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A simple model for prediction of equilibrium biomass and yield from age-structured populations

Carl Walters

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Email: c.walters@oceans.ubc.ca

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A simple model for prediction of equilibrium biomass and yield from age-structured populations

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In fisheries assessments we routinely need to predict equilibrium vulnerable biomass and catch as a function of fishing mortality rate using age-structured models, so as to provide reference points for long term management. In such predictions, we typically represent equilibrium biomass as the product of predicted equilibrium recruitment R_e times equilibrium biomass per recruit B_{PRE} :

$$B_e = R_e B_{PRE} \quad (1).$$

In such calculations, we typically need to account for effects of fishing mortality rate F on both R_e (possible recruitment overfishing) and B_{PRE} (possible growth overfishing).

Below we derive ultra-compact equations for predicting effects of fishing on B_e (and equilibrium catch). These equations are of modest theoretical interest in exposing the relative effects of changes in recruitment versus biomass-per-recruit on yields, but are not really needed for single-species, single-area assessments where the calculations need be repeated only once.

Where these compact equations may be of considerable practical value is in analyses where either the computation of B_{PRE} is costly (e.g. as a sum over a large number of “packets” of fish with different growth-vulnerability patterns) or more commonly where the calculation needs to be repeated many (e.g. 10^8) times. Large computational requirements occur for example in models for prediction and optimization of harvests over many species and spatial areas (like reefs and sport fishing lakes), where even the prediction of the spatial effort distribution (by fishermen who move in response to changing opportunities created by movement of other fishermen) may require an iterative reallocation model.

A useful property of the equations is that they are “invertible in F ”, meaning that we can either use them to predict equilibrium biomasses given fishing rate F , or to predict F given some model for predicting the equilibrium biomasses B_e . Inverse prediction of B_e from F arises for example in bio-economic modelling where fish price and fishing cost calculations lead to predictions of the bionomic equilibrium B_e , and we want to predict changes in F or fishing effort that would occur if a price or cost change causes B_e to either increase or decrease, and in modeling equilibrium changes for populations subject to compensatory natural mortality rates. Another example is in prediction of spatial fishing effort patterns over multiple spatial areas that are predicted to have different B_e due to cost factors like distance from fishing ports.

The sections below describe the R_e recruitment prediction, then a simple approximation for how B_{PRE} varies with fishing mortality rate, then how these are combined to generate overall biomass predictions. Then a section shows application of the equations to the Ricker-stock recruitment model, and a final section presents the inverse prediction equations and uses these to predict changes in Pacific herring biomass as a function of fishing mortality and compensatory predation by Steller sea lions.

Prediction of equilibrium recruitment

Most commonly, recruitment is predicted using the Beverton-Holt asymptotic model

$$R = aS / (1 + bS) \quad (2),$$

with spawning biomass S often approximated by the vulnerable biomass ($S=B$). This model can be conveniently parameterized in terms of the Goodyear compensation ratio K (ratio of maximum juvenile survival rate at low abundance to survival rate in the unfished population) and unfished biomass B_0 , while noting that $a=K/BPR_0$ (BPR_0 is unfished biomass per recruit) and $b=(K-1)/B_0$. At equilibrium, predicted recruitment must satisfy the following condition discovered by Lewis Botsford (see Walters and Martell 2004, Box 3.2):

$$R_e = aR_e BPR_e / (1 + bR_e BPR_e) \quad (3).$$

Here, BPR_e is the equilibrium biomass per recruit (which depends on F but not on R). Solving this for R_e as Lou Botsford first showed, and changing to the K, R_0 parameterization, we obtain

$$R_e = [aBPR_e - 1] / [bBPR_e] = R_0 [K - BPR_0 / BPR_e] / (K - 1) \quad (4).$$

Here R_0 is the unfished recruitment at $B=B_0$ (i.e. $R_0=B_0/BPR_0$). This equilibrium prediction for the recruitment component of B_e is a declining function of BPR_e , i.e. fishing rates that cause decrease in BPR_e are predicted to result in declining recruitment, with severity of the decline dependent on the compensation ratio (higher K leading to slower decline as F increases).

Prediction of biomass per recruit

At this point, what we typically do in fisheries assessments is to conduct an age or length structured calculation of BPR_e as a function of F , using assumed age (or length) schedules of natural mortality rate M , body weights $W(\text{age})$, and vulnerabilities at age $v(\text{age})$. That is, we calculate survivorships to age $L(\text{age})$ using $L(1)=1$ as

$$L(\text{age}) = L(\text{age}-1)e^{-M-v(\text{age})F} \quad (5),$$

then calculate vulnerable BPR_e as the sum or integral over ages of $v(\text{age})L(\text{age})W(\text{age})$; thus, effects of F on BPR_e appear in a complicated way through effects on cumulative survivorship to age $L(\text{age})$.

Having done such BPR_e calculations for a wide variety of models and growth-mortality rate patterns, ranging from the classic Beverton-Holt continuous model for biomass per recruit to cases with complex $v(\text{age})$ schedules (e.g. domeshaped) and length dynamics models, I have found that the dependence of BPR_e on F can almost always be nicely approximated by a very simple hyperbolic relationship:

$$BPR_e \approx BPR_0 / (1 + F/F_h) \quad (6),$$

where F_h is the fishing rate needed to reduce biomass per recruit BPR_e to 50% of BPR_0 . Note that F_h needs to be estimated on a case-by-case basis, using assumed growth, vulnerability, and natural mortality schedules; in particular, F_h is much lower (BPR_e is much more sensitive to F) for longer lived (low M), slower growing species and is higher for fisheries that cause dome-shaped vulnerability whatever the species. Table 1 below shows how the best-fitting F_h value is expected to vary with the von Bertalanffy growth K and mean relative length at 50% vulnerability for fish with asymptotic selectivity, for different assumptions about the M/K ratio.

Table 1. Expected changes in the Fh needed to fit the BPR vs F relationship for a typical age-structured population model, for different assumptions about the M/K ratio (natural mortality rate divided by vonBertalanffy growth K) and relative size LR/L_∞ at 50% vulnerability to fishing. (From “Fh vs LrLinf and Mk.xlsm”).

M/K=0.8		vonBertalanffy K				
		0.1	0.2	0.3	0.4	0.5
Lr/Linf	0.3	0.049	0.083	0.137	0.179	0.234
	0.4	0.058	0.094	0.146	0.216	0.272
	0.5	0.068	0.106	0.165	0.228	0.313
	0.6	0.083	0.120	0.184	0.259	0.332
	0.7	0.103	0.136	0.206	0.286	0.377
M/K=1		vonBertalanffy K				
		0.1	0.2	0.3	0.4	0.5
Lr/Linf	0.3	0.055	0.100	0.170	0.221	0.290
	0.4	0.065	0.115	0.182	0.272	0.343
	0.5	0.077	0.131	0.209	0.289	0.402
	0.6	0.092	0.148	0.233	0.332	0.428
	0.7	0.114	0.169	0.263	0.369	0.491
M/K=1.6		vonBertalanffy K				
		0.1	0.2	0.3	0.4	0.5
Lr/Linf	0.3	0.076	0.160	0.280	0.357	0.478
	0.4	0.090	0.189	0.305	0.469	0.582
	0.5	0.107	0.218	0.358	0.504	0.723
	0.6	0.127	0.249	0.405	0.589	0.774
	0.7	0.154	0.286	0.462	0.663	0.905

Combined equilibrium biomass prediction equation

If we substitute the hyperbolic BPR prediction (eq. 6), and the Botsford equilibrium recruitment prediction (eq. 4) into the basic biomass prediction (eq. 1) and then do a bit of simple algebra, we obtain the remarkably simple model for equilibrium biomass prediction that motivated writing this note:

$$Be = Bo \left[\frac{K}{(1 + F/F_h) - 1} \right] / (K - 1) \quad (7).$$

Equilibrium catch Ce is then predicted by just Ce = FBe for continuous fishing, or Ce = Be(1 - e^{-F}) for seasonal fishing. This very simple biomass model predicts monotonic decrease in Be with increasing F due to negative effects of F on both Re and BPRE, with sensitivity of the decrease depending on K and Fh. An example calculation for a long lived species (using Alberta walleye growth, mortality and vulnerability parameters to estimate Fh) is shown in Figure 1 below.

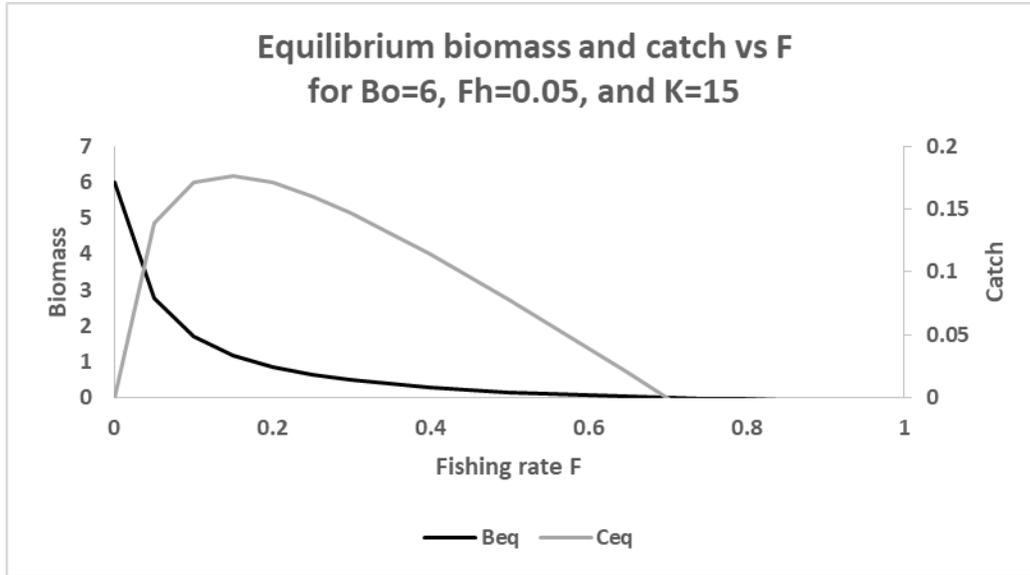


Figure 1. Prediction of equilibrium Biomass and catch for a walleye-like population (from “Prediction of equilibrium biomass and yield from R and BPR.xlsx”).

So the basic recommendation from this analysis is to first do an “offline” assessment of the equilibrium dependence of BPR on F to estimate Fh, using for example a simple spreadsheet to calculate survivorships to age (eq. 5) and associated biomasses at age per recruit, then use eq. (7) to make the equilibrium biomass and yield prediction that is needed for determination of management reference points like Fmsy and Bmsy/Bo.

A potentially important problem with the model above is that the vulnerability schedule for some fisheries implies considerable fishing impact on immature fish. In that case, the spawning stock biomass Se needed to predict recruitment can be considerably lower than the vulnerable biomass Be, and the ratio SBRe/BPre is dependent on F (gets lower as F increases) so as to imply higher risk of recruitment overfishing than predicted by treating the SBR/BPR ratio as either 1.0 or constant. In that case, users should return to the per-recruit calculation model and explicitly calculate SBR as a function of F, then approximate SBRe(F) as a hyperbolic function of F for prediction of Re; unfortunately, the result is then not quite as elegantly simple as eq. (7). All that is necessary is to use SBR instead of BPR in predicting the dependence of Re on SBRe, then multiplying the resulting Re by the eq. 6 prediction of BPre.

Prediction for the Ricker stock-recruitment model

For some populations, there may be reason to assume a dome-shaped Ricker recruitment relationship of the form

$$R = aBe^{-bB} \tag{8}$$

The Botsford equilibrium recruitment for this model is given by

$$R = -\ln(aBPR) / (bBPR) \tag{9}$$

Letting $a = K/BPR_0$, $b = -\ln(K)/(R_0BPR_0)$ and going through the same algebra to calculate Re and BPre as for eq. (7), we obtain the equilibrium biomass prediction

$$Be = \ln[K/(1+F/Fh)] * Bo / \ln(K) \tag{7a}$$

This is again a remarkably simple model for equilibrium biomass prediction. Interestingly, for the “walleye” example shown above (Figure 2), using the Ricker recruitment assumption results in a more symmetric relationship between equilibrium yield and F , and also a somewhat higher estimate of F_{msy} . These effects occur because the relatively steep Ricker model (for $K=15$) predicts increasing recruitment at first as F increases.

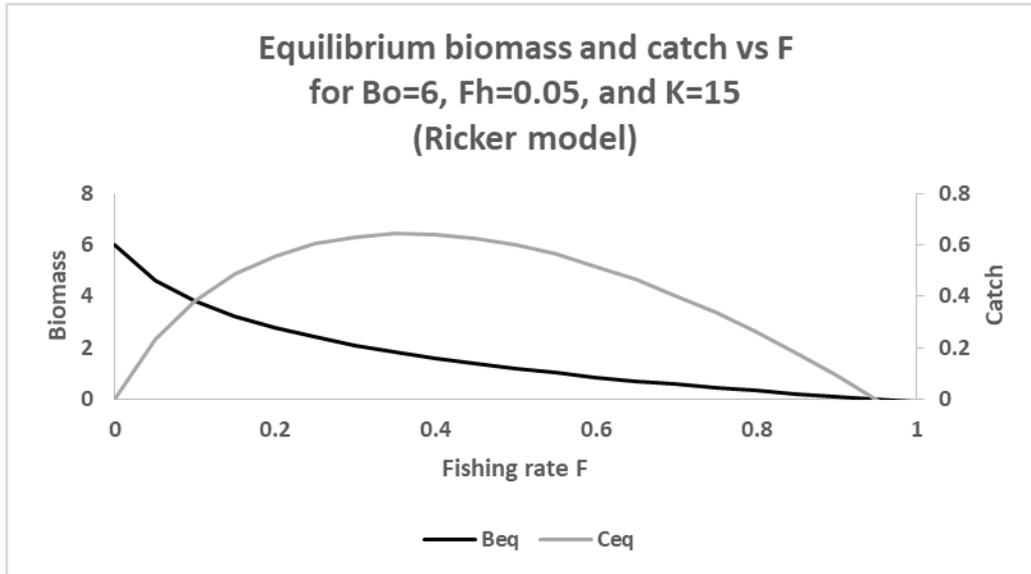
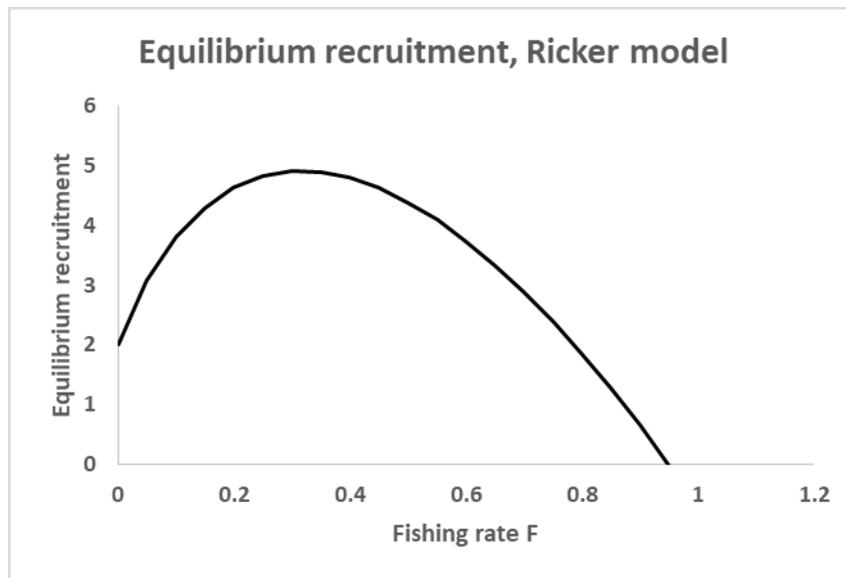


Figure 2. Walleye biomass predictions using a Ricker stock-recruitment model (from “Prediction of equilibrium biomass and yield from R and BPR.xlsx”).



(from “Prediction of equilibrium biomass and yield from R and BPR.xlsx”).

Prediction of fishing rate needed to achieve a given equilibrium biomass

Inverse equations for predicting F given Be are obtained simply by solving eq. 7, 7a for F. These are

$$\text{Beverton-Holt recruitment: } F = F_h * (\mathbf{K} / [\text{Be} / \text{Bo} * (\mathbf{K} - 1) + 1] - 1) \quad (10)$$

$$\text{Ricker recruitment: } F = F_h * (\mathbf{K} * \exp[-\text{Be} / \text{Bo} * \text{LN}(\mathbf{K})] - 1) \quad (10a).$$

Note that these predictions of F do not depend only on the depletion ratio $D = \text{Be} / \text{Bo}$, meaning that they can be applied to situations where there is information on relative stock size as measured by D, but not on absolute stock sizes. Situations like this arise for example in analysis of spatial variation across sport fishing lakes or reef areas in relative fish abundances as measured by survey sampling or catch per effort. We have also used these to predict multiple equilibria for populations subject to depensatory predation.

An example application of the inverse equation 10a is shown in Figure 3, for a situation where the equilibrium relationship between biomass and fishing rate might not be a simple one (might not display monotonic decline in biomass as F increases). Pacific herring are subject to a potentially high total mortality rate Z shortly before spawning, due to a combination of fishing rate F and predation by Steller sea lions that target the prespawning aggregations (i.e. $Z = F + Q / \text{Be}$, where Q / Be is a possibly depensatory mortality rate caused by sea lions). For this case, we first used a realistic model for age-dependent body weight, maturity, and background natural mortality rate (Table 2) to predict effect of total prespawning Z on spawning biomass per recruit, and found the best-fitting Z_h (same as F_h above) for approximating SBR (Panel A) as a function of Z. We then developed a model for predicting mortality rate Q / Be due to sea lion predation (Panel B), basically as a steep type II functional response (efficient foraging to satiation when herring are aggregated before spawning) times a logistic “numerical response” for proportion of the sea lion population electing to aggregate near herring concentrations; this model predicts low predation rates at low herring biomass, a peak in predation rates at intermediate biomass, and declining predation rate at higher herring abundance due to limits on per-predator consumption rates (satiation). Noting that eq. 10 can be written as $Z = f(\text{Be}) = F + Q / \text{Be}$, we then solve for F given Be as simply $F = f(\text{Be}) - Q / \text{Be}$, as shown in Panel C; the pattern shown in this panel has been called the “predator pit” pattern, with a decrease in sustainable F over the range of population sizes for which predation mortality rate Q / Be is highest. Then simply reversing the graph axes for Panel C to show Be vs F (Panel D) demonstrates that predation can cause a multiple-equilibrium structure with moderate Fs leading either to a high stable equilibrium or a low stable one, with an unstable equilibrium (or “critical population size”) between the two stable equilibria.

The equilibrium biomass pattern for herring shown in Figure 3, panel D is known as a “fold catastrophe”. When the Steller sea lion maximum consumption rate Q is varied from low to high levels to represent sea lion population growth, the resulting equilibrium pattern transitions from smooth decline in Be with F (for low Q) to the pattern shown in Figure 3 to a pattern where there is only a low equilibrium at high Q. This more complex pattern is known as a “cusp catastrophe”.

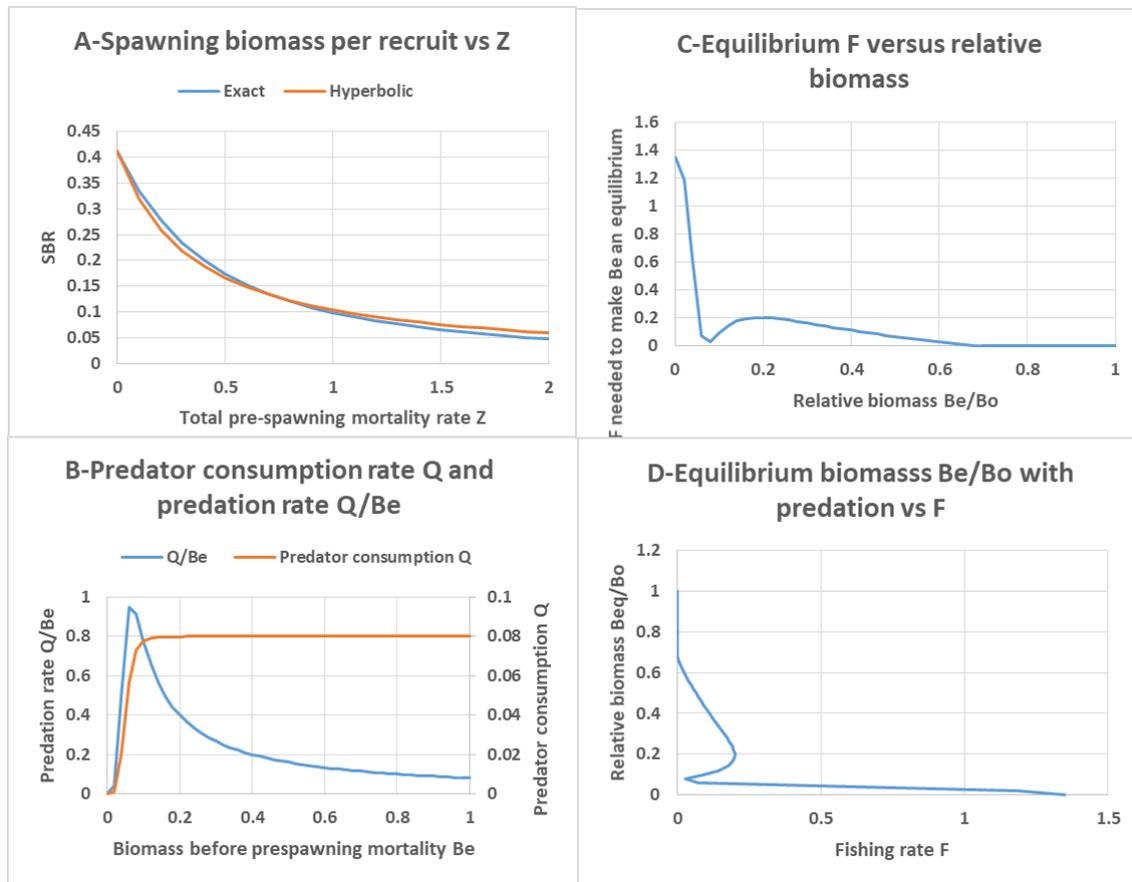


Figure 3. Components in prediction of how equilibrium biomass of Pacific herring is likely to vary in response to combined effects of fishing mortality (F) and depensatory predation mortality on pre-spawning biomass by Steller sea lions. (from “Equilibrium biomass with predation and complex age schedules.xlsx”)

Table 2. Age schedules of natural mortality rate (exclusive of sea lion predation), relative body weight, and maturity for Pacific herring. These schedules in combination with predictions of survivorship to age result in the predicted relationship between spawning biomass per recruit (SBR) and total pre-spawning mortality rate Z show in panel A, Figure 3. Age-specific natural mortality rate (M_{age}) increases for older herring so that very few fish survive past age 10. Body weights in kg. Maturity is proportion of fish maturing and joining the pre-spawning aggregation subject to total pre-spawning mortality rate Z.

Age	2	3	4	5	6	7	8	9	10
Mage	0.50	0.50	0.50	0.50	0.60	0.70	0.80	0.90	1.00
Weight	0.03	0.06	0.10	0.12	0.14	0.16	0.17	0.18	0.19
Maturity	0.00	0.25	0.50	0.80	1.00	1.00	1.00	1.00	1.00

References

Walters, C., and Martell, S. 2004. Fisheries ecology and management. Princeton University Press, Princeton NJ.