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Using time-varying asymptotic length and body condition of top piscivores to indicate ecosystem regime shift in the main basin of Lake Huron: a Bayesian hierarchical modeling approach

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Abstract:

We evaluated the ecosystem regime shift in the main basin of Lake Huron that was indicated by the 2003 collapse of alewives, and dramatic declines in Chinook salmon abundance thereafter. We found that the period of 1995-2002 should be considered as the early phase of the final regime shift. We developed two Bayesian hierarchical models to describe time-varying growth based on the von Bertalanffy growth function and the length-mass relationship. We used asymptotic length as an index of growth potential, and predicted body mass at a given length as an index of body condition. Modeling fits to length and body mass at age of lake trout, Chinook salmon, and walleye were excellent. Based on posterior distributions, we evaluated the shifts in among-year geometric means of the growth potential and body condition. For a given top piscivore, one of the two indices responded to the regime shift much earlier than the 2003 collapse of alewives, the other corresponded to the 2003 changes, and which index provided the early signal differed among the three top piscivores.

Key Words: regime shift, time-varying growth and body condition, Bayesian

hierarchical modeling and inference, top predator and ecosystem stability, and

fisheries management

Introduction

Ecological variation has been interpreted often as random events from a statistical distribution, but could be further signified by changes in parameters of the distribution. By the late 1980s, quantifying random variation was well established as a foundation of fisheries management, whereas most changes were often assumed to be captured by functional relationships such as the relationship between recruitment and the size of spawning stock (Hilborn and Walters 1992; Quinn II and Deriso 1999). It has remained much more challenging to understand changes in parameters of a distribution, which may reflect regime shifts or major changes in the structure and function of an ecosystem (Beamish et al. 1999; Chavez et al. 2003; Vert-pre et al. 2013).

A regime shift has often been described as a large, abrupt, and long-lasting change in an ecosystem (Scheffer et al. 2001; Biggs et al. 2009). Very few studies have detected early signals before abrupt changes are observed in the population abundances of major fish species. We believe that finding early signals is essential for understanding a regime shift. Prior to the abrupt change in population abundance or even stock collapse, there should be early indications that some major fish species are unable to sufficiently adjust to the increment of changes in the ecosystem.

Large changes have been observed in many ecosystems such as the Laurentian Great Lakes (Smith 1968; Vanderploeg et al. 2002). In the main basin of Lake Huron, one of the Laurentian Great Lakes, the most recent changes included the 2003 collapse of a dominant prey fish species alewives (*Alosa pseudoharengus*), a major decline in the abundance of the second prey fish species rainbow smelt (*Osmerus mordax*), and consequently the dramatic decline in Chinook salmon (*Oncorhynchus tshawytscha*)

abundance, which was the dominant piscivore before the collapse of alewives (Riley et al. 2008; Brenden et al. 2012; Bence and He 2015).

The other two top piscivores in Lake Huron are lake trout (*Salvelinus namaycush*) and walleye (*Sander vitreus*). Lake trout is the native top piscivore. Walleye is the native top piscivore in the Saginaw Bay of Lake Huron and near shore cool waters of the main basin. By the end of 1940s, fishing combined with predation by the invasive sea lamprey (*Petromyzon marinus*) led to high mortality and extirpated lake trout from Lake Huron (Hile 1949; Coble et al. 1990; Eshenroder et al. 1992). Habitat loss and impacts of exotic species also depressed walleye at about the same time (Schneider and Leach 1977). Alewives, also an invasive species from Atlantic Ocean, proliferated after the loss of top piscivores in the ecosystem (Smith 1968; Berst and Spangler 1972; Christie 1974), and generated adverse effects on natural recruitment of many native fish species (Walters and Kitchell 2001; Madenjian et al. 2008).

Chinook salmon is a piscivore introduced into Lake Huron, concurrently with the rehabilitation efforts for lake trout and walleye (Whelan and Johnson 2004). For more than 30 years until 2003, the salmonine fisheries in Lake Huron were similar to those in Lakes Michigan and Ontario, where trophic relationships were relatively stable and dominated by the interaction between alewives and Chinook salmon (Stewart et al. 1981; Madenjian et al. 2002; Mills et al. 2003; Dobiesz et al. 2005). The 2003 collapse of alewives, and then the dramatic decline in Chinook salmon abundance in Lake Huron, was abrupt and triggered new debates on fishery management strategy (Eshenroder and Burnham-Cutis 1999; Dettmers et al. 2012, 2014; Claramunt and Clapp 2014).

96 The collapse of alewives and the dramatic decline in Chinook salmon abundance
97 clearly indicates a regime shift (Bence et al. 2008; Riley 2013; Madenjian et al. 2013).
98 He et al. (2015) further suggested that the trophic interaction between alewives and
99 Chinook salmon was destabilized much earlier. Before alewives collapsed in 2003, there
100 were stepwise declines in the abundance of alewives and rainbow smelt combined (Fig.
101 1). The 2003 decline was proportionally the largest (82% of biomass) and brought the
102 stock to an almost negligible level, but the absolute magnitude of the decline (38.7 kt)
103 was much less than the declines during 1994-1996 (85.5 kt). Early studies and
104 management activities did not consider the major decline during 1994-1995 as a signal of
105 regime shift that was underway or forthcoming, probably because the emphasis was on
106 the dynamics of trophic interaction, and the large 1994-1996 decline in prey biomass was
107 not the first in the time series. Another potential reason was that, although directly
108 relying on the alewife and rainbow smelt abundance, Chinook salmon abundance did not
109 show a rapid major decline between 1995 and 2003 (Dobiesz et al. 2005; He et al. 2015).

110 The issue here has broad implications and can be summarized and generalized as
111 the follows. Prior to the dramatic decline in the abundance of the dominant piscivore in
112 responses to the final collapse of the dominant prey fish, early declines in prey abundance
113 might have sent a signal of the impending regime shift, but piscivores responses directly
114 corresponding to the early change were not recognized, and thus implications for
115 fisheries management were impossible to be recognized. To identify and understand
116 early impact on top piscivores of the impending regime shift, we also have to distinguish
117 the early start from other large variations in the ecosystem. For example, once we know

the responses of top piscivores, are there any differences among those responses to the 1990, 1995, and 2003 declines in prey fish abundance, respectively (Fig. 1)?

Our objective was to evaluate the hypothesis that time-varying growth parameters and body condition of top piscivores could be effective sensors of complex ecological changes, and could be used as early indications of an impending regime shift, prior to abrupt changes in predator abundances with dramatic fishery consequences. From the pattern of prey abundance over years (Fig. 1), a shift in among-year geometric means of growth potential and body condition might have occurred during 1994-1996 and 2002-2003, or soon after each of these times. Changes corresponding to the 1994-1996 declines in prey biomass, or through the period of 1996-2002, would mean that that body growth and condition could have been used to predict subsequent changes at the population level. We did not expect to see a major change corresponding to the 1990 decline in prey abundance, although we do need to give this an objective evaluation. Given the differences in their reliance on the declined prey fish abundance, and their capabilities of switching to alternative prey, we expected that top piscivores might have different responses to the early phase and the final regime shift.

Materials and methods

We built on recent development in modeling fish growth and separated apparent variations in fish length at age into process and observation errors (Pilling et al. 2002; Szalai et al. 2003; Helser et al. 2007; He and Bence 2007; Jiao et al. 2010). Process errors are variations in growth over time that can be captured by variations in growth

parameters. Observation errors are reflected by residuals between observed values and model predictions.

We used a cohort-and-year effect model in modeling individual growth of lake trout, Chinook salmon and walleye. We then used annual estimates of asymptotic length as an index of fish growth potential and evaluated how growth potential changed over time for the three top piscivores. He and Bence (2007) compared four growth models for lake trout in Lake Huron, including a time-invariant model, a year-effect model, a cohort-effect model, and a model that combined cohort and year effects. Their model comparisons were based on Deviance Information Criterion, an information theoretic approach for Bayesian models, similar to Akaike Information Criterion (Spiegelhalter et al. 2002), and their results strongly supported the model that integrated both cohort and year effects. Notice that both cohort and year effects reflect process errors.

In modeling the length-mass relationship (LeCren 1951; Froese 2006), we also separated process and observation errors (Szalai et al. 2003; Lai and Helser 2004; He et al. 2008). We then followed Winters and Wheeler (1994), and He et al. (2008), to use body mass at 700, 600, and 500 mm as condition indices for lake trout, Chinook salmon, and walleye, respectively. We used body mass at different sizes for the three fish species based on results from previous studies. In comparison with relatively small individuals, early studies indicated that the growth and condition of large-sized lake trout and walleye were more responsive to changes in prey supply (Mason et al. 1998; He et al. 2015). In contrast, Peters et al. (2007) found that the energetic status of small-sized Chinook salmon were more responsive than larger ones in response to changes in prey supply.

The data

We used lake trout data for 1976-2013 from spring gillnetting surveys in the main basin (He et al. 2012), Chinook salmon data for 1983-2013 from summer biological monitoring of recreational fisheries (He et al. 2008), and walleye data for 1989-2013 from fall gillnetting surveys in Saginaw Bay (Fielder and Thomas 2014). The total number of fish over years with both age and length measured, and the minimum and maximum annual number of such fish were 40145, 291, and 2197 for lake trout; 12927, 98, and 1216 for Chinook salmon; and 6907, 77, and 601 for walleye. The total number of fish over years with both length and weight measured, and the minimum and maximum annual number of such fish were 47177, 293, and 2674 for lake trout; 7419, 54, and 530 for Chinook salmon; and 8816, 116, and 698 for walleye.

Age-assignment methods differed among the three top piscivores. Scales were used for aging Chinook salmon, which have been shown in the Great Lakes to provide valid ages for known-age fish (Wesley 1996). For walleye, we used dorsal spines, a widely used standard method (Margenau 1982). Until 2012, age assignment to stocked lake trout was mostly based on year class information from fin-clips or a coded wire tag (CWT; Elrod and Schneider 1986). Since 2012, age assignment to a stocked lake trout without an implanted CWT was based on the combination of fin-clip and interpretation of scales, otolith sections, or maxilla sections (Wellenkamp et al. 2015). One of the three calcified structures was used to estimate the age of a wild lake trout, depending on the year of sample collection and the fish size. Quality control in age assignments that fully rely on calcified structure has been an ongoing process since the recent increases in the

number of old lake trout and recruitment of wild lake trout (He et al. 2012; Wellenkamp et al. 2015).

Modeling time-varying length at age and body mass at length

Length at age was modeled using the von Bertalanffy growth function (Brody 1927; von Bertalanffy 1938), with time-varying parameters (He and Bence 2007):

$$L_{y,a} = L_{y-1,a-1} + (L_{y,\infty} - L_{y-1,a-1})(1 - e^{-k_{y,a}}), \quad a > g + 1 \tag{1}$$

$$k_{y,a} = -\log_e(\rho_{y,a}) \tag{2}$$

$$\rho_{y,a} = \frac{L_{y,\infty} - L_{y-a+g+1,g+1}}{L_{y,\infty} - L_{y-a+g,g}} \tag{3}.$$

Here, y indicates year, a indicates age, ∞ represents the age of infinite old, and growth is from one year and age to the next year and age (Fabens 1965). The year-specific L_{∞} reflects the current growth potential, applicable to all age groups of fish in the year, and the length at a given age and year reflects the cohort specific growth history plus the growth influenced by the current growth condition. The growth coefficient k is derived from a year-specific asymptotic length L_{∞} and cohort specific length at age g and $g+1$, where g is the youngest age included in the growth model. This is a time-varying realization of the concept embodied in the von Bertalanffy growth function such that growth in early life and the current growth potential jointly define the Ford-Walford slope ρ and thus the growth coefficient k (Ricker 1979; He and Stewart 2002).

With time-invariant parameters, equations 1-3 can be simplified as:

$$L_a = L_g + (L_{g+1} - L_g) \frac{1 - \rho^{a-g}}{1 - \rho} \tag{4}.$$

This parameterization of the von Bertalanffy growth function was developed by Schnute and Fournier (1980), and further specified by He and Stewart (2002). We assumed time-invariant growth prior to the first year for which we had data, and thus used equation 4 to determine length at age in the first year. Following the same assumption, for those cohorts that were older than g in the first year, the same constant values of L_g and L_{g+1} were retained when the growth in subsequent years were calculated using equations 1-3 with time-varying L_∞ . In this paper, the youngest age was 2 for lake trout and 1 for Chinook salmon and walleye.

Body mass at a given body length was modeled as a power function with time varying coefficient and exponent (Szalai et al. 2003; Lai and Helser 2004; He et al. 2008):

$$W_{y,L} = a_y L^b \quad (5).$$

Here, W is body mass (kg), L is body length (mm), y indicates year, and a and b are the two time-varying parameters.

When fitting the growth model (Eqs. 1-4) or the length-mass model (Eq. 5), we did not directly estimate time-varying parameters, but rather estimated the log-scale means and annual deviations from the means:

$$\theta_y = e^{\overline{\log_e(\theta)}} \cdot e^{\varepsilon_{\theta,y}} \quad (6).$$

Here, y indicates year, θ represents one of the three growth parameters (L_∞ , L_g , L_{g+1}), or one of the two length-mass parameters (a , b), and ε is the process error, a deviation from the average of a log-scale parameter.

Bayesian hierarchical inferences

To obtain point estimates of parameters, and thereby predict length at age and year, or body mass at length and year, we minimized the objective function of our model, which was the negative log overall posterior density. The log overall posterior density was the sum of the log likelihood of data, the joint log density of parameters (priors), and the joint log density of hyper parameters (hyper priors).

We described each component of the objective functions and how we evaluated uncertainty from posterior distribution in the Appendix. In summary, (1) growth or length-mass parameters, including both the log scale means and process errors (Eq. 6) were assumed to have normal distributions. We allowed for correlations among the growth parameters, L_{∞} , L_g , and L_{g+l} (Eqs. 1-3), or between the length-mass parameters, a and b (Eq. 5), and thus the log-scale means and process errors were more specifically assumed to have multivariate normal distributions. (2) To determine the variance-covariance matrices that govern the multivariate normal distributions, we separately estimated the two components of each matrix: the correlation coefficients and standard deviations. The standard deviations were estimated on the log scale, and the correlation coefficients were estimated on Fisher's zeta scale (Fisher 1915; Zar 1999). Both were assumed to have normal distributions. (3) Observed log scale length at age or weight at length was also assumed to have normal distributions. We allowed for variance heterogeneity and estimated residual standard deviations by age for the growth model (Eqs. 1-4), and by size group for the length-mass model (Eq. 5). All of these standard deviations for observation errors were estimated on the log scale, with assumed normal distributions.

We evaluated modeling fits to the data, and estimated potential change points over years in asymptotic length and body mass at a given length. A full Bayesian change point analysis (CPA; Carlin et al. 1992) is yet to be implemented in our models, as discrete change points are notoriously challenging to be estimated (Brenden and Bence 2008), and this is especially true for nonlinear state space models like ours. In lieu of the CPA, we used the R Package ‘strucchange’ (Zeileis et al. 2015) to analyze the annual point estimates obtained from our growth and length-mass models. We used Bayesian Information Criterion (BIC) to define change points, as Akaike Information Criterion (AIC) often overestimates the number of change points (Zeileis et al. 2003). We used both BIC and AIC to compare alternative options for describing our time series, including a constant geometric mean, a linear trend, linear trends with one or more change points, and stepwise declines in the means. We then returned to our Bayesian hierarchical models to define Bayesian credibility intervals for the best descriptions of those distinct periods as identified by the CPA. The Bayesian credibility interval is a Bayesian statistic analogous to frequentist confidence intervals (Berger 1985; Bernardo and Smith 1994; Gelman et al. 2004). For example, to distinguish a major shift in the means from large random variations, we calculated geometric means before and since the year identified, and summarized their 95% Bayesian credibility intervals from posterior distributions. We expected all major shifts in piscivore body growth and condition to closely follow the pattern of prey biomass declines and to assist the comparison and evaluation we also conducted the CPA on the time series of prey biomass over years (Fig. 1).

Results

The modeling fits for length at age and body mass at age were excellent for all of three top piscivores (Fig. 2). As described in the method section, our models used many data from individual fish collected over years. To provide a concise comparison between model predictions and observations, we used geometric mean length and body mass for those ages in a year with ten or more observation. We compared those observations with corresponding model predictions of length and body mass at the age and year. The predicted body mass at age was calculated from the estimated length-mass relationship and the observed geometric mean length at age and year.

Asymptotic length L_{∞} had no or weak correlation with body length at the two youngest ages, L_g and L_{g+1} . For lake trout the 95% credibility intervals for the correlation coefficients were (-0.58, 0.12) and (-0.40, 0.31), and both overlapped zero. Similarly, for Chinook salmon, the intervals were (-1.37, 0.55) and (-1.28, 0.58), and also overlapped zero. For walleye, the intervals were (0.04, 0.78) and (0.02, 0.74), and suggested modest positive correlations. In contrast, for all of the three top piscivores, body lengths at the two youngest ages were positively correlated to each other, and the 95% credibility intervals were (0.82, 0.97), (0.88, 1.0) and (0.81, 0.97) for lake trout, Chinook salmon and walleye, respectively.

Also for all of the three top piscivores, the coefficient and exponent of the length-mass relationships had strong inverse correlations. The 95% credibility intervals for the correlation coefficients were (-1.0, -0.99), (-1.0, -0.99), and (-1.0, -0.91) for lake trout, Chinook salmon and walleye, respectively.

There was at least one major shift in each time series of point estimates from our models, including both piscivore growth potential and body condition (Fig. 3; Table 1). Those shifts corresponded to, or closely followed, the major decline in prey biomass during 1994-1996 and 2002-2003 (Fig. 1; Table 1). For Chinook salmon body condition, the CPA estimated three change points as 1996, 2003 and 2008. The second and third change points separated the years with the lowest body condition from initial declines during 1996-2002 and recent recoveries of 2008-2013. The single change point for a two-period analysis was the same as the first change point, 1996, and the recent peak of Chinook salmon body condition was still below the among-year average before the first change point. For walleye body condition, the CPA estimated two change points as 1992 and 2004. In this case, further model comparisons included three periods, as a two-period analysis would estimate a single change point between 1992 and 2004, which was inadequate. Finally, for all six time series from our models, BIC favored stepwise declines in geometric means, in comparison with a constant mean, a linear trend, or linear trends with change points (Table 1). This was consistent with the stepwise declines in prey biomass (Fig. 1; Table 1). For five out of the six time series, AIC also favored stepwise declines. The only exception was lake trout body condition, where AIC suggested three change points, instead of one, and favored trends between the change points, rather than abrupt changes.

Lake trout asymptotic length had substantial variation among years (Fig. 3). Before the change point 1998 (Table 1), the geometric mean was 834 mm, and since 1998 was only 742 mm. The posterior distributions for those means were distinct and did not overlap. Prior to 1998 the 95% credibility interval was 818-849 mm, and since 1998

the interval was 736-737 mm. The timing of the shift was 5 years before the 2003 collapse of alewives, and two years after the 1994-1996 decline in the abundance of two dominant prey fish species, alewives and rainbow smelt (Fig. 1).

Lake trout body condition was stable until the change point 2002 (Fig. 3; Table 1), and the shift toward a low level occurred right before the 2003 collapse of alewives (Fig. 1). Before 2002, the geometric mean of body mass at 700 mm had a 95% credibility interval of 3.66-3.68 kg, and since 2002 the interval was 3.30-3.32 kg.

Chinook salmon asymptotic length also had a major decline in 1997 and 1998, but then increased back to the previous level in 1999 and remained at that level until the change point 2003 (Fig. 3; Table 1). Before 2003, the among-year geometric mean was 1055 mm, and since 2003 was only 955 mm. The posterior distributions for the means did not overlap between the two periods, although there were large variations before and since 2003. Prior to 2003 the 95% credibility interval was 1031-1080 mm, and since 2003 the interval was 921-990 mm. The timing of the shift matched the 2003 collapse of alewives (Fig. 1).

Chinook salmon body condition declined to the lowest values after the alewife collapse, but then steadily increased from 2004 until 2011. With the data from the most recent years added, it became clear that the shift toward a low level actually started at the first change point 1996 (Fig. 3; Table 1). Before 1996, the geometric mean of body mass at 600 mm had a 95% credibility interval of 2.25-2.30 kg, and since 1996 the interval was 1.99-2.03 kg. The timing of the shift was 7 years before the 2003 collapse of alewives, but closely followed the 1994-1996 declines in the abundance of the two dominant prey fish species, alewives and rainbow smelt (Fig. 1).

Walleye asymptotic length had a geometric mean of 630 mm before the change point 2004, and 572 mm since 2004 (Fig. 3; Table 1). The change was less distinct visually because of the large variation since 2004. Nevertheless the difference was identified by the CPA, and the posterior distributions supported a real difference in geometric means between the two periods: prior to 2004 the 95% credibility interval was 608-653 mm, and since 2004 the interval was 550-594 mm.

The two change points in walleye body condition were 1992 and 2004 (Fig. 3; Table 1). The first was two years after a decline in prey biomass in 1990, although this decline in prey biomass was not identified as a change point by the CPA; the second was right after the 2003 collapse of alewives (Fig. 1; Table 1). We suspected another shift at 1998 based on visual inspection of the point estimates (Fig. 3), but this was not confirmed by the CPA. Between 1992 and 2003, the geometric mean of body mass at 500 mm had a 95% credibility interval of 1.19-1.20 kg, before 1992 the interval was 1.28-1.30 kg, and since 2004 was 1.09-1.10 kg.

Discussion

At the individual level, the major shift in piscivore body growth and condition closely corresponded to major prey biomass declines during 1994-1996 and 2002-2003. At the population level, a dramatic decline in Chinook salmon abundance followed the 2003 collapse of alewives. These findings suggested that the 2003 abrupt change in the trophic interaction was a response to long term ecosystem changes, to which major top piscivores had much earlier responses at the individual level.

361 Lake trout responded to the 1994-1996 declines in prey supply with reduced
362 growth potential in body length, but stable body condition. After the ultimate collapse of
363 alewives, lake trout body condition declined to a lower level, but natural recruitment
364 rapidly increased to a much higher level (He et al. 2012). In contrast, Chinook salmon
365 responded to the 1994-1996 declines in prey supply with major declines in body
366 condition. The estimated potential for body length growth was also low during 1997-
367 1998, but then returned to the previous level and did not decline until the final collapse of
368 alewives in 2003. The responses of lake trout and Chinook salmon reflected differences
369 in their abilities to adjust to a major trophic shift. Chinook salmon continued to direct
370 energy toward growth in body size, when prey supply substantially declined. He et al
371 (2008) interpreted the responses by Chinook salmon after 2003 as an indication that the
372 system was no longer able to support abundant Chinook salmon. In fact, relative to lake
373 trout, the contribution of Chinook salmon to total piscivore biomass and their total
374 consumption of prey fish already started to decrease during 1995-2002 (He et al. 2015).

375 There were some general similarities between walleye and Chinook salmon in
376 how body growth and condition changed over years. Walleye also showed the earliest
377 decline in body condition after the 1990 decline in prey biomass, probably because
378 walleye were more dependent on alewives than Chinook salmon and lake trout when
379 alewives dominated the prey fish community (He et al. 2015). Relative to other walleye
380 populations (Murphy et al. 1990), however, walleye body condition might not be
381 considered low at any point of the time series. This was also true for lake trout, when
382 comparing the body condition to that of Lake Superior lake trout (Michigan Department
383 of Natural Resources, unpublished data). At the population level, walleye abundance

increased substantially due to near elimination of the deleterious effects of alewives on natural recruitment since 2004 (Fielder et al. 2007; Fielder and Bence 2014). The increases in walleye abundance were much faster than those of lake trout, as walleye have relatively shorter life span and younger age at first reproduction. The different responses at the population level between walleye and Chinook salmon reflected a fact that walleye effectively switched to feeding on benthic prey fish such as round goby (Roseman et al. 2014; He et al. 2015).

For lake trout after 2007, and Chinook salmon after 2005, there were increases in body condition through 2011, although the peak reached by 2011 was much lower than the early peak levels. Walleye body condition in general did not increase after the alewife collapse in 2003. For Chinook salmon, the increase in body condition occurred when they had very low population abundance (Brenden et al. 2012; Bence and He 2014), and they may also have been feeding outside the main basin of Lake Huron (Richard Clark, Michigan State University, personal communication). Lake trout were able to feed on alternative prey, like walleye, but occupied a much wider habitat range than walleye (e.g., forage everywhere in the lake, Eshenroder et al. 1995).

As regime shifts indicate major changes in the structure and function of an ecosystem, they create large challenges to fisheries management (DeYoung et al. 2008; Jiao 2009). In Lake Huron, the major changes in the 1990s followed the new invasion of *Bythotrephes* in the late 1980s and dreissenid mussels and round goby (*Neogobius melanostomus*) in the early 1990s. Those new invasions started to alter the food-web dynamics dominated by fish species such as alewives, rainbow smelt, and Chinook salmon (Stetter et al. 2005; Bunnell et al. 2014; He et al. 2015). Alewives could not

adapt to the recent changes because of a continued high predation pressure (He et al. 2015). Lake trout, Chinook salmon, and walleye all had early responses to the long term process at the individual level, although the timing and the actual responses differed among these top piscivores. From the results of the CPA (Table 1), the period of 1995-2002 should be considered as the early phase of the final 2003 regime shift.

Our findings have clear management implications. First, at the individual level top piscivores may respond to the regime shift far before abrupt changes in the abundance of the dominant piscivore can be observed. While detecting and confirming the regime shift may need extra years of observation, our results suggest that when a major index of body growth and condition falls below the previous credibility interval for more than two consecutive years this should be considered as a warning that the system may be in the midst of changes that could lead to a sudden and long-lasting change in the fish community and fisheries (Walters 1987). Early detection of the impending regime shift can be used to adjust harvest levels or temper expectations (Clark 2012).

Second, major top piscivores have different life histories and may respond to a regime shift differently. Management cannot always rectify or reverse a large scale regime change, but can adapt to it by building on the natural adjustments that reflect life histories and feeding ecologies of the species in the fish community. The overall management strategy should include managing diverse fishing opportunities (Folke et al. 2004). For example, He et al. (2015) discussed different trophic interactions between piscivores and their prey in Lake Huron during two time periods. In the first period, they suggested that the alewife abundance was sufficiently high, and it was difficult to eliminate the invasive prey fish and their adverse effects on recruitment of native fish

species. They further suggested that under such conditions the best fishery inevitably relied on the most effective piscivore, the introduced Chinook salmon (Stewart and Ibarra 1991; Rand and Stewart 1998; Tsehay et al. 2014). Conversely, in the second period, they suggested that the prey supply decreased to a level, such that predation mortality increased substantially and the trophic interaction between alewives and Chinook salmon became unstable. This was exacerbated by the fact that the native top piscivore lake trout could use alternative prey effectively, and played an increasingly important role in maintaining a high and relatively stable piscivore biomass. They suggested that this led to further suppression of the alewife abundance because the alewife was the preferred diets of all major piscivores. In both periods, piscivore stability was the basis of ecosystem stability, although the shift from the early period to the next reflected substantial changes in structure and function of the ecosystem.

Overall, it is very important to identify early change points of an impending regime shift and piscivores responses. Once a transition has started, it is not feasible to manage a transitional state indefinitely. Rather than attempt to sustain the system in an implicitly assumed constant regime, the alternative management strategy is to effect the change by focusing on new key-stone fish species and diversity of the fish community.

Our method development provides a basis for future development and application. First, quantifying temporal variation in growth parameters is critical for detecting and understanding real changes in fish growth, and this is beyond of the conventional recognition of observation errors in describing fish growth. Estimated asymptotic length can encapsulate growth potential (Shuter et al. 1998; He and Stewart 2002; He et al. 2005), and our approach has estimated changes in growth potential by incorporating

453 process errors in this parameter. Second, our growth model describes year to year growth
454 of multiple cohorts, and this is a different procedure from the common practice that
455 estimates a growth trajectory based on an annual sample of length at age observations or
456 a sample pooled over a set of years. This conventional and widely applied procedure
457 implicitly treats the different cohorts represented in the sample as having experienced the
458 same constant growth conditions (Ricker 1979). Similarly, models that only use cohort-
459 specific data implicitly treat every year in a growth history as the same. Furthermore,
460 results from those conventional procedures are often influenced by a few very old and
461 large individual fish. In contrast, the asymptotic length from our model is influenced
462 mostly by inter-annual growth of representative age groups, not primarily by a few old
463 and large individual fish to be included or missed. Third, by including and estimating a
464 multivariate normal distribution for log scale growth parameters, our model is designed
465 to discourage (penalize) random variation in growth parameters, and such variations
466 would not be estimated to occur unless there are sufficient signals in the data that can
467 offset the penalties. With the potential correlations between early life growth and growth
468 potential explicitly accounted, our model parameterization also has avoided the source of
469 statistical biases that often arise from the conventional approaches to estimating
470 asymptotic length along with the growth coefficient k (Ratkowsky 1986).
471

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Table 1. The years of shifts in prey biomass, and growth potential and body condition of lake trout (LAT), Chinook salmon (CHS) and walleye (WAE) based on change point analyses using R Package ‘strucchange’. Differences in BIC and AIC between a model option and the lowest BIC or AIC option were in favor of stepwise declines over other alternatives. Periods in comparison were further explained in the text. See data sources in Figs. 1 and 3.

			Growth potential			Body condition			Prey
			LAT	CHS	WAE	LAT	CHS	WAE	
First shift			1998	2003	2004	2002*	1996	1992	1995
Second shift							2003	2004	2003
Third shift							2008		
Periods in comparison			2	2	2	2	2	3	3
Δ BIC	Constant mean		10.31	4.25	3.75	35.50	18.69	33.80	30.18
	A linear trend		4.99	4.78	3.46	8.71	8.89	5.99	4.66
	Trends w/ change point		6.47	4.30	5.99	0.48	6.06	7.61	10.99
	Stepwise decline		0	0	0	0	0	0	0
Δ AIC	Constant mean		11.88	5.65	4.97	40.11	20.12	36.14	32.92
	A linear trend		4.95	7.78	3.46	11.74	8.89	7.21	6.02
	Trends w/ change point		3.21	1.49	3.56	0	3.19	3.94	5.99
	Stepwise decline		0	0	0	3.03	0	0	0

* BIC suggested one change point, AIC suggested three.

Figure captions

Fig. 1. Biomass of age 1 and older alewives and rainbow smelt indicated two stepwise declines: 1994-1995 and 2002-2003. The figure was an update of He et al. (2015), based on USGS annual bottom trawl surveys (Riley et al. 2008; Adams et al. 2009). See change point analyses in the text and Table 1 that statistically distinguished the major shifts from other apparent large variations in the time series.

Fig. 2. Observed geometric mean length and body mass at age and year compared with model predictions. A 1:1 line is shown for reference.

Fig. 3. Growth potential as the estimated asymptotic length (left column) and body condition as the estimated body mass at a given total length (right column) varied among years. See the confirmation of major shifts in the time series by change point analysis and the 95% credibility intervals (the text, Table 1, and Appendix Fig. A1).

Figure 1

Figure 2

Figure 3 (left column)

Figure 3 (right column)

Appendix. Bayesian hierarchical models and inferences

Log likelihood of data

Observed log scale length at age was assumed to have a normal distribution, and the age ranges used in fitting the model were 4-30 for lake trout, 1-5 for Chinook salmon, and 2-13 for walleye. Summing over all ages and years, this led to the log likelihood of the data for our growth model:

$$LL_{LEN} = \sum_a \left(-n_a \cdot \log_e(\sigma_{age}) - \frac{n_a}{2} \log_e(2\pi) - \frac{1}{2} \sum_y \sum_k \frac{(\log_e L_{y,a,k} - \log_e L_{y,a})^2}{\sigma_{age}^2} \right) \quad (A1).$$

Here, n is the total number of observations across all years for a given age group, $L_{y,a}$ is the predicted length at an age (a) and year (y) from equations 1-4, $L_{y,a,k}$ is one of the observations from the age and year, and σ_{age} is the standard deviation specific to an age group. Given the assumed normal distribution of log scale observation, the predicted length at age, $L_{y,a}$, is the estimated median or equivalently the geometric mean of the length at age distribution.

Observed log scale body mass at length was also assumed to have normal distributions, which led to the log likelihood of the data for the length-mass model:

$$LL_W = \sum_s \left(-n_s \cdot \log_e(\sigma_s) - \frac{n_s}{2} \log_e(2\pi) - \frac{1}{2} \sum_y \sum_k \frac{(\log_e W_{y,s,k} - \log_e W_{L_{y,s,k}})^2}{\sigma_s^2} \right) \quad (A2).$$

Here, n is the total number of observations across all years for a given size group, $L_{y,s,k}$ and $W_{y,s,k}$ are the length and weight for one of the observations from a size group (s) and year (y), $W_{L_{y,s,k}}$ is the predicted weight at the given observed length and year from equation 5, and σ_s is the standard deviation specific to a size group. Again predicted

values are estimated medians (or geometric means) of their distributions. Based on residual plots of preliminary modeling fits, we defined the size groups with distinct standard deviations for observation errors as <450, 450–549, 550–699, and ≥700 mm for lake trout; <450, 450–649, 650–849, and ≥850 mm for Chinook salmon, and <400, 400–579, and ≥580 mm for walleye.

Prior distribution of model parameters

For a given year the vector of process errors, as associated with either growth parameters (L_∞ , L_g , and L_{g+1}) or length-mass parameters (a and b), was assumed to have multivariate normal distribution, with log density:

$$f_{MN} = -\frac{n}{2} \log_e(|\Sigma|) - \frac{n \cdot d}{2} \log_e(2\pi) - \frac{1}{2} \sum_{i=1}^n [(\underline{x}_i - \underline{\mu})^T \Sigma^{-1} (\underline{x}_i - \underline{\mu})] \quad (A3).$$

Here, n is the total number of observations and is equal to the total number of years in a time series; d is the dimension of the multivariate distribution or the number of estimates added each year, which equals three for the growth model and two for the length-mass model; $\underline{x}$ is a vector of process errors associated with the three log-scale growth parameters or two log-scale length-mass parameters, $\underline{\mu}$ is a vector of zero means for the process errors, and Σ is a variance-covariance matrix.

The variance-covariance matrix was modeled by following the same procedure of He and Bence (2007) for the growth model:

$$\Sigma = \begin{bmatrix} \sigma_{L_\infty} & & & \\ & \sigma_{L_g} & & \\ & & \sigma_{L_{g+1}} & \\ & & & \sigma_{L_{g+1}} \end{bmatrix} \begin{bmatrix} 1 & r_{L_\infty, L_g} & r_{L_\infty, L_{g+1}} \\ r_{L_\infty, L_g} & 1 & r_{L_g, L_{g+1}} \\ r_{L_\infty, L_{g+1}} & r_{L_g, L_{g+1}} & 1 \end{bmatrix} \begin{bmatrix} \sigma_{L_\infty} & & \\ & \sigma_{L_g} & \\ & & \sigma_{L_{g+1}} \end{bmatrix} \quad (A4)$$

and He et al. (2008) for the length-mass model:

$$\Sigma = \begin{bmatrix} \sigma_a & \\ & \sigma_b \end{bmatrix} \begin{bmatrix} 1 & r_{a,b} \\ r_{a,b} & 1 \end{bmatrix} \begin{bmatrix} \sigma_a & \\ & \sigma_b \end{bmatrix} \quad (\text{A5}).$$

Here, σ is the standard deviation for the deviations of a given log-scale parameter, and r the correlation coefficient between deviations of the two parameters specified by subscripts. This approach to parameterizing a variance-covariance matrix via separate consideration of standard deviations and correlations was developed in Daniels and Kass (1999, 2001), and Barnard et al. (2000). These correlation coefficients and standard deviations were estimated as hyper parameters of our models (see the next section). In comparison with the commonly used inverted Wishart distribution as a hyper prior for modeling the variance-covariance matrix, Gelman et al. (2004) provided further support for using the separation approach. Cholesky decomposition as implemented in AD Model Builder (Fournier et al. 2012) was used to ensure the variance-covariance matrix was positively definite (see also Press et al. 1992).

Our model also estimated the mean vector for the three log-scale growth parameters or the two log-scale length-mass parameters. As for the process errors, the log scale mean vector was assumed to have a multivariate normal distribution. The log density is the same as is given by equation A3, but here the number of observation n is only one. We specified the prior means as non-zero values (Table A1). The variance-covariance matrix for the log-scale means was also specified without using any additional parameter estimates. The correlation coefficients for the log-scale means were assumed to be the same as the estimates for the corresponding process errors, and the diagonal standard deviations in Eqs. A4 and A5 were specified as 2.0 (not estimated). This was a large value for log transformed growth parameters and length-mass parameters. This prior for modeling the log-scale mean vector differed from that previously used by He

and Bence (2007) and He et al. (2008). They fixed the off diagonal components of the variance-covariance matrix as zero and specified a very large value for the diagonal components (see also Pilling et al. 2002; Lai and Helser 2004; Helser et al. 2007). We modified the approach to be more consistent with the concept of correlated parameters.

Our model estimated standard deviations for observation errors (one for each age or size class) and assumed those log-scale standard deviations to have normal prior distributions, which led to a joint log prior density:

$$f_N = -n \cdot \log_e(\sigma) - \frac{n}{2} \log_e(2\pi) - \frac{1}{2} \sum_{i=1}^n \frac{(x_i - \mu)^2}{\sigma^2} \tag{A6}.$$

Here, n is the number of σ values estimated, and equals the number of age groups for the growth model (Eq. A1) or the number of size groups for the length-mass model (Eq. A2); x is a log-scale estimate of σ_{age} or σ_s , and μ and σ are the specified mean and standard deviation that jointly govern a prior distribution for the growth or length-mass model (Table A1).

Hyper prior distribution of hyper parameters

As noted above, a variance-covariance matrices Σ for process errors is determined by three correlation coefficients (r) and three standard deviations (σ) for the growth model (Eq. A4), and by one r value and two σ values for the length-mass model (Eq. A5). To govern the prior of a multivariate normal distribution (Eq. A3), those correlations coefficients and standard deviations are hyper parameters to be used.

We estimated Fisher’s Z (transformation of a correlation coefficient), and log-scale standard deviations. Fisher’s Z is an inverse hyperbolic tangent transformation, and

thus a correlation coefficient was calculated as the hyperbolic tangent of an estimated Fisher's Z:

$$r = \frac{e^{2Z} - 1}{e^{2Z} + 1} \quad (\text{A7}).$$

We assumed the Fisher's Z to have a normal hyper prior distribution (Fisher 1915; Zar 1999). The joint log hyper prior density is the same as given by equation A6, and in this case n is the number of r values estimated and equals three for the growth model (Eq. A4) and 1 for the length-mass model (Eq. A5); x is the Z value associated with each r , and μ and σ are the specified mean and standard deviation that jointly govern the hyper-prior distribution (Table A1).

Finally, we assumed the log-scale standard deviations for process errors (Eqs A4-A5) to have a normal hyper-prior distribution. The resulting joint log hyper prior density is the same as given by Eq. A6, but in this case x is one of log-scale standard deviations for process errors associated with the growth parameters ($\sigma_{L_\infty}, \sigma_{L_g}, \sigma_{L_{g+1}}$) or with the length-mass parameters (σ_a, σ_b), μ and σ are the specified average and standard deviation that jointly govern the distribution (Table A1). The number of estimates n is three for the growth model (Eq. A4), but two for the length-mass model (Eq. A5).

Approximating the Posterior Distribution and Bayesian credibility intervals

We used the Markov chain Monte Carlo (MCMC) method to approximate the marginal posterior distribution (Punt and Hilborn 1997) for estimated parameters, and for all quantities that could be calculated from these parameters. MCMC chains were generated using the Metropolis–Hastings algorithm as implemented in AD Model Builder

110 (Hastings 1970; Fournier et al. 2012). We used a chain length of 1,000,000 cycles to
111 ensure that there were no transient behaviors or any potential problems with convergence.
112 We saved every 200th cycle from the MCMC chains, and after this thinning we dropped a
113 burn-in of the initial 1,000 saved values. In essence the posterior distribution was based
114 on the 4000 sets of parameters in the saved chain, which provided a large sample of
115 values from that distribution (Fig. A1). The overall diagnostic procedure to provide
116 evidence that the saved chains were converged and provided sufficient information on the
117 posterior distribution were similar to those of He and Bence (2007) , and He et al. (2008).
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Table A1. Distributional parameters (mean and standard deviation) specified as prior or hyper-prior distributions for the listed parameters or hyper parameters. N indicated normal distribution. The vector of standard deviations for observation errors allowed for differences in observation variability among age groups in the growth model and size groups in the length-mass model. The length at the youngest age (L_g) was age 2 for lake trout from spring, age 1 for Chinook salmon from summer, and age 1 for walleye from fall. For population average parameters on log scale assumed to have a multivariate normal distribution, only hyper-prior means were specified in the table, and details are given in the text of the Appendix regarding the variance-covariance matrix. All of the prior or hyper prior distributions specified in this table were intended to be weakly informative. See Table A2 for comparisons of the priors with posterior distributions.

Model	Hyper parameter	Distributional parameter		
		Lake trout	Chinook salmon	Walleye
Growth	$Z(r_{L_\infty, L_g}, r_{L_\infty, L_{g+1}}, r_{L_g, L_{g+1}})$	$N(0, 1)$	$N(0, 1)$	$N(0, 1)$
	$\sigma_{L_\infty}, \sigma_{L_g}, \sigma_{L_{g+1}}$	$N[-1.61, 0.45]$		
	σ_{obs}	$N[-2.30, 0.28]$		
	$\overline{\log_e(L_\infty)}$	$\ln(650)$	$\ln(950)$	$\ln(600)$
	$\overline{\log_e(L_g)}$	$\ln(150)$	$\ln(450)$	$\ln(300)$
	$\overline{\log_e(L_{g+1})}$	$\ln(280)$	$\ln(650)$	$\ln(400)$
L-M	$Z(r_{a,b})$	$N(0, 1.41)$		
	σ_a, σ_b	$N[-1.61, 0.45]$		
	σ_{obs}	$N[-1.61, 0.45]$		
	$\overline{\log_e(a)}$	-20		
	$\overline{\log_e(b)}$	1.0		

Table A2. Posterior density of hyper parameters based on MCMC simulation. The averages of log scale L_{∞} , L_g and L_{g+1} in growth model and the averages of log scale a and b for length-mass model were the calculated averages over yearly estimates.

Model	Hyper parameter	Highest Posterior Density		
		Lake trout	Chinook salmon	Walleye
Growth	$Z(r_{L_{\infty}, L_g}, r_{L_{\infty}, L_{g+1}}, r_{L_g, L_{g+1}})$	$N(-0.24, 0.195)$	$N(-0.58, 0.686)$	$N(0.46, 0.232)$
		$N(-0.05, 0.188)$	$N(-0.046, 0.629)$	$N(0.41, 0.220)$
		$N(1.48, 0.191)$	$N(2.01, 0.335)$	$N(1.46, 0.201)$
	$\sigma_{L_{\infty}}, \sigma_{L_g}, \sigma_{L_{g+1}}$	$N(-2.13, 0.135)$	$N(-1.76, 0.297)$	$N(-2.00, 0.184)$
		$N(-1.10, 0.145)$	$N(-0.51, 0.116)$	$N(-1.59, 0.136)$
		$N(-2.27, 0.130)$	$N(-1.87, 0.260)$	$N(-2.01, 0.129)$
	$\sigma_{\text{obs}}, \text{min}$	$N(-2.77, 0.40)$	$N(-2.70, 0.018)$	$N(-2.60, 0.017)$
	$\sigma_{\text{obs}}, \text{max}$	$N(-2.08, 0.007)$	$N(-1.94, 0.018)$	$N(-2.07, 0.212)$
	$\overline{\log_e(L_{\infty})}$	$\log_e(789)$	$\log_e(1020)$	$\log_e(608)$
	$\overline{\log_e(L_g)}$	$\log_e(174)$	$\log_e(466)$	$\log_e(371)$
	$\overline{\log_e(L_{g+1})}$	$\log_e(334)$	$\log_e(685)$	$\log_e(439)$
L-M	$Z(r_{a,b})$	$N(-3.48, 0.346)$	$N(-2.83, 0.226)$	$N(-1.98, 0.252)$
	σ_a, σ_b	$N(-0.29, 0.210)$	$N(-0.27, 0.162)$	$N(-3.57, 0.275)$
		$N(-3.22, 0.210)$	$N(-3.33, 0.163)$	$N(-4.65, 0.222)$
	$\sigma_{\text{obs}}, \text{min}$	$N(-2.28, 0.011)$	$N(-1.97, 0.016)$	$N(-2.27, 0.011)$
	$\sigma_{\text{obs}}, \text{max}$	$N(-2.05, 0.006)$	$N(-1.56, 0.041)$	$N(-2.00, 0.032)$
	$\overline{\log_e(a)}$	-19.21	-19.4	-19.13
	$\overline{\log_e(b)}$	1.139	1.147	1.132

Figure caption for the appendix

Fig. A1. Trace-plots of MCMC simulations for among-year geometric means of asymptotic length (left column), and body mass at a given total length (right column), showed clear differences between the defined time periods.

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Figure A1 (left column)

Figure A1 (right column)