

A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates

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The red drum (*Sciaenops ocellatus*) is a popular gamefish found throughout the coastal waters of the Gulf of Mexico and along the eastern seaboard as far north as Massachusetts. Juvenile red drum grow extremely rapidly, especially during the warmer months, but adults grow very little. In fact, the change in growth with age is so abrupt that the standard von Bertalanffy curve has proven inadequate—the predicted lengths of younger fish are generally too large and the predicted lengths of older fish too small (see Beckman et al., 1988; Murphy and Taylor, 1990).

Two generalizations of the von Bertalanffy curve have been found to fit red drum length-at-age data better than the original three-parameter form. The first, dubbed the “double” von Bertalanffy growth curve (Vaughan and Helser, 1990; Condrey et al.¹), allows the rate at which an animal approaches the asymptotic length to change after some pivotal age, t_p ;

$$l_t = \begin{cases} l_\infty (1 - e^{-k_1(t-t_1)}) & \text{if } t < t_p \\ l_\infty (1 - e^{-k_2(t-t_2)}) & \text{if } t \geq t_p \end{cases} \quad (1)$$

$$t_p = (k_2 t_2 - k_1 t_1) / (k_2 - k_1),$$

where t = age;

l_∞ = asymptotic length;
 k_1, k_2 = instantaneous growth rate coefficients; and
 t_1, t_2 = age intercept parameters.

The second, dubbed the “linear” von Bertalanffy curve (Hoese et al., 1991; Vaughan, 1996), expresses the asymptotic length as a linear function of age:

$$l_t = (b_0 + b_1 t) (1 - e^{-k(t-t_0)}). \quad (2)$$

Of course other generalizations of the von Bertalanffy curve may also be appropriate, such as the Richards (1959) equation

$$l_t = l_\infty (1 - \delta e^{-k(t-t_0)})^{\frac{1}{\delta}} \quad \text{where } \delta \neq 0. \quad (3)$$

The double von Bertalanffy curve accommodates the possibility that older, larger fish might grow more slowly in proportion to their length than younger, smaller fish. (The linear von Bertalanffy curve has no biological interpretation.) In reality, one might expect the growth rate in proportion to length to decrease gradually with the age of the fish rather than at some abrupt pivotal point. Moreover, the growth pattern of juvenile red drum seems to have a

strong seasonal component (Goodyear²). In this paper a new growth equation is developed that explicitly models these two features. The new equation provided a better fit to northern Gulf of Mexico red drum age-length data than any of the above alternatives.

Materials and methods

The model

The growth rate at any given age t is assumed to be in some proportion k to the difference between the expected size at that age (l_t) and the expected maximum (l_∞):

$$\frac{dl_t}{dt} = k(l_\infty - l_t). \quad (4)$$

Further, k is assumed to decline with age and vary with the seasons such that

$$k = k_0 + k_1 e^{-\lambda_1 t} + k_2 e^{-\lambda_2 t} \sin(2\pi(t - t_c)), \quad (5)$$

where λ_1 and λ_2 are damping coefficients and t_c is a shifting parameter for the sine wave valued between 0 and 1. Substituting Equations 5 and 4 and integrating with $l = 0$ when $t = t_0$ gives

¹ Condrey, R., D. W. Beckman and C. A. Wilson. 1988. Management implications of a new growth model for red drum. Appendix D. In Louisiana red drum research, J. A. Shepard (ed.), 26 p. U.S. Dept. Commerce Cooperative Agreement NA87-WC-H-06122. Marine Fisheries Initiative (MARFIN) Program. Louisiana Department of Wildlife and Fisheries, Seafood Division, Finfish Section, Baton Rouge, Louisiana 70803-7503.

² Goodyear, C. P. 1996. Status of the red drum stocks of the Gulf of Mexico: report for 1996. Rep. MIA 95/96-47, 21 p. Miami Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149.

$$\begin{aligned}
 l_t &= L_\infty (1 - e^{\beta_1 + \beta_2 - k_0(t-t_0)}) \\
 \beta_1 &= \frac{k_1}{\lambda_1} (e^{-\lambda_1 t} - e^{-\lambda_1 t_0}) \\
 \beta_2 &= \frac{k_2}{4\pi^2 + (\lambda_2)^2} \left[\begin{array}{l} e^{-\lambda_2 t} \left(\begin{array}{l} 2\pi \cos\{2\pi(t_c - t)\} - \\ \lambda_2 \sin\{2\pi(t_c - t)\} \end{array} \right) - \\ e^{-\lambda_2 t_0} \left(\begin{array}{l} 2\pi \cos\{2\pi(t_c - t_0)\} - \\ \lambda_2 \sin\{2\pi(t_c - t_0)\} \end{array} \right) \end{array} \right] \quad (6)
 \end{aligned}$$

Assuming the animal will not shrink with age, i.e., $dl/dt \geq 0$, implies the constraint

$$k_0 + k_1 e^{-\lambda_1 t} + k_2 e^{-\lambda_2 t} \sin(2\pi(t - t_c)) \geq 0. \quad (7)$$

Equation 6 may appear formidable, but typically requires only a minute or two more to enter into standard statistical fitting packages. It reduces to a form similar to the Gompertz equation when $k_2 = 0$ and to the von Bertalanffy equation when $k_1 = k_2 = 0$.

Fitting the model to data

Equations 1, 2, 3, and 6 were fitted to observations of length-at-age from red drum collected in the northern Gulf of Mexico between September 1985 and October 1998 (see Beckman et al., 1988, or Wilson et al.³ for further details regarding the data collection and aging procedures). The fitting was accomplished by ordinary least squares by using a Nelder-Mead simplex search⁴ and, as a check, proc NLIN of SAS (1990). The least-squares solution is equivalent to the maximum likelihood solution when the distribution of length at age is normal with constant variance, which seems to be approximately true of this particular data set (Porch, unpubl. data).

Akaike's (1973) information criterion (AIC) was used to rank the growth models in terms of their ability to provide statistically parsimonious explanations of the data. The formula for the AIC may be written

$$AIC = -2 \log(L) + 2p,$$

where L is the likelihood function and p is the number of parameters (see Buckland et al., 1997). In this case, $-2 \log(L)$ is equal to the residual sums of squares.

³ Wilson, C. A., D. L. Nieland and A. L. Stanley. 1993. Variation of year-class strength and annual reproductive output of red drum *Sciaenops ocellatus* and black drum *Pogonias cromis* from the northern Gulf of Mexico. Final Report 1991-1992, 31 p. U.S. Dept. Commerce Cooperative Agreement NA90AA-H-MF724. Marine Fisheries Initiative (MARFIN) Program. Coastal Fisheries Institute. Louisiana State University, Baton Rouge, La 70803-7503.

⁴ Shaw, D. E., R. W. M. Wedderburn, and A. Miller. 1991. A Program for function minimization using the simplex method. CSIRO, Division of Mathematics and Statistics, P.O. Box 218, Lindfield, N.S.W. 2070, Australia.

Table 1

Akaike's information criteria (AIC) quantifying the fit of the various growth models to the red drum length-at-age data. Smaller AIC values indicate statistically better fits.

Model	Number of parameters	Negative log-likelihood	AIC (-25,000)
von Bertalanffy	3	16045.9	7098
Richards	4	14169.8	3348
linear von Bertalanffy	4	12883.8	776
double von Bertalanffy	5	12876.6	763
damped (Eq. 6, $k_2=0$)	5	12651.3	313
seasonal + damped (Eq. 6)	8	12584.9	186

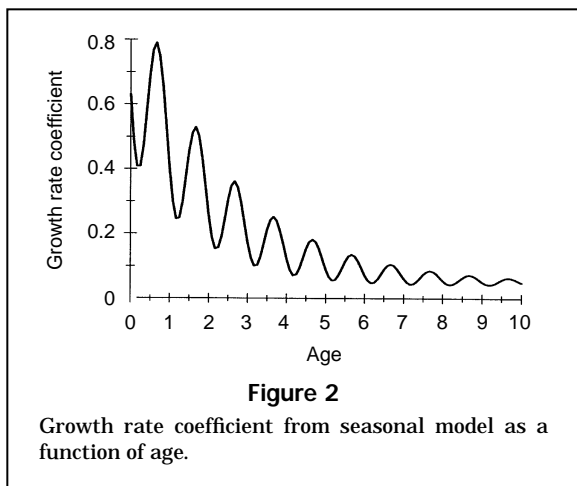
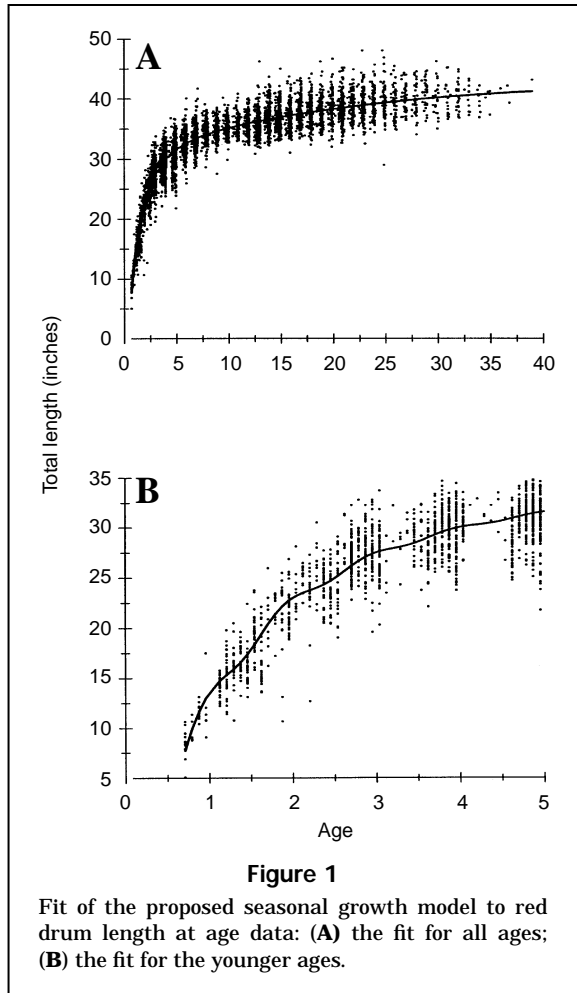
The parameter estimates for the Richards equation tended to be unstable unless good initial estimates were provided. This was accomplished by conducting the estimation in two stages. In the first stage the exponent δ was fixed to 1 and the other parameters were estimated, reducing the Richards equation to the von Bertalanffy form. In the second stage the initial guesses were set equal to the final estimates from the first stage and then all four parameters were estimated simultaneously.

Results and discussion

All five alternative growth models fitted the data significantly better than the von Bertalanffy equation according to the AIC statistic (Table 1). The Richards equation, however, did not fit the data nearly as well as the other alternative formulations and suffered from well-known instability problems (Ratkowsky, 1983), therefore it can probably be dropped from any future consideration with respect to red drum. The double von Bertalanffy curve fitted the data better than the linear von Bertalanffy curve, but the comparison is rendered moot by the performance of the new model. The five-parameter version without seasonal oscillations (Eq. 6 with $k_2=0$) fitted the data significantly better than either. The eight-parameter version with seasonal oscillations fitted the data significantly better still (see Fig. 1).

The estimated seasonal component to the growth rate was fairly substantial initially, having an amplitude at age 0 of 0.301 (k_2) and a peak in June, but declined rapidly with age (Fig. 2). It is possible that an even stronger seasonal signal would have been estimated if age-0 fish, which exhibit the strongest seasonal pattern (Goodyear⁴), had been adequately represented in the sample.

Some of the parameter estimates were highly correlated, as is the case in most growth studies. In particular, the correlations between the estimates for the growth rate and asymptotic length coefficients were typically above 0.8. However, the asymptotic variance-covariance matrix



suggests that the parameters for all of the models were estimated fairly precisely (Table 2).

The new model, either with or without the seasonal component, has both practical and theoretical advantages over the four other models examined in this study. By virtue of its greater flexibility, it was able to fit the red drum

Table 2
Parameter estimates and corresponding coefficients of variation (CV) derived from the asymptotic covariance matrix.

Model	Parameter	Estimate	CV (%)
von Bertalanffy	l_{∞}	37.7	1
	k	0.323	1
	t_0	-0.646	3
linear von Bertalanffy	b_0	32.5	1
	b_1	0.284	1
	k	0.590	9
	t_0	0.126	1
double von Bertalanffy	l_{∞}	40.0	1
	k_1	0.412	1
	t_1	0.0530	23
	k_2	0.114	2
	t_2	-8.41	3
damped (Eq. 6, $k_2=0$)	l_{∞}	44.1	1
	k_0	0.0416	7
	t_0	0.362	3
	k_1	0.667	2
	λ_1	0.464	1
	t_c	0.439	3
seasonal and damped	l_{∞}	43.4	1
	k_0	0.0475	5
	t_0	0.443	3
	k_1	0.695	2
	λ_1	0.476	1
	k_2	0.301	16
	λ_2	0.344	22
	t_c	0.439	3

data significantly better than the linear and double von Bertalanffy curves (its nearest competitors). Moreover, the Richards and linear von Bertalanffy curves are theoretically disadvantaged because their parameters have no physical interpretation. The double von Bertalanffy curve, although it has a physical interpretation, suffers because it allows only a single discontinuous change in the growth rate at one age rather than a continuous change through time. For these reasons, the new model should be more widely applicable than the others, particularly for species that change habitat preferences with age or are subject to strong seasonal environmental fluctuations.

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