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A REVIEW OF STOCK-RECRUITMENT RELATIONSHIPS WITH REFERENCE TO FLATFISH POPULATIONS

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ABSTRACT

The relationship between stock and recruitment in fish populations has been a subject of many studies and some controversy, even to the extent that it has been questioned whether the two can be related in any meaningful way. The denial of a meaningful stock-recruitment relationship has profound and disturbing influences on the science of fish population dynamics and would seem to be something of a policy of despair. A more constructive approach is to acknowledge the difficulties in establishing a stock-recruitment relationship from the available information but still to seek the best interpretation of the data for the purposes for which the analysis is intended. Among the models that have been developed to fit stock-recruitment curves to data sets are the well-known Beverton-Holt and Ricker curves, both of which have two parameters. Less commonly used is the two-parameter model of Cushing. These two-parameter models have been generalized to give three-parameter models whose shape can be varied by settings of the parameters so as to model a wide range of observed stock-recruitment curves. In this paper these models and their underlying assumptions are described. Statistical methods of fitting the curves to data are reviewed with emphasis on the appraisal of the fitted curve, concentrating on the use for which the fitted curve is intended. Methods of choosing between different curves are discussed. The review is illustrated with examples of stock-recruitment data derived for various flatfish stocks. Among the questions that are discussed is whether there are any features of stock-recruitment relationships for flatfish that differentiate them from those of other species. Methods for testing the null hypotheses that there is no relationship between stock and recruitment and that recruitment in flatfish is not influenced by environmental or other biological factors are described. Of the 20 flatfish stocks for which suitable stock and recruitment data are available, it is shown that in six cases there is a statistically significant relationship between stock size and recruitment. In one of these cases the relationship is significantly strengthened by the incorporation of an environmental measurement. Of the six significant stock-recruitment relationships one is strongly domed and three are the right-hand arm of a domed curve. In the other two cases average recruitment increases with increasing stock size, but it is not possible to differentiate between a domed and an asymptotic curve. This evidence of density-dependence in the stock-recruitment relationships for flatfish is further strengthened by an examination of those cases in which the model of constant recruitment, independent of stock size, is not rejected. In eight of these stocks it is shown that the model of constant recruitment is favoured in preference to a model in which recruitment is directly proportional to stock size. Although recruitment may vary about a constant average level over a restricted range of stock size, it is not biologically possible for a population to sustain a high level of recruitment at low stock sizes. Thus in these eight cases there is further evidence of an underlying, but as yet unidentified, stock-recruitment relationship.

1. INTRODUCTION

The scientific value of fitting stock (S)-recruitment (R) curves to data has had something of a chequered history, with alternating optimism and pessimism. Rijnsdorp (1994) gives references to authors who have called the process of fitting stock-recruitment curves into question. He also, however, refers to work (Tyler, 1992) giving a contrary opinion. There is no consensus in text books on fisheries dynamics. Wooton (1990) is doubtful about the value of fitting stock-recruitment relationships, expressing the view that although considerable ingenuity has been spent in fitting the relationships it takes an act of faith to take the resulting curves seriously. Rothschild (1986) also highlights the uncertainties, entitling his chapter

5 on the subject 'The recruitment paradox'. He does make clear, however, the fundamental importance of the concept of the stock-recruitment relationship. It is clear from all these arguments that it is the high degree of as yet unexplained variability often evident in estimates of recruitment that leads to the uncertainty. Hilborn & Walters (1992) have pointed out that the search for stock-recruitment relationships contains traps for the unwary, and that not only should the curve be fitted, giving the average recruitment at any stock level, but also that the uncertainty associated with the fitting process to actual data needs to be assessed. They give much helpful guidance to investigators of stock-recruitment relationships and certainly do not suggest that such relationships are of no value.

Some doubts have been expressed about the statistical assumptions made of the variability in recruitment that underpins simple regression models. Much ingenuity has been exercised in devising alternative methods of analysis and modifications to simple models. Rothschild & Mullen (1985) outlined a non-parametric approach assuming time variation in stock and recruitment behaviour. Moussalli & Hilborn (1986) described a method of analysis in which different stages of the life history are disaggregated, with a Beverton-Holt stock-recruitment relationship describing each stage, but with parameters that vary in time. They criticized the use of a single overall stock-recruitment relationship. Evans & Rice (1988) argued that the probability distribution of recruitment, possibly changing with stock size, was of greater value than a single deterministic function of stock size.

Walters (1985, 1990) and Hall *et al.* (1988) argued that there was a bias inherent in stock and recruitment data and suggested a method of correcting for this bias in the estimation of the parameters of a fitted Ricker stock-recruitment equation. The reason for the bias is that high observed stocks are likely to be associated with lower recruitment than average because otherwise the stock levels would have risen further. Similarly low observed stocks are associated with higher than average recruitment. It is not precisely clear to what extent this effect is moderated by lags in time between recruitment and maturity to the stock and it is beyond the scope of this review to pursue the argument further. Until this question is properly resolved, therefore, it is safest to analyse the data without any prior manipulation, but perhaps to keep in mind the possibility of bias at the end points of the stock-recruitment curve.

All of the data on flatfish stocks and recruitment analysed in this review are based on virtual population analysis (VPA). Some doubts have been expressed about the assumption of independence in the random component of any model describing variation in successive recruitment data. Hildén (1988) showed that in conditions of stable rate of exploitation and fishing mortality relative changes in stock levels are correctly identified, but that where changes occur in fishing pressure the choice of natural mortality affects perception of stock changes. Lapointe *et al.*

TABLE 1

Sources of data on flatfish stocks. The units for Pacific halibut are pounds$\cdot 10^{-6}$ both for stocks and recruitment. For all other stocks the units for stocks are tonnes$\cdot 10^{-3}$ and for recruitment numbers$\cdot 10^{-6}$.

species	*Latin name*	*stock*	*number of observations*	*assumed age at recruitment*	*source*
Pacific halibut	*Hippoglossus stenolepis*	North Pacific	42	8	Hilborn & Walters, 1992
Greenland halibut	*Rheinhardtius hippoglossoides*	N.E. Arctic	19	3	ICES, 1993a
		Iceland/Faroe	11	5	ICES, 1993b
megrim	*Lepidorhombus whiffiagonis*	Atlantic	7	1	ICES, 1993c
plaice	*Pleuronectes platessa*	North Sea	33	1	ICES, 1993d
		Skagerrak/Kattegat	12	2	ICES, 1993d
		E. English Channel	11	1	ICES, 1993d
		W. English Channel	15	1	ICES, 1993c
		Celtic Sea	14	1	ICES, 1993c
		Irish Sea	26	1	ICES, 1993e
sole	*Solea solea*	North Sea	34	1	ICES, 1993d
		E. English Channel	11	1	ICES, 1993d
		W. English Channel	22	1	ICES, 1993c
		Celtic Sea	19	2	ICES, 1993c
		Irish Sea	19	2	ICES, 1993e
		Biscay	11	0	ICES, 1993c
yellowtail flounder	*Limanda ferruginea*	S. New England	17	1	SAW, 1991
		George's Bank	17	1	SAW, 1991
American plaice	*Hippoglossoides platessoides*	E. North America	11	1	O'Brien *et al.*, 1992
summer flounder	*Paralichthys dentatus*	E. North America	9	0	SAW, 1992

(1989) and Lapointe & Peterman (1991) came to similar conclusions for data based on VPA.

The problem of fitting regression equations to data that have some autocorrelation in the random component is discussed by Judge *et al.* (1980). They showed that estimates of the parameters obtained from the ordinary least squares method are unbiased, but that the estimate of the variance of the random component is biased and thus the regression parameters may be inefficiently estimated. The direction of the bias in the variance estimates depends on the nature of the autocorrelation. Judge *et al.* (1980) showed that where the autocorrelation is of first order and moderate in degree, the efficiency of estimates obtained from ordinary least squares is high compared with that of a more complicated method of fitting (generalized least squares) incorporating the covariance structure of the random component. A fully worked out methodology for dealing with autocorrelated random components is not available (Wetherill, 1986). Judge *et al.* (1980) gave further details of a range of methods. Wetherill (1986) mentioned another point, that apparent autocorrelations may be caused by missing variables in the model. Since there is such uncertainty concerning the effects of autocorrelation, in this review models will be fitted using ordinary least squares. The possibility of autocorrelations in the residuals will, however, be tested formally, and any such significant effects will be reported.

Despite this multitude of caveats it is shown, at least for most flatfish stocks, that traditional regression assumptions can be validated. Following a careful appraisal of the different models a stock-recruitment relationship, with associated confidence bands, can be constructed in many of the cases for which data are available. It is not intended here to discuss the uses to which such relationships might be put. It is shown that the null hypothesis that recruitment is independent of stock size for all fish stocks, implying that stock size is in no way helpful in explaining any of the variability in recruitment, should be rejected. Perhaps as more data become available and the reliability of such data increases in the future the predictive power of stock-recruitment relationships will improve. The incorporation of knowledge of other factors influencing recruitment offers further potential in the derivation of meaningful stock-recruitment relationships, and this issue is briefly discussed in this review.

2. DATA

Data on flatfish stocks were obtained from two main sources (Table 1). For European stocks, reports of the findings of working groups of the International Council for the Exploration of the Sea (ICES) were consulted (ICES, 1993a, 1993b, 1993c, 1993d, 1993e). Data on some North American stocks were obtained from papers of the Northeast Regional Stock Assessment Workshops (SAW) of the Northeast Fisheries Science Center (NFSC), Woods Hole USA (SAW, 1991, 1992). Data for Pacific halibut stocks were obtained from Hilborn & Walters (1992). In a sense these data, generated by VPA calculations, are not ideal for the purposes of an investigation of stock-recruitment relationships. Estimates of both recruitment and stock size are obtained from the same table of catch-at-age data. Data on more recent year classes are less reliable than those of historically older cohorts because of the effects of estimation of terminal fishing mortality. Ideally, independent estimates of recruitment numbers and stock size should be used. Indeed, egg production should be estimated rather than spawning stock biomass. However, the VPA estimates are the best data currently available, and they will be accepted at their face value in this review.

3. MATHEMATICAL MODELS FOR S-R RELATIONSHIPS

There have been several recent reviews of stock-recruitment relationships, including those contained in most books on the dynamics of fisheries (Rothschild, 1986; Cushing, 1988; Hilborn & Walters, 1992). Little would be gained by covering this ground again here, but some additional comments may put the models in perspective for this review.

The assumed mathematical relationship is of the form

$$R = \mathrm{f}(S)$$

where $\mathrm{f}(S)$ depends on a number of parameters that have to be estimated from any given data set so as to fit the relationship to the data. For the function to give a relationship that is consistent with reality, certain constraints have to be imposed. Firstly, the function should give non-negative values for R for all non-negative S. Clearly negative stocks or recruitment have no meaning. Secondly, the function should not return a positive value for R for zero S, because if the stocks disappear so will recruitment. Thirdly, the function should not give infinite values of R, except possibly for infinite S. In this review a form of stock-recruitment relationship that satisfies these constraints will be called admissible. All the curves reviewed here can give inadmissible relationships for some values of the parameters, and this has to be borne in mind before using the results of analysis.

The stock-recruitment relationships reviewed are listed in Table 2, together with brief descriptions of their characteristics. Although other forms of relationship have been used in stock and recruitment studies (see for example Parrish & MacCall, 1978; Elliott, 1985), those chosen here are a representative selection and include those most commonly used. The familiar Beverton-Holt (Beverton & Holt, 1957) and

TABLE 2

Characteristics of stock-recruitment models. *A convex function is such that the chord joining two points on the graph is always above the graph of the function between those two points. The chord is always below the graph for a concave function.

name	*f(S)*	*conditions for admissability*	*slope at origin*	*value of S at maximum R*	*maximum R*	*value(s) of S at point(s) of inflection*	*shape*
Cushing	$R = \alpha S^{\gamma}$	$\alpha, \gamma>0$	$0\ (\gamma>1)$ $\alpha\ (\gamma=1)$ $\infty\ (\gamma<1)$	∞	∞	-	Monotonic increasing, unbounded Convex* if $\gamma>1$, Concave if $\gamma<1$.
Ricker	$R = \alpha S e^{-\beta S}$	$\alpha, \beta>0$	α	$\frac{1}{\beta}$	$\frac{\alpha}{\beta e}$	$\frac{2}{\beta}$	Domed. Concave on left hand side of maximum.
Beverton-Holt	$R = \frac{S}{b+aS}$	$a, b>0$	$\frac{1}{b}$	∞	$\frac{1}{a}$	-	Monotonic increasing to asymptote. Concave
Shepherd	$R = \frac{S}{b+aS^{c}}$	$a, b, c>0$	$\frac{1}{b}$	$\left[\frac{b}{a(c-1)}\right]^{1/c}$ $(c>1)$	$\frac{c-1}{bc}\left[\frac{b}{a(c-1)}\right]^{1/c}$ $(c>1)$	$\left[\frac{b(c+1)}{a(c-1)}\right]^{1/c}$ $(c>1)$	Domed if c>1, concave on left hand side of maximum. Beverton-Holt if c=1. Monotonic increasing unbounded and concave if c<1.
Saila-Lorda	$R = \alpha S^{\gamma} e^{-\beta S}$	$\alpha, \beta, \gamma>0$	$0\ (\gamma>1)$ $\alpha\ (\gamma=1)$ $\infty\ (\gamma<1)$	$\frac{\gamma}{\beta}$	$\alpha\left[\frac{\gamma}{\beta e}\right]^{\gamma}$	$\frac{(\gamma\pm\sqrt{\gamma})}{\beta}$	Domed. Concave on left hand side of maximum if $\gamma<1$. Two points of inflection, one each side of maximum, if $\gamma>1$.

Ricker equations (Ricker, 1954) are both two-parameter models. Cushing's equation (Cushing, 1971) is also a two-parameter model, but this has been used less often in studies of stock and recruitment. In a sense this equation is potentially limited by the fact that it is unbounded as S increases. Its use at high stock levels is therefore questionable, but in practice it may be a useful indication of the nature of the stock-recruitment relationship over the observed range of stock size. As with any fitted equation, care has to be taken in extrapolating beyond the limits of the data.

The Shepherd equation (Shepherd, 1982) is a generalization of the Beverton-Holt equation with the addition of a third parameter that allows it to be either domed or unbounded, with an asymptotic shape as an intermediate case, depending on the value of this third parameter. The Saila-Lorda equation (Saila *et al.*, 1988; Mills & Hurley, 1990) is a generalization of the Ricker equation. The third parameter here allows more variety in shape of curve than the Ricker, including the possibility of a convex region at low stock sizes (with $\gamma>1$) representing depensatory mechanisms. Of the equations reviewed here the only other that can be convex at low stock sizes is the Cushing (with $\gamma>1$), but then the values of R at high S may be too large to be representative.

Those equations defined by only two parameters are relatively inflexible. For example, the shape of the Ricker equation is determined by the single point on the stock-recruitment graph at which recruitment is a maximum. It can be seen from Table 2 that the stock size S corresponding to maximum recruitment fixes the parameter β, and then the value of maximum recruitment itself fixes α. In order to accommodate the data in the region of the dome, therefore, the Ricker equation may be a poor model at extreme stock sizes. Both the Beverton-Holt and Cushing equations are determined by any two points on the stock-recruitment plot (to be admissible the former requires that the ratio of R to S be smaller at the higher value of S). Neither of these curves can be used to represent a domed relationship. The addition of the third parameter in the Shepherd and Saila-Lorda equations gives greater flexibility, although for actual data it is often found that the best-fitting equation is inadmissible. There has to be a balance between the flexibility in potential shapes allowed by the third parameter and the difficulty in identifying suitable and admissible values for the parameters when the data are scattered.

4. STATISTICAL ASSUMPTIONS

In this paper an approach based on parametric models for theoretical stock-recruitment relationships is outlined. The scatter of data around these theoretical curves is allowed for by including an additional random component in the model that describes deviations of R from the curve. The model relating R to S then becomes

$$R = f(S) + \phi$$

The random component ϕ of this model is often called the error (Kendall & Buckland, 1982). This word will not be used in this review to avoid possible confusion between errors in estimation and other unexplained sources of variation. ϕ is assumed here to encompass not merely genuine errors in R, in the sense that the estimation of R is not equal to the true value, but also the combination of real effects both abiotic and biotic that cumulatively cause the observed R to differ from the central value defined by the mathematical model.

Implicitly the effects comprising the random component of the model are assumed to be additive, and the conventional assumption is then that their distribution is normal (Gaussian). Hennemuth *et al.* (1980) showed that the distribution of recruitment in fish stocks was better represented by a log-normal distribution than a normal, though their conclusions were based on an analysis of gross variation in R not deviations from a stock-recruitment curve. Garrod (1982) came to the same conclusion based on the evidence of deviations of R from the geometric mean of R for a number of fish stocks. He also showed that residuals from a fitted Shepherd curve after logarithmic transformation of the data were normally distributed (Garrod, 1983). Some findings from investigation of some flatfish stocks are described in this paper. In some cases the calculated residuals from fitted stock-recruitment curves indicate that the random component of the model should be represented by a log-normal distribution. In all remaining cases no clear indication is given whether the normal or log-normal model is the more appropriate. Over a limited range of R, $\ln R$ is closely approximated by a linear function of R so in cases where the deviations of R from the central value are limited in range, as is often the case for flatfish stocks, it is not surprising that it is not possible to distinguish between the normal and log-normal distributions. The log-normal assumption considerably simplifies the fitting process and in all cases the final suggested stock-recruitment relationship will carry the assumption that the random component of the model is log-normally distributed. The relationship between R and S is then:

$$\ln R = \ln f(S) + \varepsilon$$

where the random component ε is assumed to be normal. Such a relationship implies that deviations of R from the central value are represented by multiplicative effects.

Another assumption that is made in conventional regression modelling of the stock-recruitment process is that random variation is associated with the estimation of R, but not of S. Almost certainly this is not the case, but if it can be shown that unexplainable variation in R is considerably greater than that in S, then the simple regression approach is acceptable for fitting the curves to the data. As has already been mentioned, the data are taken from VPA studies. Since S comprises a number of year classes, but R is derived from a single cohort it is likely that this assumption will be acceptable. However, a further appraisal will be made before fitting is attempted.

No appraisal of variation in R or S can be made without some external information. The departure of a particular point on the stock-recruitment scatter-plot could be explained by either variation in R or in S, or indeed in both. A suggestion for testing whether it is reasonable to assume that it is R that is subject to variation is derived from collaborative work (Beverton & Iles, in prep.). This is to make use of the fact that the data on R and S are both time series. The suggestion is that any deviation from a time trend fitted to the data represents, mainly, errors in estimation together with other unexplainable sources of variation. Thus if it can be shown that variation about the trend line (in time) for $\ln S$ is small in comparison with that for $\ln R$, then the association of the random component ε with $\ln R$ rather than S can be justified.

At present this method of analysis can only be suggested as an approximate guide. The fitting of a trend curve to time series data is a subjective process. Although smoothing methods have been devised that do not make any parametric assumptions (Tukey, 1977; Velleman & Hoaglin, 1981), they do incorporate different amounts of averaging and are still not completely objective. It is unlikely that a completely objective trend fitting method will ever be devised. Where only a short run of data is available, time trends will not be apparent, and the method of checking variation may be limited. No formal statistical test of residual variation around these trend curves can be made at present since no expression appears to be available for the theoretical variance of the trend curve itself. Nevertheless, the variance about the trend curve for $\ln R$ in flatfish stocks is generally several times greater than for $\ln S$, and this is a strong indication that it is $\ln R$ that is more subject to unexplained variation than $\ln S$ (Table 3).

Diagnostic checks after calculating the fitted regression equation are strongly recommended to justify the statistical assumptions that are made about the random component ε of the stock-recruitment model. Procedures for making these checks are now standard in linear regression (Belsley *et al.*, 1980; Cook & Weisberg, 1982; Fry, 1993). Amongst the most useful are the Durbin-Watson test for independence and the normal probability plot of the residuals (Fry, 1993), also known as Filliben's test, to check for normality. Further checks are made for outliers, observations whose deviation from the usual is extreme, and influential data points. Checks for these

TABLE 3
Measurements of variation for flatfish stocks. For more information see text. For units of measurement of *S* and *R* see Table 1. n is the number of observations. SD_1 is the standard deviation of the data (after logging). SD_2 is the standard deviation of the differences between the logged data and the trend curve fitted through the logged data.

			lnS		*lnR*	
species	*stock*	*n*	SD_1	SD_2	SD_1	SD_2
Pacific halibut	Pacific	42	.34	.01	.20	.10
Greenland halibut	N.E. Arctic	19	.44	.05	.10	.07
Greenland halibut	Icelandic	11	.22	.13	.17	.04
megrim	Atlantic	7	.14	.08	.29	.16
plaice	North Sea	33	.14	.04	.42	.31
plaice	Skagerrak/Kattegat	12	.30	.09	.47	.23
plaice	E. English Channel	11	.30	.09	.37	.28
plaice	W. English Channel	15	.34	.06	.53	.35
plaice	Celtic Sea	14	.47	.10	.53	.42
plaice	Irish Sea	26	.34	.09	.34	.26
sole	North Sea	34	.48	.20	.82	.73
sole	E. English Channel	11	.18	.07	.30	.30
sole	W. English Channel	22	.32	.08	.39	.25
sole	Celtic Sea	19	.23	.09	.24	.14
sole	Irish Sea	19	.23	.11	.65	.49
sole	Biscay	11	.20	.04	.10	.07
Yellowtail flounder	S. New England	17	.73	.29	1.17	.83
Yellowtail flounder	George's Bank	17	.74	.22	1.07	.54
American plaice	E. North America	11	.73	.05	.43	.29
Summer flounder	E. North America	9	.38	.20	.52	.36

are based respectively on the residuals or studentized residuals (Fry, 1993) and the leverages, often denoted by h_i or HI (Fry, 1993). All of these test statistics and diagnostics are routinely available in statistical packages containing a linear regression fitting routine.

In nonlinear regression similar procedures have been suggested (Ross, 1990), but this is an area of current research interest in statistics (Cook & Tsai, 1985; Cook, 1986; Ross, 1987). Not all those statistical computer packages containing a non-linear regression routine enable studentized residuals and leverages to be easily obtained, but the SAS package used in the data analysis for this review does compute these statistics (SAS, 1987).

5. METHODS

The essential of the approach suggested for investigating the viability of a theoretical stock-recruitment curve in fitting a data set is to start with a simple model and progressively make it more complicated in the hope that the greater flexibility of shape allowed by the more complicated model gives a more satisfactory fit to the data. The addition of further parameters is bound to improve the fit of the curve to the data and it is necessary to test if the improvement is statistically significant. If one model is a special case of another in the sense that it can be obtained by special settings of one or more parameters, a so-called nested model, there is an established procedure for determining if the more complicated model is to be preferred. The procedure is the same as that used in variable selection in multiple regression (Fry, 1993) and is based on the decrease in unexplained (residual or error) sum of squares when the more complicated model is fitted.

Methods of choosing between models that are not special cases of one another, non-nested models, are not so well established, though some work has been done on this problem based on an original idea of Cox (1961). Some of this work is reviewed in White (1983). At present the techniques have not reached the stage where they are routinely available, and they are not available in standard statistical packages. Therefore, in this review, where comparison of models has to be made it will be done on the basis of an informal comparison of the error sums of squares of the two models.

Rothschild (1986) discusses the biological background of stock-recruitment relationships. Conceptually the simplest form of model is the case of simple linear proportionality of *R* with *S*:

$$R = \alpha S$$

The biological interpretation of the model is that mortality is density independent, with neither compensation nor depensation. The constant α depends on the scale of measurement chosen for *R* and *S* and it is convenient to investigate as a null hypothesis that the stock-recruitment relationship is a line of the above form passing through the geometric mean of the data:

$$\ln R = \overline{\ln R} - \overline{\ln S} + \ln S$$

The value $\ln\alpha = \overline{\ln R} - \overline{\ln S}$ is the least-squares estimate of the parameter α, if the log-normal error component model is assumed (Appendix 1). Cushing (1971) generalized this simple model by introducing a power of S on the right-hand side, allowing the stock-recruitment relationship to be curved:

$$R = \alpha S^{\gamma}$$

After logarithmic transformation this model becomes:

$$\ln R = \ln\alpha + \gamma \ln S$$

so that simple linear regression methods can be used for fitting and testing the model. The line of constant proportionality is a special case of the Cushing model, with γ=1 and $\ln\alpha = \overline{\ln R} - \overline{\ln S}$ so the hypothesis that this model fits the data as adequately as the Cushing model can be tested by formal statistical procedures. Note that no fitting of parameters is needed for the line of constant proportionality since these are completely determined in the equation above.

The Saila-Lorda model includes an extra term on the right-hand side of the equation:

$$R = \alpha S^{\gamma} e^{-\beta s}$$

and after logarithmic transformation this becomes:

$$\ln R = \ln\alpha - \beta S + \gamma \ln S$$

Multiple regression enables the parameters to be estimated and the goodness-of-fit of the model to be appraised. The Cushing equation is a special case of this model, with β=0. Thus a formal statistical test can be done to determine if the Saila-Lorda equation is a significantly better fit to the data than the Cushing.

The Ricker equation

$$R = \alpha S e^{-\beta s} \quad \text{is transformed to:}$$

$$\ln R = \ln\alpha - \beta S + \ln S$$

This is also linear in the parameters, and these can be estimated by regressing $\ln R/S$ on S. There appears to be some confusion in the literature about the validity of this method of fitting. Hilborn (1985) showed that the method gives unbiased estimates for the parameters. He did not, however, point out that some of the associated statistics from the regression calculations, particularly the coefficient of determination R^2 and the F statistic, are incorrect and potentially misleading. Stefansson (1992) pointed out that the regression procedure could be misleading since random but unrelated stock and recruitment could give an apparently significant relationship between $\ln R/S$ and S simply because of the presence of S on both sides of the equation. Beverton & Iles (1992b) gave an example of such an apparently significant relationship derived from artificially obtained random data. This conclusion would, however, be based on an incorrect interpretation of the value of R^2. If the assumptions of independent identically distributed normal random components in $\ln R$ are valid and if a Ricker model is appropriate for the data, then a regression of $\ln R/S$ on S gives unbiased estimates for the parameters of the Ricker equation, the correct error sum of squares and the correct confidence intervals for the parameters. For further details see Appendix 2. If it is not certain that the Ricker model is correct, a wise precaution is to make a comparison with other models using the error sum of squares as a criterion.

The Ricker equation is a special case of the Saila-Lorda (with γ=1), and the statistical significance of the improvement in prediction obtained by the inclusion of the third parameter can therefore be formally tested by comparison of the difference in error sum of squares with the error mean square. The Ricker equation is not, however, related to the Cushing equation so this formal procedure cannot be used. Similarly a model of constant recruitment is not a special case of the Ricker equation and this can lead to some difficulties in interpretation of statistical tests (see Appendix 2).

Both the Beverton-Holt and Shepherd equations need a nonlinear regression method to be used for fitting to data; they are not linear in the parameters after logarithmic transformation. The Beverton-Holt equation is a special case of the Shepherd (with c=1), so the formal statistical test based on differences in error sums of squares can be done to determine if the Shepherd equation is significantly better than the Beverton-Holt equation. It is not possible to make formal tests of either model against the Cushing, Ricker or Saila-Lorda equations.

As is the case with the Ricker equation, the Beverton-Holt and Shepherd equations do not reduce to a model of constant R (or $\ln R$) by any setting of the parameters. For that reason no formal test can be performed against this model as a null hypothesis. All three models, Ricker, Beverton-Holt and Shepherd, can, however, be tested against the null model of the line of constant proportionality discussed above, the line passing through the origin and the geometric mean of the data.

The first step in determining if there is any relationship between stock and recruitment is to fit a simple model to check whether there is a significant upward or downward trend to R with S. The simplest model is Cushing's and this is examined first. An upward trend ($\ln R$ linear in $\ln S$ with positive slope) indicates that the data are on the left-hand arm of a conventional stock-recruitment relationship and that it may be worth pursuing another model to find a better fitting curve. A downward trend (negative slope of $\ln R$ with $\ln S$) is not itself an admissible stock-recruitment relationship, but could indicate that the data are on the right-hand arm of a domed stock-recruitment curve, and thus supercompensation can be identified. The null hypothesis that recruitment is directly proportional to stock levels should be tested against the Cushing alternative.

The next step, even where the first fails to identify statistical significance, is to determine if a dome-shaped relationship is indicated. Because formal statistical tests can be done, it is most convenient to investigate the Ricker and Saila-Lorda equations at this stage. Difficulties may be experienced if the data suggest that a convex function should be fitted to the data. Although the Saila-Lorda (and also Shepherd) equation can be convex and decreasing over a range of stocks to the right of the maximum, the best-fitting equations are sometimes inadmissible. This indicates that some other form of stock-recruitment curve, not described in this review, should be used or some additional external factors should be included in the model.

The third step is to investigate whether the Beverton-Holt equation or its generalization, the Shepherd equation, gives the best fitting model. This determines whether the data rise to an asymptote, with no significant indication of a dome. Since neither model is a generalization of the Cushing, Ricker or Saila-Lorda family of curves, only informal comparisons of the error sums of squares can be made to help in deciding which model best describes the data. The evidence for an asymptote can, however, be formally tested by comparison of Beverton-Holt and Shepherd equations.

The final choice of model is thus not completely straightforward, because of the limitations of the formal statistical tests that can be done. However, it is almost always the case that one particular model emerges as the best fit. The sense in which a model is selected is that 1. it has an error sum of squares that is at least close to the minimum of all models fitted, that 2. it has admissible parameter values all of which are significantly different from 0, and 3. it complies with the principles of Occam's razor in that it is the simplest plausible fit to the data. Once this best curve is identified it is useful also to calculate confidence bands for the curve. The curve and the associated confidence bands are then displayed on a stock-recruitment diagram.

A method of calculating these confidence bands for models fitted by linear regression using statistics routinely calculated by standard statistical packages is given by Fry (1993). The essence of the method is to multiply the estimate of the standard deviation of the prediction at stock level S by a suitable factor (discussed below) to give upper and lower limits for the confidence interval of the prediction of R at S. The same calculation is repeated for a range of values of S. The upper limits of these intervals are then joined up to give the upper edge of the confidence band and similarly the lower limits give the lower edge. It is convenient to use the observed values of S used for fitting the curve for these calculations since the necessary statistics are usually easily obtained from standard statistical packages.

The variance of the prediction at the ith observed value S_i of stock size is simply the leverage h_i multiplied by the error mean square s^2. Where a statistical package is used for fitting the model both of these statistics are usually easily available. The statistic s^2 is obtained from the analysis of variance table used for testing the model. The leverages h_i are now in common use as diagnostic statistics, so these also are usually calculated by the package. The use of leverages as diagnostics is described, for example, by Fry (1993) and Rawlings (1988). The latter gives a formula, in matrix notation, for h_i. The calculation of leverages in non-linear regression is slightly more complicated. Amongst those packages that have a routine for fitting non-linear regression equations, SAS has an option for calculating leverages. The manual (SAS, 1987) gives the formula. Seber & Wild (1989) give a formula for the calculation of the hat matrix, and the leverage h_i is the ith diagonal element of this matrix.

The factor by which the standard deviation of the prediction is multipled to give the confidence interval is often chosen to be a Student's t percentile with degrees of freedom equal to the number of data minus the number of parameters in the stock-recruitment model. The theory underlying the use of this percentile shows that it gives a confidence interval with the correct confidence coefficient only if it is used for a prediction at a single value of S. One way of obtaining accurate simultaneous intervals for a range of values of S is Scheffé's method. In this method the factor is

$$\sqrt{pF_{p,\,n-p}}$$

where p is the number of constants in the model, n the number of data and F is the appropriate percentile of the F distribution. Thus the confidence interval for the prediction $\hat{R}_i$ of recruitment at stock level S_i is:

$$\hat{R}_i \pm \sqrt{pF_{p,\,n-p}s^2 h_i}$$

Miller (1981) discussed the calculation of simultaneous confidence intervals in linear regression. The formulae given above was derived for the case of linear regression, but the same formula is used as an approximation in nonlinear regression. The approximation depends on the extent to which the linear approximations used to solve the non-linear regression problem are accurate.

One of the difficulties of using non-linear regression methods is that convergence to the globally optimum solution is not guaranteed, and it is important to have initial estimates of the parameters that are close to those giving the equation of best fit. For the Beverton-Holt equation good starting values can be obtained by regressing S/R on S. The intercept of this regression is an estimate of the parameter b and the slope is an estimate of a. The values of a and b from the best-fitting Beverton-Holt equation together with a value for the third parameter c slightly different from 1 ($c \approx 1.5$) often gives convergence for the Shepherd model. Parameter estimates obtained from fitting the models after a logarithmic transformation are usually easy to obtain. For the Cushing, Ricker and Saila-Lorda equations no initial values are needed since the models are linear after logarithmic transformation. The estimates from these are then good initial values if fits to the untransformed versions of the model are investigated.

6. INCORPORATION OF ENVIRONMENTAL VARIABLES IN THE *S-R* RELATIONSHIP

If it is felt that environmental factors may influence the recruitment process it is prudent to investigate this possibility by incorporating the factors in the model. In this review attention will focus on those factors that can be quantified, and how they can be included in the model in the form of an additional component on the right-hand side of the model. Beverton & Iles (1992b) described some aspects of the incorporation of such additional components in the model. Fargo (1994) also discusses models including both stock and environmental variables.

Environmental variables can only moderate recruitment, they cannot themselves cause recruitment, only stocks can do that. Thus a formulation that allows positive recruitment to be predicted by the

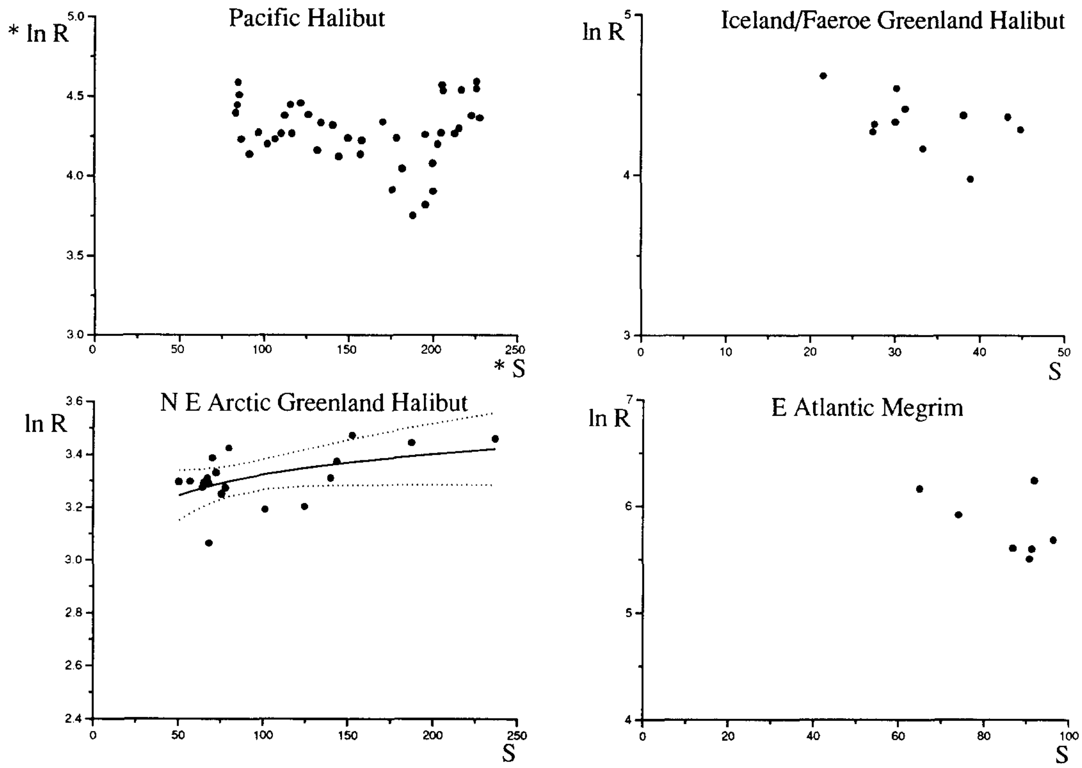


Fig. 1. Stock-recruitment diagrams for 20 flatfish stocks. Where a plausible relationship other than constant recruitment or a proportional line is identified it is shown on the diagram together with 95% confidence bands. For units see Table 1. All curves were fitted using the simple regression methods described in the text with the MINITAB statistical package.

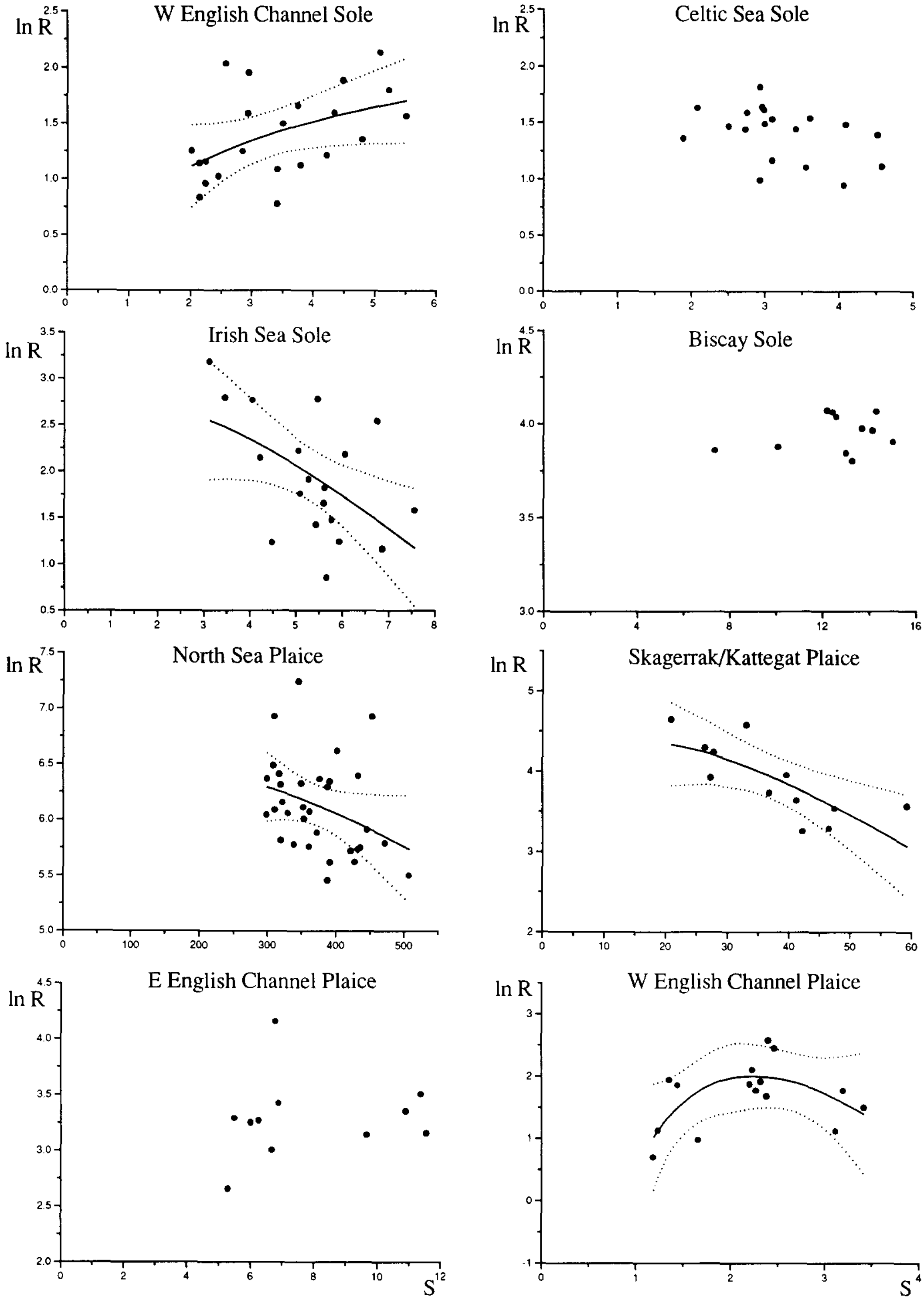
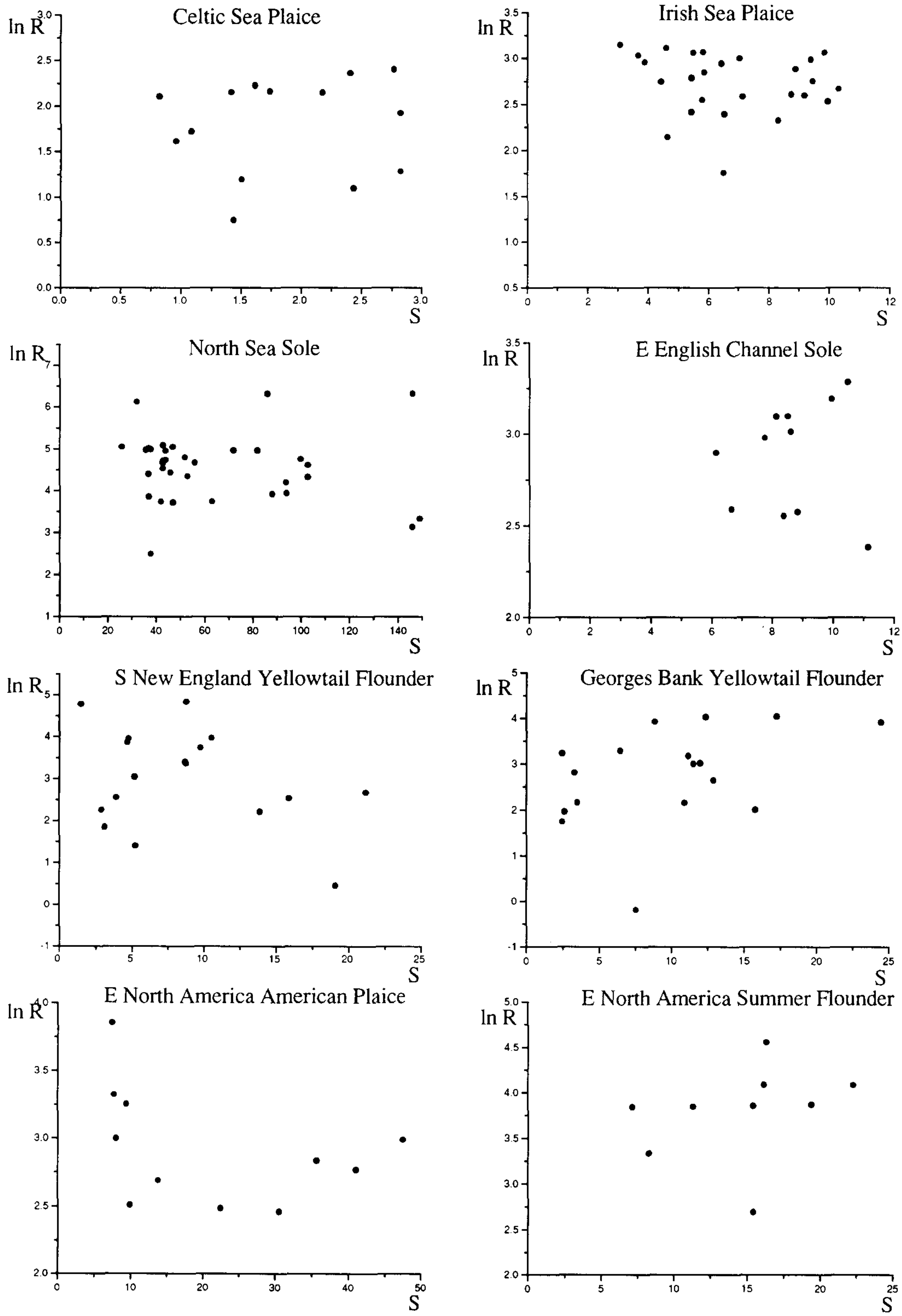


Fig. 1 (continued).


Celtic Sea Plaice
ln R
S
Irish Sea Plaice
ln R
S
North Sea Sole
$\ln R_7$
S
E English Channel Sole
ln R
S
S New England Yellowtail Flounder
$\ln R_5$
S
Georges Bank Yellowtail Flounder
ln R
S
E North America American Plaice
ln R
S
E North America Summer Flounder
ln R
S

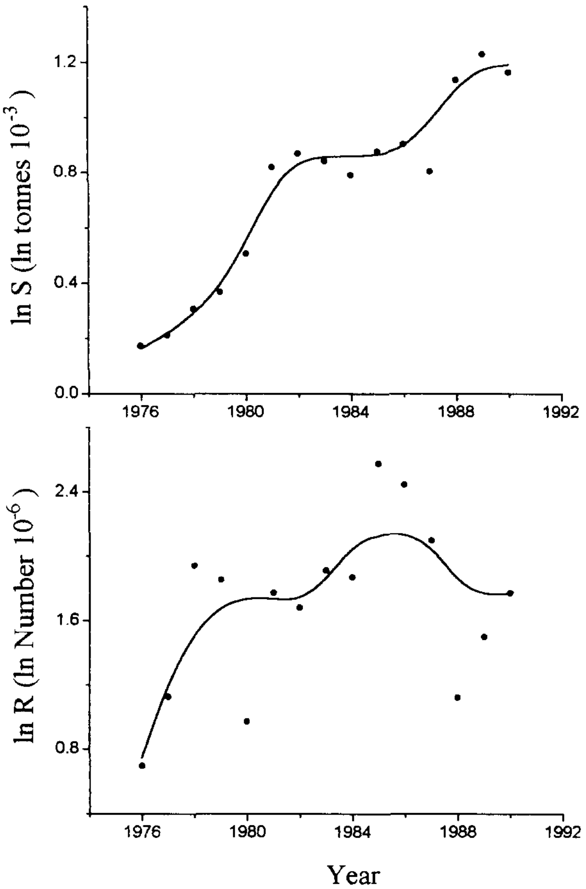


Fig. 2. Time series of logarithms of recruitment R and stock size S for western English Channel plaice.

environmental variable alone, with stocks equal to zero, is inadmissible in stock-recruitment investigations. Thus additive functions of the type:

$$R = f(S) + g(E)$$

where E is some function of environmental variables, are inadmissible. A model of the kind:

$$R = f(S) \cdot E^q$$

or, in logarithmic form:

$$\ln R = \ln f(S) + q \ln E$$

is a simple admissible form of stock-recruitment relationship incorporating a single environmental variable, and it is models of this form or of the form:

$$\ln R = \ln f(S) + rE$$

that will be investigated here. These models allow a simple statistical test to be made that the environmental variable has no significant effect on recruitment when allowance is made for the changing stock size since the null hypothesis $q=0$ or $r=0$ can be tested using the change in the error sum of squares as a criterion.

Hilborn & Walters (1992) have counselled caution in the incorporation of environmental variables in the stock-recruitment model using this approach. They have suggested that judicious choice of an environmental variable from many possibilities can be used to explain inconvenient departures from the stock-recruitment curve. This may be the case, but it is also true that a failure to take into account those variables that for biological reasons are known to affect recruitment will lead to models that are poor in explaining observed variation.

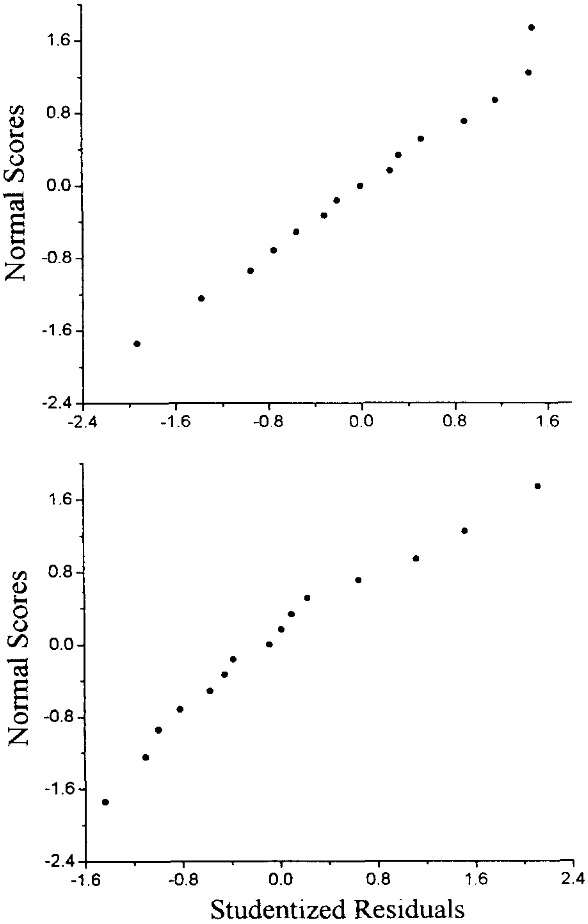


Fig. 3. Normal score plots for studentized residuals from Saila-Lorda equations fitted to log$R$ (top) and R (bottom) for the western English Channel plaice stock.

TABLE 4
Error sums of squares for western English Channel plaice. For explanation see text.

name	*df*	*ss*	*ms*	*F*	*p*
total	14	3.8919	-	-	-
proportional line P	14	3.7684	-	-	-
Cushing C	13	3.4162	0.2628	1.81	0.201
Ricker R	13	3.1998	0.2461	-	-
Saila-Lorda SL	12	2.2497	0.1875	4.38	0.037
Beverton-Holt BH	13	3.3155	0.2550	-	-
Shepherd Sh	12	2.3970	0.1998	-	-
C-SL	1	1.1665	1.1665	6.22	0.028
R-SL	1	0.9501	0.9501	5.07	0.045
BH-Sh	1	0.9185	0.9185	4.60	0.053
P-C	1	0.3522	0.3522	1.34	0.268
P-R	1	0.5686	0.5686	2.31	0.153
P-SL	2	1.5187	0.7594	4.05	0.045
P-BH	1	0.4529	0.4529	1.78	0.206
P-Sh	2	1.3714	0.6857	3.43	0.066

7. EXAMPLES

7.1. WESTERN ENGLISH CHANNEL PLAICE

This data set has been chosen for the first example since there is strong evidence of a dome-shaped relationship (see Fig. 1). It is therefore a good illustration of the step-by-step approach outlined. Fig. 2 gives time-series plots for $\ln R$ and $\ln S$ for this stock. It is clear from this plot that deviations of $\ln S$ from its trend line were small compared with those for $\ln R$. The standard deviations of the differences from the trend line were 0.064 for $\ln S$ and 0.353 for $\ln R$, so there is considerable evidence from these data that errors in measurement of R are large in comparison with those of S, and that therefore application of the models described in Section 4 is reasonable.

Table 4 gives a summary of all of the error sums of squares and associated statistical tests. All the models were fitted to the logarithms of recruitment, for reasons discussed below. It is not suggested that all these test statistics need to be formally calculated and reported in every investigation; the complete details for this data set are included for illustration only.

The first part of the table gives the error sums of squares for all models together with the standard F-test for the null hypothesis that recruitment is constant in the two cases where this is appropriate (Cushing and Saila-Lorda). Clearly the Saila-Lorda model gave the smallest error sum of squares, and this was significantly different from the error sum of squares for the null model of constant recruitment ($p=0.037$). The estimates of the parameters of this fitted equation and their standard errors are included in Table 8. All parameters were significantly different from zero. This confirms that a domed relationship is indicated for these data. Although the Shepherd equation was almost as successful in explaining these data as the Saila-Lorda, on the basis of the error sum of squares, the parameter c was estimated as 9.76 with standard error 10.25, so this equation would give similarly close fits for a wide range of parameters. This is not important if all that is sought is the set of parameters giving the closest fit, but would influence any interpretation of the parameters.

The next part of Table 8 using the methods outlined in Fry (1993) shows that the Saila-Lorda equation provided a significantly better fit than both the Cushing and Ricker equations. In both these comparisons the denominator for the F test is the error mean square for the Saila-Lorda fit. The next line shows that the Shepherd equation had an error sum of squares that was very close to being significantly smaller than that of the Beverton-Holt equation ($p=0.053$). This suggests that the hypothesis of an asymptotic relationship is somewhat questionable. Finally all of the equations are compared with the proportional line model. The correct denominators for these tests are the mean square for the model with which the proportional line is being compared. It can be seen that the Saila-Lorda model gave a significant improvement in error sum of squares ($p=0.045$).

Overall, therefore, there is little doubt that a dome-shaped relationship is indicated by these data, and that the Saila-Lorda equation gives the best fit. No outliers or lever points are indicated, using as criteria for unusual observations those given, for example, in Fry (1993). The curve and associated Scheffé confidence bands are included on the stock-recruitment

TABLE 5
Error sums of squares for North Sea plaice. For explanation see text.

name	*df*	*ss*	*ms*	*F*	*P*
total	32	5.7326	-	-	-
proportional line	32	7.7251	-	-	-
Cushing	31	5.0809	0.1639	3.98	0.055
Ricker	31	5.0833	0.1640	-	-
Saila-Lorda	30	5.0786	0.1693	1.93	0.162
Beverton-Holt	31	5.0951	0.1644	-	-
Shepherd	30	5.0806	0.1694	-	-
temperature alone	31	4.8655	0.1570	5.52	0.025
temperature + Ricker	30	4.2761	0.1425	-	-
difference	1	0.5894	0.5894	4.14	0.051
phosphate alone	31	5.2599	0.1697	2.79	0.105
phosphate + Ricker	30	5.0304	0.1677	-	-
difference	1	0.2295	0.2295	1.37	0.251
temperature + phosphate + Ricker	29	4.2747	-	-	-

diagram (Fig. 1).

Fig. 3 gives the normal score plots for the studentized residuals of this Saila-Lorda equation fitted to ln$R$ and R, respectively. It is evident that there was somewhat greater curvature in the residuals from the fit to R, indicating that a log-normal model was more realistic than the usual normal model, and that fits should be made to the logarithmically transformed data.

7.2. NORTH SEA PLAICE

This example has been chosen since data are available for two environmental variables that it has previously been suggested may influence recruitment. These are the February temperatures at Den Helder, The Netherlands (Zijlstra & Witte, 1985; Van der Veer, 1986), and the phosphate loads in the river Rhine (Boddeke & Hagel, 1994).

Ignoring the environmental data for the moment, an analysis of the stock and recruitment data (illustrated in Fig. 1) can be done following the outlines illustrated in western English Channel plaice. Errors can be assumed to be associated with R rather than S (see Table 3 for confirmation), but the conclusions from the attempts to fit different models are somewhat different. Details of the error sums of squares of the fitted models are given in Table 5. There was little with which to differentiate between them using the error sums of squares, but the parameter values of the best-fitting equations indicated that both the Saila-Lorda and Beverton-Holt fits were inadmissible, because of negative parameter values. The coefficient $\hat{\gamma}$ of the best-fitting Cushing equation was also negative and therefore inadmissible. The data indicated that recruitment was generally slightly smaller at the larger stock sizes. In fitting the Saila-Lorda equation it was evident that there was a difficulty with multicollinearity of the predictor variables S and ln$S$. Over the rather restricted range of S observed for this population S and ln$S$ were very close to being linearly related. Therefore and because of the multicollinearity, it was not possible to identify a value for the parameter γ of the Saila-Lorda equation. The (admissible) Ricker and (inadmissible) Cushing equations were informally little different in predictive power, having very similar error sums of squares. The Cushing equation had a parameter γ that was close to being statistically different from zero ($\hat{\gamma}$=-0.99, standard error 0.49, p=0.055). Tentatively therefore it is reasonable to suggest that these data were on the right-hand arm of a domed stock-recruitment relationship, probably best described by a Ricker equation. This equation and the associated confidence bands are plotted in Fig. 1. The suggestion of a domed stock-recruitment relationship has to be tentative because the significance level is not low, and Walters (1985, 1990) suggested bias in stock-recruitment data would lead to a downward tilt of the fitted curve.

It was evident from the plot and can be shown by an analysis of the studentized residuals that there are two outliers, the 1963 and 1985 year classes. Both years were preceded by cold winters and in both cases the recruitment was exceptionally good. An analysis of the leverages indicated that the 1967 year class is an influential point, with high leverage. This single observation had a disproportionate influence on the conclusion that the data are on the right-hand arm of a stock-recruitment relationship. In fact the statistical significance of the parameter γ of Cushing's equation depended on the two years, 1967 and 1968, in which stocks were highest.

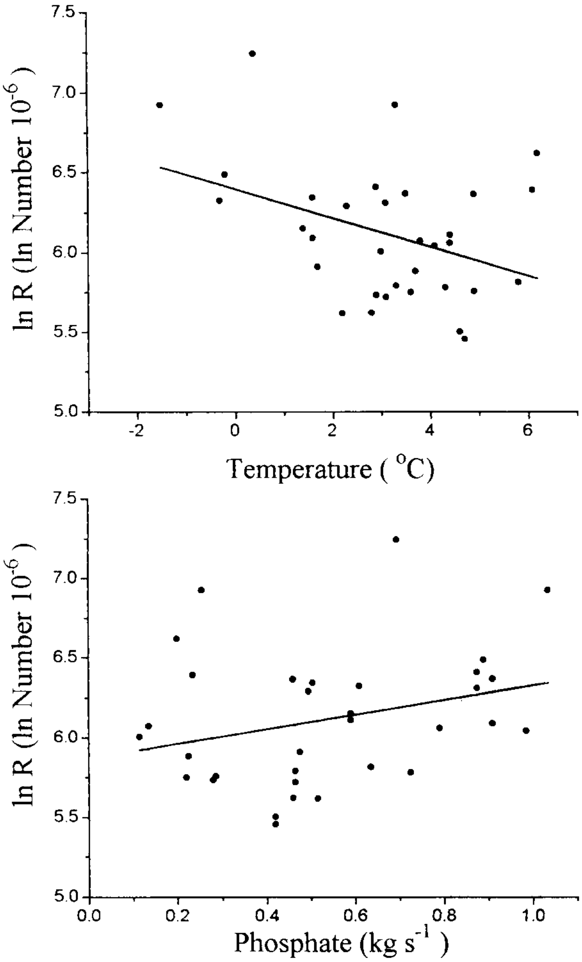


Fig. 4. Recruitment in North Sea plaice plotted against February temperature at Den Helder, The Netherlands (top) and phosphate loads in the river Rhine (bottom).

The bottom half of Table 5 gives error sums of squares and statistical tests associated with the inclusion of environmental variables in the prediction equation for recruitment. Fig. 4 shows that recruitment was negatively correlated with the February temperature at Den Helder. Table 5 shows the F ratio for the test of the null hypothesis that the slope of this relationship is zero. The p-value was small (p=0.025), so this hypothesis is rejected. Moreover there was some improvement in the Ricker stock-recruitment equation when temperature was included in the equation (p=0.051).

The relationship of recruitment to phosphate load is shown in Fig. 4. This relationship was not significant (p=0.105), but perhaps close enough to warrant further work. The difference between the error sum of squares for the Ricker model and that of the same model with phosphate included was not statistically

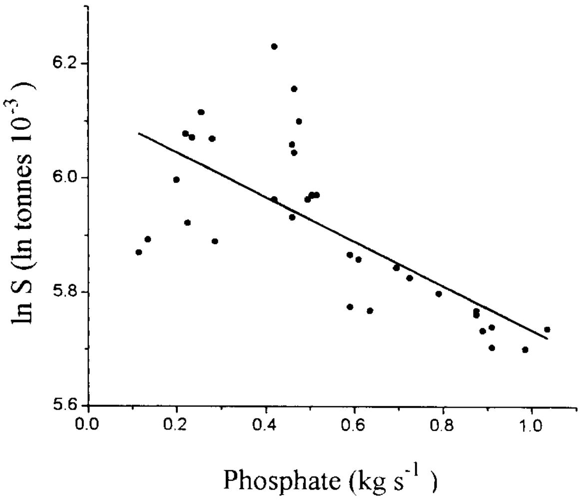


Fig. 5. Stock size in North Sea plaice plotted against phosphate loads in the river Rhine.

significant (p=0.251). Thus it is possible that the weak relationship of recruitment with phosphate was generated by a statistical relationship between stock levels and phosphate. Fig. 5 shows the scatter plot of these data. There was a strong negative correlation (p<0.0005) between stock size and phosphates. It is not suggested that there can be biological reasons for this correlation; it is more likely that it can be explained by coincidental time trends. Neither was the correlation strong enough on the basis of the variance inflation factor (see Fry, 1993, p. 158, but see footnote*) to indicate problems of multicollinearity in the multiple regression. However, the apparent relationship between recruitment and phosphate (or any suggested relationship between phosphate and the recruitment success rate *R*/S) is questionable in view of the statistical association between stock size and phosphate loads.

Stock size was not, however, related statistically to temperature, and the fact that the Ricker equation remained a plausible explanation for variability in recruitment even when allowance was made for temperature strengthens the conclusion that the dome-shaped stock-recruitment relationship is genuine for this stock.

7.3. PACIFIC HALIBUT

This data set, illustrated in Fig. 1, has been included because although the search for a viable stock-recruitment curve is fruitless, it shows that for some data a time series model may contain useful informa-

*There is an error in this author's chapter in Fry's book on page 158. The variance inflation factor should be defined as the reciprocal of (1-R^2).

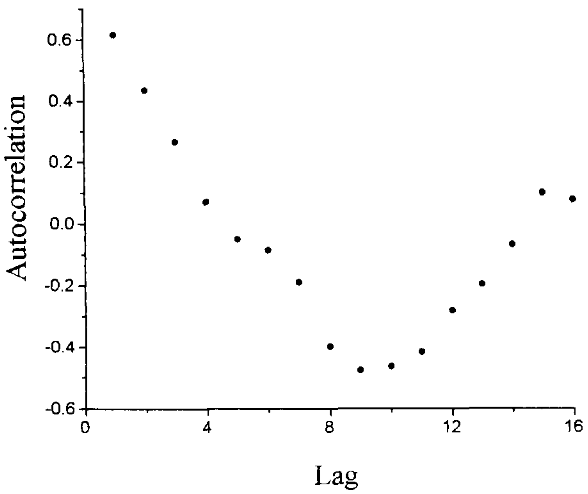


Fig. 6. Autocorrelation function for the logarithm of recruitment for Pacific halibut. Time lag in y.

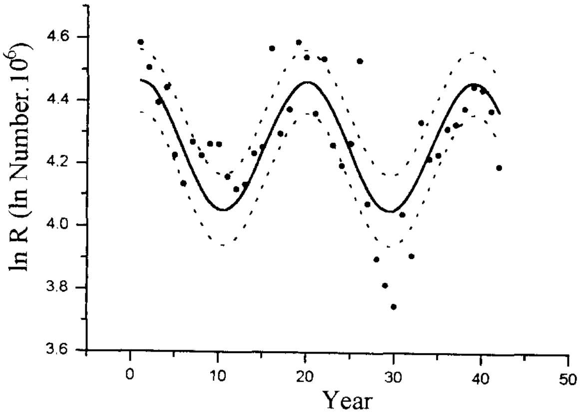


Fig. 7. Time series plot of the logarithm of recruitment for Pacific halibut together with fitted curve of period 19 years and 95% confidence bands.

tion. Table 6 summarizes the error sums of squares for the different models. Although the Saila-Lorda equation had an error sum of squares that indicated that the parameter values were strongly significantly different from zero, the estimate of the parameters β and γ were both negative, so the equation was inadmissible. Although this equation can in principle be fitted to the data, it could not be further interpreted as a stock-recruitment relationship other than giving an estimate of average recruitment over the range of observed stocks. The best-fitting Beverton-Holt and Shepherd equations were similarly both inadmissible. The error sum of squares for the best-fitting Ricker equation was greater than the total sum of squares, indicating that this was not a plausible model for these data. It is in such cases that care has to be exercised in interpreting the significance tests for individual parameters. The parameters $\ln\alpha$ and β of the Ricker equation were estimated as 0.40 and 0.0072, respectively, with standard errors 0.12 and 0.0007 and associated p values (for the null hypothesis that each is zero) of 0.001 and <0.0005. However, the null model for the Ricker equation was the line of proportionality and, as can be seen from the very large error sum of squares for this model, this was completely implausible for these data. These significance tests therefore did not indicate that a Ricker model should be fitted to these data.

The Durbin-Watson test for these data, whichever equation is fitted, indicated strongly significant autocorrelation at a lag of one year. The complete autocorrelation function for $\ln R$ is plotted in Fig. 6 and not only does this show that the data were autocorrelated, but also that there was a periodic variation of recruitment in time with a period of about 19 y. The curves plotted in Fig. 7 are a sine/cosine curve with period 19 y, together with a calculated confidence band. This confidence band does not, however, take into account errors in the estimation of the period of the fitted equation. Hilborn & Walters (1992) suggested that recruitment to the Pacific halibut stock is strongly periodic though the data they analysed are not quite the same series as that presented in this review. The period of their suggested relationship is very close to 19 y. Cabilio *et al.* (1987) showed that for a number of fish stocks in the New England-Fundy and Grand Banks areas off the east coast of North America there was a strong link between the 18.6 y nodal cycle of the tides and catches. These periodic patterns are not stock-recruitment relationships in the classical sense. Presumably the periodicity is caused

TABLE 6

Error sums of squares for Pacific halibut. For explanation see text.

name	*df*	*ss*	*ms*	*F*	*p*
total	41	1.6440	-	-	-
proportional line	41	7.0531	-	-	-
Cushing	40	1.6107	0 0403	0.83	0.369
Ricker	40	1.9916	0.0498	-	-
Saila-Lorda	39	1.3414	0.0344	4.40	0.019
Beverton-Holt	40	1.5849	0.0396	-	-
Shepherd	39	1.5023	0.0385	-	-

TABLE 7
Summary of analyses of other flatfish stocks (null model of constant recruitment). YC=year class.

species	*stock*	
Greenland halibut	Arctic	*R* increasing significantly with *S* (p=0.032 for Cushing) Ricker worse than Cushing, Beverton-Holt and Shepherd little better, Saila-Lorda inadmissible
Greenland halibut	Faroes	No fitting attempted. Large variation in *S* around trend line
megrim	Atlantic	No plausible relationship. One high outlier (1988 YC)
plaice	Skagerrak	*R* decreasing significantly with increasing *S* (p=0.002 for Cushing). Ricker worse than Cushing, others inadmissible
plaice	E. English Channel	No plausible relationship - One high outlier (1985 YC)
plaice	Celtic Sea	No plausible relationship - No outliers
plaice	Irish Sea	No plausible relationship - No outliers
sole	North Sea	No plausible relationship. Three high outliers (1958, 1963, 1987 YC's) one low outlier (1978 YC). Two influential YC's (1961, 1962). *R* negatively related to March temperature at den Helder, but outliers not explained.
sole	E. English Channel	No plausible relationship. One low outlier (1987 YC)
sole	W. English Channel	*R* increasing significantly with *S* (p = 0.023 for Cushing). Others little better than Cushing, Saila-Lorda inadmissible
sole	Celtic Sea	No plausible relationship. One high outlier (1982 YC) one low outlier (1985 YC)
sole	Irish Sea	*R* decreasing significantly with increasing *S* (p = 0.010 for Cushing). Ricker worse than Cushing. Others inadmissible
sole	Biscay	No plausible relationship
yellowtail	S. New England	No plausible relationship. One high outlier (1980 YC)
yellowtail	George's Bank	No plausible relationship. One low outlier (1989 YC)
American plaice	E. North America	No plausible relationship. Some very high R at low S
Summer flounder	E. North America	No plausible relationship. One low outlier (1988 YC)

by external factors. For the Pacific halibut data it has not proved possible to identify an admissible stock-recruitment relationship after the periodic component was removed from the recruitment data.

7.4. OTHER POPULATIONS

There is insufficient space to describe here detailed analyses for the other flatfish stocks for which data are available, but an outline of the findings completes the picture of this survey of recruitment in flatfish populations. Fig. 1 gives the stock-recruitment diagrams for all these stocks, together with the fitted stock-recruitment curve and confidence bands where such a curve can be identified. In Table 8 some values of fitted parameters and standard errors are given with a brief summary of the results of the procedures outlined in this review in Table 7 for testing a stock-recruitment relationship against the null model of constant recruitment.

In a further four out of the 20 stocks for which data are available some form of statistically significant relationship could be detected, using the traditional value of a significance level of 0.05 as the criterion for statistical significance. Of the 20 stocks, only in 11 cases were 15 or more pairs of data available and in 5 of these 11 stocks a statistically significant stock-recruitment-relationship had been identified. It is therefore generally in the stocks for which few data are available that a relationship has not been shown to exist. In several of the other data sets for which stock-recruitment relationships have not been identified, the omission of one or two extreme outliers, usually with exceptionally high recruitment, would enable

TABLE 8
Parameters and standard errors in best-fitting admissible stock-recruitment relationships.

species	*stock*	*fitted curve*	$\ln\hat{\alpha}$	*SE* $\ln\hat{\alpha}$	$\hat{\beta}$	*SE* $[\hat{\beta}]$	$\hat{\gamma}$	*SE* $[\hat{\gamma}]$
Greenland halibut	Arctic	Cushing	2.799	0.220	-	-	0.114	0.049
plaice	North Sea	Ricker	2.150	0.490	0.0052	0.0013	-	-
plaice	Skagerrak/Kattegat	Ricker	2.558	0.358	0.0602	0.0092	-	-
plaice	western English Channel	Saila-Lorda	3.123	0.782	2.622	1.051	5.890	2.172
sole	western English Channel	Cushing	0.702	0.294		-	0.587	0.239
sole	Irish Sea	Ricker	2.989	0.666	0.507	0.122	-	-

TABLE 9

Statistics for testing of stock-recruitment relationships. *The suggestion here of a model of constant recruitment independent of stocks is not intended to imply that this relationship can be extrapolated beyond the observed stock levels. It is an inadmissible relationship (see text). All the other suggested relationships are admissible. n is the number of deviations. SRR is stock-recruitment relationship.

species	*stock*	*n*	*error sum of squares*				*F-tests*		
			proportional line	*constant recruitment*	*Cushing*	*other SRR*	*prop. line vs Cushing F*	*P*	*suggested SRR**
halibut	Pacific	42	7.053	1.644	1.611	-	135.15	<.0005	constant
Greenland halibut	Arctic	19	2.851	0.183	0.139	-	332.54	<.0005	Cushing
Greenland halibut	Faroes	11	No fitting attempted. Large variation in *S* around trend line						
megrim	Atlantic	7	0.899	0.515	0.377	-	6.93	.039	constant
plaice	North Sea	33	7.725	5.733	5.081	5.083	16.13	<.0005	Ricker
plaice	Skagerrak/Kattegat	12	5.880	2.412	0.854	1.119	58.85	<.0005	Ricker
plaice	E. English Channel	11	1.865	1.308	1.348	-	3.83	.082	constant?
plaice	W. English Channel	15	3.768	3.892	3.416	2.250	1.34	.268	Saila-Lorda
plaice	Celtic Sea	14	5.362	3.625	3.602	-	5.87	.032	constant
plaice	Irish Sea	26	6.864	2.823	2.705	-	36.90	<.0005	constant
sole	North Sea	34	32.344	22.028	21.761	-	15.56	<.0005	constant
sole	E. English Channel	11	1.154	0.916	0.911	-	2.41	.055	constant?
sole	W. English Channel	22	2.864	3.245	2.490	-	3.00	.099	Cushing
sole	Celtic Sea	19	2.755	1.030	0.891	-	35.54	<.0005	constant
sole	Irish Sea	19	11.654	7.683	5.125	5.775	21.65	<.0005	Ricker
sole	Biscay	11	0.387	0.100	0.091	-	29.09	<.0005	constant
yellowtail flounder	S. New England	17	38.036	22.038	20.341	-	13.05	.003	constant
yellowtail flounder	George's Bank	17	18.045	18.417	16.040	-	1.88	.191	?
American plaice	E. North America	11	10.311	1.810	1.344	-	60.06	<.0005	constant
summer flounder	E. North America	9	2.510	2.199	2.045	-	1.59	.248	?

statistically significant curves to be fitted. On the other hand there were other cases, notably the North Sea plaice data, where one or two years with high stock levels caused the relationship to be significant. In this review all available data have been included in the analysis, and neither outliers nor lever points have been omitted in identifying the best-fitting curves.

In showing that the six stock-recruitment relationships described above were statistically significant, the models were tested against the null model of constant recruitment, independent of stock size. Such a model implies a degree of density dependence, with strong compensation giving a stable average recruitment even at lower levels of stock size. It is an inadmissable stock-recruitment relationship in the sense discussed because it assumes positive recruitment when stocks are zero. The null model of no density dependence is one of recruitment proportional to stock size ($R = \alpha S$) and it is appropriate also to test this model as a null hypothesis.

Table 9 summarizes the statistical evidence for and against the different types of model. Error sums of squares are tabulated for the models of a proportional line, constant recruitment and the best-fitting Cushing's equation. For those stocks where a form of stock-recruitment curve other than one of these three had been identified as the appropriate model the error sum of squares of this model is also tabulated. The F-statistic and associated p-value are given for testing Cushing's model against the null hypothesis of a proportional line. No formal test statistics have been tabulated for a comparison of the proportional line with the model of constant recruitment since they are non-nested models.

The statistics in Table 9 indicate that in eight cases (Pacific halibut; Celtic Sea and Irish Sea plaice; North Sea, Celtic Sea and Biscay sole; Southern New England yellowtail flounder and Eastern North American American plaice) the hypothesis of a proportional line was rejected in favour of Cushing's equation (with $p < 0.05$), and the error sum of squares for the model of constant recruitment was similar to that of Cushing's equation. Since for these cases the error sum of squares for Cushing's equation was not significantly smaller than that of constant recruitment, the indicated model for these stocks was one of constant recruitment over the range of observed stock size. This was an inadmissable model, and it cannot be assumed that the same level of recruitment would be observed were stock levels to fall below or rise above those observed in the past. In two further cases (Atlantic megrim and eastern English Channel plaice) the error sum of squares for the model of constant recruitment was somewhat less than that of the proportional line, but the difference was not so large that the former model was strongly indicated. Finally, in the cases of the George's Bank yellowtail flounder and the eastern North American summer flounder, there was little to choose between the two models.

8. DISCUSSION

The identification of plausible stock-recruitment relationships differing from the null model of constant recruitment in as many as six of the 20 stocks for which data are available is strong evidence that the general hypothesis that recruitment is not related to stock size should be rejected. Further evidence for the presence of some form of stock-recruitment relationship is the indication that in at least eight further stocks a model of recruitment varying about a constant level independent of stocks is preferred to a model of recruitment directly proportional to stocks. Recruitment is bound to be zero at zero stock size, so the model of constant recruitment is inadmissible over all stock sizes. Thus where such a model is indicated as the most satisfactory one over the observed range of stocks, there is bound to be some form of underlying stock-recruitment relationship. The failure to identify this relationship could either be because changes in recruitment would only become apparent outside of the observed range of stock size, or extraneous causes of variability have affected recruitment and have not been allowed for in fitting the relationship.

Only limited data were available to the author on biologically justifiable environmental variables that might be included in the stock-recruitment relationship in the hope of explaining the variation in recruitment. In one case, the North Sea plaice stock, one of these environmental variables, February temperature, significantly improves the stock-recruitment relationship, and goes some way in explaining the outliers. For the sole stock in the same area it is the March temperature that is most closely correlated with recruitment but this variable does not significantly improve the stock-recruitment relationship, and indeed no admissible relationship can be found for this stock with the data available. Rijnsdorp *et al.* (1991) have, however, pointed out that for this stock the low recruitment of the 1961, 1962 and 1978 year classes could be related to the severe winters of 1963 and 1979.

Beverton & Iles (1992b) reported some investigations of some non-pleuronectiform stocks and these findings will be published elsewhere. Many other authors have reported stock-recruitment relationships and the general rule would appear to be that recruitment decreases at low stock size or approaches an asymptotic value at high S. There are notable exceptions, in particular the dome shaped relationships in the stock of Windermere perch in north-western England (Mills & Hurley, 1990), and for migratory trout in a river in the same area (Elliott, 1984). It is striking amongst the flatfish stocks considered here that one stock, the western English Channel plaice, shows a definite dome and four of the others indicate the possibility that they are the right-hand arm of such a domed relationship. It is also striking that in at least eight further cases, recruitment varies about a level that is independent of the stock size.

This finding for flatfish stocks may seem to conflict with an earlier investigation of flatfish stocks (Beverton & Iles, 1992a). It was shown, by establishing a relationship between the mortality rates in 0-group plaice and the logarithm of the maximum number of fish in the 0-group population as an index of abundance, that mortality is density-dependent. Beverton & Iles (1992a) went on to suggest that this relationship is consistent with a Cushing type of stock-recruitment relationship, but should not be generalized to the stock-recruitment relationship for the adult stock. There is in any case considerable variation about the mortality/abundance relationship of the earlier paper so a domed form of stock-recruitment relationship may be consistent with that earlier work.

This review has shown that the direct approach to stock-recruitment relationships has potential value despite all the doubts that have been expressed about the process. The value of statistical models is that a plausible curve can be fitted to the data and justified by formal statistical tests. Perhaps more importantly the degree of uncertainty in the model can be expressed by calculating the confidence bands for the fitted curve. Fargo (1994) gave another similar approach to the investigation of stock and recruitment simultaneous with environmental effects. His analysis, using a response surface method, has the advantage of flexibility but the disadvantage that the fitted model is purely empirical. The stock-recruitment models used in this review have some basis in the theory of fisheries population dynamics (Harris, 1975; Rothschild, 1986). Fargo's (1994) approach would be valuable for a preliminary investigation to determine if further work should be done to identify a particular type of stock-recruitment relationship using the methods outlined in this review.

Another method of analysis that has been suggested for stock and recruitment data is the time series approach of integrated auto-regressive moving average (ARIMA) models (Box & Jenkins, 1970). Such methods are useful for the purposes of forecasting of future stocks, and perhaps recruits. Kirkley *et al.* (1982) give a typical application of the approach in fisheries research. Although these methods are very flexible and are designed to model the autocorrelation structure of the data, they do not incorporate a stock-recruitment relationship of the form discussed in this review and do not describe the structure of the relationship between stock and recruitment. Knowledge of the time dependence of stock and recruitment data may, however, assist the interpretation of data.

Because the dynamics of fish stocks are subject to changes in time, particularly due to fishing pressure but perhaps also pollution and other environmental effects, it may be the case that a particular stock will exhibit different stock-recruitment relationships over different periods of time. By looking at the sequence of data in time it may be possible to identify when such changes occur and it might be useful to include the numbers indicating the year classes on the stock-recruitment diagram.

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APPENDIX 1

FITTING A LINE OF CONSTANT PROPORTIONALITY TO THE LOGARITHMS OF RECRUITMENT

The line of constant proportionality is

$$R = \alpha S$$

After logarithmic transformation and inclusion of the random component this becomes

$$\ln R = \ln \alpha + \ln S + \varepsilon.$$

The least squares estimate of $\ln \alpha$ is the value that minimizes

$$\Sigma \varepsilon^2 = \Sigma(\ln R - \ln \alpha - \ln S)^2$$

that is,

$$\ln\hat{\alpha} = \overline{\ln R} - \overline{\ln S}$$

where $\overline{\ln R}$ and $\overline{\ln S}$ denote respectively the mean of the logarithms of R and S. When retransformed by exponentiation this gives the line passing through the geometric mean of the data with slope unity. Regression is not needed to fit the equation to data, the parameters are completely determined by the means of $\ln R$ and of $\ln S$. The model has one parameter, so the error or residual sum of squares, calculated from the formula

$$\Sigma(\ln R - \overline{\ln R} - \ln S + \overline{\ln S})^2$$

has n-1 degrees of freedom, where n is the number of data points.

If the random component of the stock-recruitment relationship is normally distributed with constant variance for R, and not $\ln R$, then the least squares fit is obtained by linear regression of R on S with the intercept term (usually referred to as the constant) excluded from the model. Most statistical packages have an option for doing this.

APPENDIX 2

FITTING THE RICKER MODEL USING SIMPLE LINEAR REGRESSION

Suppose that the random components of the model are independent and normally distributed with constant variance for the logarithms of R. The Ricker model, after logarithmic transformation is

$$\ln R = \ln\alpha - \beta S + \ln S + \varepsilon (1)$$

The maximum likelihood estimates of the parameters are those that minimize $\Sigma\varepsilon^2$ or

$$\Sigma(\ln R - \ln\alpha + \beta S - \ln S)^2$$

$$\Sigma(\ln R/S - \ln\alpha + \beta S)^2$$

and these are the estimates obtained by regressing lnR/S on S, in which the underlying model is

$$\ln R/S = \ln\alpha - \beta S + \varepsilon (2)$$

Thus the estimates of the parameters obtained from this regression are unbiased, as shown by Hilborn (1985). Since the residuals from model (2) coincide with those of model (1), the residual sum of squares and calculated residuals from the simple linear regression of $\ln R/S$ on S are also correct, and are identical with those that would be obtained from a non-linear regression fit using model (2) (excepting possibly for rounding error). The error mean square is thus the correct estimate of the variance σ^2 of the random component ε of the model. The theoretical variance of the estimate of β is $\sigma^2/S(S,S)$ where $S(S,S) = \Sigma(S-\overline{S})^2$ is the corrected sum of squares of the observed values of S, and this is also identical for both models. Similarly the theoretical variance of α is the same in both cases. Thus the confidence intervals for the parameters are also correctly calculated by a simple linear regression of $\ln R/S$ on S, but these in some cases may be misleading for a reason discussed below.

It is important to note, however, that the total sum of squares from model (2) $\Sigma(\ln R/S - \overline{\ln R/S})^2$ is not the same as that of model (1) $\Sigma(\ln R - \overline{\ln R})^2$ Hence the regression sum of squares from the simple linear regression of $\ln R/S$ on S is incorrect and the coefficient of determination R^2 calculated from this regression has no meaning and may be very misleading if interpreted in the usual way, as discussed in section 5. In fact since the Ricker model does not allow the special case of a model that $\ln R$ is constant, it is theoretically possible and sometimes happens in practice that the error sum of squares for the Ricker fit exceeds the sum of squares of deviations of the logarithms of recruitment R from the mean of the logarithms of R (the total sum of squares for $\ln R$). This is the reason why the R^2 statistic has no meaning. Ruppert & Carroll (1984) pointed out that R^2 values calculated from linearized versions of stock-recruitment curves should not be compared. In cases where a horizontal line has a smaller error sum of squares than the Ricker equation, the confidence interval calculated for the estimate of the parameter β is also liable to be misleading. It may indicate a value that is strongly significantly different from zero, but this is not for the null hypothesis that there is no relationship between stock and recruitment. Substitution of the value $\beta=0$ in the Ricker equation gives as null model a line proportional to R

$$R = \alpha S.$$

The total corrected sum of squares from the regression of $\ln R/S$ on S is the error sum of squares for this null model of a line proportional to R and passing through the geometric mean of the data. Hence the usual F test of this regression is a test of the Ricker equation against the null model of a proportional line.