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The Schnute-Deriso delay-difference model (Deriso, 1980; Schnute 1985) provides an extremely compact representation of the exact dynamics of total numbers and biomass for age-structured populations where (1) there is knife-edge recruitment to the harvested (adult) population, i.e. fishing mortality rate is independent of age for fish aged a_r and older; (2) natural mortality rate M is constant; and (3) body weight growth can be approximated by the Ford-Brody model for weight at age a, namely $w(a)=\alpha+\rho w(a-1)$. This growth model is only a good approximation for older ages, beyond the age at which weight growth rate begins to decline, but most harvested fish populations meet this condition.

The discrete time delay-difference model for total exploitable biomass B(t) and numbers N(t), summed over ages k to infinity, is given by

$$B(t)=s(t-1)[\ \alpha N(t-1)+\rho B(t-1)]+w_k R(t) \qquad (1)$$

$$N(t)=s(t-1)N(t-1)+R(t) \qquad (2)$$

where the overall survival rate s(t) for year t is given by

$$s(t)=e^{-M}(1-u(t)) \text{ or } s(t)=e^{-M-F}$$

Here, u(t) is the harvest rate in year t, and F is the instantaneous fishing rate applied over a short discrete time at the start of year t. The main advantage of eqs. (1)-(2) over full age-structured accounting is that they can be solved very quickly for very large numbers of populations, e.g. in spatial grid models, without loss of age-structure effects on average size of fish harvested and on fecundity.

This discrete-time formulation does not work well for populations that exhibit continuous reproduction over time, turn over rapidly (have high fishing mortality rates F), and/or exhibit continuous spatial mixing among local sites. Such dynamics characterize some commercially important stocks, such as shrimps and smaller tunas. For such species, it may be better to treat recruitment, growth, and mortality rates as all varying continuously over time.

Fortunately, it is simple to derive the continuous-time analog of eqs. (1)-(2), under basically the same assumptions: knife edge recruitment to fishing at age a=k, constant natural mortality rate M, and weight growth rate approximated by the same decelerating relationship

$$dw/da=\kappa(w_\infty-w(a)) \qquad (3)$$

that leads to the Ford-Brody version of the vonBertalanffy growth model. The derivation begins by noting that when reproduction is continuous over time, exploitable biomass B(t) can be represented by

$$B(t) = \int_{a=k}^{\infty} N(a,t)w(a,t)da \qquad (4)$$

Differentiating this integral with respect to t, while noting that $dB(a,t)/dt=w(a,t)dN(a,t)/dt+N(a,t)dw(a,t)/dt$, $dN(a,t)/dt=-(F+M)N(a,t)$ and noting that input rate to the biomass integral is the continuous biomass recruitment rate w(k)R(t), it is easily seen that

the rate of biomass change is given by a sum of integral terms over age, with these integral terms being B(t) and N(t). This sum of terms, along with the obvious rate equation for N(t), constitutes the continuous delay-differential model

$$dB(t)/dt = w(k)R(t) + \kappa w_\infty N(t) - (Z(t)+\kappa)B(t) \qquad (5)$$

$$dN(t)/dt = R(t) - Z(t)N(t) \qquad (6)$$

Here, $Z(t)=F(t)+M$ is the total instantaneous mortality rate, assumed to vary over time with changes in fishing mortality rate F(t). These equations can be easily extended to include emigrate rate (as an additional component of Z(t)) and immigration rates from other populations/sites, as added rate terms to both dB/dt and dN/dt. It is simple to numerically integrate the equations over time for arbitrary recruitment R(t) and F(t) rate patterns, and to link recruitment rate to biomass at time t-k using functions such as the Beverton-Holt, $R(t)=aB(t-k)/(1+bB(t-k))$, to create delay-differential model forms.

To ensure that eqs. (5)-(6) do exactly represent the dynamics of total biomass and numbers for age structured populations that meet the basic assumptions of age-independent mortality rate and linearly declining growth rate, I constructed a fully age-structured accounting model with very small age-time increments $\Delta a, \Delta t < 0.1$, and forced this model with complex R(t) and F(t) patterns. The biomasses and numbers summed over age for this model do indeed track the simple model predictions more and more precisely as the age-time increment becomes smaller (Fig. 1).

Intuitively, eq. (5) says that rate of biomass change has three components. One is the obvious recruitment addition rate w(k)R(t). The second is an addition rate proportional to fish numbers, $\kappa w_\infty N(t)$, basically representing the effect of food consumption on growth rate where the weight growth model $dw/dt = \kappa(w_\infty - w)$ in essence assumes that feeding rate per individual fish in N(t) is independent of body weight. The third term, $-(Z(t)+\kappa)B(t)$, represents biomass loss to all causes of loss, including instantaneous body mass metabolic loss represented by κ.

Equilibrium predictions of biomass, yield, and average body size

The continuous rate formulation results in very simple predictions of equilibrium biomass and numbers, under constant R(t) and F(t) conditions. Solving eq. (5)-(6) with the rates set to zero, we obtain

$$B_\infty = \frac{[w_k + \kappa w_\infty/Z]}{Z+\kappa} R \qquad (7)$$

$$N_\infty = R/Z \qquad (8).$$

Equilibrium yield Y_∞ per time is then given by just $Y_\infty = FB_\infty$, and equilibrium mean body weight B/N is given by the ratio of eq. (7) to eq. (8).

To include a stock-recruitment relationship in the equilibrium prediction, e.g. $R=aB/(1+bB)$, we simply note that B_∞ in eq. (7) can be written as $B_\infty = BPR \times R$, where biomass per recruit BPR is given as function of Z by

$$BPR = \frac{[w_k + \kappa w_\infty/Z]}{Z+\kappa} \qquad (9)$$

Using this biomass per recruit, the equilibrium recruitment rate is predicted as the stock-recruitment function function of it, e.g. $R = aR \cdot BPR/(1+bR \cdot BPR)$, which is easily solved for R, i.e.

$$R = (aBPR-1)/(bBPR). \tag{10}$$

That is, we choose an F, calculate Z and BPR from eq. 9, then predict the equilibrium R from eq. (10), while noting that R<0 implies extinction under the chosen F.

Eqs. (7)-(8) provide an interesting prediction of how equilibrium average body weight $\overline{w} = B/N$ ought to vary with Z, namely

$$\overline{w} = \frac{w_k Z + \kappa w_\infty}{Z + \kappa} \tag{11}$$

which can be solved for Z to provide an estimate of Z given $\overline{w}$ and the growth parameters:

$$\overline{Z} = \kappa \frac{w_\infty - \overline{w}}{\overline{w} - w_k} \tag{12}$$

Note that this estimator for Z approaches infinity as $\overline{w}$ decreases toward w_k, and is very similar to the one proposed by Beverton and Holt for estimating Z from mean body length.

In fact, eq. (12) points out how the whole model structure above can be used not only to predict changes in biomass, but also changes in total population length L(t) and mean body length L(t)/N(t). For modeling length dynamics and changes in mean length over time, κ becomes just the vonBertalanffy "growth" (metabolic) parameter K, and w_∞ becomes the standard vonBertalanffy L_∞.

Exact time solutions for piece-wise constant recruitment and fishing patterns

There are simple analytical solutions for the rate eqs. (5)-(6) in the case that recruitment and fishing mortality rates R and F can be treated as piece-wise constant, i.e. constant over short time intervals Δt with step changes at the start of each interval. Over any such interval, the solutions can be found by using integration factors, resulting in exact predictions of numbers and biomass at the end of each interval given starting values:

$$N(t+\Delta t) = N_\infty + [N(t)-N_\infty]e^{-Z\Delta t} \tag{13}$$

$$B(t+\Delta t) = B_\infty + w_\infty[N(t)-N_\infty]e^{-Z\Delta t} + \{B(t)-B_\infty - w_\infty[N(t)-N_\infty]\}e^{-(Z+\kappa)\Delta t} \tag{14}$$

Here, N_∞ and B_∞ are the equilibrium (asymptotic) values from eq. (7)-(8) that would result if F and Z were to remain constant for much longer that Δt. Equations (13)-(14) show that N(t) and B(t) are predicted to dampen toward the equilibrium values N_∞ and B_∞ as Δt increases, given no changes in F and R. Catch in numbers C and yield Y over the interval t to t+ Δt are given by integrating eqs. (13-14) times F over time:

$$C = FN_\infty\Delta t + F[N(t)-N_\infty](1-e^{-Z\Delta t})/Z \tag{15}$$

$$Y = FB_\infty\Delta t + Fw_\infty[N(t)-N_\infty](1-e^{-Z\Delta t})/Z + F\{B(t)-B_\infty - w_\infty[N(t)-N_\infty]\}(1-e^{-(Z+\kappa)\Delta t})/(Z+\kappa)$$
$$\tag{16}.$$

Mean body weight of fish in the catch over the interval Δt is then given by Y/C. Note that eqs. (15)-(16) each consist of an equilibrium component $FX\Delta t$ where X is equilibrium numbers or biomass under the input F and R, plus a component representing deviation of N(t) and B(t) from equilibrium. Note also that for all the piece-wise Δt predictions of eqs. (13)-(16), the equilibrium values N_∞, B_∞ used in the calculation are for the constant R predicted just for the interval Δt, not the

long-term equilibrium R predicted from a stock-recruitment relationship, i.e. not the R predicted from eq. (10).

It is common in fisheries for the weight at recruitment w_k to be less than the weight at maturity w_m, so that fish are subject to mortality rate F+M for some time period t_m before they mature. It is possible to set up the delay-differential model to explicitly model changes in spawning biomass S(t) for such cases, substituting w_m for w_k in the equilibrium biomass per recruit calculations and setting recruitment rate RS(t) to the spawning biomass to be RS(t)=R(t-t_m)e$^{-Z*t_m}$ where Z* is the mean total mortality rate over time t-t_m to t. But numerical simulations show that S(t) as a proportion of B(t) tends to closely track the moving equilibrium proportion S(t)/B(t) given by

$$S(t)/B(t) \approx e^{-Zt_m}(w_m + \kappa w_\infty/Z)/(w_m + \kappa w_\infty/Z) \qquad (16a).$$

This ratio can be multiplied by B(t) from eq. (14) to give an approximate S(t) for use in stock-recruitment equations like the Beverton-Holt, i.e. R=aS/(1+bS). Typically, the effect of such accounting for fishing mortality before maturity is to give lower estimates of Fmsy, substantially so when fish are exposed for a long t_m period (e.g. up to 5 years for long-lived species).

While the exact solution eqs. (13)-(14) look quite different from the discrete time delay-difference model of eq. (1)-(2), they can in fact be expressed in a very similar format, with "minor" differences related to the assumption of continuous recruitment and harvest mortality:

$$N(t+ \Delta t)= s^*(t)N(t)+ R(t)(1-s^*(t)))/Z+ \qquad (17)$$

$$B(t+ \Delta t)= s^*(t)[\alpha^*N(t)+\rho^*B(t)]+w_kR(t)H^* \qquad (18)$$
where the starred survival and growth rate factors are given by

$$s^*(t)=e^{-(F+M)\Delta t} \qquad (19)$$

$$\rho^*=e^{-\kappa\Delta t} \qquad (20)$$

$$\alpha^*=w_\infty(1-\rho^*) \qquad (21)$$

$$H^*=[1- \rho^*s(t)]/(Z+\kappa) +\kappa w_\infty[1- \rho^*s(t)]/[w_kZ(Z+\kappa)]-w_\infty s(t)(1- \rho^*)/(w(k)^*Z)$$
$$\qquad (22)$$

The complex recruitment "correction" factor H* looks formidable, but for reasonable survival and growth parameters typically quite close to just Δt, i.e. H* $\approx\Delta t$. Note that as for the discrete time model, s* and H* vary over time while ρ^* and α^* do not change except in cases where the growth curve varies over time.

Treating Fmsy and MSY as leading parameters for calculation of recruitment parameters

For parameter estimation, it is often convenient to follow the approach of Schnute and Kronlund (1996) and Forrest et al. (2008), where Fmsy and MSY are treated as leading parameters and the Beverton-Holt stock-recruitment parameters a,b are calculated from these. For given values of Fmsy and MSY, the calculation involves three steps:

1) calculate BPR at Fmsy: ϕ_f =[w(k)+κw_∞/(Fmsy+M)]/(Fmsy+M+κ) (23)

2) calculate $\partial\phi_f / \partial F = -\{\kappa w_\infty /[Z^2(Z + \kappa)] + (w_k + \kappa w_\infty / Z)/(Z + \kappa)^2\}$ (24)

   (evaluated at Z=Fmsy+M)

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3) calculate $a = 1/(\phi_f + \text{Fmsy}\, \partial\phi_f / \partial F)$ and $b = \text{Fmsy}^*(a^* \phi_f - 1)/\text{MSY}$ (25).

This derivation follows from noting that equilibrium yield $Y = F\phi_f (a\phi_f - 1)/(b\phi_f)$ and that the derivative of Y with respect to F must equal 0.0 at F=Fmsy. Note that the calculation can result in negative (nonsensical) values of a and b; this arises in cases where the growth parameters imply a relatively low Fmsy independent of the stock recruitment parameters, i.e. growth overfishing at lower F than the Fmsy trial value entered for the calculation. In such cases, the Fmsy trial value should be rejected as physically impossible during parameter estimation searches, MCMC trials, etc.

Using predicted changes in mean body weight in model fitting

Since the model predicts changes in mean body weight in response to changes in recruitment and fishing mortality rate, i.e. $\overline{w}(t) = B(t)/N(t)$, it is tempting to use comparisons of observed and predicted mean weights in fitting the model to data, just as we would typically use size-age composition data. Indeed, Fournier and Doonan (CJFAS, 1987) have noted that size distribution moments (mean, variance, …) appear to be just as useful as full size distributions in model fitting.

When using predicted mean weights in model fitting, care must be taken in estimation of the observed mean weight in the catch and in estimation of the weight growth parameters when the field data are body lengths and weight is estimated from a length-weight relationship ($w = aL^b$, L=body length). It is tempting to calculate mean weight at age from mean lengths predicted from a length growth curve fit, then estimate the Ford-Brody parameters from the resulting estimates of mean weight at age. This results in a downward bias in estimates of both $w(k)$ and w_∞, because of the nonlinear relationship between weight and length. Actually, mean weight is expected to differ from weight at the mean length at age by a multiplicative factor, approximately $1 + 3.0 CV^2$ if $b \approx 3.0$, where CV is the coefficient of variation in body length at age (typically in the range 0.05-0.15). More precisely, the multiplier on CV^2 for predicting mean weight from mean length is $b(b-1)/2$. So, if the estimated mean length at age a is $\overline{L}(a)$, mean weight at that age is given approximately by

$$\overline{w}(a) = (1 + 3CV^2)a\overline{L}(a)^b, \tag{26}$$

and it is this $\overline{w}(a)$ that should be used in estimating $w(k)$ and w_∞.

Failure to use corrected mean weights in estimation of the weight growth parameters leads to underestimates of the mean weights $\overline{w}(t)$, and model fitting procedures will try to increase the predicted mean weight to fit observed means (calculated from individual fish sample lengths) by reducing the modeled fishing mortality rate. That is, failure to make the mean weight correction in eq. 26 can lead to severe downward bias in estimation of historical fishing mortality rates.

Approximate estimates of recruitment rates over time given biomass over time

Suppose we have accurate annual biomass estimates $B^*(t)$ of the vulnerable biomass, e.g. from annual surveys, and of $Z(t)$ as M plus catch $C(t)$ divided by approximate mean biomass $(B^*(t+1)+B^*(t))/2$. Then assuming that numbers $N(t)$ stay fairly close to the equilibrium $R(t)/Z(t)$, eq. (14) reduces to

$$B^*(t+1) \approx R(t)BPR(t)+[B^*(t)-R(t)BPR(t)]e^{-Z(t)-\kappa} \qquad (27),$$

where $BPR(t)=[w_k+\kappa w_\infty/Z(t)]/[Z(t)+\kappa]$ is the equilibrium biomass per recruit for mortality rate $Z(t)$. We can solve eq. (27) for the approximate recruitment rate over year t, as

$$R(t) \approx [B^*(t+1)-B^*(t)\ e^{-Z(t)-\kappa}]/[BPR(t)(1-\ e^{-Z(t)-\kappa})] \qquad (28).$$

In simulation tests, this approximation typically tracks the actual recruitment rate quite closely except during periods of very rapid biomass change, provided $Z(t)$ is reasonably large (0.5 or higher). The approximate estimates can be used directly for stock-recruitment parameter estimation, or to at least provide initial estimates of recruitment anomalies from stock-recruitment models when model fitting includes estimation of the anomaly time series.

Alternative prediction of biomass per recruit using the Beverton-Holt model

The basic weight growth model (eq. 3) is not a good approximation for cases where the relative length at recruitment (L_k/L_∞) is less than 0.4 (w_k/w_∞ less than 0.064). In such cases, an option for predicting the equilibrium biomass per recruit while still assuming knife-edge selectivity is to use the classical Beverton-Holt biomass and yield-per-recruit theory based on assuming von Bertalanffy length growth and weight varying as L^3. For fish recruiting at relative age $\tau=-\ln(1-L_k/L_\infty)/K$ where K is the vonBertalanffy growth coefficient, and total mortality rate $Z=F+M$, the Beverton-Holt (their eq. 4.4 integrated to infinite age) prediction of equilibrium vulnerable biomass per recruit is given by

$$BPR=w_\infty e^{Z\tau}\{e^{-Z\tau}/Z-3e^{-(Z+K)\tau}/(Z+K)+3e^{-(Z+2K)\tau}/(Z+2K)+e^{-(Z+3K)\tau}/(Z+3K)\} \qquad (29).$$

When this equation is used for prediction of $B_\infty=BPR(t)xR$ with $BPR(t)$ from eq. (9) in equations like (13)-(14) and (27)-(28) for predicting biomass and estimating recruitment over time (with Z changing from year to year), the growth coefficient κ can simply be replaced by K, but a bit better predictions are obtained with a lower value like K/2 that implies slower damping of biomass toward its R-dependent equilibrium B_∞. An even simpler option is to just plot the predicted relationship between BPR and F for eqs. (9) and (29), then adjust the coefficient κ for eq. (9) to match the prediction from K in eq. (29) and continue using the delay-differential formulation for time dynamics and equilibrium predictions.

For cases where the length at recruitment is well below the length at maturity, BPR is not a good predictor of spawning biomass per recruit (SBPR) at high fishing rates. If fish have knife-edge maturation at relative length L_{mat} and relative age $\tau_m=-\ln(1-L_{mat}/L\infty)/K$, SBPR can be calculated simply by (1) solving eq. (29) with τ replaced by τ_m, and (2) multiplying the result by $e^{-(\tau-\tau m)Z}$ to account for cumulative mortality between fishery recruitment and maturation. The ratio SBPR/BPR behaves basically the same as the ratio S(t)/B(t) in eq. 16a above.

Representing spatial equilibrium abundances in design of Marine Protected Areas

Suppose a coastline has been divided into a large number $i=1...n_a$ spatial areas, each representing a rearing site for some species and each potentially included in an MPA. This approach to representing spatial population structure in MPA design has been widely used, eg Botsford (ref), Walters et al 2007. It is quite simple to predict equilibrium (average long

term) spatial biomass and numbers for a species across these areas, assuming delay-differential model growth and survival on each area, dispersive mixing of older fish between adjacent areas, dispersal of larvae more widely across areas, and spatial movement of fishing effort. Calculation of the equilibrium requires an iterative approach that generally converges quite rapidly. The iteration begins with initial estimates $B^{(0)}_i$ and $N^{(0)}_i$ of the by-cell biomass and numbers of fish. Here the superscript (k) designates iteration number. Then the following are calculated for each iteration $k=1,\dots$ until the estimates stop changing:

1) Larval settlement: $L^{(k)}_i = \sum_j e^{-.5(d_{ij}/sdl)^2} B^{(k-1)}_j$ (d_{ij}=distance from cell i to j, sdl=standard deviation of larval dispersal distances)

2) Local recruitment: $R^{(k)}_i = aL^{(k)}_i/(1+bL^{(k)}_i)$ (a,b are Beverton-Holt stock recruitment parameters)

3) Fishing mortality: $F^{(k)}_i = F_{tot}O_iB^{(k-1)}_i/\sum_j B^{(k-1)}_j O_j$ (O_k=1 if cell i is open to fishing, 0 otherwise; F_{tot} is total potential fishing mortality rate summed over all cells)

4) Biomass: $B^{(k)}_i = [w_kR^{(k)}_i + \kappa w_\infty N^{(k-1)}_i + m\{B^{(k-1)}_{i-1} + B^{(k-1)}_{i+1}\}]/[F^{(k)}_i + M + 2m + \kappa]$ (m=mixing rate between adjacent cells)

5) Numbers: $N^{(k)}_i = [w_kR^{(k)}_i + m\{N^{(k-1)}_{i-1} + N^{(k-1)}_{i+1}\}]/[F^{(k)}_i + M + 2m]$

Step 1) assumes that larvae are spread in a normal distribution pattern away from each source cell, with larval production in the cell proportional to biomass; alternative assumptions such as exponential decay of larval settlement with distance d_{ij} can easily be used. Step 2) assumes that larvae settling in cell i remain in that cell until recruitment at weight w_k, and are subject to density-dependent juvenile mortality during their rearing period. Step 3) is a "gravity model" prediction of the allocation of F_{tot} to cells open to fishing, with gravity model weight O_iB_i for each cell; an alternative would be to use logit choice weights $O_ie^{v_i}$ for the cells, with the utilities v_i depending on B_i and other factors such as distance from fishing ports. The step 4) and 5) biomass and numbers equations are just the model equilibria of eq. (7), with terms added to represent gain of fish from surrounding cells i-1 and i+1, and loss of fish (2m mortality terms) to those adjacent cells. Note that by including mixing of both biomass and numbers, the model effectively represents effects on average body size in cell i of dispersal into that cell of larger or smaller average sized fish from adjacent cells. For example, the model predicts increase in average body size of fish in fishing sites adjacent to marine reserves, due to dispersal of fish from the reserves that are on average older and larger than in the fished sites.

Estimation of the growth parameter κ from the vonBertalanffy K for length growth

The growth equation (eq. 3) for weight assumed above is only an approximation for weight change in fish that follow vonBertalanffy length growth. A good approximation for κ given the vonBertalanffy length growth K, at least for fish larger than $1/3L_\infty$, can be obtained by the following regression procedure:

1. Calculate relative lengths (L/L_∞) for several ages starting at the relative length L_k at recruitment, from the recursive relationship $L_{a+1}=1-e^{-K}+L_a e^{-K}$. Convert these to relative weights $W_a=L_a^3$.

2. For each age, calculate the "z-statistic" $z_a=1-W_a$.

3. The ratio $G=\sum z_a z_{a+1}/\sum z_a^2$ is then an estimate of $e^{-\kappa}$, i.e. $\kappa=-\ln(G)$.

This calculation typically results in low values of κ/K for low (e.g. 0.4) values of L_k, increasing to near 1.0 for high L_k.

As noted above, an alternative approach is to use the vonBertalanffy length growth model (and weight varying as L^3) in the basic Beverton-Holt yield model (eq. 29) to predict BPR, then vary the κ parameter in eq. (9) so as to obtain a similar pattern of change in BPR with increasing fishing rate F from eq. (9) as from the more realistic Beverton-Holt calculation.

Example application to Peru anchoveta

We used the delay-differential structure to provide a computationally efficient model for exploring effects of a wide variety of alternative harvest strategies (harvest control rules) on future fishery values for the Peru anchoveta, under a wide variety of scenarios for future recruitment variation. For this application, we treated annual fishing mortality rates F(t) and recruitment rates R(t) as constant within each year (i.e. as piece-wise variable among years), which gives basically the same predictions of year-to-year variation in biomass B(t) (using eq. 13-16 above) as would be obtained with a model that accounts for the strong seasonal variation in both catches and recruitments that actually occur in the fishery, but avoids the difficult statistical problem of estimating year-to-year changes in the seasonal pattern of recruitment variation. Using annual time steps also allowed us to fit the data to annual observed catches C(t) and acoustic survey biomass estimates S(t) available for most years since 1950, so as to obtain a long time series of estimates of how annual recruitment rates must have varied in order to have produced the observed catches and abundance trends. To check for possible bias due the annual time step, we also fit a model with monthly time steps, using historical monthly catches and with seasonality in recruitment, and a fully age-structured model with monthly time steps developed by Ray Hilborn and John Payne (U. Washington, pers. comm.).

For fitting the model to historical data, we first obtained independent estimates of the natural mortality rate M (we just assumed M=1.0) and body growth parameters w(k), κ, and w_∞. To obtain the growth parameters, we first developed a weight growth curve (weights w(a) at integer ages a) using estimates of vonBertalanffy length-growth parameters and a length weight relationship. Assuming recruitment mainly near age k=1 (when length is near 11 cm), w(k) was estimated to be 12 g and w_∞ to be 68 g. Noting that eq. (3) integrates to the Ford-Brody relationship $w(a)=\alpha+\rho w(a)$ where $\rho=\exp(-\kappa)$, we regressed w(a+1) on w(a) to obtain $\rho=0.55$ and $\kappa=0.59$.

Recruitment variation over time was modeled as a Beverton-Holt relationship with R(t) dependent on spawning biomass B(t) the previous year i.e, R(t)=aB(t-1)/(1+bB(t-1)) as in the derivations above, but modified for each year by "environmental " recruitment anomalies W(t). We examined two alternative assumptions about the W(t) cause changes in R(t): (1) "alpha" variation where the Beverton-Holt "a" parameter was multiplied each year by exp(W(t)) to simulate density-independent variation in survival rate from egg to recruitment, and (2) "beta" variation where the Beverton-Holt "b" parameter is multiplied by exp(W(t)) to simulate variation in recruitment

carrying capacity associated with factors like contraction the spawning range leading to smaller area over which juveniles are distributed (and compete). For model fitting, we used eqs. (23-25) to calculate average a,b from leading parameters Fmsy and Umsy. For the monthly time step model, we predicted relative recruitment for each month of the year, assuming similar monthly pattern for all years, and applied these monthly relative values to the predicted annual recruitment from the Beverton-Holt equation using the previous year's spawning biomass.

In some years, there has apparently been substantial discarding of juvenile anchoveta (8-10cm) too small to be attractive for processing. Absent data on such discard rates, we modeled discarding impact by multiplying the R(t) prediction for each year by exp(-FJ(t)) where FJ(t) is a guess at the fishing mortality rate experienced by juveniles year t. We set FJ equal to F(t) for years with very weak recruitment (W(t)<<0), and to values near 0 for strong recruitment years (W(t)>>0), with FJ decreasing in a logistic pattern with increasing W(t). Note absent direct data on discarding rates, we might just as well have excluded the juvenile multiplier so as to have the discarding effects estimated as a hidden component of the W(t) estimate for each year.

In order to force the model to predict catches near the historical observed values for other model parameters that predict reasonable (not too low) B(t) trends, we used the "stock reduction analysis" approach of setting F(t)=C(t)/B(t) where C(t) is observed historical catch divided by model simulated biomass B(t). This approach essentially places harsh bounds on the population dynamics model parameters, since parameter combinations that predict B(t) too low lead to huge increases in F(t) and hence "depensatory" collapse of the simulated stock size. The same approach was used with the monthly time step model and the Hilborn-Payne age-structured model.

We fitted the model to data by varying B(1950), Fmsy, Umsy, and the recruitment anomalies W(1950)-W(2014) so as to minimize a simple negative log likelihood function. To construct this function, we assumed that the survey indices had log normal variation around B(t), with a scaling parameter q representing possible incomplete surveys, i.e.

$$S(t)=qB(t)e^{v(t)} \tag{27},$$

and observation variance σ^2_v. We further assumed a normally distributed prior probability for the W(t), i.e. each W(t) distributed as N(0,σ^2_W). Under these assumptions, the concentrated negative log likelihood (actually a log posterior density under the normal prior assumption for W(t)) is given by

$$NLL = \sum_t (z(t)-lnq)^2/ \sigma^2_v +\sum_t W(t)^2/ \sigma^2_W \tag{28},$$

where z(t) is the "z statistic" z(t)=ln(S(t)/B(t) and lnq is the arithmetic mean of the z(t) as derived in Walters and Ludwig (1994). We used Solver in Excel to minimize NLL. Note that there is no way to directly estimate the observation and recruitment anomaly variances directly from the data, i.e. it is not possible to say how much of the variation (not explained by catches) in the S(t) was due to recruitment variation and how much to measurement errors. Increasing σ^2_W leads to attributing more of the S(t) variation to recruitment anomalies and less to measurement errors. To be safe in terms of assuming considerable recruitment variation, we set σ^2_v = 0.01 and σ^2_W = 0.6. This combination leads to high variability over time in the W(t) estimates, and B(t) estimates close to the observed S(t). Interestingly, the estimates of B(1950),Fmsy, and Msy that minimize NLL are quite insensitive to the assumed variances. For the monthly time step model, we included the 12 monthly relative recruitments in the set of parameters to be estimated, and predicted survey abundances for the specific times that these were collected (in addition to the average annual surveys used in the annual model fitting).

Model fits to the catch and S(t) data along with estimates of the anomaly patterns W(t) for the "alpha" and "beta" recruitment variation assumptions, for both annual and monthly time steps, are presented in the Excel spreadsheet "anchoveta fitting models.xlsx". The same Excel spreadsheet but with table functions used for policy exploration (which drastically slow model fitting) is provided in "anchoveta policy models.xlsx". Note that for fitting we forced a relatively high recruitment compensation ratio of 10 (and hence Fmsy) for all cases (this corresponds to the "steepness" parameter h=0.71); best fits when Fmsy was allowed to vary in the "beta" variation case were unrealistically high, particularly for the monthly model. All model versions, including the Hilborn-Payne age structured model, gave very similar historical biomass reconstructions (fit to historical data), predicted very similar future biomass patterns given similar harvest policies, and resulted in similar estimates of historical recruitment anomalies (Fig. 3,4,5). Biomass reconstructions were all similar to those reported in the stock assessment by Oliveros-Ramos et al. (2010), and for earlier years by Pauly et al. (1987) and Pauly and Soriano (1987) using VPA and by Santander (1987) using egg surveys.

The two alternative models for recruitment variation give similar maximum likelihood estimates for MSY, but somewhat different Fmsy estimates:

	alpha model	beta model
Fmsy	0.50	1.1
MSY	7.65	7.67

The beta model is somewhat more optimistic in its estimate of Fmsy. But when both models are simulated over time with alternative harvest control rules and future recruitment anomaly patterns, they give very similar predictions of future abundance and catches. When the model was constrained to fit the biomass survey data without any assumption about the surveys missing fish (i.e. with q=1 in eq. 27), model fits to the survey data look very similar to the case with uncertain q, but with somewhat lower MSY and higher Fmsy:

	alpha model	beta model
Fmsy	1.05	1.1
MSY	6.45	6.49

So, the basic estimates of management reference points are somewhat sensitive to assumptions about scaling of the survey data, particularly Fmsy. Further, Fmsy, which depends on the stock recruitment "a" parameter but not the "b" parameter, is poorly determined by the data, because there are no observations at very low spawning biomass (see Fig. 5).

MSY and Fmsy estimates from the monthly model with q=1 were generally similar to those for the annual model, but are not that meaningful because of predicted seasonality in catches. For the alpha variation recruitment case, the monthly model gave somewhat lower MSY (3.71 mmt) and Fmsy (0.81); for the beta case, Fmsy was higher (1.75) but time simulations with the seasonal catch

variation (seasonal allocation of annual quota) did not predict that the stock would be sustainable under such high annual F. Recruitment anomaly patterns were very similar for all four model cases (alpha variation, beta variation, annual versus monthly simulation step).

The monthly model fitting and the Hilborn-Payne age structured model gave very similar seasonal biomass patterns, with two strong recruitment peaks per year, in February and November. The February peak agrees with the two-pulse recruitment pattern found or assumed by Oliveros-Ramos and Pena (2011), but they placed the second peak earlier, in August. We obtained distinctly better fits to the pattern of seasonal variation in survey abundances for recent years, with the later peak. However, the model did not show as severe a decline in abundance for October-December as seen in a few survey years (2002-2004, 2014), suggesting that possibly the second recruitment peak did not actually occur or was much smaller than average in those years. Very similar biomass reconstructions were obtained with the Hilborn-Payne model when the seasonal recruitment pattern was forced to follow the general pattern suggested by Perea et al. (2011) with spawning peaks in September and February.

As is common in stock assessment models, there is a basic confounding between estimates of stock size and productivity, i.e. we cannot tell for sure whether the data came from a large, unproductive stock or a smaller, productive one. For the baseline model fits, we obtained survey q estimates (eq. 27) of 0.7 for the alpha model and 0.5 for the beta model, implying stock biomass approaching double the survey biomass. This does not mean that harvests could be higher, since Fmsy in both cases was low (implying low recruitment compensation ratios, i.e. high sensitivity of recruitment to stock size). If we force the estimation to use a higher q, i.e. force the model biomasses to be lower and closer to the survey estimates, the model still fits the survey data well at least for the beta recruitment case but with higher estimates of Fmsy (stronger recruitment compensation) and somewhat lower estimates of MSY. For the alpha variation case, we could not get the model biomass estimates to be close to the surveys for at least some years, though the alpha model fit better (lower NLL) when q was allowed to vary as in eq. 28. Fortunately, forced changes in the assumed survey catchability and associated changes in estimates of Fmsy and MSY do not cause large changes in predicted future catch patterns under alternative harvest control rules and patterns of recruitment variation. Interestingly, the monthly model did not give low q estimates for either the alpha or beta model, instead giving q near 0.9 (implying the surveys underestimate biomass by only 10%).

All the model fits display the strong recruitment "regime shift" pattern documented by other researchers (Cahuin et al. 2009; Oliveros-Ramos and Pena 2011), with the alpha and beta models diverging sharply in their predictions of reproductive performance at very low stock sizes (Fig. 5). But note in Fig. 5 that there are no observations for spawning biomass below 2mmt, and that the alpha and beta models predict similar recruitment rates per spawner for higher biomasses within each of the regime periods. While some of the model fits appear to statistically favor (based on nll and AIC comparisons) the alpha model, others favor the beta model. Application of Kalman filter methods to estimate alpha vs beta variation (Britten et al. 2016; Szuwalski et al. 2017 ms in review) also appear to favor the beta model. But as evident from the lack of differences in predictions over the range of observed spawning abundance, such statistical comparisons are highly suspect, and it would be prudent to heed the warnings from the alpha models that strong recruitment compensation might not lead to rapid population recovery if the stock declines to below 2mmt for any reason.

Low estimates of Fmsy and recruitment compensation can be symptoms of long-term changes in recruitment carrying capacity. It is easy to show with population simulations where the Beverton-

Holt "b" parameter is changing slowly (asymptotic maximum recruitment changing between low and high recruitment "regimes") that the stock-recruitment slope ("a" parameter) is likely to be badly biased downward, basically because both recruitment and spawning stock size decline together when recruitment carrying capacity decreases so as to make the apparent stock-recruitment relationship have a strong positive slope (low "a" value). But if this is actually what has been happening, it simply means that the stock sustain higher fishing rates at low stock size without collapsing completely, i.e. the stock is a bit more resilient than we have estimated, but it does not mean that high fishing rates should be routinely allowed during periods of low productivity and biomass.

To test sensitivity of the results to uncertainty about the natural mortality rate (M) and growth parameters, estimation trials were conducted with a wide range of M values (0.8 to 2.0) and a narrow range of alternative κ values, 0.5 to 0.65 (w_∞ does not affect the estimation because of the scaling of w_k as a value relative to it, i.e. units of weight measurement are arbitrary, and anchoveta growth has varied somewhat over time, but the parameters have been reasonably stable, see Palomares et al. 1987). These estimation trials resulted in fits to the survey data indistinguishable from the base case, i.e. Solver simply made minor adjustments to the recruitment anomaly (W(t)) estimates so as to fit the survey data equally well.

Management strategy evaluation for Peru anchoveta

We used the fitted alpha and beta annual models to explore alternative strategies for long term harvest management, by simulating the fitted models forward in time for 80 years (2014-2094) with various scenarios for future recruitment variation (anomaly patterns W(t)) and under various feedback harvest control rules for varying allowable catches with changes in stock biomass. We also ran some of these scenarios with the monthly models, to ensure that the basic policy predictions would be basically the same. We did not attempt to simulate management "tactics", i.e. the within-year implementation process for achieving target harvests or spawning abundances through the use of multiple surveys and open-closed fishing periods, and the "implementation errors" that might result from such tactics; much more complex models would be needed for that detailed evaluation. To facilitate management "gaming" for efficient exploration of a wide variety of policy alternatives, we implemented the simulations in an Excel spreadsheet ("anchoveta policy models.xlsx").

Future scenarios for recruitment variation were generated several ways: (1) repeats of historical W(t) patterns, (2) cyclic patterns with alternative periods of between 20 and 40 years, and (3) autoregressive patterns $W(t)=\rho W(t-1)+v(t)$ with high autocorrelation $\rho=0.8$ and var(v)=0.15 to give variation with peaks and lows about as frequent as seen in the model fitting. We included parameters to allow model users to generate really extreme future scenarios, such as catastrophic decline in future recruitments due to more frequent and violent El Nino events that might be associated with climate change, but did not evaluate harvest control rules for response to such scenarios since there is really nothing that can be done in the short term (5-10 yr) future to hedge against their long term impacts (the anchoveta stock turns over too rapidly to allow "stockpiling" of fish as a hedge against severe changes).

We assumed that future management responses to changing abundance will involve use of a linear control rule for varying allowable annual catch or quota Q(t) as a function of the survey estimate B*(t):

$$Q(t)=s(B^*(t)-Bmin) \text{ for } B^*(t)>Bmin \text{ and } 0 \text{ for } B^*(t)<Bmin \qquad (29).$$

Here Bmin is a stock size below which there would be no fishing, and s is basically the fishing mortality rate allowed on the surplus B*(t)-Bmin. In previous optimization studies (reviewed in Hawkshaw and Walters 2015), it has been found that predicted long term yield is typically maximized by setting Bmin to an "optimum escapement" and s=1 (i.e. harvest all the surplus over Bmin each year), with Bmin perhaps varying over time with persistent changes in recruitment rates. Walters and Parma (1996) suggested using a "fixed exploitation rate" strategy (Bmin=0 and s=Fmsy) for coping with long term recruitment variation, and showed that this rule gives near maximum long-term yields when recruitment carrying capacity but not recruitment curve slope (i.e. the beta model above) shows persistent changes. The Hawkshaw-Walters optimum control rule for maximizing risk-averse utility (sum of log catches) is basically just eq. (29) with Bmin=Becon and s=MSY/(Bmsy-Becon), where Becon is a minimum stock size below which fishers would find it uneconomical to fish (income<cost). Other control rule alternatives for coping with environmental change are reviewed in Punt et al. (2013) and King et al. (2015). We did not provide capability to evaluate arbitrary control rules such as the US "10-40 rule" since (1) there is no theoretical justification from dynamic optimization theory for using such rules with their intuitive approaches for hedging against overfishing risks via arbitrary minimum stock sizes and/or maximum fishing mortality rates at higher stock sizes, and (2) they are unnecessarily complex and difficult to explain to stakeholders.

We did limited simulation testing of a variation of eq. (29) that attempts to account for persistent changes (regime shifts) in the recruitment anomalies W(t). Motivated by the dynamic programming results in Hawkshaw and Walters (2015), we simply multiplied the Q(t) prescribed by eq. (29) times an expected "relative recruitment multiplier" (relative maximum recruitment a/b when stock-recruit a, b vary with W(t)), to give a "regime-adjusted quota" Qr(t) as

$$Qr(t)=Q(t)e^{W^*(t)} \tag{30}$$

Here, $W^*(t)$ is the arithmetic mean of the most recent three recruitment anomalies W(t). The basic effect of this quota adjustment approach is to reduce quotas when recent recruitment anomalies have been negative, and to increase it when anomalies have been positive. We numerically tested "weaker" adjustments replacing $W^*(t)$ with $kW^*(t)$, k<1, and found that values of k<1 did not give improved simulated performance.

We used three relatively simple performance measures to compare alternative harvest control rules:

(1) Total future yield (or mean annual yield over next 80 years)

(2) Total future log utility for catch (sum of ln[Q(t)+1]

(3) Number of closed years with no fishing.

Note that some policy options and future anomaly patterns resulted in complete stock collapse with little or no recovery over the 80 years; we did not include a separate performance measure such as "probability of stock collapse" since such scenarios resulted in very poor performance anyway, by all three of the measures.

For each future scenario for recruitment variation, we used the Excel "Table function" to calculate the three performance measures for a grid of (Bmin, s) combinations in eq. (29), that is we ran 80 year simulations for all combinations of Bmin=0,1,2,...,10 and s=0,0.1,0.2,...,1.0) to quickly display how each of the performance measures would vary with the harvest control parameters. This essentially results in "optimization in policy space" (Walters and Hilborn, 1978; Moxnes 2003) and

quickly reveals tradeoffs between maximization of yield (total yield) versus stability of future yields (future log utility).

Survey errors were represented by making B*(t) vary log-normally around the true January model biomass B(t), with coefficient of variation near the apparent value (0.1) that we found in the model fitting. As noted by Moxnes (2003), increasing survey error causes the optimum harvest control rule to become nonlinear, i.e. to bend so as to approach a maximum Q(t) at high B*(t); this effect is approximated in the policy space optimization by highest total yields at values of s<1.0 when the survey CV was set very high. Moxnes also noted that using a Kalman filter to represent more complicated assessment models for estimating B(t), as in Walters (2004), actually degrades management performance compared to just using the most recent survey estimate, so we did not explore more complex biomass estimation alternatives.

Policy simulations for typical future recruitment anomaly choices generally resulted in lower optimum fishing rates and yields than would be predicted from a deterministic model using the fitted estimates of Fmsy, MSY, demonstrating the strong effects of stochastic variation and survey errors on future management performance (Fig. 6). Somewhat surprisingly, the simulated pattern of variation in yield with changes in harvest control rule parameters was similar to the pattern shown in Fig. 6 for most of the patterns of future recruitment anomalies that we tested, i.e. the ranking of harvest control rule parameter options was not at all sensitive to assumptions about future recruitment variation. For all variation patterns, simply having strong variation in quotas Q(t) with changes in biomass B(t), i.e. having reasonably low s and Bmin, resulted in reasonable protection of the spawning stock and good yields; "regime shifts" in recruitment parameters were basically accounted for automatically or implicitly through the effects of those shifts on biomasses B(t), without having to explicitly vary the control rule parameters from one regime to the next.

We set up the spreadsheet models to allow "retrospective" comparisons of historical trends in catch and biomass to the trends that the model predict would have occurred if our harvest control rule options had been applied over the 1960-2016 period. A surprising finding from such comparisons is that catches would not have been much different unless very extreme control rules (high Bmin, low slope) had been applied, i.e. historical catches were not far from "optimum". None of the harvest control rules would have completely prevented the collapse in 1972, but could have made the stock size collapse less severe, nor would they have led to much more rapid recovery. This is basically because we treated the period of negative recruitment anomalies after 1971 as having been caused solely by environmental factors, i.e. we did not model the possibility that those anomalies were driven partly by reduction in recruitment carrying capacity due to spawning range contraction at lower stock biomasses.

We found a very modest increase (around 11%) in average long-term yield by using the regime-adjusted quota Q*(t) given by eq. (30), over a variety of alternative future recruitment anomaly patterns. Using the regime-adjusted quotas gave much less (around 6%) improvement in mean log utility of catches; Hawkshaw and Walters (2015) found basically the same result, i.e. the best harvest control rule for maximizing catch does involve adjustments in response to persistent W(t) changes, but the best rule for maximizing log utility is nearly independent of the current W(t) or mean W*(t) of recent anomalies. Comparing Q(t) with Q*(t) catch and stock biomass patterns, it was apparent that the modest gains from regime-adjusted quotas came mainly from increased catches during favorable recruitment regimes rather than from "protection" of the spawning stock during unfavorable regimes, i.e. predicted spawning biomasses were only trivially larger under the Q*(t) policies during negative W(t) regime periods.

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Figure 1. Two examples of how the continuous model exactly tracks total biomass and numbers predicted from a fully age-structured accounting model. In case A, recruitment and F vary in arbitrary patterns over time. In case B, there is an annual sinusoidal pattern in both recruitment and F, similar to the pattern seen in penaeid shrimp populations. F pattern over time shown on the biomass plots, R pattern shown on the numbers plots.
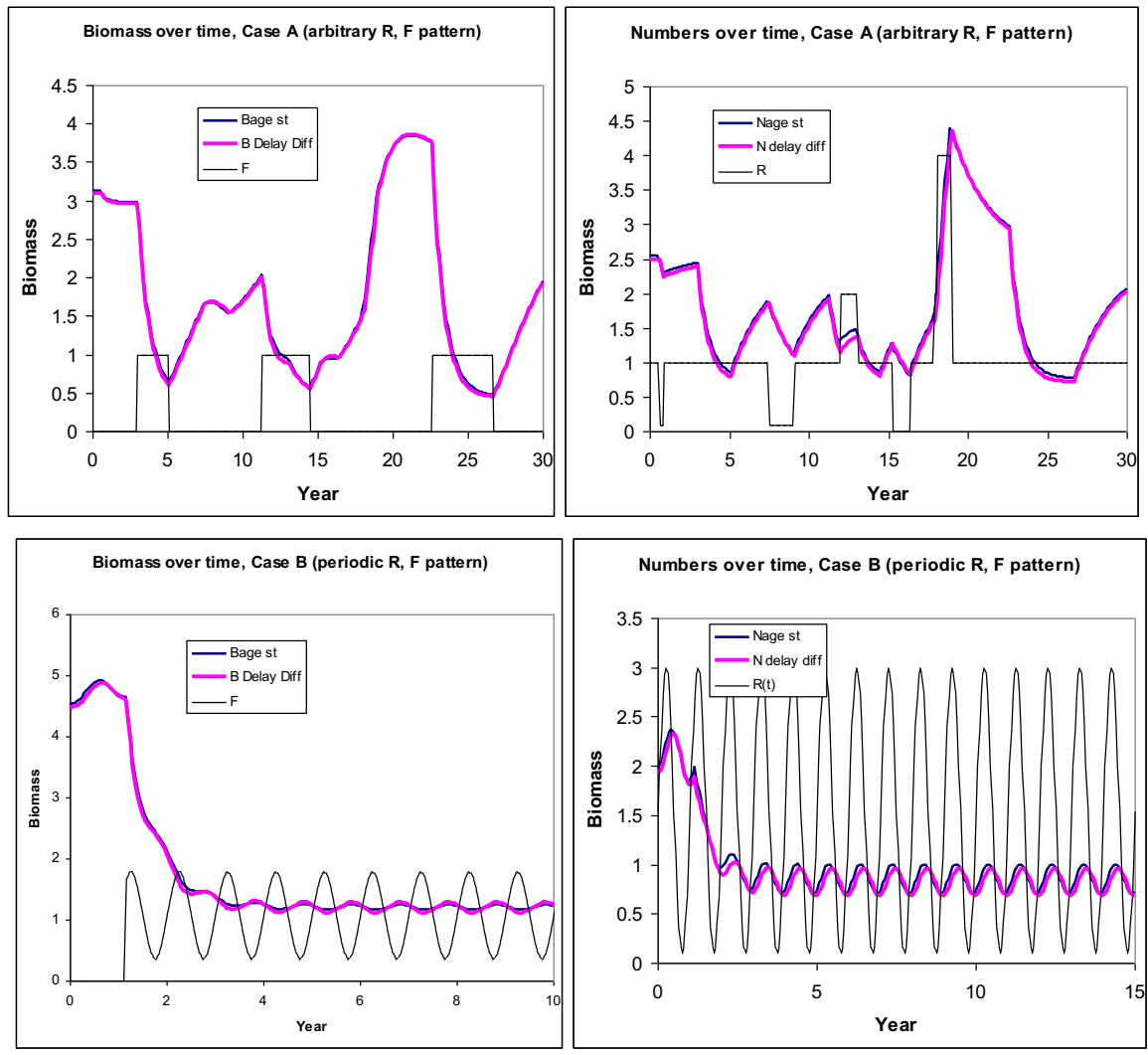
Figure 2. Comparison of fits to historical Peruvian anchoveta survey data for the annual alpha and beta recruitment variation models, and predictions of future abundance under one harvest control rule option (fixed escapement policy, 4mmt base stock) and future recruitment anomaly regime (repeat of historical anomaly pattern). From "anchoveta fitting models.xlsx", comparisons tab.
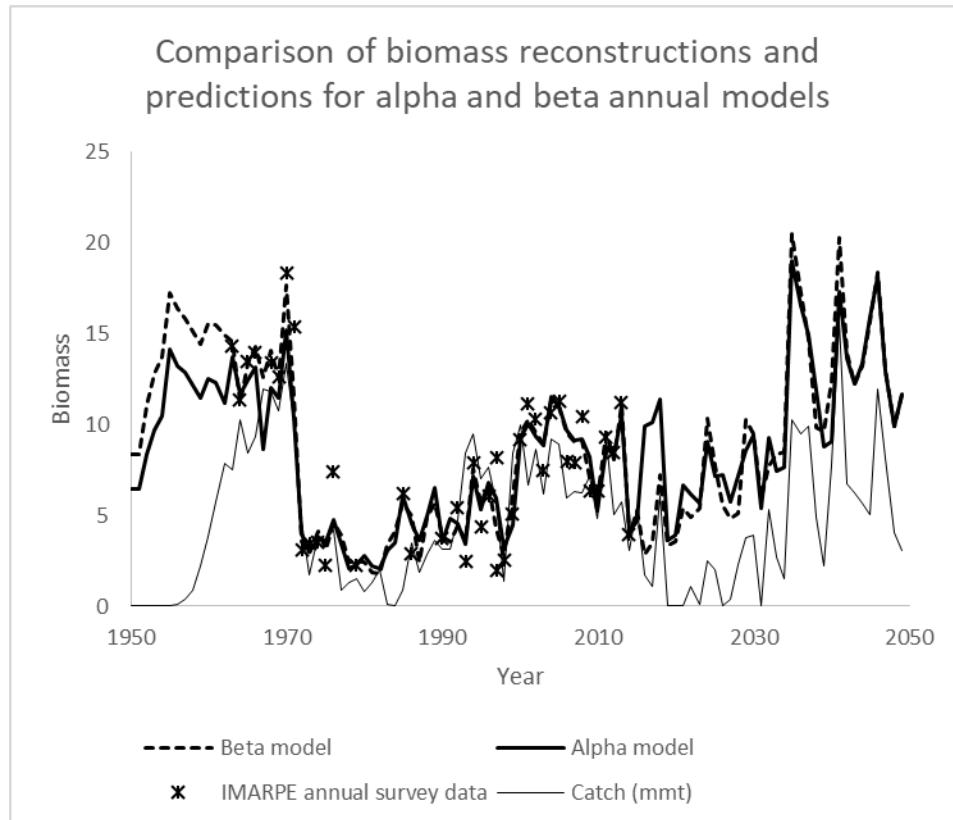
Figure 3. Comparison of monthly model fits to historical Peruvian anchoveta survey data for the alpha, beta, and Hilborn-Payne models. Annual beta model fit from Fig. 2 included for comparison. Note how the seasonal models fail to fully capture seasonal variation evident in surveys for some recent years. From "anchoveta fitting models.xlsx", comparisons tab.
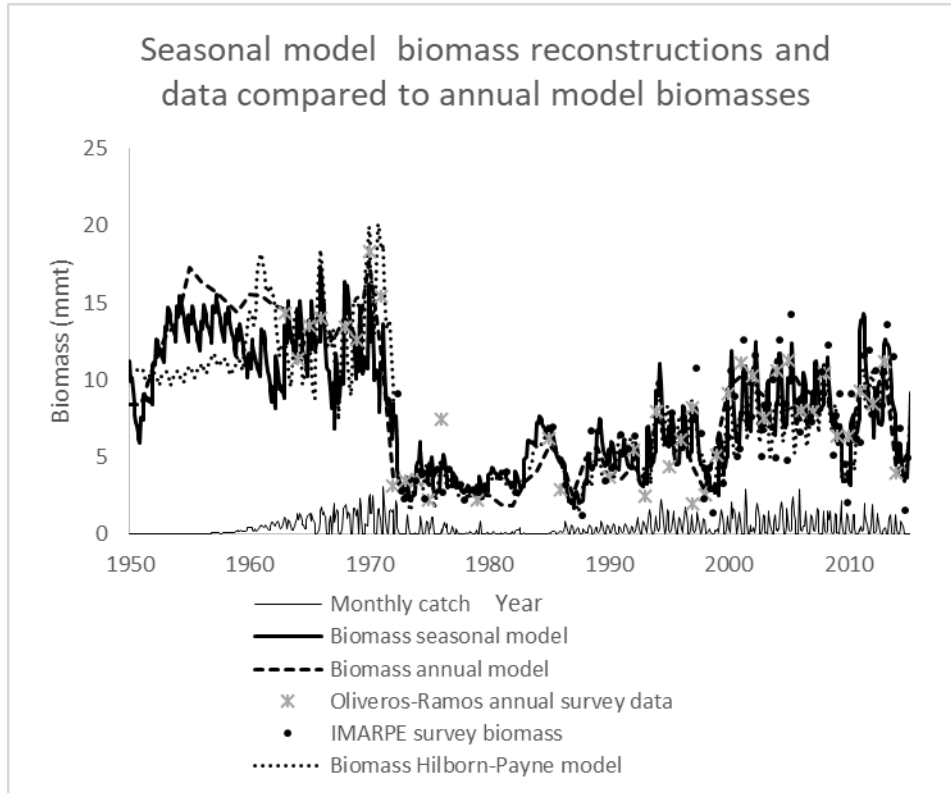
Figure 4. Annual recruitment anomaly patterns for Peruvian anchoveta estimated by fitting the various models.

Figure 5. Regime patterns in the relationship between productivity as measured by recruitment rate per spawner and spawning stock biomass. The low recruitment regime period represented by observations from 1972-1991, and the high regime periods by observations before 1971 and after 1991. Alpha and beta Beverton-Holt model predictions for the regime periods shown as solid lines. From "anchoveta fitting models.xlsx", comparisons tab.

Figure 6. Typical results from Excel table function for comparing harvest control rule choices. Table rows are alternati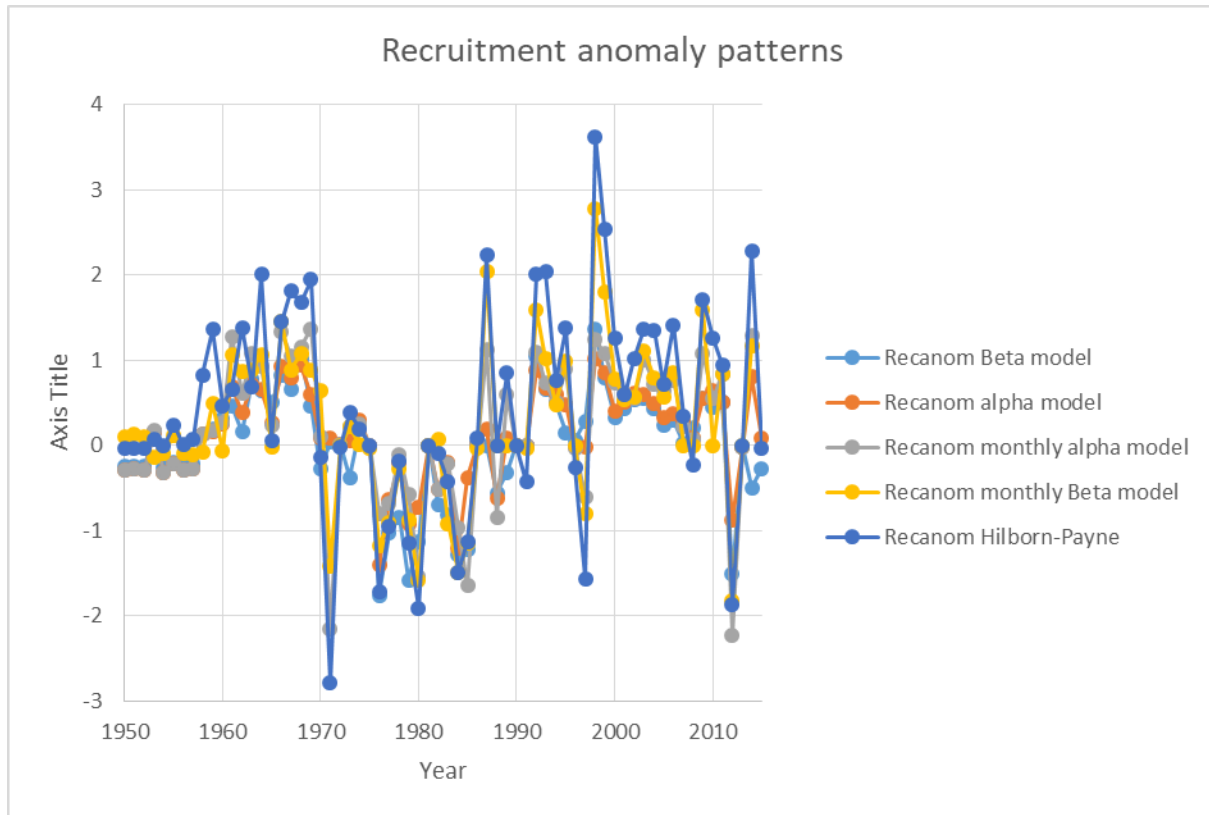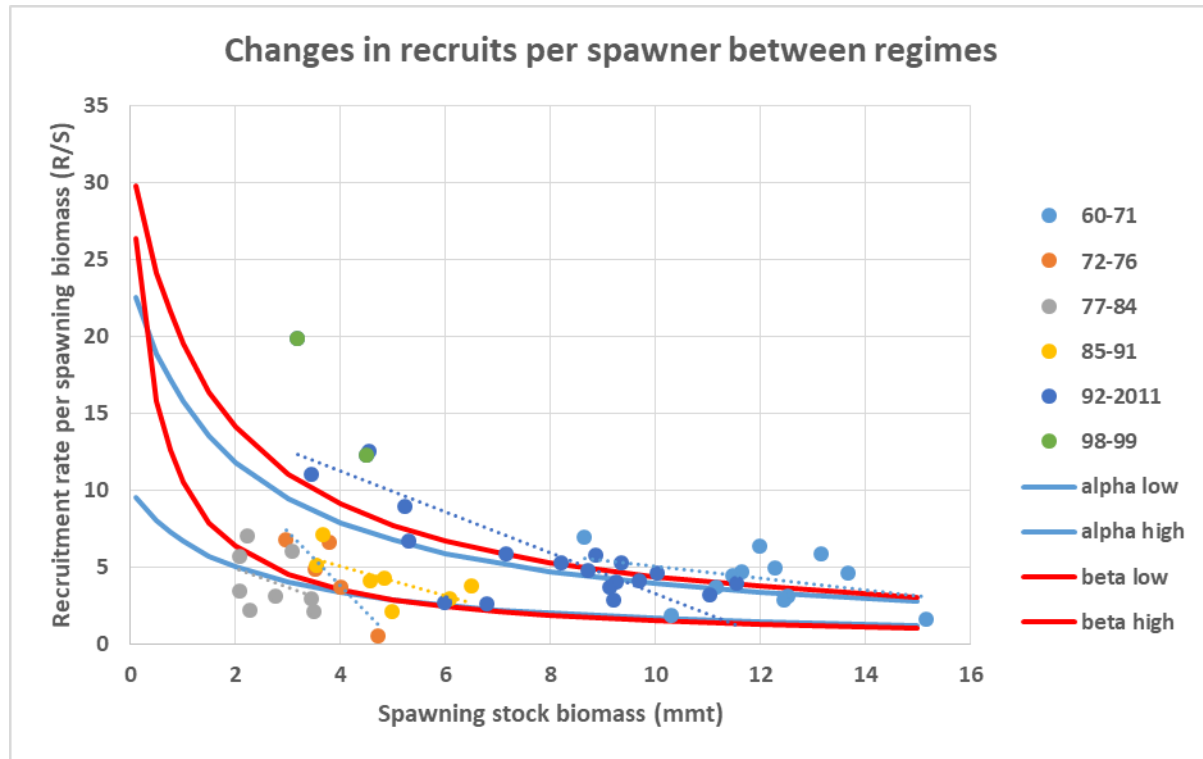ve choices for the slope s in the harvest control rule eq. (29), and columns are alternative choices for Bmin, the minimum stock size for fishing. In this example, mean future yield is maximum at s=0.8 and Bmin=3 mmt (near a fixed escapement policy) while future utility is maximized at s=0.5 and Bmin=0, i.e. a fixed exploitation rate policy with fishing rate F=0.5. Deterministic Fmsy for this case was 1.1, and MSY was 6.5, showing that stochastic recruitment effects generally result in substantially lower optimum exploitation rates and yields than would be predicted from a deterministic model. Recruitment anomaly sequence for all simulations was repeat of historical anomalies since 1950.

Mean annual catch

	0	1	2	3	4	5	6	7	8	9	10
0.2	4.01	3.86	3.71	3.55	3.39	3.23	3.07	2.91	2.74	2.58	2.42
0.3	4.74	4.59	4.44	4.28	4.11	3.93	3.74	3.55	3.36	3.17	2.98
0.4	5.04	4.95	4.83	4.69	4.52	4.35	4.16	3.96	3.76	3.55	3.34
0.5	5.07	5.07	5.01	4.91	4.77	4.61	4.43	4.23	4.03	3.82	3.60
0.6	4.92	5.06	5.07	5.02	4.91	4.77	4.61	4.42	4.22	4.00	3.79
0.7	4.64	4.96	5.06	5.06	4.99	4.88	4.73	4.55	4.35	4.14	3.92
0.8	4.29	4.81	5.01	5.07	5.04	4.94	4.81	4.64	4.45	4.25	4.03
0.9	3.92	4.65	4.94	5.05	5.05	4.99	4.87	4.71	4.53	4.32	4.11
1	3.60	4.48	4.86	5.02	5.06	5.01	4.91	4.76	4.58	4.38	4.16

Years with no fishing

	0	1	2	3	4	5	6	7	8	9	10
0.2	0	0	0	0	0	0	0	1.5	1.5	4	7.5
0.3	0	0	0	0	0	0	0	1.5	1.5	4.5	8
0.4	0	0	0	0	0	0	0	1.5	3.5	5.5	8.5
0.5	0	0	0	0	0	0	0.5	2	4	5.5	10.5
0.6	0	0	0	0	0	0	1.5	3	4	8	12
0.7	0	0	0	0	0	0	1.5	3	5.5	8.5	13.5
0.8	0	0	0	0	0	1	2	4	6	9.5	14.5
0.9	0	0	0	0	0.5	1	3.5	6	6.5	11.5	14.5
1	0	0	0	0	0.5	2	4	6	7	12.5	16

Mean log utility for future catches

	0	1	2	3	4	5	6	7	8	9	10
0.2	1.35	1.31	1.28	1.24	1.20	1.16	1.11	1.06	1.01	0.96	0.91
0.3	1.48	1.45	1.41	1.38	1.34	1.29	1.24	1.19	1.13	1.08	1.02
0.4	1.53	1.51	1.48	1.45	1.41	1.36	1.31	1.26	1.20	1.14	1.08
0.5	1.54	1.53	1.51	1.49	1.45	1.41	1.36	1.30	1.24	1.18	1.11
0.6	1.52	1.54	1.53	1.51	1.47	1.43	1.38	1.33	1.27	1.20	1.13
0.7	1.49	1.53	1.53	1.51	1.49	1.45	1.40	1.35	1.28	1.22	1.15
0.8	1.43	1.51	1.52	1.52	1.49	1.46	1.41	1.35	1.29	1.22	1.15
0.9	1.37	1.48	1.51	1.51	1.49	1.46	1.41	1.36	1.30	1.23	1.15
1	1.30	1.46	1.50	1.51	1.49	1.46	1.41	1.36	1.29	1.22	1.14