Review of paper by Potts, Murton and Myers entitled “Age, growth, and natural mortality of schoolmaster (*Lutjanus apodus*) from the southeastern United States.”

This paper provides estimates of age, growth, natural mortality, and relationships between weight and length, and total and fork length, for a species of lutjanid. The study appears to be the first to provide estimates of age and growth for this species and is thus of potential value. Although some aspects of this study are adequate, there are a range of important issues that would need to be addressed before I could recommend this paper for publication.

The authors have used a standard technique for providing estimates of age of *L. apodus*, i.e. based on counting opaque zones on sectioned sagittal otoliths, viewed microscopically, as appropriate. However, there is no mention as to whether imaging software was used, as is now fairly standard, particularly for relatively long-lived species. As such software allows the locations of the various zones to be marked and checked, this can improve reliability of results.

Given that three sections were taken of each otolith, the authors also need to state which one(s) was used as the basis for providing a zone count for each species (hopefully the one sectioned through the primordium?) (line 109). From the description of the otolith sectioning process, and otolith picture, the sections do seem unnecessarily thick (0.5 mm) (line 109). Normally, thinner sections (0.3 mm) would be expected to improve readability.

In the results, it states that when there were differences between opaque zone counts between the two independent readers, that taken by the first authors was used (line 178-179), without justification (why should this reading be considered most accurate?). Also, the plot does not indicate that the second reader “overestimated” ages, rather it just demonstrates a difference between reader 1 and reader 2 (173-180). Clear justification is needed to state why the readings of the first author were accepted over those of the second author.

The von Bertalanffy growth equation should be provided and more description given regarding the fitting procedure (line 129). For example, the authors applied a method (described by McGarvey and Fowler, 2002), to correct estimates of growth parameters for bias associated with lack of samples of below the minimum size limit. However, the method described in that paper is based on a “truncated likelihood function” whereas this paper indicates that the growth models were fitted using least squares regression? It is also important that the level of precision in the parameter estimates be reported (i.e. 95% confidence limits). The precision in the parameter values resulting from the current growth models is likely to be poor (see below).

Of greatest concern with this paper is the fit of the growth curve to the length-at-age data. Although the authors state that the growth curve (using bias-corrected growth parameters) “fit the observed data well” (lines 236-237), this is clearly not the case, and a measure of goodness of fit is not provided (e.g. value for the coefficient of determination). A residual analysis would clear show that there is an issue with quality of model fit.

In the results (line 228), the authors recognise that the growth curves are not very informative beyond age 6 (most the life span of the species), and suggest this is related to small sample sizes. However, it reflects either an issue with the data (e.g. ageing errors, large outliers) or use of an inappropriate growth model. The estimated lengths-at-age plotted in figure 4 clearly separate into two clusters of points, with the two growth curves fitted in the study (i.e. “unweighted” and “weighted” von Bertalanffy growth curves) fitting well through the lower cluster of points and completely missing the upper cluster of points. Thus, the possibility that the data should be described by two growth curves cannot be ruled out.

If this is the case, the different growth curves could reflect a difference between the sexes (but noting that this cannot easily be examined because the fish were gutted, and thus the sex is not known). Given that the samples were collected over a long period, perhaps there are also temporal differences in growth (which should be explored). Alternatively, samples were from different populations or assemblages (inshore/offshore) exhibiting different growth patterns.

In any case, the current growth models are clearly inadequate for providing a good description of the observed length-at-age data. If exploratory analyses can identify the factor(s) for this apparent divergence in growth, and the data are able to be separated according to that factor, then separate growth curves should be fitted. A statistical test, e.g. likelihood ratio test, should then be used to ascertain whether the use of separate growth curves provide a statistical improvement over the initial model, assuming that growth of all fish can be described by a single curve.

If the reason for the divergence is not able to be determined, then perhaps an alternative growth model should be used. I have provided a suggestion at the end of this review which may be useful for providing an improved description of growth.

The issues with growth estimation will impact on the reliability of the estimates of natural mortality. Given the uncertainties in estimating growth, in particular, the estimate based on maximum age from the equation of Hewitt and Hoenig (2005) may yield the most reliable value for fish that have become selected into the fisher (but noting that the recorded maximum age is based on a very low sample size, and the value of maximum age differed between the two readers).

Given the type of data collected, it is not possible to ascertain whether selectivity should be described by a dome-shaped curve or asymptotic curve (lines 264-266), and references need to be provided to support this conclusion based on similar-sized congeners.

Although the fitting of weight-length relationships assuming a multiplicative error structure (and using a bias-correction when back-transforming estimates) would appear appropriate, it would be useful to be able to evaluate the quality of the data and fit of the model based on a plot.

Relatively few references are provided in the discussion, and the research findings are not well compared with the results and conclusions of other studies for similar species. This text needs substantial development and refinement.

Suggestions for describing growth:

If deemed appropriate, a growth model allowing for divergence in growth, but without knowing the basis for that divergence, could be fitted to the length-at-age data for this species. To ensure that such a model would work, I have fitted a growth model to some simulated length-at-age data, and then to the actual length-at-age data, as provided for this species in the data file provided called "schoolmaster_agegrowth_03102016.xlsx". Initially, a model was fitted (based on the von Bertalanffy growth equation) assuming separate asymptotic lengths (L_∞), but a common growth coefficient (k) and value for the hypothetical age at zero length (t_0).

Denoting the two alternative values for the asymptotic length as L_∞^1 and L_∞^2, the estimated length at age of fish j based on the first curve, $\hat{L}_{t,j}^1$ was calculated as

$$\hat{L}_{t,j}^1 = L_\infty^1\{1 - \exp[-k(t - t_0)]\}\,,$$

and $\hat{L}_{t,j}^2$, the estimated length at age of fish j based on the second curve, as

$$\hat{L}_{t,j}^2 = L_\infty^2\{1 - \exp[-k(t - t_0)]\}\,.$$

The model was fitted using maximum likelihood estimation, where the likelihood of the length-at-age observation for each individual fish is considered as a joint likelihood, based on the observed value, and predicted values of length-at-age resulting from the two curves. Assuming normally distributed errors, on the basis of the normal probability density function, $L^1(L_{t,j})$, the likelihood of the length-at-age observation for fish j, if the growth of that fish was associated with the first curve, was

$$L^1(L_{t,j}) = \frac{1}{2\sqrt{\pi}\sigma_1}\exp\left[\frac{-\left(L_{t,j}-\hat{L}_{t,j}^1\right)^2}{2\sigma_1^2}\right]$$

where σ_1 is the standard deviation for the estimated lengths at age around the first growth curve, (assumed to be common across all ages), estimated as a parameter in the growth model. Likewise, $L^2(L_{t,j})$, the likelihood of the length-at-age observation for fish j, if the growth of that fish was associated with the second curve, was

$$L^2(L_{t,j}) = \frac{1}{2\sqrt{\pi}\sigma_2}\exp\left[\frac{-\left(L_{t,j}-\hat{L}_{t,j}^2\right)^2}{2\sigma_2^2}\right].$$

where σ_2 is the standard deviation for the estimated lengths at age around the second growth curve. As the fish must be associated with one or the other of the two curves, the contribution of the fish to the log-likelihood is λ_j, calculated as

$\lambda_j = \log_e\left[L^1\left(L_{t,j}\right) + L^2(L_{t,j})\right]$. The overall log-likelihood is $\lambda = \sum_j \lambda_j$.

Although I had no issues in fitting this model to simulated length-at-age data, there were difficulties in fitting it to the actual length-at-age data for this species. This appeared to be associated with the lack of any tendency for one of the curves to approach an asymptote. This issue was potentially overcome by using a (more robust parameterisation) of the von Bertalanffy growth curve (see Schnute, 1981). $\hat{L}_{t,j}^1$ may thus be calculated as

$$\hat{L}^1_{t,j} = L^1_1 + (L^1_2 - L^1_1)\left[\frac{1-\exp[-k^1(t-t^1_1)]}{1-\exp[-k^1(t-t^1_2)]}\right],$$

where L^1_1 and L^1_2 the estimated lengths estimated for specified reference ages t^1_1 and t^1_2, for the first growth curve, and k^1 is the growth coefficient for the first growth curve. Similarly,

$\hat{L}^2_{t,j}$ may be calculated as

$$\hat{L}^2_{t,j} = L^2_1 + (L^2_2 - L^2_1)\left[\frac{1-\exp[-k^2(t-t^2_1)]}{1-\exp[-k^2(t-t^2_2)]}\right],$$

where L^2_1 and L^2_2 the estimated lengths estimated for specified reference ages t^2_1 and t^2_2, for the second growth curve, and k^2 is the growth coefficient for the second growth curve.

Although a model of this type could be fitted (see Table 1, Figure 1), if such a model were to be used, work would be required to ensure that fitting procedure is robust. Further, a statistical test (e.g. likelihood ratio test) should be employed to determine whether the improvement in log-likelihood associated with the introduction of additional model parameters is statistically significant (i.e. to that of a single growth curve fitted to all data). If so, further research should be undertaken to elucidate whether there is a biological basis or other basis for the difference. Alternative error structures could also be explored. Although a model of this type does not overcome the issue of bias associated with gear selectivity, as highlighted in this paper, the question as to whether growth should be described by two curves rather than one curve would seem most important.

Table 1. Estimates of parameters of the above described growth model, fitted to the data for *Lutjanus apodus* in Excel.

Parameters		ln (values)	values				
curve1	L2	6.31391769	552.2041		Reference ages		
curve1	L1	5.56605637	261.4012		curve1	t1	3
curve1	k1	-14.791809	3.77E-07		curve1	t2	7
curve1	sd1	3.80250369	44.81324		curve2	t1	3
curve2	L2	5.91933805	372.1653		curve2	t2	10
curve2	L1	5.58306754	265.886				
curve2	k2	-2.4289572	0.088129		LL	-635.47425	
curve2	sd1	3.26601498	26.2067				

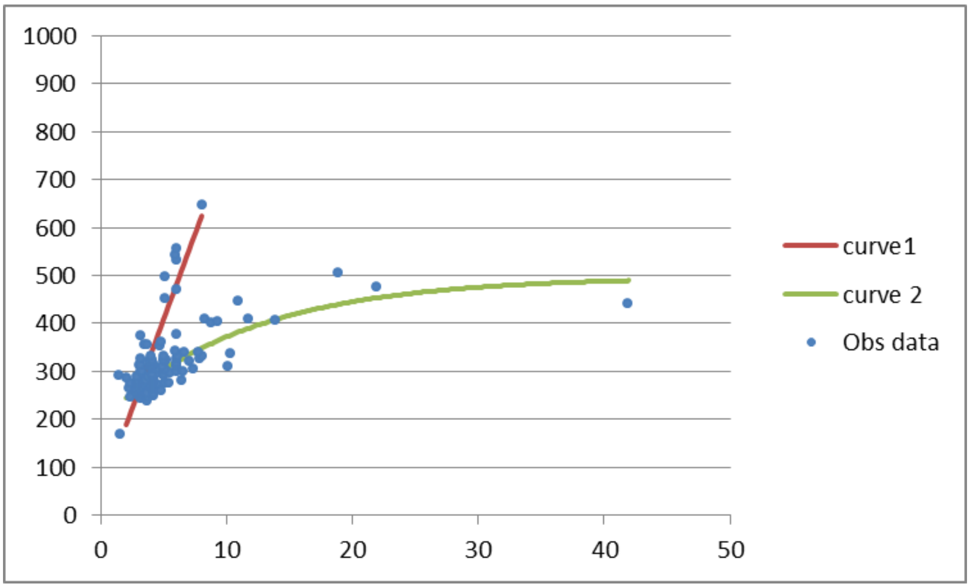

Figure 1. Preliminary fit of the growth model to the data for *Lutjanus apodus.*