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Abstract

In data-limited scenarios, indirect methods are often the best option for estimating natural mortality (M), with many utilizing maximum age-based approaches. The impact of sample size on maximum age estimates has been widely studied, yet its effects are not yet fully understood. Empirical studies establishing the relationship between M and maximum age rely on studies with sample sizes of only a few hundred to a thousand fish. The issue arises when applying these methods to fishery stock assessments which typically estimate maximum age using tens of thousands of fish. This difference in scale of sample size could lead to discrepancies in M estimates utilized in management. We investigated how sample size influences two methods for estimating maximum age: an oldest observed age (t_{max}) and a 99th percentile age (t_{99}) in a simplified population. Random samples were taken from a modeled population with a known M to determine both maximum age and M. Our findings show that smaller samples produce higher M estimates based on t_{max} than larger samples. Conversely, although the t_{99} approach consistently overestimated M, it was robust against variation in sample size. Methods to correct for the biases in M due to sample size were developed for both t_{max} and t_{99}. Therefore, we recommend using t_{99} along with our correction methods to improve the reliability of M estimates.

Keywords: natural mortality, sample size, maximum age, 99th percentile age, Hoenig, Then, Hamel and Cope

Introduction

Natural mortality rate (M) is an important parameter within stock assessments that encompasses all deaths within a stock not associated with the fishery, including predation, disease, senescence, etc. (Cope & Hamel, 2022; O. Hamel & Cope, 2022; Pauly, 1980). Natural mortality can greatly affect the setting of harvest levels and biological reference points (BRPs), assessing stock status, understanding overall stock dynamics, and can be interpreted as a proxy for productivity (Lee et al., 2011; Maunder & Wong, 2011). Moreover, M is also utilized to determine fishing mortality (F) in conjunction with estimates of total mortality (Z; Kenchington, 2014). The concern, however, is that any bias or inaccuracy in M directly affects F estimates and other parameters whose estimation is dependent on M.

Inaccurate M estimates can yield erroneous scientific information, hindering managers' ability to determine stock status (Clark, 1999) and set sustainable catch levels to achieve optimum yield and prevent overfishing (Lee et al., 2011; Punt et al., 2021; Topping & Szedlmayer, 2013). Underestimating M can result in harvest levels set below the maximum sustainable yield (MSY), leaving fish unharvested and limiting the (economic) potential of a fishery. An overestimation of M may incline fishery managers to recommend unsustainable exploitation rates, potentially depleting the stock or delaying recovery of an overfished stock (Clark, 1999; Dureuil & Froese, 2021). As a result, M is often conservatively estimated at a lower value under the precautionary approach (Pascual & Iribarne, 1993; Solinger et al., 2022; Zheng, 2003).

Efforts to accurately estimate M have long presented a significant challenge, despite numerous different approaches (e.g. Alverson & Carney, 1975; Beverton & Holt, 1959; Charnov et al., 2013; Gislason et al., 2010; Hamel & Cope, 2022; Hoenig, 1983; Lorenzen, 1996; Pauly, 1980; Then et al., 2015). Adding to the complexity is the fact that parameters, like M, within assessments are inherently estimates, and the true values are unknown (Hoenig, 2017). This further complicates the development of management recommendations and the implementation of effective management strategies.

Natural mortality rate can be estimated internally within assessment models, externally through direct methods such as tagging or telemetry, or indirectly through empirical methods that utilize meta-analysis (Gislason et al., 2010; Hewitt et al., 2007; Kenchington, 2014; Lee et al., 2011; Maunder et al., 2023; Then et al., 2015). Ideally, the estimate can be obtained directly from the stock of interest with high spatial and temporal resolution using direct methods. However, these approaches are data intensive and often impractical due to the fishery, fish behavior, and cost (Gislason et al., 2010; Hewitt & Hoenig, 2005; Kenchington, 2014; Pascual & Iribarne, 1993). Thus, reliable M estimators are essential in data-limited situations, where empirical methods are commonly used (Hoenig, 2017; Then et al., 2015).

Indirect estimation techniques require minimal data and rely on the relationships between natural mortality and other life history and/or environmental parameter(s) (e.g. Alverson & Carney, 1975; Beverton & Holt, 1959; Charnov et al., 2013; Gislason et al., 2010; Hamel & Cope, 2022; Hoenig, 1983; Hoenig et al., 2016; Kenchington, 2014; Lorenzen, 1996; Pauly, 1980; Then et al., 2015). These studies examined correlations between M and parameters such as maximum age (t_{max}), Brody growth coefficient, asymptotic length and weight (K, L_∞, and W_∞ respectively), and water temperature from a variety of different stocks. Then et al. (2015) found that maximum-age based estimators outperformed all other methods, suggesting they provide the most reliable empirical M estimates, a conclusion supported by Punt et al. (2005).

Expressions for estimating M based on maximum age were developed using previously published estimates of both maximum age and M across a wide range of species. However, the maximum age estimates were taken from studies that sampled only a few thousand individuals or fewer for a given species. Stock assessments, on the other hand, often have access to tens of thousands of fish collected over time to produce a maximum age estimate. For example, a southeastern United States (SEUSA) stock assessment of *Centropristis striata* (black sea bass) utilized over 120,000 age samples (SEDAR, 2023) – far exceeding the sample sizes in the literature underlying the published generalized maximum age estimators and deduced M. As sample sizes continue to grow, the likelihood of observing longer-lived individuals increases, resulting in lower M estimates for the same population – even if it has not changed. This creates sample size bias, where stocks with extensive samples may include a single, very old individual that does not accurately reflect population dynamics relative to M. The issue is not about "missing" older fish but rather overestimating the population's average maximum age – a factor not accounted for in empirically derived longevity-based M estimators.

This study investigates the effects of sample size through a modeling exercise that samples from a simplified, simulated population with no other factors influencing M to explore how sample size influences maximum observed age and M estimates. We utilized two methods for obtaining maximum age estimates to assess their resilience to sample size effects. Based on the biases observed, we developed correction formulas to produce improved M estimates.

Methods

Simulation Model

Hoenig (2017) used a Monte Carlo simulation to model the distribution of maximum age in a population with constant M, comparing observed maximum ages – based on sample sizes of 100 to 1,000 collected at the end of the simulation – with theoretical values from established longevity formulas. We used this model as a framework to develop a simulation that examines observed maximum ages from larger, more varied sample sizes spread across multiple years. Our simulation is a discrete-time, individual-based model that simulates a population of 40 million individuals. In contrast to Hoenig (2017), which sampled at a single point in time, this model incorporated sampling across multiple years to obtain maximum age estimates, which were then used to calculate M values, reflecting the multi-year datasets typically available to managers and stock assessments. These values are compared to the model input M experienced by the population.

Each individual model run began with a model input instantaneous M ($M_{\text{model input}}$) ranging from 0.01 to 0.5, with $M_{\text{model input}}$ fixed for a specific model run (i.e. $M_{\text{model input}}$ did not vary). This range covers many of the federally managed species assessed in the SEUSA. The $M_{\text{model input}}$ was converted to a discrete M (M_{discrete}) for each model run using the formula: $-(1 - e^{(M_{\text{model input}})})$. The M_{discrete} experienced by individuals within the population remained constant throughout each model run and did not vary with time, size, sex, age, etc. – an approach also used in the model developed by Hoenig (2017). Although substantial evidence supports M varying across these factors (Gislason et al., 2010; Lorenzen, 1996), a single value of M remains highly informative for stock assessments (Deroba & Schueller, 2013). In many cases, M estimates derived from empirical methods are used to scale approaches that calculate age-varying M (Lorenzen, 2022).

In year one of the simulation, 40 million individuals were born (age 0). Each model year consisted of a survival event followed by a recruitment event. Survival or death was determined by assigning each individual a value from a randomized uniform distribution, with individuals experiencing death if their assigned value was less than M_{discrete}. This was done to vary the numbers of survivals (or deaths) each year, while maintaining a long-term M. The annual assignment to death or survival was termed a survival event, with those surviving advanced in age by one year for the next survival event.

Each year, a recruitment event added new age-zero individuals to the population equivalent to the number of deaths to maintain a constant population size. The survival and recruitment events occurred once per model year and were independent of previous years. In other words, an individual's age did not affect its probability of death or survival (i.e. constant M). The cycle of survival and recruitment events continued for 1,000 model years to establish a stable population before sampling began over the final 20 model years.

Model years 1 – 980 served as the "burn-in" period to establish a stable population, with age sampling starting in year 981. Total sample sizes, ranging from 100 to 50,000, were taken without replacement and evenly distributed across 20 years. For example, a total sample size of 100 corresponds to sampling five individuals per year over 20 years. Independent models were run for each $M_{\text{model input}}$ and sample size combination (e.g. $M_{\text{model input}} = 0.2$ and a sample size of 100, $M_{\text{model input}} = 0.2$ and a sample size of 200, etc.), with 100 replicates per combination. The population's age structure during the sampling period was analyzed and compared to observed population age structures.

Obtaining Maximum Age Estimates

We compared two methods for obtaining maximum age values from sampled individuals to generate M estimates. Traditionally, the oldest observed age (t_{max}) of a species is used to generate an M estimate in stock assessments (e.g. SEDAR, 2015). Accordingly, the first M estimation method analyzed used this approach by selecting the oldest observed individual among all sampled fish within a simulation run.

The second method used the 99th percentile age (t_{99}) from all sampled fish within a simulation run as the maximum age estimate. This value was determined by sorting the sampled ages in ascending order, multiplying the total sample size by 0.99 to determine the index, and selecting the age corresponding to that index. It is important to note that the “maximum age” estimated using this method does not represent the true maximum observed age in a sample. Unless specified otherwise, references to maximum age will refer to the values derived from either methodology used to estimate M.

The sampled maximum age estimates from both methods were applied to three longevity-based formulas to estimate M (M_{formula}):

$$M_{\text{formula}} = 4.22 * (t_{\text{max}})^{-0.982} \qquad [1]$$

(Denoted as Hoenig Combined; Hoenig, 1983)

$$M_{\text{formula}} = 4.899 * (t_{\text{max}})^{-0.916} \qquad [2]$$

(Denoted as Then NLS; Then, 2015)

$$M_{\text{formula}} = 5.4 / t_{\text{max}} \qquad [3]$$

(Denoted as Hamel Cope; Hamel & Cope, 2022)

Characterizing Sample Size Effects

For each model run, M_{formula} values from the three longevity formulas were compared to the corresponding $M_{\text{model input}}$ value. Next, for each $M_{\text{model input}}$, we identified the sample size required to obtain the maximum age estimate that produced the most accurate M_{formula} value, which we referred to as the optimal sample size. This process was repeated for both t_{max} and t_{99} methods using the three longevity formulas [1], [2], and [3] to evaluate differences between the maximum age approaches and formulas.

Derivation of Correction Formulas

The $M_{formula}$ values derived from t_{max} and t_{99} sampling approaches were plotted against their corresponding $M_{model\ input}$ value for each sample size. If sample size was found to bias the $M_{formula}$ values relative to the $M_{model\ input}$ value, we investigated methods to address under- or overestimations. Regression models were developed to address biases in $M_{formula}$ based on longevity formula, sample size, and maximum age method. Akaike Information Criterion (AIC) values were used to identify the best models.

After identifying the best-fitting model, correction equations for $M_{formula}$ values were generated for each sample size across the three longevity formulas. To simplify the results into a single correction equation for each longevity formula, the regression model coefficients were analyzed to determine their relationship with sample size. Using this approach, the best-fit regression models, identified through AIC values, were used to create a single correction formula for each longevity-based equation for both maximum age methods. These six formulas (3 longevity formulas x 2 maximum age methods) only require an input sample size and an initial M estimate (i.e. $M_{formula}$).

Results

Sample Size Effects

Results showed a population age structure characterized by a high abundance of young fish, with numbers decreasing exponentially as age increases. The t_{max} sampling method produced the oldest sampled individuals in model runs with the largest sample sizes, while smaller sample sizes yielded younger maximum ages (Fig. 1A). Larger sample sizes produced maximum ages exceeding those predicted by each longevity estimator (i.e. Hoenig Combined, Then NLS, and Hamel Cope) for accurate $M_{\text{model input}}$ estimation. Calculating M_{formula} using t_{max} from the modeling effort showed that M_{formula} values were higher than the respective $M_{\text{model input}}$ for smaller sample sizes, while the opposite was true for larger sample sizes (Fig. 2). This produced an exponential decrease in M_{formula} values as sample size increased for all three longevity formulas.

The t_{99} ages were consistently younger than the age needed for accurate M_{formula} estimates for equations [1], [2], and [3] (Fig. 1B), causing the M_{formula} values derived from t_{99} to consistently overestimate $M_{\text{model input}}$ (Fig. 3). Although none of the longevity estimators accurately estimated $M_{\text{model input}}$ at any sample size, the t_{99} approach demonstrated reduced sensitivity to sample size compared to t_{max}. The M_{formula} values based on t_{99} ages stabilized once the total sample size reached approximately 5,000.

Optimal Sample Size

Using t_{max} to estimate M_{formula}, smaller sample sizes more accurately estimated low $M_{\text{model input}}$ values, while larger sample sizes were required for high $M_{\text{model input}}$ values across all three longevity formulas (Fig. 4). Sample sizes exceeding the optimal sample size (sample size required to produce the most accurate M_{formula} estimate) underestimated $M_{\text{model input}}$, while samples smaller than the optimal sample size overestimated $M_{\text{model input}}$. In some cases, the sampled t_{max} failed to produce an accurate M_{formula} estimate at any sample size.

Since M_{formula} estimates calculated using t_{99} consistently overestimated $M_{\text{model input}}$ values across all sample sizes, optimal sample sizes could not be determined for this approach. In other words, no sample sizes allowed for the accurate estimation of any $M_{\text{model input}}$ values, as t_{99} repeatedly produced ages younger than those needed for an accurate M_{formula}.

$M_{formula}$ Correction Formulas

Plotting $M_{formula}$ estimates against $M_{model\ input}$ values revealed that a second-order polynomial function provided the best fit to the data for the Hoenig Combined, Then NLS, and Hamel Cope formulas at each sample size. This applied for both t_{max} and t_{99} maximum age methods. The $M_{formula}$ correction equations were generated by inputting the a, b, and c coefficients from the second-order polynomial equations [4] into the quadratic formula [5]:

$$\text{Polynomial Equation: } ax^2 + bx + c = y \qquad [4]$$

$$\text{Corrected } M_{formula}\ (x) = \frac{-b \pm \sqrt{b^2 - 4a(c)}}{2a} \qquad [5]$$

In equation [4], the quadratic term is represented by the "a" coefficient, the linear term by "b", and the y-intercept by "c". The "x" term corresponds to the "true" M, referred to as "Corrected $M_{formula}$" in equation [5], and "y" represents the $M_{formula}$ estimate calculated by Hoenig Combined, Then NLS, or Hamel Cope using t_{max} or t_{99} prior to correction. Each coefficient from equation [4] was used as an input for equation [5]. These coefficients were determined for every combination of sample size and longevity formula for both t_{max} and t_{99} methods. This resulted in ten preliminary corrections equations for each longevity formula under both maximum age methods, yielding a total of 60 correction equations.

Modeling the polynomial coefficients (a, b, and c) for Hoenig Combined, Then NLS, and Hamel Cope correction formulas against sample size revealed a power or logarithmic regression fit for t_{max} and t_{99} methods. A power regression best fit all three coefficients for the t_{max} approach. For t_{99}, a power regression best fit coefficients "a" and "c", while a logarithmic regression was the best fit for "b". Using these models, a reduction from 60 to six correction formulas was developed – one for each longevity estimator under each maximum age method (Table 1).

Applying the appropriate correction equations from Table 1 to the initial $M_{formula}$ estimates from the model runs produced a linear trend in the corrected $M_{formula}$ estimates, except for an $M_{model\ input}$ value of 0.01 (Fig. 5 and 6). Regardless of the maximum age method or longevity formula, the correction formulas consistently underestimated $M_{model\ input}$ when $M_{model\ input}$ was set to the lowest level of 0.01. Larger sample sizes showed less variability in correction estimates compared to small sample sizes, while the t_{99} method produced smaller ranges in corrected $M_{formula}$ estimates compared to the t_{max} approach. Corrected $M_{formula}$ estimates were consistent across the three longevity formulas, despite substantial differences in $M_{formula}$ estimates before correction (Fig. 7).

Discussion

Sample Size Effects

In the past, small sample sizes were common, especially when aging and fishery sampling programs were limited. For example, in the Gulf of Mexico fewer than ten fishery monitoring programs existed in the 1960s and early 1970s. Since then, the number has increased to over 70 programs (Grüss et al., 2018), substantially expanding the available data for many species. Today, data from multiple surveys and monitoring programs, even those with limited sample sizes, can be integrated to develop more robust assessment models (e.g. Grüss et al., 2018; Nephin et al., 2023). However, as long time series are compiled and the number of age samples increases, the likelihood of sample size influencing a stock's maximum age estimate through an old, rare-aged individual also rises. Hoenig (1983) developed a formula that accounted for sample size, based on the rationale that increasing sample size could influence t_{max} estimates. Manooch III et al. (1998) applied both the Hoenig Combined and sample size-adjusted formula, finding that the latter produced an M estimate nearly double that of the Hoenig Combined method. These findings emphasize the need to account for sample size, as our results demonstrate its substantial influence on maximum age estimates.

Among the three longevity-based expressions examined in this study, Hoenig (1983) was one of the first to develop a longevity-based formula for estimating M using maximum age and total mortality rate data. Then et al. (2015) updated the Hoenig (1983) dataset by conducting an extensive literature search for M and maximum age estimates, resulting in a revised expression. Hamel & Cope (2022) later identified flaws in the regression used by Then et al. (2015) to derive equation [2] and, drawing on methods from Hamel (2015), addressed these biases to develop an updated longevity-based formula. Despite subsequent reviews and updates to each dataset and estimator, all three expressions remain subject to the effects of sample size on maximum age, and therefore on M estimates.

As expected, smaller sample sizes were less likely to capture the oldest age fish, resulting in higher $M_{formula}$ estimates when using t_{max}, the age of the oldest sampled fish. Similarly, larger sample sizes more frequently captured older individuals, leading to lower $M_{formula}$ estimates. In general, using t_{max} to estimate $M_{formula}$ resulted in smaller sample sizes overestimating $M_{model\ input}$, while larger sample sizes led to underestimates. As a result, current $M_{formula}$ estimates used in stock assessments derived using longevity-based methods may be biased depending on sample size and whether the species is short- or long-lived. Formulas developed for estimating the expected maximum age in a sample show that maximum age increases logarithmically with sample size (Hoenig, 1983, 2017; Holt, 1965; Kenchington, 2009, 2014; Sarhan, 1954; Then et al., 2015), a result corroborated by this study. The Then NLS, Hamel Cope, and Hoenig Combined longevity formulas all exhibited similar sample size-related biases, emphasizing the importance of accounting for sample size in data-limited situations where these formulas are commonly used to estimate $M_{formula}$.

Although an optimal sample size trend was expected, its direction was not. We initially assumed that long-lived, low M species with more age classes would require larger sample sizes to capture the oldest individuals needed for accurate $M_{formula}$ estimates. Short-lived species were expected to require smaller sample sizes to identify the oldest individuals due to their narrower age ranges. However, the opposite effect was observed, indicating that in large samples, the oldest observed individual was too old to produce an accurate $M_{formula}$ estimate for long-lived species. Large sample sizes may encounter an exceptionally old fish that is not representative of the population structure and M of species with a greater longevity and lower M. Instead, the t_{99} approach, which uses a lower, more representative maximum age, is more appropriate. Relying on the traditional t_{max} approach to estimate $M_{formula}$ has likely led to misestimating the true M for many assessed stocks.

Results for short-lived species suggest that extensive sampling is necessary to find the rare, oldest individuals needed for an accurate $M_{formula}$ estimate. This may be due to the high turnover observed in short-lived species (and potentially high recruitment), which results in younger individuals substantially outnumbering the oldest individuals. The maximum age estimate for short lived species is crucial, as a small change in the estimate can significantly affect M. For instance, increasing the maximum age estimate from four to six results in a 33% decrease in M using the Hamel Cope formula. Such a decrease in M could have significant consequences for assessments and management decisions. This counterintuitive result may stem from the established maximum age methods from literature (i.e. Hoenig, 1983; Then et al., 2015; Hamel & Cope, 2022) and the possibility that many species in the meta-analyses had sample sizes too small to accurately estimate maximum age. The results presented here call into question both the accuracy of currently reported $M_{formula}$ estimates and the adequacy of age data available for short-lived species. Under-sampling is a concern for short-lived species, as current sample sizes may be insufficient to capture the oldest age. Over-sampling is a concern for long-lived species, as accumulating age data over time may lead to an underestimate of M. The effects of sample size will vary with a species' life history, but our modeling suggests they may have caused over- or underestimation of true natural mortality rates.

Currently, minimum sample size recommendations exist for obtaining a maximum age to accurately estimate M across species, regardless of life history. Hoenig (1983) proposed that the probability of observing an older maximum age decreases once at least 200 individuals are sampled. Later, Hoenig (2017) suggested that the influence of sample size becomes less significant once annual samples reach 500 to 2,000 individuals. Yet, our modeling results demonstrate that annual sample sizes both above and below 500 significantly affects both maximum age and subsequent $M_{formula}$ estimates. Focusing on reaching a minimum sample size will likely still lead to biased estimates of maximum age and M, and we often lack the necessary knowledge to determine when a specific sample size is sufficient. Therefore, alternative methods must be employed to correct the biases caused by sample size.

99th Percentile Age

Selecting the oldest observed age (t_{max}) within a sample may introduce bias if it includes a rare individual of substantial age or size (Craig et al., 2017; Kenchington, 2014; Riginella et al., 2016). As more age data are collected and sample sizes increase, the likelihood of encountering such individuals also grows. To mitigate the sample size biases associated with

t_{max}, a percentile-based approach was explored. Dureuil & Froese (2021) proposed estimating the average maximum age as the mean age of the longest-lived n^{th} percentile of individuals. While some studies have suggested arbitrary proportions of individuals surviving to an average maximum age (e.g. 1% or 5%) (Hewitt & Hoenig, 2005), empirical data indicates this proportion is closer to 1 – 2% (Dureuil et al., 2021; See Appendix). Although not commonly used to determine maximum age, a percentile approach has been applied in some capacity for maximum age estimation in certain fish species, including *Lutjanus campechanus* (red snapper) (Buckmeier et al., 2016; Daugherty et al., 2019; Lowerre-Barbieri et al., 2015), as well as in cetaceans and marine mammals (Barlow & Boveng, 1991; Trites & Pauly, 1998). One such study modeling marine mammal populations used the 99th percentile age to define longevity, noting that this method was “less sensitive to sample size and less variable than the maximum age (100th percentile) [from a random sample]” (Barlow & Boveng, 1991). A 95th percentile age was also analyzed, but this proportion was more likely to be influenced by early-life mortality patterns (Barlow & Boveng, 1991). Consequently, a 99th percentile approach offered an opportunity to minimize the sample sizes biases observed when using t_{max} to calculate $M_{formula}$.

Sampling for t_{99} showed a significant reduction in sample size biases in our modeling efforts. After reaching a total sample size of approximately 5,000, the $M_{formula}$ estimate remained constant and insensitive to further increases in sample size, aligning with Barlow & Boveng (1991). In effect, this approach mitigates concerns about increasing sample size over time, as $M_{formula}$ estimates will remain unchanged. The 99th percentile method offers a promising alternative to the traditional t_{max} approach. However, this method resulted in a significant overestimation of $M_{model\ input}$ in all scenarios, suggesting that correction methods are still necessary to produce an accurate $M_{formula}$.

$M_{formula}$ Correction Formulas

All correction formulas for both t_{max} and t_{99} methods accurately estimated $M_{model\ input}$ across a range of sample sizes. The exception was a mortality rate of 0.01, where the correction formulas either underestimated $M_{model\ input}$ or failed to generate a corrected $M_{formula}$ estimate. This limitation is not necessarily concerning as the oldest individuals observed in simulations where $M_{model\ input} = 0.01$ approached 1,000 years old. None of the species assessed by SEDAR, nor those included in the datasets of Hoenig (1983), Then et al. (2015), or Hamel & Cope (2022) contained species near this age. The greatest maximum age in the Then et al. (2015) dataset was 205 years with an M of 0.04. For every other $M_{model\ input}$ rate assessed in our study, up to 0.5, the correction formulas produced accurate $M_{formula}$ estimates.

While there were no significant differences in performance between the t_{max} and t_{99} correction formulas, as both produced accurate $M_{formula}$ estimates, the t_{max}-corrected $M_{formula}$ values exhibited much greater variance than those of t_{99}. The 99th percentile method, in contrast, showed considerably less variation in corrected $M_{formula}$ estimates.

Differences Among Published Estimators

In the past, the choice of longevity-based M formula has been critical, as differences in their estimates can lead to varying conclusions about a stock's sustainability and catch recommendations. Before applying the correction formulas derived in our study, we observed these differences and identified a pattern in the variation of $M_{formula}$ estimates among the three formulas. All three were influenced by sample size, with smaller samples producing higher $M_{formula}$ estimates and larger samples yielding lower $M_{formula}$ estimates, but to varying degrees.

However, after applying the correction formulas, the choice of longevity formula became irrelevant, as the corrected $M_{formula}$ estimates were consistent across all three. Our study demonstrates that these correction formulas can be applied to any of the three published estimators, eliminating the need to debate which provides the most accurate $M_{formula}$ estimates.

Conclusions

We present an alternative method for estimating $M_{formula}$ using t_{99}, as the model results demonstrated the influence of sample size on $M_{formula}$ estimates when using t_{max}. Determining an optimal sample size using t_{max} is not feasible, highlighting the potential limitation of studies relying on a relatively small number of fish to establish relationships between M and maximum age. Although t_{99} alone is not reliable predictor of M, the correction formulas developed in this study effectively adjust for initial biases. The t_{99} $M_{formula}$ estimates stabilize once a total sample size threshold of 5,000 is reached, supporting a percentile-based approach with corrections as the preferred method for accurate $M_{formula}$ estimation. This approach alleviates concerns about the number of available ages for a species while minimizing the influence of outliers or rare-aged individuals.

This simulation modeled a theoretical population to examine how sample size affects maximum age estimates. It was not intended to replicate a true population or assessment model that incorporates important stock parameters such as selectivity at size and age and fishing pressure, among many others. Currently, the effects of other variables in the assessment model remain unknown; we only know that sample size influences maximum age-based M estimates. While the exponential decrease in the number of fish with age aligned with observed population age structures (Allen & Hightower, 2010; Miranda & Bettoli, 2007), assuming a constant population size over time is unrealistic, as is a constant M that does not vary with size or age. Stock sizes fluctuate over time due to various factors, including fishing pressure. In addition, the model assumed all individuals were equally susceptible to sampling, which may not always reflect real-world conditions. In fisheries, truly random sampling is rarely possible, as older fish may inhabit inaccessible areas or remain unobserved due to gear selectivity and size (Hoenig, 2017). This model also does not account for the truncation of age structure caused by fishery effects, such as size selectivity. While fisheries typically target the largest and oldest individuals, our model samples the entire population, including young-of-year fish. Since the population experienced no fishing (F = 0), mortality estimates calculated through these methods likely better reflect Z rather than M. Furthermore, historical exploitation can shape a stock's age composition, influencing the presence of older fish (Hoenig, 2017). Incorporating these factors in future research/modeling efforts could further improve the accuracy of $M_{formula}$ estimates. Additionally, recreating the work of Then et al. (2015) using t_{99} in replacement of t_{max} could mitigate biases introduced by sample size.

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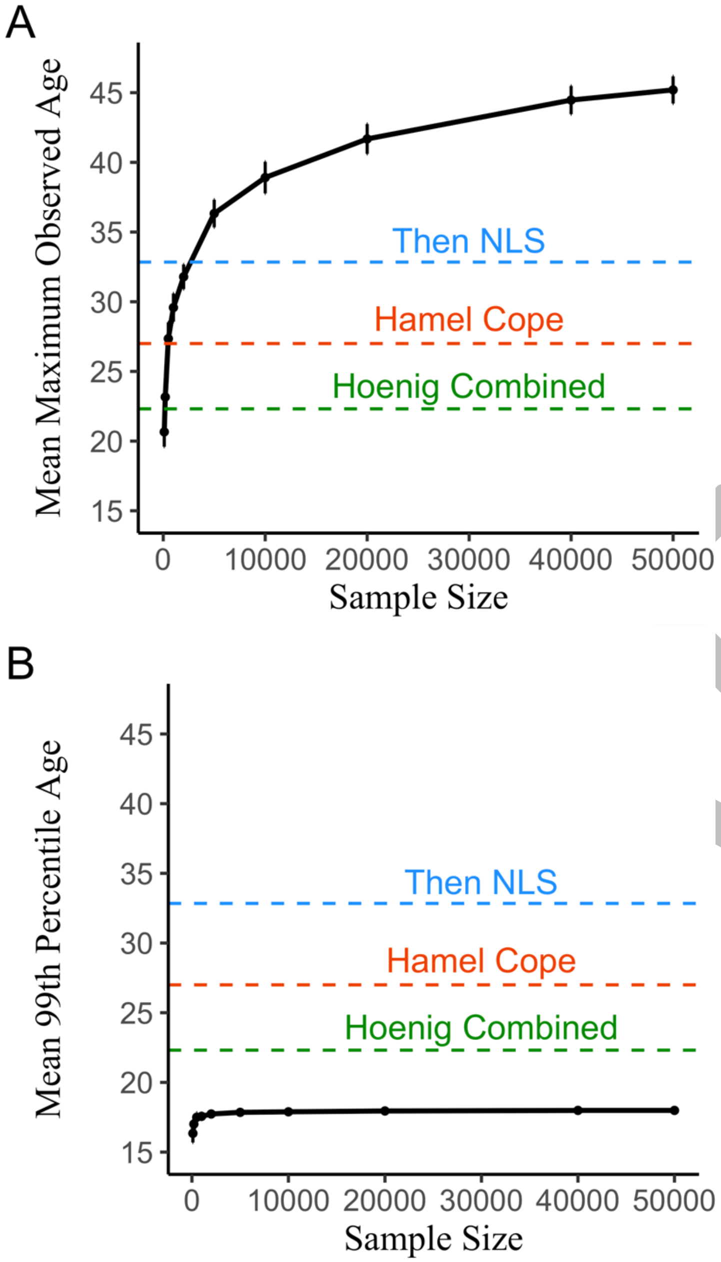

Figure 1. Mean maximum age values (Y-axis) observed for each sample size (X-axis) derived from model runs with an $M_{\text{model input}}$ of 0.2 for (A) t_{max} and (B) t_{99} methods. The 95% confidence intervals are shown for each sample size analyzed. The predicted maximum age values needed for an accurate M_{formula} estimate of 0.2 are shown for each of the three longevity equations (Hoenig Combined – green, Then NLS – blue, and Hamel Cope – orange).

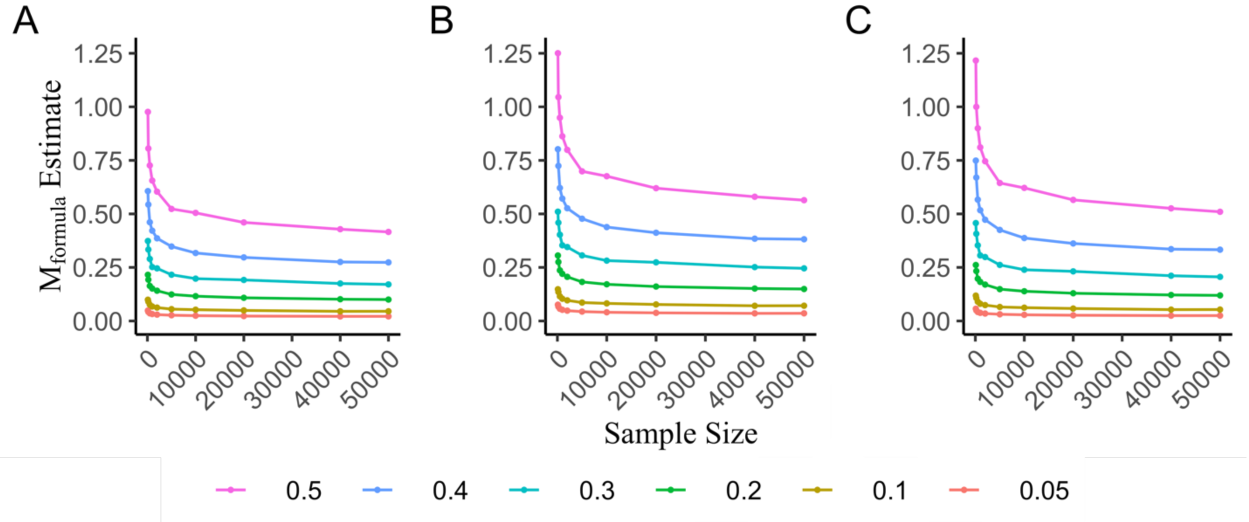

Figure 2. Lineplots of calculated $M_{formula}$ estimates (Y-axes) using the t_{max} approach across different sample sizes (X-axes). The color of the line indicates the $M_{model\ input}$ value. All panels show similar trends with lower sample sizes producing higher $M_{formula}$ estimates than larger sample sizes for Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations.

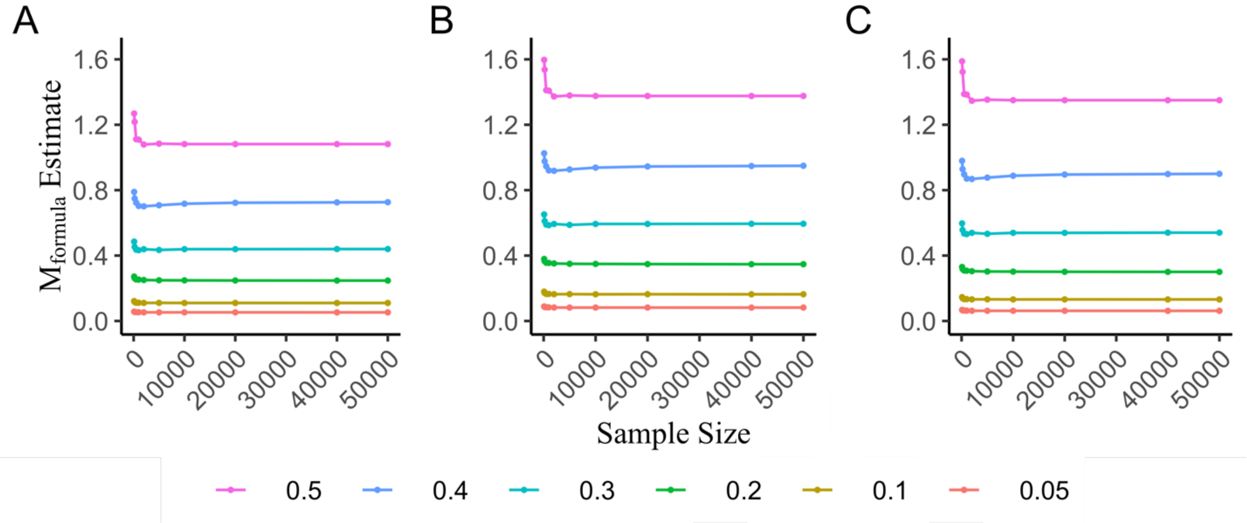

Figure 3. Lineplots of calculated $M_{formula}$ estimates (Y-axes) using the t_{99} approach across different sample sizes (X-axes). The color of the line indicates the $M_{model\ input}$ value. All panels show similar trends with lower sample sizes producing slightly higher $M_{formula}$ estimates, but estimates then level out once a sample size of approximately 5,000 is reached for Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations.

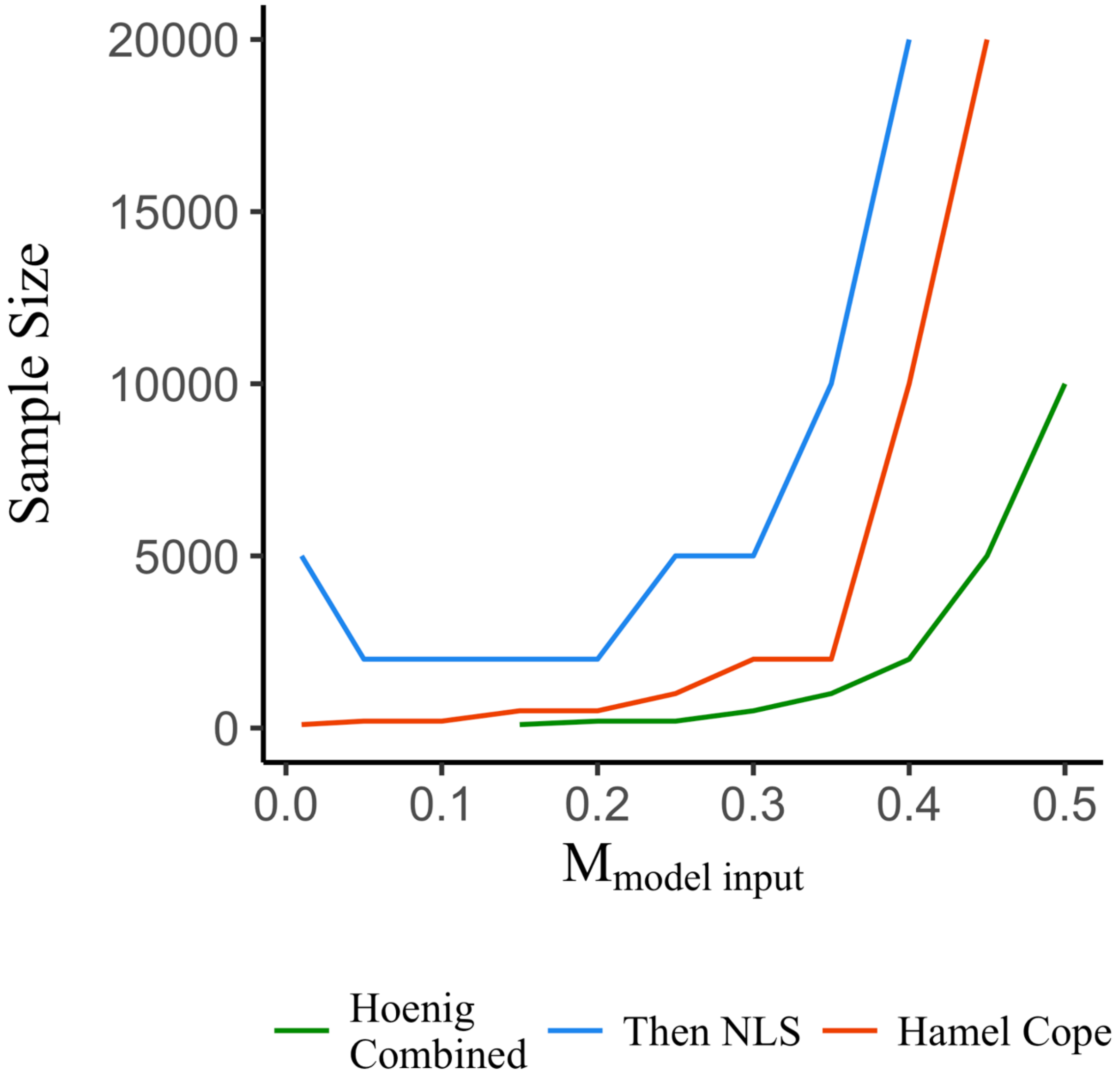

Figure 4. Optimal sample sizes (Y-axis) required to accurately estimate the $M_{\text{model input}}$ (X-axis) in the simulation using t_{max}. Results are shown for each of the three longevity formulas, with missing values at low and high motrality rates denoting instances in which the tested sample sizes could not accurately estimate $M_{\text{model input}}$. The t_{99} optimal sample sizes are omitted because the maximum age estimates from this method consistently resulted in M_{formula} estimates that overestimated $M_{\text{model input}}$, regardless of sample size.

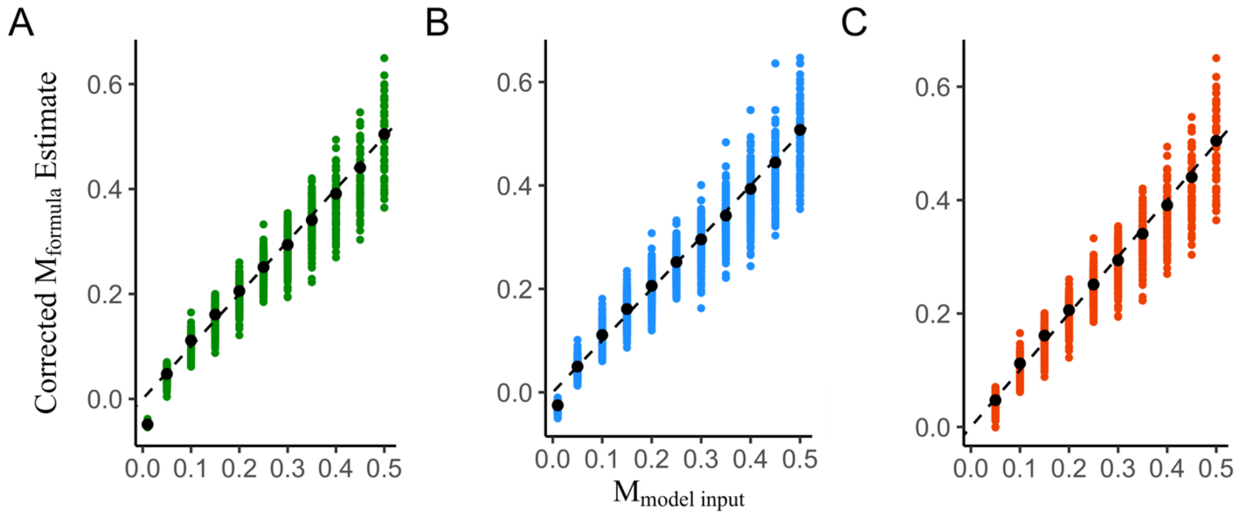

Figure 5. Resulting corrected estimates of initial $M_{formula}$ values (Y-axis) using the t_{max} correction formulas (see Equation [5] in text and Table 1) for the Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations, against $M_{model\ input}$ (X-axis). Black dots indicate means and the dotted black lines have a slope of one and intercept of zero depicting the accurate estimation of $M_{model\ input}$.

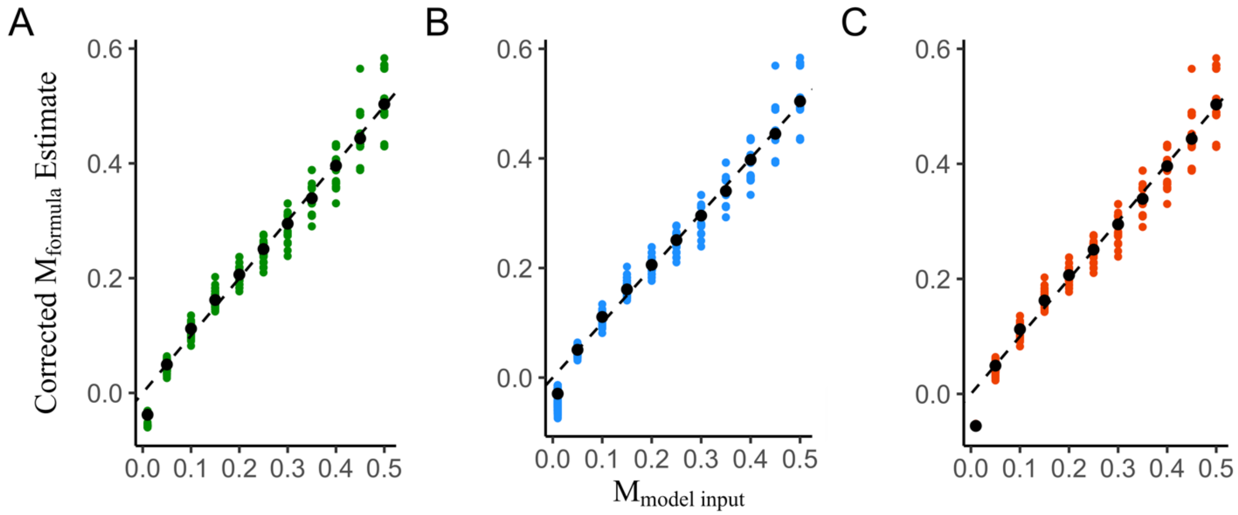

Figure 6. Resulting corrected estimates of initial $M_{formula}$ values (Y-axis) using the t_{99} correction formulas (see Equation [5] in text and Table 1) for the Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations, against $M_{model\ input}$ (X-axis). Black dots represent means and the dotted black lines have a slope of one and intercept of zero depicting the accurate estimation of $M_{model\ input}$.

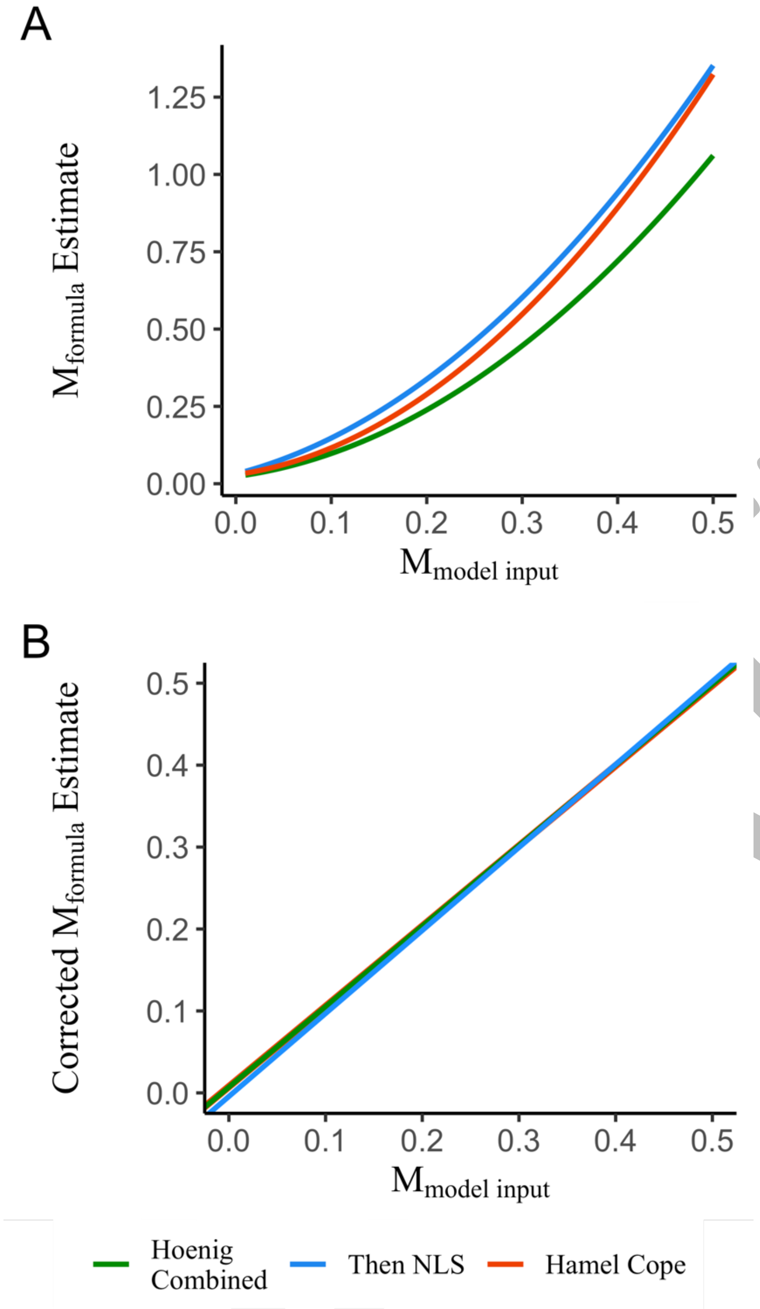

Figure 7. An example comparison of the average initial t_{99} $M_{formula}$ estimates (Y-axis) generated from a sample size of 500 by each longevity equation in comparison to the respective $M_{model\ input}$ rates (X-axis) from the simulation before (A) and after applying the correction (B). The data in 6A represent best fit polynomial trends in initial $M_{formula}$ estimates before correction.

Table 1. Polynomial coefficients a, b, and c for each maximum age method, under each longevity estimator for input into equation [5] (see text) to generate corrected $M_{formula}$ estimates. "ss" represents the sample size from which the maximum age estimate was obtained, and M_{int} indicates the initial $M_{formula}$ estimate generated using the respective longevity-based estimator before applying correction formulas.

Maximum Age Approach	Longevity Estimator	a	b	c
Oldest Observed Age	Hoenig Combined	$5.779 * ss^{(-0.143)}$	$0.470 * ss^{(-0.097)}$	$(0.047 * ss^{(-0.144)}) - M_{int}$
	Then NLS	$6.230 * ss^{(-0.135)}$	$1.019 * ss^{(-0.103)}$	$(0.060 * ss^{(-0.132)}) - M_{int}$
	Hamel Cope	$7.517 * ss^{(-0.145)}$	$0.471 * ss^{(-0.091)}$	$(0.059 * ss^{(-0.147)}) - M_{int}$
99th Percentile Age	Hoenig Combined	$5.182 * ss^{(-0.046)}$	$0.034 + 0.038 * \ln(ss)$	$(0.057 * ss^{(-0.091)}) - M_{int}$
	Then NLS	$5.454* ss^{(-0.040)}$	$0.391 + 0.041 * \ln(ss)$	$(0.070 * ss^{(-0.082)}) - M_{int}$
	Hamel Cope	$6.681 * ss^{(-0.046)}$	$-0.049 + 0.050 * \ln(ss)$	$(0.072 * ss^{(-0.092)}) - M_{int}$

Appendix: Investigating the mean age of the oldest 1% of individuals in a sample as a method for obtaining a maximum age to estimate M

While more resilient to sample size, the 99th percentile age approach still has a key limitation. Like the t_{max} method, it relies on a single individual to estimate maximum age. To address this, an alternative M estimation method was considered, based on the mean age of the oldest 1% of individuals in a sample ($t_{1\%}$). This method overcomes the reliance on a single age by utilizing multiple individuals from a sample for the maximum age estimate, while also allowing for the estimation of uncertainty around that mean age.

Additional simulations were conducted using the $t_{1\%}$ approach and analyzed in the same manner as the t_{max} and t_{99} methods to assess whether it, too, was biased or resilient to sample size. Results showed that, similar to the t_{99} method, using the oldest 1% of individuals in a sample was resilient to the effects of sample size once a threshold of approximately 5,000 individuals was reached (Fig. A.1). However, the $t_{1\%}$ approach, like t_{99}, tended to underestimate the age needed for an accurate $M_{formula}$ estimate. Although the $t_{1\%}$ method occasionally produced ages that were too old for accurate $M_{formula}$ estimation using the Hoenig Combined and Hamel Cope formulas, it generally resulted in an overestimation of the $M_{model\ input}$ for all three longevity-based formulas (Fig. A.2).

Due to the over- and underestimation of the $M_{model\ input}$ using $t_{1\%}$, we explored generating correction formulas for this method as well. The $M_{formula}$ values derived from $t_{1\%}$ were plotted against the corresponding $M_{model\ input}$ for each sample size. A second-order polynomial (equation [4]) was identified as the model that best fit the data for the Hoenig Combined, Then NLS, and Hamel Cope formulas at each sample size. The polynomial coefficients (a, b, and c) for each of the three longevity-based formulas were then modeled against sample size. These models resulted in three separate correction formulas, one for each longevity formula, as inputs into equation [5] (Table A.1). Applying these formulas to the initial $M_{formula}$ estimates from the simulation models led to a linear trend in corrected $M_{formula}$ estimates, except for an $M_{model\ input}$ of 0.01 (Fig A.3).

Calculating the mean age of the oldest 1% of individuals in a sample appears to mitigate concerns related to increasing sample size as additional age data are collected. However, small sample sizes may still pose a challenge for this method. For example, if a sample includes only 100 or 200 individuals, the oldest 1% approach yields just one or two ages, respectively, for estimating M. As a result, the estimate becomes highly sensitive to the presence of a single, exceptionally old individual, which may not accurately represent the population's age structure. Therefore, this approach is best applied when the sample size is at least 5,000. This is the point at which both the maximum age estimate and the resulting M estimate begin to stabilize with increasing sample size.

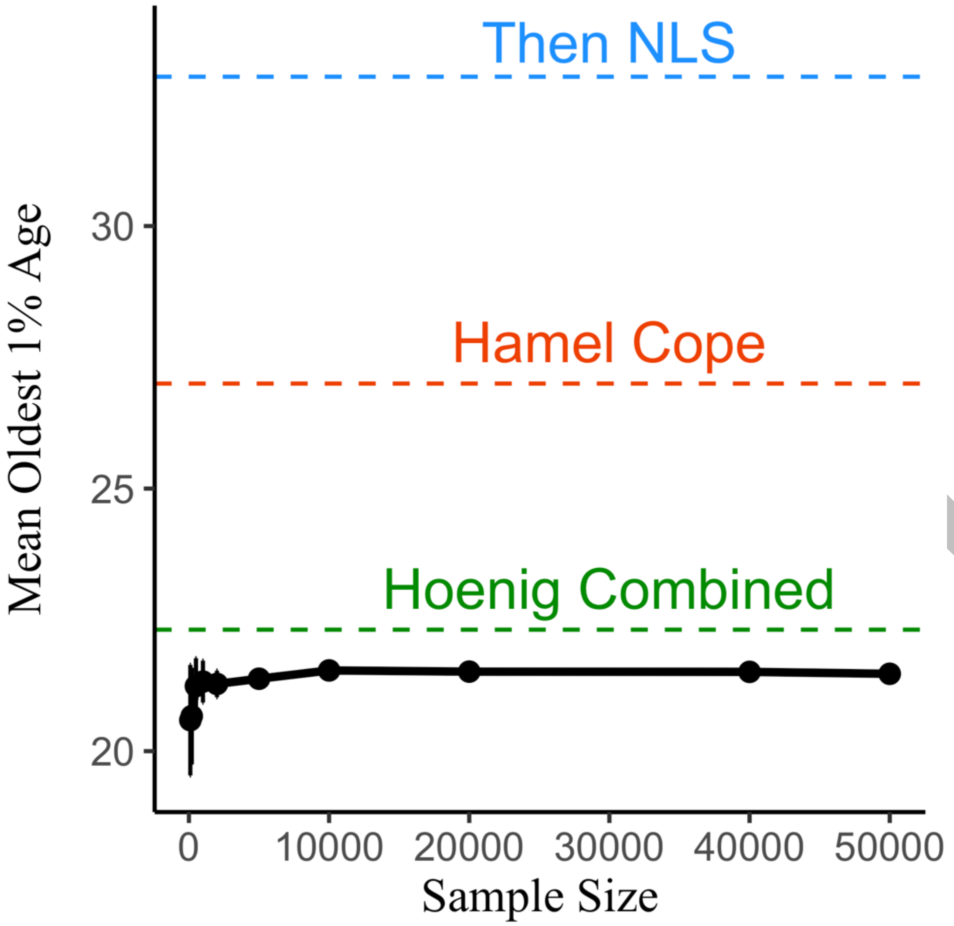

Figure A.1. Mean maximum age values (Y-axis) observed for each sample size (X-axis) derived from model runs with an $M_{\text{model input}}$ of 0.2 for the $t_{1\%}$ approach. The 95% confidence intervals are shown for each sample size analyzed. The predicted maximum age values needed for an accurate M_{formula} estimate of 0.2 are shown for each of the three longevity equations (Hoenig Combined – green, Then NLS – blue, and Hamel Cope – orange).

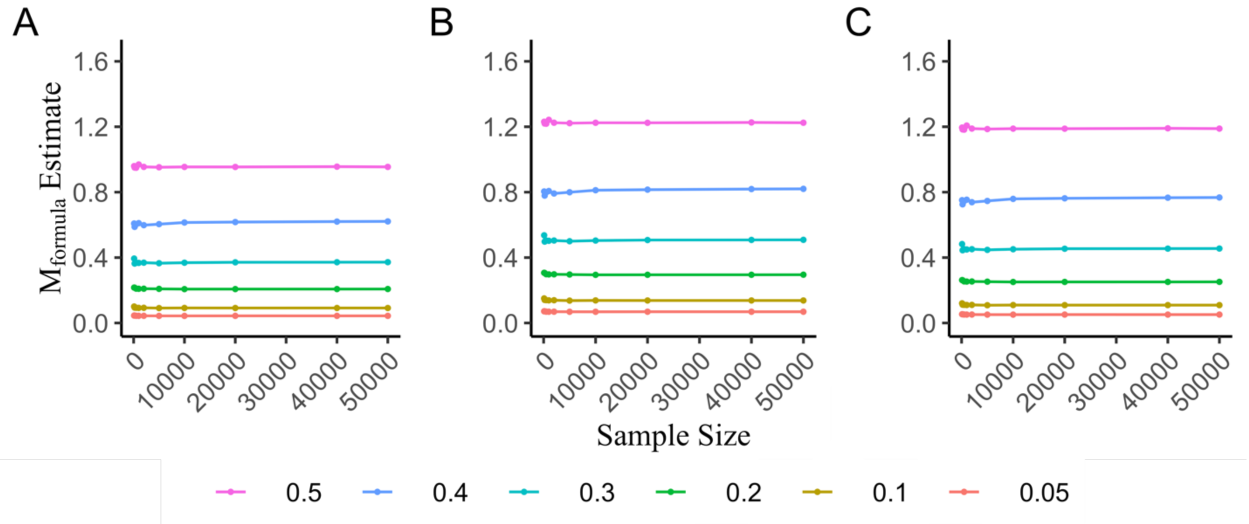

Figure A.2. Lineplots of calculated $M_{formula}$ estimates (Y-axes) using the $t_{1\%}$ approach across different sample sizes (X-axes). The color of the line indicates the $M_{model\ input}$ value. All panels show similar trends with lower sample sizes producing slightly higher $M_{formula}$ estimates, but estimates then level out once a sample size of approximately 5,000 is reached for Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations.

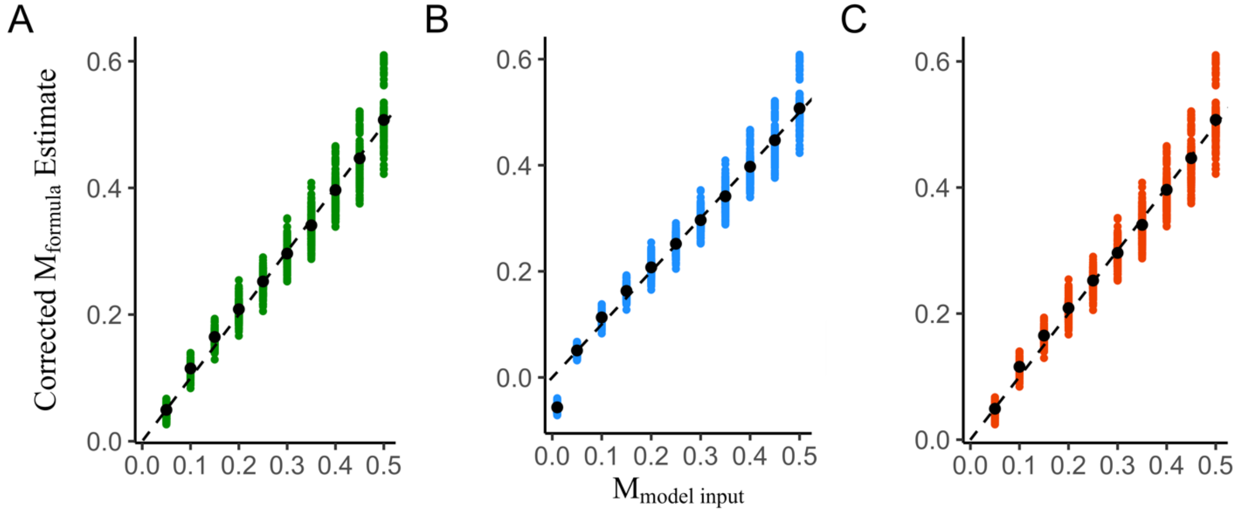

Figure A.3. Resulting corrected estimates of initial $M_{formula}$ values (Y-axis) using the $t_{1\%}$ correction formulas (see Equation [5] in text and Table A.1) for the Hoenig Combined (A), Then NLS (B), and Hamel Cope (C) longevity equations, against $M_{model\ input}$ (X-axis). Black dots represent means and the dotted black lines have a slope of one and intercept of zero depicting the accurate estimation of $M_{model\ input}$.

Table A.1. Polynomial coefficients a, b, and c for the mean top 1% age from a sample, under each longevity estimator for input into equation [5] (see text) to generate corrected $M_{formula}$ estimates. “ss” represents the sample size from which the maximum age estimate was obtained, and M_{int} indicates the initial $M_{formula}$ estimate generated using the respective longevity-based estimator before applying correction formulas.

Maximum Age Approach	Longevity Estimator	a	b	c
Mean Top 1%	Hoenig Combined	$3.420 * ss^{(-0.0073)}$	$0.207 + 9.214 * (1/ss)$	$(0.030 - 0.00055 * \ln(ss)) - M_{int}$
	Then NLS	$3.828 * ss^{(-0.0061)}$	$0.510 + 13.075 * (1/ss)$	$(0.040 * ss^{(-0.021)}) - M_{int}$
	Hamel Cope	$4.400 - 0.032 * \ln(ss)$	$0.195 + 11.089 * (1/ss)$	$(0.037 - 0.00069 * \ln(ss)) - M_{int}$