A systematic approach to estimating life-history parameters under data-limited scenarios for kawakawa (*Euthynnus affinis*) in the western and southern part of Indonesian Waters

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Abstract

Length-based stock assessment of Indian Ocean kawakawa (*Euthynnus affinis*) requires reliable life-history parameter estimates, yet regional assessments have relied on decades-old growth and mortality parameters derived from a narrow geographic range, with no associated uncertainty estimates. We developed a systematic framework to estimate the von Bertalanffy growth parameters L_∞ and K from 3,396 length-frequency samples collected from Sibolga fishing port, North Sumatra during 2016-2017. We used two optimisation algorithms (simulated annealing and genetic algorithm) across seven moving average settings, with fixed and floating L_∞, under both partial and full bootstrapping. For sensitivity analysis, we also applied a Bayesian length-interval catch-curve framework, which estimates L_∞ and K without requiring bin number or moving-average specification. The genetic algorithm consistently outperformed simulated annealing in terms of precision and resistance to local optima convergence. The Bayesian approach showed potential but failed to capture the multimodal structure of the length-frequency data and was therefore excluded from the final estimates. The resulting estimates of $L_\infty = 79.85$ cm FL and $K = 0.44\ yr^{-1}$ were broadly comparable to hard-part studies from the similar regions and the ones used in previous Indian Ocean kawakawa assessments, supporting the use of length-frequency data as a viable alternative where hard-part ageing is unavailable.

Keywords: Vital rates, data-limited fisheries, neritic tuna, stock assessment.

Introduction

For the past decade, the stock assessment of kawakawa has been hampered by catch volatility, limited fishery-dependent data, and uncertainties in the quality of initial parameter estimates (IOTC-WPNT14, 2024). Adopting a data-limited catch-only method (i.e., Catch Maximum Sustainable Yield, C-MSY), the stock status of kawakawa in 2023 was declared as overfished but not subject to overfishing, with fishing mortality (F) and biomass (B) close to the level producing maximum sustainable yield (0.98 and 0.99, respectively) (Fu, 2023). Length-Based Spawning Potential Ratio (LB-SPR) was also explored, which confirmed that the stock was heavily exploited with SPR below the 40% threshold and $F/M > 1$ (Fu, 2023). However, the length-based assessment was only focused on gillnet length frequency data from Iran, which likely do not represent the entire region (Fu *et al.*, 2019). Moreover, key input parameters were decades old: life-history parameters were derived from FishBase, which originated from a 1953 fisheries survey report in the Mauritius and Seychelles (Pauly, 1978), while natural mortality was estimated using Pauly's (1980) estimator from 1981 troll line fisheries surveys and 1990 gillnet fisheries in Oman (Yesaki and Carrara, 1993).

To address these gaps, we developed a systematic approach to estimate life-history parameters (L_∞ and K), and explore whether Bayesian estimation approach yields comparable estimates to optimisation-based methods in the western and southern part of Indonesian waters. In addition, we highlight the strengths and limitations of length-based methods under data-limited conditions.

Materials and Methods

Growth parameters

In situations where hard-part structures (e.g., otoliths) are unavailable, growth parameters are commonly estimated from length-frequency data. This procedure requires a length-frequency distribution that reflects the underlying growth process, typically with clear temporal progression of modes. Commonly used growth parameters are the asymptotic length (L_∞), the Brody growth coefficient (K) and the theoretical length at age zero (t_0) of the von Bertalanffy growth function (VBGF). The equation can be defined as follows:

$$L_t = L_\infty\{1 - e^{-K(t-t_0)}\} \qquad \text{(Eq. 1)}$$

where L_t is the total length at age t; L_∞ is asymptotic length; K is the growth coefficient; and t_0 is theoretical age at zero length.

To calculate the value of theoretical age at fish length 0 (t_0) we followed Pauly (1980):

$$\log(-t_0) = (-0.3922) - 0.2752 \times \log(L_\infty) - 1.038 \times \log(K) \qquad \text{(Eq. 2)}$$

where the coefficients were derived from 153 combinations of t, L_∞ and K, originated from Pauly (1978) to capture a wide range of fish and body sizes.

To estimate the growth parameters, we used Electronic Length Frequency Analysis (ELEFAN) which was originally developed by Pauly and David (1981) and Pauly (1982). In this study, we focused on `ELEFAN I`, which is designed for scoring length-frequency bins, scanning parameter space, and fitting a von Bertalanffy growth model (von Bertalanffy, 1938) to the temporal progression of length-frequency modes. Prior to fitting, the data are reorganised by calculating a score for each length bin based on how its count differs from a moving average (MA) of neighbouring bins using the `lfqRestructure` function within the R package `TropFishR` (Mildenberger *et al.*, 2017). This requires the value of the MA parameter to be chosen. For example, setting the MA parameter to 5 means the two bins before and the two bins after a given bin are included in the calculation (Mildenberger *et al.*, 2017). However, the choice of bins (Wang *et al.*, 2020) and the MA settings (Mildenberger *et al.*, 2017) can affect the scoring of the growth curve. We initially followed Wang *et al.* (2020) to determine the optimum bin size. However, their equation was developed using millimetres as the measurement unit, in which when converted to centimetres, it produces small bins size (e.g., ~10 mm for kawakawa). This can lead to underestimation of K and overestimation of L_∞ (Wang *et al.*, 2020). Therefore, we applied a deterministic binning approach based on Anderson and Neumann (1996), using 20 mm intervals for fish up to a maximum length of 60 mm.

Due to complexity of selecting bin size and MA values, a sensitivity analysis was performed to assess the uncertainty of estimating VBGF parameters under different settings: (1) setting MA to 5, 7, 9, 11, 13, 15, and 17, respectively, and (2) fixing L_∞ or allowing it to be estimated (floating L_∞), (3) run the model under two different optimisation and bootstrapping methods, namely `ELEFAN_SA` and `ELEFAN_GA`, and (4) conducting an additional analysis using a Bayesian length-interval catch-curve framework by supplying informative priors.

The choice of optimisation method is important. `ELEFAN_SA` employs simulated annealing, a stochastic optimisation algorithm inspired by thermodynamic annealing, designated to locate the global optimum of an objective function in the presence of multiple local optima (Press *et al.*, 2007; Xiang *et al.*, 2013). `ELEFAN_GA` uses a genetic algorithm, a stochastic search algorithm inspired by biological evolution and natural selection, dedicated to locate the global optimum through an iterative mechanism of selection, crossover, and mutation (Scrucca, 2013). However, both optimisation routines are prone to becoming trapped in local maxima (Mildenberger *et al.*, 2017). Hence, we explored the nonparametric bootstrapped versions (`ELEFAN_SA_boot` and `ELEFAN_GA_boot`) from the `fishboot` package (Schwamborn *et al.*, 2025), which additionally provide confidence interval estimates of uncertainty. The bootstrapping method involves randomly resampling from the original data with replacement and obtaining VBGF parameters from each randomly-resampled data set using multivariate kernel density estimates (Schwamborn *et al.*, 2019). However, we found that the generated confidence regions were only reliable when the posterior distribution was unimodal. In cases with multiple modes, the method only returned a single confidence interval containing the first mode, which was not always the region with the highest density. It also occasionally produced negative values, likely due to smoothing artefacts. To address these issues, we used the `hdrcde` package (Hyndman *et al.*, 2021) to obtain highest-density regions, which do not have to consist of a single interval.

For the fitting procedures, we adopted the configuration settings recommended by Schwamborn *et al.* (2019) for both `ELEFAN_SA` (`SA_temp` = 5e5, `SA_time` (sec) = 240, `maxit` = 500) and `ELEFAN_GA` (`popSize` = 100, `pmutation` = 0.2, `maxiter` = 50, `run` = 10). The fitting procedure was repeated 1,000 times with different random seed values (drawn without replacement from a discrete uniform (1, 1000) distribution), but from the same dataset. Different random seeds could only be applied in the `ELEFAN_GA` function because `ELEFAN_SA` relies on the Simulated Annealing solver `GenSA` (Xiang *et al.*, 2013), which in recent versions sets the random seed internally by default, thereby preventing external control of the optimization process (M. Taylor, Personal Communication, 12 December 2025). To explore the parameter space effectively, a different set of random initial parameter values, drawn from a uniform distribution (`init_par`) was used in each run, hereafter referred to as partial bootstrapping. For `ELEFAN_SA_boot` and `ELEFAN_GA_boot`, resampling with replacement was conducted 1,000 times. However, the simulated annealing algorithm (`ELEFAN_SA` or `ELEFAN_SA_boot`) fails when any upper bound is less than or equal to its corresponding lower bound (e.g., for L_∞). To avoid this issue, a small constant was added to the upper bound (i.e., $L_\infty + 5 \times 10^{-5}$; Table 1). This procedure is hereafter referred to as full bootstrapping.

The results were evaluated based on the maximum goodness-of-fit index ($R_{n_{max}}$), where the highest values were inspected across MA settings, optimisation methods, and bootstrapping configurations. Where R_n values were similar across MA settings, preference was given to the scenario with the most stable L_∞ and K estimates, in which defined as the lowest confidence regions across both algorithms. Where simulated annealing and genetic algorithm returned different optimal MA values, the genetic algorithm result was preferred given its superior resistance to local optima convergence (Mildenberger *et al.*, 2017; Schwamborn *et al.*, 2019).

Recently, some life-history parameters can be estimated without specifying the number of bins and MA values. The `fishblicc` package (Medley, 2025, 2025) uses a Bayesian length-interval catch-curve framework that accommodates multiple gears and flexible selectivity structures to estimate the expected number of fish in predefined length intervals, whereas individual L_∞ values were assumed to follow a gamma distribution (Medley, 2025). The model only requires minimal priors (i.e., L_∞ and M/K) which can be obtained from FishBase (Froese and Pauly, 2025) using `rfishbase` package (Boettiger *et al.*, 2012). Details of priors are given in the supplementary materials (Appendix 1). The model was fitted to length-frequency data using a Markov chain Monte Carlo (MCMC) approach under assumptions of constant recruitment, fixed selectivity (i.e., logistic, normal, and double-sided normal), a single natural mortality parameter, and von Bertalanffy growth. To improve model performance, we dynamically set `nwarmup` and `ntarget`, while also fine-tuned the `adept_delta` and `max_treedepth` to achieve model convergence. The best-fitting selectivity model was selected based on three convergence criteria: (i) absence or minimal occurrence of divergent transitions; (ii) potential scale reduction factor ($\hat{R}$) less than 1.05 for all parameters; and (iii) bulk and tail effective sample sizes (ESS) exceeding 400 for all parameters (Vehtari *et al.*, 2021). Among models meeting these criteria, the one providing the closest approximation to the observed length-frequency distributions was preferred.

All statistical analyses were conducted using R version 4.5.3 (R Core Team, 2026). For computationally intensive analyses (i.e., parallel computation), we used the University of Liverpool Barkla high-performance computing facility.

Table 1: Setting scenarios for estimating growth parameters of kawakawa (*E. affinis*) from Sibolga Port in the period of 2016-2017

Scenario	Model	MA	Parameter	Lower bound	Upper bound
Fixed L_∞	Partial bootstrapping (ELEFAN_SA/GA)	5–17 (step = 2)	L_∞ (cm FL)	84.97	84.97 + 5×10^{-5}
			K (year^{-1})	0.01	1.00
Floating L_∞			L_∞ (cm FL)	84.97	84.97 + 5×10^{-5}
			K (year^{-1})	0.01	1.00
Fixed L_∞	Full bootstrapping (ELEFAN_SA/GA_boot)		L_∞ (cm FL)	84.97	84.97 + 5×10^{-5}
			K (year^{-1})	0.01	1.00
Floating L_∞			L_∞ (cm FL)	84.97 × 0.75	84.97 × 1.25
			K (year^{-1})	0.01	1.00
Fishblicc	Bayesian length-interval catch curve framework	NA	L_∞ (cm FL)	$80.06 - 8.67$	$80.06 + 8.67$
			M/K	1.88	1.88

Results

The subset of data (i.e., Sibolga Port purse seine fleet 2016-2017) used for life-history estimation (n = 3,396) ranged from 20.0 to 57.0 cm FL with a mean length of 30.7 cm FL. Figure 1 demonstrates the suitability of this subset of data for analysis, as it showed clear modal progressions from April to December 2016 and February to November 2017.

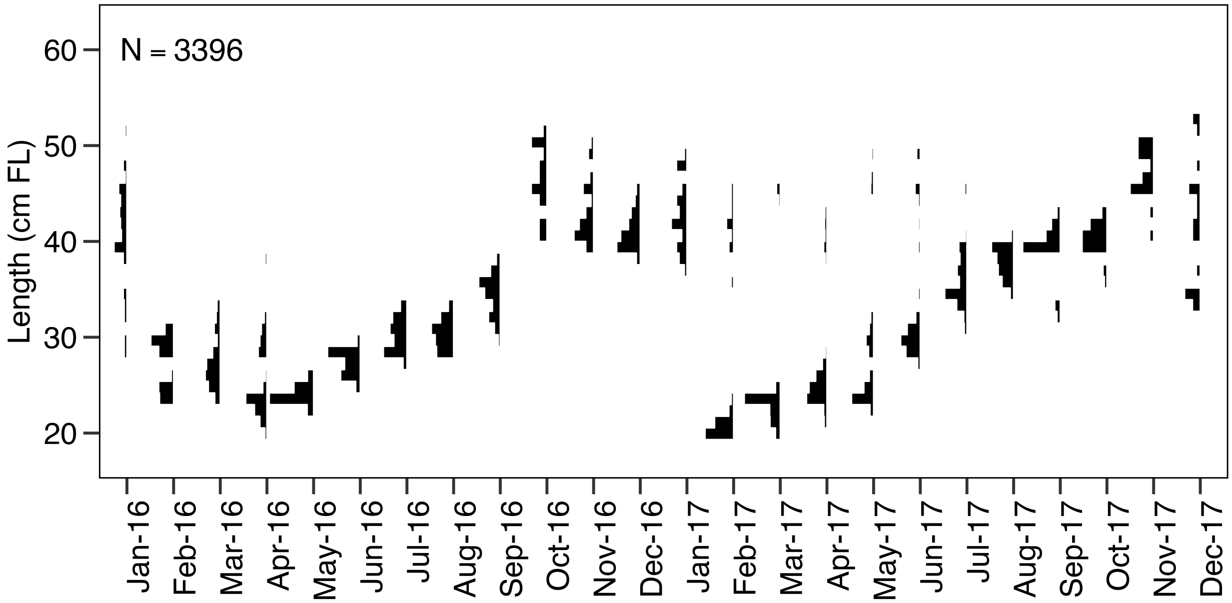

Figure 1: Monthly length frequency observations of Kawakawa (*E. affinis*) in Sibolga port from January 2016 to December 2017.

Partial bootstrapping consistently found stable solutions across both L_∞ scenarios when MA ≥ 7, regardless of the optimisation algorithm used. In contrast, full bootstrapping converged to lower K estimates before transitioning to higher estimates at MA ≥ 15 under simulated annealing, whereas genetic algorithm produced stable solutions at MA $\geq$ 11. The presence of two distinct K clusters across several panels indicates multiple local optima in the likelihood surface, which is a known challenge when fitting the von Bertalanffy growth function. In selecting the appropriate moving average (MA), Mildenberger *et al.* (2017) recommended choosing the value that maximizes the goodness-of-fit index (R_n). An MA value of 15 was chosen because it consistently produced the highest R_n values under all scenarios. Fixing L_∞ appeared to produce smaller confidence regions across scenarios, however, it may not fully capture natural variability, as individual fish can differ in growth pattern. Lower MA values (e.g., MA = 5) tended to yield lower estimates of K, whereas higher MA values (e.g., >11) generally produced more stable estimates but may also increase the risk of overfitting (Figure 2. Additionally, genetic algorithm also performed better in estimating L_∞ across MA settings, in which full bootstrapping provided a more consistent result (Figure 3). Therefore, we selected the full-bootstrapped `ELEFAN_GA` with floating L_∞ and MA = 15 as the base-case scenario, whereas $K = 0.44$ year-1 (95% CI: 0.27–0.61 $year^{-1}$) and $L_\infty = 79.85$ cm FL (95% CI: 64.90–95.82 cm FL).

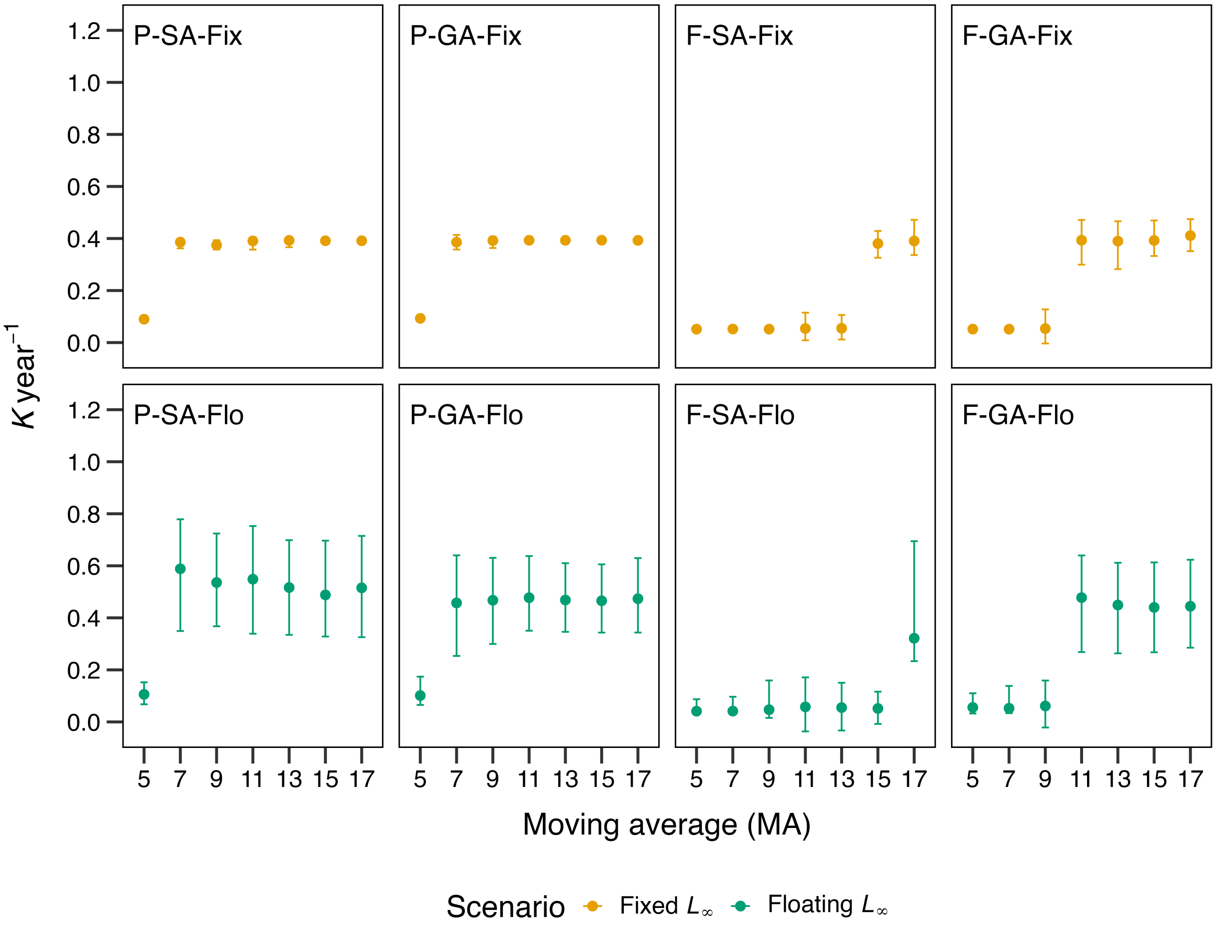

Figure 2: Estimates of the growth coefficient (K) across eight scenarios combining fixed and floating L_∞, seven moving-average (MA) settings (i.e., 5, 7, 9, 11, 13, 15, 17), and two bootstrapping approaches (partial and full) using `ELEFAN_SA_boot` and `ELEFAN_GA_boot`. Points indicate the highest density region (HDR) mode and error bars represent the 95% confidence regions.

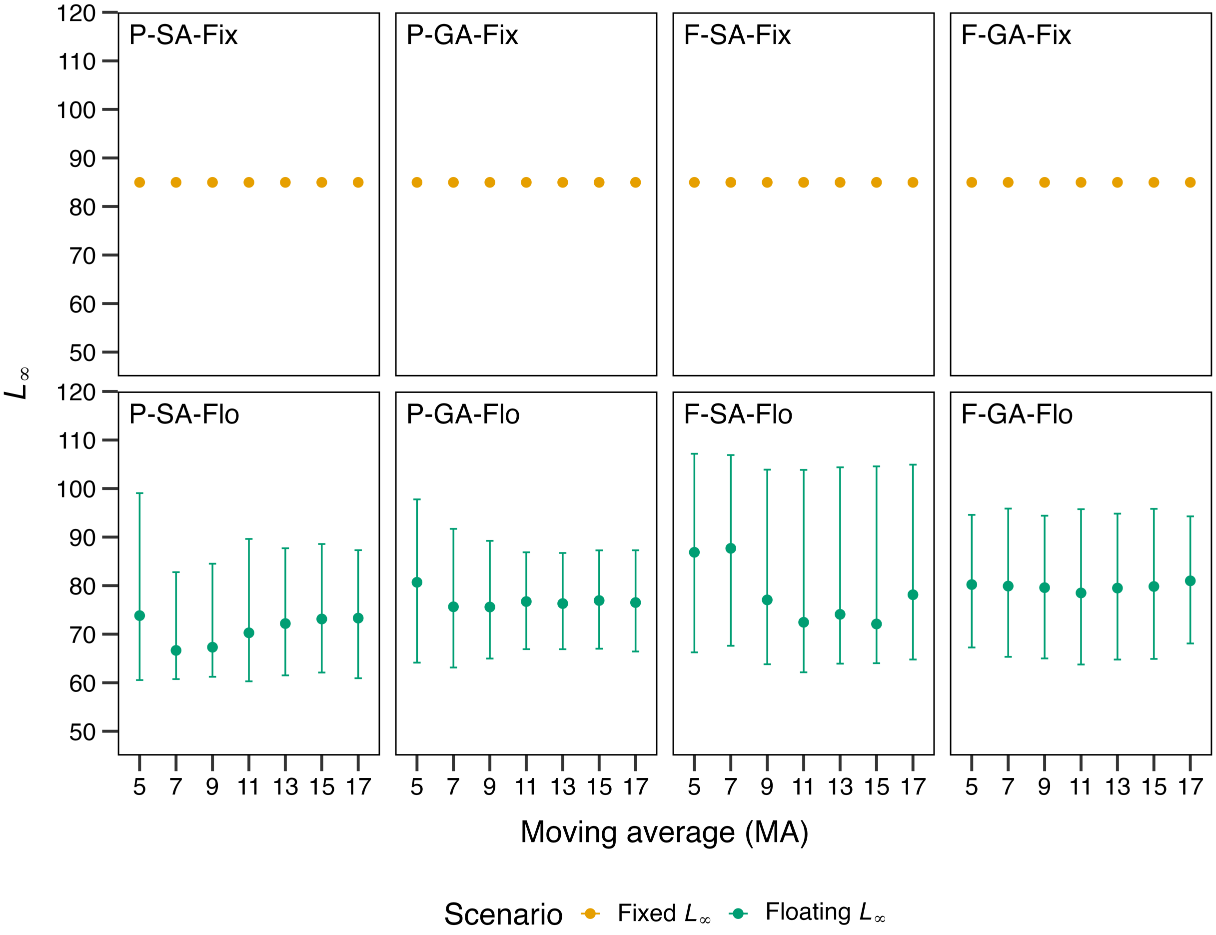

Figure 3: Estimates of the growth coefficient (L_∞) across eight scenarios combining fixed and floating L_∞, seven moving-average (MA) settings (i.e., 5, 7, 9, 11, 13, 15, 17), and two bootstrapping approaches (partial and full) using `ELEFAN_SA_boot` and `ELEFAN_GA_boot`. Points indicate the highest density region (HDR) mode and error bars represent the 95% confidence regions.

Estimating growth parameters independently outside `ELEFAN` was challenging, as improving `fishblicc` model fit came at the cost of biologically unrealistic parameter estimates. All three models with different selectivity assumption showed adequate convergence diagnostics ($\hat{R} = 1.00$, ESS > 900, no divergent transitions), indicating reliable posterior sampling. However, none of the models adequately captured the sharp recruitment peak observed at approximately 24 cm FL, as the multimodal structure in the length frequency data is more likely driven by strong recruitment cohorts than by gear selectivity. The normal selectivity model estimated L_∞ = 74.48 cm FL and K = 0.66 yr^{-1}, in which were most comparable to `ELEFAN`-based estimates, though its posterior fit (Lp = -225.20) was considerably the worst. The double-sided normal model yielded the highest Lp (0.80), indicating the closest fit to the observed length frequency distribution, but produced the lowest L_∞ estimate (53.87 cm FL) and highest K (0.71 yr^{-1}), which is considerably lower and higher than the `ELEFAN`-based estimates, respectively (Table 2). Bayesian approach offers the ability to avoid the complication of estimating the appropriate values of bin size and moving average (MA) with substantially less computing time. The poor model outputs (Appendix 2) were likely driven by strong cohort structure in the data, which the Bayesian framework could not adequately reproduce, rather than reflecting a genuine limitation of the approach itself. For this reason, we decided to drop down the fishblicc-derived life-history estimates.

Table 2: Posterior summaries from the fishblicc model under different selectivity fits. ESS denotes effective sample size, $\hat{R}$ is the potential scale reduction factor, with values near 1 indicating good mixing, and Lp denotes the log posterior.

Selectivity fits	L_∞	M/K	ESS	$\hat{R}$	Lp
Logistic	52.40	1.84	971.42	1	-190.82
Normal	74.48	1.91	1177.79	1	-225.20
Double-sided normal	53.87	1.78	1276.59	1	0.80

The theoretical age at zero length (t_0) from the `ELEFAN` model was -0.47 years, whereas `fishblicc` model produced similar value at -0.49 years. Visualisation using the von Bertalanffy growth curve indicated that kawakawa is a fast-growing species, reaching up to 40 cm in length during its first year and attaining its asymptotic length at approximately 8 years. Our estimated growth curve from full bootstrapped `ELEFAN_GA_boot` with MA = 15 and floating L_∞ scenario also falls within the range reported by previous studies in the region (Figure 4).

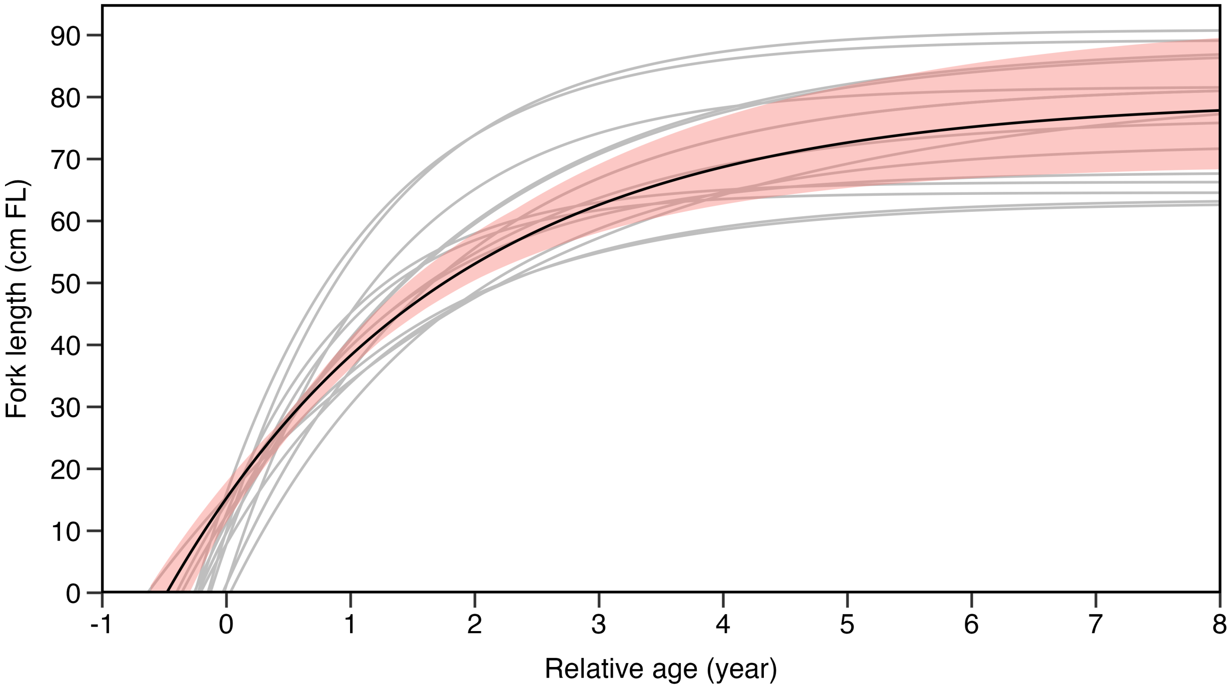

Figure 4: Von Bertalanffy growth curve from full bootstrapped ELEFAN_GA_boot with MA = 15 and floating L_∞ scenario for kawakawa (*E. affinis*) from Sibolga port (black line) with 95% confidence band (pink band). Grey lines indicate growth curves from other studies in the Indian Ocean region. See Zhou *et al.* (2019) for details on previous studies.

von Bertalanffy growth curves fitted to the length frequency data using the full bootstrapped `ELEFAN_GA_boot` approach with MA = 15 and floating L_∞ scenario approximately matched the modal progressions (Figure 5). The recruitment started in April as indicated by $t_{anchor} = 0.34$, and larger individuals were frequently observed from October to January. However, growth curves beyond 60 cm FL were poorly constrained and therefore relied heavily on estimates from ages 1-2, as no fish larger than this size were sampled due to the size selectivity of purse seine gear.

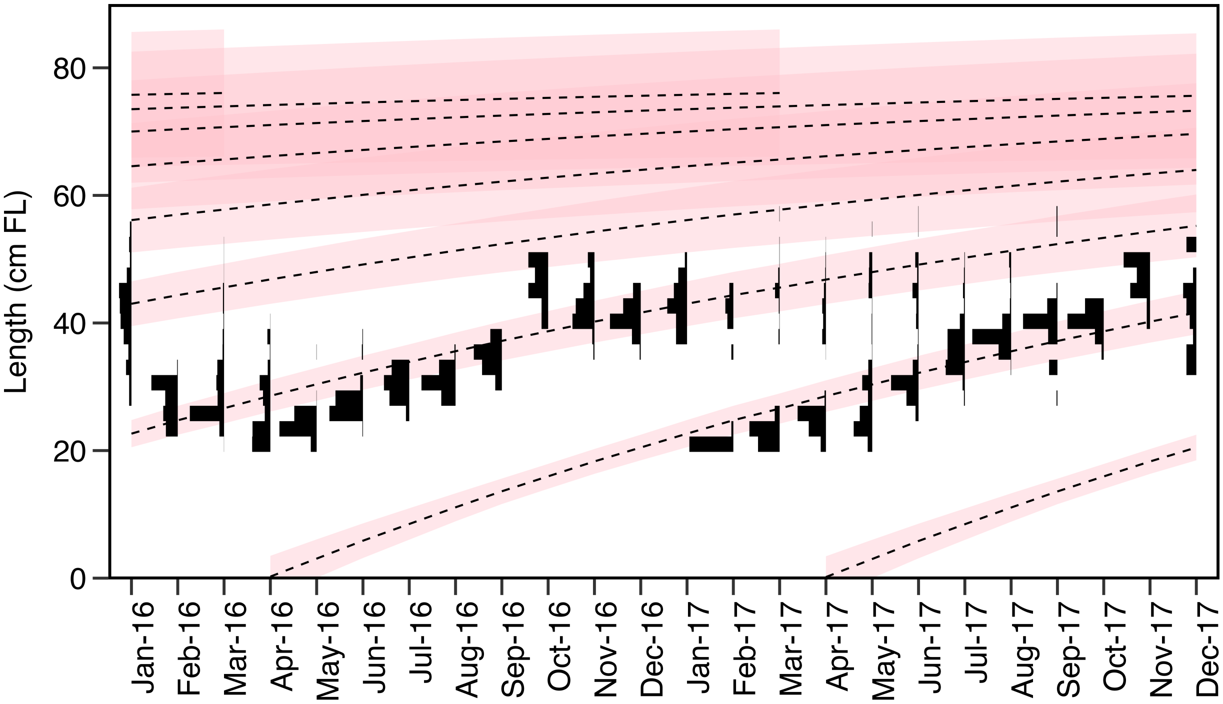

Figure 5: Fitting of von Bertalanffy growth curves (dashed lines, estimated using `ELEFAN_GA`: purple bands are 95% bootstrap confidence bands) to monthly length frequency observations of Kawakawa (*E. affinis*) in Sibolga port from January 2016 to December 2017.

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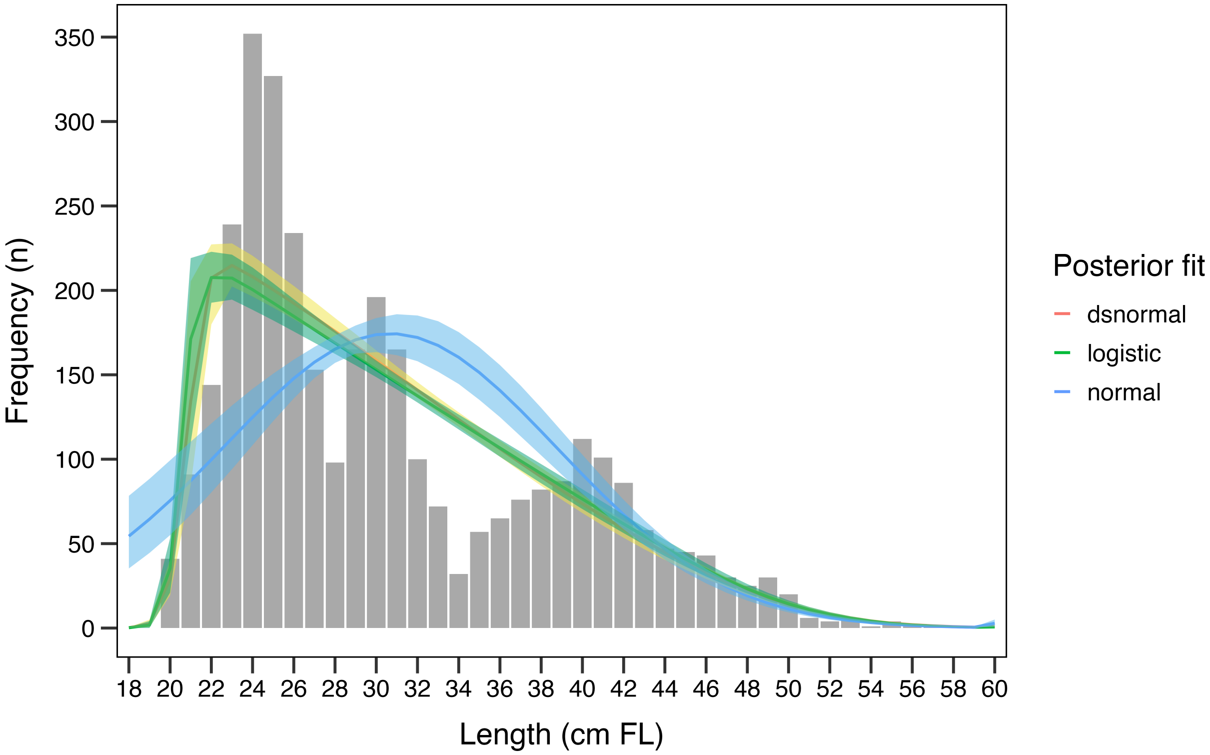
Supplementary Materials

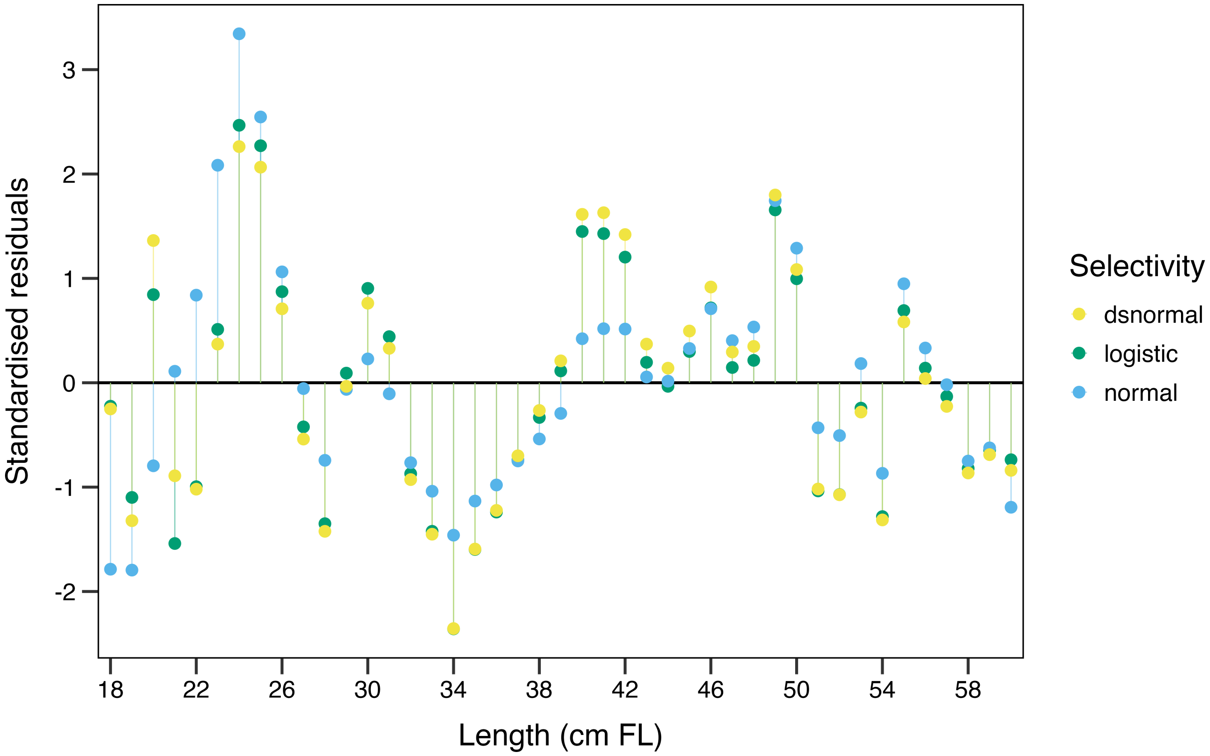
Appendix 1. Priors for Bayesian length-interval catch-curve framework (*fishblicc*)

The *fishblicc* model requires only the mean and standard deviation of asymptotic length (L_∞), which are assumed to follow a normal distribution, whereas other parameters such as the (M/K) ratio (lognormal), length-weight parameters (c and d), and the length at 50% maturity of females (L_{50}) are optional. Detailed priors are presented as follow:

Parameter	Function.type	Mean	Standard.deviation	Units
L_∞	Normal	80.06	8.67	cm FL
M	Lognormal	1.10	NA	year^{-1}
K	Lognormal	0.67	NA	year^{-1}
M/K ratio	Lognormal	1.88	NA	Dimensionless
c	NA	0.001	NA	g · cm FL^{-d}
d	NA	3.00	NA	Dimensionless
L_{50}	NA	46.54	10.61	cm FL

Appendix 2. Posterior fit diagnostics of predicted to observed length frequency distribution of kawakawa (*E. affinis*) from Sibolga port from 2016-2017 (upper) and residual variation (lower) for estimation of L_∞ under three selectivity models.




Standardised residuals
3
2
1
0
-1
-2
18
22
26
30
34
38
42
46
50
54
58
Length (cm FL)
Selectivity
dsnormal
logistic
normal