Comment

Per-recruit modelling of pulse fisheries: comment on "Modelling pulse fishery systems in data-limited situations"

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A pulse fishery is one where fishing occurs during a short period each year and is zero for the rest of the year. Grüss *et al.* proposed a continuous per-recruit model for such fisheries. However, this analysis is based on per-recruit equations that were derived under the assumption that fishing mortality is constant in time and, thus, do not apply to fisheries where F varies, such as a pulse fishery. A correct continuous per-recruit formulation for pulse fisheries is derived. In most cases, the continuous per-recruit model can be closely approximated by a discrete model, where the integrals are replaced by sums. A modification in the Baranov catch equation for pulse fisheries is also derived that can used to compute annual exploitation rates.

Keywords: catch equation, per-recruit model, pulse fisheries, yield per recruit.

A fishery where fishing occurs during a short period each year but is zero for the rest of the year is termed a pulse fishery. Grüss *et al.* (2020) proposed a continuous per-recruit model for such fisheries. However, the basis for their analysis, their (1)–(3), is only valid when fishing mortality is constant in time and, hence, does not apply to fisheries where F varies, such as a pulse fishery. All of their subsequent results are based on these equations and are therefore also incorrect. The purpose of this note is to derive a proper per-recruit formulation for a pulse fishery.

The per-recruit model tracks a cohort starting at age a_0 and ending at age $a_f = a_0 + n$. When the cohort is between ages a_k and a_{k+1} ($k = 0, 1, \ldots, n-1$), it will be assumed that there is a pulse of fishing between ages $a_k + p_{\text{start}}$ and $a_k + p_{\text{end}}$, where $0 \leq p_{\text{start}} < p_{\text{end}} \leq 1$, during which time fishing mortality F is equal to a constant F_k, with $F = 0$ for all other times. Fishing mortalities are allowed to differ by year to take into account fishery selectivity by age.

Let $S(a)$ be the fraction of the cohort remaining at age a, with $S(a_0) = 1$. Then, the per-recruit equations for this situation are (Quinn and Deriso 1999, p. 255):

$$S(a) = \exp\left[-\int_{a_0}^{a} Z(t)\,\mathrm{d}t\right], \tag{1}$$

$$b = \int_{a_0}^{a_f} S(a)G(a)\,\mathrm{d}a, \tag{2}$$

$$y = \int_{a_0}^{a_f} F(a)S(a)W(a)\,\mathrm{d}a, \tag{3}$$

where $Z = F + M$ is total mortality, M is natural mortality, $G(a)$ is some measure of fecundity (e.g. weight at age, weight times fraction mature at age, or the probability density of the number of eggs released at age a), $W(a)$ is weight at age, b is biomass per recruit (or spawning stock biomass per recruit or eggs per recruit), and y is yield per recruit.

Note that if F and M are constants, $S(a) = \exp(-Z[a - a_0])$, which can be expressed as $\exp(-F[a - a_0])\exp(-M[a - a_0])$ as in (1) and (2) of Grüss *et al.* (2020). Also, if F is constant, it can be pulled outside the integral in (3), as was done in (2) of Grüss *et al.* However, $S(a) \neq \exp(-Z[a - a_0])$ when Z is not constant,

such as in a pulse fishery. In particular, $S(a)$ declines faster during the fishing pulses than when no fishing is occurring, and hence is not a simple exponential (Figure 1). Because $\exp(-F[a - a_0]) = 1$ during the period when there is no fishing (i.e. $F = 0$), $\exp(-Z[a - a_0])$ may not even be a decreasing function of age as is required for a survival function. In addition, when F is not constant, it cannot be pulled outside of an integral.

The integral in (3) can usually be well approximated by a sum. Because in a pulse fishery, $F(a) = 0$ except between ages $a_k + p_{start}$ and $a_k + p_{end}$, (3) can be written as:

$$y = \sum_{k=0}^{n-1} F_k \int_{a_k+p_{start}}^{a_k+p_{end}} S(a) W(a) \mathrm{d}a. \tag{4}$$

The time elapsed in year a_k when there is fishing, τ, which can be computed as $\tau = a_k + p_{end} - (a_k + p_{start}) = p_{end} - p_{start}$, is typically short. Thus, the weight at age during the fishery in that year can be closely approximated by a constant W_k, the weight at age at the midpoint of the fishing period: $W_k = W(a_k + p_{start} + \tau/2)$. Also, if M is assumed to be constant, as will be done for the rest of this note, then while the fishery is occurring in year k,

$$S(a) = S(a_k) e^{-Mp_{start}} e^{-(F_k+M)(a-a_k-p_{start})}. \tag{5}$$

Substituting (5) into (4) and approximating $W(a)$ inside the integral with W_k gives:

$$y = \sum_{k=0}^{n-1} F_k W_k S(a_k) e^{-Mp_{start}} \int_{a_k+p_{start}}^{a_k+p_{end}} e^{-(F_k+M)(a-a_k-p_{start})} \mathrm{d}a. \tag{6}$$

Setting $S_k = S(a_k)$ and computing the integral gives:

$$y = \sum_{k=0}^{n-1} \frac{F_k W_k S_k e^{-Mp_{start}}}{F_k + M} (1 - e^{-(F_k+M)\tau}). \tag{7}$$

Equation (7) can be expressed using (annual) exploitation rates E_k, that represents the fraction of fish that were alive in the beginning of year k and were landed during that year. This can be computed as:

$$E_k = e^{-Mp_{start}} \int_0^\tau F_k e^{-(F_k+M)t} \mathrm{d}t = \frac{F_k e^{-Mp_{start}}}{F_k + M} \left(1 - e^{-(F_k+M)\tau}\right). \tag{8}$$
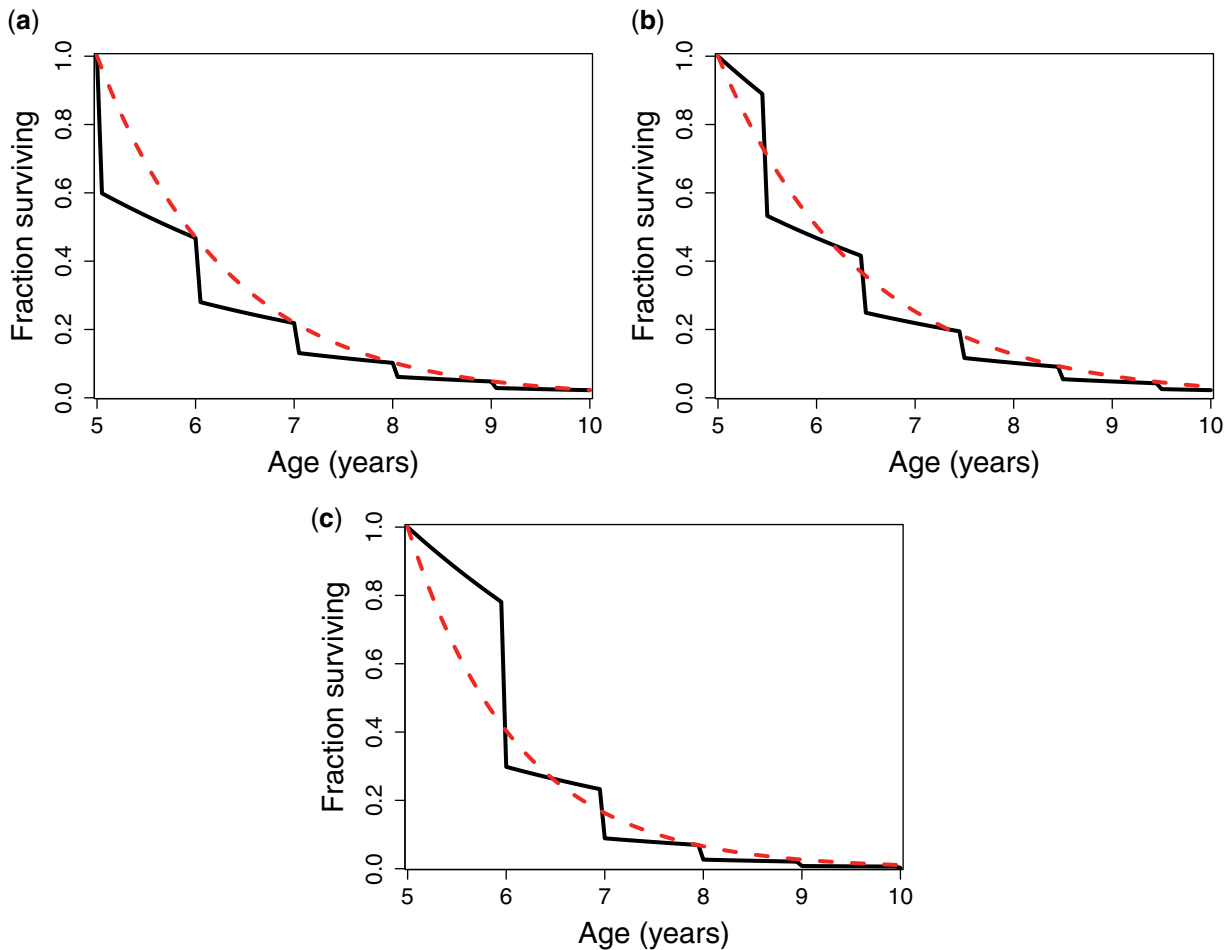
Figure 1. Actual survival at age starting at age 5 (black solid line), compared to the survival function (dashed red line) used by Grüss *et al.* (2020), and, for integer ages, Erisman *et al.* (2020), when the fishing pulse occurs in the beginning (a), middle (b), or end (c) of the year. The pulse is assumed to last for $\tau = 0.05$ years, with $F_k = 20$ during the pulse. Natural mortality is set at $M = 0.26$.

The formula given for exploitation rates in Grüss *et al.* (2020), their (3), is based on the Baranov catch equation. This equation represents the exploitation rate over a unit time period (annual in this example) under the assumption that F and M are constant over that time period (Quinn and Deriso 1999, pp. 11–12). Since F is not constant for a pulse fishery, this equation is not valid in this case. Note that (8) reduces to the Baranov catch equation based formula under the assumption that F is constant during the year, i.e. $p_{\text{start}} = 0$, $p_{\text{end}} = 1$ and thus $\tau = 1$.

Substituting (8) into (7) gives:

$$y = \sum_{k=0}^{n-1} S_k W_k E_k. \qquad (9)$$

The survival at age, S_k, can be computed recursively for each $k = 0, 1, \ldots$ using:

$$S_{k+1} = S_k e^{-M - F_k \tau}, \qquad (10)$$

or equivalently

$$S_k = \exp\left(-kM - \sum_{i=0}^{k-1} F_i \tau\right), \quad S_0 = 1. \qquad (11)$$

Both Erisman *et al.* (2020) and Grüss *et al.* (2020) attempt to use the exploitation rates E_k to compute survival at age. In the discrete Erisman *et al.* (2020) model, they effectively replaced (10) with

$$S_{k+1} = S_k e^{-M}(1 - E_k). \qquad (12)$$

This is a good approximation only if the pulse occurs at the beginning of the year and is short; if the pulse occurs later in the year, $1 - E_k$ is greater than $e^{-F_k \tau}$ by about $e^{-(p_{\text{start}} + \tau/2)M}$ (Figure 1), which would cause yield and biomass per recruit to be overestimated. Grüss *et al.* (2020) modelled survival essentially as the continuous analog of (12):

$$S(a) = S(a_{\text{OA}}) e^{-M(a - a_{\text{OA}})} (1 - E)^{(a - a_{\text{OA}})}, \quad a \geq a_{\text{OA}}, \qquad (13)$$

where a_{OA} is the age of full recruitment to the fishery. This predicts a simple exponential decline in survival that ignores the pulse nature of the fishery. If the fishing pulse is at the beginning of each year, using (13) will typically overestimate survival (Figure 1a). When the pulse is later, the situation is more complex since this equation sometimes overestimates and sometimes underestimates survival (Figure 1b and c). In any case, the correct survival function can be easily calculated using (1). For a pulse fishery, the level of fishing mortality induced by a given exploitation rate depends on the length and timing of the pulse (8), so that survival cannot be precisely predicted by the exploitation rate alone as was attempted in (12) and (13).

Example yield-per-recruit curves for Gulf corvina (*Cynoscion othonopterus*) are plotted in Figure 2. These use the same parameters as in Table 1 of Grüss *et al.* (2020), with $a_0 = 2$, $a_f = 20$, $\tau = 0.05$, $F_k = 0$ for the first 3 years of the simulation (when the fish are ages 2, 3, and 4) with the F_{ks} corresponding to the specified exploitation rate afterwards. Age-based yield per recruit is usually computed using a fixed weight at each age, which is reasonable when F is constant. However, if that approach is taken in a pulse fishery, it will often predict substantially lower yield per recruit if the fishery takes place late in the year compared to the beginning (Figure 2a) due to a nearly an extra year of natural mortality. In reality, growth and natural mortality operate continuously, so the additional growth allowed by the fishery operating later in the year will at least partially counteract the additional natural mortality. When growth is taken into account, so that the weight is taken as W_k as defined above, it is seen that, at least in this case, the timing of the fishery has only a small effect on yield per recruit (Figure 2b). Note also that at a fixed F_k, exploitation rates are lower when the pulse occurs later in the year [by a factor $e^{-M p_{\text{start}}}$ according to (8)].

The yield per recruit computed here is about twice that calculated by Erisman *et al.* (2020). Assuming the pulse occurs in the beginning of the year and an exploitation rate of zero for ages 2–4 and one for age 5, so all fish are removed at age five, yield per recruit can be simply calculated as $y = \exp(-3M)W(5) = 0.458 \times 3200 = 1466$, which agrees with Figure 2 at $E = 1$ but not with Erisman *et al.* (2020).

Spawning often occurs during a short period each year. If this is the case, and spawning occurs at age $a_k + p_{\text{spawn}}$ each year, biomass per recruit (or its variants) can also be well approximated
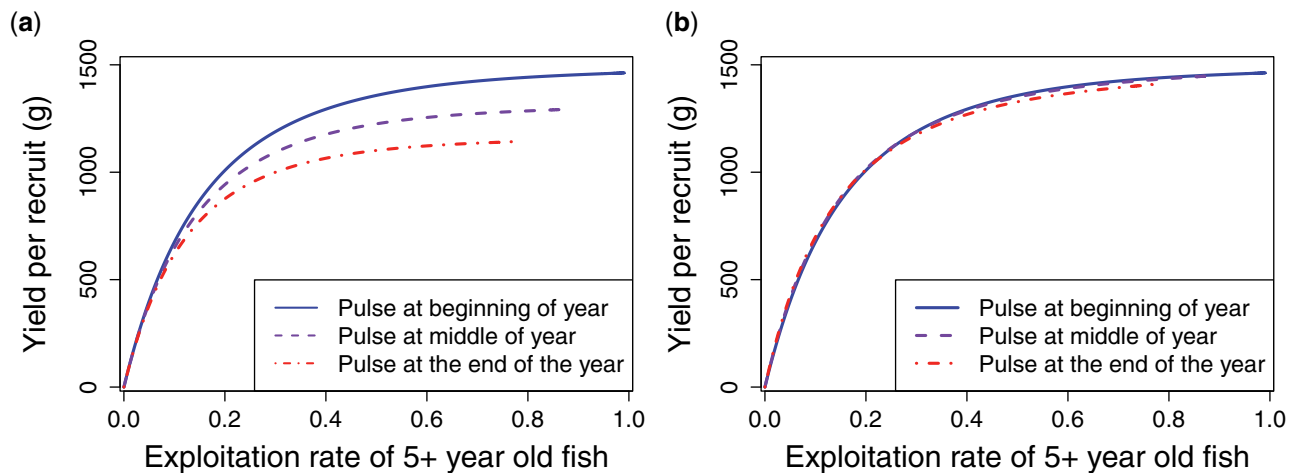
Figure 2. Yield-per-recruit curves using (a) fixed weight at age and (b) weights at age W_k that depend on the time within a year when the fishing pulse occurs (beginning of the year, solid blue line; middle of the year, dashed purple line; end of the year, dash-dotted red line).

by a sum. Let G_k be the weight (or weight times fraction mature, or number of eggs released), at this spawning time in year k. Then, biomass (or spawning biomass or eggs) per recruit b can be expressed as:

$$b = \sum_{k=0}^{n-1} S(a_k + p_{\text{spawn}}) G_k. \tag{14}$$

Note that $S(a_k + p_{\text{spawn}}) = S_k \exp(-Mp_{\text{spawn}})$ if $p_{\text{spawn}} < p_{\text{start}}$ and $S(a_k + p_{\text{spawn}}) = S_k \exp(-Mp_{\text{spawn}} - F_k\tau)$ if $p_{\text{spawn}} > p_{\text{end}}$, so (14) takes into account whether spawning occurred before or after the fishery. Similar ideas can be applied to the case where the fish spawn multiple times during the year.

Classical fishery theory is typically based on the assumption that F (as well as M) is constant with age. This assumption does not hold in many real fisheries, as in the pulse fisheries discussed here, or in rotational fisheries (e.g. Hart 2003). Even in fisheries where there is no explicit time-varying management, F can vary over time due to, for example changes in resource or economic conditions, or seasonal weather patterns. Thus, it is of interest to extend fisheries theory to include situations where F varies in time, such as what was attempted by Grüss *et al.* (2020) for pulse fisheries. However, care must be taken to assure that such analysis is not based on any result that depends on F being constant.

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