Batch-fecundity and maturity estimates for the 2004 assessment of red snapper in the Gulf of Mexico

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The previous assessment of red snapper in the U.S. Gulf of Mexico modeled the per capita fecundity of the red snapper population as the product of batch fecundity at length (based on data from Collins et al, 1994) and maturity at length (based on data from Wilson et al, 1994). Age-specific estimates were then obtained by use of a growth function (Schirripa and Legault 1999). Since then, two new unpublished data sets have become available (PCL, Fitzhugh et al., 2004; and USA, Cowan et al, 2003). Based in part on the results of some preliminary analyses presented at the 2004 Red Snapper Data Workshop, it was recommended that the two data sets be combined for use in the assessment (SEDAR, 2004). This paper presents the results of the suggested analyses.

Methods

Data

Batch fecundity was determined using the hydrated oocyte method described by Hunter et al. (1985). Maturity status was assigned to females with vitellogenic or higher stage oocytes. Note that this is a more conservative approach than originally used by Fitzhugh et al (2004) as it does not include inactive females displaying evidence of prior spawning. As a result, 41 females previously considered mature by Fitzhugh et al. (2004) are now considered immature for the sake of consistency between the two data sets. Further details regarding the data may be gleaned from the papers cited.

Models

Schirripa and Legault (1999) fitted a power function to paired observations of batch fecundity (BFE) and total length in inches (*l*) from Collins et al (1994):

$$(1) \qquad BFE = al^{b} + \varepsilon$$

where a=0.1681 and b=5.57 (ε representing random model error). They then related length to age by use of a growth function fitted to age-length pairs from another data set, essentially obtaining

$$(2) \qquad BFE = al_{\infty}(1-e^{-k(t-t_0)})^{b}$$

where t is age, l_{∞} =34.54 inches, k=0.16, and t_0 =0.04666. (In point of fact they corrected equation 2 to account for the difference between the mean fecundity at age and the fecundity at the mean length at age, however this makes very little difference to the overall trend.)

In this paper equation (2) is applied directly by fitting BFE to age. In this case a and l_{∞} are completely confounded and must be represented by a single parameter c. Moreover, in practice, b and t_0 turn out to be highly correlated and nearly identical curve shapes can be achieved with t_0 fixed to zero. Hence the actual model used was

$$(3) \qquad BFE = c(1 - e^{-kt})^{d} + \varepsilon$$

where t is age, ε represents an additive model error and c, d and k are parameters to be estimated by nonlinear regression. In principle, equations (2) and (3) should produce nearly identical curves if the parameters are estimated from the same data sets and fecundity does not depend on age beyond the dependence of length on age.

Schirripa and Legault (1999) fitted a linear function to the aggregate proportions of females mature (P) from Wilson et al (1994):

$$(4) \qquad P = \begin{cases} 0 & l < 10.5 \\ 0.35l - 3.64 & 10.5 \le l \le 13.2 \\ 1 & l > 13.2 \end{cases}$$

This in turn was converted to maturity at age using the 1999 growth function mentioned in connection with equation (2). In this paper P is modeled as a logistic function of age

$$(5) \qquad P = \frac{1}{1 + e^{-(\alpha + \beta t)}}$$

A binomial error structure is assumed and the parameters α and β are estimated by a logistic regression applied to the individual responses (mature or not). Individual responses are used rather than aggregate proportions to better accommodate small samples and account for variations in sample size.

The functions developed by Schirripa and Legault (1999) were conditioned on length and then converted to functions of age by use of the growth curve, therefore they will hereafter be referred to as length-conditioned methods (the age conversion being implied). The models fitted in this paper are conditioned on age and therefore will be referred to as age-conditioned.

Results

The trends in maturity and batch fecundity both differed significantly between data sets (PCL or USA). The data workshop participants recognized this, pointing out that the PCL data were obtained opportunistically from diverse sources over a broad time span and wide range of areas while the USA samples were obtained by more intensive sampling over a short time from two rather restricted areas. Nevertheless, there was no agreement as to which of the two data sets best represented the red snapper population as a whole and the final report indicated they should simply be combined. This being the case, all further analyses proceeded using the combined data with no distinction as to the source.

When the combined data set was used, the trends in maturity were found to differ across modes (principally commercial, charter, and scientific samples), years, and areas (east or west). There were no clear trends in the year effects and the mode effects were poorly estimated. Accordingly, both year and mode were treated as random effects in the final model. The area effect was accommodated by estimating distinct values of α and β for locations east and west of the Mississippi river, effectively the same as analyzing the data from each area separately. An additional analysis was conducted without area effects to produce a curve appropriate for a single-stock analysis. The results are shown in Figure 1.

The trends in batch fecundity did not differ significantly among areas or years when the PCL and USA data were combined. Therefore a single curve was developed to represent both areas (Figure 2). Area-specific differences are apparent, however, when the source of the data is considered (i.e., there is a significant and area/source interaction effect). More samples from a broader range of areas are needed to determine if these differences are truly reflective of the overall red snapper population or merely artifices of restricted sampling locations.

The per-capita fecundity at age vectors (product of BFE and maturity) for the area-combined and area specific cases are compared with the length-conditioned equivalent used for the previous assessment in Figure 3. The differences in the curves representing the east and west are almost indiscernible because the differences in maturity occur at ages when relatively few eggs are produce. More importantly, the new age-conditioned curves suggest the age of maximum productivity is achieved at much younger ages than indicated by the old length-conditioned curves. The difference between these to curves primarily reflects the difference between the respective batch fecundity relationships (Figure 4). There are two possible explanations for the difference between the age and length-conditioned BFE curves: (1) fecundity depends on age, perhaps in addition to length, or (2) fecundity depends primarily on length, but the growth rates implicit in the fecundity data are different from those estimated by the growth curve. Inasmuch as the new age-dependent curve ascends to near the asymptote at a much younger age than the length-dependent (age-converted) curve, the first explanation would imply that old fish produce fewer progeny than a teenage fish that has attained the same size. The second explanation implies that either the fecundity data or the growth-curve data are biased.

Nearly all of the fecundity data were obtained from various fisheries subject to a minimum size limit and are therefore clearly biased towards larger fish at age. If batch fecundity is primarily age-dependent, then this type of sampling deficiency would have little effect on the age-conditioned model (equation 3). The length-conditioned model, however, would be unable to account for any changes in fecundity with age over and above the changes that occur in length. On the other hand, if batch fecundity is primarily a function of length, then including only larger fish in the sample would tend to make younger age classes appear proportionally more productive than they actually are in the population and bias the age-conditioned model accordingly.

In the case of red snapper, nearly all fish older than age 5 are above the size limit, so the size-bias effect should be negligible for regressions on age 6 and older. This implies that, if batch fecundity is primarily a function of length and size-biased sampling is important, then the age-conditioned model fit without younger fish should be substantially different from that fit with all ages. Such a comparison is made in Figure 5. Qualitatively speaking, the curve estimated without the younger fish does predict a lower fecundity at these ages than the curve estimated with all ages, however the curves are not significantly different according to the AIC. Moreover, the difference in magnitude is far smaller than the difference between the age-conditioned model and length-conditioned models shown in Figure 3. Thus, size-bias in the fecundity data does not seem to be a major cause of the discrepancy between the age and length-conditioned models.

The length-conditioned batch fecundity model should be relatively unaffected by size-biased sampling (other than the issue of effective sample size), but the conversion to an age-dependent curve still requires the use of a growth curve. Assuming for the moment that batch fecundity depends only on length, then the minimal size-bias effect demonstrated in Figure 5 suggests that the difference between the age and length conditioned models is primarily due to the growth curve. Accordingly, a new growth curve was fit to the age-length pairs in the batch fecundity data set and subsequently used to convert the length-conditioned estimates (Figure 6). The resulting length-conditioned estimates are much more similar to the age-conditioned estimates than when the old (1999) growth curve was used.

Discussion

The choice between age-conditioned and length-conditioned estimators of per-capita fecundity depends on one's perception of whether batch fecundity is fundamentally dependent on length or age. In practice, it may be difficult to distinguish an age-effect over and above the dependence of length on age. Nevertheless, it is important to consider the implications of each view.

Implications for estimation when fecundity is dependent only on length.

The age-conditioned and length-conditioned methods presented here should produce similar curves when fecundity is predominantly a function of length, provided the data are not size-biased. In the present case, however, the data are primarily fishery dependent and fish below the minimum size limit are rare. Thus, the average size of young fish in the data set is greater than in the population and the age-conditioned approach will tend to over-estimate the fecundity of the younger fish. This bias would not affect the length-conditioned approach in terms of the fitted fecundity and maturity relationships, however it would affect the conversion to age inasmuch as a growth curve fitted to the same data would tend to overestimate the size at age of younger fish relative to the true population. Accordingly, the age-converted length-conditioned model will be biased in similar fashion to the age-conditioned model. If, however, it is possible to develop a unbiased growth curve from other data, then the length-conditioned estimates may be converted to age with little bias.

In the present case we compared the effects of two growth curves, the one used in 1999 and a new one fit to the age-length pairs in the fecundity data set itself. The old curve predicted much smaller sizes at age than the new curve, which turned out to be the primary explanation for why the 1999 and 2004 per-capita fecundity curves were so different. Both growth curves were based partly on fishery-dependent data and therefore are probably size-biased owing to the truncation effect of various minimum size limits. Nevertheless, the old growth curve predicts smaller sizes at age than can be accounted for by size limit effects alone (see Diaz and Ortiz?, in prep.). While this could reflect an increase in growth rates, it could also be a function of changing selectivity or simply an increase in the relative proportion of fishery dependent observations. In any case, it is important to identify the curve that best represents the overall population.

Implications for estimation when fecundity is dependent on age.

If fecundity depends solely on age, then the age-conditioned approach is more appropriate than the length-conditioned approach and size-bias is irrelevant beyond issues relating to sample size (excluding small fish generally implying that young fish are under-represented). There is some evidence of an age effect in Figure 6, where the age-conditioned estimates for ages 8 to 20 are seen to be consistently greater than the corresponding values from the length-conditioned estimates (even when the growth curve was from the same data set and should therefore reflect and size-bias effect if it exists). However, this does not rule out the possibility that there is also a length effect; it may simply be that youth is a contributing factor (in this case younger fish appear to be more productive than older fish of the same size). If both age and length are important determinants of fecundity, and length is a function of age, then an age-conditioned approach is required. If the data are size biased it may still be possible to filter out the effects of the bias by use of a model where the age and length effects are assumed to be separable. Otherwise, it is necessary to obtain fecundity data that is not size biased.

Implications for the assessment.

The per-capita fecundity curves based on the new data (age-conditioned or length-conditioned converted by the new growth curve) suggest that fish between the ages of six and twenty are a much more important component of the spawning population than was assumed during the previous assessment. Naturally this would be expected to raise the apparent spawning potential ratio (spr) for the stock, all other things equal. This was examined by comparing the spawning potential ratios predicted with the new age-conditioned per capita fecundity vector to those predicted with the old 1999 vector when the natural mortality, bycatch mortality and directed-fleet selectivity vectors were fixed at the levels estimated during the previous assessment. The increase appears to be substantial, between 20 and 35% for spr values between 20% and 40% (Figure 7).

Summary conclusions

1) The new per capita fecundity at age vector suggests that young fish are more productive than previously thought.
    a. The change has little to do with the additional fecundity data; the length-conditioned estimates of relative per-capita fecundity are similar to those developed in 1999 when the same growth curve is used.
    b. The change is mostly due to the difference in perceptions of growth; the growth curve developed from the age-length pairs in the fecundity data base indicate more rapid growth than the one used in 1999, with the result fish of a given size (and fecundity) are assigned younger ages.

    c. The age and length-conditioned estimators produce similar results when the growth curve is fitted to the age-length pairs in the fecundity data set.

2) The spawning potential ratio is between 20 and 35% greater with the new fecundity vector than with the 1999 vector.
3) The choice between the methods presented in this paper should be guided by the following considerations:
    a. If fecundity depends primarily on length and the data are *not* size-biased, the age-conditioned and length-conditioned (age-converted) approaches should give very similar results.
    b. If fecundity depends primarily on length and the fecundity data *are* size-biased, then
        i. if an unbiased population growth curve is available, the length-conditioned approach should be used
        ii. if an unbiased growth curve is not available, unbiased fecundity data are required
    c. If fecundity depends primarily on age then size-bias is irrelevant and the age-conditioned approach should be used.
    d. If fecundity depends on both age and length, and the data are *not* size-biased, the age-conditioned approach should be used.
    e. If fecundity depends on both age and length, and the fecundity data *are* size-biased, then either
        i. A model with separable age and length effects must be applied, in which case there may be some concerns regarding model parsimony (over-parameterization), or
        ii. Unbiased fecundity data are required.

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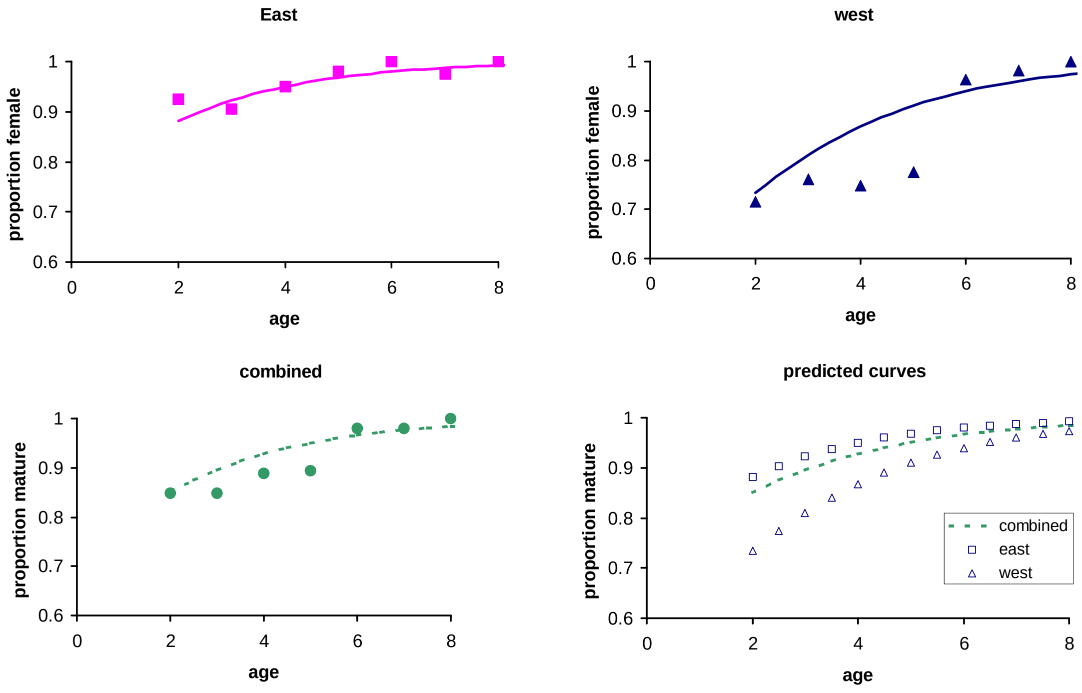


Figure 1. Logistic regressions of maturity data based upon individual responses. Proportions indicated by symbols are aggregated over year and mode; they are for reference purposes only and are not the quantities fit by the model

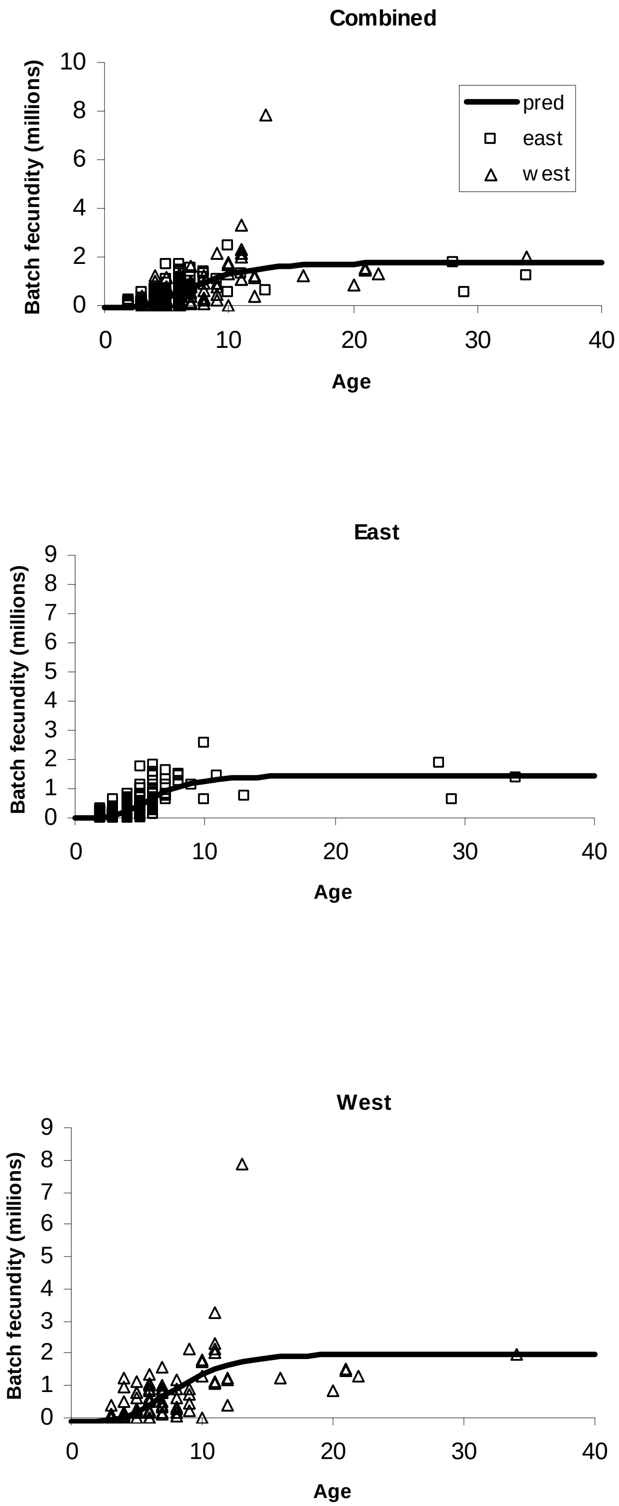
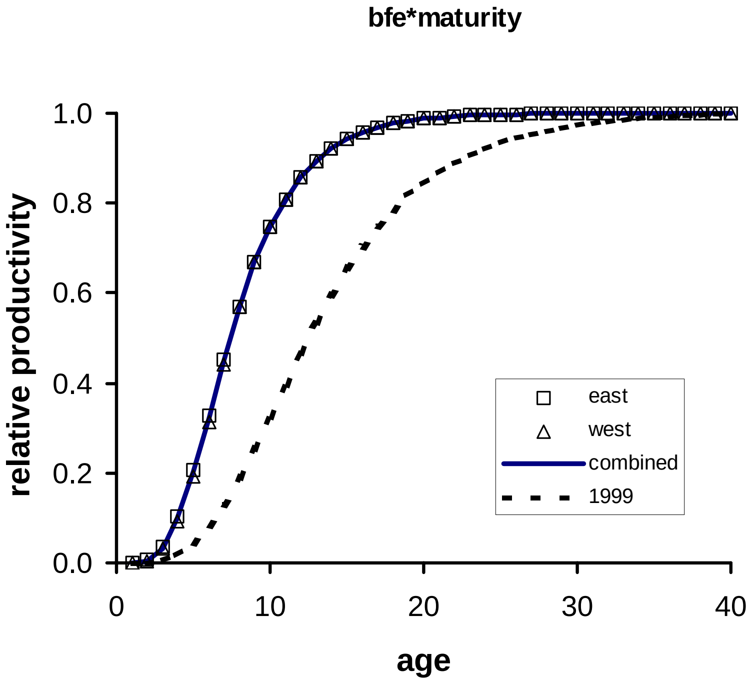


Figure 2. Nonlinear regressions of batch fecundity against age. The difference between the curves for the east and west, although discernible, was not statistically significant.



Fi**gure 3**. Product of batch fecundity at age (east and west combined) and maturity at age (east and west distinct or combined) rescaled by the maximum value. The dashed line represents the curve used in the previous assessment (Schirripa and Legault, 1999) The batch fecundity of younger animals (age 2 and 3) is so small that the differences observed in the maturation rates between the east and the west have no discernible effect on the relative production of each age class.

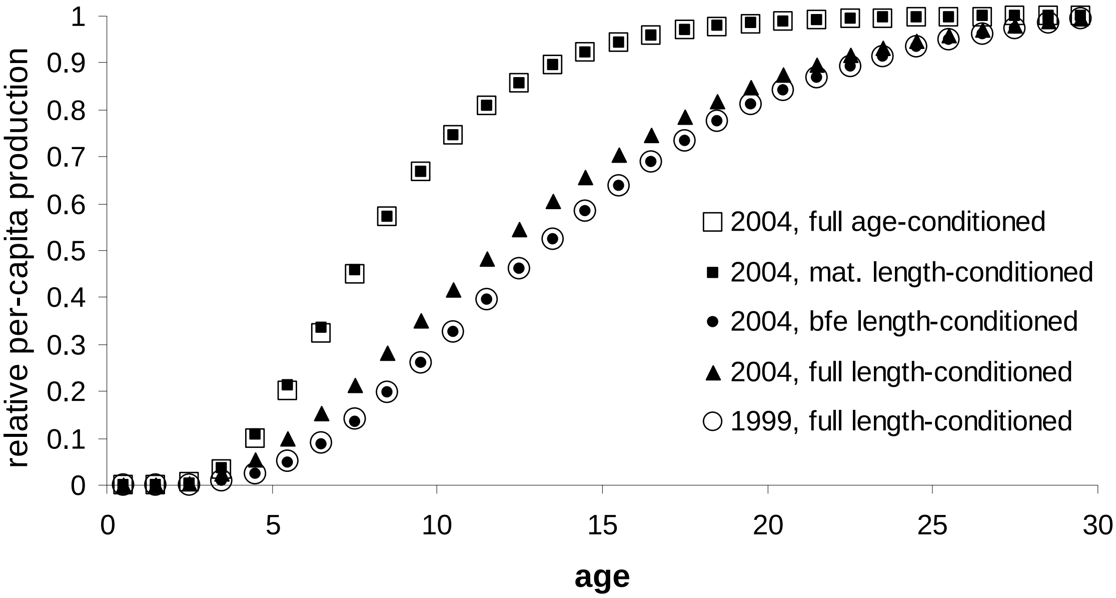


Figure 4. Comparison between the estimates of relative per-capita fecundity at age obtained with various treatments of the data. The effect of using the new data is seen in the contrast between the open circles (estimates used in 1999) and triangles (2004 data, 1999 method). The effect of using the new methods is seen in the contrast between the open squares (2004 data, 2004 method) and triangles (2004 data, 1999 method). The effect of changing the method of estimating maturity at age is isolated in the contrast between the open and closed symbols. The effect of changing the method of estimating the batch fecundity at age is isolated in the contrast between the circles and squares.

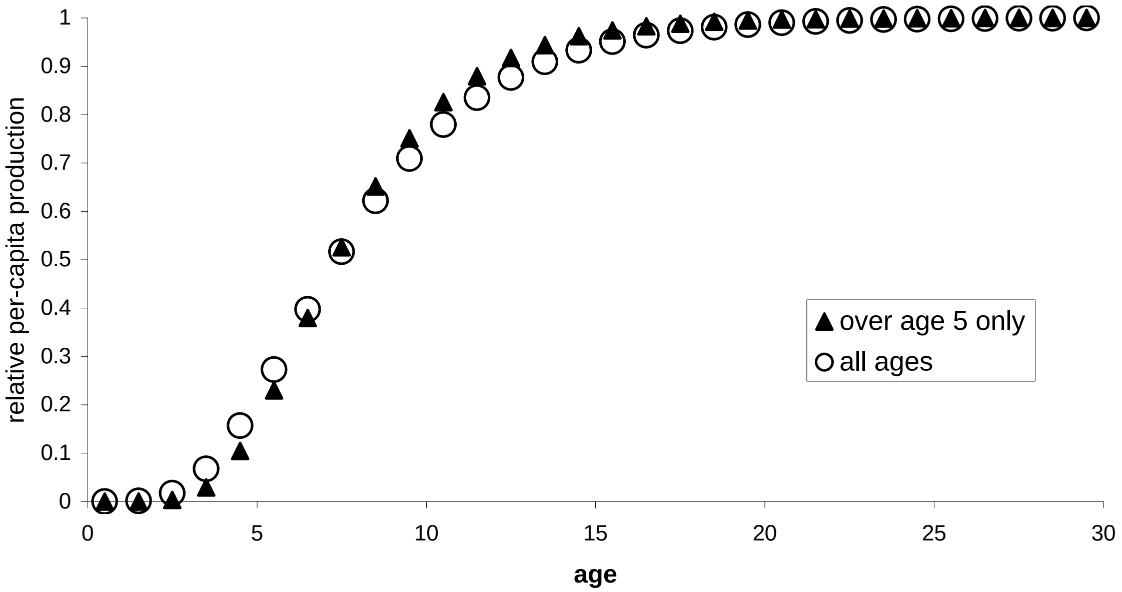


Figure 5. Effect of eliminating fish younger than 6 years old from the age-conditioned analysis of batch fecundity. The parameters obtained by fitting to ages 6 and older were not significantly different from those obtained by fitting to all ages (according to AIC).

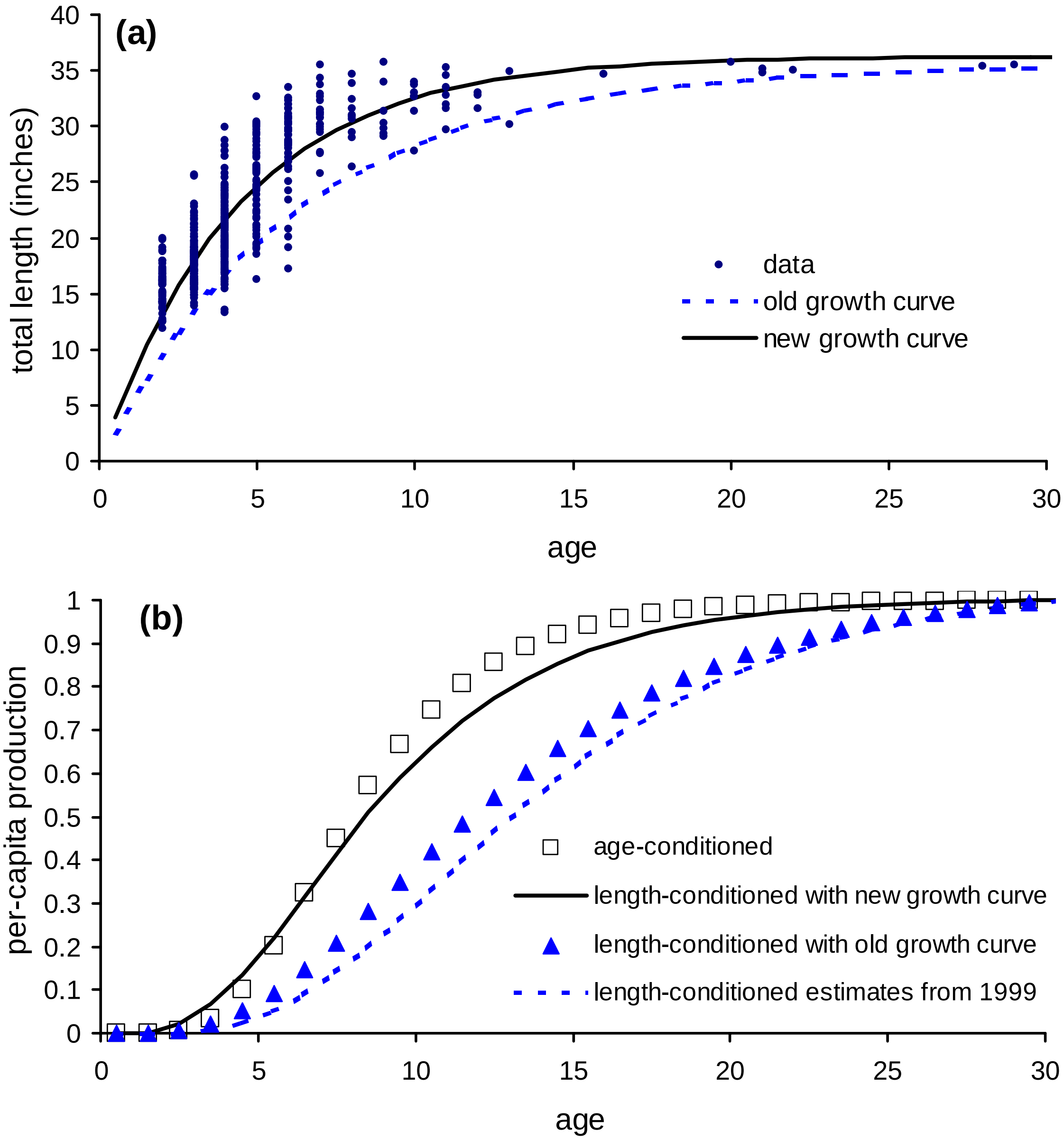


Figure 6. (a) Comparison of the ‘old’ growth curve used in the 1999 assessment and the ‘new’ growth curve estimated from the age-length pairs in the fecundity data base. (b) the trends in per capita production estimated when the batch fecundity at length relationship estimated from the 2004 data base is converted to length using the old and ‘new’ growth curves. Comparison of the triangles and dotted line reflects the effect of adding the new data. Comparison of the triangles and solid line reflects the effect of using the different growth curves to convert to age. Squares and solid line reflect the difference between applying the age-conditioned method and the length-conditioned method (when the growth curve is based on the same data as the fecundity curve).

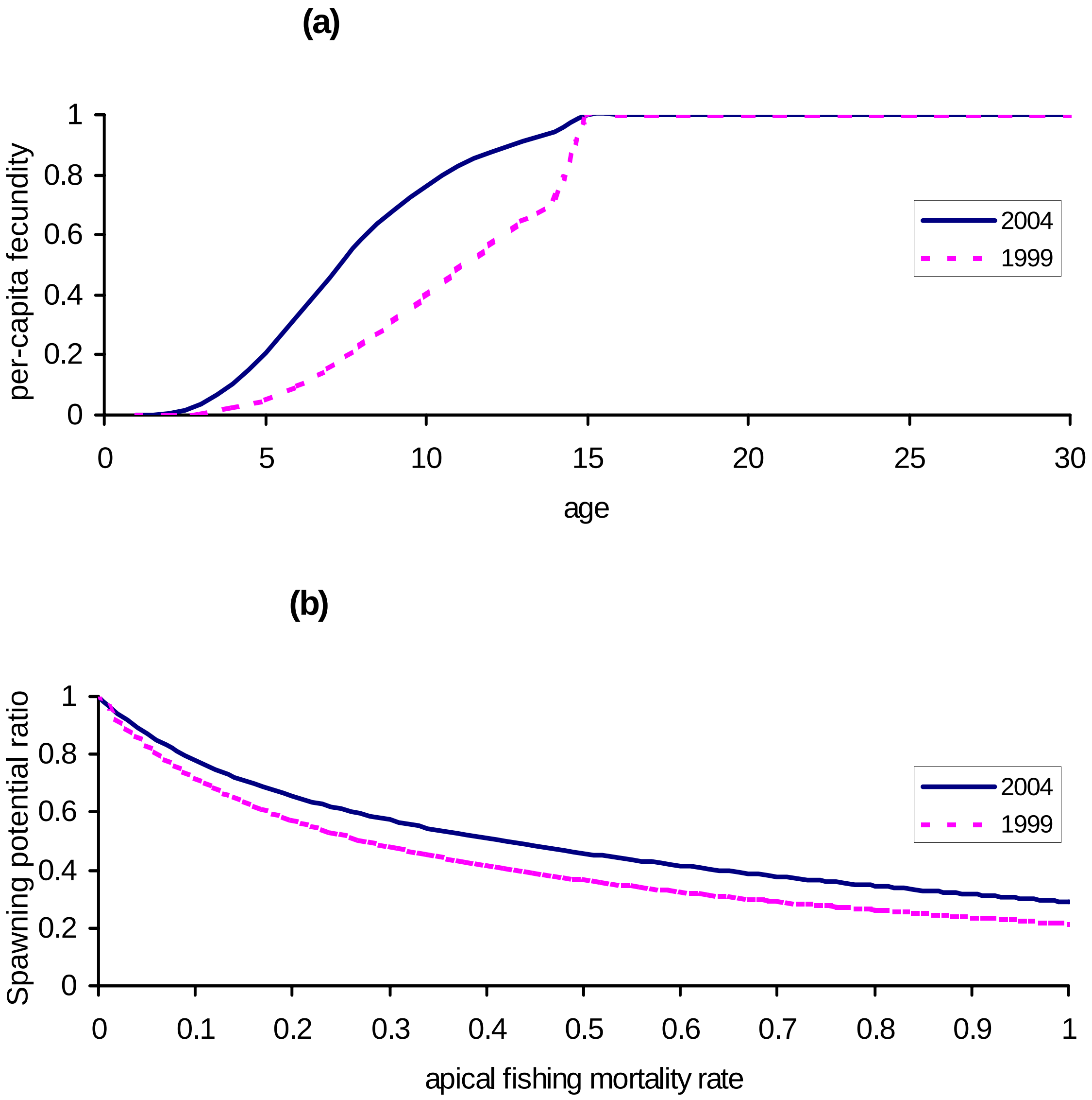


Figure 7. (a) Comparison of 2004 and 1999 per-capita fecundity vectors with a plus group at age 15 (a prorated average of ages 15-40 with an assumed total mortality rate of 0.15, as done in the previous assessment). (b) Comparison of the spaning potential ratios obtained with the two per capita fecundity curves.