Reply

On the pile-up effect and priors for L_{inf} and M/K: response to a comment by Hordyk *et al.* on "A new approach for estimating stock status from length frequency data"

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Introduction

There is a recognized need for new methods with modest data requirements to provide preliminary estimates of stock status for data-limited stocks (e.g. Rudd and Thorson, 2018). Froese *et al.* (2018) provide such a method, which derives estimates of relative stock size from length frequency (LF) data of exploited stocks. They show that their length-based Bayesian biomass estimation method (LBB) can reproduce the "true" parameters used in simulated data and can approximate the relative stock size as estimated independently by more data-demanding methods in 34 real stocks.

However, in a comment on LBB, Hordyk *et al.* (2019) claim (i) that the master equation of LBB is incomplete because it does not correct for the pile-up effect caused by aggregating length measurements into length classes or "bins", (ii) that LBB is highly sensitive to equilibrium assumptions and wrongly uses maximum observed length (L_{max}) for guidance in setting a prior for the estimation of asymptotic length (L_{inf}), and (iii) that the default prior used by LBB for the ratio between natural mortality and somatic growth rate (M/K) of 1.5 ($SD = 0.15$) is inadequate for many exploited species. These comments are addressed below.

Understanding the pile-up effect

To understand the pile-up (Baranov, 1918) of abundance observations in length classes used as bins in LF analyses (van Sickle, 1977; Pauly, 1984; Hordyk *et al.*, 2019), let us consider a thought experiment where 1000 post-larval fish of 0.5 cm length at 0.1 years of age are released in a pond. All individuals are assumed to have identical growth, with $L_{inf} = 100$ cm, $K = 0.133$ year^{-1}, and $t_0 = -0.0624$ year. Natural mortality in the pond is assumed as a constant $M = 0.2$ year^{-1} across all life stages. Fishing is conducted continuously with a gear of trawl-like selectivity retaining

50% of individuals of 50 cm length and 95% of individuals of 55 cm length. Mortality caused by fishing is set at $F = 0.2$ year^{-1}. Two hypothetical sampling strategies are applied, which obtain accurate counts of the numbers of individuals that are vulnerable to the fishing gear without harming or removing individuals. The first sampling strategy involves taking samples at time-intervals of 0.1 year and is called "fixed-time" sampling. The second strategy takes samples at intervals corresponding to the time required by the fish to grow 0.5 cm in length and is called "fixed-length" sampling. If the numbers obtained by these two sampling strategies are plotted over length and the observations are connected by smoothed curves, they give identical continuous representations of vulnerable individuals at length (see Figure 1a, where the fixed-length-based measurements are represented by a curve and the fixed-time-based measurements are represented by dots, which exactly overlay the curve).

For practical reasons, it is common to aggregate frequencies that fall within a certain length range, i.e. a length class or bin. If, for example, observed fixed-length-based frequencies are summed up in bins of 2 cm width, then four observations of 0.5 cm difference in lengths will fall into the same bin. The resulting histogram is shown in Figure 1b, and its shape is a good representation of the continuous LF, represented by the thin overlayed age-based curve.

However, if the same aggregation is done with the fixed-time-based observations, then fewer than four observations will fall into length bins at lower length, and increasingly more than four observations will fall into bins at larger lengths. This leads to a distortion of the true LF distribution, as indicated by the dots in Figure 1b. Applying the correction proposed by Hordyk *et al.* (2019) to the fixed-time-based frequencies does indeed account for this pile-up effect, as can be seen in Figure 1c, where the corrected continuous frequency curve provides a good fit for dots
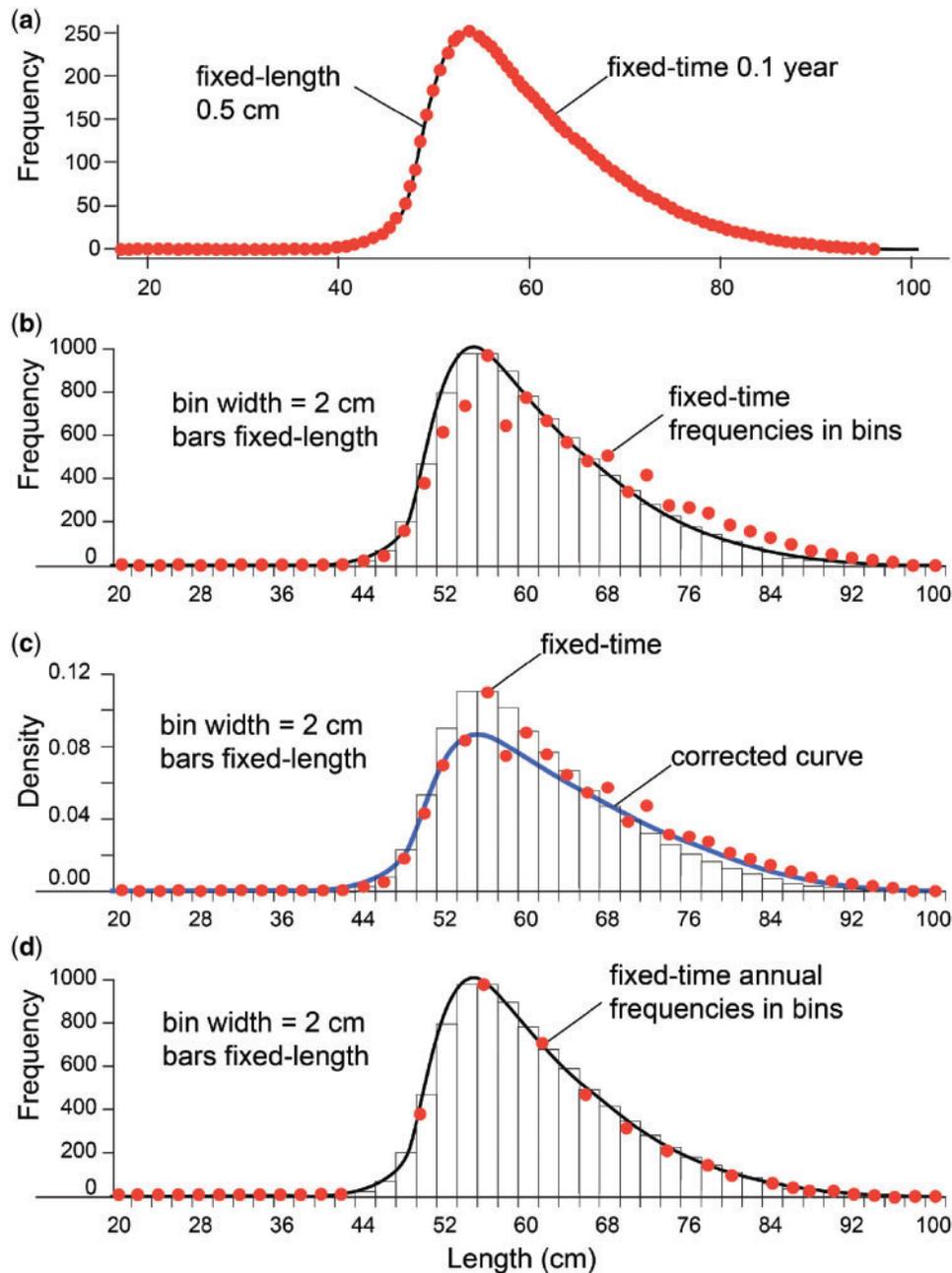
Figure 1. Length frequencies for a hypothetical cohort showing the effects of different sampling and aggregation schemes. (a) Frequencies observed at sampling intervals of 0.5 cm, represented by the black curve, and frequencies observed at 0.1 year intervals, represented by dots. (b) Histogram representing the fixed-length-interval frequencies aggregated in bins of 2 cm width, matching the original frequencies shown in (a), as indicated by the overlaid curve. The dots indicate the aggregation of the fixed-time-interval frequencies. (c) A replication of (b), but with an overlaid curve that accounts for the pile-up effect in the fixed-time-interval frequencies. (d) Replication of the histogram of (b). The dots indicate accumulated frequencies based on fixed-time-interval samples that were taken annually over the life span of the cohort, where bins without circle did not contain observations. Note that, in this case, there is no bias caused by the pile-up effect.

resulting from the uneven accumulation of fixed-time frequencies in length bins of the same width.

Thus, the "continuous time population model" proposed by Hordyk *et al.* (2019) as universally applicable to LF data assumes frequent sampling at small time-intervals. If such sampling is done across cohorts instead of following a single cohort, then the continuous time population model also assumes continuous recruitment.

But, is continuous sampling a good and general representation of the real sampling effort behind available LF data? For example, if the cohort in the thought experiment is sampled only once per year, the pile-up effect disappears and the frequencies reflect the original unbiased distribution (Figure 1d). Applying a correction for pile-up to these data would introduce a bias that overestimates exploitation rate and thus underestimates relative stock size.

Table 1. Performance comparison of three length-based methods against estimates from independent stock assessments.

Method	Different F/F_{msy} (%)	Different B/B_{msy} (%)
LBB	18 of 32 (56.3)	3 of 21 (14.3)
LBB (corr.)	25 of 32 (78.1)	9 of 21 (42.8)
LBSPR	27 of 32 (84.3)	11 of 21 (52.2)

Non-overlapping 95% confidence limits were used as indication of significantly different estimates and are shown as numbers and percentage. Note that 40% SPR was taken as a proxy for B_{msy}/B_0 and, accordingly, SPR estimates of LBSPR were multiplied by 2.5 to attain B/B_{msy}. F/M estimates produced by the three models were used as proxy for the comparison with F/F_{msy} estimates provided by the independent models.

In the real world, sampling across cohorts is the standard, and both sampling schemes and recruitment are usually not continuous. Also, fish growth and mortality in the real world are not deterministic, and different assumptions about the co-variation of L_{inf}, K, and M lead to different distributions of length-at-age and consequently to different survival schemes under length-based gear selection. Simulated data that reflect the assumptions of the model will always result in better fits than data generated with deviating assumptions (e.g. Hordyk et al., 2016). In other words, while simulations are important to verify that a model can reproduce the "true" parameter values and to test for sensitivities and limits of applicability, real-world data are needed to evaluate the usefulness of a model in comparison with results obtained with other, data-rich models.

Supplementary Tables S1 and S2 show an evaluation of exploitation and stock status based on (i) the original LBB master equation, (ii) the LBB equation with pile-up correction, and (iii) the LBSPR method of Hordyk et al. (2016) proposed by Hordyk et al. (2019) as an alternative to LBB, with all compared with respective estimates provided by independent assessments. The results are summarized in Table 1. As can be seen, both the LBB with pile-up correction and the LBSPR method gave less satisfactory results than the original (uncorrected) LBB master equation. Biased performance of LBSPR was also reported by Huynh et al. (2018).

Froese et al. (2018, pp. 2011 and 2012) stress that "LBB estimates represent the average F/M over the past years, back to when the fish now in the largest length class became vulnerable to fishing" and F/M estimates are, therefore, "not recommended as reliable proxies for current fishing pressure." Also, in the independent stock assessments used in the comparison, F_{msy} is often larger than M, thus explaining, in part, the significant positive differences found in 56% of the cases when LBB estimates of F/M were compared with independent estimates of F/F_{msy} (Table 1 and Supplementary Table S2). The target result of LBB is stock status as expressed by current biomass relative to unexploited biomass (B/B_0) or relative to the biomass that can produce maximum sustainable yields (B/B_{msy}). These LBB estimates are similar to the independent stock status estimates in 86% of the cases (Table 1 and Supplementary Table S2). In contrast, for the corrected LBB, only 57% of the stock status estimates were similar, and for LBSPR, less than half (48%). Note that LBSPR gives estimates of spawning potential ratio (SPR), where values below 0.2 (≈ 0.5 B/B_{msy}) indicate depletion and values above 0.4 (≈ 1.0 B/B_{msy}) indicate good stock status. Note also that the 95% confidence limits provided by LBSPR are unrealistically narrow,

sometimes close to deterministic, which partly explains their very low matching score.

The 34 stocks used in the evaluation were temperate and subtropical species with annual peaks in recruitment and often seasonal rather than continuous sampling schemes (Supplementary Table S1). Results may have been different if tropical species with more continuous recruitment (Pauly and Navaluna, 1983) and sampling schemes had been analysed.

The new LBB version that is available from https://oceanrep.geomar.de/44832/, therefore, contains three options: (i) use the original LBB equation, (ii) correct for the pile-up effect, or (iii) let the Bayesian model determine the degree of correction based on the best fit to the available data.

Sensitivity of LBB results to assumed or estimated values of L_{inf}

Hordyk et al. (2019) correctly note that LBB results, similar to other length-based methods, are sensitive to assumptions about asymptotic length L_{inf}, and that unrealistically high values of L_{inf} lead to an overestimation of exploitation rate, and vice versa. In LBB, asymptotic length is not a required input, but is estimated by the Bayesian model. A default prior for L_{inf} is derived by a least-squares regression of the fully selected LF data aggregated across years. Alternatively, "[i]f a good estimate of L_{inf} is available from an independent study, this value can be introduced by the user, [. . .]" (Froese et al., 2018, p. 2005). Care must then be taken to perform this potentially subjective selection of L_{inf} as guided by pre-established, objective criteria, such as taking the median of existing studies for the area from FishBase (Froese and Pauly, 2018), ignoring studies previously marked by FishBase staff as questionable.

Hordyk et al. (2019) suggest that the maximum length observed in LF data provides "an upward-biased estimator" of L_{inf} and that, as a rule, L_{inf} should be smaller than L_{max}. As stated above, LBB does not require a fixed value of L_{inf} as input, but rather estimates L_{inf} from the available data, while considering a prior derived either from aggregated LF data or provided by the user. Comparing 199 estimates of L_{inf} derived from length-at-age data with observed L_{max} for the respective stocks for 155 species in 51 countries shows that L_{max} is actually a reasonable predictor of L_{inf} (Figure 2), accounting for 96% of the variability in the data, with slope and intercept not significantly different from a 1:1 line. In other words, these data, which comprise all stocks in FishBase 06/2018 (Froese and Pauly, 2018), where sex, country, locality, and length-type were identical for independent estimates of L_{inf} and L_{max}, refute the claim by Hordyk et al. (2019) that L_{max} is an upward-biased estimator of L_{inf}. While the prior for L_{inf} does influence the results of LBB, this is actually welcome, because reasonable prior information about L_{inf} is much easier to obtain than, for example, prior information on growth or mortality rates. However, to better reflect the distribution of L_{max} values around the 1:1 line in Figure 2, the new version of LBB uses the median L_{max} across the analyzed years rather than the overall maximum length as the starting value for the least-squares regression that estimates the prior for L_{inf} and Z/K.

On the variability of M/K

Hordyk et al. (2019) claim that Froese et al. (2018) misrepresent the analysis of potential M/K values in Hordyk et al. (2015).
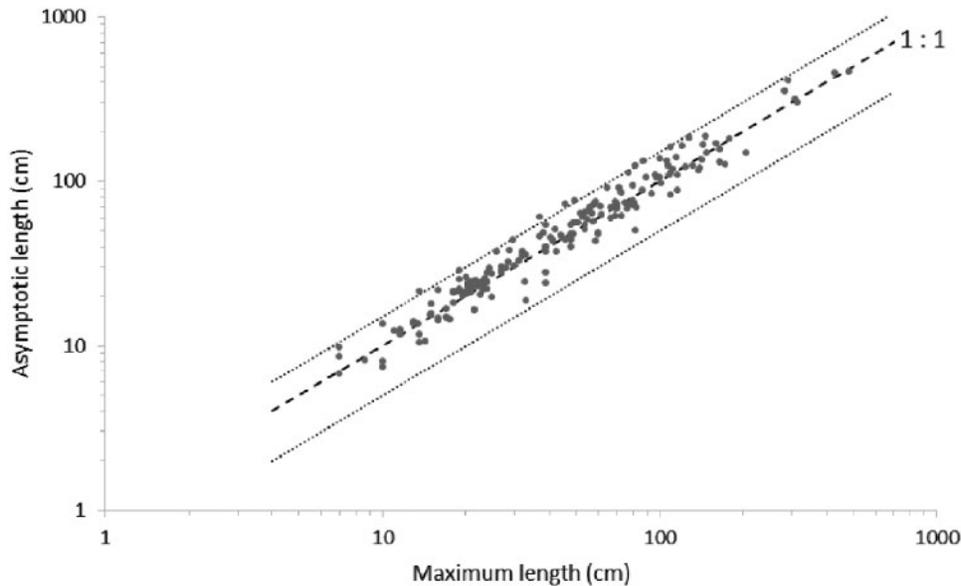
Figure 2. Scatterplot of asymptotic length (L_{inf}) as a function of maximum length (L_{max}), for 199 stocks of 155 species, where L_{inf} and L_{max} were reported independently for the same sex, length-type, country, and locality. A linear regression gives $\log_{10} L_{inf} = 0.0345 + 0.991 \times \log_{10} L_{max}$, $r^2 = 0.955$, with 95% confidence limits of the slope (0.961–1.02) including 1.0 and 95% confidence limits of the intercept (–0.0158 to 0.0848) including zero, i.e. the regression is not significantly different from the dashed 1:1 line. The dotted lines indicate 0.5:1 and 1.5:1, respectively, to put the log-scale in perspective.

While that study indeed explores a very wide range of hypothetical M/K values, it clearly states (p. 226) that "[f]or a species that conforms to the Beverton–Holt invariant $M/K \approx 1.5$, the maximum size (L_{max}; i.e. the length at [maximum age] t_{max}) is 0.95 L_{inf}." This confirms the rule of thumb proposed in Froese *et al.* (2018, p. 2009) that "[...] in LF distributions where only few individuals survive to approximate L_{inf}, it is reasonable to assume an M/K prior of 1.5."

If users of LBB have strong evidence for M/K values outside of the assumed default range of 1.2–1.8, they can easily provide their own M/K prior value. Froese *et al.* (2018, pp. 2007 and 2012) state explicitly that LBB shall only be used on "[s]uitable LF samples that show an asymmetric pattern" similar to the examples given in that paper and that LBB shall explicitly not be used on LF samples that "show an unusual normal distribution of high frequencies around reasonable estimates of L_{inf}" because such distribution violates the assumption of continuous growth. Thus, the upper and lower left frequency patterns shown in Figure 1 of Hordyk *et al.* (2019), which incidentally are not supported by any real-world data that the authors of this study are aware of, were already explicitly excluded from LBB analysis.

Consideration of recruitment in LBB

Hordyk *et al.* (2019) incorrectly suggest that the relative biomass estimates of LBB do not account for reduced recruitment at depleted stock sizes and that "[LBB] estimates of F_{msy} are equivalent to estimates of F_{max} from a conventional yield-per-recruit model [...]." Instead, LBB assumes a hockey-stick stock–recruitment relationship (Barrowman and Myers, 2000; Froese *et al.*, 2016), where relative yield per recruit and thus productivity declines linearly with biomass if predicted biomass is less than half of the

proxy used for B/B_{msy}. Also, Froese *et al.* (2018) warned (even in their abstract) that LBB results will be misleading "if LFs resulting from the interplay of growth and mortality are masked by strong recruitment pulses." Finally, LBB does not estimate F_{msy} or F_{max}, but F/M.

Summary

In summary, we thank Hordyk *et al.* (2019) for pointing out a typographical error in one of our equations, which has meanwhile been fixed in the online version of Froese *et al.* (2018) and addressed in a corrigendum for the printed version. We agree with Hordyk *et al.* (2019) that accounting for the pile-up effect in binned LF samples may be appropriate in, for example, tropical species with continuous reproduction, and we have provided for such correction as an option in the latest version of the LBB software. We note, however, that this correction as well as the LBSPR method of Hordyk *et al.* (2016) proposed by Hordyk *et al.* (2019) as an alternative to LBB leads to strong overestimation of exploitation and underestimation of stock status when compared with independent assessments of 34 real stocks from temperate and subtropical areas.

As for the points raised by Hordyk *et al.* (2019) with regard to default priors for L_{inf} and M/K, we maintain that these defaults are adequate for a wide range of exploited species. They can be easily replaced by users if better information is available. Warnings not to use LBB if LF samples do not show the typical asymmetric pattern were already provided in the original LBB paper and are repeated here.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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