A Simple Biomass-Based Length-Cohort Analysis for Estimating Biomass and Fishing Mortality

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Abstract.—A biomass-based length-cohort analysis (LCA) was examined for its performance in estimating total stock biomass and fishing mortality (F) for a population in equilibrium. We compared two LCA methods—(1) a numbers-based LCA that relies on catch numbers at length as input data and (2) a new biomass-based LCA that relies on catch biomass at length—by applying both to simulated data that generally followed characteristics of Pacific chub mackerel *Scomber japonicus* in Korean waters. We investigated the effects of using two length aggregation methods, two data simulation methods, and three expressions of weight growth (i.e., exponential growth over the length increment of the analysis, arithmetic mean growth, and geometric mean growth). Biomass and F were estimated from the new model and compared with those estimated from the numbers-based LCA model. A sensitivity analysis was performed to understand which aspect of the model parameters controlled the results. Sensitivity to estimates of terminal F was also examined. Results of the analysis showed that the allometric power coefficient β was the most important model parameter and that sensitivity of biomass-based LCA to terminal F was similar to that of numbers-based LCA. Monte Carlo simulation was used to evaluate the equilibrium assumption and to calculate confidence intervals for biomass estimates. We applied the biomass-based LCA model to data for northern rock sole *Lepidopsetta polyxystra* in the eastern Bering Sea. A comparison of biomass-based LCA population biomass estimates with northern rock sole research survey biomass estimates showed good agreement between the two types of estimates. The biomass-based LCA described in this study is unique in that it incorporates growth explicitly into the estimation procedure, which can be useful under data-deficient situations when simple length composition data and estimates of total catch biomass from just one sampling year are the only available data.

Cohort analysis and its statistical variants are the most widely used methods for estimating the size of fish stocks. These rely on catch in numbers at age (Pope 1972) or catch in biomass at age (Zhang and Sullivan 1988). These data require the use of an age–length key to estimate age. However, sometimes age determination for the stock of interest is difficult or impossible to carry out, and it is often a costly procedure.

Estimates from the Food and Agriculture Organization of the United Nations (2005) indicate that 20% of worldwide exploited fish populations either have no assessment information or the available information is not sufficiently reliable to allow an estimate of the state of exploitation. In data-deficient situations, traditional age-structured stock assessment models cannot be applied. Simple methods that rely on minimal data requirements are needed. An alternative is to use methods that rely on length composition and catch data (Jones 1979, 1984; Schnute and Fournier 1980; Pauly and David 1980; Pauly 1987; Lai and Gallucci 1988; Fournier et al. 1990; Methot 2000; Bull et al. 2005). Some methods take advantage of both data sources (Kirkwood 1983). One of the fundamental assumptions of length-cohort methods that use length composition data is that the stock is at equilibrium, with no variation in exploitation over time and no variation in year-class strength. Under equilibrium conditions, length composition data will be stable over time. We refer to this as length-cohort analysis (LCA). All of these methods produce population estimates in terms of numbers. The catch biomass has to be converted into numeric abundance, and LCA abundance estimates have to be converted back into biomass, which is often more meaningful for management purposes (i.e., total allowable catch [TAC], or catch quotas). For example, fisheries managers set TACs by weight in most marine fisheries. Fishermen themselves are usually interested in the total weight of the catch for economic reasons and often record, report, and process catch in units of

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weight. We propose a new LCA method that directly incorporates growth and produces population abundance in units of biomass. The new LCA model that accounts for growth is more accurate than one that does not, and it involves fewer computational steps, as was shown by Zhang and Sullivan (1988).

The dynamics of a fish population are determined by a balance between (1) increases due to growth and recruitment and (2) losses due to fishing mortality (F) and natural mortality (M). Another argument for examining the dynamics of fish stocks in terms of biomass is that individual growth is an important component of the fish population and should be included in analyses for a more complete picture of what is occurring in the fishery (Ricker 1975; Cushing 1981). Growth in weight is one of the best known among the important factors influencing changes in stock size (Beverton and Holt 1957). Growth will drive changes in population biomass even when mortality is zero. The influence of growth on stock changes and the relative accuracy with which growth can be measured suggest that in situations where data are collected in units of biomass and where decisions are made in terms of biomass, the analyses should be based on a biomass-oriented approach that incorporates growth. A key aim of our approach is to provide a rough first approximation of biomass in a data-limited situation. If we have sufficient data, we do not need to apply this approach and can rely on more standard approaches that take maximum advantage of data collected over multiple years.

The objectives of this paper were to (1) propose a new biomass-based LCA that directly incorporates growth and (2) investigate the performance of the biomass-based LCA and the more traditional numbers-based LCA on simulated data using four contrasting factors and applying the biomass-based LCA to actual data for northern rock sole *Lepidopsetta polyxystra* in the eastern Bering Sea. The factors included (1) use of 1- and 5-cm length interval aggregation of length composition data, (2) data simulated by the numbers-based and biomass-based LCAs, (3) three methods of calculating mean weight, and (4) the performance of the numbers-based and biomass-based LCAs in recovering simulated data. A sensitivity analysis was performed to evaluate the influence of model parameters on population biomass estimates and the sensitivity of those estimates to assumed values of terminal F (F_T). Finally, Monte Carlo simulation was used to evaluate the validity of the equilibrium assumption and to provide confidence intervals for biomass estimates. We used the Jones (1981) model to implement the numbers-based LCA; hereafter, we refer to the biomass-based LCA as the Zhang–Megrey model.

Methods

Biomass-based length-cohort analysis model.—We begin the development of the biomass-based LCA based on the time-dependent equations of Zhang and Sullivan (1988):

$$B_t = B_{t+1} \exp(M - G_t) + C_t \exp\left(\frac{M - G_t}{2}\right), \quad (1)$$

where B_t is the biomass at time t, C_t is the catch biomass at time t, M is the instantaneous natural mortality rate (per year), and G_t is the instantaneous rate of growth at time t. This equation is valid if the time increment (Δt) is 1 year. When this assumption is not valid, then a more general expression can be given by

$$B_t = B_{t+\Delta t} \exp(M \times \Delta t - G_t)$$
$$+ C_t \exp\left(\frac{M \times \Delta t - G_t}{2}\right), \quad (2)$$

where C_t and G_t are the catch biomass and the instantaneous growth rate over the time it takes to grow from length-class l_i to length-class $l_{i+\Delta l}$ (Δt^{-1}). Solving for t using the von Bertalanffy (1938) growth equation gives

$$t = t_0 - \frac{1}{K} \log_e \left(\frac{L_\infty - l_t}{L_\infty}\right), \quad (3)$$

where t_0 is the theoretical age at a zero length, K is the von Bertalanffy growth coefficient, and L_∞ is the asymptotic length. Let Δt_{l_i} represent the time needed to grow from length-class l_i to length-class $l_{i+\Delta l}$; therefore,

$$\Delta t_{l_i} = t_{l_{i+\Delta l}} - t_{l_i} = \frac{1}{K} \log_e \left(\frac{L_\infty - l_i}{L_\infty - l_{i+\Delta l}}\right). \quad (4)$$

Substituting equation (4) into equation (2) gives

$$B_{l_i} = B_{l_{i+\Delta l}} \exp\left[\frac{M}{K} \log_e \left(\frac{L_\infty - l_i}{L_\infty - l_{i+\Delta l}}\right) - G_{l_i}\right]$$
$$+ C_{l_i} \exp\left[\frac{M}{2K} \log_e \left(\frac{L_\infty - l_i}{L_\infty - l_{i+\Delta l}}\right) - \frac{G_{l_i}}{2}\right]. \quad (5)$$

Finally, we use

$$W_{l_i} = \alpha \times l_i^\beta \quad (6)$$

to convert length to weight, and we use

$$G_{l_i} = \log_e \left(\frac{W_{l_{i+\Delta l}}}{W_{l_i}}\right) \quad (7)$$

to calculate G per length-class.

We note that equation (6) is the allometric length–

TABLE 1.—Biological parameters used to simulate data generally conforming to the biology of the Korean common mackerel (Choi 2003).

Parameter	Description
Allometric length–weight parameters	
Model: $W_{l_i} = \alpha l_i^{\beta}$	
$\alpha = 0.0018$	Condition factor
$\beta = 3.567$	Allometric growth parameter
W_{l_i}	Weight (g) in length-class l_i
l_i	Fork length (cm) in length class l_i
	Minimum length = 11 cm (1-cm interval), 10 cm (5-cm interval)
	Maximum length = 46 cm (1-cm interval), 40 cm (5-cm interval)
von Bertalanffy growth parameters	
$L_{\infty} = 51.67$ cm	Asymptotic length
$t_0 = -0.428$ year	Theoretical age at zero length
$K = 0.299$ per year	Growth coefficient
Mortalities	
$M = 0.424$ per year	Natural mortality
$F = 0.424$ per year (from survey)	Fishing mortality
$F_T = 0.5\ M$	Terminal F assuming a lightly exploited fishery
$F_T = M$	Terminal F assuming a moderately exploited fishery
$F_T = 2\ M$	Terminal F assuming a heavily exploited fishery

weight relationship where α is the condition factor (Quinn and Deriso 1999) and β is the allometric growth parameter (Hilborn and Walters 1992). In our application, it relates length-class l (cm) to weight W (g) in a length-class and serves as a basis for estimating growth.

Simulated data sets.—Two simulated data sets were used to compare the different LCA methods. Since the procedural steps were different in the numbers-based versus the biomass-based simulated data sets, we describe them in Appendix A.

Biomass-based length-cohort analysis model application and analysis.—The biomass-based LCA model was applied to a simulated data set using parameter values representing growth, M, F_T, and initial population size chosen to generally reflect the dynamics of Pacific chub mackerel *Scomber japonicus* in Korean waters after Choi (2003). These data are given in Table 1.

Input data were as follows: (1) 1 year of length composition data for the catch, (2) weight of catch for each length-class, (3) estimate of M, (4) von Bertalanffy growth parameters (K, t_0, and L_{∞}), (5) allometric parameters relating length to weight (i.e., α and β), and (6) estimates of F_T for the longest length-class. Output was either (1) population biomass by length-class or (2) estimates of F by length-class.

Six steps are required to implement the biomass-based LCA. Step 1 involves calculation of weight from length for each length-class using the allometric weight equation (i.e., equation 6). Step 2 is the calculation of G_{l_i} for each length-class from weights using equation (7). In step 3, Δt is calculated for each length-class by

using equation (4). In step 4, population biomass in the longest length-class is estimated based on the biomass-based catch equation and the estimate of F_T:

$$B_{l_i} = C_{l_i} \times \frac{(M + F_T) \times \Delta t_{l_i} - G_{l_i}}{F_T \times \Delta t_{l_i}} \qquad (8)$$

when the longest class is pooled or

$$B_{l_i} = C_{l_i}$$
$$\times \frac{(M + F_T) \times \Delta t_{l_i} - G_{l_i}}{F \times \Delta t_{l_i} \times (1 - \exp\{-[(M + F_T) \times \Delta t_{l_i} - G_{l_i}]\})} \qquad (9)$$

when the longest class is truncated. Here, F_T is estimated from a direct survey or is assumed to be equal to $0.5M$ for a lightly exploited stock, M for a moderately exploited stock, or $2M$ for a heavily exploited stock.

Step 5 involves progressing from the longest length-class to the smallest length-class to calculate B_{l_i} using equation (5). In step 6, fishing mortality, $F_{l_i} \times \Delta t_{l_i}$, is calculated as

$$F_{l_i} \times \Delta t_{l_i} = \log_e \left(\frac{B_{l_i}}{B_{l_{i+\Delta l}}}\right) - M \times \Delta t_{l_i} + G_{l_i}. \qquad (10)$$

Performance metric.—Total population biomass was compared between the simulated data and the results estimated from each of the two LCA methods. Correspondence between the two sources of population biomass was compared for each LCA model by calculating the Nash–Sutcliffe model efficiency (ME) metric (Nash and Sutcliffe 1970) as a performance metric to measure differences between simulated and estimated population biomass observations. The ME

metric, which is commonly used to assess model performance, provides a measure of the ratio of model error to variability in the data. It ranges between 0 (no correspondence) and 1 (perfect correspondence) and is calculated as

$$ME = 1 - \frac{\sum\limits_{n=1}^{N} (D_n - M_n)^2}{\sum\limits_{n=1}^{N} (D_n - \bar{D})^2}, \quad (11)$$

where D_n is the data for the nth comparison, M_n is the corresponding model estimate, $\bar{D}$ indicates the mean of the data set for the chosen variable, and N is the total number of model data pairs. The squaring of the error rewards a good fit and punishes a poor fit. The ME metric was chosen over Pearson's product-moment correlation coefficient because the correlation coefficient can only detect linear dependence between two variables. The ME metric makes no a priori assumptions regarding the functional association between model estimates and observed data. Performance levels based on ME are categorized as excellent (ME > 0.65), very good (0.50–0.65), good (0.2–0.5), and poor (<0.2; from Maréchal 2004).

Examination of the equilibrium assumption.—We used Monte Carlo simulation to evaluate the sensitivity of the biomass-based LCA results to the equilibrium assumption by turning the normally deterministic process equation parameters into random variables. The Monte Carlo analysis was carried out using the eastern Bering Sea northern rock sole data. In contrast to simply adding random sampling error (normal or lognormal) to the LCA equations (e.g., see Chen et al. 2007), we evaluated the equilibrium assumption by allowing the process equation parameters to vary. In this way, the shape of the process equations changed with each Monte Carlo sample, representing parameter values that were not constant as required by the equilibrium assumption.

In the Monte Carlo simulation, we let the parameters β, K, M, and F_T be random variables drawn from a normal distribution. The choice of using a normal distribution was arbitrary. The weight–length allometric growth parameter β and the von Bertalanffy K parameter influence growth. The M and F_T parameters influence mortality. The impact of assumed stability in production and mortality estimates (i.e., equilibrium) can be quantitatively evaluated using Monte Carlo simulation. Letting β be a random variable allowed an evaluation of the impacts of variability in weight at length on variability in the biomass and F estimates.

The means for the random variables were set to the

TABLE 2.—Biological parameters of eastern Bering Sea northern rock sole after data reported by Wilderbuer and Nichol (2007).

Parameter	Description
Allometric length–weight parameters	
Model: $W_{l_i} = \alpha l_i^{\beta}$	
$\alpha = 0.00761$	Condition factor
$\beta = 3.11976$	Allometric growth parameter
W_{l_i}	Weight (g) in length-class l_i
l_i	Fork length (cm) in length-class l_i
von Bertalanffy growth parameters	
$L_\infty = 34.2$ cm	Asymptotic length
$t_0 = -0.79$ year	Theoretical age at zero length
$K = 0.26$ per year	Growth coefficient
Mortalities	
$M = 0.152$ per year	Natural mortality
2003 $F_T = 0.031$	Terminal fishing mortality
2004 $F_T = 0.044$	
2005 $F_T = 0.034$	
2006 $F_T = 0.037$	
2007 $F_T = 0.021$	

nominal values given in Table 2, and SD was determined by assuming a coefficient of variation (CV) of 10%. Since CV(x) equals σ_x/μ_x (where σ_x is the SD and μ_x is the mean), then the σ_x used to generate normal random variables (rv) is given by $0.1\mu_x$ (i.e., rv[x] $\sim N[\mu_x, 0.1\mu_x]$). A Monte Carlo solution ($n = 1,000$) to the model was calculated by simultaneously letting all four Monte Carlo parameters be random variables. The average values of the 1,000 Monte Carlo samples of the population biomass were compared with the deterministic model solution when all parameter values were set to their nominal values. Estimates of the 95% confidence intervals for each estimate of biomass and F at length were also calculated by this method.

Sensitivity analysis.—Understanding which aspect of a model controls the model's behavior is a fundamental part of model development, evaluation, and validation. Sensitivity analysis is the method most commonly used to examine model behavior. We performed a simple sensitivity analysis where the parameters α, β, L_∞, K, M, and F were each changed by 10% one at a time and the sensitivity of total population biomass was examined; sensitivity was measured as percent change from the base case in which the parameters assumed their nominal values given in Table 1. This approach is similar to the classical measure of sensitivity proposed by Tomovic (1963) and described by Saltelli et al. (2000) and Cacuci et al. (2005).

We also explored the sensitivity of the model to the assumed estimates of F_T, similar to analyses performed in classical virtual population analysis (Lassen and

Medley 2001). This analysis was performed using a 1-cm length interval and the exponential growth model.

Application to the eastern Bering Sea stock of northern rock sole.—We obtained catch biomass, biological parameters, and estimates of full-recruitment F to use as starting F_T values for eastern Bering Sea northern rock sole from Wilderbuer and Nichol (2007). Research survey length composition (T. K. Wilderbuer, National Marine Fisheries Service, personal communication) data for the years 2003–2007 were used to calculate catch biomass by length category. Survey vessels are chartered fishing vessels, so the collected data should be comparable to size composition data describing the catch of the commercial fishery. The biomass-based LCA model was applied independently to each year of the 5-year northern rock sole time series. Confidence intervals for each annual abundance estimate were obtained using the Monte Carlo simulation procedure described previously. Population biomass estimates from the deterministic and stochastic biomass-based LCA model were then compared with the survey population biomass estimates to evaluate model performance for a stock where the actual population biomass was relatively well known.

Results

Model Application and Analysis

A comparison of results from applying the numbers-based Jones LCA method and the biomass-based Zhang–Megrey LCA method to the two length aggregation methods (1 versus 5 cm), two simulated data sets (numbers- versus biomass-based), and three weight growth assumptions (W1 = mean for the exponential growth; W2 = arithmetic mean growth; W3 = geometric mean growth) is presented in Table 3. The biomass-based Zhang–Megrey LCA outperformed the numbers-based Jones LCA in every comparison (i.e., higher ME values) except for the numbers-based simulated data set using the 5-cm length aggregation. The Zhang–Megrey model fit the biomass-based simulated data almost perfectly in all comparisons.

A sample comparison between simulated and estimated quantities in terms of numbers and biomass by fork length is presented in Figure 1. This was the general pattern between simulated and estimated quantities in our study. We note that in all cases, the Jones model underestimated the true simulated population biomass values (Figure 1A, C) and the Zhang–Megrey model also underestimated the true simulated population biomass values (Figure 1B). However, the Zhang–Megrey model fit perfectly when applied to the biomass-based simulated data (Figure 1D). The Zhang–Megrey model demonstrated less bias and was more consistently accurate as calculated from the ME metric

except for the numbers-based simulated data using the 5-cm length aggregation (Table 3).

In every case, the estimated numbers from the LCA methods were higher than the simulated numbers (Figure 1), with a larger bias being demonstrated as the methods progressed from larger to smaller length categories. The bias was greater for the biomass-based simulated data (Figure 1C, D). Except for the Zhang–Megrey method applied to the biomass-based simulated data (Figure 1D), the population biomass estimates were lower than the simulated biomass (Figure 1A–C).

Table 3 shows that the MEs for the three growth models in two length intervals were not much different for both the Jones and the Zhang–Megrey methods, which indicates that the LCA models are not so sensitive to the exponential growth assumption.

The results of the aggregation contrast (Table 3) show that ME values for the 1-cm length aggregation results were always higher compared with the 5-cm length aggregation results, regardless of analysis method (Jones versus Zhang–Megrey), source of simulated data (numbers- versus biomass-based), and growth model assumption (W1, W2, or W3; Table 3). This is in agreement with the conclusions of Lai and Gallucci (1988) and Lassen and Medley (2001).

Values of ME for results calculated from biomass-based simulated data were always higher compared with results from numbers-based simulated data, regardless of length aggregation method (1 versus 5 cm), analysis method (Jones versus Zhang–Megrey), or growth model assumption (W1, W2, or W3; Table 3).

There was no clear trend in the influence of the growth model assumptions (W1, W2, and W3) when compared across analysis methods (Jones versus Zhang–Megrey), simulated data set (numbers- versus biomass-based), and length aggregation methods (1 versus 5 cm; Table 3).

The Zhang–Megrey model did not show major differences in performance between growth model assumptions (W1, W2, and W3) when simulated data were based on biomass. This was true for both length aggregation methods (1 versus 5 cm), although the ME for the 1-cm aggregation method was higher for every growth model assumption (Table 3).

Sensitivity Analysis

The sensitivity analysis for all model parameters (Table 4) indicated that the parameters most sensitive to estimated population biomass were β of the allometric growth equation (see equation 6) and then L_∞ and K. The models showed a slightly higher sensitivity to L_∞ compared with K.

There was no or little difference in the sensitivity of the parameters between length aggregation methods (1

TABLE 3.—Comparison of the Nash–Sutcliffe model efficiency (ME) metric between simulated and estimated population biomass (1,000 metric tons) contrasted between length aggregation methods (1 versus 5 cm fork length), length-cohort analysis methods (Jones versus Zhang–Megrey), methods of simulating data (numbers-versus biomass-based), and assumed growth models (exponential growth [W1], arithmetic mean [W2], or geometric mean [W3]).

Length aggregation	Analysis method	Simulated data	Assumed growth model	ME
1-cm interval	Jones	Numbers-based	W1	0.891
			W2	0.889
			W3	0.892
		Biomass-based	W1	0.961
			W2	0.960
			W3	0.961
	Zhang–Megrey	Numbers-based	W1	0.974
			W2	0.973
			W3	0.974
		Biomass-based	W1	1.000
			W2	1.000
			W3	1.000
5-cm interval	Jones	Numbers-based	W1	0.687
			W2	0.560
			W3	0.742
		Biomass-based	W1	0.865
			W2	0.895
			W3	0.848
	Zhang–Megrey	Numbers-based	W1	0.458
			W2	0.367
			W3	0.499
		Biomass-based	W1	1.000
			W2	1.000
			W3	1.000

versus 5 cm), regardless of analysis method (Jones versus Zhang–Megrey), method of simulating data (numbers- versus biomass-based), or growth model assumption (W1, W2, or W3). Estimated population biomass showed a corresponding negative or positive response to a 10% decrease or increase in the L_∞ parameter. The same was true for β and K, with population biomass showing a corresponding positive or negative response to a 10% change in the β parameter. Estimated population biomass showed a negative response to a 10% increase in the M and F parameters and a positive response to a 10% decrease in those parameters (Table 4).

Within a length aggregation method (1 or 5 cm), sensitivity of the population biomass estimate differed in relation to the source of simulated data (numbers-versus biomass-based; Table 4). The LCA methods were more sensitive to the β parameter in the numbers-based simulated data compared with the biomass-based simulated data (Figure 2).

The growth model assumptions (W1, W2, and W3) did not influence the sensitivity of the population biomass estimate when the variable length aggregation method (1 versus 5 cm), source of simulated data (numbers versus biomass), and analysis method (Jones versus Zhang–Megrey) were held constant (Table 4).

Estimated population biomass showed a consistent negative or positive response to a 10% decrease or increase in the β and L_∞ parameters regardless of the analysis model (Jones versus Zhang–Megrey), source of simulated data (numbers- versus biomass-based), and growth model assumption (W1, W2, or W3). However, biomass was more sensitive to β than to L_∞, indicating a larger response to changes in β than to changes in L_∞ (Table 4).

The sensitivity of the biomass-based LCA model to different starting values of F_T (Figure 2) showed sensitivity patterns similar to those observed in age-based cohort analysis (Pope 1972). Estimates of F converged very quickly. Compared with the case where F equals M, the largest errors (~85%) were at the longest lengths; however, the estimates converged to within 8% of each other after only seven length intervals. This represents about 22% of the fork length range (11–42 cm).

Application to Eastern Bering Sea Northern Rock Sole

In each year, the biomass-based LCA model produced trends of population biomass and F by length-class. Confidence intervals for each length category are shown as error bounds around the mean estimate. Results from the 2007 data (Figure 3) show a typical example. Biomass increased gradually until the length-class reached 29 cm, and then biomass declined. On the other hand, F remained at a low level, showing only small variations until reaching the 27-cm length-
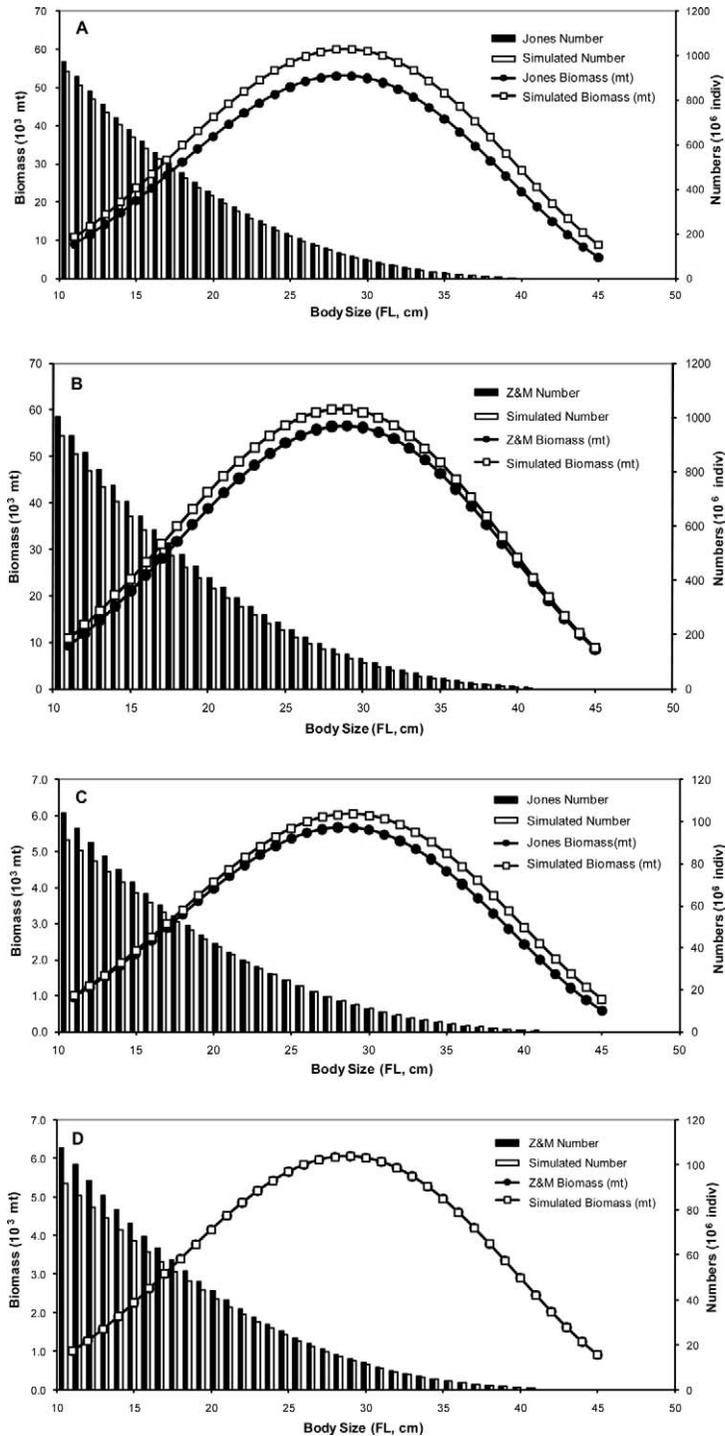
FIGURE 1.—Results (biomass, $\times 10^3$ metric tons [mt]; number, $\times 10^6$ individuals) from length-cohort analyses using **(A)** the Jones (1981) method with numbers-based simulated data; **(B)** the Zhang–Megrey (Z&M) method with numbers-based simulated data; **(C)** the Jones method with biomass-based simulated data; and **(D)** the Z&M method with biomass-based simulated data. The 1-cm fork length (FL) aggregation and the exponential growth assumption (Appendix A) were used.

TABLE 4.—Sensitivity analysis results comparing length-cohort analysis methods (Jones [1981] versus Zhang–Megrey), methods of simulating data (numbers- versus biomass-based), and growth model assumption (exponential growth [W1], arithmetic mean [W2], or geometric mean [W3]). Data are presented for the 1- and 5-cm fork length aggregation methods. Table entries represent the percent change in the estimate of total population biomass for each of the parameters (α and β from the allometric length–weight equation; $L_\infty =$ asymptotic length; $K =$ von Bertalanffy growth coefficient; $M =$ natural mortality; $F_T =$ terminal fishing mortality) relative to estimates calculated by using nominal values given in Table 1 (as a result of increasing or decreasing a parameter value by 10%).

Analysis method	Simulated data	Assumed growth model	Change	α	β	L_∞	K	M	F_T
			1-cm length aggregation						
Jones	Numbers-based	W1	+10	10.00	225.89	14.74	14.05	−7.77	−6.85
			−10	−10.00	−68.96	−24.55	−14.60	8.71	7.37
		W2	+10	10.00	226.89	14.74	14.05	−7.77	−6.85
			−10	−10.00	−68.95	−24.54	−14.60	8.70	7.36
		W3	+10	10.00	225.89	14.75	14.05	−7.77	−6.85
			−10	−10.00	−68.96	−24.55	14.60	8.71	7.37
	Biomass-based	W1	+10	0.00	36.34	14.81	14.07	−7.78	−6.85
			−10	0.00	−25.80	−24.68	−14.61	8.72	7.37
		W2	+10	0.00	36.32	14.82	14.07	−7.78	−6.86
			−10	0.00	−25.79	−24.68	−14.62	8.72	7.37
		W3	+10	0.00	36.35	14.81	14.06	−7.78	−6.85
			−10	0.00	−25.81	−24.67	−14.61	8.72	7.37
Zhang–Megrey	Numbers-based	W1	+10	10.00	227.47	37.78	17.55	−8.12	−8.14
			−10	−10.00	−69.10	−31.76	−16.87	9.16	9.17
		W2	+10	10.00	227.51	37.76	17.54	−8.12	−8.13
			−10	−10.00	−69.12	−31.75	−16.86	9.15	9.16
		W3	+10	10.00	227.44	37.79	17.55	−8.12	−8.14
			−10	−10.00	−69.10	−31.77	−16.87	9.16	9.17
	Biomass-based	W1	+10	0.00	37.00	37.86	17.56	−8.13	−8.14
			−10	0.00	−26.15	−31.85	−16.87	9.16	9.17
		W2	+10	0.00	37.00	37.85	17.56	−8.13	−8.14
			−10	0.00	−26.15	−31.85	−16.88	9.17	9.17
		W3	+10	0.00	37.00	37.85	17.56	−8.13	−8.14
			−10	0.00	−26.15	−31.86	−16.87	9.17	9.54
			5-cm length aggregation						
Jones	Numbers-based	W1	+10	10.00	231.89	19.11	15.28	−8.29	−9.19
			−10	−10.00	−69.51	−27.43	−15.67	9.39	10.62
		W2	+10	10.00	231.89	19.10	15.28	−8.30	−9.19
			−10	−10.00	−69.50	−27.43	−15.67	9.39	10.62
		W3	+10	10.00	231.89	19.11	15.28	−8.30	−9.19
			−10	−10.00	−69.50	−27.43	−15.67	9.39	10.62
	Biomass-based	W1	+10	0.00	34.18	20.56	15.62	−8.45	−9.29
			−10	0.00	−24.58	−29.29	−15.95	9.57	10.75
		W2	+10	0.00	33.75	20.72	15.72	−8.48	−9.37
			−10	0.00	−24.35	−29.49	−16.04	9.61	10.84
		W3	+10	0.00	34.40	20.48	15.57	−8.43	−9.25
			−10	0.00	−24.69	−29.18	−15.89	9.55	10.70
Zhang–Megrey	Numbers-based	W1	+10	10.00	231.02	30.19	15.84	−7.39	−7.52
			−10	−10.00	−69.41	−27.05	−15.54	8.25	8.38
		W2	+10	10.00	232.12	29.93	15.73	−7.36	−7.44
			−10	−10.00	−69.51	−26.82	−15.43	8.21	8.29
		W3	+10	10.00	230.45	30.32	15.91	−7.40	−7.56
			−10	−10.00	−69.36	−27.16	−15.60	8.26	8.43
	Biomass-based	W1	+10	0.00	33.84	31.62	16.16	−7.55	−7.62
			−10	0.00	−24.37	−28.57	−15.80	8.43	8.51
		W2	+10	0.00	33.84	31.62	16.15	−7.55	−7.62
			−10	0.00	−24.37	−28.57	−15.79	8.43	8.51
		W3	+10	0.00	33.84	31.62	16.16	−7.54	−7.62
			−10	0.00	−24.36	−28.57	−15.69	8.43	8.51

class; thereafter, F increased rapidly and exhibited greater variation. The reason for such a steep increase is that the dimension of F is multiplied by Δt, where Δt is greater for larger lengths. A comparison of population biomass estimates from the Zhang–Megrey LCA model with the survey biomass estimates (Figure 4) showed good agreement between the two estimates. In every year, the biomass-based LCA model and survey biomass estimates were equivalent, and the 95% confidence interval of the LCA model biomass
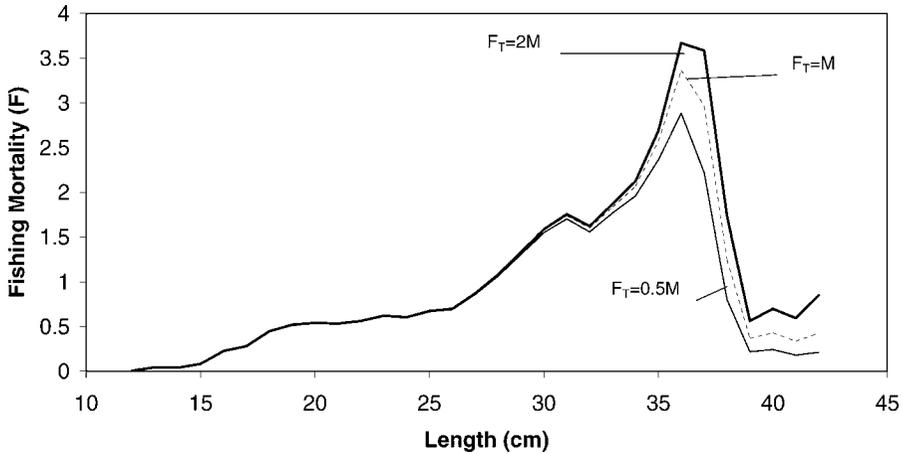
FIGURE 2.—Sensitivity of fishing mortality (F) estimates to different values of terminal fishing mortality (F_T). In this example, the analysis was performed using a natural mortality rate (M) of 0.424, a 1-cm fork length interval, and the exponential growth model (Appendix A).

estimate overlapped the 95% confidence interval of the survey biomass estimate. Also, in every year, the Monte Carlo biomass estimate was slightly higher than the deterministic estimate, although the Monte Carlo 95% confidence interval included the deterministic estimate. These results show that the Monte Carlo LCA biomass estimate was not different from the deterministic estimate. Also, the Monte Carlo LCA biomass estimate was not different from the survey estimate over the 5 years of data available for comparison.

Discussion

The model we present is based on the premise that a biomass-based analysis that incorporates growth can account for changes in population biomass resulting from changes in individual weight in addition to changes in number and thereby gives more accurate estimates of population biomass. The biomass-based LCA also facilitates the direct incorporation of data into the analysis in terms of biomass, bypassing the process of converting from biomass to numbers and then converting the numbers back into biomass in order to make management decisions based on biomass. Finally, by including growth, this biomass-based LCA incorporates three of the controlling forces that influence exploited fish stocks—namely growth, M, and F.

Worldwide, 584 fish stock groups or species groups
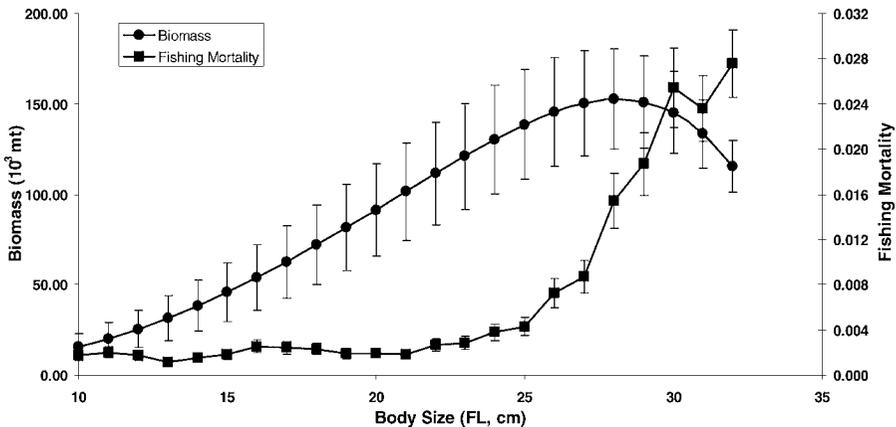
FIGURE 3.—Trends in biomass ($\times 10^3$ metric tons [mt]) and fishing mortality ($F_{l_i} \times \Delta t_{l_i}$) from application of the biomass-based length-cohort analysis method to the 2007 catch biomass and length composition data for eastern Bering Sea northern rock sole. Monte Carlo simulation was used to estimate the variability of the biomass and fishing mortality estimates (95% confidence interval) in each fork length (FL) class.
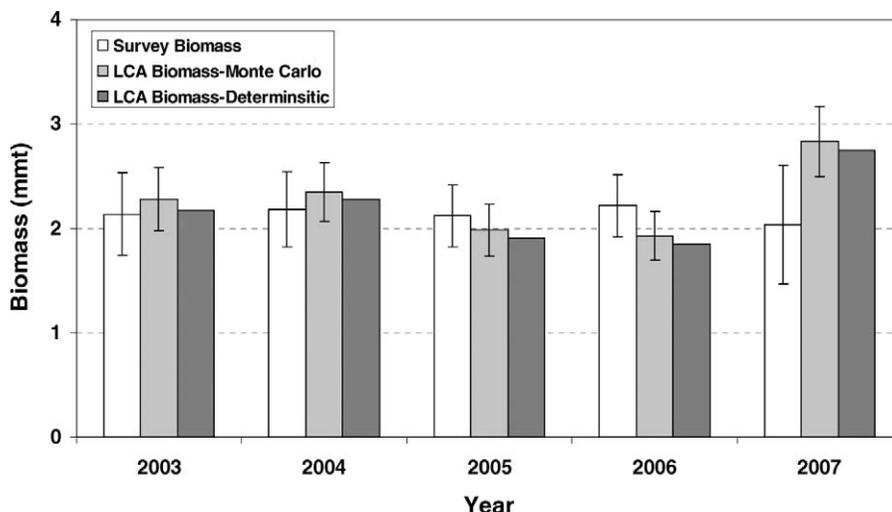
FIGURE 4.—Population biomass estimates (millions of metric tons [mmt]) from application of the deterministic and Monte Carlo biomass-based length-cohort analysis (LCA) methods to the eastern Bering Sea northern rock sole compared with actual biomass estimates from research surveys conducted during 5 years. Vertical bars for survey biomass and Monte Carlo LCA biomass estimates represent 95% confidence intervals. The LCA biomass variability was estimated using Monte Carlo simulation.

are identified as having only minimal catch trends available for monitoring resource status. Stock assessment information is available for 76% (or 441) of these groups, which produced about 80% of the total marine catches in 2002 (FAO 2005). The remaining 143 groups are not monitored or investigated with sufficient detail so as to provide a reliable assessment of their state of exploitation. Thus, the remaining 20% of the worldwide marine catches either have no assessment information or are described by information that is not sufficiently reliable to allow their state of exploitation to be estimated. A similar situation exists in the USA, where only 56% of the 230 most important fishery stocks have adequate population assessments (Murawski et al. 2008). An even smaller percentage of important stocks are assessed in developing countries, making this problem even more pervasive on the global scale compared with the United States (Johannes 1998). Furthermore, information on the biomass of species not targeted by commercial fisheries is critical and essential for conducting contemporary ecosystem-based fisheries management (EBFM; Zhang et al. 2009). Even though these species are not assessed, they are critical to a full appreciation of contemporary EBFM as they communicate aspects of important ecological interactions and issues of biodiversity. We often encounter difficulties in conducting stock assessments for some animals that lack aging structure data or for species targeted by small-scale fisheries. In these circumstances, using LCA would be a reasonable tool

to estimate biomass and fishing intensity based on length data because length data are easily obtainable in most circumstances.

Zhang and Sullivan (1988) identified several advantages to using a biomass-based analysis, especially when catch is recorded in units of biomass and when management decisions are made in terms of biomass. For example, population biomass changes result from changes in individual weight in addition to changes in numbers. Explicitly accounting for growth provides better estimates of population biomass over time. As another advantage, a biomass-based analysis gives more accurate estimates of biomass. This is true not only because weight change is incorporated more realistically but also because the form of the equation results in a mathematically more accurate approximation under the same assumptions. The approximation for the biomass-based model has a smaller error than that from the corresponding numbers-based model (Zhang and Sullivan 1988). Also, von Bertalanffy growth parameters are easily available from sources such as FishBase (Froese and Pauly 1998), and length–weight parameters can be estimated with minimal data requirements. Finally, the biomass-based analysis is simpler to perform because fewer steps are required. The biomass-based model avoids errors associated with converting biomass into numbers and numbers back into biomass. Such errors can be particularly important when the average weight of the fish in the catch is a relatively rough estimate (Rivard 1983). Also, the

variance of the mean length or mean weight usually increases as a cohort becomes older. Therefore, considerable error can be introduced in population abundance estimates simply by converting catches in weight into numbers of fish caught and in converting population numbers into population biomass. The biomass LCA performs better even when there is bias in the estimated numbers (Figure 1D). Even though the bias increases as the method progresses towards smaller length-groups, the higher numbers of smaller animals do not contribute substantially to the overall population biomass since the smaller animals weigh less than larger animals. Under the equilibrium assumption, the LCA model does not explicitly account for variability in either recruitment or mortality rates. Recruitment in the biomass-based LCA model is implicit. The Monte Carlo results indicate that LCA model estimates are robust to a violation of the equilibrium assumption.

The numbers-based method fails to account for changes in biomass that occur due to growth taking place over the fishing season. When growth is ignored, observed changes in biomass are implicitly assumed to arise solely from changes in population number. Changes in biomass due to growth that occur over the fishing season compensate, to a degree, for losses due to mortality. Higher biomass estimates arising from a numbers-based LCA will be interpreted to result from higher survivorship. Consequently, in the case where the data are collected in terms of biomass and converted into numbers in order to perform calculations, the estimates of biomass will be biased upwards when back-calculated from the catch. This will be particularly true for fast-growing species with elevated values of G. This result is clearly shown in the formula for the initial biomass estimate reexpressed from equation (9). Hence, the estimated B_{l_i} may be viewed as a decreasing function of G_{l_i}. When the growth rate is positive, estimated B_{l_i} should be lower than that calculated when growth is ignored (i.e., when $G = 0$).

The model sensitivity analysis was consistent with expectations. Since the approach is based on length, we anticipated that length parameters would be most influential. The parameter β was the most important since it affects results in a highly nonlinear manner (Table 4). It is fortunate that this parameter is easily estimated from routinely collected length and weight data—often with very high precision when the length composition is estimated on a fine level of resolution. The benefit of carrying out the sensitivity analysis is that we have quantified the influence of these parameters on the estimate of total population biomass

In data-deficient situations, there typically is no clear indication of the true state of the population. Our

application of the biomass-based LCA model to the eastern Bering Sea northern rock sole, a stock for which research surveys are conducted, indicated good agreement between Zhang–Megrey LCA biomass estimates and survey biomass estimates in every year examined. The Zhang–Megrey LCA biomass estimates were within the survey 95% confidence intervals and were not different from the deterministic LCA biomass estimate, indicating superior performance from very minimal data requirements. As a possible explanation, the better performance of the Zhang–Megrey model may be due to poor estimation of mean weight at length in the implementation of the Jones LCA model.

It is clear that fish growth is an important aspect of fish population dynamics and therefore should be incorporated into cohort analysis when catch is given in units of biomass and when management decisions are made in terms of biomass. Without consideration of growth, one of the important processes influencing changes in biomass goes undetected. The biomass-based LCA described here is unique in that it incorporates growth explicitly into the estimation procedure and uses length composition data. An additional advantage is that only a single year of length composition data is needed to perform the analysis.

The LCA method proposed here requires a single length frequency sample, assuming that the population is in equilibrium. The model is insensitive to errors in F_T (if $F \gg M$). The required F_T is not usually estimated but is assumed, and the method is known to be insensitive to the choice of F_T (Pope 1972); however, the results can be sensitive to the choice of F_T value, especially when the cumulative rate of fishing is relatively low compared with M.

The narrowest length interval that makes data reasonably smooth should be used. Considerable care should be taken with the biomass-based LCA method when only poor growth data are available or when individual variation in growth is high. If a terminal length interval ("plus" group) is required, then users should ensure that the plus group has an initial length (lower bound) that is less than 70% of L_{∞}. This will minimize errors in the model's output due to errors in estimates and variances of L_{∞} and K. Any estimate of overall F should therefore cover only the smaller size interval representing the majority of the catch. Estimates of biomass should not be considered as absolute values but rather as rough estimates of population size (Lassen and Medley 2001).

Contemporary ecosystem-based fisheries assessment approaches (e.g., Smith et al. 2007; Zhang et al. 2009) require information on the stock status of nontarget species as essential input data. The biomass-based

LCA method proposed here relies on widely available length composition data and is suitable for data-deficient situations. The major purpose of our approach is to present a simple method that can provide a first approximation of biomass in data-deficient situations. Therefore, as long as we have sufficient data, we can rely on more standard approaches, fully utilizing data collected over multiple years (see Pauly 1987; Fournier et al. 1990). Future work will extend this approach to derive metrics relevant to contemporary fisheries management yet will still be based on minimal data requirements.

Acknowledgments

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Appendix A: Procedures for Generating Simulated Data

Two methods to simulate data and three growth models were evaluated. The difference in growth models are described below. The main difference between the numbers-based and the biomass-based simulated data methods are the explicit incorporation of growth in the biomass-based method. Also, the initialization values supplied to the two simulated data methods are implemented independently. In our model, we look at a short time interval when length changes from length-class l_i to length-class $l_{i+\Delta l}$. Over this time period, growth is assumed to be exponential and is approximated with the von Bertalanffy model when accumulated over the entire life span.

Growth Assumption

Since we assumed exponential growth in weight with time in our model, we examined the sensitivity of the assumption by comparing it with other growth assumptions. Three methods were used to represent mean growth in the data simulations: exponential (i.e., assumption W1), arithmetic mean (W2), and geometric mean (W3).

Exponential growth model

The exponential growth model is

$$W_{l_{i+1}} = W_{l_i} \exp(G_{l_i} \times l_i) \qquad (A.1)$$

where i is the length-class interval and G_{l_i} is the growth rate (Δt^{-1}), which is assumed to be constant over the length interval $(l_i–l_{i+1})$. The average weight over the length interval $(l_i–l_{i+1})$ is given by

$$\overline{W_{l_i}} = \frac{1}{l_{i+1} - l_i} \int_{l_i}^{l_{i+1}} W_{l_i} \exp(G_{l_i} \times l_i)\, dl, \qquad (A.2)$$

where $l_i = 0$, $l_{i+1} = 1$, and

$$\overline{W_{l_i}} = \frac{W_{l_i}}{G_{l_i}} [\exp(G_{l_i}) - 1]. \qquad (A.3)$$

Arithmetic mean growth model

The arithmetic average growth for length-class l_i is the average over the length interval $(l_i–l_{i+1})$ and is given by

$$\overline{W_{l_i}} = \frac{W_{l_i} + W_{l_{i+1}}}{2}. \qquad (A.4)$$

Geometric mean growth model

The geometric average growth for length-class l_i is the square root of the product over the length interval $(l_i–l_{i+1})$ and is given by

$$\overline{W_{l_i}} = \sqrt{W_{l_i} \times W_{l_{i+1}}}. \qquad (A.5)$$

Simulated Data Sets

Two simulated data sets were used to compare the different LCA methods. Since the procedural steps were different in the numbers-based versus the biomass-based simulated data sets, we describe them here.

Numbers-based simulated data

The process used to simulate numbers-based data began with the parameters given in Table 1 and eight sequential steps. In step 1, for each length-class, the weight (g) is calculated from fork length (cm) using the allometric weight equation (equation 6). In step 2, the growth rate G (Δt^{-1}) is calculated from weights for each length-class by using equation (7). Step 3 involves calculating Δt for each length-class by using equation (4). Step 4 is calculation of the mean weight ($\overline{W}$, g) for each length-class by one of the three methods described above. In step 5, the population (in number) in the smallest length-class is assumed to begin with 1×10^9 individuals. Step 6 involves projecting numbers into successively larger length-classes using the exponential

survival model:

$$N_{l_{i+\Delta t}} = N_{l_i} \exp[-Z \times \Delta t_{l_i}], \qquad (A.6)$$

where Z is the instantaneous total mortality rate (per year).

In step 7, catch in numbers per length-class ($C_{l_i}^N$) is calculated using the length-based catch equation:

$$C_{l_i}^N = \frac{F \times \Delta t_{l_i}}{Z \times \Delta t_{l_i}} \times N_{l_i}[1 - \exp(-Z \times \Delta t_{l_i})]. \qquad (A.7)$$

Step 8 is the calculation of catch in biomass (1,000 metric tons) per length–class ($C_{l_i}^B$) by multiplying the catch in numbers by the mean weight from step 4:

$$C_{l_i}^B = C_{l_i}^N \times \overline{W_{l_i}}. \qquad (A.8)$$

Catch in numbers at length is used as input data to the Jones (1981) LCA model; catch in biomass at length (1,000 metric tons) is used as input data to the Zhang–Megrey LCA model.

Biomass-based simulated data

The process used to simulate biomass-based data began with the parameters given in Table 1 and eight sequential steps. Steps 1–4 are the same as for the numbers-based simulated data. The main difference in this method relative to the method used for the numbers-based data is the explicit incorporation of growth.

In step 5, the population biomass in the smallest length-class is assumed to begin at 1×10^9 metric tons. Step 6 involves projecting biomass into successively larger length-classes using the biomass-based exponential survival model:

$$B_{l_{i+\Delta t}} = B_{l_i} \exp[-(Z_{l_i} \times \Delta t_{l_i} - G_{l_i})]. \qquad (A.9)$$

In step 7, catch in biomass ($C_{l_i}^B$; 1,000 metric tons) is calculated for each length-class by using the biomass-based catch equation:

$$\begin{aligned} C_{l_i}^B = {} & \frac{F \times \Delta t_{l_i}}{Z \times \Delta t_{l_i} - G_{l_i}} \times B_{l_i} \\ & \times \{1 - \exp[-(Z \times \Delta t_{l_i} - G_{l_i})]\}. \end{aligned} \qquad (A.10)$$

Step 8 is the calculation of catch in numbers ($C_{l_i}^N$) for each length-class by dividing the catch in biomass by the mean weight from step 4:

$$C_{l_i}^N = \frac{C_{l_i}^B}{\overline{W_{l_i}}}. \qquad (A.11)$$

As in the previous section, catch in numbers at length is used as input data to the Jones model and catch in biomass at length (1,000 metric tons) is used as input to the Zhang–Megrey model.