ICES Journal of Marine Science

ICES Journal of Marine Science (2018), 75(6), 2004–2015. doi:10.1093/icesjms/fsy078

Original Article

A new approach for estimating stock status from length frequency data

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Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A. C., Dimarchopoulou, D., Scarcella, G., Probst, W. N., Dureuil, M., and Pauly, D. A new approach for estimating stock status from length frequency data. – ICES Journal of Marine Science, 75: 2004–2015.

Received 16 February 2018; revised 31 May 2018; accepted 1 June 2018; advance access publication 10 July 2018.

This study presents a new method (LBB) for the analysis of length frequency data from commercial catches. LBB works for species that grow throughout their lives, such as most commercially-important fish and invertebrates, and requires no input in addition to length frequency data. It estimates asymptotic length, length at first capture, relative natural mortality, and relative fishing mortality. Standard fisheries equations can then be used to approximate current exploited biomass relative to unexploited biomass. In addition, these parameters allow the estimation of length at first capture that would maximize catch and biomass for a given fishing effort, and estimation of a proxy for the relative biomass capable of producing maximum sustainable yields. Relative biomass estimates of LBB were not significantly different from the "true" values in simulated data and were similar to independent estimates from full stock assessments. LBB also presents a new indicator for assessing whether an observed size structure is indicative of a healthy stock. LBB results will obviously be misleading if the length frequency data do not represent the size composition of the exploited size range of the stock or if length frequencies resulting from the interplay of growth and mortality are masked by strong recruitment pulses.

Keywords: biomass depletion, data-poor stocks, healthy size structure, length frequency analysis, M/K, MSFD, proxies for MSY.

Introduction

National and regional fisheries regulations have changed in recent years to require science-based management of not only the most valuable, but of all exploited fish stocks (MSA, 2007; CFP, 2013). This has renewed interest in simple stock-reduction analysis (SRA, Kimura and Tagart, 1982) that uses available catch trends and life history data to provide estimates of exploitation and sustainable catch limits (e.g. Dick and MacCall, 2011; Costello *et al.*, 2012; Martell and Froese, 2013; Thorson *et al.*, 2013; Thorson and Cope, 2015; Froese *et al.*, 2016a; Free *et al.*, 2017; Zhou *et al.*, 2017a, b). Most of these methods require, as input, an independent estimate of biomass relative to unfished biomass in the final year and perform poorly if that estimate is wrong (Wetzel and Punt, 2011; Thorson and Cope, 2015). Using expert advice as prior for recent stock status is problematic, because it can be criticized as being subjective or a circular exercise, given the strong influence of this prior on the outcome of the analysis (see similar criticism of best-guess estimates for natural mortality and steepness in full stock assessments in Mangel *et al.*, 2013).

The size composition of exploited populations has long been used in fisheries management to estimate stock status and exploitation (Beverton and Holt, 1957; Munro, 1982; Pauly and Morgan, 1987; Gulland and Rosenberg, 1992), relative abundance of spawners and spawning potential ratio (SPR) (Goodyear, 1993; Hordyk *et al.*, 2015b), and more recently to determine whether size and age structure are comparable to that of a healthy stock (MSFD, 2008; Froese *et al.*, 2015). Size composition data have also been used directly in the assessment of data-poor fisheries (e.g. Dick and MacCall, 2011; Costello *et al.*, 2012; Martell and Froese, 2013; Thorson *et al.*, 2013; Thorson and Cope, 2015; Froese *et al.*, 2016c; Free *et al.*, 2017; Zhou *et al.*, 2017a, b), where they can provide a preliminary estimate or objective prior of current relative stock size. A recent overview of the pros and cons of length-based methods is given in Rudd and Thorson (2017).

This study presents a length-based Bayesian biomass estimation method (LBB) for the analysis of size composition, such as length frequency (LF) data from commercial catches, where all relevant parameters are estimated simultaneously with a Bayesian Monte Carlo Markov Chain (MCMC) approach. The purpose of this study is to explore the reliability of parameter estimates obtained by LBB and of derived fisheries reference points (B/B_0 or B/B_{msy}) when compared with simulated length frequencies, where the "true" parameter values are known, and with real-world length frequencies, where independent estimates of fisheries reference points were available from other assessment methods for comparison.

Material and methods

Methods

For the following conceptual development of LBB, growth in body length is assumed to follow the von Bertalanffy (1938) growth equation, in the form given by Beverton and Holt (1957), i.e.

$$L_t = L_{inf}[1 - e^{-K(t-t_0)}] \quad (1)$$

where L_t is the length at age t, L_{inf} is the asymptotic length, K is the rate by which L_{inf} is approached, and t_0 is the theoretical age at zero length. The growth parameters L_{inf} and K are used in several equations in this study.

To minimize the parameter requirements for LBB, the analytic framework is not based on absolute rates of growth and mortality, but rather on natural mortality rate (M) relative to somatic growth rate (M/K) and fishing mortality rate (F) relative to somatic growth rate (F/K), with the goal of estimating mean relative fishing mortality (F/M) and current biomass relative to unfished biomass (B/B_0). In other words, in organisms that grow throughout their lives, the increase in length can be used as a proxy for elapsed time, and by using ratios instead of absolute values the units of time and biomass cancel out.

LBB first estimates the asymptotic length L_{inf}, the length at first capture L_c where 50% of the individuals are retained by the gear, and mean M/K and F/K over the past years. If a good estimate of L_{inf} is available from an independent study, this value can be introduced by the user, thus decreasing uncertainty in LBB results. With these parameters, the current relative stock size in the form of biomass depletion B/B_0 can be calculated from standard fisheries equations.

The LBB analytical framework is shown in Figure 1 for a "synthetic" cohort (Thorson and Cope, 2015) under equilibrium conditions. Initial cohort numbers decline near linearly with length (upper curve in Figure 1) as a function of natural mortality and somatic growth with an M/K ratio of about 1.5, which is a typical value for adults of species that grow throughout their life, reaching maximum size at maximum age (Taylor, 1958; Jensen, 1996; Hordyk *et al.*, 2015b; Froese *et al.*, 2016c). The cohort is fished with a gear with length-dependent selectivity (S_L) described by an ogive function (Sparre and Venema, 1998). Total mortality increases with the onset of fishing; therefore, the number of exploited individuals (curve descending from L_x in Figure 1) declines more steeply with length than the upper curve representing no exploitation. Vulnerability to the gear increases from 0 to 1 over a certain length range until all individuals would be retained by the gear if they encounter it (S-shaped curve in Figure 1). The actual catch (lower curve in Figure 1) is determined by the amount of fishing and is a function of fishing mortality F and natural mortality M relative to somatic growth K and of gear selectivity S_L.

The decline in numbers over length as shown in Figure 1 for a cohort can also be interpreted as a snapshot of a population consisting of several year classes, with constant recruitment and life history traits (Quinn and Deriso, 1999, pp. 10 and 382; Thorson and Cope, 2015) over the time-span about equivalent to the oldest fish in the sample minus the age at first capture. Relative catch in numbers can then be observed as LF distribution in the commercial catch. The challenge is to estimate key parameters of selectivity, growth, and mortality (L_c, L_{inf}, M/K, F/K) from the catch curve in numbers. Once these parameters are known, current stock size B relative to unexploited stock size B_0 and thus current stock status B/B_0 can be estimated from a combination of standard fisheries equations (Beverton and Holt, 1957, 1966). Also, the length L_{c_opt} can be calculated, which determines the L_c value that would result in L_{opt} becoming the mean length in the catch, with the highest catch and biomass for the respective fishing mortality and a minimized impact on size structure (Froese *et al.*, 2016c). Finally, assuming $L_c = L_{c\_opt}$ and $F/M = 1$, a proxy for the relative biomass that

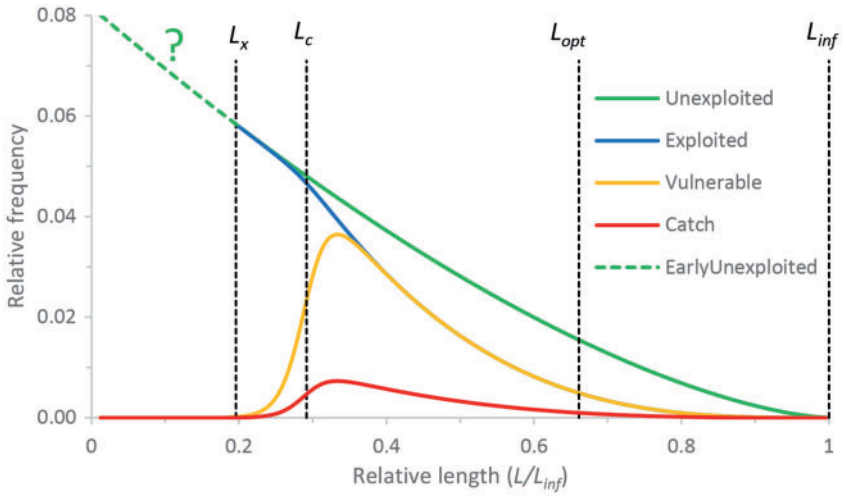

Figure 1. Conceptual framework for the analysis of length frequency data from the commercial fishery, here modelled with life history traits of Atlantic cod (*Gadus morhua*). The upper curve shows the decline in cohort numbers without fishing, with a question mark indicating that mortality and thus numbers of individuals not yet vulnerable to the gear are unknown and not relevant for the method. The curve descending from L_x shows the decline with fishing, the upper humped curve shows the fish vulnerable to the gear, and the lower humped curve is the catch in numbers resulting from a given fishing effort. The vertical dashed lines indicate the length (L_x) where fish become vulnerable to the gear, the length (L_c) where 50% of the individuals are retained by the gear, the length (L_{opt}) where the unexploited cohort would have maximum biomass, and the asymptotic length (L_{inf}).

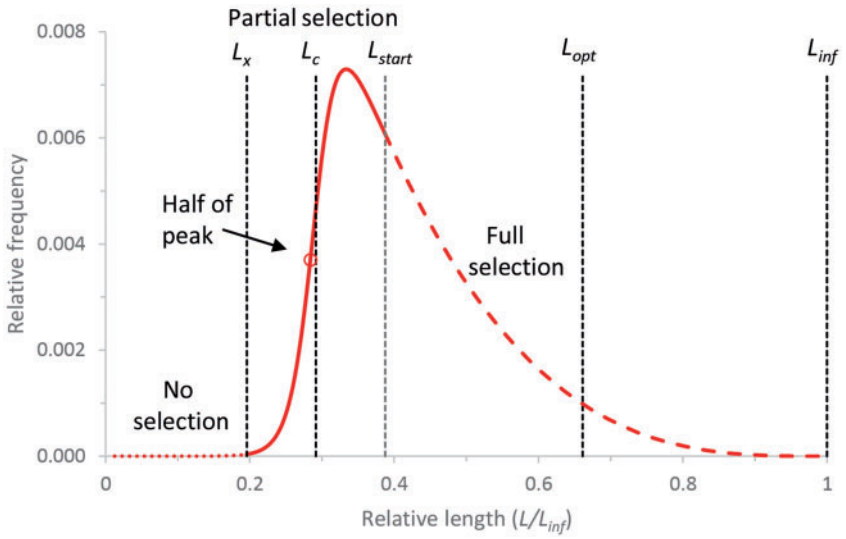

Figure 2. Schematic representation of the length frequency distribution in commercial catch, with indication of the sections that are subject to no gear selection (dotted curve), partial gear selection (solid curve), and full gear selection (dashed curve). Note the difference between the length at half of the peak of the catch curve and the slightly larger true L_c used in the model.

can produce maximum sustainable yield (MSY) can be calculated from the same standard fisheries equations.

If the gear operates with full selectivity (dashed section of red curve in Figure 2), the curvature of the catch in numbers-at-length curve is a function of total mortality rate ($Z = M + F$) relative to K; the curve is described by the equation (Quinn and Deriso, 1999, p. 369):

$$N_L = N_{L_{start}} \left(\frac{L_{inf} - L}{L_{inf} - L_{start}} \right)^{Z/K} \text{ for } L > L_{start} \text{ and } L < L_{inf} \qquad (2)$$

where N_L is the number of survivors to length L, N_{Lstart} is the number at length L_{start} with full selection, from which all individuals entering the gear are retained by the gear, and Z/K is the ratio of the total mortality rate Z to the somatic growth rate. Because

LF data do not hold any information about absolute abundance, there is no loss of information when both sides of Equation (2) are divided by their respective sums. This allows extracting the constant $N_{L\text{start}}$ out of the sum in the right-side denominator. It then cancels out against $N_{L\text{start}}$ in the numerator, and the remaining two parameters to be determined are Z/K and L_{inf}.

$$\frac{N_L}{\sum N_L} = \frac{\left(\frac{L_{\text{inf}}-L}{L_{\text{inf}}-L_{\text{start}}}\right)^{Z/K}}{\sum\left(\frac{L_{\text{inf}}-L}{L_{\text{inf}}-L_{\text{start}}}\right)^{Z/K}} \tag{3}$$

Note that in the unfished state, Z/K becomes M/K, L_{start} is zero, and $N_{L\text{start}}$ can be set to 1. Equation (2) then simplifies to

$$P_{L/L_{\text{inf}}} = \left(1-\frac{L}{L_{\text{inf}}}\right)^{M/K} \tag{4}$$

where $P_{L/\text{Linf}}$ is the probability to survive to length L/L_{inf}, which is solely a function of the M/K ratio. In other words, all populations with the same M/K ratio, whether small or large size, short or long-lived, herbivore or carnivore, occurring in warm or cold waters, will have the same probability of reaching a given fraction of their asymptotic length, independently of the absolute values of M, K, and L_{inf}. The same is true for the fully exploited part of the population, where the probability of reaching a length beyond the fully selected length L_{start} is a function of Z/K.

The catch in numbers that is subject to partial selection is, in addition to the parameters in Equation (3), a function of the selectivity of the gear (here assumed trawl-like) for the respective species, given by the ogive function in Equation (5).

$$S_{\text{L}} = \frac{1}{1+e^{-\alpha(L-L_c)}} \tag{5}$$

where S_{L} is the fraction of individuals that are retained by the gear at length L, L_{c} is as defined above, and α describes the steepness of the ogive (Sparre and Venema, 1998; Quinn and Deriso, 1999).

The length corresponding to a certain probability P of being retained by the gear can be obtained from Equation (6).

$$L_{\text{P}} = \frac{\alpha L_{\text{c}} - \log\left(\frac{1}{P}-1\right)}{\alpha} \tag{6}$$

where L_{P} is the length with probability P of being retained by the gear and L_{c} and α are as defined above. If α and L_{c} are known, Equation (6) allows calculation of the lengths where $L_x = 1\%$, $L_{\text{c}} = 50\%$, and $L_{\text{start}} = 95\%$ of the individuals are retained by the gear by setting P equal to 0.01, 0.5, or 0.95, respectively.

Because the number of survivors continues to decline as the selection ogive gradually approaches its maximum, the length at the peak catch in numbers underestimates the length of full selectivity, and consequently the length at half the peak underestimates L_{c} (see length at half of peak left of true L_{c}, as indicated in Figure 2). Therefore, the parameters of the true selection ogive cannot be estimated correctly by fitting Equation (5) to the ascending part of the catch-in-numbers curve. Rather, Equation (3) has to be replaced by a difference equation fitted to the whole catch-in-numbers curve to estimate L_{inf}, L_{c}, α, M/K, and F/K simultaneously:

$$N_{L_i} = N_{L_{i-1}}\left(\frac{L_{inf}-L_i}{L_{inf}-L_{i-1}}\right)^{\frac{M}{K}+\frac{F}{K}S_{L_i}} \text{ and } C_{L_i} = N_{L_i}\,S_{L_i}$$

where L_i is the number of individuals at length i, $L_{i\text{-}1}$ is the number at the previous length, C refers to the number of individuals vulnerable to the gear and proportionally represented in the catch, and all other parameters are as described above. By dividing both sides of the C_{Li} equation by their respective sums, the numbers are standardized and made compatible across years.

$$\frac{C_{L_i}}{\sum C_{L_i}} = \frac{N_{L_i}\,S_{L_i}}{\sum N_{L_i}\,S_{L_i}} \tag{8}$$

Fitting Equation (8) to LF data gives estimates of M/K and F/K, which can be combined to give $F/M = (F/K)/(M/K)$.

Simulated data

For the purpose of verification, simulated data were created with Equation (8) so that the parameter values underlying the simulated frequencies were known and could be compared with the results of a subsequent LBB analysis. The deterministic frequency calculated for every length class was randomized by taking its value as the mean of a lognormal distribution with a coefficient of variation of 0.1 and selecting randomly a value from that distribution. Parameter values were chosen to represent lightly to heavily fished, commercially-important species ranging from shrimp, sprat, and plaice to cod and swordfish, for a total of nine hypothetical stocks. One additional cod stock simulated higher F in specimens above 40-cm length and another additional cod stock simulated a recruitment pulse of 2-year-old fish where expected frequencies were doubled.

Equation (5) represents a selection ogive that is typical of trawls, purse-seines, and longlines (Sparre and Venema, 1998; Clarke *et al.*, 2005). As proof of concept that different types of selection functions can be accommodated by LBB, a Gaussian selection which may approximate the selection of a gillnet (Sparre and Venema, 1998) was tested for three additional simulated stocks. The spreadsheet used for creating the simulated data, the corresponding input file for the R-code, and the R-code used for adding the random noise and for the analysis are included in the Supplementary Material.

Empirical data

The data required for the analysis proposed in this study are length frequencies representative of commercial catches and collected, e.g. by on-board observers or by measuring and counting all individuals of the target species at a main landing site or in a fish market (Probst *et al.*, 2011; Pauly and Greenberg, 2013). Suitable LF samples with trawl-like selection should show an asymmetric pattern similar to Figure 2. Stocks or years which strongly deviated from the expected pattern were excluded from the analysis. For comparison with Figure 2, length frequencies for the first and last year of available data are shown for every included stock in the Supplementary Material, together with the sources for the LF data and for the independent assessments.

Length-based Bayesian estimation method

The LBB estimation was implemented within the Bayesian Gibbs sampler software JAGS (Plummer, 2003) and executed using the statistical language R (R Core Team, 2013) to fit observed proportions-at-length p_{Li} to their expected values $\hat{p}_{Li}$. Based on Equation (8), the model predicted length distribution $\hat{p}_{Li}$ is given by:

$$\hat{p}_{Li} = \frac{\hat{N}_{L_i}}{\sum \hat{N}_{L_i}} \tag{9}$$

where $\hat{N}_{L_i}$ is a function of the estimable population dynamic determents L_{inf}, M/K, and F/K [Equation (8)] and the selectivity parameters L_c and α [Equation (5)].

The observed and predicted length distributions were then fitted by assuming Dirichlet-multinomial distribution, which was proposed for fitting size and age composition in Bayesian stock assessment models because of its property of accounting for overdispersion (i.e. additional unexplained variance) compared with the standard multinomial (Mäntyniemi *et al.*, 2015; Thorson *et al.*, 2017a). Proportions-at-length assume Dirichlet-multinomial distribution with an effective sample size of $n_{\text{LF}} = 1000$, which was chosen based on desirable performance across various simulation-testing trial scenarios and on sample sizes of 800–3000 in LFs obtained from the EU Data Collection Framework.

Priors for L_{inf} and Z/K were derived by pooling available LF data across years and fitting equation 2 to the fully selected part of the catch-in-numbers curve with the nonlinear least squares estimator function nls() in R (Bates and DebRoy, 2016). The method requires start values and ranges for the parameters and these were obtained as described in Supplementary Table S2.

The following equations describe the framework of approximating the stock status from the estimated quantities L_{inf}, M/K, F/K, and L_c (Froese *et al.*, 2016c). First, with estimates of L_{inf} and M/K, the length L_{opt} where unexploited cohort biomass is maximum is obtained from Equation (10) (Holt, 1958):

$$L_{\text{opt}} = L_{\text{inf}}\left(\frac{3}{3+\frac{M}{K}}\right) \tag{10}$$

The length at first capture L_{c_opt} that maximizes catch and biomass for a given fishing pressure and leads to L_{opt} as mean length in the catch (Froese *et al.*, 2016c) can be obtained from:

$$L_{c\_opt} = \frac{L_{\text{inf}}\left(2+3\frac{F}{M}\right)}{\left(1+\frac{F}{M}\right)\left(3+\frac{M}{K}\right)} \tag{11}$$

L_{c_opt} is used below to calculate a proxy for the relative biomass that can produce MSY.

An index of yield-per-recruit (Beverton and Holt, 1966) can be expressed as a function of L_c/L_{inf}, F/K, M/K, and relative fishing mortality F/M:

$$\frac{Y'}{R} = \frac{F/M}{1+F/M}(1-L_c/L_{\text{inf}})^{M/K} \left(1-\frac{3(1-L_c/L_{\text{inf}})}{1+\frac{1}{M/K+F/K}}+\frac{3(1-L_c/L_{\text{inf}})^2}{1+\frac{2}{M/K+F/K}}-\frac{(1-L_c/L_{\text{inf}})^3}{1+\frac{3}{M/K+F/K}}\right) \tag{12}$$

An index of catch per unit of effort ($CPUE'/R$) is obtained by dividing Equation (12) by the fishing intensity F/M, assuming that fishing mortality F is directly proportional to fishing effort. Since $CPUE$ is proportional to biomass in the exploited phase of the stock, Equation (13) represents relative $CPUE'/R$ as well as an index of exploited biomass per recruit B'/R (Beverton and Holt, 1966):

$$\frac{CPUE'}{R} = \frac{\frac{Y'}{R}}{\frac{F}{M}} = \frac{1}{1+\frac{F}{M}}\left(1-\frac{L_c}{L_{\text{inf}}}\right)^{\frac{M}{K}} \left(1-\frac{3(1-L_c/L_{\text{inf}})}{1+\frac{1}{M/K+F/K}}+\frac{3(1-L_c/L_{\text{inf}})^2}{1+\frac{2}{M/K+F/K}}-\frac{(1-L_c/L_{\text{inf}})^3}{1+\frac{3}{M/K+F/K}}\right) \tag{13}$$

The relative biomass in the exploited phase of the population if no fishing takes place is given by:

$$\frac{B_0' > L_c}{R} = (1-L_c/L_{\text{inf}})^{\frac{M}{K}} \left(1-\frac{3(1-L_c/L_{\text{inf}})}{1+\frac{1}{M/K}}+\frac{3(1-L_c/L_{\text{inf}})^2}{1+\frac{2}{M/K}}-\frac{(1-L_c/L_{\text{inf}})^3}{1+\frac{3}{M/K}}\right) \tag{14}$$

where $B_0' > L_c$ denotes the exploitable fraction ($> L_c$) of the unfished biomass (B_0). An index of relative biomass depletion for the exploited part of the population B/B_0 is then obtained from (Beverton and Holt, 1966):

$$\frac{B}{B_0} = \frac{\frac{CPUE'}{R}}{\frac{B_0'>L_c}{R}} \tag{15}$$

A proxy for the relative biomass that can produce MSY (B_{msy}/B_0) was obtained by re-running Equations (12–15) with $F/M = 1$ and $L_c = L_{c\_opt}$.

Pauly and Soriano (1986) and Pauly and Greenberg (2013) point out that the assumption of knife-edge selection leads to overestimation of yield per recruit when the selection ogive overlaps with most of the life span of short-lived species. They, therefore, propose using instead the alternative approach of Beverton and Holt (1966) for yield assessment when F varies to obtain unbiased estimates of yield per recruit. This approach basically consists of calculating Y'/R_1 and Y'/R_2 for the lower L_1 and upper L_2 border of a length class with the mean fishing mortality F_1/K applicable for that size range, obtained by multiplying the F/K of full selection with the mean selectivity for that length class. Y'/R_2 is then adjusted for the decrease in number of fish due to F_1/K as they grow from L_1 to L_2. The "reduction factor" $r_{1,2}$ (Beverton and Holt, 1966) for this decrease is obtained from:

$$r_{1,2} = \frac{\left(1-\frac{L_2}{L_{\text{inf}}}\right)^{F_1/K}}{\left(1-\frac{L_1}{L_{\text{inf}}}\right)^{F_1/K}} \tag{16}$$

The relative yield per recruit contributed by the first length interval L_1 to L_2 is then obtained from:

$$Y'/R_{1,2} = Y'/R_1 - Y'/R_2 r_{1,2} \tag{17}$$

The relative yield contributed by subsequent length classes, here L_3 to L_4, is obtained from:

$$Y'/R_{3,4} = Y'/R_3(r_{1,2}\, r_{2,3}) - Y'/R_4(r_{1,2}\, r_{2,3}\, r_{3,4}) \tag{18}$$

where the parentheses contain the product of all previous reduction factors.

For the final length class from L_n to L_{inf}, relative yield is obtained from:

$$Y'/R_{n,inf} = Y^{'}/R_{n,inf}(r_{1,2}\, r_{2,3} \ldots . r_{n-1,n}) \quad (19)$$

Summing up the yield of all length classes leads to an estimate of relative yield per recruit that incorporates the effect of partial gear selection. The implementation in LBB of this procedure thus deals with the bias associated with the assumption of knife-edge selection in Equations (12–14).

Dividing yield per recruit in every length class by the respective F/M ratio (as an index of fishing effort) gives an index of cpue or abundance [same as in Equation (13)] for that length class. Summing up gives an index of cpue or abundance for the exploited length range.

Equation (14) is applied to the lower and upper bounds of each length class, and their difference is then the unexploited biomass contributed by this length class. Multiplying by selectivity and summing up gives an index of abundance in the exploited length range without fishing. Dividing exploited by unexploited abundance gives the biomass ratio B/B_0 in the exploited length range (Beverton and Holt, 1966).

Note that length classes with different F need not have the same width, i.e. subsequent length ranges with the same F can be treated as one class. This continuous estimation of relative yield and biomass per recruit can be applied for any trajectory of F as a function of length, such as selectivity of trawls or gillnets, or increasing trawl avoidance of fish as they get larger.

Uncertainty in the estimate of B/B_0 was assumed to be determined by the respective uncertainties in the estimates of F/M, M/K, F/K, and L_{inf}. The error propagation method for multiplication or division was applied, deriving the relative uncertainty of B/B_0 as the square root of the sum of the squared relative uncertainties in these four parameters.

Results

Simulation results

Fitting Equation (8) to simulated data for six hypothetical stocks with ogive selection and regular exploitation (F/M 1–1.5) gave parameter estimates that were close to the "true" values used in the simulations (Table 1). Of 36 comparisons of parameter estimates with "true" values, 25 (69%) included the "true" value within their credible intervals (~95% confidence limits) of the estimates. In the other cases, marked bold in Table 1, the central value estimated by LBB did diverge from the "true" value by 2.3–3.3% in three cases of L_{inf}, 0.8–1.6% in four cases of L_c, 6.7–7.1% in three cases of α, and 16.5% in one case of M/K. As for the predicted biomass ratio B/B_0 in the final year, the "true" value was within the confidence limits of the LBB estimate in all cases.

Simulations were also used for very preliminary exploration of LBB bias in cases of very light or heavy exploitation, variable F, or a strong recruitment pulse. This led to more cases where the "true" values were not included in the estimated confidence limits of L_{inf}, L_c, α, and F/K (see Table 1); however, "true" relative biomass was within the confidence limits of the B/B_0 estimate in all cases.

As a proof of concept, namely that LBB can also accommodate other selection functions, three stocks with simulated data for Gaussian selectivity were included. Eight (67%) of 12 parameter estimates included the "true" value within their approximated 95% confidence limits. The other cases are marked bold in Table 1. The "true" biomass ratio B/B_0 in the final year was within the predicted confidence limits in all cases.

Results based on empirical data

LBB predictions of relative biomass in the final year were evaluated against independent estimates of regular stock assessments (Supplementary Table S4). A total of 34 stocks were analysed, with a geographical range from Nova Scotia to South Africa, with a taxonomic range including cuttlefish, shrimps, anchovies, sprat, herring, flatfish, roundfish, skates, and sharks, and with a maximum length range of 7–123 cm. LBB estimates of relative fishing mortality F/M had overlapping confidence limits with and thus were similar to F/F_{msy} estimates in 16 (50%) of 32 stocks. LBB estimates of relative biomass had overlapping 95% confidence limits and thus were similar in 16 (76%) of 21 stocks with available data.

The ratios L_{mean}/L_{opt} and L_c/L_{c_opt} were below unity (<0.9) in 20 (61%) of the 33 stocks, suggesting truncated length structure and fishing of too small individuals. The ratio of the 95th percentile length to asymptotic length L_{95th}/L_{inf} was close to unity (>0.9) in 18 (55%) of 33 stocks, suggesting that at least some large fish were still present. The proportion of mature individuals in the catch was <50% in 14 (42%) of 33 stocks, suggesting that catch in these fisheries consists mostly of juveniles.

Discussion

LBB is a new Bayesian method for the analysis of fisheries-dependent LF data, which are widely available from port sampling and fisheries observers programmes. LBB is designed to require minimum data input to approximate depletion or current exploited biomass relative to unexploited biomass (B/B_0) as one of its key outputs. The assumptions, verification, caveats, and scope for application of LBB are discussed in the context of other existing methods in the following sections.

How realistic is the prior $M/K \approx 1.5$?

The M/K ratio of 1.5 proposed as a life history invariant by Jensen (1996) and Hordyk *et al.* (2015b) implies that species that reach their maximum age at about 95% of L_{inf} have an adult M/K ratio of 1.5; also, Taylor (1958) suggests that the age at 95% of L_{inf} is a realistic proxy for maximum age in many commercially-important fish. These insights can be combined into the following rule of thumb: in LF distributions where only few species survive to approximate L_{inf}, it is reasonable to assume an M/K prior around 1.5. LBB, therefore, uses a normally distributed prior for M/K with mean = 1.5 and SD = 0.15 as default, with resulting prior 95% confidence limits of 1.2–1.8.

Note, however, that some species may have different life history strategies with corresponding different M/K ratios outside this range (see Thorson *et al.*, 2017b; their Figure 3). For such species, the default setting of M/K can be replaced with other values.

To put the discussion about the most appropriate value of M/K into perspective, Froese *et al.* (2016c; their Figure 3) and Hordyk *et al.* (2015b; their Figure 5b) show that the main driver of relative yield or fished vs. unfished egg production, respectively, is fishing pressure F/M, and that M/K values of 0.3–3.0 have minor influence on the estimation of relative biomass, the main target output of LBB.

Table 1. Median estimated parameter values (est) with indication of the range that contains 95% of the Monte Carlo estimates in parentheses in comparison with "true" values used in the simulation of the data.

Simulated stock	L_{inf} true	L_{inf} est	L_c true	L_c est	alpha true	alpha est	*F/K* true	*F/K* est	*M/K* true	*M/K* est	B/B_0 true	B/B_0 est
Regular exploitation over a wide range of life history traits												
CodSim	120	122	35	**34.7**	60	**64.0**	1.54	1.60	1.54	1.58	0.26	0.25
		120–124	**0.9%**	**34.5–34.9**	**6.7%**	**61.2–66.4**		1.30–1.90		1.33–1.85		0.16–0.37
HerringSim	35	**35.8**	18	18.1	42	**39.0**	2.40	2.50	1.60	1.69	0.25	0.26
	2.3%	**35.4–36.3**		18.0–18.2	**7.1%**	**37.8–40.0**		2.09–2.70		1.43–2.00		0.16–0.35
PlaiceSim	48	47.7	26	**25.8**	48	47.9	1.33	1.10	1.33	**1.55**	0.36	0.42
		47.1–48.3	**0.8%**	**25.7–25.9**		46.3–49.2		0.82–1.35	**16.5%**	**1.34–1.79**		0.23–0.62
ShrimpSim	7.0	**6.83**	2.5	**2.54**	28	**26.1**	2.22	2.20	1.78	1.57	0.23	0.21
	2.4%	**6.74–6.94**	**1.6%**	**2.51–2.57**	**6.8%**	**25.1–26.9**		1.93–2.62		1.31–1.83		0.15–0.31
SpratSim	15	15.0	7.0	6.99	30	30.7	1.50	1.60	1.75	1.62	0.37	0.33
		14.8–15.2		6.94–7.06		29.5–31.6		1.31–1.97		1.37–1.82		0.20–0.49
SwordSim	299	**309**	90	**89.2**	60	61.7	1.82	1.90	1.36	1.59	0.20	0.21
	3.3%	**305–313**	**0.9%**	**88.6–89.8**		59.1–64.0		1.56–2.16		1.34–1.88		0.13–0.28
Different exploitation, variable *F*, and recruitment pulse												
CodLightSim	120	121	35	**34.7**	60	62.3	0.77	0.76	1.54	1.60	0.46	0.47
		120–123	**0.9%**	**34.4–34.9**		59.9–64.9		0.43–0.97		1.33–1.87		0.14–0.75
CodVeryLightSim	120	121	35	34.9	60	58.0	0.008	**0.097**	1.54	1.49	0.99	0.89
		120–122		34.7–35.1		56.0–60.7	**1112%**	**0.031–0.21**		1.37–1.59		0.03–2.4
CodHeavySim	120	**115**	35	**34.8**	60	**57.1**	6.15	**5.2**	1.54	1.55	0.05	0.06
	4.2%	**114–117**	**0.6%**	**34.6–34.9**	4.8%	**55.4–58.8**	**15.4%**	**4.86–5.50**		1.27–1.84		0.05–0.08
CodfFSim	120	120	35	**38.6**	60	**42.3**	1.54–3.08	2.7	1.54	1.49	0.14	0.14
		118–121	**10.3%**	**38.2–38.9**	**29.5%**	**40.6–43.5**		2.36–3.10		1.14–1.79		0.09–0.23
CodRecSim	120	122	35	**32.8**	60	**74.0**	1.54	1.70	1.54	1.59	0.27	0.24
		120–124	**6.3%**	**32.6–32.9**	**23.3%**	**71.5–76.6**		1.29–2.01		1.35–1.97		0.13–0.36
Gaussian selection				L_{mean}		*SD*						
SeabreamGillSim	15	14.9	8.0	7.88	2.0	1.95	2.50	**2.30**	1.25	1.26	0.37	0.41
		14.7–15.2					**8.0%**	**1.83–2.42**		0.99–1.52		0.25–0.56
CodGillSim	120	**97**	45	45.9	10	10.3	4.62	**3.10**	1.54	1.31	0.42	0.42
	19.2%	**95.5–98.8**					**32.9%**	**2.83–3.15**		1.04–1.60		0.29–0.58
CodGillVeryLightSim	120	120	45	45.6	10	10.2	0.008	**0.85**	1.54	1.51	0.99	0.84
		118–122					**10525%**	**0.05–1.59**		1.22–1.81		0.0–1.9

Parameter estimates that do not include the "true" value within their ∼95% confidence limits are marked bold and the percentage of the deviation is given under the true value. Except for L_{inf} and *M/K*, which are the median across years, all other estimates refer to the last year of simulations.

In summary, theoretical considerations as well as empirical observations suggest that $M/K \approx 1.5$ is a reasonable default prior for species where maximum length and maximum age coincide. The applicability of LBB to species that continue living after having approached L_{inf} is discussed below.

Verification

To verify the ability of LBB to correctly predict the parameters of Equations (5) and (8) from suitable LF data, the method was applied to simulated data where the "true" parameter values were known. Estimates were regarded as not significantly different if the "true" value fell inside their ∼95% confidence limits (Knezevic, 2008). Magnusson *et al.* (2013) recommend using the MCMC method for estimating approximate confidence intervals, as is done by LBB, but warn that MCMC similar to other methods generates intervals that are too narrow, thus underestimating true uncertainty. This problem is clearly visible in the very narrow confidence limits estimated by LBB for L_{inf}, L_c, and α (Table 1), which led to "true" values falling narrowly outside of the MCMC confidence limits in several cases and resulting in 69% instead of the expected 95% of the parameter estimates being not significantly different. Note that the mismatches deviated <5% from the "true" value in L_{inf} and L_c, <10% in the selection curve slope α, and <20% in one narrow mismatch of *M/K*. Given the usual uncertainties involved in estimation of these parameters with other methods, this feature of the LBB estimates appears acceptable. Note that all estimates of relative biomass B/B_0, which is the target output of LBB, included the true value within their confidence limits.

Simulations were also used for preliminary tests of extreme scenarios, such as very light (CodVeryLightSim, $F/M = 0.005$) to heavy (CodHeavySim, $F/M = 4$) exploitation, doubling of *F* in larger size classes (CodfFSim), or a recruitment pulse doubling the expected frequencies in 2-year-old specimens (CodRecSim). As for differences between heavy and light exploitation, the uncertainty in B/B_0 was considerably higher in lightly or very lightly exploited stocks, but the estimated central values were nearly identical with the true values (see CodLightSim and CodVeryLightSim in Table 1).

In the scenario with fishing pressure increasing in larger fish, the *F/K* and *F/M* ratios estimated by LBB fell about in the middle of the simulated range (see CodfFSim in Table 1). In the simulation with a strong recruitment pulse in 2-year-old fish, which overlapped with the range of gear selectivity, the estimated parameters of the selection ogive were off, but the other parameters and especially the biomass estimate were close to the "true" values.

In summary, if the assumptions of constant growth, mortality, and recruitment schedules during the period reflected by the LF

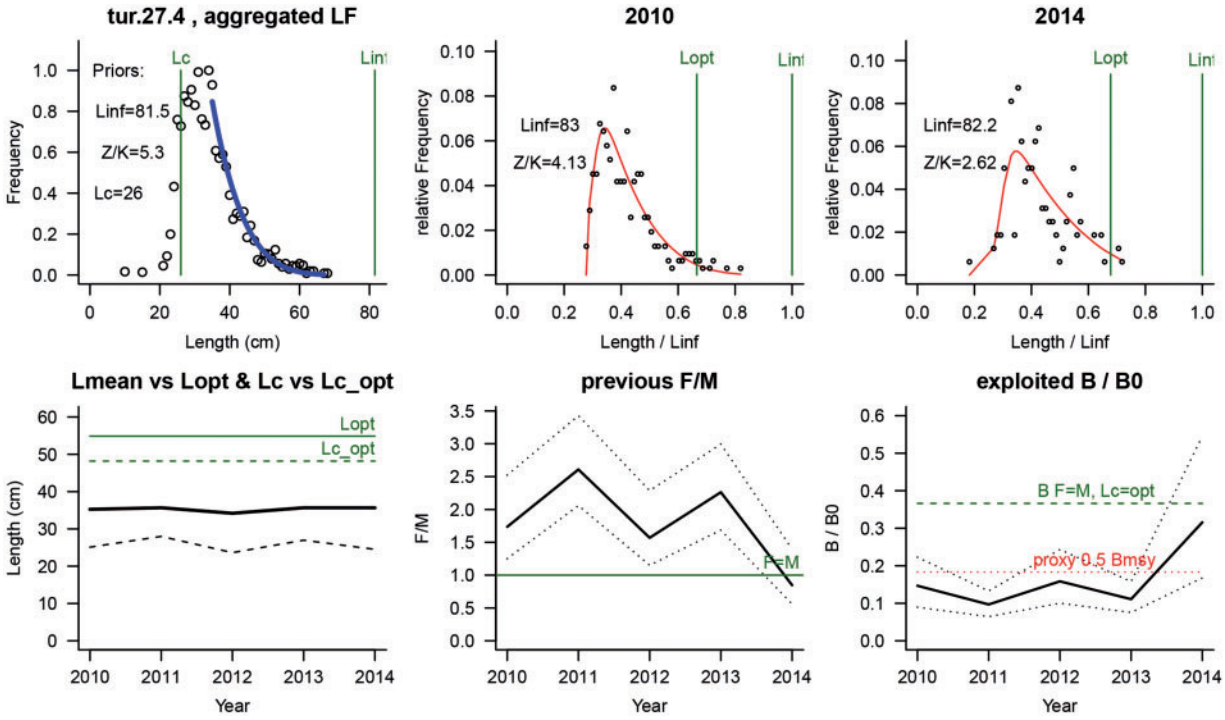

Figure 3. An example of graphical output produced by LBB, here for turbot (*S. maximus*), for the years 2010–2014. The upper left panel shows the accumulated LF data used to estimate priors L_c, L_{inf}, and Z/K. The upper middle and right panels show the LF data for the first and last year in the time-series. The curve shows the fit of Equation (8), which provides estimates of Z/K, M/K, F/K, L_c, and L_{inf}. From L_{inf} and M/K, L_{opt} is calculated and shown as reference. The lower left panel shows L_{mean} (bold curve) relative to L_{opt}, and L_c (lower dashed curve) relative to L_{c_opt}. The lower middle panel shows relative fishing pressure F/M (bold curve), with ∼95% confidence limits (dotted curves), with indication of the reference level where $F = M$ (horizontal line). The lower right panel shows relative biomass B/B_0 (bold curve) with ∼95% confidence limits (dotted curves), with indication of a proxy for B_{msy} (dashed line) and a proxy for B_{pa} or 0.5 B_{msy} (dotted line).

sample are met, LBB is capable of reliably estimating the biomass ratio B/B_0 that is compatible with the LF pattern. Because of the tendency of MCMC to underestimate uncertainty, confidence limits of other parameter estimates may not include the "true" value, but still remain close to the "true" values.

To make the case that LBB can also be used with other than trawl-like selection functions, three cases of Gaussian gillnet-like selection were included among the simulations. Sixty-seven percent of the parameter estimates and all estimates of B/B_0 included the "true" values in their ∼95% confidence limits, which may serve as a preliminary proof of concept.

Evaluation

LBB provides estimates of relative fishing mortality F/M, which can be understood as a proxy for F/F_{msy} estimates such as typically present in full stock assessments (ICES, 2017a). However, 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. This average F/M may be very different from F/F_{msy} in the final year. If fishing pressure has decreased in recent years, as is the case in several of the examined stocks, then average F/M will be higher than F/F_{msy} in the final year. Also, if F_{msy} is larger than M, as is the case in many ICES stocks [Froese *et al.*, 2016a; ICES, 2017b; see e.g. European plaice (*Pleuronectes platessa*), saithe (*Pollachius virens*), and common sole (*Solea solea*) in Supplementary Table S4], then F/M will be higher than F/F_{msy}. These differences may explain that the 50% of LBB F/M estimates with non-overlapping confidence limits were higher than the independent F/F_{msy} estimates (Supplementary Table S4).

However, average F/M across all fully exploited length classes and over the past years is a required input for yield-per-recruit equations. If recruitment and somatic growth have been reasonably stable, current biomass is a function of the cumulative fishing pressures that the stock has experienced over the exploited age range. Consequently, the LBB estimates of relative biomass agreed much better with the independent assessments, with LBB estimates having overlapping 95% confidence limits and thus being similar in 16 (76%) of 21 stocks with available data. Notably, with one exception in winter skate (*Leucoraja ocellata*) (where B/B_{msy} estimated by LBB was 1.0 (95% CL 0.6–1.6) whereas the independent estimate was 0.35), LBB estimates of depletion were typically more precautionary than the estimates from full assessments, never proposing that a stock was well above the MSY level when instead it was well below.

Note that most independent assessments did not provide estimates of B/B_0, but rather of B/B_{msy} or B/B_{pa}, where in the latter case $B/(2\ B_{pa})$ was used as a proxy for B/B_{msy} (same as in ICES, 2017c). In LBB, relative biomass predicted for $F = M$, $M/K = 1.5$ and $L_c = L_{c\_opt}$ is used as a proxy for B_{msy}/B_0, with typical values near 0.4 (see Supplementary Material). Several of the assessments used instead Schaefer models with $B_{msy}/B_0 = 0.5$. Also, LBB estimates B/B_0 for the exploited length range, whereas some of the independent assessments used total biomass or spawning-stock

biomass. For example, if L_c is significantly larger than mean length at first maturity, the depletion of biomass in the exploited length range may be much stronger than the depletion of spawning biomass or total biomass reported in assessments. These differences may explain some of the observed discrepancies.

In summary, *F/M* estimates of LBB tended to be above independent estimates of F/F_{msy} and are not recommended as reliable proxies for current fishing pressure. In contrast, LBB estimates of depletion were similar to independent estimates in about 75% of the comparisons and thus appear suitable for use as priors or as preliminary guidance in the management of data-poor stocks.

Applicability of LBB to populations that continue living after approaching L_{inf}

Tropical small reef fish typically grow rapidly towards their maximum size, which coincides with their maximum age. However, in some species, populations have been found whose adults continue to live for several decades after approaching L_{inf} (e.g. Choat and Axe, 1996; Choat *et al.*, 2003; Robertson *et al.*, 2005; Trip *et al.*, 2008). Close examination of these studies and the data they refer to (see the pertinent section in the Supplementary Material) suggest that extended survival without growth indeed occurs. In these populations, fast early growth is followed by extended longevity around maximum size when large individuals permanently relocate from warm shallow water to deep, colder water. But this life history strategy does not occur in all populations of the respective species, presumably because not all populations have access to suitable nearby deep, colder waters.

With regard to the applicability of LBB to such long-lived populations, this should be possible for the warm-water phase with typical growth and mortality patterns, but not for the cold-water phase with a wide span of ages clustering around L_{inf}, because without growth, length cannot be used as a proxy for age and, therefore, *Z/K* does not describe length-dependent mortality. True cases of high longevity without growth should be recognizable from the LF pattern, which should show an unusual normal distribution of high frequencies around reasonable estimates of L_{inf}. LBB analysis should not be performed on such populations.

Comparison of LBB with similar approaches

A similar method to LBB is the SPR approach, which basically uses the section of the length-frequency curve above the length L_{m50} where 50% of the individuals are mature, calculates the corresponding egg production by converting lengths into fecundity using a length–fecundity relationship, and then compares egg production with the one that would be present without fishing. Hordyk *et al.* (2015a, b; 2016) present a length-based implementation of SPR (LB-SPR) and demonstrate that, under the assumptions of knife-edge selectivity at length L_c and knife-edge maturation at L_m, SPR is determined by the ratios of *M/K*, *F/M*, L_m/L_{inf}, and L_c/L_{inf}. Required input to the model is *M/K*, L_{m50}, L_{m95}, L_{inf}, and CV_{Linf}. Similar as in LBB, fishing pressure *F/M* will be the average over the age range in the analyzed length-frequency sample (Hordyk *et al.*, 2015a, b). In contrast to LB-SPR, LBB does not need maturation schedules or length–fecundity parameters to be known. It accounts for the problem of knife-edge assumption and estimates *M/K*, L_{inf}, and CV_{Linf} from the available data.

In another method similar to LBB, the CC-SRA method of Thorson and Cope (2015) uses age composition data to construct catch curves and estimates mean fishing mortality for fully selected age classes as input into a modified SRA model such that prior *F/M* replaces the need for a prior on depletion. The main difference between LBB and CC-SRA is the need for age-structured data, which are often lacking in data-poor stocks.

The length-based integrated mixed effects (LIMEs) method (Rudd and Thorson 2017) was developed as a length-based extension to CC-SRA. LIME uses LF data in place of the more resource-intensive samples of age and thus is closer to the data needs of LBB, but still needs life history data such as approximations of natural mortality, growth, and maturation.

Caveats of LBB

Similar to other length-based methods, LBB will perform poorly if LF are not representative of the length composition of the exploited phase of the stock. This may be caused by gears that have a different selectivity or catchability than the main commercial gears (e.g. survey gears), or by length samples taken in areas where a non-representative subset of the exploited stock is present, such as in nursery or spawning areas. Also the availability of representative LF data can be an issue. Combining different LF samples poses an extra challenge, because the frequencies have to be weighted according to their contribution to the total catch and should stem from the same season for species with seasonal growth. For example, if landings and discards are sampled separately, incorrect weighting before adding up frequencies may lead to distributions with two distinct but unrealistic peaks. This may be one reason for the strong deviations between the LBB estimates and the independent assessment results for European plaice (*P. platessa*) in Supplementary Table S4.

LBB assumes fluctuations of mortality, growth, and recruitment around mean values over the range of ages in the LF sample and should not be used if this assumption is violated. For example, high interannual recruitment variability may lead to multiple peaks and poor analytical results (Quinn and Deriso, 1999; Hordyk *et al.*, 2015a; Thorson and Cope, 2015), because without additional information, length-based methods cannot determine whether the observed difference in the frequency of many small and few large individuals is caused by an unusually strong cohort of recruits or by strong removal of large fish (Rudd and Thorson, 2017).

In general, it is dangerous to rely too heavily on results from a fancy method that are ultimately based on limited observations combined with bold assumptions. But the same and similar problems also apply to data-rich assessment methods; as Thorson and Cope (2015, p. 40) point out, "data-poor methods such as presented here should not be held to a higher standard than their richer cousins".

Use of LBB in management of data-poor stocks

LBB may be directly useful for management of data-poor stocks with unreliable or missing catch data. Representative LF samples from the main gear used in the fishery or from the main landing site may suffice to get a preliminary impression of stock size relative to levels that can produce MSY. LBB also gives a comparison of current length at first capture L_c relative to the one (L_{c_opt}) that would maximize catch and biomass for the given fishing pressure (Froese *et al.*, 2016c). Based on this information, management can propose changes in lengths at first capture and in

fishing effort until relative biomass predicted by LF data exceeds the approximate MSY level.

Note, however, that the assumption of $F_{msy} = M$ used in the estimation of the proxy for B_{msy}/B_0 is not precautionary, because M is the upper bound rather than a surrogate of F_{msy} (Quinn and Deriso, 1999, p. 461). Consequently, the B/B_{msy} estimate of LBB should not be used as a target, but rather as a lower bound of desirable stock sizes.

Figure 3 shows an example of graphical LBB output for turbot (*Scophthalmus maximus*) in the North Sea, based on observer data from 2010 to 2014 from the German fleet (see full analysis in the Supplementary Material). Despite considerable noise in the data, the LBB assessment agrees with the full assessment (ICES, 2017c) with regard to high fishing pressure during that period and biomass fluctuating between proxies for half and full MSY level, with some recovery in recent years (see Supplementary Table S4). Throughout the time-series, L_c was well below L_{c_opt}, resulting in annual length structures with peaks well below L_{opt}.

Use of LBB in evaluating the size structure of stocks

The Marine Strategy Framework Directive (MSFD) of the EU asks for the age and size distributions of commercially exploited species to be indicative of a healthy population (MSFD, 2008, Descriptor D3.3). The corresponding implementation instructions (COM, 2017) prescribe two indicators for Descriptor D3.3: the proportion of mature individuals and the 95th percentile of length composition. The LBB estimates of these official D3.3 indicators are shown in Supplementary Table S4.

COM (2017) encourages further scientific and technical development of suitable indicators for Descriptor D3.3. In this regard, LBB estimates the mean length in the exploited population (L_{mean}) as well as the length in the unfished population (L_{opt}) where cohort biomass is maximum and, if fecundity is proportional to body weight, related reproductive potential is also maximum. The age at L_{opt} is then the mean age of parents and thus, by definition, equivalent to generation time (Pianka, 2000). An exploited population with a mean length that is close to L_{opt} has a size and age distribution similar to an unexploited healthy population. In other words, the ratio L_{mean}/L_{opt} is a theoretically sound and easy-to-estimate indicator for a healthy size and age composition of exploited stocks.

A size and age composition close to L_{opt} can be achieved by starting fishing at the length L_{c_opt}, which has the additional advantage of maximizing catch (Beverton and Holt, 1957) and biomass (Froese *et al.*, 2016c) for the applied fishing pressure (F/M).

Of 33 analysed real stocks, 13 (39%) had mean lengths close to L_{opt} with $L_{mean}/L_{opt} > 0.9$ and thus a size and age structure indicative of a healthy stock (Supplementary Table S4). Interestingly, all of these stocks also had lengths at first capture close to the optimum selectivity length with $L_c/L_{c\_opt} > 0.9$. A linear regression of L_{mean}/L_{opt} as a function of L_c/L_{c_opt} accounts for 97% of the variability in the data ($y = 0.243 + 0.74x$, $n = 32$, $r^2 = 0.97$), thus providing a first empirical confirmation of the L_{c_opt} concept, which was derived in Froese *et al.* (2016c) from basic population dynamics equations in Beverton and Holt (1957).

A very preliminary regression analysis of the size structure indicators in Table S4 shows a weak correlation for L_{95}/L_{inf} over L_{mean}/L_{opt} ($r^2 = 0.26$), and a very weak correlation of Mat (%) over L_{mean}/L_{opt} ($r^2 = 0.10$), suggesting that these indicators may reflect different properties of the analysed size distributions. In summary, the ratio L_{mean}/L_{opt} may be a suitable new indicator for MSFD Descriptor D3.3.

Conclusions

LBB is a simple and fast method for estimating relative stock size. In contrast to similar methods, it requires no information on age, maturity, recruitment, growth, effort, or mortality, just representative LF data from the commercial fishery. LBB derives priors for L_{inf} and selectivity from aggregated annual LF samples and assumes a prior M/K ratio around 1.5 (95% CL 1.2–1.8). It then performs Bayesian analyses of the annual LF data to simultaneously estimate L_{inf}, L_c, M/K, and F/K. With these inputs, a combination of standard fisheries equations (Beverton and Holt, 1957, 1966) provides an estimate of relative biomass (B/B_0 or B/B_{msy}) for the exploited size range.

LBB estimates appear especially useful as objective relative biomass priors for use in other assessment models. But the LBB estimates of length at first capture and relative biomass in comparison with their respective reference points can also be used directly in management. We thus recommend LBB as a new addition to the assessment tool box, especially for data-poor stocks.

The mean length in exploited populations relative to the length at maximum biomass in the unfished population (L_{mean}/L_{opt}) is a theoretically sound and easy-to-estimate indicator for a size and age composition indicative of a healthy stock. It should be considered as potential new indicator in the evaluation of size and age structure. Additional supplementary material is available at http://oceanrep.geomar.de/43182/.

Supplementary data

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

Acknowledgements

We thank the Department of Fisheries and Ocean (DFO) Canada, particularly Heather Bowlby and Heath Stone, for providing length composition data on elasmobranchs, and South Africa's Department of Agriculture, Forestry, and Fisheries (DAFF) for providing LF data from their handline fishery. RF acknowledges support from the German Federal Ministry for the Environment, Nature Conservation, Building and Nuclear Safety on behalf of the German Federal Agency for Nature Conservation (FKZ 3512-82-0300). MD acknowledges support from the Sobey Fund for Oceans, the Transatlantic Ocean System Science and Technology (TOSST) School, and the Nova Scotia Research and Innovation Graduate Scholarship. D.P.'s research is part of the *Sea Around Us*, supported by the Oak, Marisla, and other philanthropic foundations.

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Handling editor: Emory Anderson