A size- and age-structured model to estimate fish recruitment, growth, mortality, and gear selectivity

Matthew J. Catalano*, Micheal S. Allen

Program for Fisheries and Aquatic Sciences, Department of Forest Resources and Conservation, University of Florida, 7922 NW 71st Street, Gainesville, FL 32653, USA

ARTICLE INFO

ABSTRACT

Most stock assessment models are solely age-based and ignore variability in length-at-age, but the incorporation of length structure can improve parameter estimates. Here, we present an age- and length-structured population model to estimate fish recruitment, von Bertalanffy growth parameters, natural mortality, and gear selectivity from survey length- and age-specific catch, fishery length distributions, and total harvested biomass. We evaluated parameter bias when fitting the model to simulated data with variable fish longevity, survey sampling duration (i.e., years of data), survey gear selectivity (i.e., asymptotic or dome-shaped), instantaneous fishing mortality rate and fishing mortality trend (i.e., stable or increasing). Median proportional bias in mortality (fishing and natural), growth, and gear selectivity parameters did not exceed 0.05 across all scenarios. Median recruitment bias ranged up to 0.12 and was greatest for the short-lived species and for scenarios with increasing fishing mortality, but bias for all other scenarios was less than 0.1. The model was demonstrated using data from a whole-lake biomanipulation of gizzard shad (*Dorosoma cepedianum*) at a 2300-ha lake in Florida, USA. Model estimates of gizzard shad exploitation rate were similar to an independent estimate from an in-season depletion analysis. Estimates of gizzard shad natural mortality and growth parameters were within the range of literature values for the species. The model could be useful for estimating growth, mortality, and recruitment parameters that account for gear selectivity and the cumulative effects of size-selective harvest.

1. Introduction

Rates of mortality and reproduction in fish populations are often a function of fish size rather than age (Sauer and Slade, 1987). However, stock assessments have widely adopted methods that rely solely on fish age to estimate mortality, gear selectivity, and recruitment rates (e.g., statistical catch-at-age, virtual population analysis). Size-selective fishing practices result in differential fishing mortality rates among fish of the same age (Hansen and Chouinard, 1992), which is not accounted for in most age-based population models. Stock assessments and management policies could be improved if data on length as well as age could be incorporated into estimation procedures.

Length and age-structured models have an additional advantage because they can estimate growth parameters that account for gear selectivity and the cumulative effects of size-selective harvest (Taylor et al., 2005). Gear selectivity affects age and length

samples due to the selective properties of a survey or fishery gear. Fishing gears typically have greater capture efficiencies for larger individuals. Thus, mean length of age classes recruiting to the gear may be overestimated due to higher capture probabilities for the largest (fastest-growing) individuals of the cohort (Taylor et al., 2005). Size-selective harvest removes the largest individuals in the population over time via fishing mortality. These removal effects would be strongest on fully recruited age classes by removing the largest individuals in a cohort, and therefore the remaining fish that are collected in length–age samples may represent primarily slow-growing animals (Kristiansen and Svåsand, 1998; Sinclair et al., 2002). These effects can lead to underestimation of the asymptotic length parameter (L_∞) and overestimation of the metabolic parameter (K) of the von Bertalanffy growth model (Taylor et al., 2005).

Taylor et al. (2005) proposed a length–age structured model for estimating mortality, gear selectivity, and growth parameters simultaneously from a length–age catch matrix (collected in a single year) using a multinomial maximum likelihood framework. Growth parameters obtained using Taylor et al.'s (2005) approach were unbiased with respect to gear selectivity and the cumulative effects of size-selective harvest. This method has the potential to allow estimation of critical population parameters with realistic

* Corresponding author at: Quantitative Fisheries Center, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA.
Tel.: +1 517 355 0126; fax: +1 517 355 0138.
E-mail addresses: mcatalan@msu.edu (M.J. Catalano), msal@ufl.edu (M.S. Allen).

data requirements (i.e., 1 yr of data) and may be particularly useful for species for which large amounts of catch data are lacking. The model is unique in that it accounts for variation in length-at-age by carrying out survival calculations for each length–age bin explicitly. Here, we developed a model that uses the Taylor et al. (2005) formulation but extends the model to estimate historical recruitment (i.e., the number of age-1 fish in the population each year) for situations where sequential years of survey length–age catch matrices are available. The new model estimates recruitment, growth, mortality, and gear selectivity parameters from a time series of survey catches-at-length and age, the length distribution of the harvest, and total annual harvested biomass. The objectives of this study were to (1) introduce the model structure, (2) evaluate model performance using a series of simulation-estimation procedures, and (3) demonstrate the model using data on gizzard shad (*Dorosoma cepedianum*) from a whole-lake biomanipulation experiment in Florida, USA.

2. Methods

2.1. Model

The model estimates a recruitment time series (R_t), instantaneous natural mortality rate (M), von Bertalanffy growth parameters (asymptotic length, L_∞; metabolic coefficient, K; time at zero length, t_0), two parameters defining the time-invariant standard deviation in length-at-age (λ_1 and λ_2), and three parameters of a flexible gear selectivity function for a fishery-independent gill net survey (shape, γ_s; steepness, β_s; length at 50% selectivity, L_{s50}) and the fishery (γ_v, β_v, L_{v50}). The model is conditioned on total annual harvest (biomass) and fit to a time series of survey length–age catch matrices ($n_{l,a,t}$) and fishery length composition data ($f_{l,t}$) using a multinomial maximum likelihood function. The survey data are arranged in an array of dimensions length × age × year. The survey length–age component calculates the likelihood of the observed catch of age-a fish in length bin l at time t given a model-generated set of predicted proportions-at-age, length, and time (Taylor et al., 2005). The survey length–age log likelihood is:

$$\ln L(n|\Theta) = \sum_l \sum_a \sum_t n_{l,a,t} \ln(p_{l,a,t}), \tag{1}$$

where $n_{l,a,t}$ is the observed catch of age-a fish in discrete length interval l at time t, and $p_{l,a,t}$ is the model-predicted catch proportion of age-a fish in length interval l at time t. Predicted catch proportions $p_{l,a,t}$ are estimated as:

$$p_{l,a,t} = \frac{N_{l,a,t} s_l P(l|a)}{\sum_l \sum_a \sum_t N_{l,a,t} s_l P(l|a)}, \tag{2}$$

where $N_{l,a,t}$ is the predicted abundance of age-a fish in length interval l at time t, s_l the length-based survey gear selectivity, and $P(l|a)$ is the probability of being in length interval l given age a. The $N_{l,a,t}$ term incorporates fishing and natural mortality (described below). The likelihood term for the fishery length distribution data is calculated similarly except that the $N_{l,a,t}$ terms are summed across ages to result in predicted length distributions and the s_l term is replaced by the length-based fishery gear selectivity (v_l). Survey and fishery likelihood terms are summed to calculate the total likelihood.

Survey gear selectivity, s_l (and fishery gear selectivity, v_l) is estimated using the function (Thompson, 1994):

$$s_l = \left(\frac{1}{1-\gamma_s} \right) \left(\frac{1-\gamma_s}{\gamma_s} \right)^{\gamma_s} \left(\frac{e^{\beta_s \lambda_s (L_{s50}-l)}}{1+e^{\beta_s (L_{s50}-l)}} \right), \tag{3}$$

where γ_s determines the shape, β the steepness, and L_{s50} is the length at 50% selectivity. This selectivity function can produce

either a dome-shaped or sigmoidal curve, depending on parameter values. Values of γ_s are bounded between 0 and 1. The functional form becomes sigmoidal (i.e., knife edge selectivity) as γ_s approaches 0 and increasingly dome-shaped as γ_s approaches 1.

The probability of falling in length bin l given age a ($P(l|a)$) is calculated from a normal probability density function with mean l_a and standard deviation σ_a. Mean length-at-age, l_a, is assumed to follow the von Bertalanffy (1938) growth model:

$$l_a = L_\infty (1 - e^{-K(a-t_0)}), \tag{4}$$

where L_∞ is the asymptotic length, K the metabolic coefficient, and t_0 is the time at zero length. The standard deviation in length-at-age is estimated using (Fournier et al., 1991):

$$\sigma_a = \lambda_1 e^{(-1+\lambda_2((1-\rho^{a-1})/(1-\rho^{A-1})))}, \tag{5}$$

where λ_1 defines the magnitude of the standard deviations, λ_2 controls the trend in σ_a over ages, and ρ is the Brody growth coefficient ($\rho = e^{-K}$).

The $N_{l,a,t}$ terms are calculated as the recruitment that occurred $a-1$ years prior (R_{t-a+1}) times the survivorship to age a and length l over the time interval $t-a+1$ to time t:

$$N_{l,a,t} = R_{t-a+1} e^{-Z_{l,a,t}}, \tag{6}$$

where R_{t-a+1} is the estimated recruitment that gave rise to the age-a cohort and $Z_{l,a,t}$ is the cumulative lifetime instantaneous total mortality for age-a fish that are in length bin l at time t. Recruitments were freely estimated parameters and were not constrained to fit a stock–recruit relationship nor were they penalized for large deviations from the average recruitment. The model assumes fish recruit to the population at age 1, thus one is added to the time-specific recruitment subscript. Cumulative instantaneous mortality represents the total lifetime mortality experienced by a fish of a given length–age–time bin as they grew from age 1 to age a along a growth trajectory with an asymptotic length (Taylor et al., 2005):

$$L_{\infty(l,t)} = \frac{l}{1 - e^{-K(a-t_0)}}. \tag{7}$$

The model assumes that K is time- (years), length-, and age-invariant, thus a unique asymptotic length $L_{\infty(l,t)}$ (i.e., growth trajectory) can be calculated for each length–age bin. The cumulative instantaneous mortality is calculated separately for each length–age bin and year as (Taylor et al., 2005):

$$Z_{l,a,t} = M(a-1) + \sum_{a'} v_{l(a')} F_{t(a')}, \tag{8}$$

where a' is a vector of ages from age 1 up to age $a-1$, and $F_{t(a')}$ and $v_{l(a')}$ are vectors of annual instantaneous fishing mortality rates and length-specific fishery gear selectivities, respectively. These terms represent the fishing mortalities and fishery gear selectivities that would have been experienced in the past by fish in a given length–age–time bin. The product of the elements of vectors $F_{t(a')}$ and $v_{l(a')}$ are summed over the age interval a' to calculate the cumulative instantaneous fishing mortality experienced by fish of a given length–age–time bin over their lifetime prior to time t.

The fishery gear selectivity ($v_{l(a')}$) terms are calculated by first determining the lengths that fish of a given length–age bin would have been in past years (i.e., at ages a'), which are a function of the length–age bin specific asymptotic length $L_{\infty(l,t)}$ using:

$$l_{a'} = L_{\infty(l,t)} (1 - e^{-K(a'-t_0)}). \tag{9}$$

The length-specific fishery gear selectivity is then calculated for each of these ages using Eq. (3).

The $F_{t(a')}$ values are a year- and age-dependent subset of a vector of annual instantaneous fishing mortality rates F_t. The model is con-

ditioned on aggregate annual catch (i.e., biomass). Thus, the annual instantaneous fishing mortality rate is calculated recursively as:

$$F_t = -\ln\left(1 - \frac{C_t}{B_t}\right), \tag{10}$$

where C_t are the annual observed catches and B_t is the model-predicted vulnerable biomass. Vulnerable biomass is calculated by multiplying model-predicted numbers-at-length and age ($N_{l,a,t}$) by estimates of fishery gear selectivity (v_l) and mean weight for a given length. Mean weights were estimated external to the model using an assumed length–weight relationship of the form, $w_t = cl^b$, where l is the fish length, c the length–weight coefficient and b is the allometric parameter.

The model requires F_t values for each year during the time span of the surveys and also for the $A - 1$ years before the surveys began. The initial $A - 1$ F_t values are required to calculate the cumulative instantaneous mortality for fish that were alive before the surveys began. However, fishing mortality rates can be calculated only for years in which survey catch data are available because vulnerable biomass cannot be estimated prior to the first survey sample. If the fishery developed before the first survey occurred, the initial average fishing mortality rate (F_0) must be estimated. This parameter represents the annual instantaneous fishing mortality for the years leading up to the collection of the first survey. The first $A - 1$ values of the F_t vector are set equal to F_0, which assumes that F was relatively constant for one generation time leading up to the first sample collection.

2.2. Model performance

Model performance was evaluated by fitting the model to simulated data and estimating parameter bias for scenarios that would commonly occur in stock assessment situations. The model was used to generate data for all possible combinations of fish longevity (short-lived: $A = 8$ yrs; long-lived: $A = 15$ yrs), survey sampling duration (i.e., years of data; short: $0.5A$ yrs; long: A yrs), survey gear selectivity (asymptotic and dome-shaped), instantaneous fishing mortality rate ($F_i = 0.2$ and 0.7 yr^{-1}) and fishing mortality trend (stable and increasing). For asymptotic sampling gear selectivity, the age at 50% selectivity was $0.3L_\infty$ and fish attained 90% selectivity at $0.4L_\infty$. For dome-shaped gear selectivity, fish attained 50% selectivity at $0.3L_\infty$, maximum (100%) selectivity at $0.5L_\infty$, and 50% at L_∞. For all scenarios, fishery gear selectivity was asymptotic with 50% selectivity at $0.6L_\infty$. The increasing F scenario allowed F to increase gradually from 0 to F_i over the years in which survey data were collected. Annual recruitment variation was log-normally distributed with a coefficient of variation (CV) of 50%, and observation errors on length- and age-specific catches each year were drawn from a multinomial distribution. All other parameters were held constant in the simulations. Monte Carlo simulation was used to generate data from the model and estimate parameters for each scenario (i.e., combination of longevity, sampling duration, gear selectivity, and fishing mortality schedule). For each scenario, 200 data sets were generated and the model was fit to each. Parameter bias was calculated for each Monte Carlo iteration by dividing the difference between the estimated and true parameter values by the true values. Additional iterations (>200) resulted in no change in median bias estimates.

Preliminary simulations revealed that the first recruitment (year 1) parameter was not estimable for the short-lived species and the first three values were not estimable for the long-lived species. These recruitments produced the oldest age classes in the first year of survey catch data. The cohorts were represented in only 1 or 2 yrs of catch data, and thus the catches were very low due to cumulative mortality of the cohorts. Thus, the recruitment parameters for these cohorts were not well-defined by the data, which resulted in

large uncertainty in the estimates. We did not attempt to estimate these parameters but rather set them equal to the mean of all other recruitment parameters.

2.3. Application to gizzard shad

The model was used to estimate parameters of a gizzard shad population that experienced a biomanipulation at Lake Dora, central Florida, USA. Biomanipulation was achieved with an experimental commercial gill net fishery by the St. Johns Water Management District (SJRWMD). Prior to fish removal, the gizzard shad population was unfished. Commercial fishers removed gizzard shad during March–April 2005 and again during January–March 2006. Gizzard shad were removed using gill nets with a minimum mesh size restriction of 102 mm, which selected for fish larger than approximately 300-mm total length. The SJRWMD used onboard observers to (1) record commercial catch-per-effort in 102-mm gill nets, and (2) measure a subsample of 100 harvested gizzard shad per week to characterize the length composition of the fishery harvest. The cumulative catch and total harvest (kg) each year were estimated from mandatory trip tickets, which were submitted to the SJRWMD daily by each fisher.

An annual fishery-independent survey was conducted at Lake Dora to obtain data on the length–age composition of the gizzard shad population. Survey data were collected by setting 20 multi-panel floating gill nets at 20 fixed sites in late January or early February from 2005 to 2009. The 2005 sample was conducted prior to the initial biomanipulation and thus represented an unfished population size/age structure. The final removal occurred in 2006, thus the 2008 and 2009 samples represented a rebuilding population. Gill nets were 2.4-m deep and contained eight, 15.3-m long panels of 38, 51, 64, 76, 89, 102, 114, and 127-mm stretch monofilament mesh. Each net was set for 2–3 hrs. Captured fish were measured for total length (mm) and counted, and otoliths were removed from a subsample of 10 fish per 10-mm group for ageing. Otoliths were sectioned using a South Bay Tech©Model 650 low-speed saw and read by three independent readers using a dissecting microscope at 40× magnification. Aged fish were extrapolated to the entire catch using an age–length key to estimate the age and length composition of the catch each year.

Data inputs used in the model were 5 yrs of survey length–age catch matrices, gizzard shad length distributions from the 2005 and 2006 fishery via onboard observers, and total harvested biomass in 2005 and 2006. The model was fitted using the optim() minimization function in program R. Parameter uncertainty was evaluated by inverting the Hessian matrix to obtain the variance–covariance matrix. Parameters that must be positive values (e.g., recruitments, M, L_∞) were constrained using a logarithmic transformation and parameters on a fixed interval from 0 to 1 (i.e., g_s and g_v) were fit using the logit transformation.

As a check on the gizzard shad model performance, we compared model-predicted exploitation rates to independent estimates obtained via an in-season depletion analysis. Catalano et al. (in review, *Hydrobiologia*) estimated an annual exploitation rate of 0.7 in 2005 and 0.65 in 2006 from a depletion of fisher catch-per-effort (kg per 100 m of 102-mm net per hr) vs. cumulative catch of the fishery over the course of each annual harvest period. As a second validation, gizzard shad growth and mortality estimates were compared with alternative estimation methods and literature values. Alternative estimates of growth parameters were obtained by fitting the von Bertalanffy growth model to mean lengths-at-age calculated directly from the age–length key data using methods of DeVries and Frie (1996). Literature estimates of natural mortality were obtained from Pauly (1980; $M = f\{L_\infty, K, °C\}$), Hoenig (1983; $M = f\{A\}$), and Jensen (1996; $M = 1.5K$). We also obtained M estimates using a simple catch curve for unfished Lake Dora (2005) and

Table 1

Median proportional bias for six parameter groupings (columns) from the short-lived ($A = 8$ yrs) species and for all scenarios (rows). The medians were calculated from 200 bias estimates generated by fitting the length–age model to simulated data sets. Each parameter grouping represents several parameters (e.g., growth: L_∞, K, t_0, λ_1, and λ_2). Bias estimates of the individual parameters were pooled within each parameter grouping before median bias was calculated. Values in parentheses are the 2.5% and 97.5% quantiles.

F	F_trend	Survey selectivity	Sampling duration	Recruitment	Natural mortality	Growth	Fishery selectivity	Survey selectivity	Fishing mortality
0.2	Increase	Sigmoid	A	0.08 (−0.54,2.93)	0.01 (−0.24,0.42)	0.00 (−0.16,0.20)	0.00 (−0.10,0.11)	0.00 (−0.05,0.06)	−0.05 (−0.60,0.62)
			0.5A	0.10 (−0.56,10.34)	0.04 (−0.28,0.58)	0.00 (−0.29,0.26)	0.00 (−0.11,0.18)	0.00 (−0.08,0.10)	0.00 (−0.83,1.15)
		Dome	A	0.05 (−0.61,4.77)	−0.01 (−0.23,0.40)	0.00 (−0.23,0.18)	0.00 (−0.09,0.15)	0.00 (−0.23,0.21)	−0.03 (−0.7,0.82)
			0.5A	0.12 (−0.67,1204.36)	0.03 (−0.30,0.64)	0.00 (−0.35,0.35)	0.00 (−0.12,0.20)	0.00 (−0.38,0.27)	−0.02 (−1.00,1.21)
	Stable	Sigmoid	A	0.01 (−0.42,1.27)	0.01 (−0.19,0.24)	0.00 (−0.21,0.22)	0.00 (−0.09,0.13)	0.00 (−0.06,0.07)	0.03 (−0.72,0.71)
			0.5A	0.08 (−0.54,3.53)	0.04 (−0.33,0.53)	0.00 (−0.34,0.33)	0.00 (−0.14,0.18)	0.00 (−0.08,0.10)	0.02 (−0.99,1.00)
		Dome	A	0.10 (−0.57,4.13)	0.00 (−0.26,0.41)	0.00 (−0.24,0.24)	0.00 (−0.13,0.23)	0.00 (−0.33,0.23)	−0.01 (−0.79,1.05)
			0.5A	0.06 (−0.7,35.04)	0.02 (−0.48,0.77)	0.00 (−0.37,0.34)	0.00 (−0.20,0.27)	0.00 (−0.42,0.39)	0.03 (−0.93,1.47)
0.7	Increase	Sigmoid	A	0.03 (−0.46,1.39)	0.02 (−0.19,0.25)	0.00 (−0.21,0.20)	0.00 (−0.08,0.09)	0.00 (−0.06,0.06)	−0.01 (−0.31,0.35)
			0.5A	0.04 (−0.52,2.04)	0.03 (−0.27,0.48)	0.00 (−0.36,0.25)	0.00 (−0.11,0.13)	0.00 (−0.09,0.09)	−0.01 (−0.33,0.55)
		Dome	A	0.07 (−0.50,1.89)	0.04 (−0.25,0.35)	0.00 (−0.25,0.24)	0.00 (−0.08,0.11)	0.00 (−0.24,0.20)	−0.03 (−0.36,0.37)
			0.5A	0.05 (−0.53,3.78)	0.04 (−0.25,0.63)	0.00 (−0.37,0.32)	0.00 (−0.11,0.12)	0.00 (−0.35,0.31)	−0.01 (−0.46,0.76)
	Stable	Sigmoid	A	0.00 (−0.32,0.48)	−0.01 (−0.10,0.12)	0.00 (−0.29,0.33)	0.00 (−0.07,0.08)	0.00 (−0.07,0.07)	0.01 (−0.28,0.31)
			0.5A	0.01 (−0.47,1.03)	0.01 (−0.28,0.29)	0.00 (−0.42,0.36)	0.00 (−0.09,0.11)	0.00 (−0.08,0.10)	0.01 (−0.30,0.32)
		Dome	A	−0.04 (−0.50,0.86)	−0.03 (−0.34,0.32)	0.00 (−0.33,0.27)	0.00 (−0.19,0.21)	0.00 (−0.37,0.41)	0.02 (−0.29,0.33)
			0.5A	0.06 (−0.60,2.38)	0.04 (−0.48,0.59)	0.00 (−0.49,0.42)	0.00 (−0.20,0.33)	−0.01 (−0.56,0.52)	0.02 (−0.38,0.41)

3. Results

3.1. Model performance

Median proportional bias was less than 0.1 for all parameters and scenarios (Tables 1 and 2) except for the short-lived species with low ($F = 0.2$ yr^{-1}) and increasing F, which had three scenarios with median recruitment bias exceeding 0.1 (range: 0.1–0.12; Table 1). Simulations with low fishing mortality ($F = 0.2$ yr^{-1}) generally had greater parameter bias than those with higher fishing mortality ($F = 0.7$; Tables 1 and 2). Bias was greater for the short-lived than for the long-lived species (Fig. 1; Tables 1 and 2), and with a short (0.5A yrs) rather than long (A yrs) sampling duration. Bias was greater for scenarios with increasing F than with constant F (Tables 1 and 2). Simulations that assumed a dome-shaped survey gear selectivity function exhibited greater bias than simulations with asymptotic selectivity (Tables 1 and 2), but the model could adequately determine the shape (i.e., dome vs. sigmoidal) of the selectivity curve in most cases.

The amount of bias varied among parameters. Growth parameters had median bias of less than 0.005 across all scenarios (Tables 1 and 2). Median bias in gear selectivity parameters was low (≤0.01) across all scenarios as was bias in natural and fishing mortality (≤0.05 across all scenarios). Recruitment parameters were more biased than the other parameters, particularly for the short-lived species. Recruitment biases for the short-lived species

a pooled estimate over 5 yrs from two nearby unharvested control lakes (Lakes Eustis and Harris, 2005–2009) that had similar gizzard shad populations and were sampled with the same gear during the same time period as Lake Dora (Catalano et al., 2007).
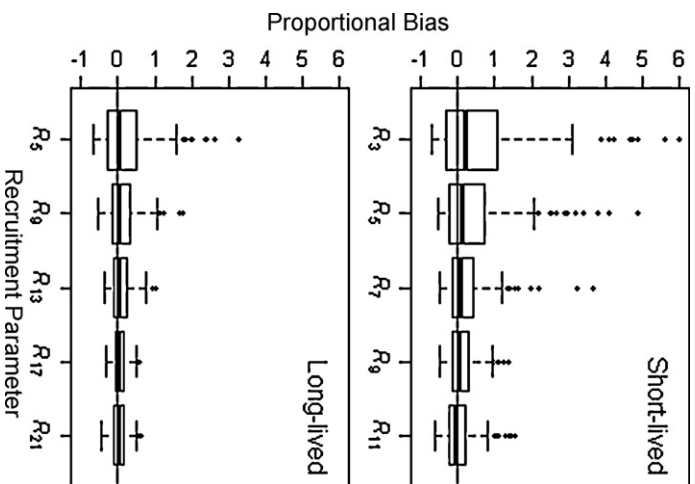

Fig. 1. Box and whisker plot showing proportional bias of recruitment estimates for a short-lived (upper) and long-lived (lower) species. The plot represents a scenario with increasing fishing mortality to 0.7 yr^{-1}, dome-shaped survey gear selectivity, and a short (0.5A) time series of data. Recruitment biases for this scenario were less than for high-bias scenarios (e.g., increasing F to 0.2 yr^{-1}, dome selectivity, short time series) but greater than low-bias scenarios (e.g., increasing F to 0.7 yr^{-1}, sigmoidal selectivity, long time series). The box represents the 25% and 75% quantiles with the median indicated by the horizontal line, and the bars signify the 2.5% and 97.5% quantiles. Every second (short-lived) and fourth (long-lived) recruitment parameter is shown for efficiency.

Table 2

Median proportional bias for six parameter groupings (columns) from the long-lived ($A = 8$ yrs) species and for all scenarios (rows). The medians were calculated from 200 bias estimates generated by fitting the length–age model to simulated data sets. Each parameter grouping represents several parameters (e.g., growth: L_∞, K, t_0, λ_1, and λ_2). Bias estimates of the individual parameters were pooled within each parameter grouping before median bias was calculated. Values in parentheses are the 2.5% and 97.5% quantiles.

| F	F_trend	Survey selectivity	Survey duration	Recruitment	Natural mortality	Growth	Fishery selectivity	Survey selectivity	Fishing mortality
0.2	Increase	Sigmoid	A	0.02 (−0.39,0.90)	0.01 (−0.15,0.17)	0.00 (−0.20,0.24)	0.00 (−0.06,0.07)	0.00 (−0.03,0.04)	−0.01 (−0.28,0.29)
			0.5A	0.01 (−0.46,1.32)	0.01 (−0.21,0.29)	0.00 (−0.32,0.29)	0.00 (−0.08,0.08)	0.00 (−0.04,0.04)	0.00 (−0.36,0.42)
		Dome	A	0.04 (−0.46,1.10)	0.02 (−0.17,0.21)	0.00 (−0.19,0.20)	0.00 (−0.06,0.08)	0.00 (−0.18,0.15)	−0.01 (−0.31,0.34)
			0.5A	0.05 (−0.45,1.66)	0.02 (−0.20,0.36)	0.00 (−0.34,0.26)	0.00 (−0.08,0.10)	0.00 (−0.23,0.20)	−0.01 (−0.4,0.45)
	Stable	Sigmoid	A	0.00 (−0.27,0.40)	0.00 (−0.10,0.09)	0.00 (−0.23,0.22)	0.00 (−0.06,0.08)	0.00 (−0.03,0.03)	0.02 (−0.31,0.3)
			0.5A	0.03 (−0.40,0.92)	0.02 (−0.21,0.26)	0.00 (−0.33,0.31)	0.00 (−0.09,0.10)	0.00 (−0.04,0.05)	0.00 (−0.39,0.4)
		Dome	A	−0.02 (−0.41,0.89)	−0.01 (−0.20,0.24)	0.00 (−0.23,0.23)	0.00 (−0.12,0.15)	0.00 (−0.23,0.23)	0.00 (−0.41,0.33)
			0.5A	−0.01 (−0.52,2.11)	−0.01 (−0.28,0.44)	0.00 (−0.32,0.29)	0.00 (−0.13,0.19)	0.00 (−0.36,0.28)	0.03 (−0.44,0.41)
0.7	Increase	Sigmoid	A	0.02 (−0.31,0.57)	0.01 (−0.16,0.15)	0.00 (−0.22,0.18)	0.00 (−0.06,0.07)	0.00 (−0.04,0.04)	−0.01 (−0.18,0.18)
			0.5A	0.01 (−0.36,0.83)	0.01 (−0.17,0.23)	0.00 (−0.28,0.26)	0.00 (−0.07,0.08)	0.00 (−0.05,0.04)	−0.01 (−0.19,0.2)
		Dome	A	0.04 (−0.42,0.81)	0.02 (−0.20,0.24)	0.00 (−0.23,0.22)	0.00 (−0.07,0.08)	0.00 (−0.21,0.17)	−0.01 (−0.17,0.17)
			0.5A	0.01 (−0.42,1.10)	0.01 (−0.21,0.28)	0.00 (−0.26,0.30)	0.00 (−0.06,0.08)	0.00 (−0.21,0.19)	0.00 (−0.22,0.22)
	Stable	Sigmoid	A	0.00 (−0.37,0.38)	0.00 (−0.08,0.09)	0.00 (−0.31,0.28)	0.00 (−0.07,0.07)	0.00 (−0.03,0.03)	0.00 (−0.14,0.15)
			0.5A	−0.01 (−0.50,0.53)	−0.01 (−0.13,0.13)	0.00 (−0.41,0.38)	0.00 (−0.07,0.10)	0.00 (−0.04,0.05)	0.00 (−0.18,0.19)
		Dome	A	0.01 (−0.47,0.84)	0.01 (−0.27,0.31)	0.00 (−0.26,0.23)	0.00 (−0.23,0.54)	0.00 (−0.32,0.27)	0.00 (−0.17,0.18)
			0.5A	0.00 (−0.59,1.50)	0.00 (−0.38,0.48)	0.00 (−0.42,0.37)	0.00 (−0.32,0.54)	0.00 (−0.49,0.39)	0.00 (−0.19,0.24)
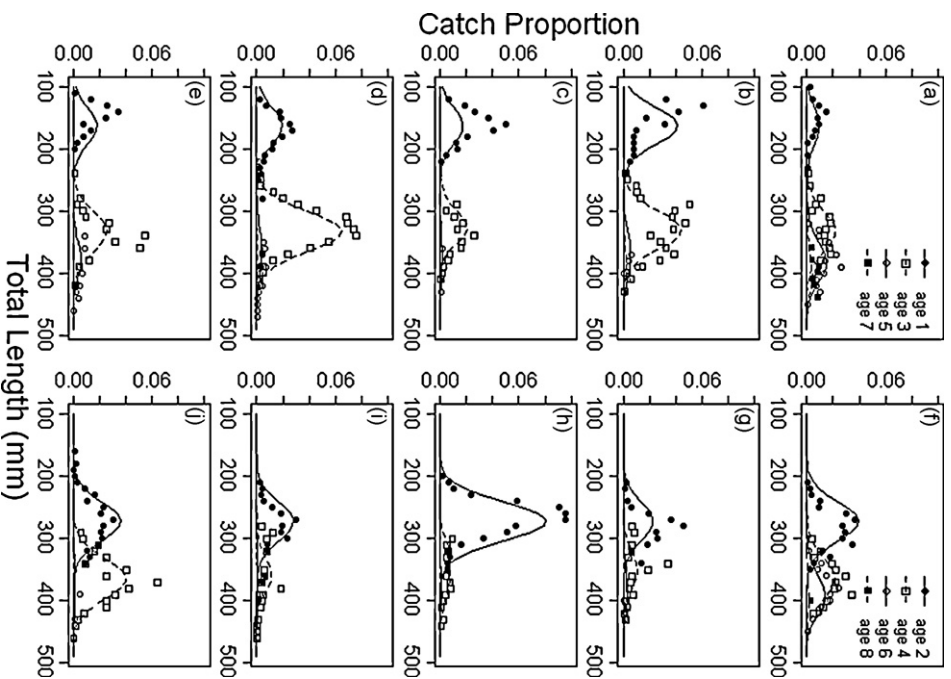
Fig. 2. Observed (points) and model-predicted (lines) length–age survey catch proportions for gizzard shad at Lake Dora, Florida from January 2005 (a and f) to January 2009 (e and j). Odd ages are shown on the left column panels (a–e) and even ages are on the right (f–j).

were driven by an upward bias in early recruitment estimates, particularly for scenarios with a short sampling duration (Fig. 1). For most other scenarios, median recruitment bias was less than 0.05. However, some of the 200 individual simulations exhibited large recruitment biases particularly for the short-lived species with low and increasing F (Table 1).

Parameter uncertainty was low with coefficients of variation (CV) less than 35% for most estimates suggesting that the data contained enough information to estimate the parameters. Recruitment parameters were the most uncertain with CVs ranging from 10% to 35%. All other parameters had CVs less than 10%

3.2. Application to gizzard shad

The total harvested biomass of gizzard shad was 124 989 kg (54 kg/ha) in 2005 and 135 095 kg (58 kg/ha) in 2006. The model fit the survey length–age data reasonably well although there was some under-prediction of proportional catches of age-1 fish in 2006, 2007 and 2009 (Fig. 2). Modal length-at-age for age-1 fish was over-predicted in 2006 and 2009 suggesting slower than average pre-recruit growth in 2005 and 2008 (Fig. 2). Length distributions from the fishery were also predicted well by the model.

Annual recruitment estimates varied from 0.5 to 4 million age-1 gizzard shad and strong year classes occurred in 2000, 2004 and 2006 (Fig. 3). Preliminary fits indicated that the first recruitment value (R_{1998}) was not estimable, and thus we fixed that value to
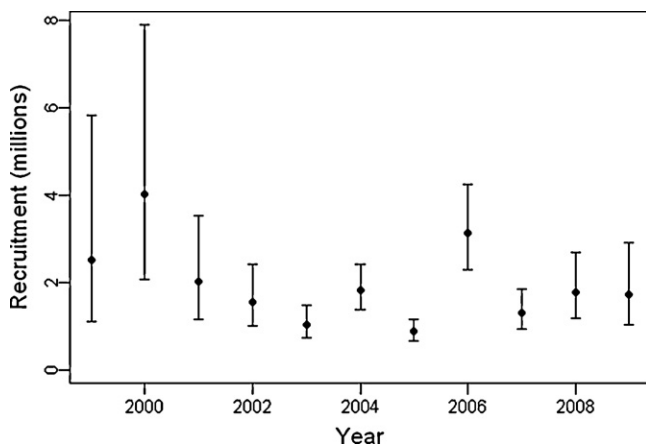
Fig. 3. Gizzard shad recruitment estimates (millions of age-1 recruits) from 1999 to 2009. Error bars represent 95% confidence intervals.

the average of all other recruitment values. There was evidence for alternating strong and weak year classes although the pattern was not evident in 2001–2002 and 2008–2009 (Fig. 3). Von Bertalanffy growth and natural mortality estimates were precise with CVs less than 10% (Table 1).

The length at 50% selectivity and γ (shape parameter) parameters were estimated precisely for all three gear selectivity functions (i.e., survey, 2005 fishery, 2006 fishery) with CVs less than 10%, but the steepness parameters were less certain (CV range: 15–36%; Table 1). The survey gear selectivity function was dome-shaped with selectivity increasing exponentially up to 400 mm then peaking at 430 mm and declining to 0.75 at 450 mm. Gear selectivity curves for the fishery were asymptotic and suggested that length at 50% selectivity decreased in 2006. This finding agreed with onboard observer data showing that fishers used mesh sizes of 102, 144 and 127 mm in 2005 but only used 102-mm mesh in 2006 due to declining catches in the large mesh sizes (unpublished data, SJRWMD). Model-predicted exploitation rates were 0.67 in 2005 and 0.75 in 2006, which were similar in magnitude to the depletion estimates of 0.7 in 2005 and 0.65 in 2006. Fitting the von Bertalanffy growth model directly to mean lengths-at-age produced growth parameter estimates of 404 mm (L_∞; 95% CI: 392–417 mm), 0.57 yr^{-1} (K; 95% CI: 0.47–0.62 yr^{-1}), and 0.11 yrs (t_0; 95% CI: −0.07 to −0.29 yrs), which were similar to the length–age model estimates of 394 mm (L_∞; 95% CI: 390–398 mm), 0.60 yr^{-1} (K; 95% CI: 0.58–0.63 yr^{-1}), and 0.17 yrs (t_0; 95% CI: 0.14–0.20 yrs; Table 3). The model natural mortality rate estimate of 0.87 yr^{-1} was greater than estimates of 0.61 yr^{-1} from Pauly (1980) and 0.53 yr^{-1} from Hoenig (1983), but was similar to an estimate of 0.9 yr^{-1} from Jensen (1996). The

model M estimate was also greater than catch curve estimates of 0.6 yr^{-1} from unfished Lake Dora in 2005 and 0.76 yr^{-1} from Lakes Eustis and Harris from 2005 to 2009.

4. Discussion

Our model extended the methods of Taylor et al. (2005) and showed that recruitment can be estimated with multiple years of data, along with M, growth and gear selectivity parameters. This model provided precise estimates with low bias for most scenarios when fit to simulated data. In addition, parameter estimates from a gizzard shad population were validated independently via alternative methods (e.g., depletion analysis). This model could be useful for assessment of fish stocks when it is desirable to model changes in cohort length distributions due to the effects of harvesting or other factors (e.g., emigration). Most processes affecting fish populations (e.g., harvesting gear, fecundity, regulations, predation rates, and metabolism) are size-based. Therefore, models that explicitly account for length-dependent processes may provide more accurate parameter estimates. An additional advantage of the approach is that length data are usually readily available and could be incorporated into the model.

4.1. Model performance

Our model, like Taylor et al. (2005), used a unique accounting structure compared to other existing length–age models. Stock Synthesis 2 (Methot, 2005) uses a growth-type-group (GTG) accounting method where the stock is divided into several growth morphs each with its own von Bertalanffy growth parameters. The dynamics of each morph are calculated separately through time as fish stay in the same morph throughout life. This method can be very efficient if only a few groups are needed but can become computationally demanding with many groups. The number of groups necessary has not been studied and likely varies depending on the species. Another approach is the matrix transition approach such as the Fleksibest model by Frøysa et al. (2002). This accounting structure calculates probabilities of transition from a given length bin and age to other length bins at the next age and time step. These calculations can be rather complicated because fish from a single length–age bin will transition to multiple length bins in the next time step.

The Taylor accounting structure can be thought of as a type of GTG model because it assumes that fish grow along a fixed growth trajectory, although it does not explicitly calculate the dynamics of each growth morph through time. Instead, the dynamics of each length–age bin are explicitly accounted for by calculating back in time rather than calculating forward as in the typical GTG for-

Table 3
Point estimates and 95% Wald confidence intervals for model parameters estimated from length–age data for gizzard shad at Lake Dora, Florida, USA.

Parameter	Description	Estimate	L95% CI	U95% CI
M (yr^{-1})	Instantaneous natural mortality	0.87	0.77	0.99
L_∞ (mm)	Asymptotic length	394.30	390.00	398.70
K (yr^{-1})	Metabolic coefficient	0.60	0.58	0.63
t_0 (yr)	Time at zero length	0.17	0.14	0.20
λ_1 (mm)	σ length-at-age scaling parameter	31.04	30.47	31.63
λ_2	σ length-at-age shape parameter	0.06	0.03	0.09
L_{s50} (mm)	Survey length at 50% selectivity	452.60	441.60	463.80
γ_s	Survey selectivity shape	0.85	0.73	0.92
β_s	Survey selectivity steepness	0.10	0.05	0.17
$L_{v50(2005)}$ (mm)	2005 fishery length at 50% selectivity	336.16	322.92	349.95
$\gamma_{v(2005)}$	2005 fishery selectivity shape	0.00	0.00	0.02
$\beta_{v(2005)}$	2005 fishery selectivity steepness	0.06	0.04	0.08
$L_{v50(2006)}$ (mm)	2006 fishery length at 50% selectivity	301.20	297.10	305.40
$\gamma_{v(2006)}$	2006 fishery selectivity shape	0.00	0.00	0.03
$\beta_{v(2006)}$	2006 fishery selectivity steepness	0.13	0.09	0.19

mulation. In addition, population numbers-at-length and age are predicted directly rather than aggregating fish into length–age bins from growth morphs (in the typical GTG formulation) by assuming a length distribution for fish of a given age and morph.

The length–age model was fit only to survey catches-at-length and age and fishery length distributions, but estimates could be improved with the inclusion of additional data types. For example, survey CPUE indices could be included to help define the magnitude of biomass reductions, which would provide information on the recruitment and mortality levels that would have been necessary to result in the observed catches and CPUE trend. Additional survey length–age catch matrices could also be included, which reduced parameter bias and uncertainty in these models in preliminary simulation analyses (Catalano, unpublished data).

We did not assess the performance of the length–age model using simulations in which the model was misspecified relative to the data-generating model. The length–age model we tested was identical in structure to the model used to generate the simulated data sets. For example, neither our data-generating model nor the length–age estimation model allowed for time, age, or cohort specific variation in growth. As another example, we assumed that instantaneous natural mortality was constant across age classes. Work by Lorenzen (2000) suggests natural mortality declines with age inversely proportional to fish length. Performance of the length–age model with time- or age-invariant parameters would likely have been reduced if fit to simulated populations with time- or age-varying growth or natural mortality. Future studies should assess the robustness of the model to misspecification errors.

The most common model bias encountered in the simulation–estimation trials was overestimation of recruitment values, particularly early in the time series. In these situations, M is often overestimated and there were trends in recruitment bias with larger recruitment biases for older cohorts than for more recent ones. These early recruitments represent cohorts that were not tracked fully through the age structure. The potential for these biases can be reduced by collecting data over a sufficiently long time series, by including additional survey data types, and by not estimating several of the earliest recruitment values but rather setting them equal to the average of the estimated recruitments. However, these approaches would probably not improve model performance for short sampling durations where few cohorts are tracked through the entire age structure.

The number of fish aged each year and the assumed width of the length bins may affect performance of the length–age model. The model requires an adequate number of aged fish. We simulated the aging of 2000 fish annually from survey data and 200 lengths from the fishery harvest, which represents a substantial data investment but is not uncommon for high-profile marine fisheries (e.g., groupers and snappers). Taylor et al. (2005) found that at least 500 fish were needed for their model to perform adequately. Model performance also depends on the number and width of the length bins. We set the length bin width at 2.5% of L_∞ because preliminary analyses indicated that parameter bias increased substantially when length bin width exceeded 10% of L_∞. Using length bins that are too wide could cause some age classes to be represented by only 1 or 2 length bins, which could introduce parameter bias due to random sampling error on these underrepresented age classes. As with other length-based models, care should be taken when setting the level of length discretization in the model.

4.2. Application to gizzard shad

The length–age model provided exploitation, growth, and natural mortality estimates for gizzard shad that generally concurred with literature and independent estimates. In particular, estimates of natural mortality from the length–age model should be closely examined relative to alternative estimates given the importance of this parameter in stock assessments. The length–age model M estimate was close to that of Jensen (1996) but exceeded those of Hoenig (1983) and Pauly (1980). The Hoenig (1983) and Pauly (1980) values were derived from empirical models based on many fish populations whereas the Jensen (1996) estimate is based on life history theory. It is not known whether any of these methods are applicable to gizzard shad. The length–age model M estimate was greater than the catch curve estimates suggesting that one of the two estimates was biased. Downward bias in the catch curve estimates could have resulted from an increase in survey gear selectivity with fish length, which would over-represent older fish in the catch, as was estimated by the length–age model. Size selectivity is common for survey gears (Bayley and Austen, 2002) but such biases are rarely considered when catch curves are estimated. Conversely, if M was overestimated by the length–age model, then there was likely a concurrent upward bias in recruitment to produce a large enough population to explain the observed harvest. It should be noted that natural mortality was estimable from our data because the fishery-independent survey captured fish for 2–3 yrs before they were fully vulnerable to the fishery. Natural mortality would be confounded with fishing mortality if surveys capture fish only after they are fully vulnerable to the fishery.

Demographic parameter estimates for gizzard shad are rare in the literature and the length–age model estimates presented here could be useful for fishery management in eastern North America. Gizzard shad are hypothesized to control food webs in eutrophic lakes through complex "middle-out" processes by larval overgrazing of zooplankton and adult detritivorous foraging (DeVries and Stein, 1992). Therefore, gizzard shad have received attention from managers as targets for biomanipulation (Kim and DeVries, 2000) and as prey for recreational fishes (Cyterski and Ney, 2005). However, there are few published estimates of gizzard shad growth, gear selectivity and natural mortality with which to inform these studies. Bodola (1965) estimated an L_∞ of 395 mm and K of 0.78 yr^{-1} for Lake Erie, and Perry et al. (2003) reported estimates of 370 mm for L_∞ and 0.58 yr^{-1} for K in the Ohio River, which are similar to our estimates. Gear selectivity estimates would be particularly useful for biomanipulation efforts that utilize gill nets as the removal method. Van Den Avyle et al. (1995) estimated retention probabilities for gizzard shad in various gill net mesh sizes but their estimates assumed equal encounter rates among fish lengths and did not represent gear selectivities that could be used in a modeling context. We could find no peer-reviewed estimates of natural mortality for adult gizzard shad.

Taylor et al. (2005) reported that prior knowledge of the shape of the gear selectivity function was required for their model. However, our simulations analysis suggested that the length–age model could obtain unbiased estimates of the shape of the gear selectivity function with no prior information. When fit to gizzard shad data from Lake Dora, gear selectivity parameter estimates suggested that survey selectivity was dome-shaped, which differed from the asymptotic selectivity assumption used by Taylor et al. (2005) for northern pike minnow (*Ptychocheilus oregonensis*). Although the gizzard shad analysis showed a dome-shaped survey gear selectivity with peak selectivity at 430 mm, it should be noted that gizzard shad exceeding 430 mm should be extremely rare in Lake Dora due to high natural mortality, an asymptotic length of 394 mm, and an estimated standard deviation in length-at-age of age-5 to age-8 fish of around 30 mm. This dome-shaped gear selectivity pattern could have been an artifact of size-dependent natural mortality rates in which faster-growing individuals had higher natural mortality rates. Nevertheless, failure to account for selectivity patterns could bias abundance estimates of large (older) fish in the age structure. Hansen et al. (1997) found that total annual mortality of Lake Superior lake trout (*Salvelinus namaycush*) was underestimated by 20%

when catch–age samples were not corrected for dome-shaped gear selectivity. This model could be useful for evaluating populations where the shape of the gear selectivity function is unknown.

4.3. Conclusion

This model could be useful for estimating critical population parameters of fishes. There have been few peer-reviewed evaluations of the parameter bias of age–length structured assessment models to date. We showed that these models can provide unbiased estimates of population parameters and tested the limits of the approach by exploring situations in which biases could arise (e.g., short time series of data). One important advantage of a fully age- and length-structured model is the ability to directly estimate growth parameters in the model. The models would likely outperform traditional age-based models when biases in growth parameters are suspected due to gear selectivity and the cumulative effects of size-selective harvest on age/size distributions.

Acknowledgements

References

Bayley, P.B., Austen, D.J., 2002. Capture efficiency of a boat electrofisher. Trans. Am. Fish. Soc. 131, 435–451.

Bodola, A., 1965. Life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in western Lake Erie. Fish. Bull. 65, 391–425.

Catalano, M.J., Allen, M.J., DeBrabandere, L., Dotson, J., 2007. Assessing Effects of Gizzard Shad Removal on Nutrient Cycling and Gizzard Shad Population Dynamics. Final Report to the St. Johns River Water Management District. University of Florida, Gainesville.

Cyterski, M.J., Ney, J.J., 2005. Availability of clupeid prey to primary piscivores in Smith Mountain Lake, Virginia. Trans. Am. Fish. Soc. 134, 1410–1421.

DeVries, D.R., Frie, R.V., 1996. Determination of age and growth. In: Murphy, B.R., Willis, D.W. (Eds.), Fisheries Techniques. American Fisheries Society, Bethesda, MD, pp. 483–512.

DeVries, D.R., Stein, R.A., 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Can. J. Fish. Aquat. Sci. 49, 1216–1227.

Fournier, D.A., Sibert, J.R., Terciero, M., 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by the MULTIFAN method. Can. J. Fish. Aquat. Sci. 48, 591–598.

Frøysa, K.G., Bogstad, B., Skagen, D.W., 2002. Fleksibest: an age–length structured fish stock assessment model. Fish. Res. 55, 87–101.

Hansen, J.M., Chouinard, G.A., 1992. Evidence that size-selective mortality affects growth of Altantic cod (*Gadus morhua* L.) in the southern Gulf of St. Lawrence. J. Fish Biol. 41, 31–41.

Hansen, M.J., Madenjian, C.P., Selgeby, J.H., Helser, T.E., 1997. Gillnet selectivity for lake trout (*Salvelinus namaycush*) in Lake Superior. Can. J. Fish. Aquat. Sci. 54, 2483–2490.

Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82, 898–903.

Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Can. J. Fish. Aquat. Sci. 53, 820–822.

Kim, G.W., DeVries, D.R., 2000. Effects of a selectively reduced gizzard shad population on trophic interactions and age-0 fishes in Walker County Lake, Alabama. N. Am. J. Fish. Manage. 20, 860–872.

Kristiansen, T.S., Svåsand, T., 1998. Effect of size-selective mortality on growth of coastal cod illustrated by tagging data and an individual-based growth and mortality model. J. Fish Biol. 52, 688–705.

Lorenzen, K., 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Can. J. Fish. Aquat. Sci. 57, 2374–2381.

Methot, R.D., 2005. Technical Description of the Stock Synthesis II assessment Program Version 1.17. NOAA Fisheries, Seattle, WA.

Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer 39, 175–192.

Perry, E., Seegert, G., Vondruska, J., Lohner, T., Lewis, R., 2003. Modeling possible cooling water intake system impacts on Ohio River fish populations. In: Dixon, Veil, Wisniewskis (Eds.), Defining and Assessing Adverse Environmental Impact from Power Plant Impingement and Entrainment of Aquatic Organisms.

Sauer, J.R., Slade, N.A., 1987. Size-based demography of vertebrates. Annu. Rev. Ecol. Syst. 18, 71–90.

Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Can. J. Fish. Aquat. Sci. 59, 361–371.

Taylor, N.G., Walters, C.J., Martell, S.J.D., 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Can. J. Fish. Aquat. Sci. 62, 215–223.

Thompson, G.G., 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Can. J. Fish. Aquat. Sci. 51, 2654–2664.

Van Den Avyle, M.J., Boxrucker, J., Michaletz, P., Vondracek, B., Ploskey, G.R., 1995. Comparison of catch rate, length distrubution, and precison of six gears used to sample reservoir shad populations. N. Am. J. Fish. Manage. 15, 940–955.

von Bertalanffy, L., 1938. A quantitative theory of organic growth. Hum. Biol. 10, 181–213.