from the most recent statistical-catch-at-age assessments, which were done by the 1836 treaty waters modeling subcommittee during spring 2009 using data through 2008. Methods and data used in these assessments are described in MSC (2009). These assessments operated on an annual basis and the abundance-at-age at the start of the year and the mortality that were estimated for each calendar year were assumed to approximate abundance at the start of the growth year on May 1 and mortality rates for years starting May 1.
2.3 Methods specific to Chinook salmon

2.3.1 Modeling structure for Chinook salmon

Bioenergetics calculations were done each year from 1968 to 2007, with one set of calculations for the entire main basin. As for lake trout, calculations were for daily time steps, in the case of Chinook salmon day 1 corresponded to September 1, assumed to represent conditions immediately after reproduction. This timing generally corresponded with timing of size-at-age estimates (largely from creel survey data) and allowed for modeling the entire year without accounting for losses due to reproduction. Fish were considered to be age-0 on September 1 after their first summer in the lake. Subsequently, ages and years were incremented by 1 year on September 1. Thus, for example a fish that was age-0 on September 1, 1968 would still be considered age-0 and in model year 1968 in August of 1969. Consumption and bioenergetics is modeled for model-ages 0 through 3, which captures consumption of fish for four piscivorous feeding seasons.

2.3.2 Size-at-age information for Chinook salmon

Length-at-age estimates assumed to correspond to day 1 of bioenergetics calculations for each age and year were obtained based on fits of a time-varying von Bertalanffy model to biological data from creel survey samples from August data (Appendix A) for ages 1-4 collected during 1983 through 2008. Although consumption is modeled only through age-3, length-at-age 4 is needed to allow calibration of the bioenergetics model to the growth increment during age-3. Age-0 length-at-age was assumed constant during 1983 through 1998 based on an estimate of the approximate length at the time of annulus formation based on limited in lake sampling. Mass-at-age values were obtained based on these length-at-age estimates and power functions relating mass to length, which had coefficients that varied over years (Appendix A). A constant set of length-at-age values for ages 1-4 were used for 1968 through 1979, based on simple averages of length-at-age data from all main basin weir samples collected during the 1973-1979. A simple average of length-at-age for ages 1-4 was estimated from weir samples collected during 1980-1982 and this was used to describe the 1979 year class through 1982, and age-4 fish in 1982. Mass-at-age corresponding to these length-at-age estimates was calculated based on the mass-length relationships. Mass-at-length for ages 1-4 not captured by the above were linearly interpolated over years for other values of fish of the same age, and corresponding length-at-age were based on the mass-length relationships. Finally, mass-at-age 0 was calculated from mass-at-age 1 during years prior to 1983, based on the assumption that the instantaneous rate of increase in mass from age-0 to age-1 would be 2.5 times the rate of increase from age-1 to age-2. This assumption was based examining how instantaneous growth rates for different sizes of fish tracked over time, extrapolated to the sizes of fish under consideration.

The fundamental bioenergetics calculations were done in terms of mass of fish, which was initiated at day one based on these mass-at-age estimates, and updated daily based on the bioenergetics calculations, which took into account the “tuning parameter” p, so as to match (or approximate) the mass-at-age for the next year and next older age. Although bioenergetics processes are based on fish
mass, fish diets were based on the length of a predator. Hence length was calculated from mass for each day of bioenergetics calculations, using the year specific mass-length relationship for that region.

2.3.3 Energy density for Chinook salmon

Energy density of Chinook salmon, as for lake trout, was assumed to follow a piece-wise linear function specified as a linear function of body mass with separate slopes and intercepts for body mass below and above a threshold, the threshold being 4 kg for this species. Different relationships were specified for four different year ranges (figure D.1). The early period (1989 and before) used the same relationship assumed in earlier applications for this species (Stewart and Ibarra 1991). The middle period (1990 through 1999) used a relationship based on data reported by Dobiesz (2003).

A late-middle period (2000-2004) and late (2005 and later) period were based on data collected or analyzed in this study and statistical models reported in appendix C. First water content was obtained from a statistical model that related this variable to fish length, which allowed for effects of sex and group (Lake Michigan, Lake Huron 2002-2004 (used to represent the late-middle period (unpublished data provided by M. Jones, MSU) and Lake Huron 2006 (used to represent the later period), and an interaction of group and length. Thus, these models allowed for intercepts that differed depending upon sex and group and slopes (of water content versus length) that depended on group. Although this model was not the lowest AIC model evaluated in appendix C, it was highly competitive, being within 0.45 of the best but more complex model that also included maturity status. Because we are seeking values to use in a pooled sex bioenergetics model, intercepts for males and females were averaged. Lipid content was then predicted from these water content values, based on a quadratic function relating arcsine square-root transformed proportion of mass that was lipid to water content. Finally energy density was calculated from lipid content based on data reported by Peters et al. (2007). In using these data to establish a relationship between energy density and mass, mass was calculated form length by using separate mass-length relationships for each year from 2002-2008 (see Appendix A) and then averaged for a given length. These years were used because although there were variations in the relationship over this time it did not appear to represent a systematic trend. Finally the predicted relationship between energy density and mass was plotted, and then this was examined and a piece-wise function was determined that approximated the relationship in this plot.

2.3.4 Diets for Chinook salmon

Although some Chinook salmon diet information was collected it is not possible to generate a full time series based solely on this. The data that are available suggests that this species has concentrated its fish consumption almost entirely on the pelagic prey species alewife and rainbow smelt, and that variations in the relative proportions of these two prey species in Chinook salmon diets has showed co-variation with the proportions in lake trout diets. Consequently, we assumed the entire fish diet was either alewife or smelt, and that the relative proportions of small alewife, large alewife, and rainbow smelt were the same as were seen lake trout during the growing season. The proportion of the diet that was invertebrates, rather than fish was also assumed to be the same as for lake trout.
2.3.5 Temperatures occupied by Chinook salmon

Temperatures occupied by Chinook salmon were based on data recorded on implanted archival tags that recorded a nearly instantaneous record of temperatures occupied (R. Bergstedt, USGS, unpublished data). Methods were similar to those used by Bergstedt (2003, 2008) for lake trout.

2.3.6 Abundance and mortality rates for Chinook salmon

Chinook salmon abundance-at-age and mortality rates were based on the most recent statistical catch-at-age assessment model developed for this species in the main basin of Lake Huron (Brenden and Bence 2009). This model operates in monthly time steps, with natural mortality constant over the calendar year for a given age of fish but with fishing mortality varying monthly. Abundance-at-age output produced by this assessment model correspond to abundance on January 1. We generated abundance at age applicable on September 1, after spawning by applying the appropriate natural and fishing mortality rates from January 1 through the end the end of August and multiplying these survivors by $1 - \text{proportion mature (for that age and year)}$, using the maturation schedule estimated as part of that assessment. Subsequently during calculations over a year starting September 1, the appropriate monthly mortality rate was calculated from the age and year specific natural mortality rate (varying over years only for age-0) and the age, year, and monthly fishing mortality rate. As a matter of bookkeeping the mortality rates for September through December in the bioenergetics model were based on the corresponding age and year mortality rates in the assessment model, whereas the mortality rates for January through August were taken from the next age and year of the assessment model (which increments age and year in January rather than in September).

2.4 Prey energy density

Prey energy densities are largely based on previously reported values, but some values or decisions are based on samples collected as part of this study. During this study, forage fish samples were collected by the USGS with additional sampling by the USFWS Alpena FRO and the MDNR. Samples were mainly collected during October from a number of sites in the U.S. waters of the main basin, and from sites near Hammond Bay and Thunder Bay during May and July. Samples were saved on ice when collected and frozen when returned to shore in bags containing individuals of the same species and size category (generally 25 g or more per bag). These samples were weighed and homogenized using a Hobart tabletop meat grinder (large samples) or a food processor (small samples). Aliquots of the resulting mixture were processed to obtain energy density following the same procedures used to obtain energy density of predators.

Prey energy density was assumed the same for prey eaten by Chinook salmon and lake trout from all three regions. Prey energy density for small (age-0, <120 mm TL) and large alewife were based on those calculated by Dobiesz (2003). Daily values were obtained by linear interpolation between the dates Dobiesz reported mean values for. During our study few samples of alewife were collected (table D.2) because this species had become uncommon in samples, and the available data were consistent with the earlier data of Dobiesz, so this same seasonal pattern of energy densities was used for alewife for the entire time series. It was evident that assumptions about the relative proportion of small and large
alewife in the diet were likely to have a larger influence on the energy content of the diet than were any possible changes in energy density within a size class. Data collected during this study for round goby during May through October 2006 and 2007 was averaged over samples and the resulting average was used for all years for which this species occurred in diets (table D.2). This value was consistent with results of Ruetz et al. (2009) for Lake Michigan. The seasonal pattern of energy density for rainbow smelt reported by Dobiesz (2003) was used from the start of modeling through model year 1999 or 2000, for Chinook salmon and lake trout respectively, for rainbow smelt and other prey species combined, with interpolation to produce daily values as for alewife. The average over the season of these values was very close to the value used in early bioenergetics applications in Lake Michigan (Stewart et al. 1983, Stewart and Ibarra 1991). Energy density of rainbow smelt and other prey species in later years was based on a single overall average from rainbow smelt samples collected during this study during May through October 2006 and 2007, excluding samples of small fish. A constant value was used because other than very small rainbow smelt energy density during May to October remained near 4700 joules per gram (figure D.2). This value was nearly identical to the average value over other prey species (table D.2). Although this value was substantially less than the value reported by Stewart et al. (1983) for Lake Michigan, and the values reported earlier for Lake Huron by Dobiesz (2003), it is comparable to values reported by Rand et al. (1994) from the Great Lakes. Invertebrate energy density was set at the value used in other bioenergetics applications (Stewart and Ibarra 1991).

3.0 Results

3.1 Proportion of maximum consumption

For Chinook salmon the proportion of maximum consumption (p) generally declined over time and with increasing total length at the start of the modeled year, with the temporal decrease tending to be larger for the smaller fish (figure D.3). This pattern, combined with a general decline in length-at-age, led to age-specific declines in p that were most evident for the youngest ages, and not evident for age-3, which had declined in length at age the most (figure D.3). As suggested by the standard errors of predicted proportion of maximum consumption versus length, these relationships with time and fish length were well established.

For lake trout temporal changes in the proportion of maximum consumption varied among regions. In the southern region, patterns were qualitatively similar to those seen for Chinook salmon (figure D.4). In the north-central region the proportion of maximum consumption for smaller fish (400 mm) appeared to generally increase until 1994 and then generally decreased (figure D.5). Fish of about 600 mm showed an increase in the proportion of maximum consumption during the 1980s after which p was roughly constant. In the north-central region these changes translated into an increase in p for age-4 until 1995 followed by a decline, and for age 7 and older sharp increases in p during the 1980s followed by no long-term trend.

In the northern region the proportion of maximum consumption by lake trout was fairly stable for small (400 mm) fish (figure D.6). For 600 mm fish there was a estimated decrease in p through about 1985, followed by an increase through 2002, followed by a modest decline. In the northern region these
temporal patterns in \( p \) with length and year translated into sharp increases in \( p \) through 1988 for age 7 and older, followed by a period without trend. For age-4 in the northern region \( p \) did not trend strongly.

### 3.2 Gross conversion efficiency

We calculated gross conversion efficiency in terms of energy (GCEE) and in terms of mass (GCEM), the latter of which accounted for the different energy density of the diet and predator fish. We only present temporal patterns for gross conversion efficiency calculated on the basis of individual fish that survive an entire year. We also calculated gross conversion efficiencies based on cumulative growth and consumption of fish surviving over the course of a year. We do not present these because they were close in value to the individual gross conversion efficiencies, but did use them when calculating population production. Note that energy gain allocated to reproduction as well as growth was considered as part of the conversion (i.e., GCE = (growth+reproduction)/growth) for lake trout (reproductive allocation was not partitioned for Chinook salmon as the last modeled day was immediately prior to reproduction for that species).

For Chinook salmon GCEE tended to decline over time starting about 1983 when annual estimates of size at age became available (figure D.7). The changes were not smooth, and there were some periods of increase and a period of particularly low values during 2001-2004. The largest fluctuations about a long-term decline occurred for the oldest fish. In contrast, GCEM for Chinook actually tended to increase over time (figure D.7). This reflects a larger decrease in predator energy density than in the energy density of their diet.

For lake trout in the southern region there was also a strong pattern of decline in GCEE over time, and this case the same qualitative pattern occurred for GCEM (figure D.8). In the north-central and northern regions there were some large fluctuations in GCE, but between 1985 and 2000 little evidence for any consistent temporal trend in either GCEE or GCEM (figures D.9&D.10). Starting about 2000 there is a downward trend in aggregate (over ages) GCEE and GCEM that is also evident in ages 7 and 10 (figures D.9&D.10).

### 3.3 Individual and population consumption

We report individual consumption calculated for predators surviving an entire year, and also population consumption based on the modeled number assumed to survive to each day of the year.

For Chinook salmon, individual annual consumption at each age and cumulative cohort consumption of an individual surviving through age-3 declined over time. This decline was substantial and a fish in the 2001 and later year classes and surviving through a third feeding season consumed about half as much as a fish stocked at age-0 in the late 1960s and early 1970s (figure D.11).

For lake trout, individual consumption varied among regions. Again temporal patterns for the southern region were most similar to those seen for Chinook salmon, although the decline in consumption per fish was not as severe, especially for older fish (figure D.12). In the north-central region there was some increase in consumption per fish during the 1980s but not much trend over time thereafter. In the
northern region the sum of individual consumption over ages and the consumption per fish for older ages showed an initial increase and decrease followed by an increase from 1985 to 2000, with a subsequent modest decrease. Age-4 fish showed little trend over time. The overall levels of individual consumption were roughly similar across regions for lake trout, particularly in the most recent years. Individual annual consumption for age 1-3 Chinook salmon was markedly higher than for lake trout of any age, even after the disproportionate temporal decline in consumption by Chinook salmon.

Total estimated population consumption by Chinook salmon increased from 1968 through 1985 (figure D.13), peaking at nearly 28 thousand MT, because increases in population biomass outpaced the decline in per fish consumption (figure D.14). After 1985 both population biomass and consumption per fish declined, leading to a rapid decline in population consumption, particularly between 1985 and 1990 and again after 2001. Average population consumption by Chinook salmon after 2002 was about 3% of peak levels. While population consumption was markedly influenced by changes in bioenergetics conditions influencing individual consumption of surviving fish, it is evident that changes in population abundance reflecting variation in recruitment and survival had even larger influences.

In the southern region total consumption by lake trout declined from 1984 through the end of the 1980s (figure D.15). Consumption then increased to peak levels in 1999-2001 followed by a decline. In the north-central region total consumption by lake trout generally increased to a peak in 1999 and then decreased (figure D.16). In the northern region total consumption varied irregularly and generally declined through 1990, followed by an increase in consumption to a peak level in 2003, then leveled off and started to decline starting in 2006 (figure D.17). Total consumption largely reflects changes in lake trout biomass (figure D.18) and individual consumption rates, but also reflects the age composition of the stocks. The common increase during the 1990s largely followed an increase in lake trout biomass across all regions, even though the patterns in consumption per fish differed. After peak total consumption occurred, declines during the 2000s appear to result from a leveling off or decline in biomass in all regions, combined with declining consumption per fish common to all regions.

We also calculated annual production and production to biomass ratios (based on start of the year biomass). Production was calculated by multiplying the age-specific consumption values by the age specific GCEpM values, adjusted for within year mortality, which were similar to the age-specific GCEM values based only on fish surviving an entire year.

Although age-specific GCEM was not influenced markedly by adjusting for within year mortality, the aggregate GCE over ages on a mass basis (GCEpM) was influenced by the age-composition of the population (figure D.13 & D18). GCEpM was found by summing daily consumption and increments in individual mass for the population over the year and taking the ratio. GCEpM was higher than GCEM (simply summing consumption and growth over ages and taking the ratio, which approximates GCEM over a lifespan) because it weights younger fish more in the calculations.

The aggregated GCEpM showed a different temporal pattern than GCEM for Chinook salmon, reflecting responses to changing Chinook salmon population age structure. While this change in GCEpM does influence the relationship between population consumption and production, it is clear that production
for Chinook salmon is largely driven by large changes in consumption, which although influenced in important ways by changing bioenergetic relationships, was most importantly influenced by the very large changes in population biomass. The ratio of production to biomass for Chinook salmon had a high value of about 5.0 in 1968 when the population consisted of age-0 fish that were growing rapidly. Over time, when in general older fish became more abundant and growth of fish of a given size was declining, the production to biomass ratio declined, generally taking values near or below 1.0 since 1985 (figure D.13).

The temporal patterns in production for lake trout largely matched temporal patterns in consumption through the 1990s (compare figures D.15,D.16, D.17 with figure D.18), reflecting the fact that aggregate population GCE was not strongly trending (figure D.18). Declines in production were more severe or started before declines in consumption, around 2000, given that aggregate population GCE in terms of mass (GCEpM) was declining (figure D.18). The production to biomass ratios for lake trout showed substantial differences among regions and over time reflecting differences in population structure and bioenergetics. P/B was generally less than 1.0 and often substantially less and even negative, showing a marked difference from the level for Chinook salmon (figures D.15, 16, and 17).

There has also been a substantial change in what prey were consumed over time. The modeled proportion alewife made up of total annual consumption by Chinook salmon increased between 1980-1989 and 2000-2003, then decreased markedly during 2004-2007 (figure D.13). The modeled proportion of invertebrates in the diet increased. We caution that the Chinook salmon diet is based on strong assumptions and extrapolations. The increase in invertebrates is based on relatively more small fish being present in the Chinook salmon population and an assumed relationship between proportion fish in the diet and predator total length. The variations on the relative proportions of alewife and rainbow smelt are extrapolated from lake trout diets.

Somewhat similar patterns were seen for lake trout diets across regions, although there were some notable differences. In general rainbow smelt dominated diets in early years, and alewife became more important through 2000-2003 (figures D.15, D.16, and D.17). For 2004 and later there was a sharp decrease in the proportion of the diet that was alewife in all regions, and substantial increase in representation of fishes other than alewife and rainbow smelt. Round goby was not present in the system during most of the time series but became an important part of the diet by 2004, particularly in the north-central region.

4.0 Literature Cited


Table D.1. Equations used in calculation of energy density. In these expressions WC = percent water of muscle wet mass, LEN = lake trout total length in mm, LIP is percent lipid of whole wet mass, and ED is specific energy density in joules per gram of total body wet mass. Note that these equations required unit conversions from Appendix C.

Lake trout

\[ WC = 79.34 - 0.00921 \times LEN \]
\[ ED = -66913.4 + 2442.50 \times WC + -19.17 \times WC^2 \]

Chinook salmon

For 2002-2004: \[ WC = 75.06 + 0.006869 \times LEN \]
For 2006: \[ WC = 84.31 - 0.01118 \times LEN \]
\[ LIP = 100 \times \sin(-3.18 + 0.108 \times WC + -0.000836 \times WC^2)^2 \]
\[ ED = 1200 + 251.21 \times LIP \]
Table D.2. Summary of energy density (joules per gram) values based on homogenized prey fish samples collected during 2006 and 2007 as part of this study. Results shown here are for small (less than 100 mm) and large size classes combined. “Months” indicate the months for which samples were available for each species.

<table>
<thead>
<tr>
<th>sample</th>
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Figures legends

Figure D.1. Energy density (ED) versus mass relationships for Chinook salmon and lake trout. For Chinook salmon 02_04 designates predicted ED from regression models for fish collected during 2002-2004 in Lake Huron, _06 indicates similar predicts for fish collected during 2006 in Lake Huron, and MI regression predictions for fish collected in Lake Michigan during 2002-2004 and in 2006. Also for Chinook salmon PW_02_04 and PW_06 indicate piece-wise approximations to the predictions for Lake Huron during 2002-2004 and 2006 used for the mid-late and late periods respectively. The piece-wise relationships used for the early and mid period are also shown. For lake trout 05-07 indicates the regression predictions for data collected during 2005-2007, pw_lin_late the approximation to these used for the mid-late and late periods, and pw_lin_early, pw_lin_midS, pw_lin_midNC, and pw_lin_midN the piece wise relationships used for the early period and for the middle period for the southern, north-central, and and northern regions.

Figure D.2. Energy density values for rainbow smelt homogenized samples from Lake Huron collected during 2006-2007. Values less than 4200 J/g were very small (age-0) fish and excluding these samples the average value was ~4700 J/g.

Figure D.3. Proportion of maximum consumption for Chinook salmon. Top panel presents proportion of maximum consumption (p) for selected sizes as function of time, with plus or minus one standard error bounds indicated by dashed lines. Bottom panel presents proportion by age over time.

Figure D.4. Proportion of maximum consumption for lake trout in the southern region. Top panel presents proportion of maximum consumption (p) for selected sizes as function of time, with plus or minus one standard error bounds indicated by dashed lines. Bottom panel presents proportion by age for selected ages over time.

Figure D.5. Proportion of maximum consumption for lake trout in the north-central region. Top panel presents proportion of maximum consumption (p) for selected sizes as function of time, with plus or minus one standard error bounds indicated by dashed lines. Bottom panel presents proportion by age for selected ages over time.

Figure D.6. Proportion of maximum consumption for lake trout in the northern region. Top panel presents proportion of maximum consumption (p) for selected sizes as function of time, with plus or minus one standard error bounds indicated by dashed lines. Bottom panel presents proportion by age for selected ages over time.

Figure D.7. Gross conversion efficiency for Chinook salmon. Top panel reports gross conversion efficiency in terms of energy (GCEE) and bottom panel in terms of mass (GCEM). The postfixes of “_1”, “_2”, or “_3” indicate that the reported GCE is for ages 1, 2 or 3. The absence of a postfix indicates that it was calculated based on the sum of growth and consumption for an individual fish of each age, with no adjustments for mortality, so growth and consumption by each age is equally weighted.
Figure D.8. Gross conversion efficiency for lake trout in the southern region. Top panel reports gross conversion efficiency in terms of energy (GCEE) and bottom panel in terms of mass (GCEM). The postfixes of 

“_4”, “_7”, or “_10” indicate that the reported GCE is for ages 4, 7 or 10. The absence of a postfix indicates that it was calculated based on the sum of growth and consumption for an individual fish of each age, with no adjustments for mortality, so growth and consumption by each age is equally weighted.

Figure D.9. Gross conversion efficiency for lake trout in the north-central region. Top panel reports gross conversion efficiency in terms of energy (GCEE) and bottom panel in terms of mass (GCEM). The postfixes of “_4”, “_7”, or “_10” indicate that the reported GCE is for ages 4, 7 or 10. The absence of a postfix indicates that it was calculated based on the sum of growth and consumption for an individual fish of each age, with no adjustments for mortality, so growth and consumption by each age is equally weighted.

Figure D.10. Gross conversion efficiency for lake trout in the northern region. Top panel reports gross conversion efficiency in terms of energy (GCEE) and bottom panel in terms of mass (GCEM). The postfixes of “_4”, “_7”, or “_10” indicate that the reported GCE is for ages 4, 7 or 10. The absence of a postfix indicates that it was calculated based on the sum of growth and consumption for an individual fish of each age, with no adjustments for mortality, so growth and consumption by each age is equally weighted.

Figure D.11. Consumption by an individual Chinook salmon that survives over a complete model year for each age, or cohort consumption by an individual in a year class that survives from age-0 through the end of age-3.

Figure D.12. Consumption by an individual lake trout that survives over a complete model year for each age, or the sum of these individual consumption values over ages 1 through 14, for each modeled region. The latter quantity can be viewed as approximating how individual consumption of a fish over a life spanning ages 1-14 is changing.

Figure D.13. Top panel: Population consumption (C), production (P), and the ratio of production to biomass for Chinook salmon in Lake Huron. Consumption and production are reported in metric tons. Middle panel: breakdown of Chinook salmon population consumption in Lake Huron by prey type. Bottom panel: aggregated gross conversion efficiencies on a mass basis. GCEM is based simply on the sum over ages of individual level consumption and growth. The population level metric GCEpM is based on weighting individual consumption each day for an age-class by the average abundance present that day.

Figure D.14. Biomass at the start of the bioenergetics modeling year for Chinook salmon.

Figure D.15. Top panel: Population consumption (C) and the ratio of production to biomass (at start of bioenergetics year) for lake trout in southern Lake Huron. Consumption and production are reported in metric tons. Bottom panel: breakdown of southern Lake Huron lake trout population consumption in Lake Huron by prey type.
Figure D.16. Top panel: Population consumption (C) and the ratio of production to biomass (at the start of the bioenergetics year) for lake trout in north-central Lake Huron. Consumption and production are reported in metric tons. Bottom panel: breakdown of southern Lake Huron lake trout population consumption in Lake Huron by prey type.

Figure D.17. Top panel: Population consumption (C) and the ratio of production to biomass (at start of bioenergetics year) for lake trout in northern Lake Huron. Consumption and production are reported in metric tons. Bottom panel: breakdown of southern Lake Huron lake trout population consumption in Lake Huron by prey type.

Figure D.18. Biomass, production, and aggregated population level GCE for lake trout in Lake Huron. Biomass is for start of bioenergetics year. Aggregated population level GCE is calculated as the ratio of population production (individual production multiplied by population abundance) calculated for each day and age-class and summed over the year and a similar sum for consumption. Production includes growth and investment in reproductive output. N, NC, and S refer to northern, north-central and southern regions.
Chinook salmon

Lake trout

Figure D.1
Figure D.2
Figure D.3
Figure D.4
Figure D.5
Figure D.6
Figure D.7
Figure D.8
Figure D.9
Figure D.10
Figure D.11
Figure D.12
Figure D.13
Figure D.14
Figure D. 15
Figure D.16
Figure D.17
Figure D.18