

Consistent ELEFAN estimation of growth curve parameters and biological reference points using medians

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Abstract. Electronic length frequency analysis (ELEFAN) is used by data-poor fisheries to assess various fish stock parameters, such as the von Bertalanffy growth curve (VBGC) parameters and biological reference points (BRPs). It is a practical tool in supporting informed fisheries management particularly in situations where age-based analysis is impractical. Although less precise than age-based analysis, ELEFAN generally achieves an acceptable level of accuracy. This study proposes an approach in which the median of the bootstrapped ELEFAN estimators is used, resulting in more consistent estimates. An operating model is employed to simulate the population dynamics of three representative fish stocks. Specified growth curve and length-weight parameters are used in the simulations and to calculate the BRPs analytically. Twelve months of length-frequency (LFQ) data containing nine hundred samples per month are simulated for various fishing mortality scenarios and selectivity parameters. The LFQ data is bootstrapped to generate 100 batches, and ELEFAN is applied to each batch 100 times. The median of the bootstrap estimator for each parameter is then calculated. The results show that median of the bootstrapped estimators produces highly consistent estimates close to the true values, with a coefficient of variation of less than 1.5% and bias of less than 2% in all scenarios for both the VBGC parameters and BRPs.

Key Words: median bootstrap estimators, bias, simulation, length frequency data, data-poor fisheries.

Introduction. Electronic length frequency analysis (ELEFAN) is a length-based method that is widely used in fisheries science to assess fish population growth and mortality parameters (Pauly 1980; Pauly & David 1981; Pauly 1982). It is commonly used in data-poor fisheries to analyze length–frequency (LFQ) data collected from local landing sites or by scientific surveys, and to estimate the von Bertalanffy growth curve (VBGC) parameters. The VBGC parameters include the asymptotic length (L_{∞}) and growth coefficient (K), which describe the average growth of fish stock (Pauly & Sparre 1991). These parameters are further used to determine the biological reference points (BRPs) related to yield-per-recruit (YPR) analysis. Overall, the VBGC parameters and BRPs are key metrics in stock assessment (Cadima 2003). However, the accuracy and precision of single-run ELEFAN's estimations are compromised by multiple sources of uncertainty (Schwamborn et al 2019; Wang et al 2020; Taufani & Matsuishi 2024). Hence, there is a need to reduce the uncertainty inherent in bootstrap estimates by generating consistently reliable estimates.

The bootstrap method is a statistical technique that resamples a dataset with replacement, enabling the precision and accuracy of the estimator to be evaluated without strong assumptions about the population (Efron 1979; Efron 1982). This approach has previously been applied in fisheries research to develop accurate analytical expressions (Cerviño & Saborido-Rey 2006; Elvarsson et al 2014; Stewart & Hamel 2014). In evaluating the accuracy of the initial estimates from single bootstrapping, numerous resampled estimates are obtained. This process can be used to evaluate the precision and accuracy of the estimator, and to establish more consistent representative values. To reduce the effects of outliers, the median is sometimes used as the representative value.

This study demonstrates, through simulations, that using the median of the bootstrap estimator provides more consistent results than relying on the initial estimates obtained by ELEFAN. In this study, consistency refers to the empirical ability of median of the bootstrap estimator to produce parameter estimates that remain close to the true value, exhibiting low bias and low coefficient of variation across repeated bootstrap resampling. Therefore, the aim of this study was to evaluate the use of median of the bootstrap estimator to achieve consistent ELEFAN parameter estimates, providing a practical approach for obtaining reliable VBGC parameters and BRPs – a critical challenge in data poor fisheries.

Material and Method

Model assumptions and data source. This study was conducted using simulated length frequency (LFQ) data representative of three life histories. Hypothetical VBGC parameter values were selected, based on expert judgment, to represent short-lived/fast-growing, medium-lived/moderately growing, and long-lived/slow growing tropical fish species (Table 1). These values were not drawn from specific species but were intended to reflect biologically plausible traits of short-lived, medium-lived, and long-lived tropical species in general. The modeling of growth, mortality, selectivity, and recruitment followed the outlines given by Taylor & Mildenerger (2017) and Chong et al (2020).

Table 1

Initial parameter values of the operating model

| <i>Parameter</i> | <i>Symbol</i> | <i>Short-lived</i> | <i>Medium-lived</i> | <i>Long-lived</i> |
|--|-------------------|--------------------|---------------------|-------------------|
| Growth curve parameters (cm) | L_{∞} | 30.0 | 70.0 | 110.0 |
| Growth coefficient (yr^{-1}) | K | 0.7 | 0.4 | 0.2 |
| Hypothetical age at 0 length (years) | t_0 | 0.0 | 0.0 | 0.0 |
| LWR parameter (intercept/condition factor) | a | 0.001 | 0.0009 | 0.00002 |
| LWR parameter (allometric growth exponent) | b | 3.0 | 3.0 | 3.0 |
| Natural mortality (yr^{-1}) | M | 0.625 | 0.313 | 0.167 |
| Fishing mortality (yr^{-1}) | F | 0.625 | 0.313 | 0.167 |
| Timestep (or time increment) | t_{incr} | 1/12 | 1/12 | 1/12 |
| Length at 50% maturity (cm) | L_{50}^m | 23.0 | 46.0 | 83.0 |
| Maturity width ogive (cm) | mwo | 5.0 | 9.0 | 17.0 |
| Spawning stock biomass (tonnes) | SSB | 1.0×10^4 | 1.0×10^4 | 1.0×10^4 |
| Recruitment upper limit parameter | α | 1.0 | 1.0 | 1.0 |
| Maximum recruitment (N) | β | 1.0×10^4 | 1.0×10^4 | 1.0×10^4 |
| Recruitment standard deviation | δ_R | 0.737 | 0.737 | 0.737 |
| Length at 50% selectivity (cm) | L_{50}^s | 8.0 | 35.0 | 72.0 |
| Selectivity width (cm) | wqs | 2.0 | 4.0 | 17.0 |
| Bin size (cm) | | 1.0 | 2.0 | 4.0 |
| Maximum age (years) | t_{max} | 4.0 | 8.0 | 15.0 |

An individual-based simulation model was developed to represent the population dynamics of a hypothetical fish species (Table 2). The model design incorporated key biological processes, including growth, natural and fishing mortality, and continuous recruitment. When using this model, the simulations proceed in discrete monthly timesteps (t_{incr}). The number of timesteps per year ($n_{\text{year}} = t_{\text{incr}}$) is set to match the length of the reproductive weight vector, ensuring that reproduction and mortality are evaluated at a consistent temporal resolution.

Simulations were conducted under the following assumptions:

- (1) Individual fish growth is described using the VBGC function. Values for L_{∞} and K are drawn for each individual from a multivariate lognormal distribution to reflect inter-individual variability. By incorporating this variability, the model represents the diversity in growth trajectories among individuals in a population (equations 1–4 in Table 2).
- (2) Individual variability in growth is incorporated by assuming a coefficient of variation (CV) of 0.1 for both L_{∞} and K . This value represents a moderate level of variability, as commonly used in individual-based models, and is consistent with the biologically plausible variability observed in fish populations.
- (3) Individual fish mature according to a length-based logistic function, such that the probability of being mature increases with body length. Maturity is characterized by a length at 50% maturity and a slope parameter defining the transition from immature to mature. Equation 5 in Table 2 specifies the probability of maturity at a given length.
- (4) Each individual experiences a total mortality (Z) that combines natural mortality (M) and fishing mortality (F), with F scaled by size-specific selectivity. The probability of death within a timestep is calculated by equation 6.
- (5) Mortality is stochastic; at each timestep, each individual is randomly designated as alive or dead. For individuals that die, the cause of death is determined probabilistically, with the likelihood of dying from natural causes or fishing proportional to the relative contributions of M and F to Z (equations 7–9).
- (6) The species is assumed to reproduce continuously throughout the year, with recruitment occurring year-round, characteristic of tropical fish (equations 10–11). Recruitment follows a hockey stick stock-recruitment relationship (Barrowman & Myers 2000). This recruitment relationship is chosen for its simplicity, precautionary nature, and suitability for simulations reflecting realistic, but conservative, recruitment dynamics.
- (7) The fish population is assumed to be in an unfished equilibrium state, where natural mortality and recruitment are balanced. The model is assumed to simulate the population over ten years without fishing (burn-in period), allowing the system to stabilize naturally (equations 12–13).
- (8) Fishing is assumed to begin after the burn-in period. Fishing mortality is applied through gear selectivity. A logistic selectivity curve, which is suitable for active gears such as trawls, is assumed to represent gear selectivity in the model (equations 14–17).

Operating model. The operating model (OM) simulated the population dynamics of hypothetical fish stocks using the “virtualPop” function of the fishdynr R package (Taylor 2017). The model was designed to reflect the life-history traits typical of short-, medium-, and long-lived tropical pelagic fish species. The hypothetical fish species were simulated using hypothetical life-history traits. The simulation spanned 50 years for the short-lived scenario and 100 years for the medium- and long-lived scenarios. A 10-year burn-in period was imposed to allow the populations to reach equilibrium, followed by 40 and 90 years of fishing, respectively. Fishing mortality remained constant within each scenario and was applied at monthly intervals. The burn-in period remained constant across all simulated life histories to allow the populations to reach a stable size structure. The simulation period was scaled with lifespan to ensure that a comparable number of generations were represented across scenarios. In each month of the final year (i.e., year 50 or 100), a random sample of 900 individuals was extracted for analysis. The sizes of the monthly LFQ samples were equal across all scenarios. These LFQ samples were bootstrapped in each month and used as the input for the ELEFAN model to estimate the stock parameters and evaluate the consistency of the median estimators.

A natural LFQ dataset of *Abra alba* (Brey et al 1988) was used to test the applicability of median bootstrap estimators’ approach to an empirical dataset with relatively small sample size. The dataset consists of shell lengths from 675 individuals collected over 7 monthly samples and grouped into 14 length classes. VBGC parameters were estimated from this dataset, and the consistency was assessed using density plots. This dataset is available in the TropFishR package.

Table 2

Equations and functions of the operating model and their descriptions

| S/n | Equation | Description |
|-----|---|--|
| 1 | $L_t = L_\infty(1 - e^{-K(t-t_0)})$ | L_t – length at time t , L_∞ – asymptotic length, K – growth coefficient, t_0 – theoretical age at length 0. |
| 2 | $L_{\infty,i} = L_{\infty,p} \cdot LN(0, L_{\infty,cv})$ | $L_{\infty,i}$ – individual asymptotic length, $L_{\infty,p}$ – population-level L_∞ , $LN(0, L_{\infty,cv})$ – a lognormal random variability in L_∞ |
| 3 | $K_i = K_p \cdot LN(0, K_{cv})$ | K_i – individual growth coefficient, K_p – population-level K , $LN(0, K_{cv})$ – a lognormal random variability in K |
| 4 | $W = aL^b$ | W – body weight of fish, a and b – length-weight relationship parameters |
| 5 | $m = \frac{1}{1 + \exp\left[\frac{L_t - L_{50}^m}{\ln\left(\frac{0.75}{0.25}\right) - \ln\left(\frac{0.25}{0.75}\right)}\right]}$ | m – maturity, L_t – length at time t , L_{50}^m – the length at which 50% of fish reach maturity |
| 6 | $p_d = 1 - \exp(-Z \cdot t_{incr})$ | p_d – the probability of death, t_{incr} – time increment |
| 7 | $p_M = \text{sample}\left((0,1), \text{prob} = \left(\frac{M}{Z}, \frac{F}{Z}\right)\right)$ | p_M – probability of death due to M , sample – is used for random sampling from a given set of values, prob – is the vector of probabilities |
| 8 | $p_F = \text{sample}\left((1,0), \text{prob} = \left(\frac{F}{Z}, \frac{M}{Z}\right)\right)$ | p_F – probability of death due to F |
| 9 | $Z = M + F$ | Z – total mortality rate, M – natural mortality rate, F – fishing mortality |
| 10 | $R = \min((\alpha \cdot SSB), \beta)$ | R – recruitment, SSB – spawning stock biomass, α – recruitment per unit of SSB (recruitment rate), β – maximum recruitment (upper limit) |
| 11 | $R_t = LN(0, \delta^2_R)$ | R_t – recruitment at time t , $LN(0, \delta^2_R)$ – lognormal-distributed random variable with mean 0 and variance – δ^2_R |
| 12 | $SSB_t = \sum_{a=0}^A N_{a,t} \cdot w_a \cdot m_a$ | SSB_t – spawning stock biomass at time t , A – maximum age, $N_{a,t}$ – number of individuals at age a and time t , w_a – the weight of individuals at age a and time t , m_a – maturity at age a . |
| 13 | $E_0 = \sum_{a=0}^A SSB_0 \cdot w_a \cdot m_a$ | E_0 – expected egg production at unfished condition, SSB_0 – spawning stock biomass in the unfished condition, A – maximum age, w_a – weight at age, m_a – maturity at age a |
| 14 | $s = \frac{1}{1 + \exp\left[\frac{L_t - L_{50}^s}{\ln\left(\frac{0.75}{1-0.75}\right) - \ln\left(\frac{0.25}{1-0.25}\right)}\right]}$ | s – gear selectivity, L_t – length at time t , L_{50}^s – length at which fish has 50% probability of being caught by the gear |
| 15 | $F = q \cdot E$ | F – fishing mortality, q – catchability coefficient, E – effort |
| 16 | $E_f = \sum_{a=0}^A (N_a \cdot w_a \cdot m_a \cdot f_a)$ | E_f – egg production under fishing conditions, N_a – number of individuals at age a , w_a – weight at age of the individuals, m_a – maturity at age, f_a – fecundity at age, A – maximum age. |
| 17 | $E_f = \sum_{a=0}^A SSB_f \cdot w_a \cdot m_a$ | E_f – egg production under fishing conditions, SSB_f – spawning stock biomass under fishing conditions, A – maximum age, a – age index, summing from 0 to A , w_a – weight at age, m_a – maturity at age a . |

Sensitivity analysis of median bootstrap estimators. Sensitivity analysis was conducted to evaluate the stability of the estimators under varying fishing mortality rates ($F \neq M$). Four alternative levels of fishing mortality levels were applied to the short-lived

life history scenario: lightly fished ($F=0.025$), underfished ($F=0.1$), medium fished ($F=0.5$), and overfished ($F=0.8$). These scenarios tested whether the median bootstrap estimators could provide consistent estimates across different fishing mortalities.

Overview of the simulations. The simulation functions were created in R (R Core Team 2024) with detailed code to simulate all essential population processes, including (i) the equilibrium period, (ii) life history parameters, (iii) parameter variability, (iv) reproduction, (v) individual growth and maturity, (vi) recruitment, (vii) natural mortality, and (viii) fishing mortality as the non-equilibrium condition of fish stock utilization. Additional functions were used to simulate gear selectivity, fishing mortality cases, and harvest rates, targeting the hypothetical fish populations. In the selected fishing mortality cases, F was increased from very low to high levels to induce variability in the fish length distributions within the sampled data. The `lfqSampSurvey` model survey sampling function was used to sample individuals with a length greater than zero to generate the 12-month synthetic LFQ dataset from 900 samples per month. These data constituted the original dataset for analysis in each scenario. The use of a one-year LFQ dataset improves analysis speed and enables analyses to be repeated more quickly (Schwamborn et al 2019). The original dataset was bootstrapped 100 times to generate bootstrapped LFQ datasets. ELEFAN was then applied to these datasets to estimate 100 sets of VBGC parameters and BRPs. A single median bootstrap estimator was then calculated for each parameter. To evaluate the consistency of the median estimator, this process was repeated 100 times. The value of 100 iterations and repetitions was considered sufficient to approximate estimates variability and for computational simplicity and speed. Consistency was evaluated using the CV, whereas accuracy was assessed using the root mean squared error (RMSE) and relative bias (RB). An overview of the simulations is illustrated in Figure 1.

Estimation of the growth curve parameters. ELEFAN was used to estimate the stock growth model parameters. First, ELEFAN was used to modify the bootstrapped LFQ dataset using bin sizes of 2.0, 3.0, and 5.0 cm for all three life-history scenarios. The bin sizes were selected using the formula given by Wang et al (2020). The modified dataset was then restructured using a moving average of five. Subsequently, the values of L_{∞} and K were estimated using `ELEFAN_GA` (Scrucca 2013; Scrucca 2016) in the `TropFishR` package, which employs a genetic algorithm-based optimization method in which the parameters are treated as genes within a population with a natural mutation rate. `ELEFAN_GA` was selected for parameter optimization because it is effective in avoiding local optima and producing stable solutions (Dang et al 2017; Taylor & Mildenerger 2017; Zhou et al 2022). The `ELEFAN_GA` optimization settings were specified as population size (`popSize`) of 50, a maximum of 30 iterations (`maxiter`), and 20 independent runs (`runs`), balancing convergence reliability and computational efficiency. The initial parameter values for L_{∞} and K were based on the values used in the OM for simulating the LFQ data. The search space spanned $\pm 20\%$ of the initial parameter values, resulting in upper and lower limits. The linearized length-converted catch curve method, as defined below (Pauly 1990; Pauly et al 1995), was used to estimate the instantaneous total mortality rate. To compare the growth curves, the growth performance index (ϕ') was calculated from the VBGC parameters (Pauly & Munro 1984). Natural mortality (M) was estimated using Tanaka's empirical formula (Tanaka 1960).

Estimation of biological reference points. The yield per recruit (YPR) model incorporates the Thompson & Bell (1934) prediction model to estimate yields and biomass. This model uses the fishing mortality, length-weight relationship parameters (a and b), and gear selectivity parameters to predict BRPs such as $F_{0.1}$, $F_{0.5}$, and F_{\max} within ELEFAN, where $F_{0.1}$ is the fishing mortality at which the slope of the YPR curve is 10% of that at the origin, $F_{0.5}$ is the fishing mortality that reduces the biomass-per-recruit (BPR) to 50% of its level in the unfished population, and F_{\max} is the fishing mortality rate that produces the maximum YPR. The assumed true values of $F_{0.1}$ and F_{\max} were analytically calculated as follows using the hypothetical VBGC parameters and mortality values:

$$YPR = \frac{F}{F+M} \cdot \left(1 - \frac{L_c}{L_\infty}\right)^{\frac{M}{K}} \cdot \sum_{n=0}^3 \frac{\Omega_n \left(1 - \frac{L_c}{L_\infty}\right)^{\frac{nK}{1+F+M}}}{1 + \frac{nK}{1+F+M}}$$

Where:

F - the fishing mortality rate;

M - the natural mortality rate;

L_c - the length of fish at first capture by the fishing gear;

Ω_n - a coefficient ($\Omega_0 = 1$, $\Omega_1 = -3$, $\Omega_2 = 3$, $\Omega_3 = -1$).

The assumed true $F_{0.5}$ value was analytically calculated using the following mathematical expression:

$$F_{0.5} = \operatorname{argmin}_F \left(BPR_F - \frac{BPR_{\text{virgin}}}{2} \right)^2$$

Where:

BPR_F - the BPR at a given F ;

BPR_{virgin} - the virgin BPR when $F = 0$.

The VBGC parameters and BRPs were estimated for each resampled dataset.

Estimator consistency analysis. The consistency of the median of the bootstrap estimators was analyzed using the CV and relative bias (RB), as defined by the following equations:

$$CV (\%) = \frac{s}{\bar{u}} \cdot 100$$

Where:

CV - the coefficient of variation of the median bootstrap estimators;

s - the standard deviation of the median bootstrap estimators;

\bar{u} - the sample mean of the median bootstrap estimators.

$$RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (u - \tilde{u}_i)^2}$$

Where:

n - the number of batches;

u - the true parameter value;

\tilde{u}_i - the predicted median value at batch i .

The RB was calculated as follows:

$$RB (\%) = \left(\frac{RMSE}{u} \right) \cdot 100$$

Where:

RB - relative bias;

RMSE - root mean squared error;

u - the true parameter value.

Results. The distribution of the original estimators from the first 100 bootstraps and the distribution of the median bootstrap estimators for each VBGC parameter and BRP for all scenarios are presented in Figures 2–4. The median bootstrap estimators of each scenario are narrowly distributed within the wider distribution zone of the original bootstrap estimates. The original bootstrap estimator produced L_∞ estimates with substantial variability, exhibiting RB and CV values within 4% across all scenarios. The significant variability was also observed in the K estimates with RB and CV around 10% across all life-history scenarios. For ϕ' , the estimates were relatively stable RB and CV less than 2% across all cases (Table 3). The BRPs; $F_{0.1}$ and $F_{0.5}$ estimates exhibited a bias greater than 10% for short-lived species, but less than 10% for medium- and long-lived scenarios. F_{\max} uncertainty remained relatively within the range of $F_{0.1}$ and $F_{0.5}$ estimates, with biases limited to approximately 7% bias across all simulated life histories.

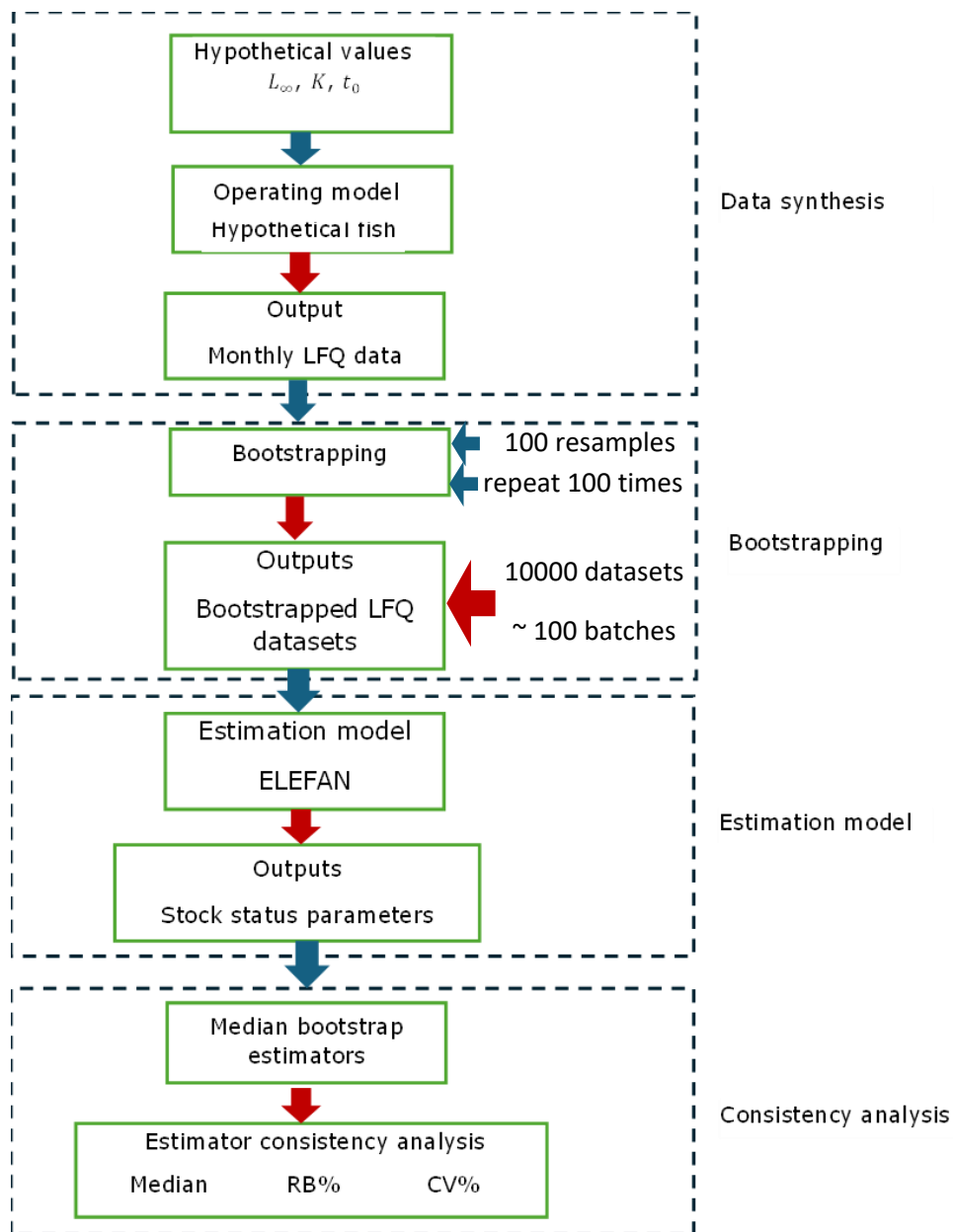


Figure 1. Overall process of the simulation study, from length frequency data synthesis to analysis of the median bootstrap estimators for each stock status parameter. CV-coefficient of variation, RB-relative bias.

Median bootstrap estimators. The median bootstrap estimators (Table 4) displayed consistent performance in estimating L_{∞} , with a CV below 0.5%, while the true initial parameter values were correctly recovered with less than 2% bias across all life-history scenarios. Similarly, K was estimated consistently (CV<1.5%) across all scenarios, with bias of less than 1.5% for short- and medium-lived scenarios and less than 3% for long-lived species. The stability of the median bootstrap estimators is also evident in the estimation of ϕ' , with a CV below 0.5% and bias of less than 1% across all scenarios. For all BRPs across all scenarios, the medians consistently produced estimates with a bias of less than 2% and CV of approximately 1%.

When applied to the *Abra alba* dataset to estimate VBGC parameters, the results showed that the median bootstrap estimators were narrowly concentrated around the center of the widely spread original bootstrapped ELEFAN estimates (Figure 5). The distribution of the median bootstrap estimators followed similar trend to that observed in the simulated scenarios. This pattern indicates that, even with relatively small empirical dataset, the proposed approach yields consistent parameter estimates.

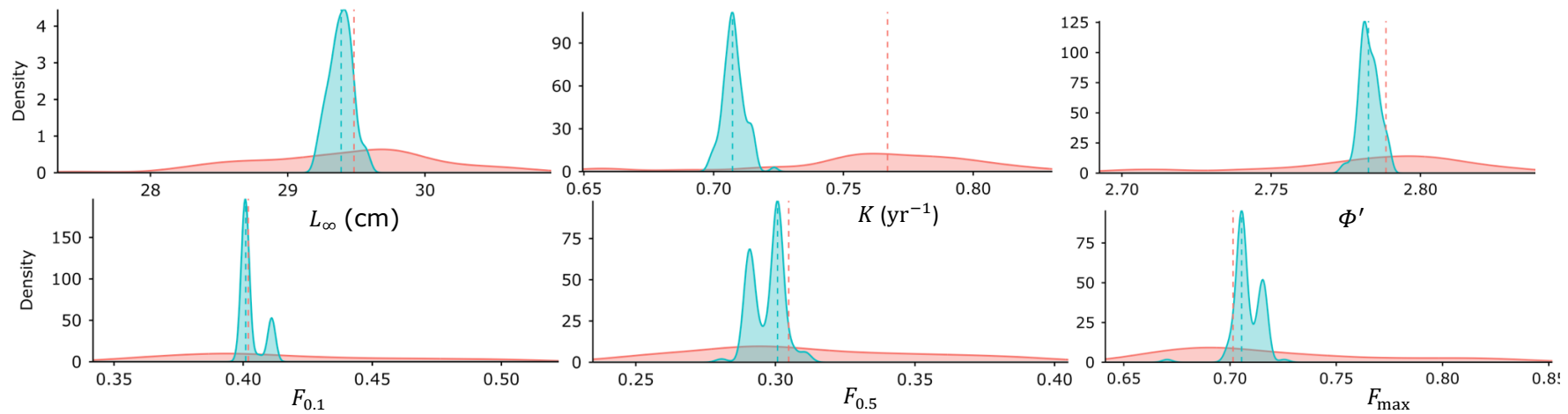


Figure 2. Comparison of original and bootstrap estimators in estimating VBGC parameters and BRPs of simulated short-lived life history. Pink color - the original bootstrap estimates, light blue - the medians of bootstrap estimators; dashed vertical lines the medians of the distributions.

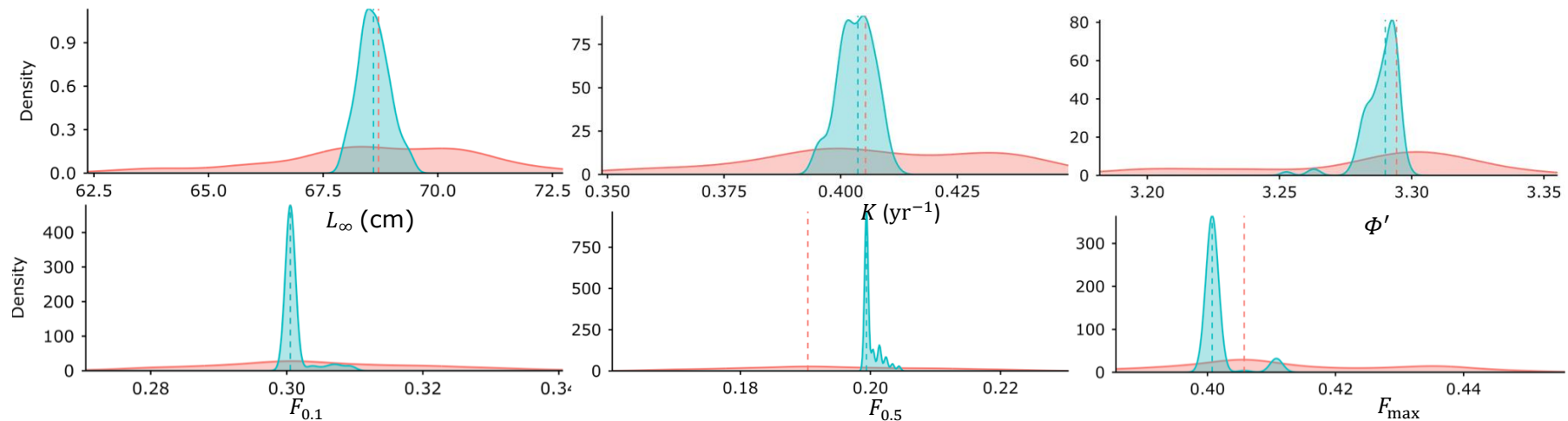


Figure 3. Comparison of original and median bootstrap estimators in estimating VBGC parameters and BRPs of simulated medium-lived life history. Pink - original bootstrap estimates, light blue - medians bootstrap estimators, dashed vertical lines - the median values.

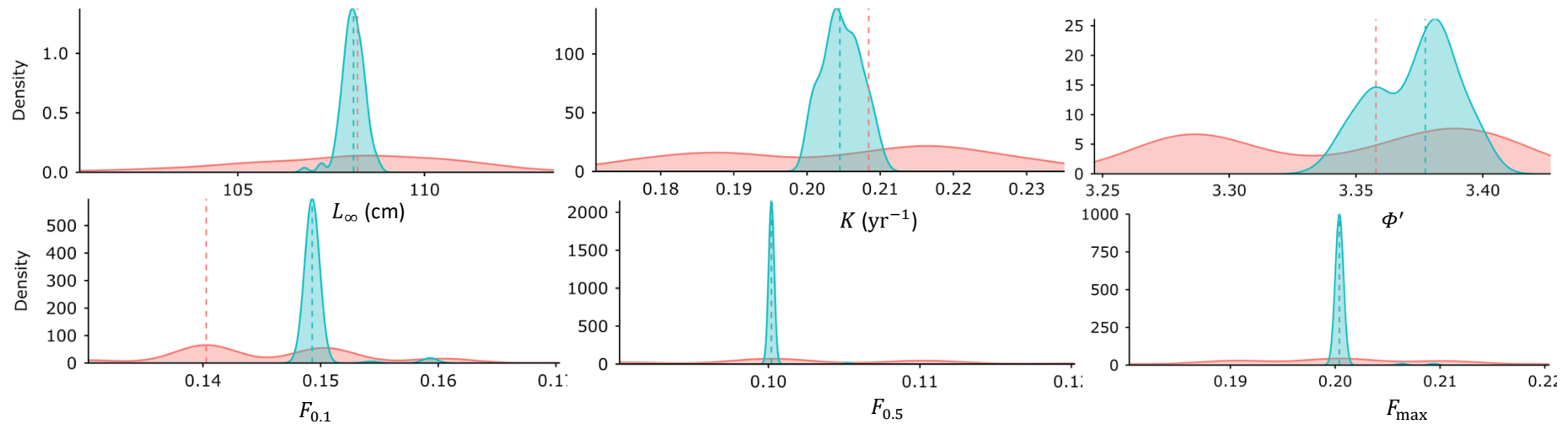


Figure 4. Comparison of original and median bootstrap estimators for estimating VBGC parameters and BRPs of simulated long-lived life-history. Pink - the distribution of original bootstrap estimates, light blue - the medians of bootstrap estimators, dashed vertical lines - the median values.

Table 3

Comparison of original bootstrap estimators in estimating VBGC parameters and BRPs from different life histories scenarios using simulated length frequency data

| Variables | True value | Short-lived scenario | | | Medium-lived scenario | | | | Long-lived scenario | | | |
|---------------------------------|------------|----------------------|-------|-------|-----------------------|--------|------|------|---------------------|--------|------|------|
| | | Median | RB% | CV% | True value | Median | RB% | CV% | True value | Median | RB% | CV% |
| L_{∞} (cm) | 30 | 29.48 | 3.06 | 2.32 | 70 | 68.71 | 3.75 | 3.18 | 110 | 108.21 | 3.18 | 2.56 |
| K (yr^{-1}) | 0.7 | 0.77 | 9.62 | 5.21 | 0.4 | 0.41 | 6.33 | 6.12 | 0.2 | 0.21 | 8.79 | 8.67 |
| ϕ' | 2.8 | 2.79 | 1.40 | 1.25 | 3.30 | 3.29 | 1.35 | 1.33 | 3.38 | 3.36 | 1.93 | 1.60 |
| $F_{0.1}$ (yr^{-1}) | 0.4 | 0.40 | 11.68 | 10.56 | 0.3 | 0.30 | 5.27 | 4.99 | 0.15 | 0.14 | 6.56 | 5.64 |
| $F_{0.5}$ (yr^{-1}) | 0.3 | 0.30 | 14.23 | 13.34 | 0.2 | 0.19 | 8.28 | 7.61 | 0.1 | 0.10 | 8.67 | 7.95 |
| F_{\max} (yr^{-1}) | 0.7 | 0.70 | 7.90 | 7.10 | 0.4 | 0.41 | 5.35 | 4.18 | 0.2 | 0.20 | 4.95 | 4.98 |

Table 4

Comparing median bootstrap estimators from different life histories in estimating VBGC parameters and BRPs using simulated length frequency data

| Variables | Short-lived | | | | Medium-lived | | | | Long-lived | | | |
|---------------------------------|-------------|--------|------|------|--------------|--------|------|------|------------|--------|-------|------|
| | True value | Median | RB% | CV% | True value | Median | RB% | CV% | True value | Median | RB% | CV% |
| L_{∞} (cm) | 30 | 29.39 | 2.10 | 0.29 | 70 | 68.60 | 2.08 | 0.48 | 110 | 108.10 | 1.80 | 0.28 |
| K (yr^{-1}) | 0.7 | 0.71 | 1.25 | 0.59 | 0.4 | 0.40 | 1.25 | 0.93 | 0.2 | 0.21 | 2.65 | 1.25 |
| ϕ' | 2.8 | 2.78 | 0.63 | 0.12 | 3.29 | 3.29 | 0.22 | 0.21 | 3.38 | 3.38 | 0.507 | 0.47 |
| $F_{0.1}$ (yr^{-1}) | 0.4 | 0.40 | 1.27 | 1.03 | 0.3 | 0.30 | 0.78 | 0.68 | 0.15 | 0.15 | 1.21 | 1.19 |
| $F_{0.5}$ (yr^{-1}) | 0.3 | 0.30 | 2.11 | 1.92 | 0.2 | 0.20 | 0.63 | 0.62 | 0.1 | 0.100 | 0.56 | 0.50 |
| F_{\max} (yr^{-1}) | 0.70 | 0.71 | 1.49 | 0.92 | 0.4 | 0.40 | 0.79 | 0.69 | 0.2 | 0.200 | 0.60 | 0.54 |

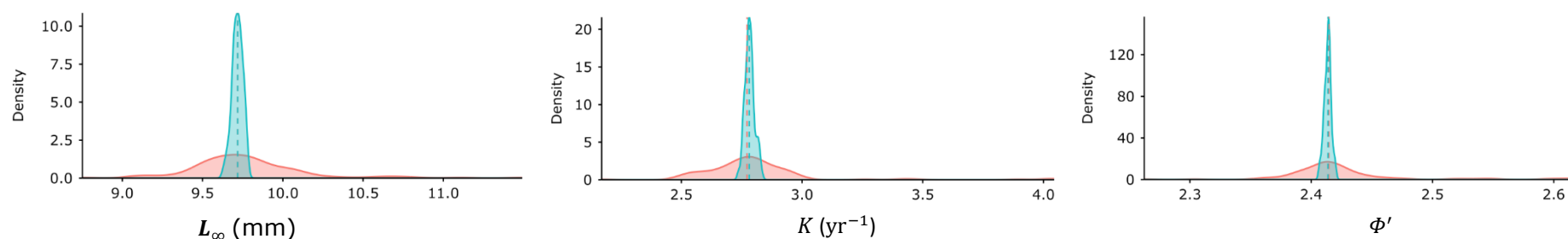


Figure 5. Comparing the original and median bootstrap estimators calculated using *Abra alba* empirical data in estimating VBGC parameters. Pink color - distribution of original bootstrap estimates, light blue color - median bootstrap estimators, dashed vertical lines - median values.

Table 5

Comparing sensitivity of median bootstrap estimators across a range of fishing mortality rates on estimating VBGC parameters and BRPs of a short-lived life history using simulated length frequency data

| Variables | True value | F = 0.025 | | | F = 0.1 | | | F = 0.5 | | | F = 0.8 | | |
|-------------------------------|------------|-----------|------|------|---------|------|------|---------|------|------|---------|------|------|
| | | Median | RB% | CV% | Median | RB% | CV% | Median | RB% | CV% | Median | RB% | CV% |
| L_{∞} (cm) | 30 | 30.02 | 0.29 | 0.29 | 29.84 | 0.61 | 0.32 | 29.79 | 0.80 | 0.33 | 29.26 | 2.56 | 0.18 |
| K (yr ⁻¹) | 0.7 | 0.701 | 0.84 | 0.39 | 0.70 | 0.66 | 0.39 | 0.71 | 0.44 | 0.82 | 0.70 | 0.58 | 0.27 |
| ϕ' | 2.8 | 2.81 | 0.18 | 0.09 | 2.82 | 0.70 | 0.14 | 2.81 | 0.99 | 0.18 | 2.810 | 0.35 | 0.05 |
| $F_{0.1}$ (yr ⁻¹) | 0.4 | 0.39 | 2.17 | 0.85 | 0.40 | 1.60 | 1.61 | 0.41 | 1.58 | 0.46 | 0.40 | 0.45 | 0.27 |
| $F_{0.5}$ (yr ⁻¹) | 0.3 | 0.31 | 2.86 | 0.32 | 0.30 | 1.97 | 1.88 | 0.31 | 1.82 | 0.80 | 0.30 | 0.70 | 0.52 |
| F_{max} (yr ⁻¹) | 0.65 | 0.66 | 1.72 | 0.24 | 0.66 | 2.12 | 1.59 | 0.66 | 1.67 | 0.67 | 0.66 | 2.02 | 0.63 |

Sensitivity analysis. Sensitivity analysis of the median bootstrap estimators demonstrated strong consistency across varying F values (Table 5). L_∞ remained close to the true value across all F values, with RB not greater than 2.6% and CV below 0.4%, indicating highly consistent estimates. K also had a relatively low RB and a CV of less than 1%, reflecting consistent estimation of the median across all F scenarios. ϕ' was particularly stable, with an RB below 1% and CV below 0.2%. The BRPs ($F_{0.1}$, $F_{0.5}$, and F_{\max}) also exhibited strong consistency across different F values, with an RB generally below 3% and a CV of less than 2%. F_{\max} remained slightly more consistent, with RB values below 2.2% across all scenarios. Overall, these results indicate that median bootstrap estimators maintained a high degree of consistency in estimating the VBGC parameters and BRPs close to the true values across the range of simulated fishing mortalities. These findings suggest that median bootstrap estimators are stable and relatively insensitive to variations in fishing mortality.

Discussion. The original bootstrap estimators (Table 3) provide a measure of variability in the VBGC parameters and BRPs for the short-, medium-, and long-lived hypothetical fish species. L_∞ and ϕ' were relatively uncertain, with K and the BRPs exhibiting higher variability, particularly in short-lived species. This variability reflects the sensitivity of the VBGC parameters and BRPs estimations that may be caused by either sampling process errors inherent in the original sample or natural variability in fish growth in a population (Isaack 1990; Schwamborn et al 2019). Highly uncertain parameter estimates, such as VBGC parameters and BRPs may propagate bias when applied in other stock assessment models or used as benchmarks for decision-making. Using the median of the bootstrap estimators (Table 4) markedly improves the consistency of parameter estimates. The median bootstrap estimators approach effectively smooths out the variability present in the individual bootstrap samples, providing stable and consistent estimates. This approach enhances the reliability of the growth efficiency comparisons across populations or species, independent of body size (Pauly & Munro 1984; Taufani & Matsuishi 2024). Relatively to conventional bootstrap resampling, the median bootstrap estimators demonstrate clear advantage in producing more consistent estimates. While the original bootstrap approach captures variability and uncertainty inherent in the original sample, it can yield inflated bias and variability for sensitive parameters (Figures 2–4). The median bootstrap estimators reduce these effects, producing estimates that are consistently closer to the true value and reliable across all life-history scenarios. This demonstrates their potential for improving reliable parameter estimation in fish stock assessments, particularly for species with short lifespans (Quinn & Deriso 1999; Collie & Gislason 2001; Pennino et al 2022).

The consistency of the estimates produced using the median bootstrap estimators as resampling medians comes from the central limit theorem, leading to a reduction in CV proportional to $1/\sqrt{n}$, where n is the number of resampling iterations. However, increasing the number of bootstrapping iterations does not increase the amount of information known about the population, because the bootstrap samples only come from the original dataset. This reduction in variability does not necessarily imply enhanced precision, as demonstrated by Tables 4 and 5 and Figures 2–4 (Efron & Tibshirani 1994; Casella & Berger 2002; Glover & Mitchell 2016). Median bootstrap estimators consistently captured the VBGC parameters of the *A. alba* with lower variability than the original bootstrap estimators. This pattern, which closely resembled that observed in simulated scenarios, suggests that the proposed approach can reliably summarize variability and provide stable parameter estimates even with empirical data (Figure 5). The approach maintained consistent estimation despite the relatively small sample size, illustrating its feasibility for use in data-poor situations. Overall, the similarity between the empirical and simulated patterns indicates that the method behaves consistently across both simulated and real-world datasets. The results of the sensitivity analysis further highlight the stability of the median bootstrap estimators in maintaining consistent parameter estimates across a range of fishing mortality scenarios (Table 5). The VBGC parameters exhibit minimal variations in RB and CV, suggesting that the median bootstrap estimators reliably estimate parameter close to the underlying true values, regardless of variable fishing mortality. This consistency is particularly important in data-poor and overfished fisheries, where the

traditional approach can lead to biased estimates. The BRPs also display strong consistency, with the RB and CV values remaining below 3% in most cases. This suggests that the median bootstrap approach stabilizes estimates that might otherwise be highly sensitive to the exploitation level. The observed stability of F_{\max} across all F values further underscore the stability of key management benchmarks when using the median estimators. Overall, these findings suggest that median bootstrap estimators provide a reliable approach for fish stock assessments, ensuring consistent VBGC parameter and BRP estimates even under simulated overfishing scenarios. While they do not directly reduce the statistical uncertainty inherent in the original sample, their ability to maintain consistent estimates closer to the true values across scenarios enhances the interpretability and comparability of results for fisheries management purposes.

A common challenge with LFQ data is the scarcity of large individuals, which is typical of overfished stocks or surveys biased by selectivity. This scarcity hampers cohort tracking and often causes traditional approaches to yield biased estimates (Schwamborn et al 2019; Wang et al 2021). The stability of the median bootstrap estimators under the simulated overfishing scenario directly addresses this limitation, providing stable VBGC parameter estimates. Overall, the findings of this study enhance confidence in the estimation of reliable VBGC parameters. These parameters may be applied in other fish stock population models to improve stock assessments and the resulting management advice in data-poor fisheries (Bertignac & Pontual 2007; Hufnagl et al 2012; Schwamborn et al 2018).

Generally, the median of the bootstrap estimators shows broad potential applicability across a range of assessment contexts. However, additional research is required to confirm their performance under more diverse conditions. Future studies should therefore examine these median bootstrap estimators across a wider spectrum of scenarios, including varying sample sizes and data resolutions, various length-frequency structures arising from changing mortality regimes, gear selectivity patterns, seasonality, temperate ecological scope, and pulsed recruitment. In addition, the reproducibility of the estimators should also be assessed under varying levels of individual growth variability that deviate from ideal steady-state conditions, as well as across different bin-size configurations. Finally, applying the framework to multiple empirical datasets spanning different fish species would further substantiate its generalizability in data-poor fisheries.

Conclusions. In summary, this study confirms that the median of the bootstrap estimators provides a consistent framework for estimating the VBGC parameters and BRPs. They are effective in data-poor fisheries, where continuous sampling is costly and reliable estimates are often scarce, as demonstrated through simulations and application to *A. abra* dataset. This approach enables fisheries scientists and managers to obtain reliable VBGC parameters and BRPs from less costly, readily available LFQ data.

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