Dynamics of lake trout production in the main basin of Lake Huron

Ji X. He, James R. Bence, Charles P. Madenjian, Randall M. Claramunt

J. X. He Michigan Department of Natural Resources, Lake Huron Fisheries Research Station, 160 East Fletcher Street, Alpena, Michigan 49707, USA (hej@michigan.gov)

J. R. Bence Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824, USA (bence@msu.edu)

C. P. Madenjian. U. S. Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, Michigan 48105, USA (cmadenjian@usgs.gov)

R. M. Claramunt. Michigan Department of Natural Resources, Fisheries Division, 8258 South Ayr Road, Alanson, MI 49706 (ClaramuntR@michigan.gov)

Corresponding author:

Ji X. He (hej@michigan.gov; 989-356-3232 x2573; fax: 989-356-1951)

Abstract:

To inform lake trout (*Salvelinus namaycush*) fishery management in Lake Huron that has undergone rapid ecosystem changes, we quantified lake trout production dynamics by coupling age-structured stock assessment and fish bioenergetics models. Our approach revealed the connection between piscivore production and prey consumption, included growth compensation to reproduction losses, and allowed comparisons between long-term dynamics of fishery harvests and fish production. We found that despite the collapse of alewives, a major non-native pelagic prey fish, lake trout production appeared to be sustainable. To a certain degree, the effect of recent recruitment declines on lake trout production was offset by release of harvest pressure from subadult lake trout, and reduction of fishing and sea lamprey induced mortality on adult lake trout. Evidence for sustainability also included the finding that no changes in average ratios of annual production to beginning-of-the-year biomass. Juvenile P:B ratio remained as high as 2.1. The effect of growth declines on adult and subadult production was offset by reduction in population mortality. Body growth and condition did not continue to decline when lake trout became more and more reliant on round goby as food, and the dynamics of total consumption of prey fish continued to be recipient controlled.

Key Words: Fish production, Fisheries and ecosystem management, Salmonids, Stock assessment, Bioenergetics models

Introduction

54   Fish production is the ecological process that determines sustainable fishery yield

55   (Mertz and Myers 1998). Fish production also plays a major role in structuring fish and

56   invertebrate communities (Downing and Plante 1993). The production of apex predators

57   in a food web, i.e., the piscivore production in an aquatic ecosystem, is crucial to shaping

58   ecosystem structures and functions (Estes et al. 2010, 2011). Thus, when fishery harvests

59   have substantial impacts on fish production (Repel et al. 2015), fishery management is

60   also ecosystem management (Larkin 1996). These connections between fishery harvest

61   and fish production can be further elucidated by studying dynamics of fish production.

62   Production of a fish population is typically formulated as a time-averaged

63   measure with the concept that, to maintain a steady state, the combination of natural

64   mortality and fishing mortality should equal the production to biomass (P:B) ratio (Mertz

65   and Myers 1998). For an age structured fish population, this P:B ratio is the average

66   growth rate weighted by biomass ratio of each age group to total population biomass:

67    $$P = \sum_{age}^{max} \bar{B}_a \cdot G_a$$

68   where P stands for production, B_a stands for biomass of an age group, and G_a stands for

69   growth rate of average individual fish in an age group. The ratio of annual production to

70   the average biomass within a year is also believed to be approximately a constant for a

71   fish species in a food web and habitat (Randall and Minns 2000; Hays et al. 2007).

72   The practice of fishery management, however, is more often about managing

73   fisheries in a changing environment, where the average biomass within a year does not

74   necessarily represent a balance between growth and mortality rates, and the ratio of

75   annual production to the average biomass within a year does not necessarily represent the

76   turnover rate of a fish population. Thus, fishery management is much less about

77   maintenance of a steady state, but more about adjusting to changes in stock size, such as

78   stock depletion and recoveries, as well as to major changes in ecosystem structures and

79   functions, e.g., regime shifts (Beamish et al. 1999; Scheffer et al. 2001).

80   To address this management challenge, we recognize two alternative options for

81   the measure of biomass to be defined. Recall that annual production is a summation of

82   daily production while fish abundance declines through a year. With the conventional

83   measure of average biomass within a year (Ricker 1946; Chapman 1971; Repel et al.

84   2015), the P:B ratio is always equal to the average growth rate of body mass. An

85   alternative measure is beginning-of-the-year biomass. We used the alternative measure

86   in this paper, to make P:B ratio adequately reflecting the process that, for a given level of

87   recruitment, annual production can be altered by changes in body growth or changes in

88   population mortality. A time-invariant average P:B ratio will indicate sustainability of

89   the energy flows that are driven by environmental changes and can be altered also by

90   fishery management and fishing mortality.

91   In the main basin of Lake Huron in North America, lake trout (*Salvelinus*

92   *namaycush*) is the native top piscivore in cold water, and sustainability of lake trout

93   production represents stability of the lake ecosystem (DesJardine et al. 1995). In the

94   middle of the last century, the lake trout population collapsed (Hile 1949), due to

95   predation by the invasive sea lamprey (*Petromyzon marinus*) and the fishery harvest that

96   failed to be adaptive to the change that had a major impact on lake trout population

97   dynamics. Since then, the loss of piscivore predation pressure on the prey fish

98   community is regarded as a benchmark of decreases in ecosystem stability (Smith et al.

99   1968; Estes et al. 2010).   Concurrent with the control of sea lamprey abundance, a major

100   salmonine stocking program has helped to rebuild the lake trout population, along with

101   the introduction of Pacific salmons to the lake (Eshenroder et al. 1995; Whelan and

102   Johnson 2004; Claramunt et al. 2013). Recruitment of wild lake trout was rare when lake

103   trout abundance was not sufficiently high, and the prey fish community was dominated

104   by alewives (*Alosa pseudoharengus*). The detrimental impacts of alewives on lake trout

105   natural reproduction and wild recruitment have been well recognized (Walters and

106   Kitchell 2001; Madenjian et al. 2008a; Riley et al. 2011). By 2003, concurrent with the

107   disruption of pelagic food web due to decreases in nutrient loads, and invasion and

108   proliferation of dreissenid mussels, piscivore abundance and predation pressure continued

109   to increase. These conditions led to a crash in the alewife population (Riley et al. 2008;

110   Barbiero et al. 2011; He et al. 2015), followed by lake wide increases in recruitment of

111   wild lake trout, but also major declines in post-stocking survival of hatchery stocked lake

112   trout yearlings (He et al. 2012; Johnson et al. 2015).

113   Major piscivores in the main basin of Lake Huron also include walleye (*Sander*

114   *vitreus*), and Chinook salmon (*Oncorhynchus tshawytscha*). The main basin walleye

115   mostly come from Saginaw Bay, and about 50% of Saginaw Bay walleye feed in the

116   main basin (Hayden et al. 2014; Fielder and Bence 2014). Chinook salmon used to be the

117   dominant piscivore since the 1970s and contributed over 70% of total piscivore biomass

118   in the 1980s. After the collapse of alewives, however, Chinook salmon contribution to

119   total piscivore biomass decreased to only about 13% (He et al. 2015), and more than 80%

120   of Lake Huron Chinook salmon started to consume prey fish in Lake Michigan before

121   they returned and spawned in the tributaries to Lake Huron (Clark et al. 2016). Lake

122   trout has resumed its place as the keystone piscivore in the main basin of Lake Huron.

123   The contribution by lake trout to total piscivore biomass and total consumption of prey

124   fish increased from below 20% in the 1980s to near 50% by 2002 and over 70% by 2010

125   (He et al. 2015).

126   With all of these profound changes in the ecosystem, fishery managers have

127   become concerned that lake trout abundance might have exceeded carrying capacity of

128   the lake even though the abundance is still below the historical level prior to the collapse

129   in the middle of the 20th century. Fishery management, however, has continued to build

130   on the early recommendation that a maximum annual mortality of 40-45% was

131   sustainable for lake trout in North America, including the Great Lakes (Healey 1978;

132   Nieland et al. 2008). Madenjian et al. (2013) have reviewed the most recent trophic shift

133   in Lake Huron. He et al. (2015) have described the shift as from a pelagic energy

134   pathway to a benthic energy pathway. From previous investigations, He et al. (2015)

135   have also suggested that recent abundance declines of pelagic prey fish, such as the

136   alewife and rainbow smelt (*Osmerus mordax*), may not be the end of non-stationary

137   variations of Lake Huron food web. Thus, an evaluation of Lake Huron carrying capacity

138   for lake trout can be confounded by profound changes over time in the ecosystem.

139   The real challenge to managing fisheries in Lake Huron is indeed the continued

140   ecosystem change. We interpret the carrying capacity concern as a question about

141   sustainability of lake trout population and lake trout fisheries. Such sustainability is

142   influenced by both environmental change and fisheries management (Larkin 1996). Our

143   objective in this paper is to determine what are the major impacts of recent ecosystem

144   changes on lake trout, and to understand how the production of adult lake trout has been

145   developed and sustained during the recent rapid ecosystem changes.

146

Materials and methods

147

148   We estimated annual production by coupling age structured stock assessment and

149 fish bioenergetics models. In comparison with commonly used methods, such as the

150 Instantaneous Growth Rate Method and the Increment Summation Method (Ricker 1946;

151 Chapman 1971; Newman and Martin 1983; Hayes et al. 2007), our approach has three

152 major advantages. The first is to realize the close connection between fish production

153 and prey consumption. The second is to explicitly take account of growth changes within

154 a year and growth compensation to reproduction losses. The third is not to assume a

155 steady state from very limited sampling events. We quantified long-term dynamics of

156 fish production and made direct comparisons between annual fishery harvests and fish

157 production.

158   Building on the previous development (He et al. 2015, 2016), we focused on the

159 time period from 1985 through 2016. Data sources included commercial and recreational

160 fisheries, and fishery independent surveys. The commercial fishing effort and lake trout

161 harvests were dominated by large-mesh gillnetting, and additional harvests from trap nets

162 and small-mesh gillnets were added to total annual catch in stock assessment (Brown et

163 al. 1999; Brenden et al. 2013). The recreational fishing effort and lake trout catch were

164 estimated from Michigan waters since 1985 (Su and Clapp 2013; Su and He 2013). The

165 fishery independent surveys used graded-mesh gill nets and were conducted in late April

166 through June, from the mouth of St. Marys River at northern end of the lake to the port of

167 Port Sanilac near southern end of the lake (He 2019). Hundreds of lake trout samples

168 from each of the three data sources every year had their ages assigned. For hatchery

169 stocked lake trout without a coded-wire tag, age assignments were based on a six-year

170 cycle of fin clips before 2012, and a combination of fin-clip and a maxilla or otolith

171   method in recent years. Scales were used in early years to estimate ages of juvenile wild

172   lake trout, and maxillae or otoliths were used in recent years to estimate ages of all wild

173   lake trout (Wellenkamp et al. 2015).   Biomass-based diet compositions were measured

174   periodically from lake trout samples of commercial gillnetting and recreational fisheries,

175   and every year since 1996 from samples of fishery independent annual surveys (Diana

176   1990; Dobiesz 2003; Madenjian et al. 2006; Roseman et al. 2014). In this study,

177   following He et al. (2015), all measures from individual fish were summarized for three

178   lake trout size groups: <400 mm, 400-600 mm, and >600 mm, although the differences

179   between the last two size groups were almost negligible in the most recent years (e.g.,

180   Katie Kierczynski and Brian Roth, Michigan State University, unpublished data).

181   He et al (2015) have provided a schematic presentation of our models. Below and

182   in the subsections followed, we describe specifics of each model component for the

183   synthesis of production dynamics. The main basin of Lake Huron was divided into two

184   regions (He 2019). For the descriptions of lake wide status and trends, we summarized

185   population biomass, production, and total consumption from modeling syntheses

186   conducted in each of the two regions. We also rederived growth indices by fitting growth

187   and length-mass models using lake-wide data without distinguishing the two regions as

188   we did when fitting the models to derive inputs for stock assessment and lake trout

189   bioenergetics models. The growth and length-mass models were based on data from

190   annual fishery independent spring surveys that the survey design aimed at making sample

191   distribution closely reflecting lake trout distribution in the lake (He 2019).

192

193   *Time-varying status of average individual lake trout*

194   Body mass at age was used for applying the fish bioenergetics model, and for

195   calculating biomass. The body mass was calculated from body length at age, using a

196   power function with time varying coefficient and exponent (He et al. 2008):

197          $$W_{y,a} = a_y \cdot L_{y,a}{}^{b_y} \tag{1}$$

198   where the length at age ($L_{y,a}$) was from a von Bertalanffy growth function (VBGF) with

199   time-varying parameters. The time-varying VBGF was fitted to length-at-age data and

200   described how cohort-specific growth changed every year (He and Bence 2007):

201          $$L_{y,a} = L_{y-1,a-1} + \left(L_{y,\infty} - L_{y-1,a-1}\right)\left(1 - e^{-k_{y,a}}\right) \qquad a > g + 1 \tag{2a}$$

202          $$k_{y,a} = -ln\left(\rho_{y,a}\right) \tag{2b}$$

203          $$\rho_{y,a} = \frac{L_{y,\infty} - L_{y-a+g+1,g+1}}{L_{y,\infty} - L_{y-a+g,g}} \tag{2c}$$

204   where the Ford-Walford slope ρ and growth coefficient k were determined by asymptotic

205   length L_∞ and body lengths (L) at the two youngest ages, g and $g+1$ (He and Stewart

206   2002). The body lengths (L) at the two youngest ages were estimated to vary among year

207   classes, and the asymptotic length L_∞ was estimated to vary among years.

208   The average total length at an age and year was estimated against observations of

209   individual total length at the age and year (He and Bence 2007). The average body mass

210   at an age and year was estimated against observations of individual body mass at the age

211   and year (He et al. 2008). The model implementation and the evaluation of model

212   estimates in a Bayesian framework were also reported in He et al. (2016). We used the

213   models to describe total length and body mass at age 2 and older based on data from

214   fishery independent annual spring gillnetting surveys (He 2019). Total length at age 1

215   was assumed to be a constant over years at a value of 120 mm, and the over-year vector

216 of average body mass at age 1 was calculated based on the model estimated time-varying

217 length-mass relationships.

218   Maturity schedules were determined by body size and body growth at age, based

219 on analyses of logistic regression (Appendix 1) with fishery independent survey data up

220 to 2010 (Bence et al. 2010). Annual sample sizes of recent data were not adequate for

221 updating the analyses but allowed us to conduct empirical calculation for some age

222 groups. Based on the empirical calculation available, we assumed that lake trout maturity

223 schedule in recent years did not change from previous predictions of the latest model.

224   Time-varying growth parameters were used also as indices to track lake trout

225 responses to ecosystem changes. Length at beginning of ages 2 and 3 were growth

226 indices for juveniles (age 1-2) that depend on consumption of invertebrates. After age 3,

227 length at age is determined by cohort-specific growth histories and year-specific growth

228 potential (Equations 3). Thus, asymptotic length and the body mass at a length of 700

229 mm were indices for adult and subadult lake trout that depend on consumption of prey

230 fish. In this paper, we emphasized the body mass at 700 mm of total length because its

231 turning point corresponded to the 2003 collapse of alewives, and only adult growth

232 indices were influenced by declines in the alewife and rainbow smelt abundances (He and

233 Bence 2007; He et al. 2008, 2016).

234

235 *Time-varying status of lake trout population*

236   Age-specific abundance and mortality were needed for estimating annual

237 production and consumption of prey fish, and for calculating population biomass and P:B

238 ratios. The abundance and mortality matrices were estimated from statistical catch at age

239   assessments. The total instantaneous mortality Z was year- and age-specific, and the

240   value was equal to the sum of four sources of mortality.

241    $$Z_{y,a} = F_{c_{y,a}} + F_{r_{y,a}} + M_{s_{y,a}} + M_{b_a} \tag{3}$$

242   Background natural mortality (M_{b_a}) for age 3 and older was estimated as a constant,

243   using a log scale prior mean of ln (0.1) from Brenden et al. (2011). The sea lamprey

244   induced mortality rates ($M_{s_{y,a}}$) was estimated from wounding rate

245    $$M_{s_{y,a}} = \omega_{L_{y,a}} \frac{1-p_s}{p_s} \tag{4}$$

246   where, ω is the number of wounds per fish in spring each year (April-June), and p_s is the

247   probability that a fish survives an attack (Madenjian et al. 2008b). Wounding rate was

248   observed specific to lake trout with a given length at year and age ($L_{y,a}$) and was

249   estimated as a logistic function of body length (Rutter and Bence 2003). The estimated

250   value was converted to year and age-specific rates based on annual distribution of length

251   at a given age.

252   Commercial fishing mortality ($F_{c_{y,a}}$) and recreational fishing mortality ($F_{r_{y,a}}$)

253   differed from each other in the measure of fishing effort, as well as catchability and

254   selectivity. Equations 5-7 below were applied separately by fishery, although the

255   subscript for fishery is suppressed. In general, a fishing mortality ($F_{y,a}$) was calculated as

256   a product of annual fishing effort (E_y), catchability (q_y), and age-specific selectivity ($S_{y,a}$):

257    $$F_{y,a} = E_y \cdot q_y \cdot S_{y,a} \tag{5}$$

258   Fishing efforts were taken from fishery data. Catchability was estimated as a first order

259   autoregressive process, reflecting changes in fish distribution over years along with

260   changes in the food web:

261    $$q_y = e^{\overline{lnq} + \rho(lnq_{y-1} - \overline{lnq}) + \varphi_y} \tag{6}$$

262   where $\overline{lnq}$ is the average of log scale catchability q, ρ is the autocorrelation coefficient,

263   and ψ is the deviation from the autoregressive process on log scale and was assumed to

264   follow a normal distribution with a mean of zero. Note that when ρ equals zero, the

265   process on log scale will be reduced to an average plus white noise error, and when ρ

266   equals 1.0, the process on log scale will be simplified as a random walk (Schnute 1994).

267   Selectivity was estimated as a normal function of log scale body length at age:

268
$$S_{y,a} = \frac{1}{\sigma_y\sqrt{2\pi}} exp\left(-\frac{(ln(L_{y,a})-\mu)^2}{2\sigma_y^2}\right) \tag{7}$$

269   where, σ_y is the standard deviation in year y that determines the shape of a dome-shaped

270   function of log scale fish length. $L_{y,a}$ is the mean length at age a in year y. When the log

271   scale body length is equal to μ, selectivity is at the peak of the dome-shaped curve. The

272   peak parameter was estimated on log scale $\mu = e^{ln(\mu)}$ and the shape parameter σ_y was

273   modeled to change over year as random walk (Equation 6 with $\rho=1$).

274   Population numbers at year and age were projected with the assumption of

275   exponential mortality

276
$$N_{y+1,a+1} = N_{y,a}e^{-Z_{y,a}} \tag{8}$$

277   The maximum age was set as 30 based on observations from fisheries and surveys, and

278   recruitment was estimated at age 3, as a random walk:

279
$$N_{y,3} = e^{ln(N_{y_1,3})} \qquad \text{if } y = y_1 \tag{9a}$$

280
$$N_{y,3} = e^{ln(N_{y-1,3})+\varphi_y} \qquad \text{if } y > y_1 \tag{9b}$$

281   where ψ is a deviation that describes how much the log scale recruitment changes each

282   year from the previous year. Those log scale deviations were assumed to follow a normal

283   distribution with zero mean.

284   Overall, the estimation of number and mortality at age and year, along with

285   estimation of fishery parameters, were based on modeling fits to annual harvests of

286   commercial and recreational fisheries, catch per unit effort of the fishery independent

287   surveys, and age composition from each of these three data sources. The model

288   implementation and evaluation in a Bayesian framework was first reported in Sitar et al.

289   (1999). Since then, the original model was improved and evaluated continuously, and

290   was used in fishery management annually, particularly in the 1836 Treaty ceded waters

291   (United States v. Michigan. 2000; Truesdell and Bence 2016). Note that the fits to age

292   composition allowed the model to track every year class and estimate recruitment. Each

293   of the three data sources also included hatchery-versus-wild composition based on fin-

294   clips applied to all hatchery stocked lake trout. Our model also fitted the wild-ratio-at-

295   age data with the assumption that adult and subadult mortalities were the same for

296   hatchery stocked and wild lake trout, and the wild ratio should be the same over years

297   and ages (age 3 and older) for a given year class.   Thus, the estimates of recruitment at

298   age 3 were allocated between hatchery stocked and wild lake trout.

299   To characterize long-term rehabilitation of the lake trout population and the

300   development of lake trout fisheries, we also calculated average age of fishery harvest lake

301   wide. An average age was calculated first separately for commercial and recreational

302   fishery in northern and southern Lake Huron, and standard deviation was estimated by

303   using the assessment model that fitted age composition for each fishery every year. The

304   average age of overall fisheries lake wide was calculated as a harvest-number weighted

305   average age, and its standard error was the square-root of the sum of variances of the

306   components.

307   Numbers at ages 1 and 2 were not estimated directly from the recent catch-at-age

308   assessments. In some of earlier years, when recruitment was mostly from hatchery

309   stocking of age-1 lake trout, the mortality rates at age 1 and 2 were estimated as size

310   dependent based on Gislason et al. (2010), plus the estimated random effects of stocking

311   event.   Based on those early assessments, we assumed in the current study that the

312   survival rate from age 2 to age 3 was a constant of 0.75 and the survival rate from age 1

313   to age 2 was a constant of 0.40, and thus the numbers at ages 1 and 2 were back

314   calculated from number at age 3. Potential deviation from the assumed average survival

315   rates will not influence the estimates of over-year patterns of juvenile abundance,

316   biomass, production, and food consumption (mostly invertebrates), because the vector of

317   recruitments at age 3 was estimated from the assessment model.

318

319   *Implementation of fish bioenergetics model of lake trout*

320   Daily growth ($\Delta W_{y,a,d}$) and daily food consumption ($C_{y,a,d}$) were estimated from

321   simulation of lake trout bioenergetics model that was used to fit body mass changes from

322   one year and age to the next year and age. Structures, parameters, and implementation of

323   the lake trout bioenergetics model have been well documented (Stewart et al. 1983; He

324   and Stewart 1998, Madenjian and O'Connor 1999), although a new evaluation and

325   synthesis with the recent Bayesian framework on parameter and estimate uncertainty is

326   desirable. Environmental variables for applying the model to Lake Huron lake trout were

327   taken from He et al. (2015), along with samples and data analyzed in more recent years

328   using the same methods. It was assumed that lake trout use of thermal habitats

329   (temperature profile within a year) did not change over time. At each daily step of the

330   model simulation, diet composition was assigned based on the initial body length for the

331　day that was calculated from initial body mass based on the time-varying length-mass

332　relationships (Equation 1). Invertebrates contributed a large proportion to the diet of lake

333　trout <400 mm, and prey fish contribution to the diet was modeled as linear functions of

334　body length for lake trout in this size group. As detailed in He et al (2015) and citations

335　therein, there were changes in energy density of lake trout and major prey fish species

336　over time, although there was no evidence to suggest further changes after 2010.

337

338　*The synthesis of production dynamics*

339　　　Our coupling of population dynamics and fish bioenergetics did not use a constant

340　population trajectory or a constant individual growth trajectory. Elements of the dynamic

341　processes, such as mortality and growth, were cohort specific in a time-varying

342　environment. Our models tracked these elements of all cohorts from one year and age to

343　the next year and age. For computation and data fitting of the time-varying growth

344　model, the time-varying length-mass model, the statistical catch-at-age assessments, and

345　the bioenergetics simulation of every age and year interval, we used AD Model Builder

346　(Fournier et al 2012; He et al. 2015, 2016).

347　　　Annual summary as described below was done for each of three age groups:

348　juvenile (ages 1-2), subadults (ages 3-5) and adults (age 6+), because fish production and

349　P:B ratio are typically dependent on body size and whether a fish is reproducing. Age-0

350　lake trout were not included, because the estimation of age-0 abundance, production and

351　food consumption would require another large set of investigations. We included

352　reproduction in the calculation of production. We followed the assumption that male to

353　female ratio was 1:1, and mature lake trout on average lost 6.8% of body mass at

354　spawning on the 20th of October (Stewart et al. 1983). This loss to reproduction was

355   recompensed when body mass was simulated to grow from one year and age to the next

356   year and age. The biomass was summarized on the 1st of May, which was also day 1 for

357   annual summaries of production and food consumption, because fishery independent data

358   were collected from the annual spring surveys (He 2019).

359   From the estimates of number ($N_{y,a}$) and body mass ($W_{y,a}$) at year and age,

360   biomass at the beginning of a year (B_y) was calculated as:

361                  $$B_y = \sum_{age} N_{y,a} \cdot W_{y,a} \tag{10}$$

362   Annual production (P_y) and annual food consumption (C_y) were summarized from daily

363   growth of body mass ($\Delta W_{y,a,d}$) and daily food consumption ($C_{y,a,d}$) as estimated from

364   simulations of lake trout bioenergetics model:

365                  $$P_y = \sum_{age} \sum_{d=1}^{365} N_{y,a,d} \times \Delta W_{y,a,d} \tag{11}$$

366                  $$C_y = \sum_{age} \sum_{d=1}^{365} N_{y,a,d} \times C_{y,a,d} \tag{12}$$

367   The number at age every day in a year ($N_{y,a,d}$) was calculated with the assumption that

368   total mortality (Z) was a constant over time for a given age within a year:

369                  $$N_{y,a,d} = N_{y,a} \times e^{\left(-\frac{day}{365}\right) \times Z_{y,a}} \tag{13}$$

370   We assumed normal distribution for biomass, production and total consumption.

371   The variance of a summary of biomass, $V(\hat{B})$, was calculated as:

372      $$V(\hat{B}) = \sum_{age} \left[\overline{w}_a^2 V(\hat{N}_a) + \hat{N}_a^2 V(\overline{w}_a) - V(\hat{N}_a) V(\overline{w}_a) \right] \tag{14}$$

373   where the variance of an estimated number at age, $V(\hat{N}_a)$, for age 3 and older, was from

374   SD report of the assessment model. The variance of average body mass at age, $V(\overline{w}_a)$,

375   for age 2 and older, was from SD report of the length-mass relation model. For

16

376   calculating standard deviation and variance of some model components and some overall

377   estimates (Table 1), we also applied the general variance property that, with a constant b:

378    $$sd(bX) = |b|sd(X) \tag{15}$$

379   Overall, very similar approximations of variances were used also in Bence et al. (2016).

380

381   **Results**

382   *Biomass and body mass*

383   A major turning point was that juvenile biomass dramatically declined in 2003

384   (Figure 1). The peak of juvenile biomass in 2001 led to the peak of subadult biomass in

385   2003, and the peak of adult biomass in 2006-2007. Prior to 2008, over 77% of variation

386   in adult biomass was explained by juvenile biomass with a five-year time lag, and over

387   88% of the variation was explained by subadult biomass with a three-year time lag. The

388   2003 sharp decline in juvenile biomass was closely followed by rapid decline in subadult

389   biomass, but a large decline in adult biomass did not occur until 2014, although the 95%

390   probability interval for the estimates of adult biomass increased since 2003.

391   The timing of the turning point was also approximated by the timing of a

392   substantial decline in body mass at 700 mm of total length, and no density effect on this

393   measure of condition was detected (Figure 1d). In the plot of the body mass of a 700-mm

394   lake trout versus biomass of adult and subadult lake trout, the slopes were negligible (p >

395   0.6), when two intercepts were estimated separately for two time periods. AIC

396   comparison did not support the use of a single regression line (-22 vs -36), in comparison

397   with the use of two intercepts or averages for each of the two periods of years, which

398   were sufficiently different from one another (p < 0.0002) to warrant a horizontal line fit

399   for the period of 1985-2001 and a second horizontal line fit for the period of 2002-2016.

400

401   *Consumption and P:B ratios*

402   After the collapse of alewives, annual total consumption continued to be the same

403   linear function of the biomass of adult and subadult lake trout (Figure 2a), and the same

404   linear function of adult and subadult production (Figure 2b). Thus, the decline in total

405   consumption (Figure 2c) was recipient controlled, rather than donor controlled, although

406   the contribution of major prey fish changed (Figure 2d). The total annual consumption

407   was mostly of alewives and rainbow smelts before 2003, then mostly rainbow smelt and

408   round goby (*Neogobius melanostomus*), and almost exclusively goby after 2014. The

409   total annual consumption of rainbow smelt showed substantial variations since 2003.

410   Most of variation in lake trout production was explained by lake trout biomass,

411   and the ratio of annual production to beginning-of-the-year biomass did not change after

412   the alewife collapse ($p > 0.1$; Figure 3).   For adult lake trout (age > 5), biomass

413   explained 79% of variation in production, and the P:B ratio averaged 0.22. For subadults

414   (ages 3-5), biomass explained 67% of variation in production, and the P:B ratio averaged

415   0.46. For juveniles (ages 1-2), over 74% of variation in production was explained by

416   biomass, and the average P:B ratio was as high as 2.1.

417   Based on the average age of fishery harvests (Figure 3d), adult and subadult

418   production and P:B ratios were influenced by fishery harvests. Juvenile production and

419   P:B ratio were influenced only by the natural mortality. Sea lamprey predation also did

420   not influence juvenile production and P:B ratio because juvenile body size was small and

421   sea lamprey predation rate depends on lake trout size.

422   The time-invariant average P:B ratios for adult and subadult lake trout implied

423   substantial reduction in fishing and sea lamprey induced mortalities. Otherwise, adult

424   and subadult production and P:B ratios should reflect the negative impact of substantial

425   declines in body growth and condition (e.g., Figure 1d). Among-year variations of adult

426   P:B ratio substantially increased after 2002 (Figure 3a), which was associated with the

427   fact that fishery harvest became mostly from adult lake trout after 2002 (Figure 3d). This

428   was consistent with the findings that a large decline in adult biomass was delayed until

429   2014, but uncertainty of biomass estimates increased since 2003 (Figure 1a-c).

430

431   *Production and fishery harvest*

432   Juvenile, subadult, and adult production showed distinct patterns over time

433   (Figure 4). The dynamics of subadult production followed the dynamics of juvenile

434   production, which peaked in 2000. Both subadult and adult productions, as well as

435   fishery yield, steadily declined to the lowest point by 1992, when fishery harvest was

436   mostly from subadult lake trout, and fishery yield was about the same as subadult

437   production. From 1992 through the early 2000s, when fishery yield from subadult lake

438   trout was far less than subadult production, adult biomass and production steadily

439   increased. The peak of adult production was in 2010, 3-4 years after the peak of adult

440   biomass. This was because adult production included reproduction, adult mortality was

441   sufficiently low, and lake trout older than age 6 had higher maturity and fecundity.

442   During 2004-2016, subadult production decreased to a very low level, but the

443   pressure of fishery harvest was released from subadult lake trout. Adult production

444   remained relatively stable and even continued to increase slowly, when fishery yield was

445   less than adult production. The extended long period of low juvenile and subadult

446   production, however, plus the occasionally excessive harvest, appeared to have delayed

447   effect on adult production.

448

Discussion

Impacts of food-web changes and sustainability of lake trout production

There were complex interactions in the fish community along with rapid changes in the food web. Prior to the ultimate collapse of alewives in 2003, the alewife population blocked the recruitment and production of wild lake trout (Walters and Kitchell 2001; Madenjian et al. 2008a; Riley et al. 2011), but abundant alewives and rainbow smelts also functioned as a predation buffer during the events of hatchery stocking to protect hatchery-stocked age-1 and age-0 lake trout (Johnson et al. 2015). After the alewife collapse, the increases in recruitment of wild lake trout so far did not fully compensate the loss of stocked recruitment (He 2019). Also, following the major declines in the abundance of pelagic prey fish such as alewives and rainbow smelt since the middle 1990s, the growth and body condition of adult and subadult lake trout substantially declined (He and Bence 2007; He et al. 2008, 2016).

Lake trout adult biomass and production continued to increase after the collapse of alewives in 2003. Adult biomass reached its peak in 2006-2007, adult production peaked in 2010, and lake wide large declines did not occur until 2013-2014. Prior to 2008, increases in adult biomass were mostly explained by strong year classes of hatchery-stocked recruitment. Thereafter, the effect of recruitment decline was offset to a certain degree by reduction in mortality, including the nearly complete release of harvest pressure from subadult lake trout, and reduction of fishing and sea lamprey induced mortality of adult lake trout.

Lake trout production appeared to be sustainable as evidenced also by the lack of changes in average P:B ratios. The effect of growth decline on adult and subadult

472   production was fully offset by reduction in population mortality, while body growth and

473   body condition did not continue to decline when lake trout became more and more reliant

474   on round goby as food. Potential density effects on lake trout growth were still

475   negligible, and the dynamics of total consumption continued to be recipient controlled,

476   rather than donor controlled.

477   The lesson is that fishery management may not have much control on

478   environmental changes, but has major impact on mortality, and thus on fish production.

479   Prior to 2000, based on Johnson et al. (2004, 2015), lake trout age range from fisheries

480   was 3-13 years, model estimated annual mortality at the age of peak selectivity was in the

481   range 45-63% in southern Lake Huron and 45-83% in northern Lake Huron. Since 2000,

482   lake trout age range from fisheries rapidly increased to 3-24 years, annual mortality at the

483   peak selectivity was in the range 32-45% in southern Lake Huron, and 26-30% in

484   northern Lake Huron, far below the maximum limit of 40-45% that was believed to be

485   sustainable when the recruitment and growth of lake trout were relatively stable. The

486   large reduction in mortality, particularly in northern Lake Huron, was because of

487   reduction in sea lamprey induced mortality and effective fishery regulation that was a

488   combination of harvest quota and the establishment of no-fishing zones and large areas of

489   no commercial fishing zones (He 2019).

490   A large decline in adult biomass finally occurred in 2014, after a delay of more

491   than 10 years. Thus, aggressive control of sea lamprey induced mortality and fishing

492   mortality will continue to be crucial for maintaining and further expanding the biomass

493   and production of adult lake trout. A serious concern is whether the fixed harvest control

494   rule, i.e., annual mortality of 40-45%, will continue to be closely implemented in the

495   future. Relaxation of the harvest control will likely lead to a downward trend in adult

496   biomass and production, unless recruitment increases to such a level as to fully

497   compensate for the expected increase in fishing mortality. Our findings also imply that

498   the annual mortality might need to be further reduced unless substantial increases in

499   recruitment occur soon.

500   The juvenile P:B ratio was not influenced by fishing and sea lamprey induced

501   mortality and the ratio remained as high as 2.1.   From this result, we expect that natural

502   reproduction and wild recruitment will continue to increase. We also caution managers

503   to proceed with care in making decisions to fully terminate lake trout stocking, because

504   changes in Lake Huron food web are still ongoing, the dynamics of lake trout recruitment

505   is uncertain, and a constant source of recruitment has been a key factor for the success of

506   lake trout rehabilitation in Lake Huron. We recommend that stocking success in the

507   current food-web condition can be improved with adequate use of temporal and spatial

508   heterogeneity of the food-web and habitat conditions. In Lake Huron, commercial

509   fishing efforts were still mostly driven by the harvests of lake whitefish (*Coregonus*

510   *clupeaformis*), rather than lake trout. The hatchery component of lake trout recruitment

511   may contribute substantially to protecting wild lake trout from fishery harvests, by

512   reducing migration of wild lake trout along the gradient of lake trout density, and

513   reducing the population sink in southern Lake Huron where the strength of wild

514   recruitment has become much weaker than northern Lake Huron (He 2019).

515

516   *Managing fisheries with non-stationary ecosystem variations*

517   It is well known that a sustainable fishery yield should be less than fish

518   production (Leach et al. 1987; Downing and Plante 1993; Mertz and Myers 1998), but

519   this principle has not been used routinely in fishery management. Applications of the

520   surplus production model were not built on the reality that fish populations are age

521   structured (Polacheck et al. 1993; Prager 2002; Maunder 2003), and practical harvest

522   control rules were developed and applied mostly based on stock-recruitment relationship

523   (Mace 1994; Deroba and Bence 2008; Rothschild and Jiao 2009). When an ecosystem

524   undergoes major changes in structure and function, and recruitment variations are non-

525   stationary, general guidance for using a consistent management strategy to conduct a

526   timely fishery regulation is much less clear (Jiao 2009), because the near future

527   recruitment is essentially unknown, and recognizing a new ecosystem and stock-

528   recruitment regime always requires time. While we cannot exhaust all different

529   approaches to evaluating how production and biomass relate to each other, we agree with

530   that evaluating production versus stock size is an informative complement to the

531   evaluation of sustainable harvests based on stock-recruitment relationships (Jacobson et

532   al. 2001; MacCall (2002).

533   From our model development and application, we described fish population

534   dynamics in terms of production, not just in number and biomass. The results have

535   allowed us to directly compare fishery harvest to lake trout production in the main basin

536   of Lake Huron. When the average age of annual harvest is 5 and younger, if the fishery

537   yield is less than 50% of the recent three-year average of subadult production, adult

538   biomass and production should increase rapidly. When the average age of annual harvest

539   is 6 and older, if the fishery yield is less than 50% of the recent three-year average of

540   adult production, adult biomass and production should be stable or continue to increase.

541   Note that in the above two scenarios, fish production is already influenced by fishing

542   mortality and sea lamprey predation mortality. The potential of maximum production

543   can be quantified through simulations with a range of combinations of natural mortality

544   and sea lamprey induced mortality. The simulations could also include potential density

545   dependent growth when a relationship is supported by data (e.g. Lorenzen and Enberg,

546   2001). Regardless of the status of an ecosystem, the principle that fishery harvest should

547   be less than fish production can be routinely implemented in fishery management.

548

558 **References**

559 Barbiero, R. P., Lesht, B. M., and Warren, G. J. 2011. Evidence for bottom-up control

560   of recent shifts in the pelagic food web of Lake Huron. Journal of Great Lakes

561   Research 37:78–85.

562 Beamish, R. J., Noakes, D. J., McFarlane, G. A., Klyashtorin, L., Ivanov, V. V., and

563   Kurashov, V. 1999. The regime concept and natural trends in the production of

564   Pacific salmon. Canadian Journal of Fisheries and Aquatic Sciences 56:516–526.

565 Bence, J. R., Nye, N., and He, J. X. 2010. Responses of lake trout and Chinook salmon to

566   unprecedented declines in major prey fish abundance in Lake Huron. Final

567   Report, Great Lakes Fish and Wildlife Restoration Act, FWS Agreement No.

568   301815G124. Quantitative Fisheries Center, Department of Fisheries and

569   Wildlife, Michigan State University, East Lansing, Michigan.

570   Bence, J. R., Madenjian, C. P., He, J. X., Fielder, D. G., Pothoven, S. A., Dobiesz, N. E.,

571   Johnson, J. E., Ebener, M. P., Cottrill, R. A., Mohr, L. C., and Koproski, S. R.

572   2016. Reply to comments by Riley and Dunlop on He et al. (2015). Canadian

573   Journal of Fisheries and Aquatic Sciences 73:865-868.

574   Brenden, T. O., Bence, J. R. Lantry, B. F., Lantry, J. R., and Schaner, T. 2011.

575   Population Dynamics of Lake Ontario Lake Trout during 1985–2007, North

576   American Journal of Fisheries Management 31: 962-979.

577   Brenden, T. O., Brown, R. W., Ebener, M. P., Reid, K., and Newcomb, T. J. 2013. Great

578   Lakes commercial fisheries: historical overview and prognosis for the future. In

579   Great Lakes Fisheries Policy and Management, pp 339-397. Ed. by N. J.

580   Leonard, C. P. Ferreri, and W. W. Taylor. Michigan State University Press, East

581   Lansing, Michigan.

582   Brown, R. W., Ebener, M., and Gorenflo, T. 1999. Great Lakes commercial fisheries:

583   historical overview and prognosis for the future. In Great Lakes Fisheries and

584   Policy Management: A Binational Perspective, pp. 307-354. Ed. by W. W. Taylor

585   and C. P. Ferreri. Michigan State University Press, East Lansing.

586   Chapman, D. W. 1971. Production. In Methods for assessment of fish production in fresh

587   waters. IBP Handbook 3. pp 199-214. Ed. by W. W. Ricker, Blackwell Scientific

588   Publications, Oxford, UK.

589   Claramunt, R. M., Madenjian, C. P., and Clapp, D. F. 2013. Pacific salmonines in the

590   Great Lakes basin. In Great Lakes Fisheries Policy and Management, pp 609-

591   650. Ed. by N. J. Leonard, C. P. Ferreri, and W. W. Taylor. Michigan State

592   University Press, East Lansing, Michigan.

593   Clark Jr., R. D., Bence, J. R., Claramunt, R. M. Johnson, J. E. Gonder. D. Legler, N. D.,

594   Robillard, S. R., and Dickinson, B. D. 2016. A Spatially Explicit Assessment of

595   Changes in Chinook Salmon Fisheries in Lakes Michigan and Huron from 1986

596   to 2011. North American Journal of Fisheries Management 36:1068-1083.

597   Deroba, J. J. and Bence, J. R. 2008. A review of harvest policies: understanding relative

598   performance of control rules. Fisheries Research 94:210-223.

599   DesJardine, R. L., Gorenflo, T. K., Payne, R. N., and Schrouder, J. D. 1995. Fish-

600   community objectives for Lake Huron. Great Lakes Fishery Commission. Special

601   Publication 95-1. 38 p. Ann Arbor, Michigan.

602   Diana, J.S. 1990. Food habits of angler-caught salmonines in western Lake Huron.

603   Journal of Great Lakes Research 16:271–278.

604   Dobiesz, N.E. 2003. An evaluation of the role of top piscivores in the fish community of

605   the main basin of Lake Huron. Ph.D. dissertation, Michigan State University, East

606   Lansing, Michigan.

607   Downing, D. A. and Plante, C. 1993. Production of fish populations in lakes. Canadian

608   Journal of Fisheries and Aquatic Sciences 50:110-120.

609   Eshenroder, R. L., Payne, N. R., Johnson, J. E., Bowen, C., and Ebener, M. P. 1995.

610   Lake trout rehabilitation in Lake Huron. Journal of Great Lakes Research

611   21(Supplement 1): 108–127.

612   Estes, J. A., Peterson, C. H., and Steneck, R. 2010. Some effects of apex predators in

613   higher-latitude coastal oceans. *In* Trophic Cascades: Predators, Prey, and the

614   Changing Dynamics of Nature, pp. 37-53. Ed. by J. Terborgh and J. A. Estes.

615   Island Press, Washington DC.

616   Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J.,

617   Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J.,

618   Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S.

619   A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E.,

620   Virtanen, R., and Wardle, D. A. 2011. Trophic downgrading of planet Earth.

621   Science 333:301-306.

622   Fielder, D. G., and Bence, J. R. 2014. Integration of auxiliary information in statistical

623   catch-at-age (SCA) analysis of the Saginaw Bay stock of walleyes in Lake Huron.

624   North American Journal of Fisheries Management 34: 970-987.

625   Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N.,

626   Nielsen, A., and Sibert, J. 2012. AD Model Builder: using automatic

627   differentiation for statistical inference of highly parameterized complex nonlinear

628   models. Optimization Methods and Software 27: 233–249.

629   Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. 2010. Size, growth, temperature and

630   the natural mortality of marine fish. Fish and Fisheries 11: 149-501.

631   Hayden, T. A., Holbrook, C. M., Fielder, D. G., Vandergoot, C. S., Bergstedt, R. A.,

632   Dettmers, J. M., Krueger, C. C., Cooke, S. J. 2014. Acoustic Telemetry Reveals

633   Large-scale Migration Patterns of Walleye in Lake Huron. PLoS ONE 9(12):

634   e114833. doi:10.1371/journal.pone. 0114833

635   Hayes, D. B., Bence, J. R., Kwak, T. J. and Thompson, B. E. 2007. Abundance,

636   biomass, and production estimation. *In* Analysis and interpretation of freshwater

637   fisheries data, pp. 327-374. Ed. by C. S. Guy and M. L. Brown. American

638   Fisheries Society, Bethesda, Maryland.

639   He J. X. 2019. Regions and Sub-regions of Lake Trout in the Main Basin of Lake

640   Huron. Journal of Aquatic Research and Marine Sciences 2019: 97-105.

641   He, J., and Stewart, D. J. 1998. Ontogeny of energetic relationships and potential effects

642   of tissue turnover: a comparative modeling study on lake trout. Canadian Journal

643   of Fisheries and Aquatic Sciences 55: 2518–2532.

644   He, J. X., and Stewart., D. J. 2002. A stage-explicit expression of the von Bertalanffy

645   growth model for understanding age at first reproduction of Great Lakes fishes.

646   Canadian Journal of Fisheries and Aquatic Sciences 59:250–261.

647   He, J. X., and Bence, J. R. 2007. Modeling annual growth variation using a hierarchical

648   Bayesian approach and the von Bertalanffy growth function, with application to

649   lake trout in southern Lake Huron. Transactions of American Fisheries Society

650   136: 318-330.

651   He, J. X., Bence, J. R., Johnson, J. E., Clapp, D., and Ebener, M. P. 2008. Modeling

652   variation in mass-length relations and condition indices of lake trout and Chinook

653   salmon in Lake Huron: a hierarchical Bayesian approach. Transactions of

654   American Fisheries Society 137: 801-817.

655   He, J. X., Ebener, M. P., Riley, S. C., Cottrill, A., Kowalski, A., Koproski, S., Mohr, L.,

656   and Johnson, J. E. 2012. Lake trout status in the main basin of Lake Huron,

657   1973-2010. North American Journal of Fisheries Management 32:402-412.

658 He, J. X., Bence, J. R., Madenjian, C. P., Pothoven, S. A., Dobiesz, N. E., Fielder, D. G.,

659   Johnson, J. E., Ebener, M. P., Cottrill, R. A., Mohr, L. C., and Koproski, S. R.

660   2015. Coupling age-structured stock assessment and fish bioenergetics models: a

661   system of time-varying models for quantifying piscivory patterns during the rapid

662   trophic shift in the main basin of Lake Huron. Canadian Journal of Fisheries and

663   Aquatic Sciences 72:7-23.

664 He, J. X., Bence, J. R., Roseman, E. F., Fielder, D. G., and Ebener, M. P. 2016. Using

665   time-varying asymptotic length and body condition of top piscivores to indicate

666   ecosystem regime shift in the main basin of Lake Huron: a Bayesian hierarchical

667   modeling approach. Canadian Journal of Fisheries and Aquatic Sciences 73:1092–

668   1103.

669 Healey, M. C. 1978. The dynamics of exploited lake trout populations and implications

670   for management. The Journal of Wildlife Management 42: 307-328.

671 Hile, R. 1949. Trends in the lake trout fishery of Lake Huron through 1946.

672   Transactions of American Fisheries Society 76: 121-147.

673 Jacobson, A. D., DeOliveira, J. A. A., Barange, M., Cisneros-Mata, M. A., Félix-Uraga,

674   R., Hunter, J. R., Kim, J. Y., Matsuura, Y., Ñiquen, M., Porteiro, C., Rothschild,

675   B., Sanchez, R. P., Serra, R., Uriarte, A., and Wada. T. 2001. Surplus

676   production, variability, and climate change in the great sardine and anchovy

677   fisheries. Canadian Journal of Fisheries and Aquatic Sciences 58:1891–1903.

678 Jiao, Y. 2009. Regime shift in marine ecosystems and implications for fisheries

679   management, a review. Reviews in Fish Biology and Fisheries 19: 177-191.

680   Johnson, J. E., He, J. X., Woldt, A. P. Ebener, M. P., and Mohr, L. C. 2004. Lessons in

681   rehabilitation stocking and management of lake trout in Lake Huron. *In*

682   American Fisheries Society Symposium 44, Propagated fish in resource

683   management, pp. 157–171. Ed. by M. J. Nickum, P. M. Mazik, J. G. Nickum, and

684   D. D. MacKinlay. American Fisheries Society. Bethesda, Maryland.

685   Johnson, J. E., He, J. X., and Fielder, D. G. 2015. Rehabilitation stocking of walleyes

686   and lake trout: restoration of reproducing stocks in Michigan waters of Lake

687   Huron. North American Journal of Aquaculture 77: 396-408.

688   Larkin, P. A. 1996. Concepts and issues in marine ecosystem management. Reviews in

689   Fish Biology and Fisheries 6:139-164.

690   Leach, J. H., Dickie, L. M., Shuter, B. J., Borgmann, U., Hyman, J., and Lysack, W.

691   1987. A review of methods for prediction of potential fish production with

692   application to the Great Lakes and Lake Winnipeg. Canadian Journal of Fisheries

693   and Aquatic Sciences 44 (Supplement 2): 471485.

694   Lorenzen, K., and Enberg, K. 2001. Density-dependent growth as a key mechanism in

695   the regulation of fish populations: evidence from among-population comparisons.

696   Proceedings Royal Society of London B. 269: 49-54.

697   MacCall, A. D. 2002. Use of known-biomass production models to determine

698   productivity of West Coast groundfish stocks. North American Journal of

699   Fisheries Management 22:272-279.

700   Mace, P. M. 1994. Relationships between common biological reference points used as

701   thresholds and targets of fisheries management strategies. Canadian Journal of

702   Fisheries and Aquatic Sciences 51:110–122.

703   Madenjian, C.P., and O'Connor, D.V. 1999. Laboratory evaluation of a lake trout

704   bioenergetics model. Transactions of American Fisheries Society 128: 802–814.

705   Madenjian, C.P., Holuszko, J.D., and Desorcie, T.J. 2006. Spring–summer diet of lake

706   trout on Six Fathom Bank and Yankee Reef in Lake Huron. Journal of Great

707   Lakes Research 32:200–208.

708   Madenjian, C. P., O'Gorman, R., Bunnell, D. B., Argyle, R. L., Roseman, E. F., Warner,

709   D. M., Stockwell, J. D., and Stapanian, M. A. 2008a. Adverse effects of alewives

710   on Laurentian Great Lakes fish communities. North American Journal of Fisheries

711   Management 28: 263–282.

712   Madenjian, C. P., Chipman, B. D. and Marsden, J. E. 2008b. New estimates of lethality

713   of sea lamprey (*Petromyzon marinus*) attacks on lake trout (*Salvelinus*

714   *namaycush*): implications for fisheries management. Canadian Journal of

715   Fisheries and Aquatic Sciences 65: 535-542.

716   Madenjian, C. P., Rutherford, E. S., Stow, C. A., Roseman, E. F., and He, J. X. 2013.

717   Trophic shift, not collapse. Environmental Sciences and Technology. 47: 11915-

718   11916.

719   Maunder, M. N. 2003. Is it time to discard the Schaefer model from the stock

720   assessment scientist's toolbox? Fisheries Research 61:145-149.

721   Mertz, G., and Myers, R. A. 1998. A simplified formulation for fish production.

722   Canadian Journal of Fisheries and Aquatic Sciences 55:478-487.

723   Newman, R. M., and Martin, F. B. 1983. Estimation of fish production rates and

724   associated variances. Canadian Journal of Fisheries and Aquatic Sciences

725   40:1729-1736.

726 Nieland, J. L., Hansen, M. J., Seider, M. J., and Deroba, J. J. 2008. Modeling the

727   sustainability of lake trout fisheries in eastern Wisconsin waters of Lake Superior.

728   Fisheries Research 94:304-314.

729 Polacheck, T., Hilborn, R., and Punt, A. E. 1993. Fitting surplus production models:

730   comparing methods and measuring uncertainty. Canadian Journal of Fisheries

731   and Aquatic Sciences 50: 2597-2607.

732 Prager, M. H. 2002. Comparison of logistic and generalized surplus-production models

733   applied to swordfish, *Xiphias gladius*, in the north Atlantic Ocean. Fisheries

734   Research 58:41-57.

735 Randall, R. G., and Minns, C. K. 2000. Use of fish production per unit biomass ratios

736   for measuring the productive capacity of fish habitats. Canadian Journal of

737   Fisheries and Aquatic Sciences 57:1657-1667.

738 Ricker, W.E. 1946. Production and utilization of fish populations. Ecol. Monograph 16:

739   373–391.

740 Riley, S. C., Roseman, E. F., Nichols, S. J., O'Brien, T. P., Kiley, C. S., and Schaeffer, J.

741   S. 2008. Deepwater demersal fish community collapse in Lake Huron.

742   Transactions of American Fisheries Society 137:1879-1890.

743 Riley, S. C., Rinchard, J., Honeyfield, D. C., Evans, A. N., and Begnoche, L. 2011.

744   Increasing thiamine concentrations in Lake Trout eggs from Lakes Huron and

745   Michigan coincide with low Alewife abundance. North American Journal of

746   Fisheries Management, 31:1052-1064.

747 Roseman, E. F., Schaeffer, J. S., Bright, E., and Fielder, D. G. 2014. Diets of angler

748   caught piscivores in Lake Huron reflect community-level changes following food-

749   web paradigm shift. Transactions of American Fisheries Society 143:1419–1433.

750 Rothschild, B. J. and Jiao Y. 2009. The structure of complex biological reference points

751   and the theory of replacement. Transactions of American Fisheries Society 138:

752   949–965

753 Rutter, M. A., and Bence, J. R. 2003. An improved method to estimate sea lamprey

754   wounding rate on hosts with application to lake trout in Lake Huron. Journal of

755   Great Lakes Research 29(Supplement 1): 320-331.

756 Rypel, A. L., Goto, D., Sass, G. G., and Vander Zanden, M. J. 2015. Production rates of

757   walleye and their relationship to exploitation in Escanaba Lake, Wisconsin, 1965–

758   2009. Canadian Journal of Fisheries and Aquatic Sciences 72: 834-844.

759 Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., and Walkerk, B. 2001. Catastrophic

760   shifts in ecosystems. Nature 413:591-596.

761 Schnute, J. T. 1994. A general framework for developing sequential fisheries models.

762   Canadian Journal of Fisheries and Aquatic Sciences 51:1676–1688.

763 Sitar, S. P., Bence, J. R., Johnson, J. E., Ebener, M. P., and Taylor, W. W. 1999. Lake

764   trout mortality and abundance in southern Lake Huron. North American Journal

765   of Fisheries Management 19: 881–900.

766 Smith, S. H. 1968. Species succession and fishery exploitation in the Great Lakes.

767   Journal of The Fisheries Research Board of Canada 25: 667-693.

768 Stewart, D.J., Weininger, D., Rottiers, D.V., and Edsall, T.A. 1983. An energetics model

769   for lake trout, Salvelinus namaycush: application to the Lake Michigan

770   population. Canadian Journal of Fisheries and Aquatic Sciences 40: 681–698.

771 Su, Z., and Clapp, D. 2013. Evaluation of Sample Design and Estimation Methods for

772   Great Lakes Angler Surveys, Transactions of the American Fisheries Society

773   142:234-246.

774   Su, Z., and He, J. X. 2013. Analysis of Lake Huron recreational fisheries data using

775   models dealing with excessive zeros. Fisheries Research 148:81-89

776   Truesdell, S. B., and Bence, J. R. 2016. A review of stock assessment methods for lake

777   trout and lake whitefish in 1836 Treaty Waters of Lake Huron, Lake Michigan

778   and Lake Superior. Michigan State University, Quantitative Fisheries Center,

779   Technical Report T2016-01. East Lansing, Michigan.

780   United States v. Michigan. 2000. Consent Decree. Case No. 2:73 CV 26.

781   Walters, C., and Kitchell, J. F. 2001. Cultivation/depensation effects on juvenile survival

782   and recruitment: implications for the theory of fishing. Canadian Journal of

783   Fisheries and Aquatic Sciences 58: 39–50.

784   Whelan, G. E., and Johnson, J. E. 2004. Successes and failures of large-scale ecosystem

785   manipulation using hatchery production: the upper Great Lakes experience. *In*

786   American Fisheries Society Symposium 44, Propagated fish in resource

787   management, pp. 3–32. Ed. by M. J. Nickum, P. M. Mazik, J. G. Nickum, and D.

788   D. MacKinlay. American Fisheries Society. Bethesda, Maryland.

789   Wellenkamp, W., He, J. X., and Vercnocke, D. 2015. Using maxillae to estimate ages of

790   Lake Trout. North American Journal of Fisheries Management 35:296-301.

791   **Table 1.** Calculations using the general variance property of Equation 15 which relates

792   the standard deviation of a quantity bX to the standard deviation for X. The first

793   three calculations were inputs to the summary using Equation 14. The values of

794   0.75 and 0.4 were assumed annual survival rates.

sd (bX)	b	Source of sd(X)
SD of number at age 2	1/0.75	SD of number at age 3 from SD report of statistical catch at age assessment
SD of number at age 1	1/0.40	SD of number at age 2 as calculated above
SD of body mass at age 1	$(\overline{w}_{y,1}/\overline{w}_{y+1,2})$	SD of mean body mass in year (y+1) from SD report of time-varying length-mass model
SD of annual production	year-specific P:B ratio	SD of beginning-of-the-year biomass from Equation 14
SD of annual consumption	year-specific C:B ratio	SD of beginning-of-the-year biomass from Equation 15

795

796

797   **Appendix 1** A summary of Bence et al. (2010). Changing patterns of maturity schedules

798   of lake trout in Lake Huron.

799   The probability of maturity (P) was modeled using a logistic relationship:

800
$$P = \frac{1}{1 + exp(-Z)}$$

801   where Z is a linear predictor function:

802
$$Z = a + b_1 X_1 + b_2 X_2 + \ldots + b_k X_k$$

803   and the Xi are the values of predictor variables such as fish age or length. This is the

804   standard model and assumed distribution for logistic regression, and parameter estimation

805   was accomplished using the R statistical programming language and the glm function

806   with the "binomial family" specified. We considered alternative models that included

807   different subsets of the predictor variables and we evaluated these alternative models

808   based on Akiake's Information Criterion (AIC). We used MDNR Spring gillnetting

809   survey database that provided biological data on over 56 thousand individual fish from

810   1976 through 2008. Biological data that are routinely collected include age, length (mm),

811   mass (kg), and maturity status, although not all variables were recorded for each fish.

812   Our first set of logistic regressions considered maturity to be a function of fish age

813   (year), total length (mm), body mass (kg), and condition factor (unitless). The analysis

814   only included fish samples that had no missing values for the Base4 variables (male

815   n=24,442; female n=21,475). For each sex, we evaluated all possible models with

816   different combinations of predictor variables.

817   Our second set of analyses added three region-and-year specific average growth

818   variables to the best model from the Base4 analysis. These average growth variables

819   included the increment in length (LI), the increment in body mass (WI), and the

820   instantaneous growth rate of body mass (G). Average length at age was based on a fitted

821 time-varying von Bertalanffy model (He and Bence 2007). Average body mass was

822 calculated by applying a mass versus length power function, where the coefficient and

823 exponent of the relationship were also allowed to vary over time for each region (He et

824 al. 2008). Only observations that had non-missing values for the ADD3 variables were

825 used, so sample sizes were further reduced from BASE4 analyses (male n=24,027;

826 female n=21,131).

827   A third set of logistic regressions were referred as "ADD6" that added six region-

828 and-year specific average growth variables to the best model from the Base4 analyses. In

829 addition to LI, WI, and G in "ADD3", we further considered changes in the average

830 growth. For example:

831 $$LI2_{a,y} = LI_{a-1,y-1} - LI_{a,y}$$

832 WI2 and G2 were defined similarly. We considered all possible combinations of the six

833 growth variables (LI, WI, G, LI1, WI2, G2). Only observations that had non-missing

834 values for all 10 potential predictor variables were used, so sample sizes were further

835 reduced (male N = 22,668; female N = 19,897).

836   The best models from the BASE4, ADD3, and ADD6 groups produced

837 qualitatively similar predictions of how maturity schedules have changed over time. Our

838 analyses also provided a more comprehensive understanding of the relationship between

839 maturity schedule and predictor variables (Table A1). When considering only variables

840 available from individual measurements (BASE4 analyses), the best model contained all

841 four variables (fish age, length, mass, and condition factor) for both sexes, and this model

842 was far superior over any of those reduced models (ΔAIC > 40). Estimated coefficients

843 for length, age, and condition were all positive for both sexes, as was expected, indicating

844 that longer and older fish that were heavy for their length had a greater probability of

845 mature (table below). Somewhat counter-intuitively, the coefficient for body mass was

846 negative. It should be kept in mind, however that this is the effect of mass in concert

847 with other variables. When considering models with average growth variables (ADD3

848 analyses), the model included all three growth variables added was superior over any of

849 reduced models (ΔAIC > 13). Increment in length and increment in body mass had

850 negative coefficients whereas the coefficient for instantaneous growth in body mass was

851 positive. Given that instantaneous growth rates tend to be largest for smaller fish and

852 vary the most for these fish, this differential response allows smaller versus larger fish to

853 respond to growth conditions in different ways. When considering models that included

854 changes in growth variables (ADD6 analyses), there were multiple competitive models,

855 with ΔAIC < 10. From the best (lowest AIC) model, G was only included for males, as

856 was seen in the ADD3 model. The coefficient for WI2 was positive for both sexes. The

857 coefficient for LI2 was positive for females. For males the coefficient was nominally

858 negative, but its magnitude was small and uncertain (SE about the same as estimate).

859   To construct matrices of mature proportion at age over time, our approach was to

860 first calculate average values of the probability of maturation for each age and year on a

861 management unit and sex basis using the best logistic model (from ADD6). These results

862 were supplemented by similar estimates based on the best ADD3 model for age 2.

863 Proportions mature for age-1 were assumed to be zero and proportions mature for ages 13

864 and older were assumed to be 1.0. A few anomalous values based on small sample sizes

865 were treated as though missing. The resulting matrix had missing values that were filled

866 in by using averages from adjacent years, or interpolation over gaps of several years.

867 Once this preliminary matrix was generated for each sex it was smoothed by using a

868   three-year centered average (with first and last year using the average of first three or last

869   three years, respectively).

870 **Table A1.** Parameter estimates from best logistic regression models for lake trout chosen

871   by AIC. L is fish total length (mm), W is fish mass (kg), C is condition factor, LI

872   is growth in length, WI is growth in mass, and G is instantaneous growth in mass.

873   Changes in growth are denoted by a "2" after corresponding growth variable.

874

	Males			**Females**	
Best BASE4 model					
	Estimate	SE		Estimate	SE
Intercept	-30.327	1.135	Intercept	-23.831	1.269
Age	0.453	0.023	Age	0.921	0.026
L	0.047	0.002	L	0.029	0.002
W	-2.185	0.183	W	-1.037	0.171
C	5.625	0.383	C	3.043	0.448
Best ADD3 mode					
	Estimate	SE		Estimate	SE
Intercept	-30.25	1.166	Intercept	-22.426	1.271
Age	0.252	0.037	Age	0.605	0.041
L	0.05	0.002	L	0.031	0.002
W	-2.262	0.187	W	-1.011	0.17
C	6.4	0.381	C	3.702	0.432
LI	-0.023	0.003	LI	-0.021	0.004
WI	-1.36	0.179	WI	-1.694	0.193
G	1.785	0.215	G	1.351	0.325
Best ADD6 model					
	Estimate	SE		Estimate	SE
Intercept	-28.413	1.272	Intercept	-20.216	1.288
Age	0.282	0.04	Age	0.431	0.046
L	0.048	0.002	L	0.03	0.002
W	-1.879	0.205	W	-0.866	0.173
C	5.99	0.418	C	3.693	0.44
LI	-0.017	0.004	LI	-0.022	0.003
WI	-2.969	0.214	WI	-2.012	0.233
G	0.37	0.324	LI2	0.021	0.003
LI2	-0.0011	0.0013	WI2	1.545	0.199
WI2	3.242	0.22	G2	-0.558	0.228

875

Figure captions

Figure 1. Dynamics of beginning-of-the-year biomass and a decline in adult body mass:
a) Juvenile biomass (ages 1-2). b) Subadult biomass (ages 3-5). c) Adult biomass
(age > 5). d) Body mass at total length of 700 mm plotted against beginning-of-the-
year biomass of adult and subadult lake trout. In the plots a-c), dots and solid lines
are average estimates of the biomass, dashed lines are 95% probability intervals. In
panel d), dots represent average estimates of the body mass prior to 2002, open
circles represent average estimates of the body mass for the rest of years, the distance
between a pair of gray bars represents 95% probability intervals of an annual
estimate, and horizontal lines represent the average within a period of years or the
intercept of a regression line with the slope equal to zero.

Figure 2. Annual total consumption by lake trout. a) The relationship between annual
consumption and beginning-of-the-year biomass of adult and subadult lake trout. b)
The relationship between annual consumption and annual production of adult and
subadult lake trout. In both panels a-b, dots represent average estimates of annual
consumption prior to 2003. Open circles represent the average estimates after 2002.
The regression line in each panel was based on all estimates in the time series. c)
Average estimates of annual consumption (dots and solid line) with 95% probability
intervals (dashed lines). d) Annual consumption of prey fish partitioned among prey
fish species, including alewives (alew), rainbow smelt (smlt), sculpins (sclp), and
other fish species (other), which includes sculpins, sticklebacks, and coregonines.

899 **Figure captions** (continued)

900 **Figure 3.** The relationships between annual production and beginning-of-the-year

901   biomass of a) adult, b) subadult, and c) juvenile lake trout. Dots represented

902   average estimates of annual production prior to 2003. Open circles represent

903   those after 2002. The regression line in each panel was based on all estimates in

904   the time series. Also, d) The average age of lake wide fishery harvests (diamonds

905   and the solid line) with 95% probability intervals (dashed lines).

906

907 **Figure 4.** Average estimates of annual production (dots and solid lines) with 95%

908   probability intervals (dashed lines). a) Juvenile (age 1-2) production. b) Subadult

909   (age 3-5) production compared with fishery yield mostly from subadult lake trout

910   (open squares and the line). c) Adult (age > 5) production compared with fishery

911   yield mostly from adult lake trout (open circles and the line).

912