Red Snapper Compensation in the Stock-Recruitment Function and Bycatch Mortality

--- ***J.E. Powers and E.N. Brooks, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149***

In this, we are concerned with the interaction of bycatch mortality before, during and after the stock-recruitment process.

Start with Beverton-Holt compensation during a period of time Δt:

$$(1) \qquad \frac{dR_t}{dt} = -AR_t^2 - M_c R_t \quad \Rightarrow \quad R_{t+\Delta t} = \frac{R_t \beta}{1+\alpha R_t} \qquad \text{or} \qquad R_t = \frac{R_{t+\Delta t}}{\beta - \alpha R_{t+\Delta t}}$$

where β=exp(-$M_c\Delta t$) and α= A(1-exp(-$M_c\Delta t$))/ M_c . The Beverton-Holt S-R function essentially models the process in terms of a density-dependent component of the natural mortality rate (AR_t) added to a density-independent component (M_c). Normally we think of M being density-independent and we use the equation:

$$\frac{dR_t}{dt} = -MR_t \quad \Rightarrow \quad R_{0+\Delta t_1} = R_0 e^{-M\Delta t}$$

However, in equation (1) the Beverton-Holt equation defines *M* as a density-dependent function $M(R_t)$=$A(R_t)$ + M_c. It is interesting to note is that as $t \to \infty$, then $M(R_t) \to M_c$. Thus, as the recruitment process goes along, the $M(R_t)$ function approaches a constant (approaches being density-independent). Also, we can relate the parameter M_c (the asymptotic value) to the parameterizations that we normally use with red snapper, i.e. the steepness (h) and the ratio of spawners to recruits at equilibrium with no fishing (ϕ):

$$(2) \qquad e^{-M_c\Delta t} = \frac{4h}{\varphi(1-h)} \qquad \frac{5h-1}{E_0(1-h)} = \frac{A}{M_c}\left[1-\exp(-M_c\Delta t)\right],$$

or

$$M_c = \frac{1}{\Delta t}\left[\ln\left(\frac{\varphi}{4}\right) + \ln\left(\frac{1-h}{h}\right)\right] \qquad A = \frac{1}{E_0}\left(\frac{5hM_c\varphi}{\varphi - h(\varphi+4)}\right)$$

where $E_0 = R_{0,eq}$, the number of egg produced in equilibrium when there is no fishing. Note that in (2), the spawner per recruit ratio (φ) is calculated with "spawners" being defined as the number of fish initiating the recruitment process, i.e. $E_0 = R_{0,eq}$, as well.

For M_c to be positive, then $\varphi > 4h/(1-h)$ and $h < \varphi/[4+\varphi]$. However, φ (the equilibrium ratio of eggs to recruits when there is no fishing) will be a large number for most recruitment processes. Therefore, $\varphi/[4+\varphi]$ will approximately equal 1, which always will be larger than h. Also, since φ will probably be a large number for red snapper (on the order of 10^6), then $M_c \approx \ln(\varphi/4)/\Delta t$.

Case I: bycatch mortality occurs *before* compensation

Assume bycatch mortality occurs during time period Δt_1 at a level of F_1, when natural mortality is density-independent at M_1 and that compensation occurs during time period Δt_2 .

$$\frac{dR_t}{dt} = (-F_1 - M_1)R_t \quad \Rightarrow \quad R_{0+\Delta t_1} = R_0 e^{-(F_1+M_1)\Delta t_1}$$

(3)

$$R_{0+\Delta t_1+\Delta t_2} = \frac{R_{0+\Delta t_1}\beta_2}{1+\alpha_2 R_{0+\Delta t_1}} = \frac{R_0\beta_2 e^{-(F_1+M_1)\Delta t_1}}{1+\alpha_2 R_0 e^{-(F_1+M_1)\Delta t_1}} = \frac{R_0 e^{-(F_1+M_1)\Delta t_1 - \mathrm{M}_c\Delta t_2}}{1+\frac{\mathrm{A}}{\mathrm{M}_c}R_0 e^{-(F_1+M_1)\Delta t_1}\left(1-e^{-\mathrm{M}_c\Delta t_2}\right)}$$

Note that the beta and alpha are specific to the duration of the second stage (Δt_2), hence the subscripts. Also, the bycatch during the first stage is calculated by the usual catch equation:

(4) $$C_{by,\Delta t_1} = R_0 F_1 (1 - e^{-(F_1+M_1)\Delta t_1})/(F_1 + M_1)$$

Case II: bycatch mortality occurs *during* compensation at a rate of F_d.

$$\frac{dR_t}{dt} = -\mathrm{A}R_t^2 - (\mathrm{M}_c + F_d)R_t \quad \Rightarrow \quad R_{t+\Delta t_d} = \frac{R_t\beta_d}{1+\alpha_d R_t}$$

(5)

$$= \frac{R_t e^{-(\mathrm{M}_c+F_d)\Delta t_d}}{1+\frac{\mathrm{A}}{\mathrm{M}_c+F_d}R_t\left(1-e^{-(\mathrm{M}_c+F_d)\Delta t_d}\right)}$$

where $\beta_d = \exp(-\mathrm{M}_c\Delta t_d - F_d\Delta t_d)$

and $\alpha_d = \mathrm{A}(1-\exp(-\mathrm{M}_c\Delta t_d - F_d\Delta t_d))/(\mathrm{M}_c + F_d)$

(6) $$C_{by,\Delta t} = \frac{F_d}{\mathrm{A}}\ln\left[1+\frac{\mathrm{A}}{\mathrm{M}_c+F_d}R_t\left(1-e^{-(\mathrm{M}_c+F_d)\Delta t}\right)\right]$$

Case III: bycatch mortality occurs *after* compensation

Bycatch Mortality occurs during time period Δt_2 at a level of F_2, when natural mortality is density-independent at M_2. Compensation occurs during time period Δt_1 .

$$R_{0+\Delta t_1} = \frac{R_0 \beta_1}{1 + \alpha_1 R_0}$$

(7)

$$R_{0+\Delta t_1+\Delta t_2} = R_{0+\Delta t_1} e^{-(F_2+M_2)\Delta t_2} = \frac{R_0 \beta_1 e^{-(F_2+M_2)\Delta t_2}}{1 + \alpha_1 R_0} = \frac{R_0 e^{-\mathrm{M}_c \Delta t_1 - (F_2+M_2)\Delta t_2}}{1 + \frac{\mathrm{A}}{\mathrm{M}_c} R_0 \left(1 - e^{-\mathrm{M}_c \Delta t_1}\right)}$$

Note again that the beta and alpha are time duration dependent. The bycatch equation is

(8) $$C_{by,\Delta t_2} = R_{0+\Delta t_1} F_2 (1 - e^{-(F_2+M_2)\Delta t_2}) / (F_2 + M_2)$$

We now have the Beverton-Holt equations for computing all combinations of before, during and after.

One *could* fit an S-R curve (i.e. the R_0 vs $R_{\Delta t_1+\Delta t_2+\Delta t_3+\Delta t_4+\Delta t_5+\ldots}$ curve) and get the parameters M_c and A using the normal fitting routines and solving for F_0 and F_1 using the appropriate catch equations. However, by doing so, it is being implicitly assumed that the timing and the mortality rates of the various stages have been resolved satisfactorily. Many renditions could be hypothesized depending upon the durations of the various time periods, density-dependent or density dependent mortality during each time period, and, indeed, if the compensation parameters change over time.

Comparison of Instantaneous and average M's

For comparison purposes we can calculate the average M over a particular time period as:

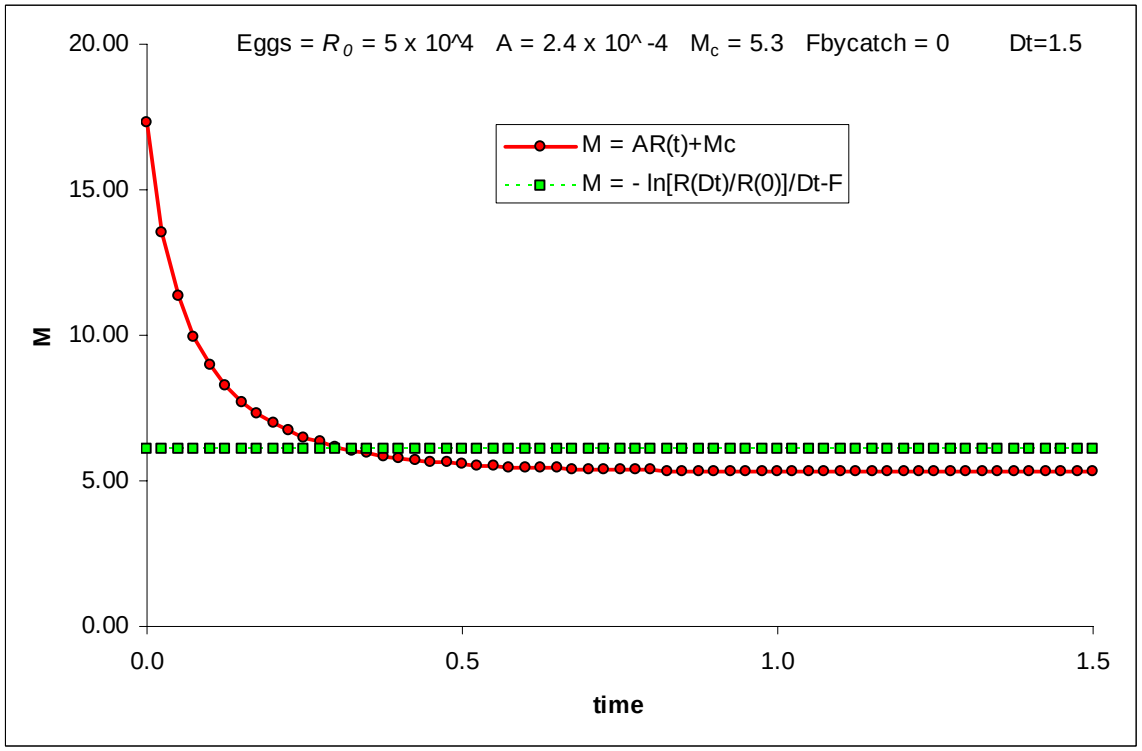
$$(9) \qquad R_{\Delta t} = \frac{R_0 \exp[-(\mathrm{M}_c + F)\Delta t]}{1 + \frac{\mathrm{A}}{\mathrm{M}_c + F} R_0[1 - \exp(-(\mathrm{M}_c + F)\Delta t)]}$$

$$Z_{\Delta t}\Delta t \cong (M_{ave} + F)\Delta t \cong -\ln\left[\frac{R_{\Delta t}}{R_0}\right]$$

$$M_{ave}\Delta t \cong -F\Delta t - \ln\left[\frac{\exp[-(\mathrm{M}_c + F)\Delta t]}{1 + \frac{\mathrm{A}}{\mathrm{M}_c + F} R_0[1 - \exp(-(\mathrm{M}_c + F)\Delta t)]}\right]$$

$$M_{ave} \cong \mathrm{M}_c + \frac{1}{\Delta t}\ln\left[1 + \frac{\mathrm{A}}{\mathrm{M}_c + F} R_0[1 - \exp(-(\mathrm{M}_c + F)\Delta t)]\right]$$

This difference between the average M and the instantaneous $M(R_t)$ are shown in the following **Fig 1**:



Implications of compensation timing for equilibrium calculations

Following are the equations for the number of age 2.25 recruits ($R_{2.25}$), according to the assumed timing of compensation (Figure 2), and previous derivations. Also, in what follows, the notation for the density independent mortality parameter, M_c given in equation (1) has been replaced by the notation M_x, with x being specified for the appropriate time period. F_{b0} and F_{b1} refer to bycatch mortality of age 0 and age 1 fish, respectively.

Case I – Bycatch occurs **before** compensation

$$R_{2.25} = \frac{E_0 \beta_2 \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1})}{1 + \alpha_2 E_0 \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1})} \quad \text{, where}$$

$$\beta_2 = \exp(-0.25M_2) \qquad \beta^I = \beta_2 \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1})$$

$$\alpha_2 = \frac{A}{M_2}(1 - \exp(-0.25M_2)) \quad \Rightarrow \text{ Let} \quad \alpha^I = \alpha_2 \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1})$$

Case II – Bycatch occurs **during** compensation [in this we are assuming that compensation occurs during the period 0 to 2 years and that the density-independent component of the mortality rate M_c is being denoted by $M_c = ½(M_0 + M_1)$; this is done so that Case II can be more easily compared to the other Cases].

$$R_{2.25} = \frac{E_0 \beta_{0-2} \exp(-.25M_2)}{1 + \alpha_{0-2} E_0} \quad \text{, where}$$

$$\beta_{0-2} = \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1})$$

$$\alpha_{0-2} = \frac{A}{0.5(M_0 + M_1) + F_{b0} + F_{b1}}(1 - \exp(-M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1}))$$

$$\beta^{II} = \beta_2 \exp(-.25M_2)$$

$\Rightarrow$ Let

$$\alpha^{II} = \alpha_2$$

Case III – Bycatch occurs **after** compensation

$$R_{2.25} = \frac{E_0 \beta_0 \exp(-0.75M_0 - M_1 - 0.25F_{b0} - 0.5F_{b1}) \exp(-.25M_2)}{1 + \alpha_0 E_0} \quad \text{, where}$$

$$\beta_0 = \exp(-0.25M_0)$$

$$\alpha_0 = \frac{A}{M_0}(1 - \exp(-0.25M_0))$$

$$\beta^{III} = \beta_0 \exp(-.75M_0 - M_1 - .25M_2 - .25F_{b0} - .5F_{b1})$$

➔ Let

$$\alpha^{III} = \alpha_0$$

Given the stock recruit relationship $R = \frac{E\beta}{1+\alpha E}$, then equilibrium statistics are as follows (*cf.* Ricker 1975: Computation and Interpretation of Biological Statistics of Fish Populations, Appendix III).

(10) The replacement line is $R = \frac{\mathrm{E}}{\varphi_0}$, where φ_0 is unfished spawners per recruit.

(11) setting (1) equal to the S-R curve and solving for E_0 (equilibrium unfished egg production):

$$E_0 = \frac{\varphi_0\beta - 1}{\alpha}$$

(12) equilibrium unfished recruits are then:

$$R_0 = \frac{\varphi_0\beta - 1}{\varphi_0\alpha} \quad .$$

(13) To find equilibrium egg production at Maximum Excess Recruitment[1] (MER), find the point on S-R curve with the same slope as the replacement line:

$$E_{MER} = \frac{\sqrt{\varphi_0\beta} - 1}{\alpha}$$

(14) equilibrium recruits at MER are then:

$$R_{MER} = \frac{\beta}{\alpha}\left[1 - \frac{1}{\sqrt{\varphi_0\beta}}\right]$$

(15) SPR_{MER} is the ratio of φ_{MER} to φ_0:

$$SPR_{MER} = \frac{E_{MER} \big/ R_{MER}}{\varphi_0} = \frac{1}{\sqrt{\varphi_0\beta}}$$

(16) MER (in number of surplus recruits) is:

$$R_{MER} - \frac{E_{MER}}{\varphi_0} = \frac{E_{MER}\beta}{1+\alpha E_{MER}} - \frac{E_{MER}}{\varphi_0} = \frac{1}{\alpha}\left[\sqrt{\varphi_0\beta} - 1\right]^2$$

[1] Note that if age structure and growth effects are small, then equilibrium statistics for MER and MSY are approximately equivalent. However, in the case of red snapper, it is not expected that MER and MSY statistics will be equivalent. Nevertheless, since MER statistics may be calculated independent of the growth and selectivity factors, they are used for purposes of demonstrating the effects of timing on equilibrium recruitment statistics.

Now, from the derivations on the previous page, substituting α^I and β^I, α^{II} and β^{II} or α^{III} and β^{III} from the three compensation timing scenarios, we can see the implications for equilibrium statistics of when bycatch is assumed to occur. First, notice that the redefined β parameters (β^I, β^{II} and β^{III}) are all equivalent, i.e.

$$\beta^I = \beta^{II} = \beta^{III} = \beta = \exp(-M_0 - M_1 - 0.25M_2 - 0.25F_{b0} - 0.5F_{b1}) .$$

The question of interest is how the timing of compensation affects the equilibrium statistics. One way to examine this is to take the ratio of E_{MER}, R_{MER}, and MER between Case I (or Case II) and Case III (the "base" case). Noting that the β parameters are all equal, and that φ_0 is the same for all scenarios, then the ratios all reduce to a comparison of α terms:

$$\frac{E_{MER,I}}{E_{MER,III}} = \frac{\sqrt{\varphi_0\beta} - 1}{\alpha^I} \times \frac{\alpha^{III}}{\sqrt{\varphi_0\beta} - 1} = \frac{\alpha^{III}}{\alpha^I} ,$$

$$\frac{R_{MER,I}}{R_{MER,III}} = \frac{\frac{\beta}{\alpha^I}\left[1 - \frac{1}{\sqrt{\varphi_0\beta}}\right]}{\frac{\beta}{\alpha^{III}}\left[1 - \frac{1}{\sqrt{\varphi_0\beta}}\right]} = \frac{\alpha^{III}}{\alpha^I} ,$$

$$\frac{MER_I}{MER_{III}} = \frac{\frac{1}{\alpha^I}\left[\sqrt{\varphi_0\beta} - 1\right]^2}{\frac{1}{\alpha^{III}}\left[\sqrt{\varphi_0\beta} - 1\right]^2} = \frac{\alpha^{III}}{\alpha^I} .$$

Given the derived values for α', α'', and α''', as defined by the timing assumptions in Figure 2, and the assumption that A is constant between the three cases, comparing equilibrium statistics for Case I (bycatch **before** compensation) to Case III (bycatch **after** compensation) leads to the following:

$$(17) \qquad \frac{\alpha^{III}}{\alpha^I} = \frac{M_2}{M_1} \times \exp(M_0 + M_1 + .25F_{b0} + .5F_{b1}) \times \frac{[1 - \exp(-.25M_0)]}{[1 - \exp(-.25M_2)]} .$$

In the above equation, one can assume that, in general, $M_0 > M_1 > M_2$. Thus, the first term on the right hand side is <1, while the second and third terms are >1. Therefore, whether there are more recruits at age 2.25 ($R_{2.25}$) when bycatch occurs before compensation as compared with the present assumption (bycatch occurs after compensation), depends on the magnitudes of the natural and bycatch mortalities as well as the amount of time that each force operates. However, for most reasonable values of M, the second term dominates and the ratio (17) is expected to be greater than 1 (see example below in Table 1).

Additionally, if A (the density-dependent component of natural mortality) differs with the age (or equivalently, the size) of a fish, then a further term in the above equation is A^{III} / A^{I} . One might argue that the magnitudes of A at age follow the same pattern as M at age, i.e. $A^{I} > A^{II} > A^{III}$. However, that notion will not be pursued any further in this report.

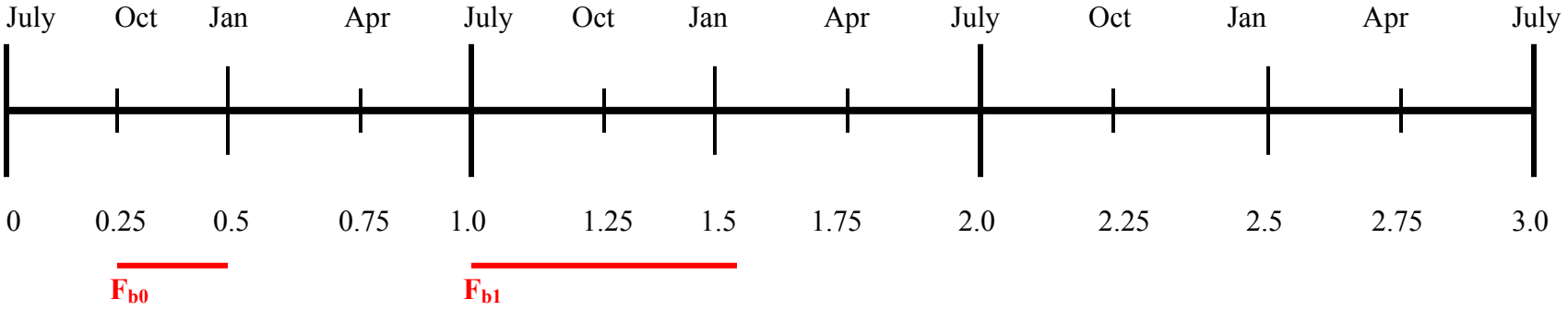
Similarly, comparing equilibrium statistics for Case II (bycatch **during** compensation) to Case III (bycatch **after** compensation) leads to:

$$(18) \quad \frac{\alpha^{III}}{\alpha^{II}} = \frac{0.5(M_0 + M_1) + .25F_{b0} + .5F_{b1}}{M_0} \times \frac{[1 - \exp(-.25M_0)]}{[1 - \exp(M_0 + M_1 + .25F_{b0} + .5F_{b1})]} \quad .$$

As before, arguing that $M_0 > M_1 > M_2$, then the first term on the right hand side is >1 (unless $0.5M_1$ and bycatch fishing mortality sum to less than half of M_0) , while the second term is <1. This implies that the magnitude and duration of natural and bycatch mortalities will determine whether more or less recruits survive to age 2.25 at equilibrium MER if bycatch occurs during the compensatory phase as opposed to after compensation (Table 2).

Note that the above alpha ratios invert the comparisons done in equation 18. For example, if you are comparing $E_{MER,I} / E_{MER,III}$, this is equal to $\alpha^{III} / \alpha^{I}$. So if $\alpha^{III} / \alpha^{I}$ is greater than one, then this implies that $E_{MER,I} / E_{MER,III}$ is greater than one and that $E_{MER,I}$ is greater than $E_{MER,III}$.

Figure 2. Assumed Timing of Mortality Processes.



Assumptions:
- **M_0 is constant from age 0 – 1;**
- **M_1 is constant from age 1 – 2;**
- **M_2 is constant from age 2 – 3;**
- **A from equation (1) – the density dependent component of mortality – is constant regardless of the timing of compensation ;**

Table 1. Examples of α^{III}/α^{I} from equation (17) using various input mortality rates. F_b is the cumulative mortality due to shrimp fishery bycatch.

Parameter	Value					
M_0	0.5	0.5	1	0.5	0.5	0.05
M_1	0.3	0.3	0.3	0.6	0.3	0.05
M_2	0.1	0.1	0.1	0.1	0.2	0.05
F_b	2.12	0	2.12	2.12	2.12	0
α^{III}/α^{I}	17.65	2.12	27.39	23.82	17.87	1.11

Table 2. Examples of α^{III}/α^{II} from equation (18) using various input mortality rates. F_b is the cumulative mortality due to shrimp fishery bycatch.

Parameter	Value					
M_0	0.5	0.5	1	0.5	1	3
M_1	0.3	0.3	0.3	0.6	0.6	2.5
M_2	Note: The value of M2 is not involved in this calculation					
F_b	2.12	0	2.12	2.12	4.24	3
α^{III}/α^{II}	0.63	0.17	0.63	0.65	1.12	1.01

Note that in Tables 1-2 the alpha ratio inverts the comparisons done in equation 18. For example, if you are comparing $E_{MER,I}/E_{MER,III}$, this is equal to α^{III}/α^{I}. So if α^{III}/α^{I} is greater than one, then this implies that $E_{MER,I}/E_{MER,III}$ is greater than one and that $E_{MER,I}$ is greater than $E_{MER,III}$.

For Reference: Below is the size at age from the von Bertalanffy model estimated with the truncated distribution (as a result of minimum size limits). Total length (TL) is in inches. This table may be useful for future discussions about survival or density-dependent components of mortality, and/or applications of a Lorenzen-type curve to relate magnitude of survival at age to length at age.

AGE	TL inches
0	0
0.5	1.0
1.0	4.5
1.5	7.6
2.0	10.4
2.5	12.9
3.0	15.2