Biomass dynamic models

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Contents

1 Overview

Kingsland (1982) gives a review of biomass models.

2 Schaefer (1954)

2.1 Same + Growth − Removals

The Schaefer model is:

$$B_t \quad = \quad B_{t-1} \; + \; rB_t\left(1-\frac{B_t}{K}\right) \; - \; C_t$$

3 Surplus production

The second term describes the relationship between surplus production (growth) and abundance:

$$g(B) \quad = \quad rB\left(1-\frac{B}{K}\right)$$

In biological terms, the surplus production combines recruitment, body growth, and natural mortalities.

Conceptually, the model describes the simplest case of linear recruitment, where all individuals have the same body weight, and the natural mortality rate is constant. Individiuals reproduce as 1-year-olds and then die. After a period of removals, the population rebuilds towards K until the number of individuals dying from natural causes equals the recruitment.

3.1 Original equation

Schaefer (1954, Eq. 2):

$$g(B) \quad = \quad k_2 B\,(L-B)$$

Replace $k_2 = \frac{r}{K}$ and $L = K$:

$$\begin{aligned} g(B) \quad &= \quad \frac{r}{K}\,B\,(K-B) \\ &= \quad rB\left(\frac{K-B}{K}\right) \\ &= \quad rB\left(1-\frac{B}{K}\right) \end{aligned}$$

3.2 $B_{\text{MSY}} = 0.5K$

The surplus production is maximized where the derivative of the growth function is zero. It's easiest to find the derivative by using elementary calculus notation,

$$
\begin{aligned}
f(x) &= rx\left(1 - \frac{x}{K}\right) \\
&= rx - \frac{rx^2}{K} \\
&= rx - \frac{r}{K}x^2 \\
f'(x) &= r - 2\frac{r}{K}x \\
&= r - \frac{2r}{K}x
\end{aligned}
$$

so:

$$
g'(B) = r - \frac{2r}{K}B
$$

B_{MSY} is where the derivative equals zero,

$$
0 = r - \frac{2r}{K}B_{\text{MSY}}
$$

and we can isolate B_{MSY}:

$$
\begin{aligned}
\frac{2r}{K}B_{\text{MSY}} &= r \\
2rB_{\text{MSY}} &= rK \\
B_{\text{MSY}} &= \frac{rK}{2r} \\
&= \frac{r}{2r}K \\
&= 0.5K
\end{aligned}
$$

3.3 $\mathrm{MSY} = 0.25\,rK$

Knowing $B_{\mathrm{MSY}} = 0.5K$ we can evaluate $\mathrm{MSY} = g(B_{\mathrm{MSY}})$:

$$
\begin{aligned}
g(B) &= rB\left(1 - \frac{B}{K}\right) \\
\mathrm{MSY} &= rB_{\mathrm{MSY}}\left(1 - \frac{B_{\mathrm{MSY}}}{K}\right) \\
&= 0.5\,rK\left(1 - \frac{0.5K}{K}\right) \\
&= 0.5\,rK\,(1-0.5) \\
&= 0.5\,rK\,(0.5) \\
&= 0.25\,rK
\end{aligned}
$$

3.4 Relative growth rate

The relative growth rate, as a fraction of current abundance, is $\mathrm{Rate}(B) = g(B)/B$,

$$
\begin{aligned}
g(B) &= rB\left(1 - \frac{B}{K}\right) \\
\mathrm{Rate}(B) &= rB\left(1 - \frac{B}{K}\right)\Big/B \\
&= r\left(1 - \frac{B}{K}\right) \\
&= r - \frac{rB}{K}
\end{aligned}
$$

so the relative growth rate approaches r when the abundance is close to zero, and declines linearly with B until zero growth occurs at abundance K.

4 Variations

4.1 Gompertz (1825)

Applied in stock assessment by Fox (1970, Eq. 8):

$$
\begin{aligned}
g(B) &= rB\,(\log K - \log B) \\
&= rB\,\log\left(\frac{K}{B}\right) \\
&= rB\,\log K\left(\frac{\log K - \log B}{\log K}\right) \\
&= rB\,\log K\left(\frac{\log K}{\log K} - \frac{\log B}{\log K}\right) \\
&= rB\,\log K\left(1 - \frac{\log B}{\log K}\right)
\end{aligned}
$$

The surplus production is maximized where the derivative of the growth function is zero. It's easiest to find the derivative by using elementary calculus notation,

$$
\begin{aligned}
f(x) &= ax\,(b - \log x) \\
&= abx \;-\; ax\log x \\
f'(x) &= ab \;-\; \left[(ax)'\log x \;+\; (ax)(\log x)'\right] \\
&= ab \;-\; \left[a\log x \;+\; (ax)\frac{1}{x}\right] \\
&= ab \;-\; \left[a\log x \;+\; a\right] \\
&= ab \;-\; a\log x \;-\; a
\end{aligned}
$$

so:

$$
g'(B) = r\log K \;-\; r\log B \;-\; r
$$

B_{MSY} is where the derivative equals zero:

$$0 \;=\; r\log K \;-\; r\log B_{\text{MSY}} \;-\; r$$

First isolate $\log B_{\text{MSY}}$,

$$\begin{aligned} r\log B_{\text{MSY}} &= r\log K \;-\; r \\ \log B_{\text{MSY}} &= \log K \;-\; 1 \end{aligned}$$

then exponentiate:

$$\begin{aligned} \exp(\log B_{\text{MSY}}) &= \exp(\log K - 1) \\ B_{\text{MSY}} &= \exp(\log K) \;\times\; \exp(-1) \\ &= \frac{K}{e} \\ &\approx 0.368K \end{aligned}$$

Knowing $B_{\text{MSY}} = \frac{K}{e}$ we can evaluate $\text{MSY} = g(B_{\text{MSY}})$:

$$\begin{aligned} g(B) &= rB\,\log\!\left(\frac{K}{B}\right) \\ \text{MSY} &= rB_{\text{MSY}}\,\log\!\left(\frac{K}{B_{\text{MSY}}}\right) \\ &= r\,\frac{K}{e}\,\log\left(\frac{K}{\frac{K}{e}}\right) \\ &= \frac{rK}{e}\,\log\!\left(\frac{e}{K}\times K\right) \\ &= \frac{rK}{e}\,\log(e) \\ &= \frac{rK}{e} \\ &\approx 0.368\,rK \end{aligned}$$

4.2 Pella-Tomlinson (1969)

Pella and Tomlinson (1969, Eq. 5):

$$g(B) \quad = \quad \mathcal{H} B^m \; - \; \mathcal{K} B$$

Replace $\mathcal{H} = -\frac{r}{pK^p}$, $m = p+1$, and $\mathcal{K} = -\frac{r}{p}$:

$$\begin{aligned}
g(B) \quad &= \quad -\frac{r}{pK^p} B^{\,p+1} \; + \; \frac{r}{p} B \\
&= \quad \frac{rB}{p} \; - \; \frac{r}{pK^p} B^{\,p+1} \\
&= \quad \frac{rB}{p} \; - \; \frac{r}{pK^p} B^p \times B \\
&= \quad \frac{rB}{p} \; - \; \frac{rB}{p} \times \frac{B^p}{K^p} \\
&= \quad \frac{rB}{p} \left(1 \; - \; \frac{B^p}{K^p} \right) \\
&= \quad \frac{rB}{p} \left[1 \; - \; \left(\frac{B}{K} \right)^p \right]
\end{aligned}$$

The surplus production is maximized where the derivative of the growth function is zero. It's easiest to find the derivative by using elementary calculus notation,

$$
\begin{aligned}
f(x) &= \frac{ax}{c}\left[1-\left(\frac{x}{b}\right)^c\right] \\
&= \frac{ax}{c} - \frac{ax}{c}\left(\frac{x}{b}\right)^c \\
&= \frac{ax}{c} - \frac{ax}{c}\left(\frac{x^c}{b^c}\right) \\
&= \frac{ax}{c} - \frac{a}{c}\left(\frac{x^{\,c+1}}{b^c}\right) \\
&= \frac{ax}{c} - \frac{a}{c\,b^c}\,x^{\,c+1} \\
f'(x) &= \frac{a}{c} - \left(\frac{a}{c\,b^c}\right)(c{+}1)\,x^c \\
&= \frac{a}{c} - \left(\frac{ac+a}{c\,b^c}\right)x^c
\end{aligned}
$$

so:

$$
g'(B) = \frac{r}{p} - \left(\frac{rp+r}{pK^p}\right)B^p
$$

B_{MSY} is where the derivative equals zero:

$$
0 = \frac{r}{p} - \left(\frac{rp+r}{pK^p}\right)B_{\mathrm{MSY}}^p
$$

First isolate B_{MSY}^p,

$$\begin{aligned}
\left(\frac{rp + r}{pK^p}\right) B_{\text{MSY}}^p &= \frac{r}{p} \\
B_{\text{MSY}}^p &= \frac{r}{p}\left(\frac{pK^p}{rp + r}\right) \\
&= r\left(\frac{K^p}{rp + r}\right) \\
&= \frac{rK^p}{rp + r} \\
&= \frac{K^p}{p + 1}
\end{aligned}$$

then log-transform,

$$\begin{aligned}
\log\left(B_{\text{MSY}}^p\right) &= \log\left(\frac{K^p}{p+1}\right) \\
p \log B_{\text{MSY}} &= \log(K^p) \; - \; \log(p+1) \\
\log B_{\text{MSY}} &= \frac{p \log K \; - \; \log(p+1)}{p} \\
&= \log K \; - \; \frac{\log(p+1)}{p} \\
&= \log K \; + \; \left(-\frac{1}{p}\right) \log(p+1) \\
&= \log K \; + \; \log(p+1)\left(-\frac{1}{p}\right)
\end{aligned}$$

and exponentiate:

$$\begin{aligned}
\exp(\log B_{\text{MSY}}) &= \exp\left[\log K \; + \; \log(p+1)\left(-\frac{1}{p}\right)\right] \\
B_{\text{MSY}} &= \exp(\log K) \; \times \; \exp\left[\log(p+1)\left(-\frac{1}{p}\right)\right]
\end{aligned}$$

Noting that $x^{ab} = (x^a)^b$, we rearrange the last term:

$$
\begin{aligned}
B_{\text{MSY}} &= K \times \exp\left[\log(p{+}1)\left(-\frac{1}{p}\right)\right] \\
&= K \times \left(\exp\left[\log(p{+}1)\right]\right)^{-\frac{1}{p}} \\
&= K \times (p{+}1)^{-\frac{1}{p}} \\
&= K\left(\frac{1}{p{+}1}\right)^{\frac{1}{p}}
\end{aligned}
$$

When $p{=}1$ we get Schaefer:

$$
\begin{aligned}
B_{\text{MSY}} &= K\left(\frac{1}{1{+}1}\right)^{\frac{1}{1}} \\
&= K\left(\frac{1}{2}\right) \\
&= 0.5K
\end{aligned}
$$

When $p \to 0$ we get Gompertz,

$$
\begin{aligned}
B_{\mathrm{MSY}} &= \lim_{p\to 0} K\left(\frac{1}{p+1}\right)^{\frac{1}{p}} \\
&= K \times \lim_{p\to 0}\left(\frac{1}{1+p}\right)^{\frac{1}{p}} \\
&= K \times \lim_{p\to 0}\left[\left(1+p\right)^{-1}\right]^{\frac{1}{p}} \\
&= K \times \lim_{p\to 0}\left(1+p\right)^{-\frac{1}{p}} \\
&= K \times \exp\left(\lim_{p\to 0} \log\left[\left(1+p\right)^{-\frac{1}{p}}\right]\right) \\
&= K \times \exp\left[\lim_{p\to 0} -\frac{1}{p}\log(1+p)\right] \\
&= K \times \exp\left[-\lim_{p\to 0}\frac{\log(p+1)}{p}\right]
\end{aligned}
$$

noting that $\lim_{x\to c}\frac{f(x)}{g(x)} = \lim_{x\to c}\frac{f'(x)}{g'(x)}$:

$$
\begin{aligned}
B_{\mathrm{MSY}} &= K \times \exp\left[-\lim_{p\to 0}\frac{\frac{1}{1+p}}{1}\right] \\
&= K \times \exp\left[-\lim_{p\to 0}\frac{1}{1+p}\right] \\
&= K \times \exp\left[-\frac{1}{1+0}\right] \\
&= K \times \exp(-1) \\
&= \frac{K}{e} \\
&\approx 0.368K
\end{aligned}
$$

Knowing $B_{\mathrm{MSY}} = K\left(\frac{1}{p+1}\right)^{\frac{1}{p}}$ we can evaluate MSY$=g(B_{\mathrm{MSY}})$:

$$
\begin{aligned}
g(B) &= \frac{rB}{p}\left[1 - \left(\frac{B}{K}\right)^{p}\right] \\
\mathrm{MSY} &= \frac{rB_{\mathrm{MSY}}}{p}\left[1 - \left(\frac{B_{\mathrm{MSY}}}{K}\right)^{p}\right] \\
&= \frac{r\,K\left(\frac{1}{p+1}\right)^{\frac{1}{p}}}{p}\left[1 - \left(\frac{K\left(\frac{1}{p+1}\right)^{\frac{1}{p}}}{K}\right)^{p}\right] \\
&= \frac{rK}{p}\left(\frac{1}{p+1}\right)^{\frac{1}{p}}\left(1 - \left[\left(\frac{1}{p+1}\right)^{\frac{1}{p}}\right]^{p}\right) \\
&= \frac{rK}{p}\left(\frac{1}{p+1}\right)^{\frac{1}{p}}\left(1 - \frac{1}{p+1}\right) \\
&= \frac{rK}{p}\left(\frac{1}{p+1}\right)^{\frac{1}{p}}\left(\frac{p+1}{p+1} - \frac{1}{p+1}\right) \\
&= \frac{rK}{p}\left(\frac{1}{p+1}\right)^{\frac{1}{p}}\left(\frac{p}{p+1}\right) \\
&= \frac{rK}{p}\left(\frac{p}{p+1}\right)\left(\frac{1}{p+1}\right)^{\frac{1}{p}} \\
&= rK\left(\frac{1}{p+1}\right)\left(\frac{1}{p+1}\right)^{\frac{1}{p}} \\
&= rK\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}}
\end{aligned}
$$

When $p=1$ we get Schaefer:

$$
\begin{aligned}
\mathrm{MSY} &= rK\left(\frac{1}{1+1}\right)^{1+\frac{1}{1}} \\
&= rK\left(\frac{1}{2}\right)^{2} \\
&= 0.25\,rK
\end{aligned}
$$

When $p \to 0$ we get Gompertz,

$$\begin{aligned}
\text{MSY} &= \lim_{p\to 0} rK\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}} \\
&= rK \times \lim_{p\to 0}\left(\frac{1}{1+p}\right)^{1+\frac{1}{p}} \\
&= rK \times \exp\left(\lim_{p\to 0} \log\left[\left(\frac{1}{1+p}\right)^{1+\frac{1}{p}}\right]\right) \\
&= rK \times \exp\left[\lim_{p\to 0}\left(1+\frac{1}{p}\right)\log\left(\frac{1}{1+p}\right)\right] \\
&= rK \times \exp\left[-\lim_{p\to 0}\left(1+\frac{1}{p}\right)\log(1+p)\right] \\
&= rK \times \exp\left[-\lim_{p\to 0} \log(1+p) + \frac{\log(1+p)}{p}\right] \\
&= rK \times \exp\left[-\lim_{p\to 0} \frac{\log(1+p)}{p}\right]
\end{aligned}$$

noting that $\lim_{x\to c} \dfrac{f(x)}{g(x)} = \lim_{x\to c} \dfrac{f'(x)}{g'(x)}$:

$$\begin{aligned}
\text{MSY} &= rK \times \exp\left[-\lim_{p\to 0} \frac{\log(1+p)}{p}\right] \\
&= rK \times \exp\left[-\lim_{p\to 0} \frac{\frac{1}{1+p}}{1}\right] \\
&= rK \times \exp\left[-\lim_{p\to 0} \frac{1}{1+p}\right] \\
&= rK \times \exp\left[-\frac{1}{1+0}\right] \\
&= rK \times \exp(-1) \\
&= \frac{rK}{e} \\
&\approx 0.368\, rK
\end{aligned}$$

The Pella-Tomlinson shape parameter p does not only shift B_{MSY} away from $0.5K$, but also changes the maximum height of the production curve. This is unfortunate, as the modeller might be interested in exploring different shapes without altering the maximum productivity.

Since we know the maximum surplus production for a given p,

$$\mathrm{MSY} \quad = \quad rK\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}}$$

the production can be scaled to any given range.

Starting from the original Pella-Tomlinson,

$$g(B) \quad = \quad \frac{rB}{p}\left[1 \; - \; \left(\frac{B}{K}\right)^{p}\right]$$

we first divide by MSY to scale the production between 0 and 1,

$$
\begin{aligned}
g_1(B) &= \frac{\frac{rB}{p}\left[1-\left(\frac{B}{K}\right)^p\right]}{rK\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}}} \\
&= \frac{\frac{B}{p}\left[1-\left(\frac{B}{K}\right)^p\right]}{K\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}}} \\
&= \frac{B\left[1-\left(\frac{B}{K}\right)^p\right]}{pK\left(\frac{1}{p+1}\right)^{1+\frac{1}{p}}} \\
&= \frac{B\left[1-\left(\frac{B}{K}\right)^p\right]}{pK\left[\frac{1}{(p+1)^{1+\frac{1}{p}}}\right]} \\
&= \frac{B\left[1-\left(\frac{B}{K}\right)^p\right]}{\frac{pK}{(p+1)^{1+\frac{1}{p}}}} \\
&= \frac{(p+1)^{1+\frac{1}{p}}}{pK} \quad \times \quad B\left[1-\left(\frac{B}{K}\right)^p\right] \\
&= \frac{B}{pK}\,(p+1)^{1+\frac{1}{p}}\left[1-\left(\frac{B}{K}\right)^p\right]
\end{aligned}
$$

and then multiply by $0.25\,rK$ to use that as maximum production at any given p:

$$
\begin{aligned}
g^\star(B) &= 0.25\,rK \;\times\; \frac{B}{pK}\,(p+1)^{1+\frac{1}{p}}\left[1-\left(\frac{B}{K}\right)^p\right] \\
&= \frac{0.25\,rB}{p}\,(p+1)^{1+\frac{1}{p}}\left[1-\left(\frac{B}{K}\right)^p\right]
\end{aligned}
$$

4.3 Theta-logistic (1973)

Gilpin and Ayala (1973, Eq. 3):

$$g(B) \quad = \quad rB\left[1-\left(\frac{B}{K}\right)^{\theta}\right]$$

where θ gives the asymmetry of the growth.

Different from Pella-Tomlinson, which has $\frac{r}{p}$ as the first term. The theta-logistic model has the nice property that r is the initial growth rate, independent of θ. The Pella-Tomlinson model has the nice property that it becomes the Gompertz model as $p \to 0$.

The theta-logistic model has a problem with low θ values. Maximum production tends towards zero with decreasing θ, so the model will need very large K when θ is small.

4.4 Fletcher (1978)

From Prager (2002, Eqs 2–4):

$$
\begin{aligned}
g(B) &= \gamma m \frac{B}{K} - \gamma m \left(\frac{B}{K}\right)^n \\
&= \gamma m \left[\frac{B}{K} - \left(\frac{B}{K}\right)^n\right] \\
&= \gamma m \frac{B}{K} \left[1 - \left(\frac{B}{K}\right)^{n-1}\right]
\end{aligned}
$$

where

$$
\gamma = \frac{n^{n/(n-1)}}{n-1}
$$

and $m = \frac{1}{4}\, rK$, i.e. MSY:

$$
\begin{aligned}
g(B) &= \gamma m \left[\frac{B}{K} - \left(\frac{B}{K}\right)^n\right] \\
&= \gamma \frac{rK}{4} \left[\frac{B}{K} - \left(\frac{B}{K}\right)^n\right] \\
&= \gamma \frac{rK}{4} \frac{B}{K} - \gamma \frac{rK}{4} \left(\frac{B}{K}\right)^n \\
&= \gamma \frac{r}{4} B - \gamma \frac{rK}{4} \left(\frac{B}{K}\right)^n \\
&= \gamma \frac{1}{4} rB - \gamma \frac{1}{4} rK \left(\frac{B}{K}\right)^n \\
&= \frac{\gamma}{4} rB - \frac{\gamma}{4} rK \left(\frac{B}{K}\right)^n \\
&= \frac{\gamma}{4} r \left[B - rK \left(\frac{B}{K}\right)^n\right]
\end{aligned}
$$

The Schaefer model corresponds to $n=2$ where $\gamma=4$,

$$\begin{aligned}
\gamma &= \frac{n^{n/(n-1)}}{n-1} \\
&= \frac{2^{2/(2-1)}}{2-1} \\
&= \frac{2^{2/(1)}}{1} \\
&= 2^{2/(1)} \\
&= 2^2 \\
&= 4
\end{aligned}$$

as verified here:

$$\begin{aligned}
g(B) &= \frac{\gamma}{4}\, rB \;-\; \frac{\gamma}{4}\, rK\left(\frac{B}{K}\right)^n \\
&= \frac{4}{4}\, rB \;-\; \frac{4}{4}\, rK\left(\frac{B}{K}\right)^2 \\
&= rB \;-\; rK\left(\frac{B}{K}\right)^2 \\
&= rB \;-\; rK\,\frac{B^2}{K^2} \\
&= rB \;-\; r\,\frac{B^2}{K} \\
&= rB \;-\; rB\,\frac{B}{K} \\
&= rB\left(1 \;-\; \frac{B}{K}\right)
\end{aligned}$$

Prager (2002) describes the shape of the production curve with the unitless ratio $\phi = \frac{B_{\mathrm{MSY}}}{K}$, which has a more intuitive meaning than the n exponent. The relationship is:

$$\phi = \left(\frac{1}{n}\right)^{1/(n-1)}$$

Insert $n=2$ and note how the Schaefer model corresponds to $\phi = 0.5$, as expected:

$$\begin{aligned} \phi &= \left(\frac{1}{n}\right)^{1/(n-1)} \\ &= \left(\frac{1}{2}\right)^{1/(2-1)} \\ &= \left(\frac{1}{2}\right)^{1/(1)} \\ &= \frac{1}{2} \end{aligned}$$

4.5 Polacheck et al. (1993)

Polacheck et al. (1993, Eq. 1):

$$g(B) = \frac{r}{p}\, B\left[1-\left(\frac{B}{K}\right)^{p}\right]$$

where p controls the asymmetry of the sustainable yield versus stock biomass relationship.

The authors note that the $\frac{r}{p}$ term is often omitted when the formula is presented.

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5.1 Look up later

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