1 **SUBMITTED MANUSCRIPT (UNDER REVIEW):**

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3 **Robust estimation of fish life history parameters from unfished populations**

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5 *Wanwan Kurniawan*[a,b]

6 [a] Institute of Marine and Antarctic Studies (IMAS), University of Tasmania, Castray Esplanade,

7 Battery Point TAS 7004, Australia

8 [b] National Research and Innovation Agency (BRIN), Jl. M.H. Thamrin No. 8, Jakarta Pusat 10340,

9 Indonesia

10 wanwan.kurniawan@utas.edu.au

11

12 *Shane A. Richards*[c]

13 [c] School of Natural Sciences, University of Tasmania, Dynnyrne TAS 7005, Australia

14 shane.richards@utas.edu.au

15

16 *Pia Bessell-Browne*[d]

17 [d] Commonwealth Scientific and Industrial Research Organization, Castray Esplanade, Battery Point

18 TAS 7004, Australia

19 pia.bessell-browne@csiro.au

20

21 *Asta Audzijonyte*[a]

22 [a] Institute of Marine and Antarctic Studies (IMAS), University of Tasmania, Castray Esplanade,

23 Battery Point TAS 7004, Australia

24 asta.audzijonyte@utas.edu.au

25

26 Corresponding author: Wanwan Kurniawan

27 Email: wanwan.kurniawan@utas.edu.au

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Abstract

Asymptotic length (L_∞) and the ratio of natural mortality to the von Bertalanffy growth coefficient (M/K) underpin fish population dynamics and are central in data-poor stock assessments. These parameters are traditionally generated from length–age keys, mark–recapture studies, or inferred from other life-history traits, yet remain unknown for about 80% of fished species. Because M/K and L_∞ shape the length distribution of unexploited populations, they should be estimable directly from unfished length distribution. Until recently this was impractical, as most length data came from exploited stocks; however, the rapid growth of diver and camera-based visual surveys now provides thousands of length observations from largely unfished populations. Using simulations, we identified conditions under which direct estimation of M/K and L_∞, together with two observational selectivity parameters, is feasible for such fish observation datasets. Parameter estimation was done using a modified widely used length-based assessment model LB-SPR. Our simulation scenarios spanned diverse life-history parameters and realistic sampling regimes with varying selectivity, length binning, and sample sizes. We showed that the model produced unbiased M/K and L_∞ estimates (<15% and <10% biases respectively) for populations with both continuous and pulsed recruitment, provided the coefficient of variation in length-at-age was specified accurately, length distribution spanned >10 length bins and samples included >500 individuals. The parameter estimation approach presented here enabled reliable estimation of life-history parameters for hundreds of diverse fish species and populations distributed across environmental gradients.

Keywords: data-poor, LB-SPR, life history, population dynamics, stock assessment, underwater survey

Highlights

- Growth and mortality parameters are essential but unknown for most species
- A new method is presented to estimate these parameters from length observations
- Life-history parameters can now be estimated for hundreds of fish populations
- The new method can be used with AI-assisted and citizen science data collections

1. Introduction

Population dynamics of fish are governed by three main processes: growth, mortality, and recruitment (Quinn II and Deriso 1999, Andersen 2020a). Understanding these processes and estimating their associated parameters is an essential component of fisheries research and stock assessment (Allen and Hightower 2010, Sparre and Venema 1998). In the absence of strong environmental variation, the abundance of an unexploited fish population is expected to stabilize at its ecological carrying capacity with recruitment staying relatively constant (Andersen 2020a). Consequently, it is often assumed that for stable populations length structure is predominantly determined and shaped by growth and natural mortality parameters (Hordyk et al. 2015a).

In fisheries models, individual growth is typically modelled using the von Bertalanffy growth function (VBGF) characterized by three parameters - asymptotic length (L_∞), the growth coefficient (K), and theoretical age at zero length (a_0). These VBGF parameters have been traditionally estimated from aging studies using otoliths, vertebrae, or spines, but such studies cover only a fraction of fish species, are expensive, and sometimes produce biased estimates due to limited sampling of fish across all age groups (Green et al. 2009, Goldman 2005, Prince, Wilcox and Hall 2023). Likewise, natural mortality, represented by its instantaneous rate per year (M), can be estimated from mark-recapture studies or catch at age data (Maunder et al. 2023, Thorson et al. 2017, Bowlby et al. 2021), however, these methods are also costly and can be imprecise. Consequently, M is often inferred through correlations with other life history (LH) parameters (e.g., maximum age, asymptotic length, and growth coefficient), or environmental conditions (Pauly 1980, Hoenig 1983, Then et al. 2014, Hamel 2014, Dureuil et al. 2021) and is usually modelled as a constant, independent of fish age, length, and time (Maunder et al. 2023, Kai, Yokoi and Fujinami 2023). Despite its critical role in population assessments, M remains one of the most uncertain parameters within fisheries models (Maunder et al. 2023, Miethe, Reecht and Dobby 2019, Thorson et al. 2017, Kai et al. 2023).

It has been shown that population length distributions under equilibrium conditions are determined not by the individual parameters M and K, but by their ratio M/K, with L_∞ serving as a scaling factor (Prince et al. 2014, Hordyk et al. 2015b, Hordyk et al. 2016). Conveniently, M/K ratio varies less among species than the individual M and K values (Prince et al. 2014, Hordyk et al. 2015b, Froese et al. 2018). Recent efforts to estimate M/K values for various fish species include correlative analysis while accounting for evolutionary relatedness (Thorson et al. 2017), as well as compilations of empirically estimated growth rates and maximum age-based natural mortality inferences (Prince et al. 2023). Yet, despite extensive work, validated estimates are available only for a few hundred fish species. Moreover, given that LH parameters are likely to be affected by temperature and other environmental conditions, it is likely that M/K and L_∞ should be estimated at a local population level (Prince et al. 2023, Audzijonyte et al. 2020). This presents an even bigger challenge to obtain accurate

estimates using traditional approaches. Alternative methods are needed to improve the availability of LH parameters across diverse fish species. One such method could be statistical parameter estimation from unfished population length frequencies.

The use of length data to infer LH (e.g., growth) and fisheries (e.g., fishing mortality rate) parameters is a well-established practice in fisheries science (Gulland and Rosenberg 1992, Andersen 2020b). However, the existing approaches either rely on length compositions derived from catch or focus on evaluating the impacts of fishing to populations (Hordyk et al. 2015a, Froese et al. 2018, Beverton and Holt 1956, Pauly 1983, Pauly and David 1980, Taylor and Mildenberger 2017). Among these approaches, length-based, data-poor stock assessment methods typically estimate fisheries-related parameters, using the length composition from catches, and *a priori* estimates of LH parameters (e.g., M/K and L_∞). Yet, by removing the fishing component, these methods could, in theory, be adapted to estimate LH parameters from length composition data of unfished populations. Such length composition data is now available through rapid accumulation of diver and camera operated visual surveys (e.g., Edgar and Stuart-Smith 2014). These datasets include hundreds of fish species with diverse LH and represent thousands of populations from around the globe. Importantly, many of the surveyed fish species are not subject to fishing pressure, providing an opportunity to apply length-based methods to estimate LH parameters. Ultimately, having better estimates of LH parameters will help subsequent assessments of fished populations.

In this study, we introduce a modified version of the length-based spawning potential ratio method (LB-SPR, Hordyk et al. 2015a, Hordyk et al. 2015b), with the focus on LH parameter estimation in unfished populations. Fitting is performed using Bayesian methods and the performance is tested using simulated datasets with realistic sampling regimes. Our analysis focuses on identifying conditions that will affect the estimation accuracy and precision of the method, and we offer recommendations for applying this approach to real-world datasets.

2. Materials and methods

To develop the method to estimate LH parameters, we modified the LB-SPR method introduced by Hordyk et al. (2015a) and tested the performance of the newly developed method using a range of simulated datasets, across various LH and sampling conditions. LB-SPR applies user-provided LH (M/K and L_∞) parameters to estimate fishing mortality, fisheries selectivity, and spawner potential ratio using length composition data from catch. In contrast, our LH estimation method removes the fishing component of the model and estimates M/K and L_∞ and two observation selectivity parameters (length at 50% and 95% observed in logistic function) using length composition samples from unfished populations.

2.1. Model structure of our LH estimation method

Our LH estimation method assumes an unfished population with a stationary age distribution, which in turn yields a stationary length distribution. Stationarity arises from the model assumption of constant and continuous recruitment, age-invariant natural mortality, and time-invariant growth parameters. Growth is described by the VBGF model.

A constant natural mortality implies an exponentially declining abundance with age. Just like in LB-SPR, our model tracks individuals to a maximum age ($a_{\max}$), by discretising lifespan into X equally spaced age classes of arbitrary time length, $x = 0, 1, \ldots, X - 1$. The annual natural mortality rate (M) is replaced by a generic natural mortality rate ($\dot{M}$) expressed in the same time unit as x. We obtain $\dot{M}$ from the assumed number of cohorts X and the cohort survivorship at $a_{\max}$, denoted ε, which allows age and length distribution to be modelled without specifying the true M and $a_{\max}$.

The relative abundance at age x satisfies the following equation:

$$\dot{N}_x = e^{-\dot{M}x} \tag{1}$$

Note that the recruitment rate is arbitrarily set to 1, because the model uses relative abundances.

Age distribution is then converted to length distribution facilitated by VBGF model. In this VBGF model, we set the theoretical age at zero length (a_0) to 0 (Table 1; see also Hordyk et al. 2015a to see why this assumption is necessary) and treat L_∞ as the population mean asymptotic length. Asymptotic length for individual fish is normally distributed around L_∞ with coefficient of variation CV. These lead to a growth equation parameterized by L_∞ and M/K:

$$L_x = L_\infty \left(1 - \varepsilon^{\frac{x}{M/K(X-1)}} \right) \tag{2}$$

with L_x the population mean length at age x and that individual length at age (l_x) is also normally distributed about the mean L_x and coefficient of variation CV:

$$l_x \sim Normal(L_x, (CVL_x)^2). \tag{3}$$

In practice, lengths are usually allocated to length bins which partition the length range of individuals and have either equal or varying bin widths. Combining (1) to (3), the relative abundances in ages can be transformed to relative abundances in length bins. Specifically, suppose there are J length bins, where the jth bin is bounded by lengths l_{j-1} and l_j. The relative abundance of fish expected to be associated with j^{th} length bin ($\dot{N}_j$) is given by:

$$\dot{N}_j = \begin{cases} \sum_{x=0}^{X-1} \dot{N}_x \Phi\left(\frac{l_j - L_x}{CVL_x}\right), & \text{if } j = 1; \\ \sum_{x=0}^{X-1} \dot{N}_x \left(\Phi\left(\frac{l_j - L_x}{CVL_x}\right) - \Phi\left(\frac{l_{j-1} - L_x}{CVL_x}\right) \right), & \text{if } 1 < j < J; \\ \sum_{x=0}^{X-1} \dot{N}_x \left(1 - \Phi\left(\frac{l_j - L_x}{CVL_x}\right) \right), & \text{if } j = J \end{cases} \tag{4}$$

where Φ is the cumulative probability density function of the standard normal distribution.

176   The proportion of fish observed in j^{th} length bin ($\widetilde{N}_j^o$) will differ from the expected proportion

177   ($\dot{N}_j / \sum_{j=1}^{J} \dot{N}_j$) if the probability of observing fish (observation selectivity) is affected by their length.

178   Usually, smaller fish are more difficult to observe than larger fish. Therefore, similar as with fishing

179   selectivity in LB-SPR, we model observation selectivity with a logistic function defined by

180   parameters L_{50} and L_{95}, representing the lengths at which fish have 50% and 95% chances of being

181   observed. For the jth length bin with midpoint $\frac{l_{j-1}+l_j}{2}$, selectivity (s_j) is given by:

182    $$s_j = \left(1 + \exp\left(-\frac{\ln 19}{L_{95}-L_{50}}\left(\frac{l_{j-1}+l_j}{2} - L_{50}\right)\right)\right)^{-1}.$$ (5)

183   Given this length-dependent selectivity, the expected proportion of fish observed in the jth length bin

184   is given by:

185    $$\widetilde{N}_j = \frac{s_j \dot{N}_j}{\sum_{j=1}^{J} s_j \dot{N}_j}$$ (6)

186   We used $X = 200$ age classes to balance a good approximation to continuous recruitment with

187   computational efficiency. Consistent with LB-SPR, our LH estimation method assumes that 1% of

188   fish survive to the maximum age ($\varepsilon = 0.01$) and that coefficient of variation of l_x is 10% ($CV = 0.1$)

189   (Table 1). We examined sensitivity to ε and CV as well as to a_0 in the simulations. More complete

190   description of the model structure of our LH estimation method is provided in Supplementary

191   Materials.

192

193   **2.2.   Parameter estimation**

194

195   Our LH estimation method uses length composition sample provided by the user and assumptions

196   described above, to estimate four parameters. The model requires a dataset where the lengths of N fish

197   are assigned to J length bins and N_j^o is the number of fish observed in each of the jth length bin ($N =$

198    $\sum_{j=1}^{J} N_j^o$). We expect proportion $\widetilde{N}_j$ to be associated with j^{th} length bin. Given counts across multiple

199   length bins, our LH estimation method will estimate four parameters: $\theta = \{M/K, L_\infty, L_{50}, L_{95}\}$ using

200   Bayesian method that fits the expected and observed proportions of fish in each length bin. Observed

201   fish counts are assumed to follow a Dirichlet-multinomial distribution. This distribution allows for

202   overdispersion of observational data compared to a Multinomial distribution, that would normally be

203   used to model observed fish proportions across length bins. The overdispersion arises because in

204   practice fish are sampled non-independently, leading to greater variation in the observed proportions

205    $\widetilde{N}_j^o$ compared to the expected proportions $\widetilde{N}_j$. Non-independence may arise from samples being

206   collected at multiple times or across multiple locations. Additional variation my also arise because the

207   model does not fully describe the processes that generate the length frequency data in natural

208   populations.

209   The Dirichlet-multinomial distribution requires the estimation of an additional positive

210 parameter, θ_0, that quantifies the level of overdispersion. Therefore, the likelihood function of the

211 model parameters given the data can be written as:

212 $$L(\theta, \theta_0 | N_1^o \cdots N_J^o) = \frac{\Gamma(\theta_0)\Gamma(N+1)}{\Gamma(\theta_0+N)} \times \prod_{j=1}^{J} \frac{\Gamma\left(\theta_0\tilde{N}_j+N_j^o\right)}{\Gamma(\theta_0\tilde{N}_j)\Gamma\left(N_j^o+1\right)}. \tag{7}$$

213   Bayesian analysis was implemented using the *rstan* package (Stan Development Team 2024),

214 which applies Hamiltonian Monte-Carlo (HMC) algorithms. Estimations were conducted using one

215 chain with 3,000 posterior samples and 500 burn-in samples to be discarded from the final posterior

216 estimates. Full details of parameter estimation procedure are provided in Supplementary Materials.

217

218 **2.3. Data-generating model**

219

220 To evaluate the performance of our LH estimation method and its sensitivity to violations of

221 underlying assumptions, we used a simulation-estimation procedure. Data-generating models (DGMs)

222 were developed to simulate length composition samples from unfished populations across a range of

223 LH and sampling parameters (Fig. 1, Table 2). The simulated data were then fed to the estimation

224 model (EM; i.e., our LH estimation method) that returns the estimates of two LH (M/K and L_∞) and

225 two observation selectivity (L_{50} and L_{95}) parameters. To assess the sensitivity of parameter estimates

226 to the violation of the assumed continuous recruitment, DGMs incorporated both continuous and

227 pulsed (annual) recruitment. A summary of these DGMs is provided below, with methodological

228 details available in Supplementary Materials.

229   Briefly, the continuous-recruitment DGM shared the same assumptions as the EM, except that

230 a_0 of the VBGF was not always fixed at zero. As in the EM, the DGM generated length composition

231 sample from age structure defined in X equally spaced classes where we set $X = 1,000$ to obtain

232 smooth length distributions. In the DGM, age (a) was defined in years, instead of arbitrary unit as in

233 the EM. The relative numbers of fish at each age were computed assuming a particular value of

234 annual instantaneous mortality rate M. The M was set to an arbitrary value of 0.3 year^{-1}, but this value

235 does not affect results since length distributions are largely determined by M/K, rather than on M and

236 K individually. The exception occurs when a_0 is not 0 (see Hordyk et al. 2015b), which we examined

237 in sensitivity analyses. From this, length at age was computed using the original VBGF equation

238 parameterized by K, L_∞ and a_0, with K obtained from the target M/K and $M = 0.3$.

239   Both EM and DGMs produce length compositions, but the length binning differs. The EM

240 binned lengths directly into observational length bins, either equal or variable in width (see below). In

241 contrast, DGMs first binned the simulated data into 0.5 cm equal-width bins, to represent "true

242 population length structure". This length structure was then randomly sampled using the specified

243 sampling parameters (Table 2), and then re-binned into the observational length bins.

244   The pulsed-recruitment DGM assumed recruitment occurred only for three months each year

245 (February-April), altering age structure relative to continuous recruitment. In this pulsed-recruitment

246 DGM, we used the same $X \approx 1,000$ time steps, but the effective number of populated age groups was

247 considerably smaller because most time steps lacked recruits. Once the age structure was established,

248 length composition was generated in the same manner as with continuous-recruitment DGM.

249

250 **2.4.   Simulations and evaluations**

251

252 Fig. 1 outlines the general structure of simulations, with parameters listed in Table 2. In the base

253 simulations, we explored the ability of the EM to estimate LH and selectivity parameters from

254 populations characterized by M/K values of 0.5, 1.0, 1.5, 2.3, and 3.5. These values span most

255 empirical estimates of M/K ratios (Prince et al. 2023) and were also used in previous studies (Prince

256 et al. 2014, Hordyk et al. 2015a, Prince et al. 2023). In the base simulations, we assumed continuous

257 recruitment, $a_0 = 0$, $\varepsilon = 0.01$, $CV = 0.1$, i.e. the same as in the EM. We also assumed L_∞ of 40 cm, a

258 common maximum length of fish observed in coastal rocky and coral reefs (Audzijonyte et al. 2020).

259 For each of the five M/K scenarios, the true population length distribution in I bins $\{N_1^o, \ldots, N_I^o\}$ was

260 sampled 10 times with a sample size (N) of 5,000 length observations per sample, using observation

261 selectivity parameters of $L_{50} = 5$ cm and $L_{95} = 7.5$ cm (representative of underwater visual surveys,

262 Ackerman and Bellwood 2000). Sampled fish lengths were then re-binned into J length bins (in base

263 scenario resulting in 2 cm equally spaced bins), representing the observed length distribution.

264   First, we tested the sensitivity of the EM to violations of assumptions about LH parameters a_0,

265 ε, and CV. The a_0, specifying fish length at zero age (L_0) and assumed to be 0 in the EM, was varied

266 from 0 to 20% of L_∞ ($L_0 = 0$ to 8 cm as $L_\infty = 40$ cm) in the DGMs. For ε, which was set to 1% in the

267 EM, we explored values ranging from 0.1% to 2%. Finally, we simulated data using CV values

268 ranging from 0.05 to 0.2 (0.1 in the EM). Since we found that violation of CV assumption strongly

269 affected parameter estimates, we also explored whether estimates can be improved when EM assumed

270 different CV values (0.05 to 0.2).

271   Second, we explored how observation selectivity might affect accuracy and precision of LH

272 parameter estimation. For each of the five M/K scenarios described above (other parameters

273 following baseline values), we sampled fish with L_{50} values ranging from 2 to 20 cm (5% to 50% of

274 L_∞) and L_{95} ranging from 1.2 to 2 times L_{50}. We also explored the effects of bin width by sampling

275 into equal and unequal binning schemes. For equal bin widths, we tested bin sizes ranging from 1 to 8

276 cm. For unequal bin widths, we used increasing bin sizes, as is commonly used in underwater visual

277 surveys. Specifically, we used the Reef Life Survey (RLS) binning, where bin width starts from 2 cm

278 in the smallest fish, increasing to 3.75, 5, etc (see Table 2). For the base scenario of $L_\infty = 40$ cm, the

279 RLS binning resulted in 10-12 length bins, depending on M/K ratio. Sensitivity of parameter

280   estimation to sample sizes was evaluated by varying sample size from 200 to 20,000 length

281   observations, reflecting the variability observed for common fish species in the RLS data.

282   In theory, length structure is only sensitive to the M/K ratio and not its L_∞ value (Prince et al.

283   2014, Hordyk et al. 2016). However, because observational data is usually collected in a fixed length

284   binning (e.g., RLS binning), resolution of observational data will be different depending on the L_∞ of

285   the species, and this will affect model's ability to estimate LH parameters. Therefore, for each of the

286   five M/K scenarios in base simulations, we also tested the accuracy of parameter estimation for L_∞

287   values ranging from 10 to 90 cm. To examine potential effects from where the maximum observed

288   length falls within a bin, we perturbed L_∞ by ±10%, yielding five evenly spaced L_∞ values within

289   each of 10 to 90 cm above.

290   Finally, we explored the performance of the EM to the violation of the continuous recruitment

291   assumption. For this we used the length frequency data simulated using five M/K values and baseline

292   values of other parameters, but using recruitment only for three months (February-April). The

293   simulated populations were then sampled with the frequency of 1, 2, 6, or 12 times. In cases where

294   sampling occurred only once, we compared sampling during the recruitment event (March) versus six

295   months later (September). When sampling occurred 2, 6 and 12 times, we spaced sampling events

296   evenly across months with the initial sampling occurring in March. The timing of sampling matters

297   because pulsed recruitment leads to non-stationary length structures through the year.

298   The sensitivity analysis described above results in 380 tested parameter combinations, each

299   replicated 10 times, giving 3,800 simulated length distributions provided to the EM for parameter

300   estimation. From this we generated posterior distributions for each of the four estimated parameters

301      $\theta = \{M/K, L_\infty, L_{50}, L_{95}\}$ and quantified the relative error (RE) following equation

302          $$\text{RE} = \frac{\hat{\theta}-\theta}{\theta}$$ (8)

303   where $\hat{\theta}$ is the median of the posterior estimate and θ is the true value used in the simulation (Hordyk

304   et al. 2015b, Rudd and Thorson 2018). All analyses were conducted in R (R Core Team 2024). Data

305   and code are available on GitHub at https://github.com/wanw001 and will be archived on Zenodo

306   upon the acceptance of this publication.

307

308   **3. Results**

309

310   **3.1. M/K and L_∞ could be estimated accurately when observations include small fish**

311

312   The shape of the observed length distribution in unfished population strongly depended on the M/K

313   ratio and observation selectivity parameters (Fig. 2). The length distribution transitioned from left-

314   skewed to right-skewed as M/K ratio goes from <1 to >1 (see also Miethe et al. 2019). Above M/K

315 of 2, the general shape of the distribution was highly right-skewed and less sensitive to M/K values,
316 but very high M/K ratios (3.5) resulted in lower maximum length, relative to L_∞.

317   The EM gave accurate and precise estimates of both M/K and L_∞ parameters when selectivity
318 parameters were sufficiently low (Fig. 3). Specifically, when L_{50} was no more than 25% of L_∞, the
319 estimates of M/K and L_∞ were within 25% and 10% of their true values for all M/K ratios,
320 respectively. However, when L_{50} was set at half of L_∞, estimates were within the same error ranges
321 only in cases when the logistic selectivity curve was very steep (i.e., L_{95} was 120% of L_{50}). For all
322 selectivity parameters, the bias in both M/K and L_∞ estimates generally increased with increasing
323 M/K. This bias was mostly positive but became negative for M/K of 3.5 at high selectivity
324 parameters. The negative bias at M/K of 3.5 occurs because the overall shape of the length
325 distribution was similar to that of M/K of 2.3, but maximum observed lengths were small relative to
326 their L_∞ values (Fig. 2), hence our method estimated smaller M/K and L_∞values relative to the true
327 values.

328   Accuracy of L_{50} and L_{95} estimates showed a slightly different pattern from that of M/K and
329 L_∞. The estimates of L_{50} were slightly negatively biased for low true L_{50} and positively biased for
330 high L_{50}, especially for low M/K values. Meanwhile, the biases of L_{95} estimates tended to be higher
331 for low L_{50}, especially for low M/K values (Fig. 3).

332

333 **3.2. M/K and L_∞ estimates were accurate for >10 length bins, sample sizes > 500 and $L_\infty \geq$**
334   **30 cm**

335

336 Accurate and precise estimates of M/K and L_∞ were obtained when observations were done in equal
337 length bin widths of 4 cm or smaller, as well as for progressively increasing bin widths as adopted in
338 RLS surveys (Fig. 4, left column). The relative errors of M/K and L_∞ were within 12% and 7% of
339 their true values respectively. For the baseline case of L_∞ 40 cm, the 4 cm equal bin, and the RLS bins
340 resulted in 10 to 13 actual observed length bins, depending on the M/K ratio. Using 8 cm equal length
341 bins led to a large decline in the accuracy and precision of parameter estimates, with large positive
342 errors in estimated values (Fig. 4, left column).

343   As expected, increasing sample size decreased bias and increased precision for all four
344 estimated parameters (Fig. 4, middle column; see also Fig. S1 for non-truncated plot). Sample sizes of
345 5,000 resulted in very accurate and precise M/K and L_∞ estimates, i.e. the estimates were within 9%
346 and 6% of their true values. However, even a sample size of 500 provided reasonable accuracy, with
347 nearly all estimates within 30% of their true values. For a sample size of 200, parameter estimates
348 were generally inaccurate. Generally, for simulations exploring length bin and sample sizes, higher
349 M/K values resulted in higher positive errors in M/K and L_∞ estimates, except for M/K of 3.5,
350 where the bias was reduced and errors became negative. Estimates of selectivity parameters behaved

351 similarly to M/K and L_∞ estimates in that parameter values were estimated accurately for all except 8

352 cm length bins and smallest sample sizes of 200.

353   Finally, given that the use of finite and especially progressively larger length bins is likely to

354 affect parameter estimation accuracy depending on the absolute length of the fish, we assessed the

355 accuracy of parameter estimates for L_∞ ranging from 10 to 90 cm (Fig. 5 & S2). Results showed that

356 when increasing bin widths are used to record observations, estimates of M/K and L_∞ were strongly

357 biased for L_∞ of 10 cm. However, when true L_∞ was at 20 cm and especially 30 cm or larger, all

358 parameter estimates improved rapidly. Accuracy improvements were also observed in the estimates of

359 L_{50} and L_{95} as the true L_∞ increased. The only exception was the case of L_∞ at 90 cm, where biases

360 of L_{50} and L_{95} increased for the low M/K of 0.5. In some cases we observed abrupt changes in the

361 accuracy of M/K and L_∞ estimates with small changes in L_∞, for example when L_∞ was increased

362 from 19 to 20 cm for M/K of 3.5.

363

364 **3.3. M/K and L_∞ could be estimated accurately for fish with pulsed recruitment when**

365 **sampling was conducted over multiple months**

366

367 Pulsed recruitment diminished the accuracy of M/K and L_∞ when estimates were made from just a

368 single sample (Fig.4, right column), although sampling in the middle of recruitment time (March),

369 yielded slightly better results than estimates from a single sampling event in September. Even two

370 sampling events separated by 6 months produced considerably better estimates of M/K and L_∞,

371 except for the smallest M/K values of 0.5. When sampling frequency was higher, parameter estimates

372 were generally reliable and similar to those of continuous recruitment.

373

374 **3.4. M/K and L_∞ estimates were sensitive to the misspecification of CV**

375

376 Overall, the estimates of M/K and L_∞ were robust to violation of the assumption that age at zero

377 length was 0 ($a_0 = 0$) (Fig. 6, left column). Even when a_0 corresponded to a high L_0, i.e. 20% of L_∞,

378 the two parameters were estimated within 20% accuracy, with highest positive bias at high M/K

379 values. In contrast, estimates of the two selectivity parameters were more sensitive to the violation of

380 $a_0 = 0$, and were highly biased when a_0 corresponded to an L_0 higher than 10% of L_∞.

381 Misspecification to cohort survivorship at maximum age ε (proxy for a_{max}) had the opposite effect of

382 parameter estimates in that it mostly affected M/K and L_∞ estimates, leading to positive bias for

383 values lower than the default, i.e., $\varepsilon = 1\%$, and low M/K ratios, but having negligible impact on

384 selectivity parameter estimates. Finally, M/K and L_∞ estimates were highly sensitive to the

385 misspecification of CV (Fig. 6, right column; see also Fig. S3 for non-truncated plot). Deviations from

386 the default assumption of 0.1 strongly biased M/K and L_∞ estimates, in either negative or positive

387 direction, depending on the values of true CV. Estimates of selectivity parameters were less affected,

388 except for cases with the lowest M/K values.

389   Given that misspecification in CV had a large impact on parameter estimates, we further tested

390 whether assuming a different CV value in the EM (currently set at 0.1) could give better estimates of

391 the four parameters. As expected, parameter estimates were most accurate when the CV assumed in

392 the EM was the same as the value used to simulate the data (Fig. 7; see also Fig. S4 for non-truncated

393 plot). Yet, when the CV value was mis-specified, using a CV of 0.15 in the EM resulted in the least

394 biased parameter estimates. Notably, for low M/K values, estimates of L_{50} and L_{95} were often highly

395 biased.

396

4. Discussion

397

398

4.1. Overall performance of our method

399

400

401 Building on a widely popular LB-SPR method described by Hordyk et al. (2015a), we developed a

402 method to estimate two LH (M/K and L_∞) and two observational selectivity (L_{50} and L_{95})

403 parameters, using length data from unfished populations. Overall, we found that the new method

404 performs reasonably well, typically estimating parameters with less than 15% and 10% bias for M/K

405 and L_∞ respectively (30% and 20% bias in extreme data cases), assuming that the observation data

406 was generated by processes that do not strongly violate the model assumptions. Good performance of

407 the method required moderate observation selectivity (L_{50} and L_{95} $<0.5L_\infty$), sufficient number of

408 length bins (≥ 10) and reasonable sample sizes (≥ 500). These conditions are necessary for the data to

409 accurately reflect the shape of the underlying length distribution. We found that our method was

410 sensitive to the misspecification of the variation of length at age, CV (assumed to be 0.1 in the

411 method, but other values can also be used), but violations to the assumed theoretical age at length zero

412 (a_0) or fish survivorship at the maximum modelled age (ε) had smaller effects. Performance was best

413 for fish species that exhibit continuous recruitment, although continuous recruitment throughout the

414 year rarely occurs in nature. However, even under pulsed recruitment, pooling samples from different

415 seasons smoothed the composite length distribution and improved the accuracy and precision of

416 parameter estimates.

417   The M/K and L_∞ parameters are central to describing the expected unfished length structure

418 needed for population assessments. Two most widely used length-based methods – LB-SPR (Hordyk

419 et al. 2015a) and LBB (Froese et al. 2018) – require M/K and L_∞ to generate expected unfished

420 length distributions and estimate reference points for evaluating population status. However,

421 estimating reliable values for M, K, and L_∞ through traditional approaches such as aging or tagging

422 studies remains challenging and costly. With the rapid growth in underwater monitoring, either

423   through underwater surveys, deployments of underwater cameras, or AI-assisted data extraction, fish
424   length observations from both fished and unfished populations are becoming increasingly available.
425   Our method is designed to utilize these data to estimate M/K and L_∞ across a broad range of species
426   and populations.

427

428   **4.2.   Comparison with other LH estimation methods and with original LB-SPR**

429

430   The estimation of LH parameters using length-frequency data has a long history in fisheries science,
431   with examples including electronic length frequency analysis (ELEFAN, Pauly and David 1981) and
432   Bayesian growth model (BGM, Zhou et al. 2022). Both ELEFAN and BGM infer VBGF parameters
433   (L_∞ and K) from length data by analysing modal or mean-length shifts across cohorts, either from a
434   single snapshot or a time-series sample. Alternative methods (Ebert 1973, Sparre 1987) estimate
435   growth and total mortality (Z) parameters, with Z derived from the right-hand limb of the length
436   distribution. Broader adoption of these methods is sometimes hindered by the lack of clear separable
437   cohorts due to low sampling resolution or extended recruitment times. In fact, a large scale study
438   spanning 800 species and nearly 3,000 populations from mostly unfished populations, showed that,
439   when pooled over temporal scales, most length compositions are largely unimodal (Heather et al.
440   2025). Another limitation of previous LH estimation methods is that they typically estimate growth
441   and mortality separately, using different parts of length distribution - growth from cohort spacing and
442   mortality from the slope of the right-hand limb. Estimating growth and mortality parameters
443   individually is more prone to bias, as they tend to exhibit higher variability than their ratio (Prince et
444   al. 2014, Prince et al. 2023).

445   Until recently, LH parameter estimation, including using methods above, typically use length
446   data from fished population or catch, which is already affected by length-selective fishing (Hordyk
447   al. 2016). When used in estimation, the "distorted" length distribution can bias the parameter
448   estimates. The LH estimation method presented here avoids reliance on length progression or the
449   slope of the right-hand limb of length distribution. Instead, it uses the overall shape of length
450   distribution from unfished population, building on the modelling foundation established by Hordyk et
451   al. (2015a) in the development of the LB-SPR method.

452   Developed from LB-SPR framework, our method retains the same underlying model structure
453   and assumptions. Both approaches use the shapes of the length distribution to infer growth to
454   mortality ratio and selectivity. In our method it is the relative natural mortality rate and observation
455   selectivity, whereas in LB-SPR it is the relative total mortality rate, which translates to relative fishing
456   mortality rate (F/M), and fishing selectivity. Importantly, our method also estimates L_∞, a parameter
457   that determines the absolute scale of the length distribution. In contrast to fishing selectivity in LB-
458   SPR, observation selectivity in our method does not impact population length structure.
459   Methodologically, our method employs Bayesian inference (as in LBB; Froese et al. 2018), allowing

460 the incorporation of prior knowledge and direct quantification of uncertainty (Hoff 2009), while LB-
461 SPR employs maximum likelihood. It should also be noted that we followed the original version of
462 LB-SPR introduced by Hordyk et al. (2015a), rather than the Growth-Type-Group (GTG LB-SPR)
463 extension (Hordyk et al. 2016), which addresses the Rosa Lee's phenomenon, where length-at-age
464 distribution in older age groups become increasingly skewed due to selective removal of fastest
465 growing fish. The GTG modification, while important for fished populations, is unnecessary here
466 because we focus on unfished populations with length-independent natural mortality.
467
468 **4.3. Conditions for high performance of our LH estimation method**
469
470 Overall, we found that, despite the challenge of estimating four parameters from relatively low-
471 resolution length data (e.g., unequal bin widths from 2 to 10 cm), our LH estimation method
472 performed surprisingly well. As expected, parameter inference generally improved with increasing
473 sample size. When total sample size fell below 500 length observations, the length distribution often
474 failed to adequately represent the underlying population length-structure, resulting in reduced method
475 performance (see Fig. S7). Although 500 lengths may seem large, the assumption of equilibrium in
476 the population allows data pooling across temporal and spatial scales. This makes sample sizes of 500
477 to 1,000 lengths achievable for many commonly observed species in underwater surveys.
478 The binning resolution is another key factor influencing the accuracy of parameter estimation,
479 as it determines how well the underlying shape of the length distribution is captured by the data (see
480 Figs. S6 & S10). We found that binning with 10 length bins, whether of equal 2 cm width or
481 increasing width (as in RLS surveys), provided good accuracy and precision, with minimal
482 improvement beyond 13 bins. This minimum bin count also sets the lowest L_∞ for which the method
483 remains effective. When we considered RLS binning we found that our method performed well for
484 species where L_∞ is at least 30 cm, as it resulted in 9 to 11 length bins containing counts. Smaller L_∞
485 (e.g., ~10–20 cm) produced only 5–9 bins that leads to lower accuracy. The abrupt changes of bias
486 shown in Fig. 5 arise when small shifts in L_∞ move the maximum observed length (L_{max}) across bins,
487 changing the number of informative bins (e.g., shift of L_∞ from 19 to 20 cm at M/K of 3.5 increases
488 the number of bins from 6 to 7). When the bin count remains unchanged, accuracy is largely
489 unaffected even if L_{max} shifts from lower to higher end of the bin.
490 For similar reasons, our method may produce highly biased parameter estimates when
491 observational selectivity excludes fish of sizes up to half of L_∞. Such extreme selectivity - either due
492 to inability of the observer to see small fish present within the study site or because young fish occur
493 in different habitats - obscures the left side of the length distribution (Fig. 2; see also Fig S5). As a
494 result, the model is unable to distinguish whether the absence of small fish is caused by selectivity or
495 a low M/K ratio. Consequently, our method is not suitable for estimating LH parameters for species

496 that undergo pronounced ontogenetic habitat shifts, unless standardised length frequency data can be
497 collected across all relevant habitats.

498   Finally, our simulation also showed that for species with high M/K ratios, where length
499 distributions are strongly right-skewed, the model tended to produce more biased estimates of M/K
500 and L_∞. This bias is again linked to the number of informative length bins. Higher M/K ratios result
501 in fewer larger fish, reducing $L_{\max}$ and the number of informative bins. However, it is unclear why
502 the bias tends to be increasingly positive. This is possibly due to differences in how observation
503 selectivity and age resolution are implemented in the DGM and the EM. For example, the DGM uses
504 $X \sim 1,000$, while EM uses $X = 200$. Interestingly, when the true M/K reaches 3.5, the bias suddenly
505 drops or becomes negative. Two mechanisms likely explain this pattern: (i) length distributions
506 become increasingly similar for $M/K > 2$ (Fig. 2), so the method may ascribe the distribution to a
507 lower M/K and L_∞ combination; and (ii) with finite samples, observations in the upper right-tail
508 become increasingly rare, reducing the observed $L_{\max}$. When sample sizes are very large (e.g.,
509 20,000; Fig. 4 right column), more observations capture the upper right-tail, reinforcing the trend of
510 increasing positive bias. Therefore, counterintuitively, smaller sample sizes can sometimes reduce bias
511 at high M/K values by limiting the influence of rare large individuals.

512

513 **4.4.   Violations of model assumptions and impacts on LH parameter estimates**

514

515 Like all models, the LH estimation method presented here relies on a set of assumptions about the
516 processes that generated the observed length data, and violations of these assumptions can affect the
517 accuracy of the model results. A common assumption in data-poor approaches is constant and
518 continuous recruitment. While we did not explore the impact of varying recruitment intensity, we
519 found that pulsed recruitment can impair parameter estimation accuracy when observations are drawn
520 from a single time period. This is because the shape of the length distribution varies depending on the
521 timing of sampling relative to the recruitment event (see Fig. S8). However, our sensitivity analyses
522 showed that pooling even two samples collected by six months apart is sufficient to smooth the length
523 distribution toward that expected under continuous recruitment, thereby improving our method's
524 performance (Figs. 4, S8, & S9).

525   Three additional assumptions in our method are related to a_0, ε, and CV. Both LB-SPR and our
526 method require that $a_0 = 0$, even though it is well known that good fits of VBGF are obtained mostly
527 when a_0 is negative, corresponding to positive length at zero age ($L_0 > 0$) (e.g., Shih, Hsu and Chen
528 2014, Wilson and Nieland 2001, Pardee, Wiley and Springer 2021). Fortunately, our simulations show
529 the violation to $a_0 = 0$ assumption has minimal impact, consistent with findings from LB-SPR
530 (Hordyk et al. 2015b). Varying ε between 0.1% to 2% also had limited effect on parameter estimates
531 (Fig. 6), indicating robustness to model misspecification. While species-specific values of ε have been

532　　　suggested (e.g., 1-2% in some Teleost and Elasmobranch, Dureuil and Froese 2021, Nadon and Ault

533　　　2016), our method adopted $\varepsilon = 1\%$ following the original LB-SPR formulation. Although Dureuil

534　　　and Froese (2021) estimated an average ε of 1.5% across species, our simulations show that using $\varepsilon =$

535　　　1% has a negligible influence on M/K and L_∞ estimates.

536　　　　　In contrast to the relatively minor effects of misspecifying a_0 and ε, we found that inaccurate

537　　　assumption about CV can lead to substantial bias in LH parameter estimates. Our method, following

538　　　LB-SPR, assumed a baseline CV of 10%. However, if the true value was 20%, estimates were

539　　　positively biased by 35-100% for M/K and 18-40% for L_∞. In comparison, LB-SPR is reported to be

540　　　insensitive to CV (Hordyk et al. (2015b), though this conclusion was made based on a narrower range

541　　　of CV (0.075-0.125), compared to our study (0.05-0.20). Interestingly, when comparing our results

542　　　with Fig. 2 in Hordyk et al. (2015b) for the same CV value, the relative errors in our LH parameter

543　　　estimates were generally smaller. It remains to be determined which baseline CV value performs best

544　　　with our method, or whether the CV parameter should also be estimated together with main LH

545　　　parameters.

546　　　　　Notably, errors in M/K and L_∞ estimates are positively correlated - overestimation in one

547　　　parameter often accompanies overestimation in the other and *vice versa*. However, observation

548　　　selectivity (L_{50} and L_{95}) trades off negatively with M/K and L_∞, such that improving the accuracy of

549　　　one pair can lead to reduced accuracy in the other. When applied to assess the status of fished

550　　　population, LB-SPR is sensitive to M/K and L_∞ (Hordyk et al. 2015b). Overestimating M/K tends

551　　　can result in an underestimation of F/M and inflation of the SPR, whereas overestimating L_∞ has the

552　　　opposite effect. This interaction can be beneficial when M/K and L_∞ estimates from our method are

553　　　used for LB-SPR to assess the population status of the same species. If M/K and L_∞ are both

554　　　overestimated, their opposing effects in LB-SPR could partly offset each other, leading to more

555　　　accurate estimates of F/M and SPR. Naturally, the overall reliability of LB-SPR-based assessments

556　　　depends on the magnitude of bias in LH parameters and potential misspecifications of other model

557　　　parameters.

558

559　　　**4.5.　Limitations and future work**

560

561　　Estimating LH parameters from length frequency data alone is challenging, and any method applied to

562　　address it must rely on a set of assumptions and simplifications. A key assumption of our method, as

563　　in other length-based methods, is that the M/K ratio is defined under the conditions that fish growth

564　　follows VBGF and natural mortality is independent of both length and age. These conditions are often

565　　violated (Lorenzen, Camp and Garlock 2022, Fahmi et al. 2021). While the VBGF provides a

566　　reasonable approximation for many species, it can misrepresent juvenile growth (Quinn II and Deriso

567　　1999, Lester, Shuter and Abrams 2004), and mortality is unlikely to be length-independent. When

body growth follows a different model, or mortality changes across length, M/K may lose interpretability. We did not test sensitivity of L_∞ estimate to departures from VBGF or length-independent M, but such violations will likely bias L_∞.

In our DGM, we used a steady-state, one-snapshot population with constant recruitment, rather than dynamic populations through time (cf. Hordyk et al. 2015b, Rudd and Thorson 2018, Huynh et al. 2018). This choice is reasonable, as we did not explore variable recruitment effect on parameter estimation. Like LB-SPR, our model treats recruitment as constant, although it is well known that in natural populations recruitment can fluctuate dramatically around its average level (Hordyk et al. 2015b, Rudd and Thorson 2018). Our random sampling design might not have sufficiently represented this fluctuation, potentially leading to weaker performance of our LH estimation method in real-world applications.

Finally, just like fishing selectivity in LB-SPR, our method assumes logistic observation selectivity. Yet, some species or observation methods may have dome-shaped selectivity, where largest fish are harder to observe. In such cases, our method will likely underestimate L_∞ and bias M/K. Unfortunately, accounting for dome-shaped selectivity in LH parameter estimation is challenging (Hordyk et al. 2015a). If large individuals are absent, it is difficult to identify whether this is caused by the LH parameters, or selectivity. Hence, the model should not be applied in cases where observational selectivity is likely to be strongly dome-shaped.

Despite these limitations, the LH parameter estimation method presented here offers valuable potential for estimating M/K and L_∞ across a wide range of fish and invertebrate species, where growth can be reasonably described by the VBGF and other model assumptions are approximately met. With the increasing availability of length data from citizen science, automatic monitoring and other emerging sources, the method could help illuminate variable LH traits across hundreds of species and support data-poor stock assessments. Importantly, the method presented here requires data from a largely unfished population, which may be obtained from well-managed marine reserves, remote ecosystems, or historical surveys conducted prior to the onset of fishery.

Future studies could extend the current LH estimation method to incorporate environmental gradients using hierarchical models that allow population-specific estimates of M/K and L_∞. Another extension could be reformulating our method with dome-shaped observation selectivity particularly for species with clear ontogenetic shift in habitat for oldest individuals.

6. Author contributions: CRediT

WK: Conceptualization, Methodology, Formal analysis, Writing-original draft. **SAR**: Conceptualization, Methodology, Writing – review and editing. **PB-B**: Methodology, Writing – review and editing. **AA**: Conceptualization, Methodology, Writing – review and editing, Funding acquisition.

7. Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used ChatGPT in order to improve the wording and overall clarity of the text. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

8. References

Ackerman, J. L. & D. R. Bellwood (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series,* 206**,** 227-237.

Allen, M. S. & J. E. Hightower. 2010. Fish population dynamics: mortality, growth, and recruitment. In *Inland Fisheries Management in North America, Third Edition,* ed. W. A. H. M. C. Quist, 43-80. Bethesda, Maryland: American Fisheries Society.

Andersen, K. H. 2020a. *Fish Ecology, Evolution, and Exploitation: A New Theoretical Synthesis*. Princeton: Princeton University Press.

Andersen, K. H. (2020b) Size-based theory for fisheries advice. *ICES Journal of Marine Science,* 77**,** 2445-2455.

Audzijonyte, A., S. A. Richards, R. D. Stuart-Smith, G. Pecl, G. J. Edgar, N. S. Barrett, N. Payne & J. L. Blanchard (2020) Fish body sizes change with temperature but not all species shrink with warming. *Nature Ecology & Evolution,* 4**,** 809-814.

Beverton, R. J. H. & S. J. Holt (1956) A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *Journal du Conseil / Conseil Permanent International pour l'Exploration de la Mer,* 14**,** 67-83.

Bowlby, H. D., H. P. Benoît, W. Joyce, J. Sulikowski, R. Coelho, A. Domingo, E. Cortés, F. Hazin, D. Macias, G. Biais, C. Santos & B. Anderson (2021) Beyond Post-release Mortality: Inferences on Recovery Periods and Natural Mortality From Electronic Tagging Data for Discarded Lamnid Sharks. *Frontiers in Marine Science,* 8.

639   Dureuil, M., W. H. Aeberhard, K. A. Burnett, R. E. Hueter, J. P. Tyminski & B. Worm (2021) Unified
640   natural mortality estimation for teleosts and elasmobranchs. *Marine Ecology Progress Series,*
641   667**,** 113-129.

642   Dureuil, M. & R. Froese (2021) A natural constant predicts survival to maximum age.
643   *Communications Biology,* 4**,** 641.

644   Ebert, T. A. (1973) Estimating growth and mortality rates from size data. *Oecologia,* 11**,** 281-298.

645   Edgar, G. J. & R. D. Stuart-Smith (2014) Systematic global assessment of reef fish communities by
646   the Reef Life Survey program. *Scientific Data,* 1**,** 140007.

647   Fahmi, W. Kurniawan, I. R. Tibbetts, S. Oktaviyani, C. L. Dudgeon & M. B. Bennett (2021) Age and
648   growth of the tropical oviparous shark, *Chiloscyllium punctatum* in Indonesian waters.
649   *Journal of Fish Biology,* 99**,** 921-930.

650   Froese, R., H. Winker, G. Coro, N. Demirel, A. C. Tsikliras, D. Dimarchopoulou, G. Scarcella, W. N.
651   Probst, M. Dureuil & D. Pauly (2018) A new approach for estimating stock status from length
652   frequency data. *ICES Journal of Marine Science,* 75**,** 2004-2015.

653   Goldman, K. J. 2005. Age and growth of elasmobranch fishes. In *Management techniques for*
654   *elasmobranch fisheries,* ed. J. A. M. R. Bonfil, 76-102. Rome: FAO.

655   Green, B. S., B. D. Mapstone, G. Carlos & G. A. Begg. 2009. Introduction to Otoliths and Fisheries in
656   the Tropics. In *Tropical Fish Otoliths: Information for Assessment, Management and Ecology,*
657   eds. B. S. Green, B. D. Mapstone, G. Carlos & G. A. Begg, 1-22. Dordrecht: Springer
658   Netherlands.

659   Gulland, J. A. & A. A. Rosenberg. 1992. *A review of length-based approaches to assessing fish stocks.*
660   Rome: FAO.

661   Hamel, O. S. (2014) A method for calculating a meta-analytical prior for the natural mortality rate
662   using multiple life history correlates. *ICES Journal of Marine Science,* 72**,** 62-69.

663   Heather, F. J., S. A. Richards, N. C. Krueck, R. D. Stuart-Smith, S. J. Brandl, J. M. Casey, G. J. Edgar,
664   N. Barrett, V. Parravicini & A. Audzijonyte (2025) Consistent unimodal body length
665   distributions in hundreds of reef fishes across diverse life histories. *Fish and Fisheries,* 26**,**
666   533-545.

667   Hoenig, J. M. (1983) Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin,* 81**,**
668   898-903.

669   Hoff, P. D. 2009. *A First Course in Bayesian Statistical Methods*. New York: Springer.

670   Hordyk, A., K. Ono, K. Sainsbury, N. Loneragan & J. Prince (2015a) Some explorations of the life
671   history ratios to describe length composition, spawning-per-recruit, and the spawning
672   potential ratio. *ICES Journal of Marine Science,* 72**,** 204-216.

673   Hordyk, A., K. Ono, S. Valencia, N. Loneragan & J. Prince (2015b) A novel length-based empirical
674   estimation method of spawning potential ratio (SPR), and tests of its performance, for small-
675   scale, data-poor fisheries. *ICES Journal of Marine Science,* 72**,** 217-231.

676 Hordyk, A. R., K. Ono, J. D. Prince & C. J. Walters (2016) A simple length-structured model based on
677　　　　life history ratios and incorporating size-dependent selectivity: application to spawning
678　　　　potential ratios for data-poor stocks. *Canadian Journal of Fisheries and Aquatic Sciences,* 73**,**
679　　　　1787-1799.

680 Huynh, Q. C., J. Beckensteiner, L. M. Carleton, B. J. Marcek, V. Nepal KC, C. D. Peterson, M. A.
681　　　　Wood & J. M. Hoenig (2018) Comparative performance of three length-based mortality
682　　　　estimators. *Marine and Coastal Fisheries,* 10**,** 298-313.

683 Kai, M., H. Yokoi & Y. Fujinami (2023) Modeling of age-dependent natural mortality rates for long-
684　　　　lived fishes based on the Richards model family. *Canadian Journal of Fisheries and Aquatic*
685　　　　*Sciences,* 80**,** 1289-1300.

686 Lester, N. P., B. J. Shuter & P. A. Abrams (2004) Interpreting the von Bertalanffy model of somatic
687　　　　growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London. Series*
688　　　　*B: Biological Sciences,* 271**,** 1625-1631.

689 Lorenzen, K., E. V. Camp & T. M. Garlock (2022) Natural mortality and body size in fish populations.
690　　　　*Fisheries Research,* 252**,** 106327.

691 Maunder, M. N., O. S. Hamel, H.-H. Lee, K. R. Piner, J. M. Cope, A. E. Punt, J. N. Ianelli, C.
692　　　　Castillo-Jordán, M. S. Kapur & R. D. Methot (2023) A review of estimation methods for
693　　　　natural mortality and their performance in the context of fishery stock assessment. *Fisheries*
694　　　　*Research,* 257**,** 106489.

695 Miethe, T., Y. Reecht & H. Dobby (2019) Reference points for the length-based indicator Lmax5% for
696　　　　use in the assessment of data-limited stocks. *ICES Journal of Marine Science,* 76**,** 2125-2139.

697 Nadon, M. O. & J. S. Ault (2016) A stepwise stochastic simulation approach to estimate life history
698　　　　parameters for data-poor fisheries. *Canadian Journal of Fisheries and Aquatic Sciences,* 73**,**
699　　　　1874-1884.

700 Pardee, C., J. Wiley & S. Springer (2021) Age, growth and maturity for two highly targeted jack
701　　　　species: and. *Journal of Fish Biology,* 99**,** 1247-1255.

702 Pauly, D. (1980) On the interrelationships between natural mortality, growth parameters, and mean
703　　　　environmental temperature in 175 fish stocks. *ICES Journal of Marine Science,* 39**,** 175-192.

704 Pauly, D. (1983) Length-converted catch curves: a powerful tool for fisheries research in the tropics
705　　　　(part I). *Fishbyte,* 1**,** 9-13.

706 Pauly, D. & N. David (1980) An objective method for determining fish growth from length-frequency
707　　　　data. *ICLARM Newsletter,* 3**,** 13-15.

708 --- (1981) ELEFAN I, a basic program for the objective extraction of growth parameters from length-
709　　　　frequency data. *Berichte Der Deutschen Wissenschaftlichen Kommissuib Für*
710　　　　*Meeresforschung,* 28**,** 205-211.

Prince, J., A. Hordyk, S. R. Valencia, N. Loneragan & K. Sainsbury (2014) Revisiting the concept of Beverton-Holt life-history invariants with the aim of informing data-poor fisheries assessment. *ICES Journal of Marine Science,* 72**,** 194-203.

Prince, J. D., C. Wilcox & N. Hall (2023) How to estimate life history ratios to simplify data-poor fisheries assessment. *ICES Journal of Marine Science.*

Quinn II, T. J. & R. B. Deriso. 1999. *Quantitative fish dynamics.* New York: Oxford University Press.

R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rudd, M. B. & J. T. Thorson (2018) Accounting for variable recruitment and fishing mortality in length-based stock assessments for data-limited fisheries. *Canadian Journal of Fisheries and Aquatic Sciences,* 75**,** 1019-1035.

Schlosser, I. J. (1990) Environmental variation, life history attributes, and community structure in stream fishes: Implications for environmental management and assessment. *Environmental Management,* 14**,** 621-628.

Shih, C.-L., C.-C. Hsu & C.-Y. Chen (2014) First attempt to age yellowfin tuna, *Thunnus albacares*, in the Indian Ocean, based on sectioned otoliths. *Fisheries Research,* 149**,** 19-23.

Sparre, P. 1987. A method for the estimation of growth, mortality, and gear selection/recruitment parameters from length-frequency samples weighted by catch per effort. ed. D. M. Pauly, G.R., 75-102. International Center for Living Aquatic Resources Management.

Sparre, P. & S. C. Venema. 1998. *Introduction to Tropical Fish Stock Assessment. Part 1. Manual.* Rome: FAO.

Stan Development Team. 2024. RStan: the R interface to Stan. R package version 2.32.6.

Taylor, M. H. & T. K. Mildenberger (2017) Extending electronic length frequency analysis in R. *Fisheries Management and Ecology,* 24**,** 330-338.

Then, A. Y., J. M. Hoenig, N. G. Hall, D. A. Hewitt & H. e. E. Jardim (2014) Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science,* 72**,** 82-92.

Thorson, J. T., S. B. Munch, J. M. Cope & J. Gao (2017) Predicting life history parameters for all fishes worldwide. *Ecological Applications,* 27**,** 2262-2276.

Wilson, C. A. & D. L. Nieland (2001) Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. *Fishery Bulletin,* 99**,** 653-664.

Zhou, S., T. Hutton, Y. Lei, M. Miller, T. van Der Velde & R. A. Deng (2022) Estimating growth from length frequency distribution: comparison of ELEFAN and Bayesian approaches for red endeavour prawns (*Metapenaeus ensis*). *ICES Journal of Marine Science,* 79**,** 1942-1953.