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ARTICLE

An Improved Method for the Estimation and Comparison of Mortality Rates in Fish from Catch-Curve Data

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Abstract

Catch-curve analyses are routinely used to estimate instantaneous mortality (Z) in fish, and as the age-frequency data are often overdispersed, the application of a variance bias-correction factor has been recommended. The extensions of the Poisson generalized linear model ($GLM_{Poisson}$) may, however, constitute a better alternative, as they model the variance (SE) in counts more adequately with their specific dispersion parameter for more accurate estimations and statistical comparisons. To test this idea, simulated age-frequency data generated under four dispersion scenarios were analyzed according to six currently available methods and compared with the results of a $GLM_{Poisson}$ and five of its extensions to evaluate each method-specific bias in $Z \pm$ SE estimates. Empirical age-frequency data from sampled Walleye *Sander vitreus* and Arctic Char *Salvelinus alpinus* populations in Québec, Canada, were then used to illustrate the applicability of our GLM-based method, which relies on the behavior of Pearson residuals to assess model adequacy and an information-theoretic approach for model selection. All analyses revealed that Z-estimates were generally accurate among the methods considered, except under the most likely situation of quadratic overdispersion met in ecological studies, for which only the negative binomial type 2 and the mean-parametrized Conway–Maxwell–Poisson (CMP) extensions were adequate to estimate both Z and its SE. Linearly overdispersed data were best modeled by the negative binomial type 1 and generalized Poisson (GLM_{GP}) extensions; the GLM_{CMP} and GLM_{GP} were the most appropriate to model underdispersed data, whereas the $GLM_{Poisson}$ adequately modeled equidispersed data, similar to the Chapman and Robson (1960) method. Statistical comparisons of $Z \pm$ SE for grouping factors, such as year or site, were correctly achieved when the most adequate and statistically supported $GLM_{Poisson}$ extension was applied. Altogether, the proposed GLM-based method should help to circumvent the identified issues related to SE estimation for statistical inferences about mortality rates for fisheries management decision making.

The age-frequency data obtained from sampled fish, also referred to as catch-curve data, are often used to estimate instantaneous mortality (Z) on the logarithmic scale, which can then be converted into total annual mortality ($A = 1 - e^{-Z}$) on the more practical response scale (Miranda and Bettoli 2007). Such catch-curve analyses are generally conducted under strict assumptions that are often only partially met (Smith et al. 2012; Ogle 2016): (1) the population is closed to emigration and immigration, (2) recruitment is constant or at least varies without a trend over time, (3) Z is constant across ages and years for ages on the descending limb of the catch curve, (4) vulnerability follows the same conditions as for Z, and (5) the sample is not biased regarding any specific age-group. The last

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assumption implies that age estimates are accurate. Given these assumptions associated with a steady-state population, Z and its estimated uncertainty will almost always be biased to some degree (Murphy 1997; Nelson 2019) but are nonetheless useful to approximatively assess mortality rates in the absence of more accurate estimates derived from effort-intensive capture–mark–recapture data (Zabel et al. 2005; Dudgeon et al. 2015). For instance, comparing mortality rates between time periods for the same study site implies that some of the listed assumptions would not be met. However, the results obtained may still provide useful biological information for the assessment of a given population, especially when combined with other biodemographic parameters (e.g., Barbieri et al. 1994). Therefore, efforts should be made to use the least biased method for the estimation of Z and its associated error given the known limitations of this commonly used approach.

Among the different currently available methods for the estimation of mortality rates are that of Heincke (1913), the maximum likelihood approach of Chapman and Robson (1960; hereafter, "CR method"), the linear regression (LR) method of Ricker (1975), and its weighted version (WLR; Maceina and Bettoli 1998). Based on a simulation study aimed at assessing the bias in Z-estimates, Dunn et al. (2002) found that the CR method outperformed the LR method, which often underestimates Z. In a larger simulation study, Smith et al. (2012) assessed the previously mentioned methods to evaluate their respective bias and made four recommendations that should be applied to catch-curve analyses: (1) the CR method should be preferred using the "peak plus" criterion (see Figure 1), (2) the CR variance estimator should be corrected for overdispersion (CR with correction for bias [CRCB] method), (3) the LR method should no longer be used, and (4) the Heincke (1913) method generally performs poorly and should in most cases be disregarded. Smith et al. (2012) recognized that the WLR method often slightly outperformed the CR method, but they also indicated that its associated weighting procedure was purely ad hoc. More recently, Millar (2015) proposed the use of generalized linear models (GLMs) with a Poisson distribution to estimate Z, as Chapman and Robson (1960) reported that their approach was equivalent to considering that the age frequencies were Poisson distributed, with expected values decreasing geometrically with age. Building on the work by Smith et al. (2012) and Millar (2015), Nelson (2019) proposed an adapted "Poisson model" (PM) that also corresponds to a GLM fitted with a Poisson distribution, but it is applied to an artificially extended age structure with zero counts (see Millar 2015) and the SE estimate is corrected for overdispersion afterward, similar to the CRCB method. Nelson (2019) showed through simulations that the two CR methods and his adapted PM were the least biased for the estimation of Z.

Despite the variance bias-correction factor used to account for the often-overdispersed (i.e., variance > mean) age-frequency data, Nelson (2019) cautioned that the estimated SE obtained will almost always be downwardly biased and should thus not be used in statistical comparisons. Although obtaining the least biased Z-estimates is desirable for biological inferences, modeling the associated variance adequately is as important to draw valid inferences between and among different grouping variables of interest. The current statistical approach for the comparison of Z-estimates from catch curves relies on the LR method and the use of a GLM with a Gaussian (i.e., normal) distribution to compare the slopes ($\hat{Z}$) of $\log_e$ transformed age-class counts from, for instance, two lakes (Miranda and Bettoli 2007; Ogle 2016). This GLM approach allows an evaluation of whether the interaction between the variables "age" and "site" is statistically supported, which would then provide evidence of different mortality rates. However, use of the LR method as mentioned above is no longer recommended (Smith et al. 2012), and more importantly, count data in ecological studies should not be log transformed (O'Hara and Kotze 2010). Moreover, such a parametric test would require that the residuals of the investigated model are normally distributed and homoscedastic to produce valid statistical inferences. Fitting an error structure that is specifically designed for the modeling of age-frequency data is therefore more adequate to determine the rate at which counts decrease with age.

The Poisson distribution has been specifically developed for discrete variables and should thus be primarily used for the analysis of count data (Hilbe 2014). However, to produce reliable estimates, this distribution requires that the variance in counts be approximately equal to the mean (i.e., equi-dispersion), which is rarely observed in ecological studies, whereas overdispersion is far more frequent (Richards 2008). When counts are overdispersed, several extensions of the Poisson distribution can be considered to find the most adequate at modeling the extra variance observed in the age-frequency data, such as the negative binomial type 2 (NB2) extension that was previously suggested by Millar (2015). The NB2, along with the quasi-Poisson (QP), have been among the most commonly used extensions to model overdispersed data in ecological studies (Bliss and Fisher 1953; Ver Hoef and Boveng 2007; Demétrio et al. 2014), as both have a specific dispersion parameter that models the extra variance as a function of the mean (Hilbe 2014), which will generally allow a better fit to the observed data instead of applying a correction factor afterward. The Conway–Maxwell–Poisson (CMP; Sellers and Shmueli 2010), which has been more recently parametrized on its mean (Huang 2017), is also gaining
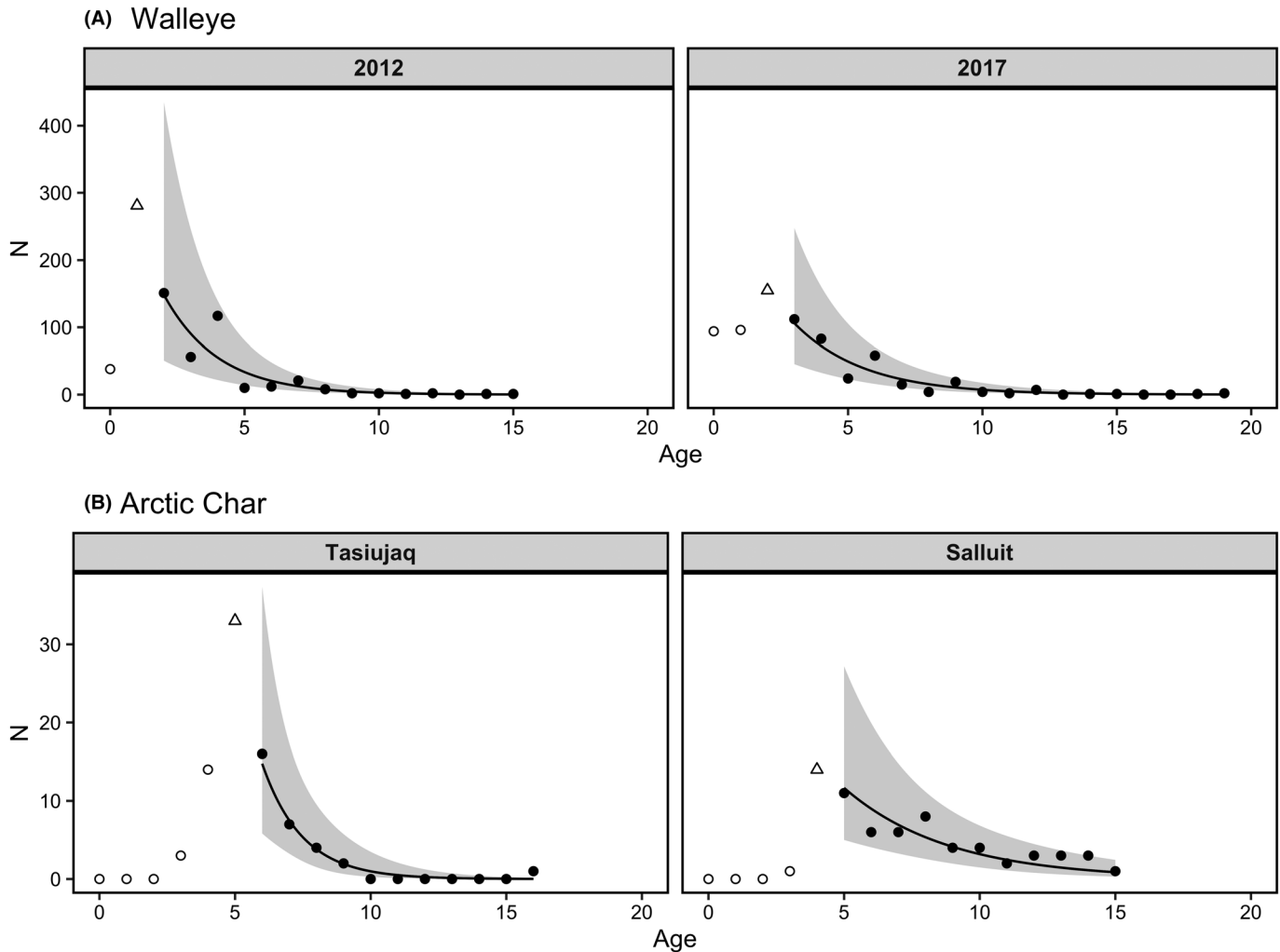
(A) Walleye

(B) Arctic Char

FIGURE 1. Age-frequency data of monitored fish populations in Québec, Canada, used for the estimation of instantaneous mortality rates (*Z*) from catch-curve analyses: **(A)** Walleye population (Baskatong Reservoir in 2012 and 2017) and **(B)** anadromous Arctic Char (Tasiujaq and Salluit) populations. The "peak" age (i.e., mode) is illustrated by the open triangle, whereas younger age-classes that are not fully recruited to the fishing gear are represented by open circles. The "peak plus" criterion (i.e., peak + 1) was used for the catch-curve analyses; thus, only the filled circles were considered for the estimation of *Z*, often referred to as the "descending limb" of the catch curve. Predicted values with their respective 95% CI (shaded area) according to each of the top-ranking log-linear models retained (see Table 3) are shown.

attention due to its ability to model both over- and underdispersed data (Lynch et al. 2014). The generalized Poisson (GP; Consul 1989), which can also be used when the assumption of equi-dispersion is not satisfied and especially with underdispersed data (Hilbe 2014), should also be considered with the mean-parametrized CMP in such circumstances, as they can sometimes provide better model adequacy for ecological inferences (e.g., Brooks et al. 2019). Determining whether these extensions fitted in GLMs may outperform the currently available methods is one of the main motivations behind the present investigation for both the estimation and statistical comparison of mortality rates.

In this study, six currently available methods and GLMs fitted with either the Poisson distribution ($GLM_{Poisson}$) or five of its derived extensions (Table 1) were first compared for the estimation of $Z \pm SE$ to assess their accuracy and precision according to the analysis of simulated catch-curve data. Our objective was to evaluate the relative performance of these different methods under the rationale that accounting for the variance with a dispersion parameter within the modeling of count data is expected to produce more reliable estimates, especially when the age-frequency data are overdispersed. Four dispersion scenarios were investigated for the simulation analyses: (1) equi-dispersion, (2) linear overdispersion, (3)

TABLE 1. Mean (±SD) estimated instantaneous mortality rate (Z) from 100 simulated data sets generated under four dispersion scenarios (equi-dispersion, linear overdispersion, quadratic overdispersion, and underdispersion) for six currently available methods and six generalized linear models (GLMs) considered when the true Z was fixed to 0.500 and the dispersion parameter was set to 1.0, 2.0, 2.0, and 0.5, respectively. The observed bias between the mean estimated Z under each dispersion scenario and the true value is expressed as a percentage of bias (%), and the sign (+ or −) is used to indicate the direction of the bias. The least biased method for each dispersion scenario is indicated in bold.

Method	Equi-dispersion	Linear overdispersion	Quadratic overdispersion	Under dispersion
Heincke	0.499 ± 0.040 (−0.15%)	0.502 ± 0.064 (+0.43%)	0.387 ± 0.453 (−22.5%)	0.502 ± 0.027 (+0.33%)
Linear regression (LR)	0.425 ± 0.057 (−14.9%)	0.429 ± 0.079 (−14.2%)	0.306 ± 0.118 (−38.8%)	0.457 ± 0.037 (−8.62%)
Weighted linear regression (WLR)	**0.500 ± 0.037 (+0.05%)**	**0.500 ± 0.060 (−0.03%)**	0.359 ± 0.182 (−28.2%)	0.503 ± 0.027 (+0.68%)
Chapman–Robson (CR)	0.498 ± 0.027 (−0.32%)	0.503 ± 0.043 (+0.56%)	0.442 ± 0.196 (−11.6%)	0.502 ± 0.017 (+0.30%)
Chapman–Robson corrected for bias (CRCB)	0.498 ± 0.027 (−0.45%)	0.502 ± 0.043 (+0.42%)	0.441 ± 0.195 (−11.7%)	0.501 ± 0.017 (+0.18%)
Adapted Poisson model (PM)	0.499 ± 0.027 (−0.11%)	0.504 ± 0.043 (+0.78%)	0.444 ± 0.196 (−11.3%)	0.503 ± 0.017 (+0.51%)
Poisson	0.492 ± 0.026 (−1.70%)	0.502 ± 0.026 (+0.48%)	0.429 ± 0.028 (−14.2%)	0.502 ± 0.026 (+0.45%)
Quasi-Poisson (QP)	0.492 ± 0.016 (−1.70%)	0.502 ± 0.025 (+0.48%)	0.429 ± 0.076 (−14.2%)	0.502 ± 0.011 (+0.45%)
Negative binomial type 1 (NB1)	0.492 ± 0.027 (−1.64%)	0.503 ± 0.039 (+0.53%)	0.311 ± 0.077 (−37.8%)	0.502 ± 0.026 (+0.45%)
Negative binomial type 2 (NB2)	0.492 ± 0.027 (−1.61%)	0.505 ± 0.040 (+1.07%)	**0.485 ± 0.103 (−2.95%)**	0.502 ± 0.026 (+0.45%)
Conway–Maxwell–Poisson (CMP)[a]	0.491 ± 0.023 (−1.77%)	0.503 ± 0.037 (+0.64%)	0.475 ± 0.083 (−4.90%)	**0.501 ± 0.017 (+0.11%)**
Generalized Poisson (GP)	0.492 ± 0.023 (−1.68%)	0.503 ± 0.039 (+0.59%)	0.319 ± 0.074 (−36.2%)	0.502 ± 0.017 (+0.38%)

[a] Mean-parametrized Conway–Maxwell–Poisson (Huang 2017).

quadratic overdispersion, and (4) underdispersion, knowing that the third scenario represents the most likely one encountered with ecological count data (White and Bennetts 1996; Alexander et al. 2000; Lindén and Mäntyniemi 2011). Fisheries data sets from (1) two Walleye *Sander vitreus* gill-net surveys that were conducted in two different years at the same study site and (2) two anadromous Arctic Char *Salvelinus alpinus erythrinus* populations that were monitored in different river systems in Nunavik (Québec, Canada) were used as examples (i.e., empirical data) to illustrate the applicability of our GLM-based method for the estimation and comparison of $\hat{Z}$. For the different GLMs considered, we aimed to determine which one provided the most statistically supported estimate of $Z \pm$ SE under the assumption that the age-frequency data analyzed from our samples offered a good approximation of the unknown age structure of each studied population. Lastly, comparisons of $\hat{Z}$ between years (Walleye) or between sites (Arctic Char) were investigated by testing

whether the interaction term with age obtained statistical support, similarly as described by Miranda and Bettoli (2007). Altogether, this investigation may provide further insights regarding the statistical interpretation of Z obtained from sampled age-frequency data for fisheries management purposes.

METHODS

Simulated age-frequency data.— A total of 100 simulated age-frequency data sets were generated under each of the four dispersion scenarios. The true β-value for the "age" parameter (Z) was fixed to 0.500 (i.e., $A = 39.3\%$), and then $\hat{Z}$ and its estimated SE were obtained for each of the currently available methods and GLMs when the simulated data were (1) equi-dispersed according to a $GLM_{Poisson}$ using a value of 1 for the dispersion parameter; (2) overdispersed, with the variance modeled as a linear function of the mean according to a negative binomial

type 1 model (GLM_{NB1}) and a value of 2 for the dispersion parameter; (3) overdispersed, with the variance modeled as a quadratic function of the mean according to a GLM_{NB2} and a value of 2 for the dispersion parameter; and (4) underdispersed according to a double Poisson (Efron 1986) model and a value of 0.5 for the dispersion parameter. Each $\hat{Z}$ obtained was compared to the true Z, and the observed mean difference over the 100 simulation runs was then converted into a percentage (%) of bias. The same was done for each estimated SE, which was compared to a reference SE obtained for each of the four dispersion scenarios considered to calculate bias (%). The reference SE was determined based on the weighted mean of the SE estimates obtained over the 100 simulated data sets of each dispersion scenario according to the five maximum likelihood GLMs by adjusting the mean SE relative to their mean Akaike weights (based on Akaike's information criterion [AIC]; Akaike 1973) following an information-theoretic approach (Burnham and Anderson 2002). When a given model for a given simulated data set did not converge, such as the GLM_{NB1} on some occasions when applied to under- or equi-dispersed data, the mean $\hat{Z}$ and estimated SE were calculated using fewer than 100 simulation results, whereas the Akaike weight assigned under such conditions for a given simulated data set was zero. Precision was evaluated according to the SD around the mean calculated over the ≤100 simulation results and also visually according to the width of the interquartile range of either the estimated Z or SE values obtained.

Empirical age-frequency data.— The Walleye data were collected as part of a large, standardized gill-net provincial monitoring program (Service de la Faune Aquatique 2011), whereas the Arctic Char data originated from a northern program aimed at establishing reference states (Mainguy and Beaupré 2019). Many data sets were available for the Walleye surveys; we selected the Baskatong Reservoir near the city of Mont-Laurier because its 2012 and 2017 data sets were among the largest sample sizes of specimens caught. The gill nets used are made of a series of eight panels of increasing mesh sizes to allow the capture of a wide range of lengths and, thus, ages—except for young specimens (Figure 1A). Because catchability bias related to fish size is almost inevitable with gill nets, this can affect the estimated age structure (Finstad et al. 2000). Therefore, the Z-estimates may be further biased given the limitations already associated with catch-curve analyses, but nonetheless they will still be comparable when done on the same basis, especially at the same study site. The two Arctic Char studies near the Nunavik communities of Tasiujaq (Aipparusik River) in 2017 and Salluit (Tasiallujuak River) in 2019 were less likely to introduce age-structure biases, as Arctic Char returning from the sea will be captured in the counting cage of the weir used if they attempt to go any further upstream. Ages of all sampled Walleye and Arctic Char were determined based on the examination of year-increment annuli of their otoliths with a binocular microscope.

Catch-curve analyses of simulated and empirical data.— As recommended by Smith et al. (2012), we applied the "peak plus" criterion, which consists of using the age that is 1 year beyond the age of full recruitment by the fishing gear (Figure 1). Each of the 400 simulated and empirical data sets was analyzed according to the six currently available methods to estimate $Z \pm$ SE using the R package fishmethods (Nelson 2019). These estimates were obtained by fitting the "full" age to that corresponding to "peak plus" and the "last" age to that of the oldest observed age. For the simulated data sets, the 2-year-old age-class was systematically used as the "full" age, whereas the "last" age was determined for each of the 400 simulated age-frequency data sets. The mean ($\pm$SD) number of age counts that were analyzed for the descending limb of the 400 simulated catch curves was 357 ± 97, which was similar to although independent of that of the Walleye data. The GLMs were then used to analyze how the variable "counts" varied according to the continuous variable "age." The age-frequency data analyzed with GLMs were artificially extended with ages having each a count of zero past the oldest age up to three times that age, as performed in fishmethods for the adapted PM of Nelson (2019). For the simulated data, the oldest extended age was fixed at 45 in all dispersion scenarios to facilitate the large number of GLM analyses performed, knowing that the addition of age-classes with zero count is done to minimize the underestimation of A (see Millar 2015). The candidate GLMs were all fitted according to the methodological details provided in the Appendix.

To identify the GLMs that best fit the simulated and empirical data, we first assessed model adequacy based on the behavior of their Pearson residuals by using the R package hnp (Moral et al. 2017), which produces an intuitive goodness-of-fit diagnostic plot (e.g., Demétrio et al. 2014). Briefly, the sorted absolute values of the Pearson residuals are plotted against the quantiles of the half-normal distribution (hereafter, "half-normal scores") to determine whether they fall within the limits of a simulated envelope according to the distributional assumptions of the investigated model (Moral et al. 2017). Model adequacy can then be verified visually (Figure 2) and by calculating the percentage of residuals falling outside the envelope (Appendix). As the envelope used to assess fit is simulated and thus its lower and upper bands slightly vary from one simulation to the next, a set of 100 simulations was run for each GLM tested and the mean percentage of residuals falling outside the envelope was used to categorize model adequacy as follows: (1) excellent (mean < 1%); (2) good (1% ≤ mean < 5%); (3) acceptable (5% ≤ mean < 10%); and (4) inadequate (mean ≥ 10%). These
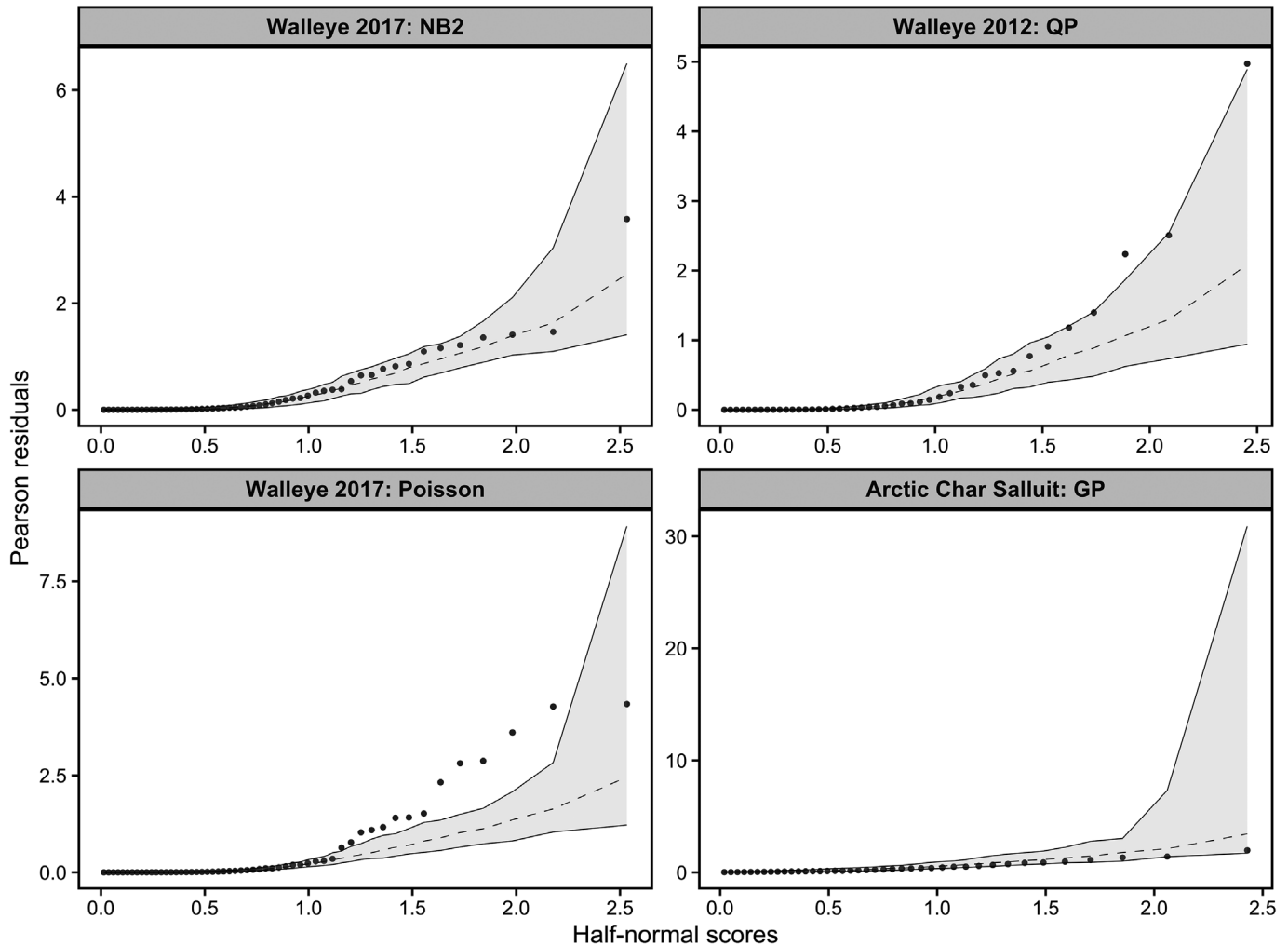
FIGURE 2. Half-normal plots with a simulated envelope for the Pearson residuals obtained for four different models by using the R package hnp. The residuals (filled circles) should be found within the limits (solid lines) of the simulated envelope and ideally should be located near the median (dashed line). A negative binomial type 2 (NB2) generalized linear model (GLM) fitted to the overdispersed Walleye 2017 data (top left) provides an excellent fit. A Poisson GLM fitted to the same Walleye 2017 data (bottom left) provides an inadequate fit. A quasi-Poisson (QP) GLM fitted to the overdispersed Walleye 2012 data (top right) provides a good fit, but as the residuals are moving away from the median with increasing half-normal scores, this is suggestive of a poorer fit. A generalized Poisson (GP) GLM fitted to the Arctic Char data from Salluit (bottom right) has an excellent fit, with all the residuals found within the simulated envelope. However, these residuals are systematically following the lower limit of the simulated envelope, indicating rather problematic behavior that is suggestive of a poorer, questionable fit. [Color figure can viewed at afsjournals.org.]

strict, arbitrarily determined categories have been elaborated according to how the lower and upper limits of the envelope are generated, as they respectively correspond to the 2.5th and 97.5th percentiles of the residuals obtained from re-fitting the model to simulated data (Moral et al. 2017). This indicates that around 5% of the residuals are expected to fall outside the simulated envelope for a well-fitting model. Models identified as being inadequate should be discarded, except in the case of small sample sizes (e.g., $n \le 30$), for which the percentage of residuals found outside the simulated envelope is more likely to exceed 10% (i.e., 3 points outside of the simulated envelope) despite sometimes

having a reasonable fit; thus, just the visual examination is recommended in such cases. The Akaike weights of the adequate GLMs retained were then used to objectively identify the most statistically supported model (Burnham and Anderson 2002). For the simulated data, model adequacy was assessed according to the mean of the 100 hnp runs averaged over each of the 100 simulated data sets under a given dispersion scenario, whereas the mean Akaike weight obtained was used to establish the relative statistical support among the different GLMs considered.

Comparison of mortality rates.— The GLMs were used to compare Z by fitting the variable "year" or "site" and

an interaction term with the age parameter when the two groups for a given species were pooled into a single data set. The adequate GLM found to have the most statistical support based on Akaike weights was then used to determine whether A statistically differed between the considered groups. Statistical support for a difference was obtained by comparing the best-ranking model to its counterpart without the interaction term, relying on Akaike weight (expressed in %) to determine whether the model with this additional parameter allowing for different regression slopes received more support (i.e., >50%) compared to the reduced model that included only the additive effects.

Statistical analyses.— To avoid model selection issues that could be attributable to the low sample sizes of the Arctic Char age-frequency data, the second-order (small-sample) AIC (AIC_c; Burnham and Anderson 2002) was used for all comparisons. Candidate models with an AIC_c difference (ΔAIC_c) greater than 7 were discarded (Burnham et al. 2011) prior to the last step of model selection, even if they were found to be adequate. To determine whether the assumption of equi-dispersion was met for each of the empirical data sets, we first used a two-sided dispersion test conducted on the results of a $GLM_{Poisson}$, which was applied to the observed age-frequency data prior to extending them with zero counts using the R package AER (Kleiber and Zeileis 2008). According to the sign of the z-score statistic and the estimated dispersion parameter obtained, a specific one-sided dispersion test was then conducted to determine whether the data were sufficiently equi-dispersed (Appendix). To provide a complete description of the results obtained following our GLM-based method, the AIC_c scores obtained for the empirical data sets for each of the five GLMs considered (i.e., excluding GLM_{QP}) are presented, including those categorized as inadequate, for comparison purposes and to highlight any potential inconsistencies between model adequacy and selection. All statistical analyses were performed in R version 4.0.3 (R Core Team 2020). All R scripts that were used in this study for the analysis of the empirical data are available in the Appendix, with detailed examples applying to the Baskatong Reservoir Walleye 2012 data. Data files and R scripts for both simulated and empirical data analyses are available at https://github.com/rafamoral/catchcurve.

RESULTS

Simulated Age-Frequency Data

The estimates of Z and its associated SE revealed some discrepancies among the currently available methods and GLMs (Table 1; Figures 3, 4). Omitting the LR method, which systematically produced the least accurate estimates

by underestimating Z in all four dispersion scenarios, all of the other methods produced a mean $\hat{Z}$ that was sufficiently accurate (bias < 2%), but this was only true for the less-likely scenarios in which the simulated age-frequency data were equi-dispersed, linearly overdispersed, or underdispersed (Table 1; Figure 3). The WLR method produced a highly accurate but slightly less-precise mean $\hat{Z}$ of 0.500 when the simulated age-frequency data were either equi-dispersed or linearly overdispersed, whereas for the underdispersion scenario the GLM_{CMP} and GLM_{GP} were the most accurate (Table 1; Figure 3). Under the more plausible ecological scenario of quadratic overdispersion, all of the currently available methods were downwardly biased, with the worst being the WLR method by 28% and the best being the adapted PM by 11% (Table 1; Figure 3). Among the log-linear models, the GLM_{NB2} and GLM_{CMP} provided the most accurate estimates, with a respective underestimation bias of 3% and 5%, whereas those obtained with the GLM_{GP} and GLM_{NB1} were downwardly biased by 36% and 38%, respectively (Table 1; Figure 3).

More variation was observed for the estimated SEs among the currently available methods and GLMs (Figure 4). Given that (1) the two CR methods (CR and CRCB) and the adapted PM were recently considered the least biased methods to estimate Z (Nelson 2019) and (2) two of these methods also apply a variance bias-correction factor that should produce more accurate SEs, we only report below the results of the two CR methods and the adapted PM for the assessment of the bias. The simulation results describing accuracy and precision for all six currently available methods are nonetheless presented in Figure 4. For the equi-dispersion scenario, the reference SE was 0.025 and similar to that of the most supported $GLM_{Poisson}$ (0.026), which had an overestimation bias of 4%, identical to that of the CR method (Figure 4). The use of a correction factor inflated this overestimation bias for the CRCB method (11%) and the adapted PM (12%; Figure 4). Although ranked as the third best-supported model for the linear overdispersion scenario, the GLM_{CMP} produced an estimated SE (0.037) nearly identical to the reference SE, with an underestimation bias of 0.05%, whereas the second-ranking GLM_{GP} had an overestimation bias of 6% and the best-ranking GLM_{NB1} had an overestimation bias of 7% (Figure 4). The CR method underestimated the reference SE by 29% for this dispersion scenario, whereas the CRCB method and the adapted PM overestimated it by 24% and 16%, respectively (Figure 4). Under quadratic overdispersion, the reference SE obtained was 0.090, which was comparable to that of the most supported GLM_{NB2} (0.103), although with an overestimation bias of 15%. Upward bias was, however, much more pronounced with the CRCB method (62%) and the adapted PM (59%), whereas the CR method had an
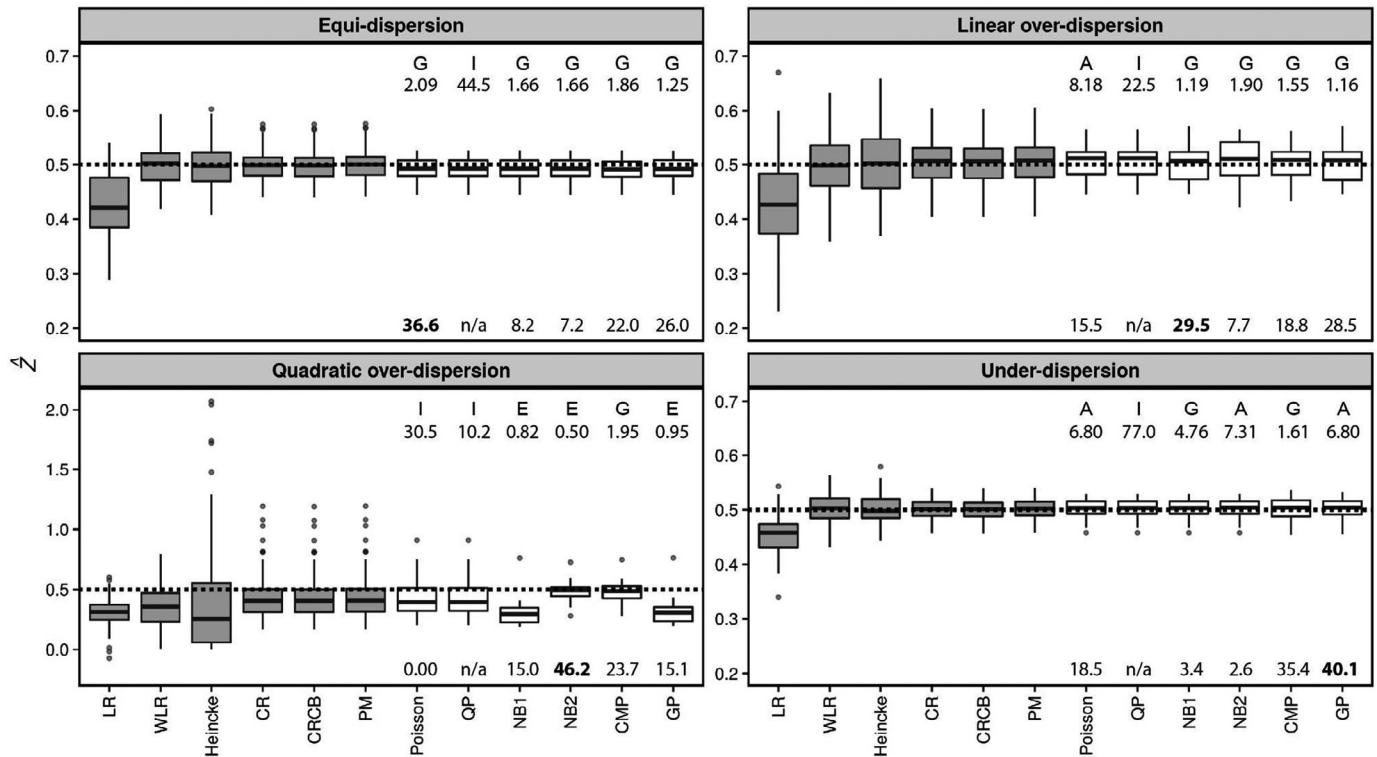
FIGURE 3. Box plots showing the performance of six currently available methods (gray filled boxes) and six generalized linear models (GLMs; unfilled boxes) in estimating the true instantaneous mortality rate (Z) of 0.500 (dashed reference lines) from which 100 simulated data sets were produced under four different dispersion scenarios (acronyms are defined in Table 1). Box plots are delimited by the first and third quartiles, the horizontal black solid line represents the median, and the whiskers correspond to the most extreme observation within 1.5 times the interquartile range, whereas the filled gray circles represent potential outliers. For the $GLM_{Poisson}$ or one of its five extensions, model adequacy is indicated by a single letter at the top of each plot and is categorized as excellent (E), good (G), acceptable (A), or inadequate (I) based on the mean percentage of Pearson residuals falling outside of a simulated envelope (see Methods and Figure 2), which is also indicated under each letter. The Akaike weight (%; based on the second-order Akaike's information criterion) of each model is also provided at the bottom of each plot, with the most supported model being highlighted in bold.

underestimation bias of 69% (Figure 4). The reference SE for the underdispersion scenario was 0.019 and comparable to that obtained with the most supported GLM_{GP} (0.017), yielding an underestimation bias of 12%. The estimate obtained from the CRCB method underestimated the reference SE by only 0.2%, whereas an upwardly biased estimate was obtained with the CR method (37%) and the adapted PM (39%; Figure 4). Although the WLR method generally estimated Z accurately except for the most commonly encountered quadratic overdispersion scenario (Table 1; Figure 3), the estimation of the SE with this method was poor under all scenarios: overestimation bias was at best 20% for the underdispersed simulated data and was as much as 73% for the quadratic overdispersion scenario (Figure 4).

Empirical Age-Frequency Data

The estimates of $Z \pm$ SE of the currently available methods for the Walleye and Arctic Char data sets are presented in Table 2. For example, the estimates of Z

obtained from the analysis of the Walleye 2012 data set provided A-values of 39.3% (Heincke method), 33.6% (LR), 40.5% (WLR), and 38.7% (CR, CRCB, and adapted PM), revealing moderate variation among these methods and less so when the LR method is not considered. According to the $GLM_{Poisson}$, the observed Walleye data had a tendency of being overdispersed or were overdispersed (2012: z-score = 1.47, $P = 0.07$; 2017: z-score = 2.57, $P = 0.005$), whereas the observed Arctic Char data showed a tendency of being underdispersed or were underdispersed (Tasiujaq: z-score = −1.35, $P = 0.09$; Salluit: z-score = −6.17, $P < 0.001$). Thus, the $GLM_{Poisson}$ assumption of equi-dispersion was either met or not satisfied, indicating that alternative models could in some cases be more appropriate. The estimates of Z from the $GLM_{Poisson}$ and its five extensions applied to the extended age-frequency data are presented in Table 3, together with a categorization of their fit according to the behavior of their Pearson residuals, their AIC_c scores and Akaike weights, and other model statistics.
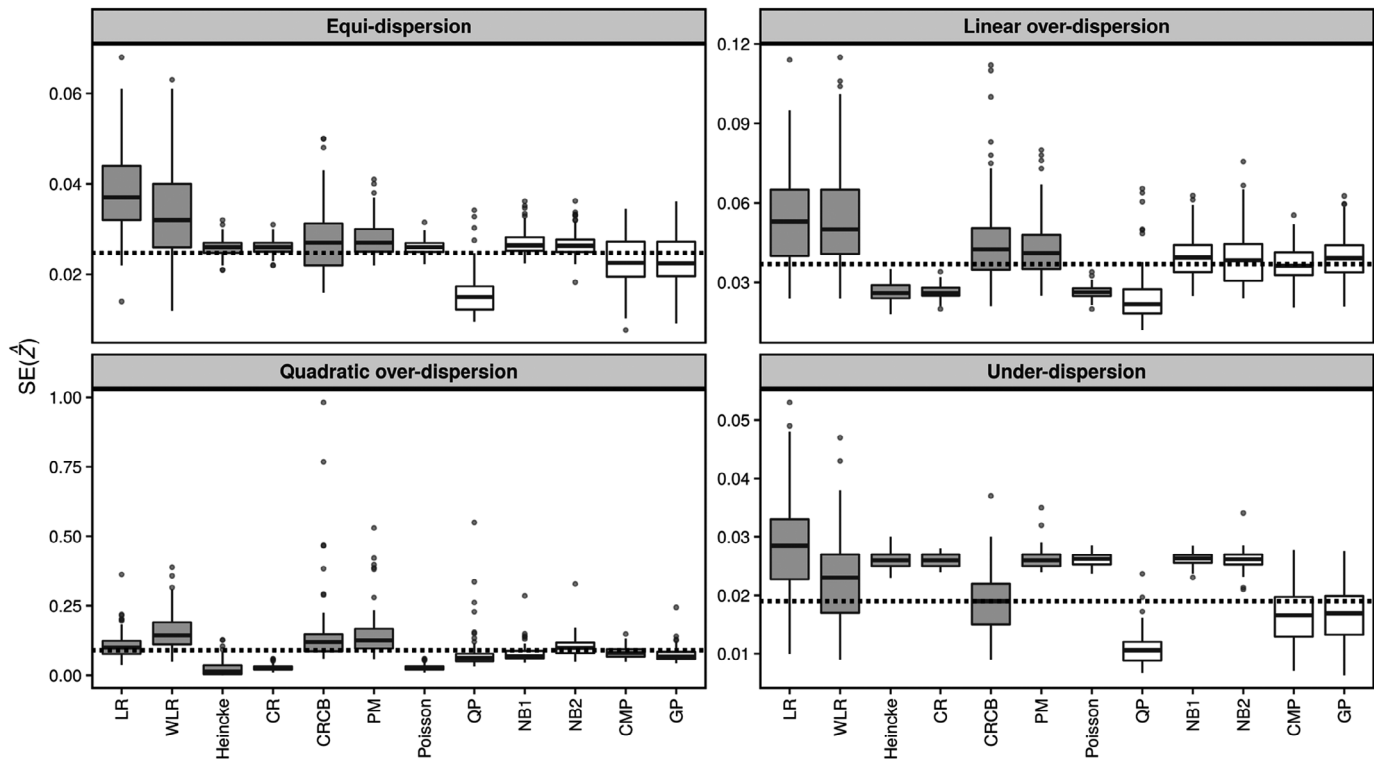
FIGURE 4. Box plots showing the performance of six estimators (gray filled boxes) and six generalized linear models (GLMs; unfilled boxes) in estimating the reference SE (black dashed line) of the estimated instantaneous mortality rate ($\hat{Z}$), which corresponds to the most statistically supported mean SE estimate based on Akaike weights according to the 100 simulated data sets that were produced under each of the four different dispersion scenarios (acronyms are defined in Table 1). Each dispersion scenario thus has a specific reference SE value (0.025 for equi-dispersion, 0.037 for linear overdispersion, 0.090 for quadratic overdispersion, and 0.019 for underdispersion). The box plots are delimited by the first and third quartiles, the horizontal thick line represents the median, and the whiskers correspond to the most extreme observation within 1.5 times the interquartile range, whereas the filled gray circles represent potential outliers.

TABLE 2. Instantaneous mortality rate (Z; $\pm$SE) estimates obtained from six currently available methods (acronyms are defined in Table 1) for Walleye sampled in Baskatong Reservoir during 2012 and 2017 and for Arctic Char sampled in rivers near Tasiujaq and Salluit, Québec, Canada.

	Walleye		Arctic Char	
Method	2012	2017	Tasiujaq	Salluit
Heincke	0.500 ± 0.026	0.410 ± 0.023	0.762 ± 0.143	0.243 ± 0.034
LR	0.405 ± 0.050	0.292 ± 0.045	0.238 ± 0.075	0.177 ± 0.032
WLR	0.518 ± 0.075	0.410 ± 0.061	0.683 ± 0.037	0.175 ± 0.031
CR	0.490 ± 0.025	0.400 ± 0.022	0.660 ± 0.123	0.255 ± 0.036
CRCB	0.490 ± 0.075	0.399 ± 0.050	0.646 ± 0.278	0.254 ± 0.032
PM	0.491 ± 0.089	0.401 ± 0.055	0.677 ± 0.126	0.260 ± 0.037

Estimates of Z were often similar across the currently available methods and GLMs in both species (Tables 2, 3), especially between the two CR methods, the adapted PM, and the GLM-derived estimates. As for the simulated data, the LR method again produced systematically lower Z-estimates, whereas those obtained with the WLR method were generally more comparable, although this method likely underestimated Z in a manner similar to the LR method for Salluit Arctic Char (Table 2). Differences in SE estimates were more evident (Tables 2, 3), with the CR and Heincke methods and the GLM$_{Poisson}$ having lower SEs when compared to the other methods for the overdispersed Walleye data in both years. The most supported GLMs for the analysis of the two Walleye

TABLE 3. Instantaneous mortality rate (Z; ±SE) estimates obtained from generalized linear models (GLMs) fitted with a Poisson distribution and five different extensions for Walleye sampled in Baskatong Reservoir in 2012 and 2017 and for Arctic Char sampled in rivers near Tasiujaq and Salluit, Québec, Canada (model acronyms are defined in Table 1). Model adequacy is categorized as either excellent, good, acceptable, or inadequate depending on the mean percentage (shown in parentheses; $n \leq 100$ simulation runs) of Pearson residuals falling outside a simulated envelope (see Methods and Figure 2). The log-likelihood, number of parameters (k), second-order Akaike's information criterion (AIC_c), AIC_c difference (ΔAIC_c), and Akaike weight of each model are presented. The best-supported adequate model is highlighted in bold.

GLM	$Z \pm$ SE	Model adequacy	Log-likelihood	k	AIC_c	ΔAIC_c	Akaike weight
			Walleye 2012				
Poisson	0.491 ± 0.025	Inadequate (18.6)	−78.595	2	161.5	72.46	Discarded
QP	0.491 ± 0.042	Good (4.05)	n/a	3	n/a	n/a	n/a
NB1	0.398 ± 0.059	Excellent (0.67)	−46.819	3	100.2	11.21	Discarded
NB2	**0.495 ± 0.055**	**Excellent (0.20)**	**−41.212**	**3**	**89.0**	**0.00**	**0.767**
CMP[a]	0.489 ± 0.054	Excellent (0.00)	−42.405	3	91.4	2.39	0.233
GP	0.388 ± 0.060	Excellent (0.02)	−45.185	3	97.0	7.95	Discarded
			Walleye 2017				
Poisson	0.401 ± 0.022	Inadequate (23.6)	−64.188	2	132.6	31.15	Discarded
QP	0.401 ± 0.028	Inadequate (21.9)	n/a	3	n/a	n/a	n/a
NB1	0.363 ± 0.045	Excellent (0.00)	−49.417	3	105.3	3.85	0.083
NB2	0.380 ± 0.042	Excellent (0.20)	−48.415	3	103.3	1.84	0.225
CMP[a]	**0.384 ± 0.038**	**Excellent (0.04)**	**−47.494**	**3**	**101.5**	**0.00**	**0.564**
GP	0.359 ± 0.048	Excellent (0.16)	−48.972	3	104.4	2.96	0.129
			Tasiujaq Arctic Char				
Poisson	**0.677 ± 0.126**	**Good (2.21)**	**−13.306**	**2**	**30.9**	**0.00**	**0.615**
QP	0.677 ± 0.151	Good (2.14)	n/a	3	n/a	n/a	n/a
NB1[b]	0.677 ± 0.126	n/a	−13.306	3	33.2	2.32	0.193
NB2	0.677 ± 0.126	Good (2.28)	−13.306	3	33.2	2.33	0.192
CMP[a,c]	0.743 ± 0.085	n/a	n/a	3	n/a	n/a	n/a
GP[d]	0.743 ± 0.032	Inadequate (21.8)	[−8.337]	3	[23.3]	n/a	Discarded
			Salluit Arctic Char				
Poisson	**0.260 ± 0.037**	**Excellent (0.00)**	**−24.073**	**2**	**52.5**	**0.00**	**0.421**
QP	0.260 ± 0.019	Inadequate (56.5)	n/a	3	n/a	n/a	n/a
NB1[c]	0.260 ± 0.037	n/a	n/a	3	n/a	n/a	n/a
NB2	0.260 ± 0.037	Excellent (0.00)	−24.073	3	54.8	2.33	0.131
CMP[a]	0.245 ± 0.031	Excellent (0.00)	−23.328	3	53.3	0.84	0.276
GP[e]	0.254 ± 0.033	Questionable (0.61)	−23.807	3	54.3	1.80	0.171

[a] Mean-parametrized CMP (Huang 2017).

[b] The model converged and allowed us to obtain AIC_c scores, but the Pearson residuals could not be extracted to inspect model adequacy.

[c] The model did not converge; thus, no Pearson residuals or AIC_c score could be used, despite obtaining parameter estimates.

[d] Although the model was inadequate, the log-likelihood and AIC_c values are presented in brackets to emphasize the importance of testing model adequacy prior to model selection.

[e] Although the model had an apparent excellent fit, inspection of the Pearson residuals revealed an unusual behavior that was indicative of a poorer fit and its adequacy was thus judged as questionable (see Figure 2).

data sets provided, as expected, SE estimates that were greater than those of the CR method and the $GLM_{Poisson}$ but lower than those produced by the CRCB method and the adapted PM (Tables 2, 3). The overdispersed Walleye 2012 data were best modeled by the GLM_{NB2}, with an SE estimate of 0.055 (Table 3). As observed with the simulated data, the corresponding estimates for the CRCB method and the adapted PM were higher: 0.075 and 0.089, respectively (Table 2). The variance bias-correction factor therefore produced SE estimates that were 36% and 62% greater than that of the best-supported model. For

the 2017 Walleye data, the CRCB method and the adapted PM again inflated the SE estimates by 32% and 45%, respectively, compared to the best-ranking GLM_{CMP} (Tables 2, 3). The two Arctic Char data sets were best independently described by a $GLM_{Poisson}$, which produced $Z \pm$ SE estimates that were identical to those of the adapted PM (Tables 2, 3).

Comparison of Mortality Rates

In the Walleye data set, the top-ranking model estimated A at 39.0% (95% CI = 32.1–45.3%) in 2012 and

31.9% (95% CI = 26.6–36.8%) in 2017, indicating a decline in mortality rates of approximately 7 percentage points over the 5-year period, although statistical support for this interpretation may be weak due to the partly overlapping 95% CIs. In the Arctic Char data set, the most supported GLM$_{Poisson}$ provided A-estimates of 49.2% (95% CI = 35.0–60.3%) at Tasiujaq and 22.9% (95% CI = 17.1–28.3%) at Salluit. Note that for both of the Arctic Char data sets, the GLM$_{NB1}$ and GLM$_{NB2}$ produced $\hat{Z}$ and estimated SE values that were identical to those of the GLM$_{Poisson}$ (Table 3), likely because their additional dispersion parameter specifically designed at modeling any "extra" variance was not required in the presence of equi-dispersed or underdispersed data; therefore, both were reduced to a GLM$_{Poisson}$ while simultaneously being AIC$_c$ penalized. With non-overlapping 95% CIs, the estimated A for the sampled Arctic Char was statistically higher at Tasiujaq than at Salluit.

Once the observed age-frequency data were regrouped according to either year (Walleye) or site (Arctic Char), the Walleye data were still overdispersed (z-score = 2.21, $P = 0.01$), whereas the Arctic Char data were underdispersed (z-score = −3.61, $P < 0.001$). After the overdispersed Walleye data set was artificially extended, the most supported models based on Akaike weight were the GLM$_{NB2}$ (65.6%) and the GLM$_{CMP}$ (34.4%). In a second step, the Akaike weight of each of these two models was then separately compared to that of their respective counterpart that excluded the interaction term. Both the GLM$_{NB2}$ (57.1%) and the GLM$_{CMP}$ (56.8%) provided weak but statistically detectable support for the inclusion of the interaction term, indicating different mortality rates between years and, oppositely, about 43% of statistical support for a lack of difference in both cases. For the underdispersed Arctic Char data set, all of the models obtained an excellent fit, except for the GLM$_{NB1}$, which did not converge. The GLM$_{CMP}$ received the most statistical support (46.7%), followed by the GLM$_{GP}$ (23.2%), GLM$_{Poisson}$ (22.8%), and GLM$_{NB2}$ (7.3%). All models indicated that the interaction term was strongly supported (≥99.5%) when compared to a model containing only the additive effects of age and site, providing unequivocal statistical support for a difference in A between the Tasiujaq and Salluit Arctic Char populations.

DISCUSSION

The assessment of model adequacy with Pearson residuals (Moral et al. 2017) followed by the use of an information-theoretic approach (Burnham and Anderson 2002) offers a statistically proven method to objectively identify the most supported GLMs from which mortality rates can be estimated and compared, therefore providing a clear advantage over the currently available methods for which no such assessment can be made. Our simulation analyses indicated that the NB2 extension performed generally well at modeling overdispersed count data, which explains in part its widespread use (Hilbe 2014). This finding is consistent with those of other ecological studies that have promoted the use of the negative binomial distribution to model overdispersed count data (Bliss and Fisher 1953; White and Bennetts 1996; Alexander et al. 2000), although some of its generalizations may sometimes prove more adequate (Lindén and Mäntyniemi 2011). When the count data have been generated under both demographic and environmental processes, such as with catch-curve data, the variance–mean relationship will be more likely quadratic (Engen et al. 1998), providing further support for the use of the GLM$_{NB2}$. Under such conditions, other, more complex extensions should ideally also be considered, such as the Poisson–normal (Hinde 1982), the Poisson–inverse Gaussian (Dean et al. 1989), and the hyper-Poisson (Sáez-Castillo and Conde-Sánchez 2013) extensions, on top of the mean-parametrized CMP, although a trade-off has to be made regarding the advantage of considering multiple extensions to obtain a better fit to the count data on the one hand and the analytical time this would require on the other. Our GLM-based method also offers a more reliable statistical approach that should be adopted by fisheries biologists to compare mortality rates between grouping factors, as it outperforms the one currently proposed (Miranda and Bettoli 2007; Ogle 2016), especially given the inadvisable use of the LR method (Smith et al. 2012; this study) on which it is based.

Nelson (2019) cautioned that any downwardly biased SE estimates are likely to indicate that a statistically supported difference between two mortality rates can be found, whereas in some instances it should not. For example according to the only two adequate GLMs used to compare years for the Walleye data set, weak statistical support was found for a difference between the mortality rates, which corresponded to $P < 0.10$ for the interaction term for both extensions, whereas the use of the inadequate GLM$_{Poisson}$ would have indicated much stronger support for a difference (Akaike weight = 93%, corresponding to $P = 0.007$), thus creating a potential to lead to an incorrect interpretation of the results. We also found the opposite pattern when the two methods relying on a variance bias-correction factor were used. For the simulated data sets that were generated under quadratic overdispersion, the adapted PM, which was the least biased of the currently available methods, estimated A at 35.9% (95% CI = 15.1–51.5%) due to its SE being artificially inflated by its correction factor, somewhat contrary to its purpose, whereas the true Z and its reference SE yielded A of 39.3% (95% CI = 27.6–49.2%). Using the adapted PM for these simulated data sets produced a 95% CI with a width that was inflated by 69%, in addition to

underestimating A by 9%. Therefore, the use of either the adapted PM or the CRCB method to compare grouping factors when the age-frequency data are overdispersed has the potential to statistically mask a difference between mortality rates when it does exist. On the other hand, our GLM-based method identified the GLM_{NB2} as the best-ranking model with an accurate A estimation of 38.4% (95% CI = 24.7–49.7%), corresponding to an underestimation bias of only 2%, whereas the width of the 95% CI obtained was increased by 16%. Altogether, these results clearly indicate that using a method derived from a $GLM_{Poisson}$ to estimate Z and its SE, whether or not a variance bias-correction factor is applied, will likely lead to less-reliable estimates under the most common overdispersion scenario met with age-frequency data.

Interestingly, if the age-frequency data are equidispersed, they can be adequately modeled with the $GLM_{Poisson}$, which produced results nearly identical to those of the CR method (Millar 2015; this study). Under such circumstances, the application of a variance bias-correction factor is in fact unnecessary because it can potentially induce an upward bias in the estimated SE obtained, as demonstrated with the analysis of the simulated equi-dispersed data. Furthermore, the analysis of the site-specific Arctic Char data sets also showed that a $GLM_{Poisson}$ can sometimes be sufficient to adequately model underdispersed data (Zuur et al. 2009). When overdispersion is detected, the GLM_{NB1} and GLM_{GP} both seem to be well adapted to analyze age-frequency data but apparently only when they are linearly overdispersed. For instance, Ver Hoef and Boeng (2007) showed that for the estimation of abundance of harbor seals *Phoca vitulina* from aerial surveys, a GLM_{QP} that closely resembles a GLM_{NB1} was more adequate than the GLM_{NB2} to analyze their overdispersed count data by looking graphically at how the partitioned variance behaved compared to its partitioned mean, which was found to follow a linear pattern. This visual assessment of the variance–mean relationship was important to investigate since the two extensions greatly diverged for the abundance estimates produced (Ver Hoef and Boeng 2007). Most of the time, however, the extra variance in counts will be better taken into account with a GLM_{NB2} (Hilbe 2014). Under such a case, the GLM_{QP}, GLM_{NB1}, and GLM_{GP} often offered an inadequate fit for both the simulated and empirical data analyzed in this study. Interestingly, the mean-parametrized CMP (Huang 2017) was adequate not only to model quadratic overdispersion but also to model underdispersion according to our analysis of both the simulated and empirical data, providing further support to its already recognized flexibility in ecological studies (Lynch et al. 2014; Brooks et al. 2019). Given the many inadequate fits obtained with the GLM_{QP} and the fact that AIC_c cannot be used to compare it with other log-linear models, this extension appears to be of little practical use. We suggest that only the GLM_{NB1} should be considered instead, as it is based on maximum likelihood and produces estimates similar to those obtained with a GLM_{QP} for the analysis of linearly overdispersed data (Hilbe 2014). Overall, selecting the most adequate extensions of the Poisson distribution according to the dispersion of the catch-curve data being analyzed should generally produce more accurate mortality rates than those obtained with the currently available methods, which can then help to provide a more reliable assessment of a given population status, especially when combined with other biodemographic parameters (Barbieri et al. 1994; Bisping et al. 2019).

It is important to note that the best adequate model in each of the analyses conducted received rather moderate AIC_c support ranging from as low as 30% up to as much as 77%. This is clearly indicative that more than one distributional assumption can accommodate different randomly selected age-frequency data originating from the same sampled population—and possibly more so when the sample sizes used are small. This finding highlights the importance of considering more than one Poisson distribution extension, especially when overdispersion is detected, in an attempt to estimate Z and its uncertainty. Therefore, to more accurately reflect the age structure of the studied population and its inherent distribution profile at any given point in time, the use of the least biased fishing gear relative to fish age (Finstad et al. 2000) combined with efforts to increase the sample size should ultimately allow one to identify with more certainty the adequate Poisson distribution extension that should be used according to the Akaike weight obtained, thus reducing model uncertainty for biological inferences. However, for the more likely situation in which the Akaike weights are distributed through two or more adequate candidate models, as observed in this study, one can use the "model averaging" approach (Dormann et al. 2018), which incorporates the estimate from each retained adequate model by weighing its contribution respective to its Akaike weight, similar to what was done to calculate the reference SE. The single Z-estimate that results from this approach will represent a compromise that better reflects model selection uncertainty and can even potentially reduce prediction error (Dormann et al. 2018).

Modeling of $Z \pm$ SE under diverse simulation scenarios would be the next logical step to determine the circumstances under which the GLM extensions of the Poisson distribution examined in this study—and possibly other, more complex ones—are the most adequate for statistical inferences specifically related to catch-curve analyses, benefiting from the significant amount of simulation work already existing on this subject (Murphy 1997; Dunn et al. 2002; Thorson and Prager 2011; Smith et al. 2012; Millar 2015; Nelson 2019; this study). For instance, how does varying the dispersion parameter under biologically plausible scenarios affect the estimation of Z and its SE when sample

size is also allowed to vary? Such simulation studies could thus help to determine the conditions under which a given extension will likely be less biased and more precise, knowing, however, that other potential explanations must be considered besides the distributional assumptions to reach better model adequacy (Moral et al. 2017). As such, added covariates—for example, the annual variability in recruitment when such data are available—may increase model adequacy and thus can result in a more accurate estimate of Z (Millar 2015). Altogether, GLMs fitted with Poisson distribution extensions definitely offer greater flexibility than the currently available methods for statistical inferences. More importantly, our GLM-based method is also applicable to other fisheries studies relying on count data, such as those based on CPUE. Given the already recognized ability of the NB2 extension to take into account the presence of many zeros in the modeling of count data (Warton 2005), it should thus be considered not only for the estimation and comparison of mortality rates for overdispersed age-frequency data but also for other fisheries management purposes, such as comparing abundance indices between or among grouping variables of interest.

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Appendix: R Scripts and Model Equations

R Scripts

These R scripts allow the analysis of the six generalized linear models (GLMs) that were considered in this study (i.e., $GLM_{Poisson}$, GLM_{QP}, GLM_{NB1}, GLM_{NB2}, GLM_{CMP}, and GLM_{GP}; defined in Table 1) using the 2012 data set for Baskatong Reservoir Walleye (Figure 1A) as an example. More specifically, the required scripts for the dispersion test to be performed on the $GLM_{Poisson}$, the modeling of the five other GLMs, the way to conduct the 100 simulation runs to calculate the mean percentage of residuals falling outside the simulated envelope according to the half-normal scores as a goodness-of-fit diagnostic, and how to compare the candidate log-linear models based on Akaike weights are provided. An example of how to test whether mortality rates differ between two compared groups is also shown using the surveyed years (2012 and 2017) of the Walleye data set. Model equations for the Poisson family distribution and five of its extensions that were considered in this study are presented.

R Packages

The following packages need to be installed according to the package name using `install.packages("nameofpackage")` and then loaded into R for specific analyses to be performed with `library(nameofpackage)`:

```
library(AER)
library(MASS)
library(glmmTMB)
library(hnp)
library(tidyverse)
library(MuMIn)
```

Fitted Model Acronyms

Model fitting uses the following acronyms: **p** = Poisson, **qp** = quasi-Poisson, **nb1** = negative binomial type 1, **nb2** = negative binomial type 2, **cmp** = mean-parametrized Conway–Maxwell–Poisson, and **gp** = generalized Poisson.

Dispersion Test

To be statistically meaningful, a dispersion test can only be applied to the results of a $GLM_{Poisson}$ for the analysis of count data: "overdispersion is irrelevant for models that estimate a scale parameter" (B. Bolker: https://bbolker.github.io/mixedmodels-misc/glmmFAQ.html#overdispersion). Here, we show how to first apply a $GLM_{Poisson}$ to the original age-frequency data—that is, prior to artificially extending them with zero counts (Millar 2015)—to then conduct a two-sided dispersion test with the R package AER. The original data set is referred to as `baskatong2012` to distinguish it from the extended data set used in all of the subsequent GLM analyses (`walleye2012`). Therefore, the $GLM_{Poisson}$ applied to the original data will be referred to as `baskatong2012_p`. The first (two-sided) dispersion test is conducted to determine whether the estimated dispersion parameter and the z-score statistic obtained indicate that the age-frequency data *may* be either overdispersed (i.e., dispersion parameter > 1.0; positive z-score statistic) or underdispersed (the opposite). At this step, a lack of equi-dispersion in the age-frequency data can already be detected at $P < 0.05$. Nevertheless, we recommend conducting a second specific one-sided over- or underdispersion test to determine whether the assumption of equi-dispersion is statistically satisfied given the actual dispersion of the observed age-frequency data revealed by the first test; the dispersion parameter and the z-score statistic will both remain the same as those obtained with the two-sided test, but the ability to detect an apparent lack of equi-dispersion will be increased. Lack of statistical support under such a specific test will indicate that the variance in the age-frequency data is likely sufficiently similar to the mean for a $GLM_{Poisson}$ to produce valid statistical inferences. Generally, however, the age-frequency data will more likely have a variance that is greater than the mean, often leading to a ratio greater than 1 between the residual deviance and its associated degrees of freedom, which as a rule of thumb are both suggestive of overdispersion. Only a proper dispersion test should be used, however, to statistically determine whether the data are sufficiently equi-dispersed. The more appropriate extensions of the Poisson distribution for the analysis of the age-frequency data can then be identified, such as the use of the NB1, NB2, and CMP extensions if the data are overdispersed, for instance. Note also that the `hnp()` function applied to a $GLM_{Poisson}$ that was used to analyze overdispersed data will indicate an inadequate fit, with most Pearson residuals found above the upper limit of the simulated envelope as a result of overdispersion (see Figure 2, bottom left).

$GLM_{Poisson}$ applied to the original data set with the `glm()` function:

```
baskatong2012_p<-glm(N~AGE,
family=poisson,data=baskatong2012)
```

The model results (i.e., output) can be obtained with the `summary()` function:

```
summary(baskatong2012_p)
```

Performing a **two-sided dispersion test** with the `dispersiontest()` function:

```
dispersiontest(baskatong2012_p,
alternative="two.sided")
```

Performing a one-sided **overdispersion test**:

```
dispersiontest(baskatong2012_p,
alternative="greater")
```

Performing a one-sided **underdispersion test** (just as an example):

```
dispersiontest(baskatong2012_p,
alternative="less")
```

The P-value associated with the overdispersion test corresponds to $1 - P$ for the underdispersion test, such that if the z-score statistic obtained has, for instance, a negative value for an overdispersion test and is associated with $P = 0.96$, then this result would provide statistical support for underdispersion ($P = 0.04$).

$GLM_{Poisson}$ applied to the extended age-frequency data set (`walleye2012`):

```
walleye2012_p<-glm(N~AGE,
family=poisson,data=walleye2012)
```

GLM_{QP}:

```
walleye2012_qp<-glm(N~AGE,
family=quasipoisson,data=walleye2012)
```

GLM_{NB1} with the function `glmmTMB()` from the R package glmmTMB:

```
walleye2012_nb1<-glmmTMB(N~AGE,
family=nbinom1,data=walleye2012)
```

GLM_{NB2} with the R package MASS. Note that the `family=` argument is implicitly invoked by the `glm.nb()` function to use the NB2 extension, such that it is not indicated in the script:

```
walleye2012_nb2<-glm.nb(N~AGE,
data=walleye2012)
```

GLM_{NB2} can also be tested with the `glmmTMB()` function. Note here that `nb2` has been changed to **NB2** to differentiate it from the previous model obtained with `glm.nb()`:

```
walleye2012_NB2<-glmmTMB(N~AGE,
family=nbinom2,data=walleye2012)
```

GLM_{CMP}:

```
walleye2012_cmp<-glmmTMB(N~AGE,
family=compois,data=walleye2012)
```

GLM_{GP}:

```
walleye2012_gp<-glmmTMB(N~AGE,
family=genpois,data=walleye2012)
```

Goodness-of-Fit Diagnostic Plots with hnp

We provide below helper functions to compute the half-normal plots with a simulated envelope for the GLMs fitted using the R package glmmTMB (GLM_{NB1}, GLM_{CMP}, and GLM_{GP}). The $GLM_{Poisson}$, GLM_{QP}, and GLM_{NB2} obtained with the package MASS can all be directly assessed for model adequacy by the R package hnp (Moral et al. 2017). The three GLMs depending on the R package glmmTMB all require the following additional functions to allow the visual inspection of the Pearson residuals according to a simulated envelope:

Function to obtain GLM diagnostics (Pearson residuals):

```
dfun<-function(obj)
{residuals(obj,type="pearson")}
```

Function to simulate a new response variable from the fitted GLM:

```
sfun<-function(n,obj)
{simulate(obj)[[1]]}
```

Function to refit a GLM analyzed with the R package glmmTMB (GLM_{NB1}, GLM_{CMP}, and GLM_{GP}). Characters in bold need to be changed according to the data and variables analyzed and the extension of the Poisson distribution fitted in a given GLM. Here is an example for the GLM_{NB1} in which family=nbinom1, whereas compois or genpois should be used instead following the same approach for the GLM_{CMP} and GLM_{GP}, respectively:

```
ffun_nb1<-function(response) {
fit<-try(glmmTMB(response~AGE,
family=nbinom1,data=walleye2012),
silent=TRUE)
while(class(fit)=="try-error") {
response2<-sfun(1,walleye2012_nb1)
fit<- try(glmmTMB(response2~AGE,
family=nbinom1,data=walleye2012),
silent=TRUE)
}
return(fit)
}
```

All hnp results in this study were obtained with the seed 2020 (using year 2020; just used to assure the reproducibility of the results), but any other seed can be used:

```
set.seed(2020)
```

For the $GLM_{Poisson}$, GLM_{QP}, and GLM_{NB2}, the diagnostic plots for model adequacy can be obtained using the following script. The argument how.many.out=TRUE provides the number of Pearson residual points falling outside of the simulated envelope to further assess each model's adequacy:

```
hnp_walleye2012_p<-hnp(walleye2012_p,
plot=FALSE,resid.type="pearson",
how.many.out=TRUE)
```

For the GLM_{NB1}, GLM_{CMP}, and GLM_{GP}, the diagnostic plots require references to the additional functions that were previously performed. Here is the script for the assessment of model adequacy, with the GLM_{NB1} again used as an example. Note that once the dfun and sfun have been executed once, they do not need to be run again. Just the fitfun is required for each considered GLM to be specifically executed:

```
hnp_walleye2012_nb1<-
hnp(walleye2012_nb1,
plot=FALSE,newclass=TRUE,
diagfun=dfun,simfun=sfun,fitfun=ffun_nb1)
```

Here, we organize all results into a single data set (for instance, if only the $GLM_{Poisson}$, GLM_{QP}, and GLM_{NB2} were the models to be summarized). Note that the walleye2012 data set has $n = 44$ ages when considering the extended ages with counts of zero past the maximal age. Thus, at the end of this script, "each=44" refers to the sample size:

```
hnp_walleye2012<-data_frame(residuals=
    c(hnp_walleye2012_p$residuals,
    hnp_walleye2012_qp$residuals,
    hnp_walleye2012_nb2$residuals),
lower=c(hnp_walleye2012_p$lower,
    hnp_walleye2012_qp$lower,
    hnp_walleye2012_nb2$lower),
median=c(hnp_walleye2012_p$median,
    hnp_walleye2012_qp$median,
    hnp_walleye2012_nb2$median),
upper=c(hnp_walleye2012_p$upper,
    hnp_walleye2012_qp$upper,
    hnp_walleye2012_nb2$upper),
x=c(hnp_walleye2012_p$x,
    hnp_walleye2012_qp$x,
    hnp_walleye2012_nb2$x),
model=factor(rep(c("Poisson","Quasi-Poisson",
"Negative binomial type 2"),each=44),levels=c
("Poisson","Quasi-Poisson","Negative binomial type 2")))
```

Including the results in hnp plots:

```
plot_walleye2012<-hnp_walleye2012%>%
    ggplot(aes(x=x,y=residuals))+
    theme_bw()+ facet_wrap(~model,
     scales="free")+
```

```
geom_point(cex=1,pch=16,alpha=.75)+
geom_line(aes(y=median),lty=2,lwd=.2)+
geom_line(aes(y=upper),lty=1,lwd=.2)+
geom_line(aes(y=lower),lty=1, lwd=.2)+
geom_ribbon(aes(ymin=lower,
ymax=upper),fill="gray",alpha=.2)+
xlab("Half-normal scores")+
ylab("Pearson residuals")+
 theme(panel.grid.major=element_blank
 (),panel.grid.minor= element_blank())
```

Saving the desired plot with a high resolution (800 dpi):

```
png("walleye_2012.tiff",res=800,
units="in",w=10,h=6)
print(plot_walleye2012)
dev.off()
```

Viewing the final plots (one hnp simulation run per model) in a single figure in R:

```
print(plot_walleye2012)
```

Next, we produce 100 half-normal plots for each model to obtain the average number of points (residuals) that fell outside of the simulated envelope, with $GLM_{Poisson}$ as an example for the GLMs that can be directly modeled by the R package hnp and GLM_{NB1} as an example for those that can only be obtained with the R package glmmTMB, which require additional simulation functions.

$GLM_{Poisson}$ (100 hnp simulation runs):

```
set.seed(2020)
walleye_hnp_p<-list()
for(i in 1:100) {
    walleye_hnp_p[[i]]<-
    hnp(walleye2012_p,
    resid.type="pearson",
    how.many.out=TRUE,
    plot.sim=FALSE)
}
```

$GLM_{Poisson}$ (summary of the 100 simulations):

```
walleye2012_p_hnp_summary<-
sapply(walleye_hnp_p,function(x)
x$out/x$total*100)
```

GLM_{NB1} (100 hnp simulation runs):

```
set.seed(2020)
walleye_hnp_nb1 <- list()
for(i in 1:100) {
    walleye_hnp_nb1[[i]]<-
    hnp(walleye2012_nb1,
    newclass=TRUE,
    diagfun=dfun,simfun=sfun,
    fitfun=ffun_nb1,
    how.many.out=TRUE,
```

```
    plot.sim=FALSE)
}
```

GLM_{NB1} (summary of the 100 simulations):

```
walleye2012_nb1_hnp_summary<-
sapply(walleye_hnp_nb1,function(x)
x$out/x$total*100)
```

Including all results into a single data set:

```
results <- data.frame(model=factor(rep(c ("Poisson",
    "Quasi-Poisson",
    "Negative binomial type 2"),
    each=100),levels=c("Poisson",
    "Quasi-Poisson",
    "Negative binomial type 2")),
    perc_out=c (walleye2012_p_hnp_summary,
    walleye2012_qp_hnp_summary,
    walleye2012_nb2_hnp_summary))
```

Result summaries:

```
results %>%
group_by(model) %>%
summarise(mean=mean(perc_out),
sd=sd(perc_out))
```

Model Selection Based on Akaike Weights

The function `model.sel()` of the R package MuMIn allows us to compare candidate models using an information-theoretic approach based on the second-order Akaike's information criterion (AIC_c). We recommend that only the GLMs found to be adequate according to the previous goodness-of-fit assessment step should be considered for model selection. The most supported model will obtain the lowest AIC_c score and the highest Akaike weight. Note that a GLM_{QP} cannot be included in the candidate models being compared, as it is based on quasi-likelihood rather than maximum likelihood, thus preventing the calculation of Akaike weight for all models. Models with convergence issues either should not be included or should be included only with caution:

```
model.sel(walleye2012_p,
walleye2012_nb1,walleye2012_nb2,
walleye2012_cmp,walleye2012_gp)
```

Comparing Mortality Rates

Below are the scripts to compare the mortality rates between years 2012 and 2017 for the Baskatong Reservoir Walleye population, where `walleye1217` regrouped the extended age-frequency data of both years and the NB2 extension is used as an example to test the interaction AGE* YEAR (**nb2_int**). Note that for `walleye1217`, both survey years are referred to as Y2012 and Y2017 for the

categorical variable `YEAR`, instead of `2012` and `2017`, as otherwise `YEAR` would be wrongly interpreted by R as a numeric, continuous variable:

```
walleye1217_nb2_int<-
glm.nb(N~AGE+YEAR+AGE*YEAR,
data=walleye1217)
```

The same extension is used to test the model, this time only containing the additive effects of `AGE` and `YEAR` (**nb2_add**):

```
walleye1217_nb2_add<-
glm.nb(N~AGE+YEAR,data=walleye1217)
```

The function `model.sel()` seen above can then be used to determine which of these two candidate models obtain most of the Akaike weight. More statistical support (>50% and up to 100%) for the inclusion of the interaction term would indicate different slopes and, thus, different mortality rates.

Model Equations

In the model equations below, Y represents the response variable; μ is the mean parameter; ϕ is the dispersion parameter; β_0 and β_1 are the intercept and slope of the linear predictor for the mean, respectively; n is the sample size; p is the number of regression coefficients; and Γ is the gamma function.

Poisson model:

$$Y \sim \text{Poisson}(\mu)$$

$$P(Y=y) = \frac{e^{-\mu}\mu^y}{y!}$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\phi = 1\,(\text{known dispersion parameter})$$

$$\text{Var}(N) = \phi\mu = \mu$$

QP model:

$$Y \sim \text{Poisson}(\mu)$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\tilde{\phi} = \sum_{i=1}^{n} \frac{y_i - \hat{\mu}_i}{\hat{\mu}_i(n-p)}\,(\text{estimated through Pearson residuals})$$

$$\text{Var}(N) = \phi\mu$$

NB1 model:

$$Y \sim \text{NegBin}(\mu, \phi)$$

$$P(Y=y) = \frac{\Gamma(y+\mu\phi^{-1})}{y!\Gamma(\mu\phi^{-1})} \left(\frac{\phi^{-1}}{\phi^{-1}+1}\right)^{\mu\phi^{-1}} \left(\frac{1}{\phi^{-1}+1}\right)^y$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\text{Var}(N) = \mu + \phi\mu$$

NB2 model:

$$Y \sim \text{NegBin}(\mu, \phi)$$

$$P(Y=y) = \frac{\Gamma(y+\phi^{-1})}{y!\Gamma(\phi^{-1})} \left(\frac{\phi^{-1}}{\phi^{-1}+\mu}\right)^{\phi^{-1}} \left(\frac{\mu}{\phi^{-1}+\mu}\right)^y$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\text{Var}(N) = \mu + \frac{\mu^2}{\phi}$$

Mean-parametrized CMP model:

$$Y \sim \text{CMP}(\mu, \phi)$$

$$P(Y=y) = \left(\mu + \frac{e^\phi - 1}{2e^\phi}\right)^{ye^\phi} \frac{(y!)^{-e^\phi}}{Z(\mu, \phi)},$$

$$\text{with}\, Z(\mu, \phi) = \sum_{j=0}^{\infty} \frac{\mu^j}{(j!)^\phi}$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\text{Var}(N) = \mu e^{-\phi}$$

GP model:

$$Y \sim \text{GP}(\mu, \phi)$$

$$P(Y=y) = \mu[\mu + (\phi-1)y]^{y-1}\phi^{-y}\frac{e^{-\left[\frac{\mu+(\phi-1)y}{\phi}\right]}}{y!}$$

$$\log(\mu) = \beta_0 + \beta_1 \times \text{age}$$

$$\text{Var}(N) = \phi^2\mu$$