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Unveiling the recovery dynamics of Walleye after the invisible collapse

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Abstract—Walleye (*Sander vitreus*) populations in Alberta, Canada collapsed by the mid-1990s and were a case study in the paper *Canada's Recreational Fisheries: The Invisible Collapse?* Here we fit age-structured population dynamics models to data from a landscape-scale monitoring program to assess Walleye population status and reconstruct recruitment dynamics following the invisible collapse. Assessments indicated that populations featured low F_{msy} values of approximately 0.2-0.3 under conservative assumptions for the stock-recruitment relationship but that many populations were lightly exploited during 2000-2018. Recruitment reconstructions showed that recovery from collapse in 33/55 lakes was driven in part by large positive recruitment anomalies that occurred during 1998-2002. Additionally, 15/55 lakes demonstrated cyclic recruitment dynamics. The documented recruitment anomalies and cyclic fluctuations could be due to environmental effect(s) or cannibalism, and experimentation is likely necessary to resolve this uncertainty. These findings contribute new information on the recovery dynamics of Walleye following the invisible collapse, and demonstrate the effectiveness of coupling traditional fisheries science models with broad-scale monitoring data to improve understanding of population dynamics and sustainability across landscapes.

Keywords: Walleye, invisible collapse, inland recreational fisheries, population dynamics, cyclic recruitment fluctuations

Introduction

The invisible collapse of inland recreational fisheries is among the most influential papers published in fisheries science (hereafter “invisible collapse”; Post et al. 2002 *in* Sass and Allen 2014). This paper used data, qualitative information, and expert judgement from inland recreational fisheries in Canada and theoretical arguments to demonstrate that inland fisheries were not immune to overharvest or collapse (Post et al. 2002). Declines were said to have gone unnoticed or were “invisible” because of the long timeframes across which the declines were believed to have occurred (e.g., see arguments in Pauly 1995) and because of the difficulties of monitoring and assessing populations across landscapes (see Lester et al. 2003). While Post et al. (2002) increased awareness of several aspects of inland fisheries sustainability, their claims regarding fishery status were not based on the analysis of long-term data using stock assessment models. This nuance is noteworthy because assessment models fitted to survey trend and size-age data via a likelihood function serve as a means through which beliefs about sustainability might be contrasted against data (Hilborn and Walters 1992; Hilborn and Mangel 1997). In many inland fisheries, standardized survey data do not exist—and indeed did not exist for all the case studies examined in Post et al. (2002). However, since Post et al. (2002) several inland fisheries management agencies in North America have invested in broad-scale monitoring programs (e.g., see Bonar and Hubert 2002; Lester et al. 2003). It is in these systems that it may now be possible to fit assessment models to snapshots of standardized monitoring data (Ricker 1975; Lorenzen et al. 2016), which in turn might inform understanding of inland fisheries ecology and sustainability across landscapes.

It is a well-known concern, however, that the assessment models developed for large-scale fisheries might not be applicable “as-is” to the analysis of small-scale inland fisheries data

due to lingering data limitations or lack of technical expertise (e.g., see Lorenzen et al. 2016). This is problematic because the total value of small-scale inland fisheries often rivals or surpasses the value of their large-scale fisheries counterparts (Lynch et al. 2016b; Funge-Smith 2018) and because the application of assessment methodologies like those used in large-scale fisheries could improve scientific understanding and fisheries management outcomes in inland settings (Post et al. 2002; Welcomme et al. 2010; Beard et al. 2011; De Graaf et al. 2015; Cooke et al. 2016; Lorenzen et al. 2016; Lynch et al. 2016b). Because assessment models have not been fitted to data collected across landscapes, a variety of simpler methodologies have emerged to fill this gap. For example, a major focus of inland fisheries has been on the development of data-limited tools that use life history theory or social-ecological-systems approaches to rank population status or sensitivity to overharvest across large spatial-temporal scales (e.g., Shuter et al. 1998; Lester et al. 2014a; Carpenter et al. 2017; Embke et al. 2019; Wilson et al. 2019). These frameworks are used to determine status because of data limitations or because of the technical difficulties of fitting population dynamics models to data collected across landscapes (see arguments in Shuter et al. 1998; Arlinghaus et al. 2017). In the context of inland fisheries, a limitation of these data-limited methodologies is that all ignore time-series data on population dynamics, which masks important ecological processes and may render both assessment advice and management actions ineffective (Hilborn and Walters 1992; Quinn and Deriso 1999). Consequently, nearly 20 years after Post et al. (2002) understanding of the dynamics and hence sustainability of fisheries across landscapes remains veiled beyond a few high-value locations where intensive data collection occurs and traditional assessment techniques can be applied (e.g., Treml et al. 2014; Jones et al. 2016).

Walleye *Sander vitreus* support valuable fisheries throughout North America (Bozek et al. 2011), display highly variable recruitment dynamics (see Hansen et al. 1998), and populations in Alberta, Canada were used as a key case study in Post et al. (2002). Post et al. (2002) hypothesized that overharvest occurred in these fisheries because of the dual challenges of managing low productivity northern fisheries coupled with Alberta's high fishing pressure relative to other jurisdictions, where licence sales were used as a proxy for fishing effort per hectare of fishable water (see also Sullivan 2004). Thus, Alberta Walleye were said to be a precursor to the challenges facing inland fisheries management as human populations grow and angling effort increases into the future (Post et al. 2002). Walleye fisheries in Alberta collapsed by the mid-1990s, and in response to declines managers implemented stringent harvest regulations in 1996 to recover populations (i.e., high minimum length limits or catch-and-release regulations; Sullivan 2003). Additionally, fisheries managers initiated a province-wide standardized monitoring program to survey Walleye populations in 2000. Walleye populations in Alberta are stated to have recovered since collapse and after the implementation of regulations (Sullivan 2003; Spencer 2010). However, no published work on the population dynamics of these fisheries exists despite the central role they have played in shaping understanding of inland fisheries sustainability more generally (e.g., see Post et al. 2002; Sullivan 2003).

This paper addresses the challenge of fitting traditional fisheries models (*sensu* Ricker 1975; Hilborn and Walters 1992) to snapshots of data and assessing inland fisheries status across landscapes. While it is impossible to monitor and assess all fish populations across a landscape (see Shuter et al. 1998; Cooke et al. 2016; Arlinghaus et al. 2017), we seek to demonstrate that much can still be learned by fitting assessment models to data from as many populations as is feasible. Thus, our goal is to develop a general population dynamics model that can be fitted to

data collected from broad-scale inland fisheries monitoring programs. To confront this challenge, we use the Alberta Walleye fishery as a case study and fit assessment models to as many populations as was possible using survey data collected during 2000-2018. Upon fitting models to data from 55/123 surveyed lakes, our objectives were to 1) examine patterns in mortality rates and survey biomass estimates among lakes, 2) assess population sustainability using Kobe plots, and 3) reconstruct recruitment dynamics during 1980-2018 to inform understanding of Walleye recovery following the invisible collapse. Our work unveils the invisible or hidden (*sensu* Post et al. 2002; Embke et al. 2019) population dynamics of Alberta Walleye and highlights several ecological complexities that often go unrecognized during the analysis of landscape-scale inland fisheries data.

Methods

Standardized monitoring program

Biological data were collected using the FWIN protocol (Morgan 2002). The FWIN program uses multimesh gillnets that are eight panels each 7.6 m in length and which are set in randomly stratified locations across the 2-5 and 5-15 m depth strata. Nets were fished for 21-27 h during September when water temperatures were 10-15°C. Twenty-three percent of the surveys used half-nets, which were half the length of a normal net but featured the same proportion of mesh sizes (Paul et al. 2020). Fish were sampled for age estimation structures, weight (g), and fork length (mm). Age was estimated for fish using either fin rays (most fish during 2000-2003) or otoliths (2004-2018), and the proportions of fish that had age estimated in each survey was high (min = 0.09, median = 0.99, max = 1.0). A total of 123 lakes were surveyed during 2000-2018, but we only considered lakes with ≥ 3 surveys because this seemed like a reasonable minimum number of surveys with which to fit an assessment model (Fig. 1;

model described below). Given these constraints, our analyses included a total of 236 FWIN surveys conducted in 55 lakes (i.e., 45% of all surveyed lakes) during 2000-2018, totalling 43 790 sampled fish.

Lake-specific life history traits

We conducted meta-analyses of all life history characteristics for Walleye in lakes with ≥ 3 FWIN surveys during 2000-2018 to obtain lake-specific values of these quantities for assessment models. We summarized von Bertalanffy growth, weight-length, and age-maturity relationships using the methods in Cahill et al. (2020). All models were fitted using template model builder (Kristensen et al. 2015), and we ensured the maximum gradient of the objective function was ≤ 0.001 and that the Hessian matrix was positive-definite to test for consistency with convergence for each fit. We also evaluated model fits using plots of fitted values vs. data and residual plots. Finally, we tested for the presence of density-dependence in the traits we examined. We found no evidence for density-dependent juvenile growth, either among lakes or in any lake singly (Cahill et al. 2020). Analogous analyses for the k lake-specific weight-length relationship exponents (β_k) and age at 50 percent maturity (a_{50k}) yielded similar results.

Stocking and creel survey data

We used data from two other sources in addition to the FWIN data. First, we queried the provincial database for all Walleye stocking records, which we then linked to the FWIN data above. Second, we also used all available creel surveys on lakes to inform our assessment modeling below. Angling catch-per-effort (CPE) for Walleye was calculated using standardized methods in Walker et al. (2007). These surveys began in 1984, represent 169 lake-years of data, and were conducted in 64 distinct lakes.

Visualizing Paloheimo's "design effects" in catch-at-age data

We created bubble plots of the catch-at-age survey data for each lake to visualize the information contained within the age-structure data across the Alberta landscape. A typical example of the information contained in a lake's catch-at-age data is presented in Fig. 2. Such plots contain three "design effects," with *age effects* along the y-axis, *year effects* along the x-axis, and *recruitment effects* along the plot diagonal (Paloheimo 1980). These effects contain information on key processes such as recruitment and mortality rates (e.g., see Ricker 1975; Fournier and Archibald 1982). Additionally, Fig. 2 reveals an aspect of Walleye biology in Alberta that we exploit: fish may live to 20 years of age, and thus the catch-at-age data in some lakes contain information on recruitment and mortality rates in years before standardized monitoring began in 2000. Thus, bubble plots contain information from FWIN surveys on Walleye population dynamics during the latter stages of the invisible collapse and before the province instituted restrictive harvest regulations in 1996 (see also Sullivan 2003).

Model structure

Here we develop an age-structured population model to extract information from the FWIN survey data, which is similar to the catch-free assessment models of Porch et al. (2006) and the stock reduction analysis of Walters et al. (2006). This model is a straightforward age-structured population dynamics model that estimates quantities relevant to assessing the sustainability of fish populations using catch-at-age survey data, and similar models and age-structured equations have been used in fisheries science and assessment and fitted to survey trend and size-age data for nearly 40 years (see Beverton and Holt 1957; Ricker 1975; Fournier and Archibald 1982). We provide a summary of indices, symbols, equations, and their definitions in Table 1, and describe all estimated parameters and their prior distributions in Table 2.

First, we note that netting surveys provide observations of age-specific catch-per-unit-efforts (cpue) for each lake-year survey as

$$(1) O_{a,t,k} = \text{cpue}_{a,t,k} \cdot p_{t,k},$$

where $O_{a,t,k}$ is the observed cpue of age a fish in year t from lake k , $\text{cpue}_{a,t,k}$ is the catch per net of age a fish in year t and lake k , and $p_{t,k}$ is the proportion of fish which had an age estimate in survey t , k . A population dynamics model to predict the observed cpues in Eq. 1. for fish $a > 1$ is

$$(2) N_{a,t,k} = \begin{cases} R_{t,k} & \text{if } a = 2 \\ N_{a-1,t-1,k} \cdot e^{(-M_{a,k} - v_{a-1,k} \cdot F_{\text{period}, k})} & \text{if } 2 < a \leq 20 \end{cases}$$

Here, $R_{t,k}$ is the age-2 recruitment for year t in lake k , the modeling of which is described below. For fish of age 3 and older, $N_{a,t,k}$ represents the numbers of fish at age a in year t and lake k and which was calculated recursively as a function of the number of fish in that lake the year previously at $a - 1$ multiplied by the finite annual survival rate. We limited calculations to fish of ages ≤ 20 , since visual inspection of the data indicated that most useful information was contained in younger ages (with larger sample numbers and less contamination from age estimation errors).

The total finite annual survival rate term in eqn. 2. featured three components. First, size-dependent instantaneous natural mortality $M_{a,k}$ was modeled as

$$(3) M_{a,k} = \left(\frac{M_0}{l_{a,k}} \right)^\theta,$$

where $M_{a,k}$ was dependent upon an asymptotic value of instantaneous natural mortality M_0 , the relative length of fish at age $l_{a,k}$, and an exponent parameter which scales the relationship

(Lorenzen 2000, 2005). We assumed M_0 was 0.1 for all analyses, because higher values of M_0 such as those obtained using data-poor methods (e.g., Kenchington 2014) resulted in a substantial mismatch between preliminary model fits and the observed survey data, while lower values seemed unlikely given the empirically observed longevity of Walleye in the province (e.g., fewer than 0.0001 of all Walleye sampled in Alberta survived beyond 25 years). We used a value of 0.85 for θ because Walleye in well-studied systems demonstrate modest increases in M at young ages (Hansen et al. 2011; Vandergoot and Brenden 2014). Relative length of fish at age a in lake k was calculated using lake-specific von Bertalanffy growth parameters from the life history meta-analyses as

$$(4) \ l_{a,k} = \frac{l_{\infty k}}{\bar{l}} [1 - e^{(-vb_{k,k} \cdot a)}].$$

In this equation $l_{\infty k}$ is the lake-specific asymptotic average size of fish, $\bar{l}$ represents the global average l_{∞} among lakes, and $vb_{k,k}$ represents the von Bertalanffy metabolic rate parameter. The term $\frac{l_{\infty k}}{\bar{l}}$ scaled weight-at-age from absolute values to relative values and changed the interpretation of the fecundity-at-age relationships from relative to absolute units which was useful for recruitment modeling (see below).

The remaining terms in the finite annual survival rate component of Eq. 2 determined the instantaneous fishing mortality rate. The term $F_{\text{period}, k}$ represented an estimate of instantaneous fishing mortality F during two periods. The first of these periods was during 1980-1996 (i.e., $F_{\text{early}, k}$), while the second mortality regime represented an average F during 1997-2018 (i.e., $F_{\text{late}, k}$). These periods coincided with major regulation changes that occurred throughout the province in 1996, and this model features a mathematical constraint between the estimated

fishing mortality rates and recruitment values. This constraint can be seen in the algebraic structure of eq. 2. In this equation, if the F terms increase or decrease the corresponding $R_{t,k}$ values must also increase or decrease. Thus, without annual survey data and (or) better effort data, it is not possible to estimate F for each year, either by sharing information among lakes or in any single lake. This distinction represents a difference between the models developed here and modeling approaches such as statistical catch at age models or virtual population analysis, both of which use information on absolute removals or effort to disentangle the interacting effects of fishing mortality rates and recruitment in age-structured models (e.g., see Quinn and Deriso 1999; Walters and Martell 2004).

The final term $vf_{a-1,k}$ in Eq. 2 represented the relative vulnerability to fishing, and thus adjusted the instantaneous fishing mortality experienced by fish of a given size. We assumed relative vulnerability to angling increased with fish length according to

$$(5) \quad vf_{a,k} = l_{a,k}^{\psi},$$

where ψ is a parameter that describes the increase in vulnerability to angling as fish size increases and which was assumed to be $\psi = 2$. We evaluated this assumption using an independent analysis and catch-at-age data from creel surveys conducted in 17 lakes during 1984-1988 and conduct a sensitivity test assuming a different structural form of this relationship in Supplement A. We chose these creel surveys to inform the fishing vulnerability relationship because lakes had a five fish bag limit with no size limit during this period, and thus anglers were free to harvest any Walleye they sought (Sullivan 2004). Thus, we modeled fishing vulnerability for a given lake as a function of the growth characteristics in that lake and the assumed $\psi = 2$.

Stock and recruitment

We imposed both Beverton-Holt (asymptotic) and Ricker (dome-shaped) stock-recruitment relationships on $R_{t,k}$ values (Ricker 1954; Beverton-Holt 1957). These relationships result in different advice on sustainable harvest rates and so we consider both here to ensure our findings are robust to this key structural uncertainty (Quinn and Deriso 1999; Brännström and Sumpter 2005). We modeled Beverton-Holt dynamics as

$$(6) R_{t,k} = SSB_{k,t} - 2 \cdot \frac{e^{ar_k + w_{k,t}}}{1 + br_k \cdot SSB_{k,t} - 2},$$

where

$$(7) br_k = \frac{(e^{ar_k \cdot sbro_k} - 1)}{R_{0k} \cdot sbro_k}$$

$$(8) SSB_{k,t} = \sum_a N_{a,t,k} f_{a,k}$$

and

$$(9) f_{a,k} = \begin{cases} 0 & \text{if } a < a50_k \\ \max(0, l_{a,k}^{\beta_k}) & \text{if } a \geq a50_k \end{cases}$$

Here ar_k 's represent lake-specific average maximum egg survival to age-2 and are unknown parameters to be estimated, $w_{k,t}$ represent observation errors estimated from the data, br_k are lake-specific density-dependent effects on egg survival, and $SSB_{k,t}$ represents female spawning stock biomass in units kg/ha. In Eq. 7, br_k terms were derived from ar_k and two other terms. The first of these terms, R_{0k} , represented lake-specific average unfished recruitment values and was estimated. The second term $sbro_k$ was the lake-specific spawner biomass per recruit in the unfished state, which was calculated as $\sum_a f_{a,k} l_{a,k}$ where unfished survivorship $l_{a,k}$ was calculated recursively as

$$(10) \quad l x_{a,k} = \begin{cases} 1 & \text{if } a = 2 \\ l x_{a-1,k} \cdot e^{-M_{a-1,k}} & \text{if } 2 < a \leq 20 \end{cases}$$

Next, we modeled Ricker stock-recruitment dynamics as

$$(11) \quad R_{t,k} = SSB_{k,t-2} \cdot e^{ar_k + w_{k,t} - br_k \cdot SSB_{k,t-2}}$$

and

$$(12) \quad br_k = \frac{ar_k + \ln(sbro_k)}{R_{0k} \cdot sbro_k},$$

where all remaining quantities were defined as in the Beverton-Holt case. Walleye in Alberta were declining or fully collapsed by 1980 (Post et al. 2002; Sullivan 2004), which was 20 years before the first standardized survey occurred and when models were initialized. Thus, we were unable to initialize models using the commonly used unfished equilibrium assumptions (e.g., see methods in Ahrens et al. 2020). To overcome this challenge, we specified initial recruitment values in 1980-81 as

$$(13) \quad N_{a=2,t=1 \text{ and } 2,k} = G_k \cdot R_{0k}$$

for both the Beverton-Holt and Ricker cases. In this parameterization, G_k are additional estimated parameters that represent the proportion of the mean unfished recruitment level expected during the first two years in the model.

We attempted to estimate average Walleye stocking survival in our assessment models but were unable to because this quantity was often low and highly variable (e.g., stocking to age two survivorship was typically ≤ 0.01 and sometimes apparently greater than 0.1). Because this quantity was inestimable, we instead multiplied the number of fish per hectare stocked two years previously by an assumed stocking survival rate of 0.01 percent, and plotted this alongside estimated recruitment trends. This helped visualize the influence and efficacy of stocking

practices on Walleye population dynamics throughout Alberta. The two-year staggering was required because fish did not appear in the population dynamics models until age two. We assumed this stocking-to-age-two survivorship value because it allowed us to visualize stocking data and recruitment trends on the same scale.

Predicting survey catch-at-age, likelihood, and an analytical solution for recruitment

Equations 2-13 define the framework with which to calculate numbers at age in each lake during 1980-2018, and we now extend this to predict survey catch-at-age in any lake-year combination $C_{k,a,t}$ using

$$(14) \quad C_{k,a,t} = N_{a,t,k} \cdot nnet_{t,k} \cdot p_{t,k} \cdot v_{a,k}.$$

The term $nnet_{t,k}$ represents total net effort for a survey, where half-nets were given a value of 0.5 and regular nets a value of 1. The final term $v_{a,k}$ describes increasing vulnerability to the survey nets which was assumed to increase with the swimming speed of fish, where relative length of fish was used as a proxy for swimming speed (Taylor et al. 2005):

$$(15) \quad v_{a,k} = [l_{a,k} \cdot (1 - e^{vbk_k \cdot a})]^\varphi.$$

Here, φ is a parameter describing the increase in vulnerability to the survey gear and assumed shared among lakes, which seemed reasonable given lakes were surveyed using standardized methods (see arguments in Smith et al. 2017). We estimated φ for all lake-year surveys and read this into our model as a fixed value (Supplement A).

A statistical model for the $O_{a,t,k}$ values is the Poisson likelihood, which can be used to contrast the observed data against model predictions via

$$(16) \quad \ln L = \sum_k \sum_{t(k)} [-C_{a,t,k} + O_{a,t,k} \cdot \ln(C_{a,t,k})].$$

Here the outer sum is over lakes and the inner sum is over years $t(k)$ for which lake k was surveyed, and we note that this specification ensures each catch-at-age observation contributes to the total log-likelihood $\ln L$. This specification leverages the duality between the multinomial and Poisson distributions and can improve mortality rate estimates, particularly when recruitment variability is high (Millar 2015). This model can be fit by maximum likelihood or Bayesian methods (Hilborn and Mangel 1997), the latter of which is developed in the next section.

If one assumes Poisson distributed catch-at-age values, an analytical solution to the maximum likelihood estimates of the recruitment values $R_{t,k}^*$ can be obtained by differentiating the likelihood function in Eq. 16 with respect to the $R_{t,k}$ terms and then setting this derivative to zero. This solution leads to a direct conditional maximum likelihood estimate of $R_{t,k}^*$ for any lake k as

$$(17) \quad R_{t,k}^* = \frac{\sum_{a'} O_{a'+2, t+a', k}}{\sum_{a'} S_{a'+2, t+a', k} \cdot n_{t+a', k} \cdot p_{t+a', k} \cdot v_{a', k}},$$

where a' is a vector of ages from 2 to 20 and $S_{a,t,k}$ is the survivorship matrix for fish in lake k . This solution is noteworthy because it requires no assumption that the $R_{t,k}$ values are distributed around a stock-recruitment relationship and because it removes t by k parameters from the nonlinear estimation procedure in statistical catch at age models. We originally fit models using the analytical approach because it improved estimation speed and allowed us to quickly evaluate model runs and visualize emergent recruitment trends throughout Alberta. We ultimately elected to forgo the analytical approach and chose to explicitly incorporate stock-recruitment relationships into models because this allowed us to “see” further back in time and explore what recruitment levels must have been before the $SSB_{k,t}$ estimates were available. Additionally, inclusion of the stock-recruitment relationships enabled us to project models forward in time and

compare policy options for managers. Nonetheless, the analytical solution presented here is a useful way to recreate recruitment trends when computational efficiency is important.

Extension to Bayesian estimation

We extended the model above to the Bayesian framework because we sought to incorporate prior information on Walleye declines during the invisible collapse and because this allowed us to calculate derived quantities of use to fisheries managers (Punt and Hilborn 1997). Extending the $\ln L$ in Eq. 16 to a posterior density is done by adding the natural logarithms of the priors to the $\ln L$ as

$$(18) \quad \text{posterior} = \ln L + \sum_{k,t} \ln(w_{k,t}) + \sum_k [\ln(ar_k) + \ln(R_{0k}) + \ln(G_k) + \ln(F_{\text{early},k}) + \ln(F_{\text{late},k})]$$

and then using an algorithm such as Markov chain Monte Carlo (MCMC) to simulate the posterior distribution.

We estimated ar_k , $w_{k,t}$, R_{0k} , G_k , $F_{\text{early},k}$, and $F_{\text{late},k}$, and list all priors for these parameters in Table 2. We specified lake-specific informative priors for ar_k as

$$(19) \quad ar_k \sim \text{normal}(\mu_{ar_k}, \sigma_{ar_k} = 0.1),$$

where

$$(20) \quad \mu_{ar_k} = \ln\left(\frac{\phi}{s_{brok}}\right).$$

Here the lake-specific mean μ_{ar_k} used to inform the ar_k estimates was based on the Goodyear Compensation ratio ϕ (Goodyear 1980) and s_{brok} . Compensation ratio represents the slope of the stock-recruitment relationship at low stock sizes as the ratio of juvenile survival rate at low

population size to the juvenile survival rate of an unfished population (Walters et al. 2006). In addition to both Beverton-Holt and Ricker dynamics, models were run assuming two different values for ϕ . We selected ϕ values of 6 and 12 because meta-analyses indicate that fish with life history characteristics similar to Walleye in Alberta demonstrate ϕ values in this range (Goodwin et al. 2006; Hilborn and Walters 2021). Additionally, we used small σ_{ar_k} values to safeguard against the known time-series bias that occurs when estimating stock-recruitment relationships in age structured models and note that failure to account for this bias results in substantial overestimation of stock productivity and hence sustainable harvest rates (Walters 1985; Korman et al. 1995). We conducted sensitivity tests of this assumption by using larger values for σ_{ar_k} for all model fits and runs (e.g., $\sigma_{\text{ar}_k} = 5.0$). These tests showed modest increases in ar_k for many lakes, similar to what we expected *a priori* for reasons elaborated upon in Walters (1985). To model recruitment anomalies we set the observation error component of recruitment to

$$(21) \quad w_{k,t} \sim \text{normal}(0, \sigma_w = 1.2).$$

We used an informative σ_w prior of 1.2 for the observation error terms because we encountered numerical issues when we assumed wider values. However, both our main findings and policy advice to managers were robust during prior sensitivity tests where we systematically varied σ_w from low to high values (i.e., runs from $\sigma_w = 0.1$ to $\sigma_w = 5.0$).

The final component of recruitment that we modeled was R_{0_k} , and we assumed prior distributions for these parameters as

$$(22) \quad R_{0_k} \sim \text{lognormal}(\mu_{R_0} = \ln(6), \sigma_{R_0} = \ln(3)).$$

These priors were used because they represented a plausible range of unfished recruitment values in the province (e.g., we expected R_{0k} to range from ~5 to 50 age-2 recruits). We had little information with which to inform estimates of G_k , and thus assumed vague priors for these parameters as

$$(23) \quad G_k \sim \text{normal}(\mu_G = 0, \sigma_G = 1)$$

and bounded G_k such that it had positive support.

In addition to the general knowledge that Walleye collapsed throughout Alberta by the mid-1990s (e.g., Sullivan 2003; Sullivan 2004), we used angling catch rates from the creel surveys to inform priors for $F_{\text{early}, k}$ and $F_{\text{late}, k}$. We chose this approach because there were not enough creel surveys to fit assessment models using traditional estimation methods. Angling catch rates from creel surveys conducted throughout Alberta show that average angling catch rate increased from approximately 0.2 to 1.25 fish/hr during 1984-2018 (Fig 3.). Assuming an age structured model with parameters similar to ours, we noted that the number of vulnerable Walleye (i.e., $\sum_a N_{a,t,k} \cdot v_{f,a,k}$) would have to increase by approximately 6-fold across lakes on average for this increase in angler catch to occur. This increase in the number of vulnerable Walleye implies that many lakes had higher mortality rates during the early period and were likely near

$$(24) \quad F_{\text{early}, k} \sim \text{normal}(\mu_{F_{\text{early}}} = 0.3, \sigma_{F_{\text{early}}} = 0.1)$$

while fishing mortality during the late period was lower on average and closer to

$$(25) \quad F_{\text{late}, k} \sim \text{normal}(\mu_{F_{\text{late}}} = 0.1, \sigma_{F_{\text{late}}} = 0.5).$$

The tight $\sigma_{F_{\text{early}}}$ value was necessary because there were no FWIN surveys during this period and thus fishing mortality was difficult to estimate. An exception to this were lakes where FWIN

surveys were conducted in the early 2000s and which also contained old fish, in which case mortality estimates could be informed by the available age-structure data collected during the netting surveys.

Generated management quantities

We assessed sustainability of Alberta Walleye fisheries during 2000-2018 using Kobe plots. For a single population, Kobe plots show the ratio of late period instantaneous fishing mortality to the fishing mortality rate thought to achieve maximum sustainable yield on the y-axis. The x-axis of a Kobe plot indicates the current spawning stock biomass relative to a spawning stock biomass thought to achieve maximum sustainable yield. The y-axis of the Kobe plot was calculated as

(26)
$$\frac{F_{late, k}}{F_{msy, k}}$$

and the x-axis of the Kobe plots as

(27)
$$\frac{\xi_k}{SSBo_k}$$

where ξ_k represented the average spawning stock biomass across years surveyed in a lake, $0.4 \cdot SSBo_k$ represented the proportion (40%) of the average unfished biomass assumed to achieve maximum sustainable yield (see below), and $SSBo_k$ was calculated as $R_{0_k} \cdot sbro_k$ (see also Mace 1994).

Fitting age-structured assessment models to survey data

We fit all models in Stan, which implements Hamiltonian Monte Carlo via the No-U-Turn sampling algorithm and which is more efficient than standard MCMC for many ecological models (Monnahan et al. 2017; Cahill et al. 2018). We fit a total of 220 Bayesian state-space

stock assessment models (i.e., 55 lakes x 2 structural assumptions about stock-recruitment relationships x low and high ϕ values = 220 total fits). All models were run with 10 chains and starting values for all parameters were initiated randomly for each chain. We discarded the first 1000 draws as a warmup and retained the next 1000 draws with a thinning rate of 1 to summarize posterior distributions for the parameters of interest. We visually inspected chains for mixing using ShinyStan (Gabry 2015), used Gelman-Rubin statistics to test for convergence to a common posterior mode among chains, and visually assessed parameter pairs plots for collinearity. We ensured model fits contained no divergent transitions, which is a diagnostic indicating whether the results from Stan's samplers are valid (Carpenter et al. 2016). We chose an adapt delta step size parameter of 0.999 and a maximum treedepth parameter of 15. These control parameters ensured estimated parameters for all fits had ≥ 1000 effective samples. We manipulated data and made figures using the R statistical computing environment and tidyverse (Wickham et al. 2019; R Development Core Team 2020) and made maps using open source information (South 2017). We also used the tidybayes package to manipulate Bayesian model output (Kay 2018). All code required to conduct these analyses is available at <https://github.com/ChrisFishCahill/unveiling>.

We developed an interactive web application (see Wszola et al. 2017; Chang et al. 2020) that provides access to all assessment model runs and key outputs that are useful for fisheries managers. This application also links to a one-page tableau summarizing key information from each lake's stock assessment for a given model run and is available at <https://fw-habitat-aep.shinyapps.io/BERTA/>. For the remainder of the manuscript we present results from the Beverton-Holt stock-recruitment relationship with $\phi = 6$ scenario unless noted otherwise.

Results for other stock-recruitment relationships and ϕ scenarios are available on the web application.

Results

Instantaneous fishing mortality rates

Models showed that the survey data were uninformative for most $F_{\text{early},k}$ estimates and that $F_{\text{late},k}$ estimates were often low but variable among lakes (e.g., $F_{\text{late},k}$ often ≤ 0.1 ; Fig. 4). Early period mortality rate estimates tracked the prior mean of 0.3 for most lakes, but there were exceptions to this as assessment models estimated lower values for $F_{\text{early},k}$ in three lakes (see Gods Lake, Unnamed 5, Winefred Lake; Fig. 4). Inspection of the age structure data for a subset of lakes showed that the difference between $F_{\text{early},k}$ estimates that tracked the prior and those which estimated off of the prior was due to the presence or absence of fish older than age 15 in surveys conducted during the early 2000s (see Gods and Winifred lakes vs. all other lakes; Fig 5). Conversely, late period fishing mortality rate estimates were well-informed by the netting data for all lakes and estimates of this quantity for 23/55 lakes were ≤ 0.1 (Fig. 4). Comparison of the age structure data for lakes with low vs. high $F_{\text{late},k}$ estimates indicated that the difference between these two groups was due to the truncation of age structure in lakes with higher estimates of fishing mortality (e.g., compare Pigeon Lake, Winefred Lake, and Lac Ste. Anne vs. Lac La Biche; Fig. 5).

Kobe plot results

Assessments showed that population sustainability according to Kobe plot quadrant rankings varied widely across the province (Fig. 6). Kobe plots indicated that 31/55 Walleye fisheries were sustainable (bottom right quadrant), 11/55 lakes were not overfished but

overfishing was occurring (upper right quadrant), 2/55 lakes were overfished but rebuilding (bottom left quadrant), and that 11/55 fisheries were overfished and still experiencing overfishing (upper left quadrant; Fig. 6). A total of 18/55 fisheries had mean survey spawning stock biomasses (SSB) values at or above the mean SSB estimated to occur at carrying capacity (i.e., posterior median estimates ≥ 1.0 along the x-axis; Fig. 6). Mapping the Kobe plot rankings across the Alberta landscape showed there was no clear spatial pattern to the assessment rankings, although the four southernmost systems assessed were in the upper left quadrant (inset Fig. 6). Status assessments were robust for most lakes across both structural forms of the stock-recruitment relationship and for both ϕ values (e.g., Fig. 7; upper two rows). Exceptions to this statement included some of the lakes in the upper left quadrant of Fig. 6 with relatively high values of F_{late} , which shifted to a different Kobe plot quadrant under the Ricker structural form with $\phi = 12$ (Fig. 7; bottom two rows). Additionally, post hoc inspections comparing assessment outputs and several potential predictor variables and maps of assessment quantities across the Alberta landscape are presented in Supplement B.

Stocking results

A total of 147 stocking events occurred in the lakes-years relevant to this study, and an average of 4.6 fish per ha were introduced per stocking event (min: <0.1 fish stocked per ha; max: 40.8 fish stocked per ha). Visualizing stocking data alongside reconstructed recruitment trends from assessments showed that survival of stocked fish to age-2 was low (e.g., often < the assumed value of 1% survival from time of stocking to age-2; Fig. 8) and poorly correlated with age-2 recruitment values estimated from models. For example, assuming all estimated age-2 recruits from the assessment models resulted from stocking showed stocking survival to age-2 to be approximately 1% for Lac La Biche but also showed that stocking survival was likely lower

in other systems like Lake Newell (left hand column; Fig. 8). Stocking data for Pigeon Lake showed that stocking activities potentially contributed to the age-2 recruitment pulse observed in the early 2000s (upper right panel; Fig. 8). However, Buck Lake also showed an age-2 recruitment pulse in 2000 and was only 50 km away from Pigeon Lake but was not stocked (bottom right panel; Fig. 8).

Recruitment dynamics

Age-2 recruitment reconstructions revealed that 33/55 assessed lakes demonstrated large recruitment pulses that were on average 10-40 times the average recruitment level for a given lake during 1998-2002 (Fig. 9). These large recruitment events were present throughout the province, in lakes that were near and distant from population centers, and in systems for which survey data also showed evidence of low F_{early} estimates (e.g., Unnamed 5 in remote northeastern Alberta; Fig. 9). Recruitment anomalies occurred in lakes that were both stocked and unstocked (e.g., Pigeon Lake vs. Buck Lake; Fig. 9). Inspection of age-2 recruitment trends alongside spawning stock biomass (SSB) trajectories showed that recruitment anomalies first occurred at low spawning stock biomasses for most lakes, and that subsequent increases in SSB have in general not resulted in larger recruitment events (see panels for Amisk Lake; Baptiste Lake; Gods Lake; Lac Ste. Anne; Lesser Slave Lake; Pigeon Lake; Fig. 10). A smaller subset (15/55) lakes demonstrated cyclic age-2 recruitment dynamics (see panels labeled “cycle” in Fig. 10; Supplement C). Cycles had periods of 6-10 yrs (e.g., see Buck Lake Figs 8-9 and Baptiste Lake Figs 9-10), and these dynamics were also present in lakes throughout the province. The earliest evidence of cyclic recruitment dynamics occurred in Unnamed 5 in 1989 (see Fig. 9).

Discussion

By fitting stock assessment models to data from 55/123 surveyed Alberta Walleye lakes our work challenges the belief that neither the data nor the technical capacity exists with which to assess inland fish population dynamics and inform policy across broad spatial-temporal scales (e.g., Cooke et al. 2014; Arlinghaus et al. 2017). Because of this belief, many tools have been developed to replace the assessment models used in data-rich fisheries more generally. These data-limited tools often rely on static representations of the population(s) in question or fail to incorporate observation or process considerations required to reliably assess fish populations (see Hilborn and Walters 1992; Quinn and Deriso 1999). For example, some methods used to assess fisheries across landscapes do not account for fishing or survey vulnerability (e.g., MacPherson et al. 2014) or neglect to incorporate density dependence in juvenile survival via a stock-recruitment relationship as the key ecological factor determining sustainable harvest rates (see Lester et al. 2014b; Embke et al. 2019). In doing so these approaches ignore the wealth of knowledge and experience gained from assessing data-rich fisheries throughout the world (Hilborn and Liermann 1998; Myers et al. 1999). Furthermore, assessing fishery status across landscapes using age-structured models is more attainable now than ever before as several agencies coordinate monitoring programs similar to the Alberta FWIN program (e.g., see Lester et al. 2020). While stock assessment models were mathematically explicit, none of our findings required methodological advances for fisheries science more generally (see similar methods used in Beverton and Holt 1957; Fournier and Archibald 1982; Punt and Hilborn 1997; Millar 2015; Monnahan et al. 2019).

Stock assessments provided new insights into the sustainability of Alberta Walleye fisheries when late period fishing mortality rates and survey biomasses were compared to lake-specific F_{msy} and SSB_0 reference points. Examination of fishing mortality rate and survey

biomass patterns among lakes indicated that many fisheries have been lightly exploited in recent years and thus could safely sustain higher fishing rates. For example, assessments showed that one-third of fisheries had fishing mortality rates that were close to zero and featured average survey biomasses that were at or above their average unfished biomass estimates (i.e., ≥ 1.0 on the x-axis of the Kobe plot in Fig. 6), the combination of which indicates that additional harvests could have been safely taken during 1997-2018 (e.g., most MSY estimates were approximately 1-2 fish / ha per yr). The finding that foregone harvest opportunities existed in many lakes during 1997-2018 contradicts the widespread belief that most Alberta Walleye populations are heavily or even fully exploited (e.g., see Pigeon Lake in Fig. 6; Post et al. 2002; Sullivan 2003; Spencer 2010; Government of Alberta 2018). While this finding contradicts earlier work, the present study was the first to use both survey trend and size-age data to estimate current mortality rates and biomass trends relative to standard reference points like F_{msy} or SSB_0 . Without explicit estimation of reference points it is not possible to identify when new fishing opportunities become available or whether overfishing is occurring (Hilborn and Walters 1992; Walters and Martell 2004). The unexpected finding of foregone harvest opportunities in many Alberta Walleye lakes demonstrates the importance of fitting stock assessment models to data in situations where it is now possible to do so (see also Hilborn and Mangel 1997).

While some of our findings contradict previous work on Alberta Walleye, other results support earlier hypotheses. For example, we estimated low F_{msy} values for all lakes (i.e., typically ≤ 0.2 - 0.3 depending on assumptions about stock productivity). The finding that all populations had relatively low F_{msy} values provides the first quantitative evidence that Alberta Walleye are vulnerable to overexploitation and thus that regulations are important for conserving their populations. This corroborates a central claim from Post et al. (2002) and Sullivan (2003),

as both authors hypothesized that Alberta Walleye should be vulnerable to overharvest because these fish experience cold climates near the range limits of the species and because of their longevity. Whereas Post et al. (2002) and Sullivan (2003) hypothesized that Walleye fisheries were vulnerable to overharvest, we estimated the magnitude of instantaneous fishing mortality rates and annual removals that could be considered sustainable by managers. A rule-of-thumb emerging from our work for Alberta managers is that policies that allow instantaneous fishing mortality rate to exceed approximately 0.2-0.3 or total removals to exceed 1-2 fish / ha per yr should be viewed with caution from a conservation perspective, and if policies exceed these levels they should be evaluated using adaptive management (Walters 1986; Hilborn and Walters 1992). More stringent policies could be targeted on precautionary grounds (see Carpenter et al. 2017 for a qualitative example), but such objectives should be explicitly (i.e., quantitatively) defined (Edwards and Dankel 2016).

In addition to assessing fish populations across a landscape, our work unveils the population dynamics of Alberta Walleye following the invisible collapse and contributes new information on the ecological processes leading to their recovery. Recruitment reconstructions indicated that positive recruitment anomalies first occurred at low SSB during 1998-2002, that these strong year classes were present in 33/55 fisheries, and that recruitment pulses were present in lakes whether they had low or high F_{early} or F_{late} . The observation that strong year classes occurred in both remote and accessible lakes and regardless of fishing mortality rate suggests that environmental forcing or overcompensation due to cannibalism drove recovery in many Walleye populations (see Parma and Deriso 1990; Claessen et al. 2004). Additionally, SSB recovery from heavily exploited or even collapsed states occurred more rapidly than would be expected had regulations alone been responsible for the observed SSB increases. This finding

indicates that Walleye recovery was not exclusively due to the implementation of regulations as has been previously reported (see Sullivan 2003), but rather that favorable recruitment events drove recovery of SSBs in many lakes, and that these cohorts were then protected by the regulations described in Sullivan (2003).

While it is possible that Walleye were headed toward extinction due to recruitment failures that occurred at low SSB in at least some lakes (i.e., compensatory stock-recruitment; Walters and Kitchell 2001; Sass et al. 2021), assessments showed that many of these populations were “rescued” by strong recruitment events that occurred in the late 1990s to early 2000s and before SSB could have recovered following fishing mortality reductions in 1996. This finding raises the important possibility that at least some Walleye populations have always been sustained by occasional episodic recruitment events, and persisted under high fishing pressure because favorable recruitment events occurred even though population age structures and egg production were severely impacted by high fishing rates (see Sullivan 2003; Sullivan 2004; this study). Simulation studies indicate that the same basic fixed-escapement harvest policies that achieve maximum average yield in fish populations with less variable recruitment should also result in maximum average yield for stocks that feature episodic or spasmodic recruitment dynamics (Koslow 1989, 1992), and that moderate but stable fishing mortality rates should result in sustainable fisheries with less variation in fishing opportunity than implied by fixed-escapement policies. However, future work evaluating these and other policies specific to inland fisheries using management strategy evaluation is needed (see approaches in Edwards and Dankel 2016).

In addition to demonstrating that recruitment pulses drove recovery in many Alberta Walleye lakes, the discovery of cyclic recruitment dynamics in an inland fishery is a striking

reminder of the difficulty of analyzing landscape-scale data, particularly when invoking theories or methodologies that ignore the potential for fish population dynamics (Hilborn and Walters 1992). Cycles are a hallmark of complex population dynamics (Turchin 2003), and population reconstructions in 15/55 lakes showed at least some evidence of cyclic recruitment behavior with periods of 6-10 years. Cyclic recruitment fluctuations are not well documented for Walleye even though it is among the most well-studied fish species worldwide (see Ritchie and Colby 1988; Bozek et al. 2011), and such dynamics could be caused by delayed mortality (e.g., cannibalism) or environmental effect(s) which can both influence juvenile survival (see Parma and Deriso 1990; Botsford and Hobbs 1995). Walleye recruitment has been associated with cannibalism and environmental variables such as growing degree days (GDD) or water levels (e.g., Cuff 1980; Quist et al. 2003; Nate et al. 2011; Honsey et al. 2020), but it is difficult to determine the relative importance of intrinsic vs. extrinsic factors regulating recruitment using observational data (see Parma and Deriso 1990). Thus, adaptive management is likely necessary to evaluate the degree to which these factors influence recruitment patterns in Alberta Walleye populations (see Walters 1986; McAllister and Peterman 1992).

While not a primary objective of our work, qualitative examination of stocking records plotted alongside age-2 recruitment trajectories yielded insights into the efficacy of Walleye stocking practices in Alberta. For example, even though stocking survival to age-2 was an assumption in our models, there was low correlation between the number of Walleye stocked at age-0 and estimates from the survey data of age-2 recruitment two years later. This low correlation between stocking rates and estimated age-2 recruitment rates does not change depending on our assumed value of stocking survival; instead, this assumption scales the stocking values appearing on our recruitment trajectory plots (e.g., see Supplement A). This

617 finding of low correlation between stocking rate and subsequent age-2 numbers aligns with
618 literature showing that the outcome of Walleye stocking is highly variable and often
619 unsuccessful (see Kerr 2011; Raabe et al. 2020). Recent public pressure in Alberta has renewed
620 interest for a supplemental stocking program that proponents claim will improve angling
621 opportunities, the economy, and offset the effects of exploitation in Walleye fisheries. However,
622 such a program is unlikely to achieve all these objectives as highly variable proportions of
623 stocked fish apparently survive to age-2, and because these fish do not become fully vulnerable
624 to angling until ages 5-7 (Supplement A). Additionally, Lac La Biche—a regionally important
625 fishery—was the most heavily stocked lake in this study but assessment models showed this
626 fishery was heavily exploited and likely unsustainable (Fig. 6).

627 Some of our assessment assumptions are questionable, particularly about vulnerability,
628 natural mortality, and temporal patterns in fishing mortality. First, the survey vulnerability
629 exponent φ and the instantaneous natural mortality rate M_0 represented key assumptions in our
630 models. Sensitivity tests showed that varying these parameters altered the scale of the
631 recruitment estimates but did not affect the trends. However, uncertainty in M_0 also influenced
632 estimates of $F_{\text{late},k}$, particularly in lakes with higher estimates of late period fishing mortality.
633 We used a value of $M_0 = 0.1$ as a conservative starting point, but post hoc inspections revealed
634 there was a weak positive relationship between $F_{\text{late},k}$ and growing degree days, with the highest
635 $F_{\text{late},k}$ estimates coming from the four southernmost (warmest) systems included in our study
636 (Fig. 6). This suggests that natural mortality may be higher in southern Alberta, which is
637 consistent with metabolic theory and empirical estimates of M_0 for Walleye in similar climates
638 (see Pauly 1980; Hansen et al. 2011) and which means that assessments were too conservative in
639 the southern systems. Models also had difficulty “seeing” backward in time to estimate

recruitment events that occurred before surveys began. The age composition at the time of the first survey in a lake is a function of the fishing mortality and recruitment rates in the years leading up to that survey (Porch et al. 2006), and inconsistent creels meant that we had to assume fishing rates were relatively stable to obtain reliable recruitment estimates. The hindcasting of early recruitments would have been more credible had we been able to inform the estimates of pre-survey fishing mortality rates with more consistent information on historical catches (Hilborn and Walters 1992), and which is opposite to what occurs in saltwater data-limited assessments where information on total removals is available but fishery independent surveys are unavailable (Free et al. 2020). In situations where creel and FWIN surveys overlapped we approximated direct fishing mortality rate estimates as catch divided by the vulnerable abundance estimated from the assessment models (see Ricker 1975), and the resulting values were all low and consistent with assessments. Nonetheless, a direction for future work in Alberta is the development of inexpensive monitoring tools to quantify fishing effort and the pairing of these with the ongoing FWIN surveys (see approaches in Trudeau et al. 2021), which would enable direct mortality rate estimates and reduce assessment uncertainty.

It is neither new nor novel to fit age-structured models to fisheries data (Fournier and Archibald 1982), and yet coupling old methods with existing data from a landscape-scale monitoring program has allowed us to reconstruct the recovery dynamics of Walleye following the invisible collapse (Post et al. 2002). In doing so, we have unveiled a remarkable complexity of ecological dynamics that has gone unrecognized for over two decades and which has far-reaching implications for inland fisheries conservation. We believe this juxtaposition says much about the development of inland fisheries science and management since Post et al. (2002), and implies that in some cases where data have accumulated traditional assessment models have been

written off because they are mathematically difficult or perhaps because such methods are not in vogue among inland researchers (e.g., Ricker 1975). As a discipline we seem to assume that because *all* fisheries across a landscape cannot be assessed using age-structured methods that there will be little or no use in assessing as many *as is feasible* (see Arlinghaus et al. 2017), despite the fact that even a handful of assessments could contribute a wealth of ecological information beyond simply estimating population status (Hilborn and Walters 1992; this paper). Perhaps the best scientific rationale for adopting approaches like those used here is that they provide a consistent and explicit framework through which competing hypotheses about the dynamics and sustainability of fisheries can be contested against data (Hilborn and Mangel 1997). Thus, these approaches provide an effective means through which prevailing views can either be refuted or turned into evidence (Walters 1986; Punt and Hilborn 1997), and from where we can advance the science of inland fisheries assessment and management.

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Table 1. Symbols, definitions, and sources used to develop models. See Table 2 for all estimated parameters and prior distributions.

Symbol	Definition	Value(s)	Source(s)
a	Age	2-20	-
t	Year	1980-2028	-
k	Lake	1-55	-
$O_{a,t,k}$	Observed catch per unit effort	-	-
$P_{t,k}$	Proportion of fish with age estimates in survey t,k	0.09 to 1.0	-
$N_{a,t,k}$	Numbers at age	-	-
$R_{t,k}$	Age 2 recruits	-	-
$M_{a,k}$	Instantaneous natural mortality at age	-	Lorenzen 2000, 2005
M_0	Asymptotic instantaneous natural mortality	0.1	Assumed, based on empirical longevity of ~ 25 yrs for Walleye in Alberta
$l_{a,k}$	Relative length at age	-	-
θ	Power coefficient for age-specific instantaneous natural mortality	0.85	Assumed, based on Hansen et al. 2011 and Vandergoot and Brenden 2014
$l_{\infty,k}$	Lake-specific asymptotic maximum length (cm)	-	Cahill et al. 2020
$\bar{l}$	Average among lake value for asymptotic maximum length	58	Cahill et al. 2020
$\nu b k_k$	Brody growth coefficient	-	Cahill et al. 2020
$F_{period,k}$	Instantaneous fishing mortality during "early" or "late" period	-	-
$\nu f_{a,k}$	Relative vulnerability to fishing	-	-
ψ	Parameter describing increase in vulnerability to angling	2	Creel survey data from 17 lakes during 1984-1988
$R_{t,k}$	Age-2 recruitment	-	-
$SSB_{k,t}$	Female spawning stock biomass	-	-
$sbro_k$	Spawner biomass per recruit unfished	-	Calculated using life history characteristics and M
br_k	Density- dependent effects on egg survival	-	Ricker 1954 and Beverton and Holt 1958
$w_{k,t}$	Observation error terms for recruitment	-	-
$f_{a,k}$	Fecundity at age	-	-
β_k	Weight-length regression growth exponent	-	Life history meta-analysis
$a50_k$	Age at 50% maturity	-	Life history meta-analysis
$lx_{a,k}$	Unfished survivorship	-	Walters and Martell 2004
$C_{a,t,k}$	Predicted catch at age	-	-
$nnet_{t,k}$	Number of nets in survey	-	-
$v_{a,k}$	Fish vulnerability to the survey gear	-	Taylor et al. 2005
ϕ	Parameter describing increase in vulnerability to survey gear	2.42	Estimated from FWIN catch-at-age data in all lakes-years
$R_{t,k}^*$	Conditional maximum likelihood estimate of recruitment	-	This manuscript
$F_{msy,k}$	Instantaneous fishing mortality rate at maximum sustainable yield	-	-
ξ_k	Average SSB during survey years	-	-

Table 2. Parameters, definitions, and prior distributions or values used to fit models. Bold font indicates an estimated parameter while normal font indicates this value was fixed (e.g., ϕ), or calculated using lake-specific life history characteristics (e.g., $sbro_k$). Models were fit assuming both Beverton-Holt and Ricker stock-recruitment models and two different ϕ values.

Parameter	Definition	Prior distribution or value
ar_k	Average maximum egg survival to age 2	Normal(μ_{ar_k} , $\sigma_{ar_k} = 0.1$)
μ_{ar_k}	Lake-specific mean for ar_k	$\ln\left(\frac{\phi}{sbro_k}\right)$
ϕ	Goodyear compensation ratio	6 or 12
$sbro_k$	Spawner biomass per recruit in the unfished condition	Dependent on lake-specific life history parameters
$w_{k,t}$	Observation error terms for recruitment anomalies	Normal($0, \sigma_w = 1.2$)
R_{0k}	Average unfished recruitment	Lognormal($\mu_{R_0} = \ln(6)$, $\sigma_{R_0} = \ln(3)$)
G_k	Proportion of the mean unfished recruitment level for initial years	Normal($\mu_G = 0, \sigma_G = 1$)
$F_{early,k}$	Average instantaneous fishing mortality during 1980-1996	Normal($\mu_{F_{early}} = 0.3, \sigma_{F_{early}} = 0.1$)
$F_{late,k}$	Average instantaneous fishing mortality during 1997-2018	Normal($\mu_{F_{late}} = 0.1, \sigma_{F_{late}} = 0.5$)

Figure 1. Distribution of lakes in Alberta where Fall Walleye Index Netting occurred ≥ 3 times during 2000-2018 (black points) versus lakes where Walleye are known to occur, but which were not assessed (open points). Inset: location of study area in Canada. Map created in R using publicly available datasets. See Materials and methods for information on datasets.

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920 **Figure 2.** Catch-at-age data collected using Fall Walleye Index Netting from Buck Lake,
 921 Alberta during 2003-2017. Bubble size corresponds to the relative number of fish caught each
 922 year at a given age. This plot demonstrates Paloheimo's "design effects" in catch-at-age data
 923 and age effects are visible along the y-axis, year or temporal effects are apparent along the x-
 924 axis, and recruitment effects occur along the diagonal of the plot.

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Figure 3. Average angler catch per unit effort from 169 creel surveys conducted in 64 lakes throughout the Alberta during 1984-2018 using the standardized methods in Walker et al. (2007).

Figure 4. Instantaneous fishing mortality estimated for “early” (1980-1996) and “late” periods (1997-2018) using catch-at-age data collected via the Alberta Fall Walleye Index Netting program during 2000-2018. Circles represent posterior medians, while thick and thin lines represent the 0.25-0.75 and 0.10-0.90 quantiles, respectively.

Figure 5. Bubble plots of catch-at-age data from a subset of 9/55 lakes surveyed using Fall Walleye Index Netting during 2000-2018. Bubble size corresponds to the relative number of fish caught each year at a given age, while posterior median estimates of instantaneous fishing mortality rates for an early period (F_{early} ; 1980-1996) and late period (F_{late} ; 1997-2018) are indicated in the upper-left corner of each panel.

Figure 6. Kobe plot lake status estimates using average instantaneous fishing mortality rate during the late period (1997-2018) and average spawning stock biomass during surveyed years for a given lake relative to their maximum sustainable yield reference points (crosshairs). Points indicate posterior median estimates. Inset: location of assessed lakes in Alberta, and point colors correspond to Kobe plot quadrant colors in the main figure. Note: uncertainty intervals for the Kobe plot quantities are available for each lake and model run in the online portal available at <https://fw-habitat-aep.shinyapps.io/BERTA/>. Map created in R using publicly available datasets. See Materials and methods for information on datasets.

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Figure 7. Sensitivity of Kobe plot status rankings for 4/55 lakes (rows) given different assumptions about the structural form of the stock-recruitment relationship and value of compensation ratio (i.e., Beverton-Holt or Ricker shapes and $\phi = 6$ or 12; columns). Yolks represent the 0.25-0.75 posterior quantile, the edge of the egg-white represents the 0.9 quantile, and the salt-and-pepper flecks indicate posterior draws. Crosshairs indicate maximum sustainable yield reference points.

Figure 8. Age-2 recruitment trajectories (solid lines; posterior medians) for a subset of 4/55 lakes surveyed using Fall Walleye Index Netting during 2000-2018. Diamonds indicate the number of Walleye stocked per hectare two years earlier assuming 1% of these fish survived to age-2. Buck lake was not stocked during 1980-2018 and is approximately 50 km from Pigeon Lake.

Figure 9. Mean standardized age-2 recruitment trends using Fall Walleye Index Netting data collected during 2000-2018. Solid lines indicate posterior medians, while dark shaded and light shaded regions indicate 0.25-0.75 and 0.10-0.90 credible intervals, respectively. Vertical shaded regions indicate that a recruitment pulse of 10-40x average recruitment levels occurred during 1998-2002. Panels labeled “cycle” exhibit evidence of cyclic recruitment dynamics.

Figure 10. Female spawning stock biomass and age-2 recruitment trajectories for a subset of 9/55 lakes surveyed using Fall Walleye Index Netting during 2000-2018. Solid lines indicate posterior medians, while dark shaded and light shaded regions indicate 0.25-0.75 and 0.10-0.90 credible intervals, respectively. Black points denote “observed” spawning stock biomass (SSB) values and thus are only present in surveyed years. Black bars indicate the observed SSB value ± 0.3 coefficient of variation. See Supplement C for trajectory plots for all lakes including stocking icons, which are not shown here for simplicity.