Equilibrium Yields and Yield Isopleths from a General Age-Structured Model of Harvested Populations

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The equilibrium properties of an age-structured model that includes any arbitrary age-specific weights, vulnerabilities, fecundities, and natural mortality rates, combined with stock–recruitment relationships, are derived. The numbers, biomass, and catch at each age can be calculated quite simply. These relationships can be used to construct yield-isopleth diagrams, or to plot equilibrium yield and biomass against harvest intensity. We used the results to compute yield isopleths for the Pacific halibut (*Hippoglossus stenolepis*) fishery. The analysis can also include a fishing season of any specified length. Relationships are given to translate the aggregate properties of the age-structured models into several alternative surplus production models.

On a calculé les propriétés d'équilibre d'un modèle structuré selon l'âge qui comprend différents poids, vulnérabilités, fécondités et taux de mortalité naturelle arbitraires en fonction de l'âge combinés à des relations stock–recruitment. Les nombres, biomasses et prises selon l'âge peuvent être facilement calculés. Ces relations peuvent servir à l'élaboration de diagrammes des lignes isoplèthes du rendement ou à tracer un graphique du rendement d'équilibre et de la biomasse en fonction du niveau d'exploitation. Les auteurs ont utilisé les résultats pour calculer les lignes isoplèthes du rendement de la pêche du flétan du Pacifique (*Hippoglossus stenolepis*). L'analyse peut aussi porter sur une saison de pêche de diverse durée. On présente des relations pour transformer les propriétés globales des modèles structurés selon l'âge en plusieurs autres modèles de production excédentaire.

Age-structured models of fish stocks are increasingly used in the analysis of fisheries management options; such models follow the general form outlined by Walters (1969). These models can include age-specific natural mortality rates, fecundity, weight, and vulnerability to fishing, as well as stock–recruitment relationships. Normal practice is to use such models in simulations of alternative fishing policies, although a literature has developed on the optimal harvesting strategies for these models: Rorres and Fair (1975), Reed (1980), Getz (1980a, 1980b). Fisheries managers often want to explore the relationship between harvest intensity and some aspect of age-specific vulnerability, a method popularized by the yield-isopleth diagrams of Beverton and Holt (1957). Beverton and Holt's work did not include any stock-recruitment relationships and therefore is often inadequate for stocks when stock and recruitment are thought to be related.

In this paper we explore the properties of a generalized age-structured model for generation of yield-isopleth diagrams, and we present a worked example using data from Pacific halibut (*Hippoglossus stenolepis*). The equations we derive are

closely related to those of Getz (1980a) who analyzed an age-structured model that differs primarily in the timing of the breeding season in relation to the harvest season.

In addition we explore a number of properties of the model to see if biologically meaningful parameters for stock and recruitment can be derived. Finally we see to what extent the properties of the generalized age-structured model can be compressed into simple two-parameter surplus production models.

Reconsideration of the Catch Equation

Since the catch equation was introduced over 60 yr ago (Baranov 1918), methods of fish stock assessment have assumed that fishing mortality and mortality due to causes other than fishing act simultaneously over the course of the entire year. However, the fishing season for most stocks has been greatly reduced since Baranov's day and it is therefore often assumed that fishing and natural mortality occur separately (e.g. the method of Deriso 1980). Both assumptions are extreme. An intermediate model, in which fishing takes place over a proportion of each year but where natural mortality takes place over the entire year, is shown below.

If we let our year begin with the onset of fishing and if the season lasts until time $\tau(0 < \tau < 1)$, then it is easily shown that the catch C and abundance at the end of the fishing season N_τ are

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TABLE 1. Effect of adjusting the catch equation for length of the fishing season on calculations of abundance at end of fishing season. The abundance at the end of the year is computed as a proportion of abundance at the beginning of the year for several annual harvest rates. A natural mortality rate of $M = 0.2$ was used.

Catch rate	Length of fishing season (mo)				
	1	3	6	9	12
0.1	0.80	0.78	0.76	0.74	0.73
0.3	0.67	0.64	0.60	0.58	0.55
0.5	0.48	0.46	0.42	0.40	0.37
0.7	0.29	0.27	0.24	0.22	0.20
0.9	0.09	0.08	0.06	0.05	0.04

given by

$$(1) \quad C = N_0 \frac{F}{F + M}(1 - e^{-\tau(F+M)})$$

$$(2) \quad N_\tau = N_0 e^{-\tau(F+M)}$$

where N_0 is the abundance at the beginning of the year and F and M are instantaneous rates of fishing and natural mortality (in units of year^{-1}). The abundance at the end of the year N_1 is simply

$$(3) \quad N_1 = N_0 e^{-(\tau F + M)}.$$

Table 1 illustrates how calculations of abundance depend on the length of the fishing season. For short seasons with moderate catch rates, estimates of abundance at the end of the year, calculated assuming that fishing occurs throughout the year, will be about 90% of the true value. By comparing across rows of Table 1 we can see how much the length of the fishing season affects the total loss from the population. For short seasons with high catch rates, estimated stock size can be as low as 50% of the true value. Adjusting the catch equation for length of season will thus afford an increase in precision for only a slight increase in computational complexity.

Equilibrium Formula for Age-Structured Models

Formulae are here derived for computing values of several model variables at the equilibrium reached when a constant harvest rate is applied indefinitely. Data required include age-specific parameters, such as weight, relative vulnerability to harvesting, and reproductive potential (either egg production or whatever may be chosen to represent "stock" in the stock and recruitment model), and estimates of the stock–recruitment model parameters. Variables to be determined are total biomass before and after fishing, recruitment, total reproductive potential, and the catch. Getz (1980a) provided similar equations except that he assumed that the spawning population was measured after harvest and we assume that spawning occurs before harvest.

The equations depend on the annual order of events. The year starts with recruitment, followed by harvesting. Natural mortality occurs throughout the year. Reproductive potential is assumed to be determined by abundance after recruitment but before the onset of fishing.

Let N_i be the number of fish at age i after recruitment but before harvesting. At equilibrium:

$$(4) \quad N_i = R_\infty, \quad i = r$$
$$= R_\infty \exp\left[-\sum_{j=r}^{i-1}(\tau F V_j + M_j)\right],$$
$$i = r + 1, \ r + 2, \ldots, n$$

where R_∞ = equilibrium recruitment in numbers of fish, V_j = the relative vulnerability to harvesting at age j, M_j = the rate of natural mortality at age j (although M_j will usually be assumed constant over ages), r = the age at recruitment, and n = the oldest age accounted for in the model.

The total equilibrium biomass after recruitment but before fishing is B_∞, given by substituting from 4:

$$(5) \quad B_\infty = \sum_{i=r}^{n} W_i N_i$$
$$= R_\infty Q_1$$

where

$$Q_1 = W_r + \sum_{i=r+1}^{n} W_i \exp\left[-\sum_{j=r}^{i-1}(\tau F V_j + M_j)\right]$$

and W_i = weight at age i.

Total reproductive potential E_∞ is

$$(6) \quad E_\infty = \sum_{i=r}^{n} f_i N_i$$
$$= R_\infty Q_2$$

where

$$Q_2 = f_r + \sum_{i=r+1}^{n} f_i \exp\left[-\sum_{j=r}^{i-1}(\tau F V_j + M_j)\right].$$

If reproductive potential is represented by egg production, then f_i = fecundity at age i adjusted for the sex ratio. If reproductive potential is simply proportional to biomass, then $f_i = W_i$, and if reproductive potential is numbers of fish, then $f_i = 1$.

The biomass of catch is given by

$$(7) \quad C_\infty = \sum_{i=r}^{n} W_i N_i \frac{F V_i}{F V_i + M_i}(1 - \exp[-\tau(F V_i + M_i)])$$
$$= R_\infty Q_3$$

where

$$Q_3 = W_r \frac{F V_r}{F V_r + M_r}(1 - \exp[-\tau(F V_r + M_r)])$$
$$+ \sum_{i=r+1}^{n} W_i \frac{F V_i}{F V_i + M_i}(1 - \exp[-\tau(F V_i + M_i)])$$
$$\times \left(\exp\left[-\sum_{j=r}^{i-1}(\tau F V_j + M_j)\right]\right).$$

Total equilibrium biomass after fishing B_∞' is given by

$$(8) \quad B_\infty' = \sum_{i=r}^{n} W_i N_i'$$
$$= R_\infty Q_4$$

where

$$Q_4 = W_r \exp[-\tau(F V_r + M_r)]$$
$$+ \sum_{i=r+1}^{n} W_i \exp\left[-\tau(F V_i + M_i)\right.$$
$$\left.- \sum_{j=r}^{i-1}(\tau F V_j + M_j)\right].$$

Note that if breeding takes place after the fishing season, then

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N_i' should be used in equation 6 instead of N_i. Substituting f_i for W_i in equation 8 would provide the reproductive potential appropriate for postharvest spawning.

Equations 5–8 have been derived in terms of equilibrium recruitment. It remains to derive an expression for R_∞ in terms of stock and recruitment parameters. If the Ricker (1954) model is used, we have

$$(9) \quad R_\infty = \alpha E_\infty e^{-\beta E_\infty}$$

where α and β are model parameters. Substituting equation 6 into equation 9, we obtain

$$(10) \quad R_\infty = \frac{\ln(\alpha Q_2)}{\beta Q_2}.$$

If the Beverton and Holt (1957) model is used, we have

$$(11) \quad R_\infty = \frac{E_\infty}{(\alpha E_\infty + \beta)}.$$

Substituting equation 6 into 11, we get

$$(12) \quad R_\infty = \frac{Q_2 - \beta}{\alpha Q_2}.$$

Finally, substituting either equation 10 or 12 into equations 5–8, we obtain the equilibrium values in terms of the harvest rate, length of the season, the age-specific parameters, and the stock and recruitment parameters.

Stock–Recruitment Parameters for Age-Structured Models

For age-structured models, the biological interpretation of the parameters α and β is not immediately obvious and can be quite difficult to interpret. Fortunately, α and β can be combined with the other parameters of the age-structured model to calculate more biologically meaningful quantities. There are several possibilities, but we suggest the use of (1) the unfished equilibrium biomass and (2) the rate of biomass recruitment at half the unfished equilibrium biomass. These two quantities, when taken together, are equivalent to α and β, as shown in the next two paragraphs.

The unfished equilibrium biomass can be determined from equation 5 with $F = 0$. The rate of recruitment θ at proportion p of the equilibrium biomass B_∞ (assuming the same age distribution) is given for the Ricker model by equation 13 (details of the derivation are given in the appendix):

$$(13) \quad \theta = W_r \frac{(\alpha Q_2)^{1-p}}{Q_1}.$$

And for the Beverton Holt model:

$$(14) \quad \theta = W_r \frac{Q_2}{Q_1} \frac{1}{(pQ_2 + (1-p)\beta)}.$$

For modeling purposes, it would be convenient if we could set α and β from values of B_∞ and θ. For the Ricker model, it can be shown (details in appendix) that

$$(15) \quad \alpha = \frac{1}{Q_2} \left(\frac{Q_1 \theta}{W_r} \right)^{1/(1-p)}$$

and

$$(16) \quad \beta = \frac{Q_1}{Q_2} \ln \left(\frac{Q_1 \theta}{W_r} \right) \frac{1}{(1-p)B_\infty}$$

while for the Beverton and Holt model:

$$(17) \quad \alpha = \frac{Q_1}{B_\infty} \left[1 - \frac{1}{1-p} \left(\frac{W_r}{Q_1 \theta} - p \right) \right]$$

and

$$(18) \quad \beta = \frac{Q_2}{1-p} \left(\frac{W_r}{Q_1 \theta} - p \right).$$

Simplification to Surplus Production Models

It is increasingly recognized that complex age-structured models can be compressed into a much more manageable form with little sacrifice in accuracy. Deriso (1980) presented the most elegant reduced form, compressed a generalized age-structured model into a delay-difference equation with seven parameters. Hilborn (1979), Ludwig and Hilborn (1983), and Ludwig and Walters (1985) have shown that simple two-parameter surplus production models can be used as surrogates for the more complex age-structured models. Hilborn (1979) used a discrete form of the standard Schaefer model:

$$(19) \quad B_{t+1} = B_t + rB_t \left(1 - \frac{B_t}{k} \right) - C_t$$

where B_{t+1} is the biomass at time $t + 1$, B_t is the biomass at time t, r is the rate of growth of biomass as B approaches zero, k is the unfished equilibrium stock size, and C_t is the catch at time t.

Ludwig and Hilborn (1983) and Ludwig and Walters (1985) have used Ricker's recruitment model as a surplus production model of the form

$$(20) \quad B_{t+1} = B_t e^{\alpha(1 - B_t/\beta)}$$

where e^α is the rate of growth of biomass as B approaches zero and β is the unfished stock size.

There are several ways to compress the behaviour of the age-structured model into the simple surplus production model. We suggest the following.

The properties of the Schaefer model are

$$(21) \quad \begin{aligned} B_\infty &= k \\ C^* &= \frac{rk}{4} \\ B^* &= \frac{k}{2} \end{aligned}$$

where B_∞ is the unfished stock size, C^* is the maximum sustainable yield, and B^* is the biomass at maximum sustainable yield. Parameter B_∞ can be derived from the age-structured model by setting $F = 0.0$. Parameters C^* and B^* can both be found by a numerical search over values of F. Once B_∞, C^*, and B^* are determined, the values of r and k can be computed using (21).

The parameters of the Ricker equation can be calculated in several ways. The simplest is to use the following equation from Ricker (1975):

$$(22) \quad \alpha = u^* - \ln(1 - u^*)$$

where u^* is the annual harvest rate C^*/B^*. The β of the Ricker model is the unfished stock size and therefore B_∞.

Equilibrium Properties of Pacific Halibut

Age-specific population parameters for the Pacific halibut fishery (R. B. Deriso, International Pacific Halibut Commis-

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TABLE 2. Weight, vulnerability, and reproductive potential schedules for Pacific halibut. Reproductive potential is the weight times the percent of females who reproduce at that age. Natural mortality rate (M) was assumed to be 0.2 for all ages.

| Age	Average weight (kg)	Relative vulnerability	Reproductive potential
8	8.0	0.18	1.0
9	10.3	0.32	2.6
10	12.7	0.47	4.8
11	15.8	0.59	7.9
12	19.5	0.76	12.2
13	22.7	0.81	17.1
14	26.4	0.92	23.1
15	28.7	1.00	28.7
16	30.8	1.00	30.8
17	33.8	1.00	33.8
18	41.3	1.00	41.3
19	45.7	1.00	45.7
20	44.7	1.00	44.7

FIG. 1. Yield-isopleth diagram for Pacific halibut using the data from Table 2. Contours are in thousands of tonnes per year. Fishing mortality rate is τF.
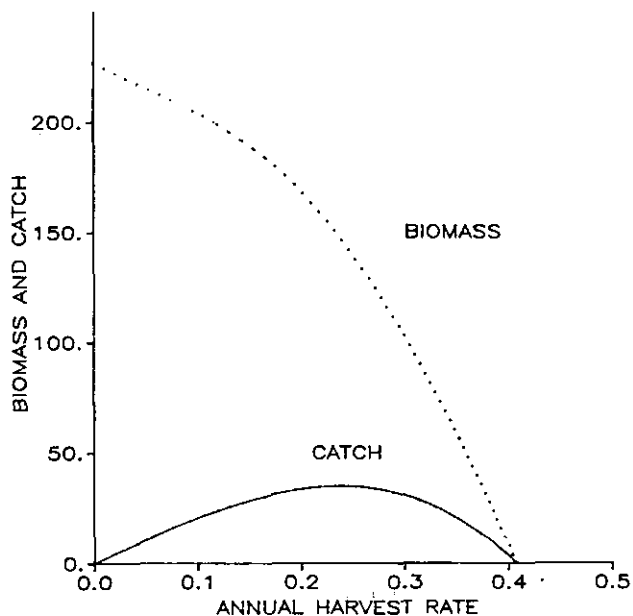

FIG. 2. Equilibrium stock size and yield versus harvest rate for Pacific halibut. Annual harvest rate is the catch divided by the preharvest biomass.

sion, University of Washington, Seattle, WA, pers. comm.) are listed in Table 2. Recruitment to the gear occurs at age 8, and the oldest age in the model is 20. Natural mortality is assumed constant over all ages, with $M = 0.2$. The length of the fishing season is currently about 4 wk, so $\tau = 4/52 = 0.0769$.

Reproductive potential for the stock and recruitment model was defined to be the sum over ages 8–20 of a fraction of the total biomass at each age, where the fraction begins at 1/8 for age 8, and increases by 1/8 for each age from age 9 to age 14, and is equal to unity for ages 15–20. Recruitment in thousands of fish is determined from a Ricker model with the parameters $\alpha = 0.187$ and $\beta = 0.016$.

The optimal harvest rate is not available in closed form, so the equilibrium properties were calculated numerically by varying F between 0 and 22 in increments of 0.25. The apparently high values of F are a result of the very intense but short fishing season. The unfished stock size (B_∞) is 226 KMT, and the maximum sustainable harvest (C^*) is 35 KMT, which takes place when $F^* = 8.0$. The biomass at optimum harvest rate (B^*) is 147 KMT, and the annual harvest rate at optimum (u^*) is 0.24.

The alternative stock–recruitment parameters were also calculated. The unfished equilibrium biomass is 226 KMT, and the rate of recruitment at half the unfished equilibrium biomass (θ) is 0.30. The latter value seems reasonable for a long-lived species. For short-lived, highly fecund species, we would expect θ to be larger.

Figure 1 shows the yield-isopleth diagram for the fishery, where the x-axis represents the annual catch divided by the preharvest biomass (harvest rate), and the y-axis represents the first year of vulnerability. The vulnerability of all older ages is unchanged. While this is somewhat unrealistic, it does let us examine the potential increase in yield that could be obtained by increasing the age at first capture. Although this is not a yield-per-recruit diagram, its general shape is quite similar.

Figure 2 shows the equilibrium stock size and the equilibrium yield versus harvest rate. This curve conforms to the general shapes we have come to expect from surplus production models. Given the relationship between the Schaefer parameters r and k and the three numbers available from the age-structured model (B_∞, B^*, C^*), there are four possible combinations of r and k
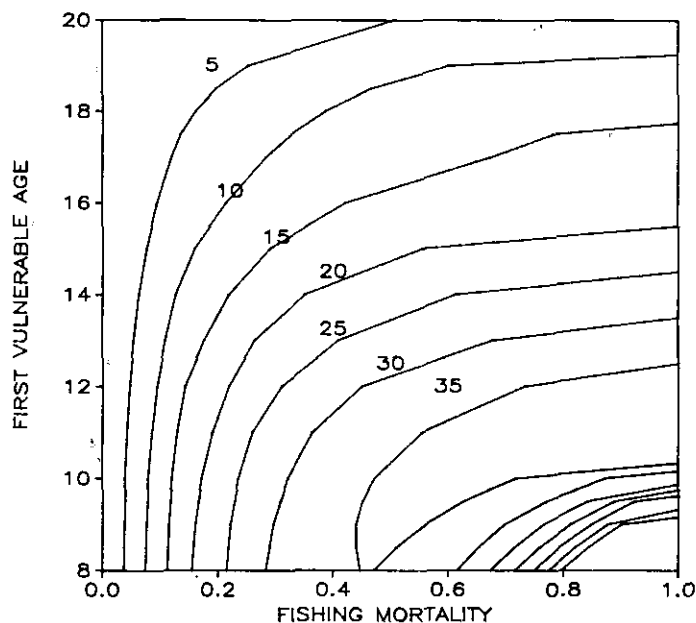
that can be calculated. These are shown in Table 3, along with the parameters that can be calculated from r and k using the Schaefer model. In each set, some of the biologically meaningful parameters $(B_\infty, B^*, C^*,$ and $u^*)$ are equal to those of the "real" age-structured model, and some of the parameters are not the same. The best approach is the upper right-hand set, in which k is estimated by multiplying the optimum stock size of the age-structured model by 2, and r is obtained by multiplying the ratio of catch to biomass at optimum by 2.

While there may appear to be some circularity in these calculations, whenever the use of the surplus production model is desired, the best way to calculate parameters may be to use the age-structured model. The surplus production model would be

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TABLE 3. Optimal equilibrium properties of Schaefer model parameters using parameters derived from equilibrium properties of an age-structured model. The Schaefer parameters r and k can each be estimated in two different ways from B_∞, C^*, and B^*.

	$k = B_\infty = 227$	$k = 2B^* = 296$
$r = \dfrac{2C^*}{B^*} = 0.48$	$B_\infty = 226$ $C^* = 27$ $B^* = 113$ $u^* = 0.24$	$B_\infty = 296$ $C^* = 35$ $B^* = 147$ $u^* = 0.24$
$r = \dfrac{4C^*}{B_\infty} = 0.62$	$B_\infty = 226$ $C^* = 35$ $B^* = 113$ $u^* = 0.31$	$B_\infty = 296$ $C^* = 46$ $B^* = 147$ $u^* = 0.31$

used for optimization, simulation, or gameing. Therefore we want to have our compressed surplus production model behave as much like the full age-structured model as possible. The upper right hand set in Table 3 is probably preferred because we would like our compressed model to have the same optimum stock size, sustainable yield, and optimum harvest rate as the full age-structured model.

Using equation 22 to estimate the parameters of a Ricker-type surplus production model produces $B_\infty = 226$, $C^* = 33$, $B^* = 105$, and $u^* = 0.24$. In this case the optimum stock size and yield are underestimated.

The utility of any of these surplus production representations of the full age-structured model will depend on the exact use of the compressed model, and the choice of which parameter estimation method to use is left to potential users. Potential users are reminded that many other methods can be used, including a Beverton–Holt stock–recruitment curve as a surplus production model, or the Pella and Tomlinson (1969) surplus production model.

Discussion

We have presented a simple method for summarizing age-structured data for harvested populations. Weight and fecundity schedules are usually easily obtained from data collected in association with age sampling. If a time series of age composition of catch is available, the remaining data required can be determined by the method of Fournier and Archibald (1982), or by cohort analysis (Pope 1972) used in conjunction with a method for the estimation of stock–recruitment parameters (Ludwig and Walters 1981).

Model dynamics will in general depend largely on the relationship between the fecundity and vulnerability schedules. Density-dependent growth and species interactions are the two biological factors not included in this analysis that may be significant. Nevertheless, useful statistics characterizing the population are the equilibrium properties and alternative stock–recruitment parameters as described above. The equations are simple enough to solve on a programmable calculator, and yet enable one to analyze yields for different vulnerability schedules and fishing intensities.

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Appendix: Derivation of Stock–Recruit Parameters for Age-Structured Models

For the Ricker stock–recruitment curve (equation 9), the rate of biomass recruitment at proportion p of equilibrium biomass, assuming the same harvest rate F, is given by

$$(A.1) \qquad \theta = \frac{W_r R_\theta}{p B_\infty}$$

where R_θ = recruitment in numbers of fish at proportion p of the unfished biomass. It remains to express R_θ in terms of α, β, and p and B_θ in terms of α and β.

To begin, substituting equation 10 into equation 5, we obtain

$$(A.2) \qquad B_\infty = \frac{Q_1}{Q_2} \frac{\ln(\alpha Q_2)}{\beta}.$$

Now, rewriting R_θ, we have

$$(A.3) \qquad R_\theta = \alpha E_\theta e^{-\beta E_\theta}$$

where E_θ = reproductive potential at proportion p of the equilibrium biomass. Assuming the same age distribution as for B_θ, then

$$(A.4) \qquad E_\theta = \sum_{i=r}^{n} f_i p N_i$$
$$= p E_\infty.$$

Substituting equation 10 into equation 6 and then using the result in equation A.4 gives

$$(A.5) \qquad E_\theta = p \frac{\ln(\alpha Q_2)}{\beta}.$$

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Now, rewriting equation A.3 using equation A.5, we obtain

(A.6) $R_\theta = \dfrac{\alpha}{\beta} p \ln (\alpha Q_2)(\alpha Q_2)^{-p}.$

Finally, substituting equation A.2 and equation A.6 into our expression for θ, we derive

(A.7) $\theta = W_r \dfrac{(\alpha Q_2)^{1-p}}{Q_1}.$

As derived above, equation A.2 and equation A.7 are valid for any value of the harvest rate. For B_∞ and θ to refer specifically to the *unfished* equilibrium biomass and rate of recruitment at proportion p of the *unfished* equilibrium biomass, respectively, we need only write Q_1 and Q_2 with $F = 0$.

Following the same line of argument, for the Beverton–Holt curve (equation 11), we have

(A.8) $B_\infty = \dfrac{Q_1}{Q_2} \dfrac{(Q_2 - \beta)}{\alpha}$

and

(A.9) $R_\theta = \dfrac{E_\theta}{\alpha E_\theta + \beta}$

  $= p\dfrac{(Q_2 - \beta)}{\alpha} \cdot \dfrac{1}{pQ_2 + (1-p)\beta}.$

Finally, substituting equation A.8 and equation A.9 into our expression for θ, we obtain

(A.10) $\theta = \dfrac{W_r Q_2}{Q_1} \cdot \dfrac{1}{pQ_2 + (1-p)\beta}.$

To derive α and β in terms of θ and B_∞ for the Ricker curve, rewriting equation A.7 gives α directly (equation 15). To derive β, simply solve the equation obtained when equation 15 is substituted into equation A.2.

Similarly, to derive α and β in terms of θ and B_∞ for the Beverton–Holt curve, first solve equation A.10 for β. Then to derive α, solve the equation obtained when equation 18 is substituted into equation A.8.

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