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

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Introduction

He et al. (2015) described piscivory patterns in the main basin of Lake Huron for 1984–2010, during which there was also a pattern of stepwise declines in the abundance of dominant prey fish species. The approach of He et al. (2015) was to couple age-structured stock assessment and fish bioenergetics models to estimate prey fish consumption and to compare these patterns with prey fish biomass from a bottom trawl survey. Riley and Dunlop (2016) were highly critical of the methods and conclusions reached by He et al. (2015). They claimed that we incorrectly interpreted the bottom trawl survey data and did not account for uncertainty. We respond to these and other criticisms below, which we find do not undermine our findings.

Catchability

In the Discussion of He et al. (2015), we argued that predation had an important role in the collapse of alewives (Alosa pseudoharengus) during 2003 in the main basin of Lake Huron, and in subsequently suppressing the alewife abundance, because the estimated total consumption of alewives was large relative to the absolute abundance of alewives. In this context, we stated that our view was based on “the swept-area indices of biomass for age-1 and older alewives are close to the actual biomass in the main basin”, which in turn as we indicated was based on (i) the work done in Lake Michigan that estimated survey catchability using a 12 m headrope small trawl (Tsehaye et al. 2014) and (ii) the work done by Adams et al. (2009), who estimated fishing power corrections (FPCs) between the small trawl and a 21 m headrope large trawl. The small trawl was used in the USGS Lake Huron surveys during 1973–1991, and the larger trawl has been used since 1992. The criticisms that Riley and Dunlop level against our evaluation reflect several misinterpretations and misunderstandings of our work and the work we have built on. Their claims also include several misleading summaries of other past work and some fairly dogmatic statements.

1 Incorrect statements regarding published catchability estimates and fishing power corrections. We define survey catchability as a ratio of the estimated number to the actual number of fish in the lake. This is the same definition used by Tsehaye et al. (2014). Riley and Dunlop incorrectly stated that “the “catchability coefficient” estimated by Tsehaye et al. (2014) is essentially a correction factor used to estimate the biomass of prey fish that was present in Lake Michigan at a time previous to the trawl survey based on model predictions of predator consumption and is not an estimate of trawl catchability per se”. They then added further confusion by claiming that “the FPCs developed by Adams et al. (2009) were specifically designed to correct catch per unit effort between the two trawls, not to correct estimates of catchability.” Following the definition presented by Riley and Dunlop, “the proportion of a population caught with one unit of survey effort”, catchability is (catch/effort)/N, where N is the true population size. Thus, for differences in gear, there is no difference between catch-per-effort correction and catchability correction. With our definition of catchability, the catchability equation is modified only by the total area of the lake and the swept area per unit of survey effort. The bottom line is that given estimates of the small trawl catchabilities, using the FPCs to estimate catchabilities of the large trawl is certainly appropriate (J. Adams, USGS GLSC, personal communication).

2 Incorrect speculations regarding the basis for our claim that swept-area abundance was close to actual abundance. Riley and Dunlop (2016) stated “the “catchability coefficient” estimated by Tsehaye et al. (2014) is for age-3 and older alewife, not YAO alewife, and the product of this estimate (0.29) and the FPC (7.85) is equal to 2.28, not 1.0.” Here, YAO stands for yearling and older. They further speculated “He et al. (2015) may have mistakenly used the estimated age-0 alewife “catchability coefficient” from Tsehaye et al. (2014), which was 0.13, and which multiplied by the YAO FPC would yield an estimate of 1.02”. In fact, we did calculations for both age-0 and YAO alewives, and both suggested that the biomass estimates were close to absolute biomass. For age-0, the calculation was fairly direct. We multiplied the catchability estimate of 0.13 for the small bottom trawl by an FPC of 6.89 to obtain a catchability estimate of 0.90 for the large trawl. For YAO alewives, we did not assume equal catchability for all age groups because the small bottom trawl was especially ineffective at catching age-1 alewives (Eck and Brown 1985). From the catch curve data for the small bottom trawl (Eck and Brown 1985), the catchability for age-1 alewives was less than half that for age-0, and the catchability for age-2 alewives was equal to that for age-0. Thus, we assigned small trawl catchability values of 0.06 and 0.13 for age-1 and age-2 alewives, respectively, and only used the value of 0.29 for age-3 and older. We also weighted these values by typical relative abundances of these age categories, assuming an
annual mortality rate of 60%. The weighted mean catchability of the small trawl was 0.113, which we then multiplied by the FPC estimate of 7.85 for YAO alewives to obtain a catchability estimate of 0.89 for the large trawl. We did not present those details on our calculations in He et al. (2015), given this was an argument presented in one paragraph in the Discussion, and perhaps we should have.

(3) A misleading summary of the evidence for bias in the swept-area estimator of biomass. Riley and Dunlop argued that “It is well recognized that estimates of fish abundance from daytime bottom trawl surveys in the Great Lakes are likely to be highly negatively biased”. They were implying that the biomass estimates in Lake Huron’s main basin were similarly biased. In fact, however, Riley and Dunlop (2016) failed to provide any evidence specifically showing that the estimates of alewife biomass in the main basin of Lake Huron based on the 21 m headrope large trawl were significantly biased. Not a single reference they cited specifically addressed catchability of alewives with the large trawl. Results from Tsehaye et al. (2014) showed that the small trawl was indeed negatively biased. To the extent that all biases also apply to Lake Huron, however, the greater fishing power of the large trawl, as indicated by the FPCs, approximately counterbalances these biases.

(4) A dogmatic statement that a “valid inference about the catchability of a given tow cannot be made from tows conducted in another lake with different gears”. While we agree many factors that vary in space and time can influence catchability, it does not logically follow that one cannot appropriately combine evidence between lakes and gears to address catchability. Riley and Dunlop’s claim regarding general negative biases of bottom trawl surveys in the Great Lakes appears to be the kind of inference they argue against. In our view, we made strong but reasonable assumptions when we used the FPCs from Adams et al. (2009) and the catchability estimates from Tsehaye et al. (2014). We acknowledged the assumptions and uncertainty by stating that “We recognize there is substantial uncertainty in both the catchability estimate and fishing power correction and a strong assumption involved in applying a Lake Michigan catchability estimate to Lake Huron. Further research in this area is clearly warranted.”

Our argument, that the large trawl provides biomass estimates of YAO alewives roughly on the same scale as absolute biomass, does not entirely depend on those details in our use of FPCs and our calculations of catchability. For example, assuming equal catchability per unit area trawled in the two lakes during 1973–1991, biomass density was 4.0 times higher in Lake Michigan than in the main basin of Lake Huron (Madenjian et al. 2008). Further taking into account the differences in lake area, total biomass was 6.1 times as high. If the differences in biomass density persist through 1995–2002 (the 8 years prior to the collapse of alewifes), the implied biomass of YAO alewives should be about 30 kt in Lake Huron, given a mean biomass of 184 kt in Lake Michigan during that period (I. Tsehaye, Wisconsin Department of Natural Resources, personal communication). This value corresponds closely to the large trawl estimated mean of 28.9 kt during this period. While obviously relative biomass density cannot remain unchanged over time, we believe this result does suggest that the swept-area estimates of biomass are plausibly close to absolute biomass.

**Documentation of methods and discussion of uncertainty**

Riley and Dunlop criticized our work for not fully documenting modeling methods and for not providing model uncertainty. In regard to the modeling methods, it is not clear to us what details they were concerned about. From He et al. (2015): “A compendium of all equations and parameters of our model system, including hierarchical Bayesian statistics, and detailed explanations, across the four species for each area and for each process, would be of book length. For each level process we modelled, however, model equations and parameters have been well documented in peer-reviewed publications (see Appendix A, Table A2). In the subsection below, we only emphasize critical details for the couplings of those complex models.” We stand by this original statement.

In several places, Riley and Dunlop (2016) criticized our work by incorrectly summarizing our methods. For example, they stated that we used constant diet composition during 1987–2008 for Chinook salmon (Oncorhynchus tshawytscha) and that our models did not include spatial structure. Such descriptions are in contradiction to the actual methods presented by He et al. (2015). We encourage readers who remain concerned regarding these issues to read our original publication.

Riley and Dunlop’s claim that “the consumption estimates are highly uncertain” was unsubstantiated. Direct calculation of uncertainty measures for consumption estimates is indeed challenging because of the many components involved, such as diets, energy density of prey and predator, seasonal temperature of habitat occupied, predator size-at-age, abundance, and mortality rates. Previous analyses and our sensitivity analysis, however, have strongly suggested that the major uncertainty in such estimates resides in the estimate of predator abundance, which can be summarized by predator biomass (Stewart et al. 1983). Modest changes in the water temperature regime experienced by fish have been shown to result in very small changes in estimates of food consumption (Madenjian et al. 2003). Laboratory evaluations of fish bioenergetics models have revealed that the estimates of cumulative food consumption by Chinook salmon, lake trout (Salvelinus namaycush), walleye (Sander vitreus), and lake whitefish (Coregonus clupeaformis) over an extended period (3–14 months) are typically within 10% of the observation (Madenjian and Wang 2013; Madenjian et al. 2004, 2006, 2012, 2013).

The mean weight-at-age, for the age groups most dominant in the populations we estimated consumption for, was derived from large sample sizes with standard errors (SEs) generally less than 6% of the estimates. Given the weight-at-age schedules, we used the delta method to propagate uncertainty for stock assessment parameters from the asymptotic variance–covariance matrix and then estimated SEs for annual biomass values using automated procedures available in AD Model Builder (Seber 1982; Fournier et al. 2012). For lake trout and walleye, the estimated coefficient of variation (CV) for stock biomass ranged from 1.5% to 12%, with the highest values at the end of the time series (2011 and 2012). All CVs were 8% or less prior to 2011. Aggregated biomass for the three predators combined had CVs ranging from 4% to 10%. We believe the relatively low CVs for lake trout, walleye, and the aggregated total biomass support our approach to presenting results based on descriptions of the patterns of point estimates.

CVs for Chinook salmon biomass were substantially higher, ranging from 14% to 30%, with the highest values over 25% during the period 2002–2012. We thus calculated the ratios of Chinook salmon biomass in 2002 to the mean in 2004–2012 (9-year period after collapse) and to the mean in 1993–2001 (9-year period prior to 2002). We also calculated the difference between the two ratios and propagated errors to estimate SEs for the ratios and their difference. The first ratio was 3.11 (SE = 0.35), the second ratio was 0.90 (SE = 0.11), and the difference between them was 2.21 (SE = 0.27). This confirmed a major pattern we presented that Chinook salmon biomass (and consumption) was similar in 2002 to previous years but declined dramatically to a much lower level for the period starting in 2004.

Additional uncertainty is associated with equations used in the assessment models. In published work we cited in He et al. (2015), and in other unpublished analyses, we explored such additional uncertainty. Nothing from these analyses suggested our conclusions about biomass (and hence consumption) patterns were sensitive to the particular equations we used.
The role of predation and other factors in the alewife collapse

Riley and Dunlop (2016) also claimed that the ratio of consumption to prey biomass did not provide valid information regarding the importance of predation, because the prey biomass we used was from the fall, which did not fully reflect prey availability. Essentially they were saying that the “right” denominator should be something like prey production. They presented this critique as though it was an issue we had not considered, ignoring our statement: “While the predation was substantial relative to standing stock of YAO alewife, production to biomass ratios for similar prey fish can sometimes exceed 1.0.” While there is a great need for estimating annual and seasonal prey fish production, and certainly this is needed to fully evaluate the predation rates that any given prey fish population can sustain, we think it is entirely reasonable to conclude, as we did, that if annual consumption of alewives during the collapse was 50%–70% of the fall 2002 standing stock of alewives, it is likely that predation played an important role in the collapse. Our argument regarding the role of predation was based on the alewife biomass immediately prior to the collapse and the consumption during the collapse, not on the ratio of consumption during a period to the biomass at the end of that period.

We also presented the ratio of annual consumption of alewives and rainbow smelt to the swept-area estimates of biomass for those two species as an index of predation intensity. We believe that, for example, the order of magnitude increase in the ratio between 1990–1995 and 2003–2010 is compelling evidence for an increase in predation intensity. We neither believed nor implied that this ratio represented the proportion of the available prey that was eaten. We are puzzled by the claim of Riley and Dunlop that the mere calculation of this index implies that we viewed the swept-area estimate as an absolute measure of prey available to be consumed. This would clearly not be reasonable, as this ratio averaged over 1.6 for the period of 2003–2010.

While we indicated that predation was important, we did not argue this was the sole cause of the collapse of alewives and acknowledged that higher levels of mortality could be partly due to environmental factors. We did not address the potential role of temperature specifically on the collapse because we were not convinced by the arguments in Dunlop and Riley (2013), and in a failed effort, we attempted to avoid controversy on this topic. While some of us think temperature could have played some role in the collapse, the empirical support is weak. If this occurred, it is puzzling that dead alewives were not observed as in past large-scale die-offs in the Great Lakes, including Lake Huron. Moreover, in both Lakes Huron and Michigan, regression analyses have failed to detect any relationship between variables reflecting winter severity and age-3 alewife recruitment or standing stock (Madenjian et al. 2005; Dunlop and Riley 2013; Collingsworth et al. 2014). Despite the lack of any significant statistical relationship between winter severity and alewife survival, Dunlop and Riley (2013) concluded that “the cold winter of 2003 was likely the catalyst that induced a largescale die-off of alewife in Lake Huron”. Riley and Dunlop (2016) cited O’Gorman et al. (1987) and Ridgway et al. (1990) as linking alewife mass mortality to winter severity “in other lakes”. Those two studies were conducted in different areas of Lake Ontario. For the main basin of Lake Ontario, O’Gorman et al. (1987) suggested that the most substantial overwinter mortality occurred in severe winters following mild winters when the alewife abundance had exceeded carrying capacity. The more recent analysis of O’Gorman et al. (2004), based on a longer time series, found an effect of temperature on recruitment at age 1, but not on survival from age 1 to age 2 during the period 1978–2000. Dunlop and Riley (2013) did not specifically invoke the mechanism suggested by O’Gorman et al. (1987), although they used the winter-to-winter change as part of their description of winter severity and did not provide an alternative mechanism for why this might matter. It is unlikely Lake Huron alewives exceeded carrying capacity of the lake, given their low stock size in 2002. Despite changes in lower trophic level productivity, alewife individual growth did not show large obvious changes prior to the collapse (Dunlop and Riley 2013), and during the collapse that might indicate the population exceeding carrying capacity. Riley and Dunlop (2016) also stated that “Several studies have experimentally investigated cold-temperature mortality in this species (Snyder and Hennessy 2003; Lepak and Kraft 2008; Snyder and Murray 2009).” These studies actually do not support Riley and Dunlop’s claims. Lepak and Kraft (2008) did not find any evidence for higher mortality of alewives kept at cold (<3 °C) temperatures. The studies of Snyder and Hennessy (2003) and Snyder and Murray (2009) were designed to evaluate responses in fatty acid composition to a cold challenge, in which temperature was dropped from 12 to 2 °C during a 20-day period. Such a cold challenge is not representative of how Lake Huron (or other large lakes) cools over an extended period during the late fall and winter.

Conclusion

The criticisms leveled against our work stem from numerous factual, logical, and technical flaws on the part of Riley and Dunlop (2016). We stand by our original conclusions regarding temporal patterns of predator consumption and predation intensity and the argument we made in the discussion that predation played an important role in the collapse of alewife during 2002–2004 (He et al. 2015).

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References


