Evaluating a dynamic approach to yield-mortality models

Omar Defeo and John F. Caddy

Production modelling using fishery yield but total mortality rate in place of fishing effort (yield-mortality models) does not suffer from undetected changes in catchability or fishing power from technological change, is easier to apply to multi/gear fisheries for the same species, and produces biologically meaningful reference points. They can be calibrated against analytical models and may use the same data sets. Their disadvantage has been the equilibrium assumption as per Csirke and Caddy (1983). Annual mortality rates may come from procedures such as catch curve analysis which make local equilibrium assumptions, but becomes dynamic if the mortality estimates are annual. Theory and problems in fitting this model are described using the same data sets as illustrated in the equilibrium yield-mortality (Y-Z) model in Caddy and Defeo (1996), but also for North Sea cod using data from the working group report on the ICES website. A non-linear quasi-Newton fitting procedure was used in which all three parameters, (r, B_{∞}, and M) are constrained to positive values by a penalty function in the minimisation algorithm. For short time-series with high inter-annual variations in yield, the model is very sensitive to initial values. We suggest using the equilibrium model to generate seed values for dynamic fitting. Trials with the North Sea cod data show that with a long term and robust data set the dynamic model explains a large proportion of the variance and provides a good fit to trends in the catch series. It recovered a value for natural mortality rate similar to that used in other assessments. We also demonstrate that data sets for conventional VPA/cohort analysis can be successfully reused to deduce values of M, r, and B_{∞} from Y-Z models. For all data sets, the dynamic model is more sensitive to time series trends than the equilibrium model although M values were generally lower, but fairly consistent with published values. Guidelines for future work are suggested.

© 2001 International Council for the Exploration of the Sea

Keywords: production models, yield-mortality models.

Received 20 November 2000; accepted 6 August 2001.

O. Defeo and J. F. Caddy: Laboratorio Biología Pesquera, CINVESTAV IPN Unidad Mérida, A.P. 73 Cordemex, 97310 Mérida, Yucatán, México; J. F. Caddy: T.H. Huxley School of Environment, Earth Sciences and Engineering, Imperial College, London, UK. Correspondence to: O. Defeo: tel: 5299-812960; fax: 5299-812334; e-mail: odefeo@mda.cinvestav.mx

Introduction

Conventional surplus production models based on catch and effort data have been intensively studied and applied for management advice throughout the second half of the 20th century. These models provide insights into long-term fishery performance and are flexible tools for fishery analysis with low parameter requirements (Laloë, 1995). Among the possible approaches, catch-effort surplus production models, either assuming equilibrium conditions (Schaefer, 1954; Fox, 1970) or framed as dynamic models (Schnute, 1977; Prager, 1994; Punt and Hilborn, 1996), have been most commonly applied for fishery advice. They also have the advantage of the easy generation of Biological Reference Points, either as targets or limits for fishery management (Caddy and Mahon, 1995).

Although the focus in the recent literature has been largely on the need for dynamic as opposed to equilibrium-based approaches, whatever their characteristics, standard catch-effort models are potentially subject to serious errors in the absence of fishing effort calibration. Such errors come from unquantified changes in q with fishing intensity and biomass, but these are often neglected in the fitting process. Indeed, fishing effort is usually assumed proportional to fishing mortality (qf=F), even though catch rate as an analogous index of abundance (qB=cpue) is frequently

questioned nowadays as an unbiased abundance estimator. The assumption of constant catchability coefficient (q) implicit in both dependent and independent variables of production modelling with catch and effort, is also at variance with technological aspects of the evolution of fishing power. This is one reason why production modelling has been abandoned in some areas of the world in favour of more complex analytical models. Improvements in fishing gear design such as the use of synthetic fibres, and technologies for fish detection, with increased precision in the application of fishing power, are rarely explicitly considered when standardising fishing effort (Caddy, 1996, 1999).

We believed that this important source of uncertainty when fitting production models expressed in terms of fishing effort can be reduced using surplus yield models in which total mortality rate is substituted for fishing effort where such estimates are available (Csirke and Caddy, 1983; Caddy and Defeo, 1996). As long as the natural mortality rate for fishable components of the stock remains more or less constant during the time period considered, this approach is a valid alternative to effort-denominated models for the reasons detailed by Caddy and Mahon (1995) and Caddy and Defeo (1996). It can provide alternative estimates to analytical models, often using the same data sets. Yield-mortality (or Y-Z) models link the yield Y as the dependent variable to an overall risk of death given by the instantaneous total mortality coefficient Z. Production modelling of Y against Z also allows one to generate an index of biological production, which includes natural deaths plus harvested yield for the population as a whole (Caddy and Csirke, 1983). This can be the basis for useful precautionary fishing strategies (Die and Caddy, 1997). Y can be measured with a relatively narrow margin of error and Z can be estimated by different approaches, including the classical age-based (Ricker, 1975) and length-based (e.g. Sparre and Venema, 1992) catch curves. Alternatively, but not tested here, total mortality rate at age may be estimated from cohort analyses, using the same age-structured data for comparison. Thus, sources of uncertainty with Y-Z models are likely to be relatively well known and quantifiable, or at least as easy to estimate as they are with fishing effort as the independent variable.

Perhaps the main reason why Y-Z models are not being used more frequently despite the growing availability of annual series of mortality data, has been that the version available assumes pseudo-equilibrium conditions (*sensu* Caddy, 1996), and as such, are criticized as time-invariant. Thus, since our 1996 joint paper (Caddy and Defeo, 1996), we have looked for approaches to building a Y-Z model with dynamic characteristics, which can be used to predict variations in yield through time as a direct function of the total risk of death to which the population is subjected. In this paper we explore a simple dynamic Y-Z model and highlight the advantages and pitfalls associated with fitting it. We also suggest some guidelines for future work.

Methods

Model formulation

Variations in biomass through time could be expressed as:

$$B_t = B_{t-1} + rB_{t-1}\left(1 - \frac{B_{t-1}}{B_\infty}\right) - Y_{t-1} \tag{1}$$

where Y is the yield, B is the biomass, t is time, B_∞ is the pristine (or, preferably, unexploited) population biomass or carrying capacity of the environment and r is the intrinsic rate of population growth (Hilborn and Walters, 1992).

The instantaneous total mortality rate Z is classically defined as:

$$Z_t = M + F_t \tag{2}$$

where F_t and M are, respectively, the instantaneous fishing and natural mortality rates. As $F_t = Y_t/B_t$, where Bt is the average biomass present during the year, then:

$$Z_t = M + \frac{Y_t}{B_t} \tag{3}$$

and:

$$B_t = \frac{Y_t}{Z_t - M} \tag{4}$$

Substituting (4) in (1) we have:

$$\frac{Y_t}{Z_t - M} = \frac{Y_{t-1}}{Z_{t-1} - M} + r\frac{Y_{t-1}}{Z_{t-1} - M}\left[1 - \frac{Y_{t-1}}{B_\infty(Z_{t-1} - M)}\right] - Y_{t-1} \tag{5}$$

$$Y_t = \frac{Y_t - M}{Z_{t-1} - M}\left[Y_{t-1} + rY_{t-1}\left(1 - \frac{Y_{t-1}}{B_\infty(Z_{t-1} - M)}\right)\right] - (Z_t - M)Y_{t-1} \tag{6}$$

Catch variations through time could then be expressed as:

$$Y_t = \left(\frac{Y_t - M}{Z_{t-1} - M}\right)Y_{t-1}\left[1 + r\left(1 - \frac{Y_{t-1}}{B_\infty(Z_{t-1} - M)}\right)\right] - (Z_t - M)Y_{t-1} \tag{7}$$

where yield in year t (Y_t) is expressed solely in terms of the present mortality rate and the values of yield and mortality in the previous year.

Fitting the model

The silver and Peruvian hake data sets

The dynamic Y-Z function proposed in Equation (7) was fitted to the Gulf of Maine silver hake and the Peruvian hake on the basis of information provided, respectively, by Almeida and Anderson (1978) and Espino and Wosnitza-Mendo (1984). In the latter study, the authors separated catch data by sex, and thus Y-Z models were also fitted separately by sex. These data-bases were selected to allow comparison of their per-formance with respect to the equilibrium Y-Z models described by Caddy and Defeo (1996) for the same stocks [see Equations (8) and (9) below]. These fittings were based on the following linearised logistic approach:

$$\frac{Y_t}{Z_t - M} = a - b(Z_t - M) \qquad (8)$$

We also used estimates derived from the equilibrium logistic Y-Z model described by the following quadratic form (Caddy and Csirke, 1983):

$$Y_t = aZ_t^2 + bZ_t + c \qquad (9)$$

Equation (9) is the classical logistic used to relate annual values of yield to total mortality, and was fitted here by multiple regression. An estimate of M was obtained by solving this equation for $Z = M$ (Y_t and $F = 0$), as shown by Csirke and Caddy (1983).

The non-linear procedure (quasi-Newton) used for fitting Equation (7) includes a penalty function in the minimisation algorithm (sum-of-squares criterion) by which all three parameters to be estimated (r, B_∞, and M) are constrained to positive values. We then provided seed values for parameters obtained from previous esti-mates using the equilibrium approach (Caddy and Defeo, 1996), and this sequence is the procedure we now recommend for further testing and application. Input parameters (median values derived from bootstrapping analysis in the earlier paper) were (a) for silver hake: $r = 0.722$, $M = 0.266\,\mathrm{yr}^{-1}$, and $B_\infty = 147\,055$ t; (b) for Peruvian hake (males): $r = 2.554$, $M = 0.44\,\mathrm{yr}^{-1}$, and $B_\infty = 120\,760$ t, and Peruvian hake (females) $r = 2.731$, $M = 0.38\,\mathrm{yr}^{-1}$, and $B_\infty = 127\,880$ t. We assessed the quality of the estimation procedure through the distri-bution of errors. The M values chosen as input for running the model were obtained from Caddy and Defeo (1996).

Sensitivity analyses were performed by sequentially fixing one parameter to be estimated and allowing the remaining two parameters to vary randomly. The fixed parameter was input under a wide range of values (e.g. M and r from $0.1–6.0\,\mathrm{yr}^{-1}$, see Figure 3), in order to evaluate the robustness of the convergence of the non-linear fitting procedure. The range of trial values for natural mortality also included those estimates for the

silver hake from the equilibrium procedure of M: 0.144 (regression analysis) and $0.266\,\mathrm{yr}^{-1}$ (bootstrapping) (see Caddy and Defeo, 1996) from direct fitting of Equation (9) and $0.400\,\mathrm{yr}^{-1}$ from Equation (8).

The North Sea cod

One obvious application of the model is to provide an alternative assessment for stocks for which Virtual Population Analysis (VPA) or other age-structured methods have already been applied. Here, age-structured data allow Z values at age and year to be reconstructed by adding a trial M value to the mean F values resulting from analysis of age composition by VPA or similar procedures. One question in this context was whether we could recover the value of M by equilibrium or dynamic fittings.

The data set used was for the North Sea cod (*Gadus morhua*) from ICES working group reports (http://www.ices.dk). We added the independent value of M used in assessments for this species by ICES (i.e., $M = 0.20\,\mathrm{yr}^{-1}$) to the mean F values listed by the working group for age groups 2–4, in order to reconsti-tute the total mortality estimates. Although we could have performed the fitting using mean F values for all ages, this would have been biased towards fully recruited age groups abundant in the early years, and it was felt that the overall yield was probably most sensitive to F values for newly recruited age groups. However this fitting is meant to illustrate the procedure followed, and does not preclude other options. The resulting series of $Z_{2–4}$ values was then fitted against the annual landings for the species coming from the same report.

The three input parameters were allowed to vary randomly (i.e. the solution was unconstrained), with only seed values provided for fitting Equation (7). Knowing the M value allowed us to evaluate the per-formance of both the dynamic and equilibrium Y-Z models in retrieving it from the trend of mean Z value.

Results

Silver hake

For silver hake, random parameter variation did not lead to model convergence. The sensitivity analysis performed with three fixed values of M from the pre-vious equilibrium fits reported as inputs to Equation (7) (Table 1), showed a trend in improved goodness of fit for lower M values. M estimates derived from the dynamic model were about a third lower than for the linearised logistic (equilibrium version) with Equation (8), where the goodness of fit criterion (r^2) was maxi-mized for $M = 0.4\,\mathrm{yr}^{-1}$ (see Caddy and Defeo, 1996 for details). The equilibrium model tended to show higher values for B_∞ and lower for r than for the dynamic model. Nevertheless, the use of $M = 0.144\,\mathrm{yr}^{-1}$ as input

Table 1. Silver hake. Parameter estimates obtained by fitting the dynamic Y-Z model [Equation (7)] with three M values (0.144, 0.266, and 0.400 yr^{-1}) obtained from the equilibrium Y-Z models detailed by Caddy and Defeo (1996). B_∞ and r were allowed to vary randomly. Bootstrap estimates of population parameters from fitting Equation (8) (details in Caddy and Defeo, 1996) are shown for comparative purposes. This model was fitted by using different trial values of M estimated by Equations (8) and (9) (details in Caddy and Defeo, 1996).

	Static model	Dynamic model		
		Natural mortality (yr^{-1})		
Parameter	0.400	0.144	0.266	0.400
B_∞ (t)	147 055	98 816	108 246	115 282
s.e.	16 254	26 199	25 470	16 621
p	0.0000	0.0013	0.0004	0.0000
r	0.722	0.934	0.781	0.683
s.e.	0.063	0.270	0.277	0.291
p		0.0027	0.0109	0.0299
r^2	0.649	0.383	0.290	0.035

to the new approach yielded estimated catches that fitted fairly well the observed data (K-S test: p>0.10) and provided a good description of long-term trends in yields for silver hake (Figure 1). These results were more convincing than using the equilibrium approach which predicted an unreliable negative value of yield due to an unusually high Z value in one year of the time series (Figure 1). The Shapiro-Wilk W test for normality revealed a normal error structure (W test=0.97; n=21; p=0.70) for the dynamic model. This was also true for the other two M values used for seeding Equation (7) (W test: p=0.77 and p=0.15 for M=0.266 and 0.400 yr^{-1}, respectively). It is worth noting that the standard error of the parameters for the equilibrium approach tended to be smaller than in the dynamic approach (Table 1), even though different estimation procedures preclude exact comparison.

Peruvian hake

Figure 2 shows the fitting of Equations (7) and (8) to annual values of yield for males and females separately

in the Peruvian hake fishery. Estimates of natural mortality were similar for both sexes (i.e. ≈ 0.40 yr^{-1}) and for both methods (Table 2). In contrast, B_∞ and r estimates tended to differ between the two models, with the dynamic model converging towards higher values of B_∞ and lower r-values (Table 2). This is expected, given the substantial covariance between variables (see Caddy

Figure 2. Dynamic [continuous line, Equation (7)] and equilibrium [broken line, Equation (8)] Y-Z models fitted to Peruvian hake yields (filled circles): (a) males and (b) females.
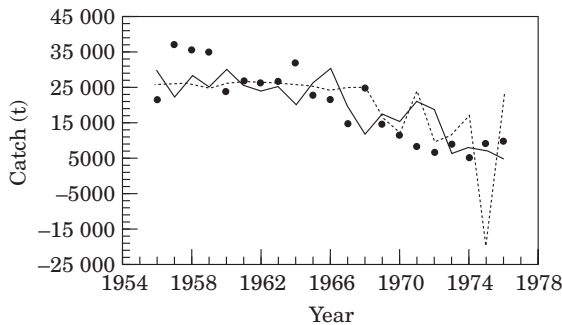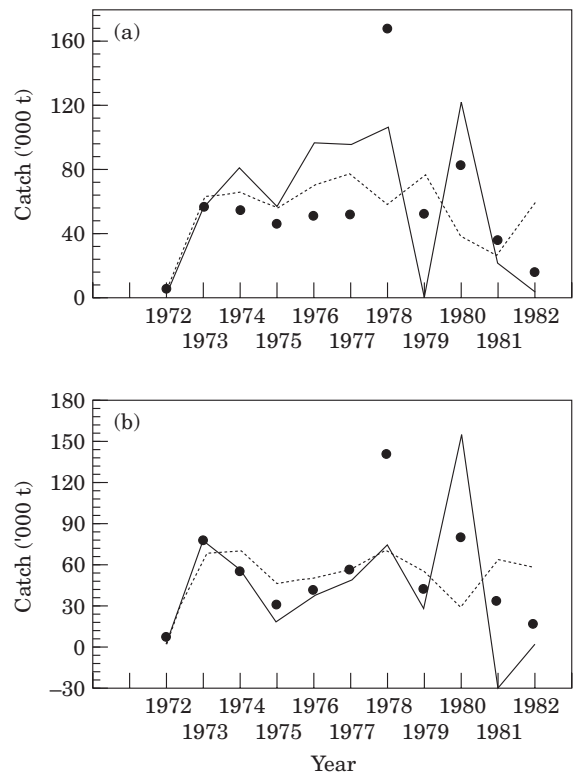
Figure 1. Dynamic [continuous line, Equation (7)] and equilibrium [broken line, Equation (8)] Y-Z models fitted to silver hake yields (filled circles).

Table 2. Peruvian hake. Parameters estimated by the dynamic Y-Z model [Equation (7)]. Only seed values were used for fitting the model and thus the minimisation of least squares was performed allowing all parameters to vary randomly. Bootstrapping estimates obtained y fitting Equation (8) are shown for comparative purposes. This model was fitted by sex using different trial values of M, and the selected values of M were those that maximized a goodness-of-fit criteria for Equation (8) (details in Caddy and Defeo, 1996).

	Static model			Dynamic model		
	Median	s.e.	p	Mean	s.e.	p
Males						
B_∞	120 922	12 926	0.0000	181 665	28 109	0.0002
r	2.504	1.430		1.839	0.294	0.0002
M	0.440			0.438	0.025	0.0000
r^2		0.255			0.283	
Females						
B_∞	130 850	9 441	0.0000	224 780	148 459	0.1685
r	2.304	0.355		0.730	0.419	0.1199
M	0.380			0.39	0.0164	0.0000
r^2		0.267				

and Defeo, 1996; Punt and Hilborn, 1996). For males (W test=0.93; p=0.41), the normal distribution of error structure revealed model adequacy, but this is only partially true for females (W test=0.84; p=0.03). Indeed, neither dynamic nor equilibrium Y-Z models could reproduce the drastic change in catches observed in 1978. This was a response to the abrupt entrance of factory midwater trawlers to the fishery in that year and consequent pulse fishing (Wosnitza-Mendo and Guevara-Carrasco, 2000). This outlier generated wide fluctuations in predicted yield in subsequent years for the dynamic model, whereas predicted yields derived from the equilibrium approach followed roughly the historical mean of landed catches (Figure 2). Nevertheless, sensitivity analysis performed by sequentially fixing one of the parameters to be estimated under a wide range of trial values (e.g. r from 0 to 6, Figure 3) confirmed the robustness of the above mentioned estimates for both male and female Peruvian hake. The strategy of fixing one parameter at a time was useful for detecting the existence of a global minimum through the non-linear minimization process.

North Sea cod

Analysis of the North Sea cod data set showed the advantages of having long-term, high contrast data for model fitting. The strategy of adding an input M value to the weighted mean F values coming as output from the VPA analysis generated total annual mortality rates that were compared with the overall yield in the same year. Figure 4 shows the trajectory of the dynamic model [Equation (7)] and the relationship between annual values of Y and Z for the full North Sea cod data set fitted by the equilibrium logistic [Equation (9)]. The fitting of the dynamic model to this cod data set

explained a very high percentage of the variance (r^2=0.82) and reproduced fairly well the trends in catches for the 35 years analyzed (Figure 4a). The model rapidly converged to the same global minimum, irrespective of the initial values used for fitting, which for M and r varied between 0.1 and 8 yr^{-1} and for B_∞ from 500 000 to 8 000 000 t; i.e. a value slightly larger than the
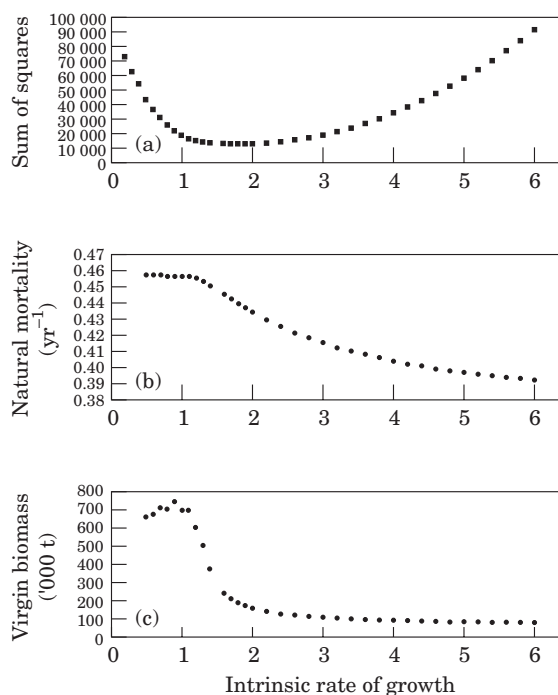

Figure 3. Effect of different assumed values of the intrinsic rate of growth r on the (a) non-linear estimation of the dynamic Y-Z model, (b) natural mortality M, and (c) virgin biomass B_∞ for the Peruvian hake (males).
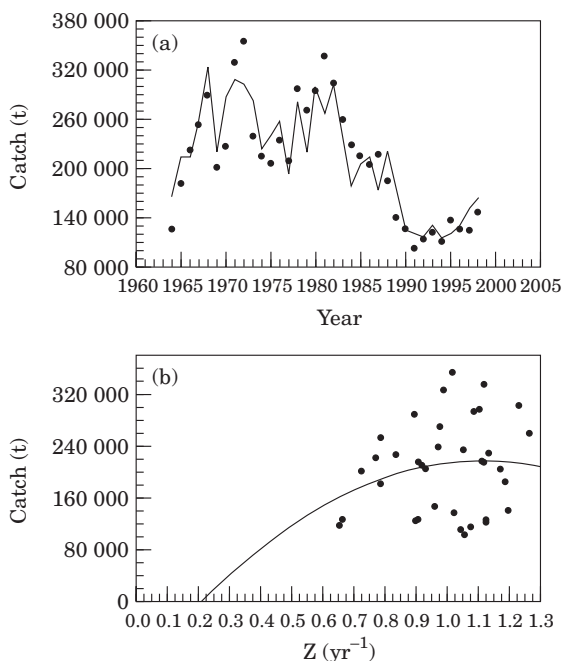
Figure 4. North Sea cod. (a) Dynamic and (b) equilibrium [Equation (9)] Y-Z models fitted to 35 years of data (filled circles).

than the input value used for adding to F values derived from VPA.

Discussion

We have presented here a dynamic procedure for modelling estimates of catch and overall annual mortality rate based on a time-series of annual data and several approaches to its fitting. The new model provided a close projection of the actual long-term trends in yield and also gave independent estimates of vital parameters for stock assessment and management purposes (i.e. M, B_∞, and r). Our results also fit well the conclusions from other investigations of silver and Peruvian hakes (males and females). However, based on trial fittings, it is evident that future research should be directed to the following issues:

(1) The Y-Z model is very sensitive to initial conditions and to the seed values used, especially if short data series are used. A poor choice of initial parameter values for the non-linear fitting procedure can lead to non-convergence or even to a convergence on local minima instead of at the global minimum. In these cases, following the strategy suggested by Punt and Hilborn (1996) for fitting biomass dynamic models, it is suggested that one of the parameters to be estimated be given a range of fixed values. This is relatively more easily achieved than with catch-effort models since parameter values for M for the same or similar species usually exist in the literature. Additional sensitivity analysis performed under a wide range of initial guesses strongly suggests that fixing one parameter (or more, depending on the quality of the data set) helps to improve the performance of the model. Combining biological knowledge with goodness-of-fit results in this way was considered desirable when fitting a mathematical model (Laloë, 1995). From our results to date, we also suggest that the equilibrium model be fitted first to obtain seed values, which can then be used in a second fitting of the dynamic model. This is because experience suggests that despite our doubts expressed in the earlier paper (Caddy and

total cumulative catch. Residuals were normally distributed (W test=0.97; p=0.37) and independent. The lack of temporal trends was verified by a not statistically significant first-order autocorrelation (r=0.12; Box & Ljung Q test=0.58: p=0.44).

The estimate of M obtained by fitting the logistic directly as a quadratic equation [Equation (9)] was $0.207 \, \text{yr}^{-1}$, which coincided closely with the input used in VPA and roughly with the value obtained by non-linear fitting of the dynamic ($M=0.138 \, \text{yr}^{-1}$). On the contrary, the M value that maximized the goodness of fit criterion, using the linearized logistic approach for Equation (8) was almost three times higher ($0.59 \, \text{yr}^{-1}$)

Table 3. North Sea cod. Parameters estimated by the dynamic [Equation (7)] and equilibrium quadratic [Equation (9)] Y-Z models. In the former, parameters were allowed to iterate randomly, with only seed values used for fitting.

	Static model			Dynamic model		
	Mean	s.e.	p	Mean	s.e.	p
B_∞	477 124		0.0000	1 087 860	244 286	0.0000
r	1.823		0.0000	1.149	0.188	0.0000
M	0.207		0.138	0.195	0.4832	
r^2		0.045			0.821	

Defeo, 1996), it appears that M values obtained from the equilibrium model are often close to those in the literature.

(2) Sensitivity analysis shows that dynamic model parameters, especially r and B_∞, are strongly cross-correlated, hence their values are not independent. This was already noticed by Caddy and Defeo (1996) for different static Y-Z models fitted to the same data sets. The substantial covariance between estimates also suggests that B_∞/r ratios can be more precisely determined than for the parameters themselves (Punt and Hilborn, 1996). Thus, in applying the dynamic model it could also be useful to consider: (a) an independent estimate or likely range of M values, possibly by fitting the static model or estimating M by another methodology; (b) a ratio of probable r/B_∞ values derived from conventional static or dynamic effort-yield models.

(3) In the case of the Peruvian hake, neither the dynamic nor static versions of the Y-Z model were able to predict the abrupt and substantial increase in yield that occurred in 1978 (Figure 2). The dynamic model was destabilized by this data point, leading to substantial variations in predicted catch subsequently (1979–1982). The dynamic approach was clearly more sensitive to fishery trend than its static counterpart, perhaps as a result of the high r values estimated (i.e. between 0.8 and 2.5). Punt and Hilborn (1996) also showed that at high r values, the results using biomass dynamic models (see Hilborn and Walters, 1992) tend to be unreliable, because fluctuations in population size are then mainly driven by large recruitment fluctuations. Other adaptive responses to high fishing intensity (e.g. increasing length at first maturity with decreasing stock size) could take place in the Peruvian hake, as mentioned by Wosnitza-Mendo and Guevara-Carrasco (2000).

(4) As for the equilibrium approach, the dynamic model is not immune to error if the data set does not span a wide range of mortality rates, and estimates are particularly vulnerable to outlying values of the independent variable in short data series (e.g. the Peruvian hake). Even though examination of residuals of the fit did not show systematic patterns or departures from normal distribution, the existence of an obvious outlying data point in the Peruvian hake destabilizes the behaviour of the dynamic model, thus suggesting that alternative estimates could be obtained by omitting this point. We suggest evaluating the relative performance of the estimation procedure when outliers are excluded from model fitting. Bootstrap methods can also be applied to estimate confidence intervals for the parameters, as suggested by Caddy and Defeo (1996) for equilibrium Y-Z models.

(5) As noted, the estimates of total mortality used for the hake examples for the dynamic model assume "pseudo-equilibrium" conditions (*sensu* Caddy, 1996). Catch curve analysis, commonly used to estimate total

mortality, assumes constant recruitment and time-invariant natural mortality, and because mortality (and catch data) are only estimates, the observation error estimation procedure is the appropriate one. However, this "pseudo-equilibrium assumption" is not believed to change the validity of the modelling approach *per se*, and may be seen as introducing a form of "smoothing" or "equilibrium approximation" to the data. Mean values of Z represent the impact of fishing on all harvestable year classes, and thus aggregate information on the age structure and dynamics of the population (Caddy, 1986; Defeo and Seijo, 1999). In this sense, as noted by Caddy (1986), this is effectively a flexible version of Gulland's (1961) procedure for equilibrium approximation by effort averaging over a fixed number of years corresponding to the average number of years an age class is in the fishery.

(7) The proportion of the variance explained by the model from the data sets tested so far seems to be higher for the equilibrium model. This happens with other surplus production models; i.e. correlations derived from linearized surplus production functions are usually high because the control variable (fishing effort or Z depending on the case) appears on both sides of the equation. Thus, the variance estimates from dynamic fitting appear more realistic and free of the noise imposed by this interdependence between control and response variables. This was also noted for M estimates derived from r^2 maximization of Equation (8) (in which the term (Z-M) appears on both sides of the equation) for the silver hake and the North Sea cod.

In both cases, M estimates provided by the dynamic model were close to those derived from the quadratic fitting [Equation (9)], but disagreed with values found using the linearized logistic. With the latter, M estimates that maximized the goodness-of-fit criterion (r^2) were almost three times higher than those provided by the dynamic and quadratic models. These results confirm that this approach is dangerous if estimates of M are close to the observed minimum Z (Pin and Defeo, 2000) and probably should not be used.

(8) One criticism of the model could be that M may not be constant through the time-series. Two opposing factors might have been in play: (a) mean ages decline with increased exploitation, though this is probably less important if the data series begins after the unexploited cohorts have passed through the fishery. (b) If the general depletion of top predators suggested by Pauly *et al.* (1998) is valid, M will have declined along with overall rates of predation.

A simple three parameter model cannot hope to account for such contrary effects, but the bias introduced seems likely to be much smaller than the unidirectional change in q resulting from technological improvements and increased fishing power over recent decades.

In summary, we have shown that the dynamic Y-Z model developed here has utility as a flexible simulation tool for exploring fishery trends: it has low parameter requirements and can use the same data as currently employed for fitting virtual population analyses and similar age-based analytical models.

Acknowledgements

References

Almeida, F. P., and Anderson, E. D. 1978. Status of the Gulf of Maine silver hake stock – 1978. National Marine Fisheries Service, North East Fisheries Center, Woods Hole Laboratory. Laboratory Document: Reference No 78–56, 19 pp.

Caddy, J. F. 1986. Stock assessment in data-limited situations – the experience in tropical fisheries and its possible relevance to evaluation of invertebrate resources. Canadian Special Publication of Fisheries and Aquatic Sciences, 92: 379–392.

Caddy, J. F. 1996. Regime shifts and paradigm changes: is there a place for equilibrium thinking? Fisheries Research, 25: 219–230.

Caddy, J. F. 1999. Fisheries management in the twenty-first century: will new paradigms apply? Reviews in Fish Biology and Fisheries, 9: 1–43.

Caddy, J. F., and Csirke, J. 1983. Approximations to sustainable yield for exploited and unexploited stocks. Oceanographie Tropicale, 18: 3–15.

Caddy, J. F., and Defeo, O. 1996. Fitting the exponential and logistic surplus yield models with mortality data: some explorations and new perspectives. Fisheries Research, 25: 39–62.

Caddy, J. F., and Mahon, R. 1995. Reference points for fishery management. FAO Fisheries Technical Paper No 347, 83 pp.

Csirke, J., and Caddy, J. F. 1983. Production modelling using mortality estimates. Canadian Journal of Fisheries and Aquatic Sciences, 40: 43–51.

Defeo, O., and Seijo, J. C. 1999. Yield-mortality models: a precautionary bioeconomic approach. Fisheries Research, 40: 7–16.

Die, D., and Caddy, J. F. 1997. Sustainable yield indicators from biomass: are there appropriate reference points for use in tropical fisheries? Fisheries Research, 32: 69–79.

Espino, M., and Wosnitza-Mendo, C. 1984. El uso del modelo Csirke-Caddy para la merluza peruana (*Merluccius gayi peruanus*). Boletín Instituto del Mar del Perú, 8: 191–205.

Fox, W. W. 1970. An exponential surplus yield model for optimizing exploited fish populations. Transactions of the American Fisheries Society, 99: 80–88.

Gulland, J. A. 1961. Fishing and the stocks of fish at Iceland. Ministry of Agriculture, Fisheries and Food (UK). Fishery Investigation Service II, 23: 1–52.

Hilborn, R., and Walters, C. J. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman and Hall, New York.

Laloë, F. 1995. Should surplus production models be fishery description tools rather than biological models? Aquatic Living Resources, 8: 1–16.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. Jr 1998. Fishing down marine food webs. Science, 279: 860–863.

Pin, O., and Defeo, O. 2000. Modelos de producción captura-mortalidad para la pesquería de corvina (*Micropogonias furnieri*) (Desmarest, 1823) en el Río de la Plata y Zona Común de Pesca Argentino-Uruguaya (1975–1986). *In* Modelos de Producción Excedente Aplicados a los Recursos Corvina y Pescadilla, pp. 31–65. Ed. by M. Rey, and G. Arena. INAPE-PNUD. 89 pp.

Punt, A. E., and Hilborn, R. 1996. Biomass dynamic models. User's Manual. FAO Computerized Information Series (Fisheries). No 10, FAO, Rome, 62 pp.

Prager, M. H. 1994. A suite of extensions to a non-equilibrium surplus production model. Fishery Bulletin, 92: 374–389.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada, 191: 382.

Schaefer, M. B. 1954. Some aspects of the dynamics of populations important to the management of commercial marine fisheries. Bulletin of the Inter-American Tropical Tuna Commission, 1: 27–56.

Schnute, J. T. 1977. Improved estimates from the Schaefer production models: theoretical considerations. Journal of Fisheries Research Board of Canada, 34: 583–603.

Sparre, P., and Venema, S. C. 1992. Introduction to tropical fish stock assessment. Part 1 – Manual. FAO Fisheries Technical Paper 306/1 Revision 1, FAO Rome, 376 pp.

Wosnitza-Mendo, C., and Guevara-Carrasco, R. 2000. Adaptive responses of Peruvian hake to overfishing. Naga, The ICLARM Quarterly, 23: 24–28.