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Stock and recruitment - again

D.J. GARROD

LOWESTOFT , 1982

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The author:

D J Garrod, B Sc Ph D, is Deputy Director of Fisheries Research and is Head of the Fish Stock Management Division of the Directorate of Fisheries Research. He is based at the Fisheries Laboratory at Lowestoft.

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1. Introduction

A number of stocks have suffered recruitment collapse during the last two decades. Environmental change has no doubt contributed to the collapse but in each case it has occurred under continued high levels of exploitation and at a time when the spawning stock has been reduced to relatively low levels. Estimation of the stock and recruitment relationship therefore remains a cause for concern. Ideally it should be based upon a definition of the biological mechanisms involved, but this does not appear to be a practicable solution for any stock in the foreseeable future. It therefore remains necessary to extract as much information as possible from the empirical analysis of time series data, bearing in mind the reality that any relationship so determined can only represent the average outcome of a very complex biological process. A return to this approach is justified by the evident need to find some acceptable description of the relationship, if only to capture its general form and the approximate magnitude of parameters as a basis for estimating sustainable yield (as opposed to yield per recruit) and for further development of multispecies models.

This paper therefore looks again at the empirical approach by applying a model developed by Shepherd (1982) to a selection of stocks for which time series data are readily available and including stocks which are known to have 'collapsed'. The stocks and time series are:

California sardine,	1932-62
Atlanto-Scandian herring (Norwegian spring-spawners only),	1950-69
North Sea herring,	1952-74
St Lawrence mackerel,	1966-75
Arcto-Norwegian cod,	1950-75
North-east Arctic haddock,	1950-75
Greenland cod,	1958-77
St Lawrence cod,	1950-74
North Sea haddock,	1920-36 and 1946-76
Georges Bank haddock,	1936-63
North Sea plaice,	1947-76
North Sea sole	1957-76

Data for California sardine have been provided by Dr P E Smith and for Georges Bank haddock by Dr R Hennemuth. Otherwise the basic data have been taken from sources listed in Appendix 1. The only amendments to published material have been the adjustment of year-class strength to give recruitment of one-year-old fish in each stock, using the appropriate estimates of natural mortality and abundance of the youngest exploited age group given by the source.

The intention is to fit the Shepherd model to the data for individual stocks and, by comparison of the parameter estimates for each stock, to seek generalizations that may help to explain the apparent variations in recruitment between stocks and hence lend credibility to the estimates.

2. The Shepherd model of stock and recruitment

Any stock and recruitment relationship reflects the variation in pre-recruit (i.e., eggs to recruitment) mortality with stock size. That mortality is in turn composed of density independent and density dependent components, however these may be defined. Typically the density dependent component generates a compensatory mortality where increased egg production is offset by increased pre-recruit mortality, causing a less than proportional increase in recruitment (Shepherd and Cushing, 1980). This can lead to the asymptotic form proposed by Beverton and Holt (1957) but other workers, notably Ricker (1954), Cushing and Horwood (1977), and Ware (1980), have shown that dome-shaped stock and recruitment curves can be generated by postulating plausible but more complex biological models, and still other workers have incorporated depensatory mechanisms that might exist at low stock size. Each is possible, but the use of any one of these models necessarily imposes the particular underlying biological rationale on the data set as an assumption which may not be valid and which cannot be tested.

The Shepherd model (Shepherd, 1982) makes no implicit assumption concerning the form of the density dependent compensation process: it can take any form dictated by the data, including the asymptotic or dome-shaped characteristic if these are appropriate. It is a three parameter model:

$$R = \frac{aE}{1 + (E/K)^{\beta}} \qquad (1)$$

where R is the recruitment,
E is the spawning stock as eggs,
a is the density independent survival,
β is the degree of compensation, and
K is a parameter that defines the stock size above which density dependent processes predominate over density independent processes; it reflects some 'carrying capacity' of the system.

Equation (1) defines the functional form of the stock and recruitment relationship, but the actual mechanism involves variation in the mortality of pre-recruits with stock size which can be seen more readily in the transformation:

$$\ln (E/R) = \ln \left\{ 1 + (E/K)^{\beta} \right\} + \ln \ (1/a) \qquad (2)$$

where R is the recruitment of one year olds and hence $\ln (E/R)$ is the mortality in the first year.

Equation (2) describes a relationship between pre-recruit mortality and stock size which, in a plot of $\ln (E/R)$ against $\ln E$, has the form of two straight line segments joined by a transitional curve where $E \simeq K$. For $E << K$ the relationship is a horizontal straight line $\ln (E/R) = \ln (1/a)$ and for $E >> K$, a straight line with slope β.

Note that fitting the relationship to data by standard least squares methods assumes that the variance of recruitment at any stock size is log normally distributed. Figure 1 is a frequency distribution of the log-transformed estimates of year-class strength for all of the stocks listed in Section 1 combined. The data have been standardised relative to the individual stock means and grouped to show that the distribution is approximately log normal and not in conflict with the assumption. (See also Garrod (In press)).

fit is itself difficult in an inherently 'noisy' set of data: the variance explained by the relationship is usually rather small and can be equally well satisfied by a range of parameter combinations. The prospective advantage of examining data from a range of stocks lies in the possibility that similarities in the parameter estimates will provide mutual support for the interpretation insofar as they may indicate the existence of common mechanisms.

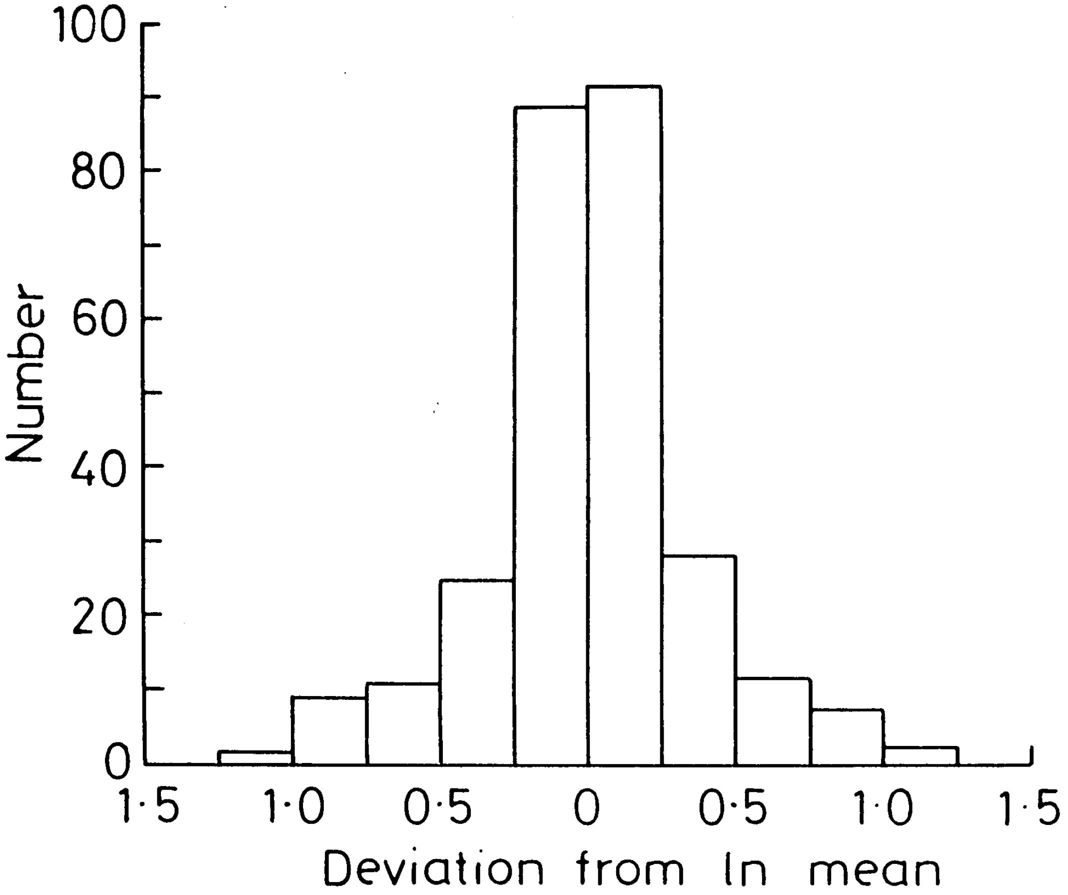


Figure 1 Aggregate frequency distribution of year-class strength for all of the stocks listed in Section 1 expressed as the deviation from the geometric mean for each stock.

The fitting of Equation (2) to the time series data itself raises two other statistical problems – the lack of independence of the variables and the choice of the most appropriate combination of three parameters, β, K and ln $(1/a)$ in a data set characterized by high variance. The crucial issue in defining the stock and recruitment relationship is the variance of pre-recruit mortality with stock size. With the data available that mortality can only be estimated as the ratio of stock (as eggs) to recruits, so the statistical objection cannot be avoided. A random distribution of recruitment with respect to stock size will, when transformed in terms of mortality, lead to an estimate of Equation (2) with $\beta = 1$. A 'stock and recruitment' relationship can only be distinguished if β is significantly different from 1, or if the non-linear form provides a significantly better representation of the data than linear regression.

The estimation of the three parameters in the non-linear

3. Application of the Shepherd model to selected stocks

Preliminary inspection of the individual stock data plotted as ln (E/R) against ln E indicates that the points do not cluster around horizontal straight lines, or show clear curvature, and we may conclude that the observations lie mainly in the region $E >> K$. This reflects the common experience that the conventional plot of recruitment on stock size has not shown any obvious non-linearity within the range of data available.

A preliminary comparison of the compensation coefficients can therefore be obtained by linear regression. These are summarised in Table 1 using the predictive regression of ln (E/R) on ln E since the main source of variability (random variation) is in recruitment, likely random errors in estimation of the stock as eggs being small in the logarithmic transformation. The estimates of β with the

Table 1 Estimates of the Compensation Coefficient (β) from linear regression.

	β	s d	P	Range of ln$E$ Lower	 Upper	ln $\bar{E}$	ln $(\bar{E}/R)$	ln (E/R) Virgin stock †	ln E Virgin stock ‡
California sardine	0.044	0.073		29.32	34.22	32.32	10.58	10.8	36.87
Norwegian spring spawning herring	0.430	0.209	*	30.12	34.94	33.96	11.41	12.2	35.80
North Sea herring	0.643	0.151	****	31.48	33.59	32.81	10.26	12.3	35.98
Greenland cod	0.215	0.193		29.91	33.72	32.52	14.14	14.6	34.66
St Lawrence cod	0.693	0.155	****	31.05	32.54	31.84	13.37	14.6	33.61
Arcto-Norwegian cod	0.870	0.252	***	31.54	33.53	32.58	11.90	15.0	36.14
North-east Arctic haddock	0.289	0.485		30.41	32.31	31.18	11.85	15.0	42.08
North Sea haddock	0.926	0.179	****	28.42	33.05	31.27	11.25	13.5	33.70
Georges Bank haddock	0.551	0.254	**	29.96	31.58	30.57	12.49	14.6	34.40
North Sea sole	0.791	0.433	*	30.38	31.64	30.96	12.54	13.8	32.55
North Sea plaice	0.877	0.315	***	30.97	31.64	31.27	11.44	12.6	32.59
St Lawrence mackerel	1.538	0.228	****	32.86	34.61	33.97	12.29	13.2	34.56

$P < 0.10$ *
< 0.05 **
< 0.01 ***
< 0.001 ****

† ln (E/R) Virgin stock is the egg production per recruit in the unexploited stock (see Appendix 2)

‡ ln E Virgin stock is the value ln E at which the fitted relationship has the value ln (E/R) Virgin stock.

Table 2 Parameters of the Shepherd model estimated by least squares minimisation

Group	Stock	Initial values Sum of squares (%)	 ln $(1/a)$	 ln K	 β	Terminal values Sum of squares (%)	 ln $(1/a)$	 ln K	 β
1	California sardine					1	9.7	28.3	0.08
2.	Norwegian spring spawning herring	9	6.9	29.3	0.91	19	6.7	23.2	0.44
	North Sea herring	46	7.6	29.1	0.70	48	9.4	32.9	1.73
	Greenland cod	4	12.3	29.0	0.46	8	11.7	22.6	0.24
	St Lawrence cod	1	11.0	29.0	0.82	13	9.8	26.1	0.60
	Aggregate of Group 2	39	9.8	29.1	0.83	65	11.6	32.2	1.07
3	Arcto-Norwegian cod	21	8.2	30.0	1.35	33	8.3	28.6	0.90
	North-east Arctic haddock	1	10.6	29.9	0.68	2	9.8	25.8	0.33
	North Sea haddock	29	9.2	29.6	1.26	35	5.1	24.6	0.92
	Georges Bank haddock	11	11.5	30.0	0.94	16	9.4	25.0	0.55
	North Sea sole	13	11.3	29.2	0.55	19	12.1	31.3	2.28
	North Sea plaice	22	9.5	29.5	0.99	23	10.9	31.4	2.01
	St Lawrence mackerel	80	6.2	29.6	1.37	85	6.1	29.9	1.54
	Aggregate of Group 3	66	9.0	30.1	1.29	70	9.5	30.9	1.81

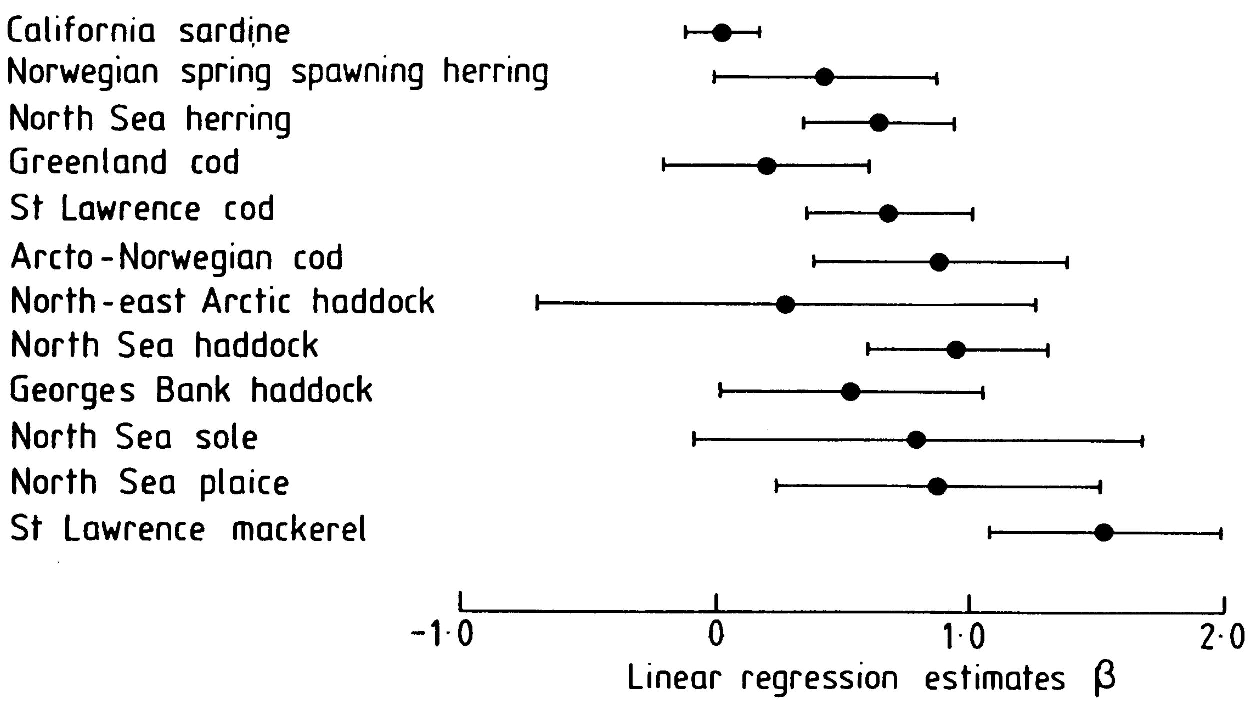


Figure 2 Mean and 95% confidence interval of β estimated from the functional linear regression for individual stocks, fitted to non-scaled data

95% confidence limits are illustrated in Figure 2. The standard deviation of β for California sardine is rather small but the regression coefficient itself is only slightly greater than zero. For this stock, Norwegian and North Sea herring and Greenland and St Lawrence cod the compensation coefficient is significantly less than 1 suggesting that a real relationship exists; it is not simply an artefact of the statistical transformation of a set of random observations (see above). The compensation coefficient for St Lawrence mackerel is greater than 1 but for the remainder of the listed stocks it is less than, but not significantly different from 1.

The initial estimates of β have then been used as values to initiate the estimation of the three parameters of the Shepherd model by a least squares minimisation routine. As may be expected from the variance of the provisional estimates of β (Table 1), this approach does not provide a clearly defined minimum sum of squares. The 'efficiency' of the minimisation can be judged from the percentage of the total sum of squares accounted for at each iteration to follow the trajectory of the procedure. This makes is possible to identify one limit where the gradient of improvement in the minimisation is minimal. However, because the overall reduction in least squares is rather small, for some stocks this 'minimum' is not necessarily a significant improvement on some previous combination. The results are given in Table 2 showing for each stock parameter combinations from the iterations giving the sum of squares closest to the initial sum of squares about the means of the data sets, and the terminal minimum. For most stocks the minimisation leads to a reduction in the estimate of β but, for North Sea herring, sole and plaice and St Lawrence mackerel, β is increased because some marginal reduction on sum of squares has been achieved by a parameter combination which takes greater account of outlying values caused by the occasional very good or poor survival. Closer inspection of the results also shows that for many stocks the estimates of $\ln(1/a)$ and $\ln K$ are coupled and can vary in combination with almost constant β with very little change in the sum of squares. This again reflects the distribution of data points $\ln E >> K$. In effect, the analysis establishes a probable range of β, but the estimates of $\ln(1/a)$ and $\ln K$ are doubtful.

Some further information is necessary to enable some choice of parameters in the range given. The parameter β is the asymptotic slope of the Shepherd model. There is no *a priori* reason to select a particular value of stock as eggs at which this asymptotic value of β would obtain. However, it would seem appropriate to assume that for all practical purposes the asymptotic value would occur in the region of the virgin spawning stock size. An estimate of this initial stock size can be obtained from the population fecundity in terms of the number of eggs per recruit to an unexploited stock. This defines the level of pre-recruit mortality to which the stock is adapted, so that the value of $\ln E$ at which the regression intersects the value of $\ln(E/R)$ of the unexploited stock then estimates the unexploited stock size. A fuller explanation of this calculation is given in Appendix 2. Data are not available to take density dependent growth and fecundity into account in this calculation but using the recorded growth rate leads to estimates of $\ln(E/R)$ of the unexploited stock and hence estimates of the unexploited stock size itself. The latter are listed in Table 1.

Bearing in mind that the population fecundity of even very small stocks lies in the order of 10^{12} eggs (i.e., $> \ln 27.6$), it can be seen that for many of the stocks analysed here the observations cover a very wide range and approach the estimated size of the virgin stock. The true value of β for

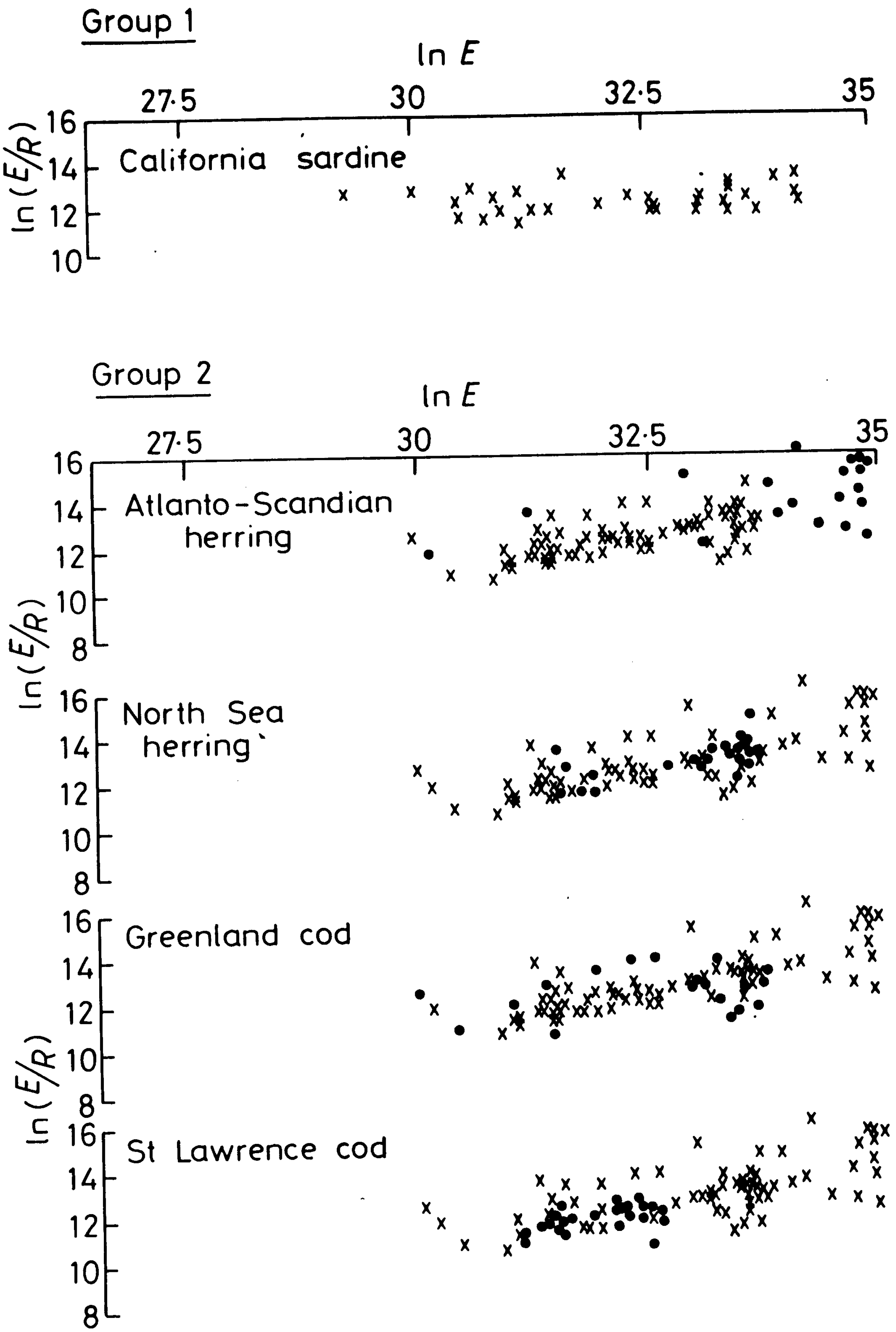
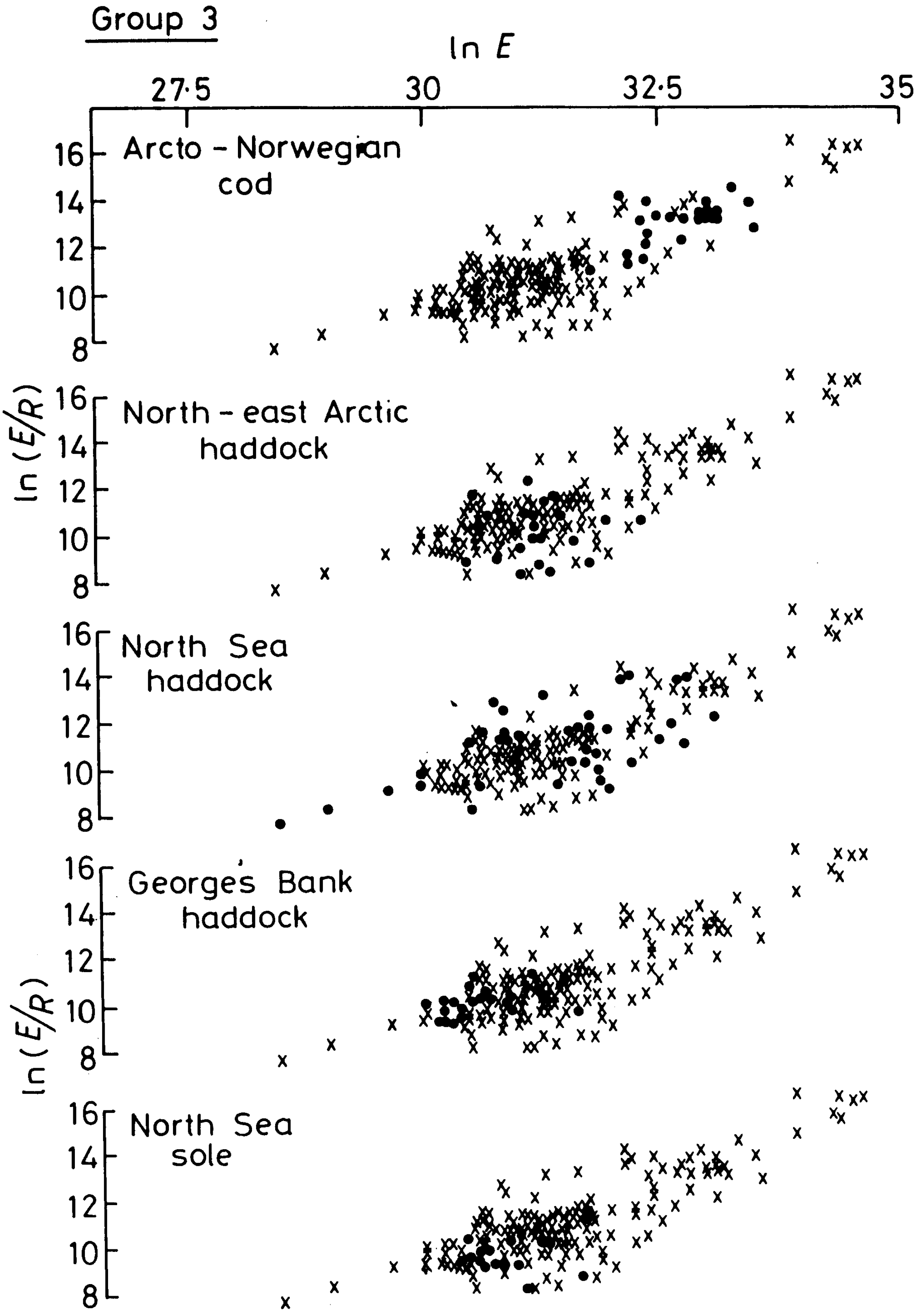


Figure 3 Plot of log survival ($\ln E/R$) against egg production ($\ln E$) for individual stocks using scaled data within the grouped stock data: ● named stock; x other stocks in the same group.



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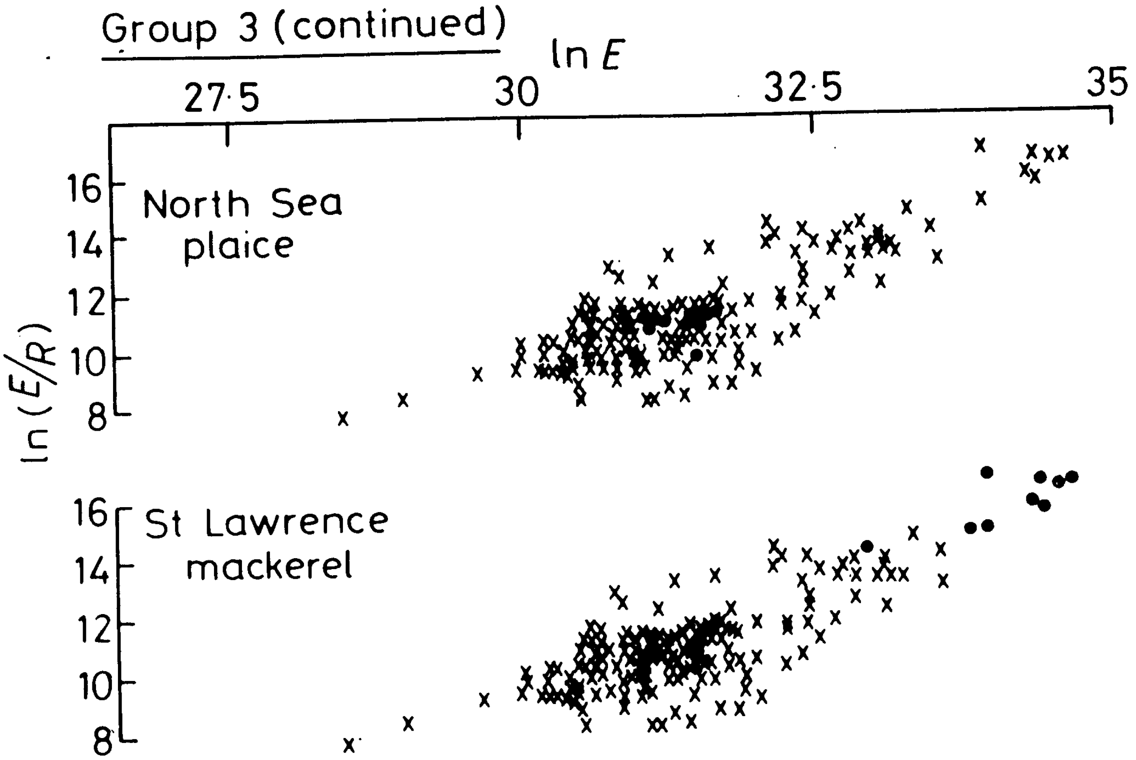


Figure 3 Continued

these stocks may not therefore be heavily distorted by non-linearity concealed in the variance. The stocks and value of β concerned are, from Table 1:

California sardine	0.044	Group 1
Norwegian spring spawning herring	0.430	Group 2
North Sea herring	0.643	
Greenland cod	0.215	
St Lawrence cod	0.693	
Arcto-Norwegian cod	0.870	Group 3
North Sea haddock	0.926	
St Lawrence mackerel	1.538	

Figure 2 illustrates the mean and standard deviation of β. There is no statistical justification for choosing a particular order but the stocks examined have been allocated to three groups based on the estimates of β. For the remaining stocks (North-east Arctic haddock, Georges Bank haddock, North Sea sole and North Sea plaice) the range of observations is small; in the first two this range lies well below the unexploited stock size, and the last two are comparatively small stocks. Theoretical curves based on the Shepherd model with a parameter β at the level of Group 3 above would show a very much lower slope in the range of the data for the four stocks listed in parentheses above. They could be in a restricted range of the same curve and for this reason they have been included in Group 3.

Reviewing the parameter estimates and stock grouping it is clear that the California sardine data are different from stocks in Groups 2 and 3. However, there is no reason to postulate any difference *between* Groups 2 and 3 except to note that the values of β for Group 2 are generally lower and that three of the Group 2 stocks are known to have collapsed whereas the Group 3 stocks have a history of recruitment varying without obvious trend in the time period concerned. There is no reason to draw any distinctions between the stocks *within* Groups 2 and 3. The idea is that within groups the pre-recruit mortality may be following the same density dependent functional relationship, and that with appropriate scaling an analysis based on the data amalgamated in these groups may improve the definition of the parameters. This may seem surprising, but, if it is considered that the density dependent mortality is generated by interaction between the pre-recruits and their predators or prey, it means no more than that the ecosystems in which they occur have similar ratios of biomass between the 'trophic' layers concerned. If it is observed that given ecosystems support similar numbers of pre-recruits, then it is likely that their predators and prey will also exist in similar numbers and hence that the density dependent mortality is also similar.

This biological rationale for expecting some generality in the density dependent pre-recruit mortality does *NOT* however mean that the total mortality should be the same in each stock. The density independent component may vary so that each group comprises a family of curves defined by Equation 2, having the same curvature but lying at different levels of ln E/R. In order then to analyse the data within groups as a single set of observations so far as the density dependent mortality is concerned, it is necessary to correct for the density independent element. So far no estimates of ln $(1/a)$ are available. Instead, the linear regressions have been scaled using ln (E/R) for each stock

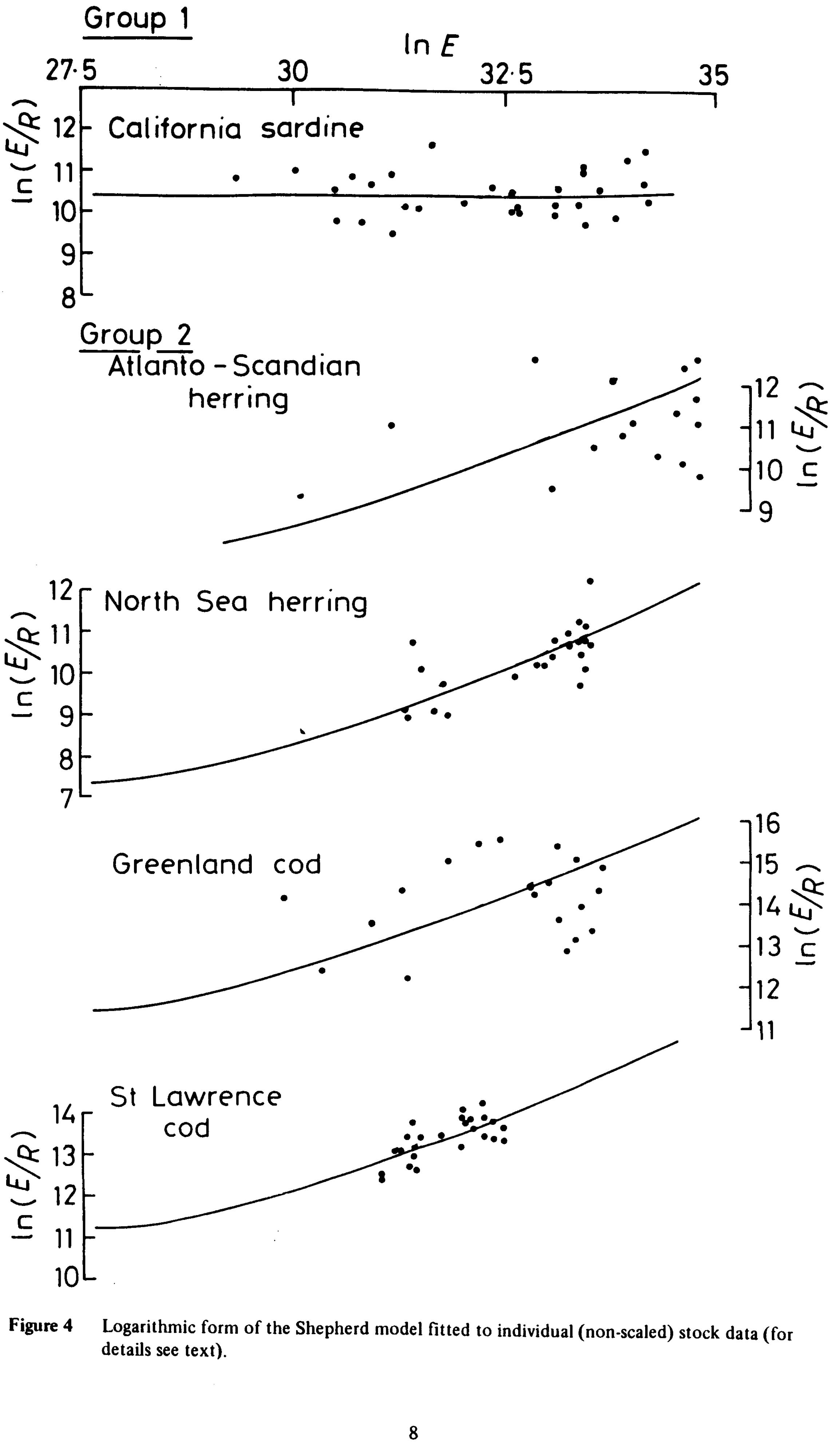
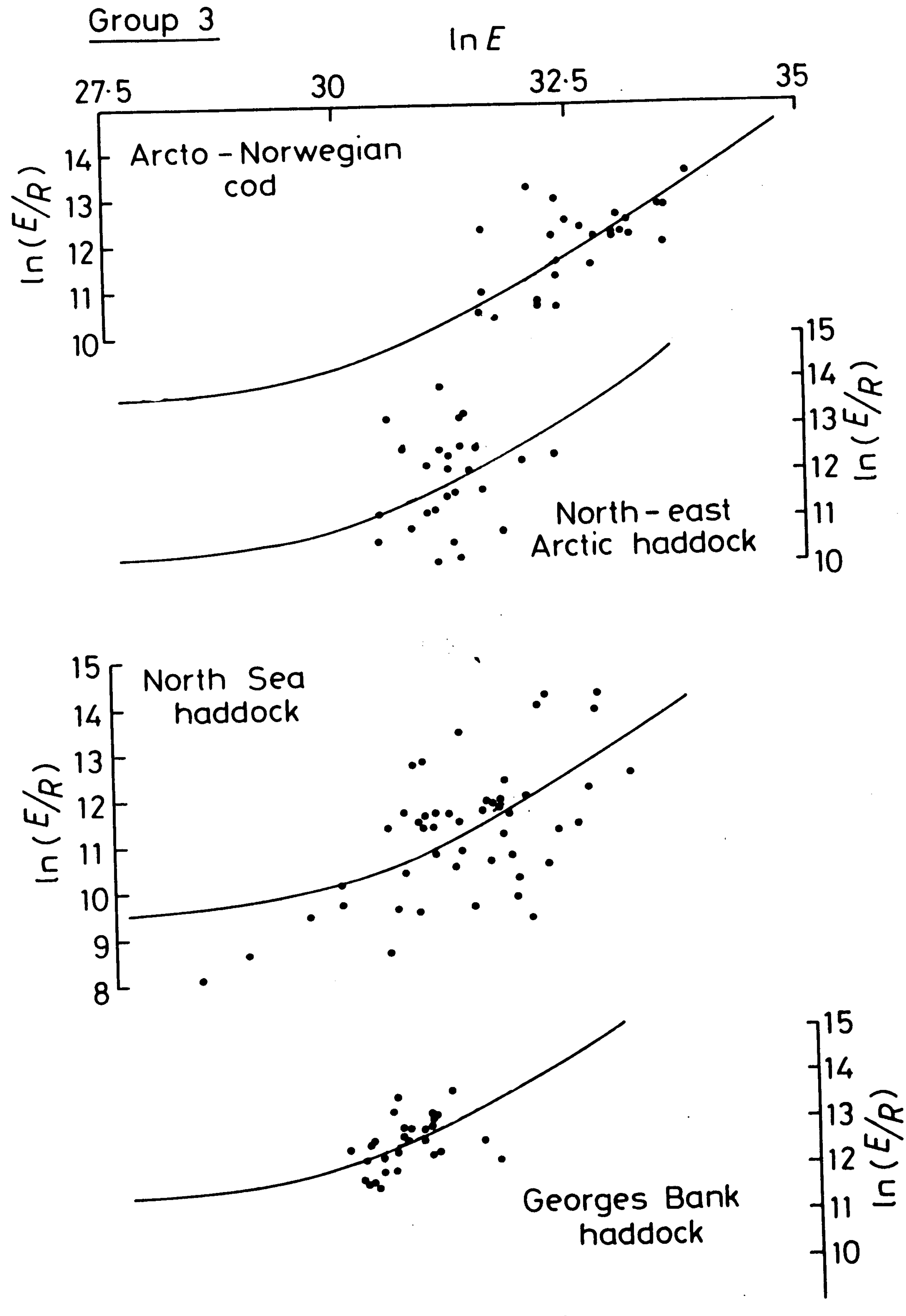


Figure 4 Logarithmic form of the Shepherd model fitted to individual (non-scaled) stock data (for details see text).



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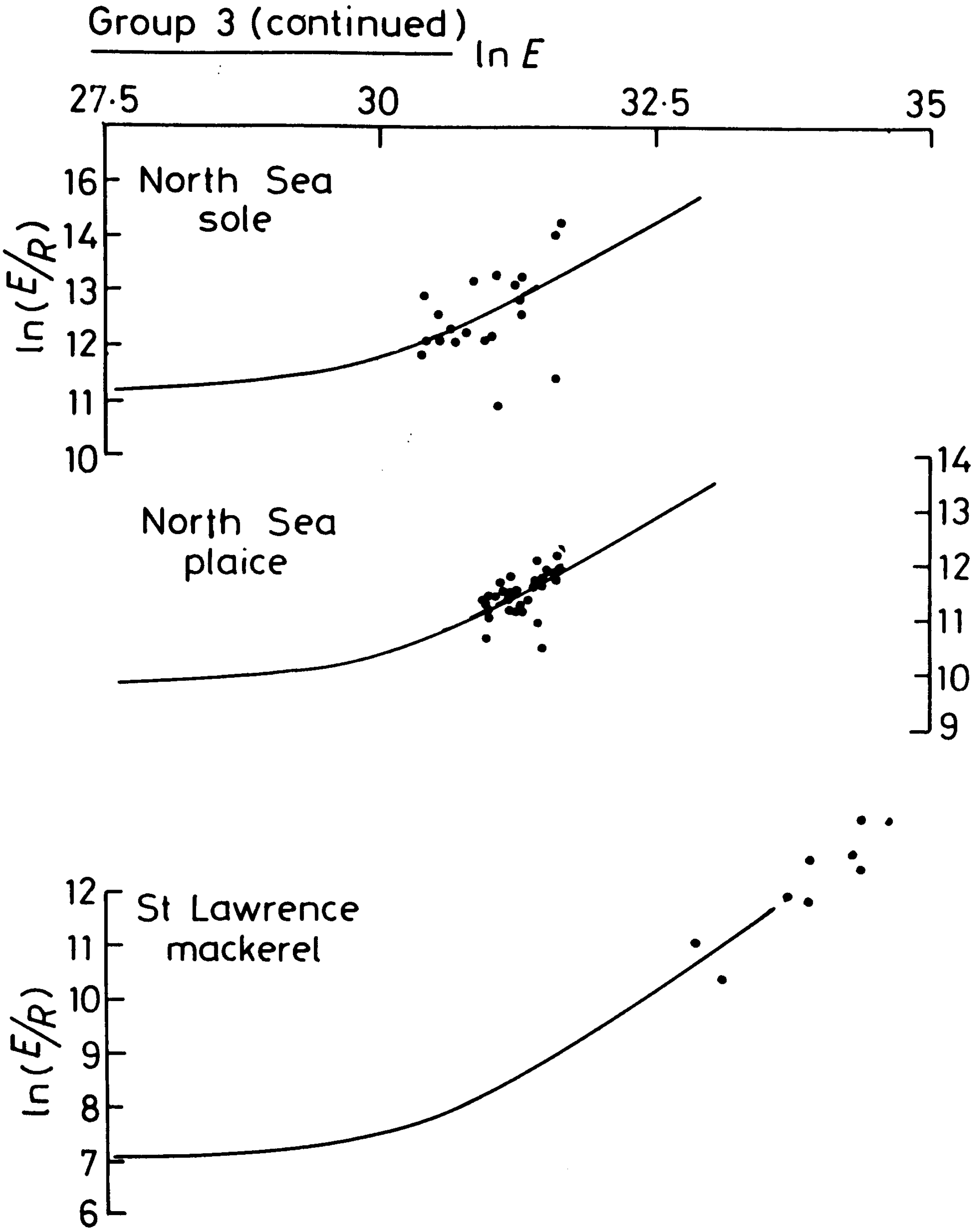

Figure 4 Continued

at the average value ln E for the total data set. This average (ln 32.1) lies within or close to the range of ln E for every stock. The value of ln (E/R) at ln E = 32.1 has been calculated (from the linear regression) for each stock and then the deviation of this from the average ln (E/R) at ln E = 32.1 for all stocks has been substracted from the data. This correction, ln (E/R) at ln 32.1 for individual stocks minus the average ln (E/R) at ln 32.1 for all stocks, has been applied to each observation for the appropriate stock. It shifts the data for each stock vertically on a plot like Figure 3, bringing the data for different stocks to coincide at the overall mean stock size.

These scaled estimates of ln (E/R) are plotted against ln E for the stock groupings in Figure 3, with the data points for each stock identified within each group. The underlying form of these relationships has then been examined using the least squares minimisation routine to estimate the variance accounted for by (i) the predictive (Y on X) linear regression model, (ii) a Beverton and Holt model (i.e., Shepherd model where $\beta = 1$) and (iii) the Shepherd model itself. The results are summarised below.

	Residual sum of squares		
	Group 1	Group 2	Group 3
Total	8.8	118.3	535.5
Linear regression	8.7	102.2	171.3
Beverton and Holt	8.3	65.5	200.9
Shepherd	8.7*	65.5	161.4

*The sum of squares 8.7 reflects the identification of a local minimum as the iteration converged.

None of the models gives any improvement in the interpretation of the Group 1, California sardine data, beyond what is achieved by the variance around the mean of the two variables. This corresponds with McCall's (1979) recent analysis of the data. There is no evidence of a density dependent response of any practical significance. For Group 2 stocks both non-linear models achieve a considerable reduction in sum of squares and there is nothing to chose between them. For Group 3 stocks the Beverton and Holt model (where $\beta = 1$) is less efficient than a linear regression but the Shepherd model does achieve a slightly improved reduction in the residual sum of squares. The conclusions are (i) that the Group 2 data which, it will be recalled, cover the widest range of stock sizes as ln E, are consistent with $\beta = 1$ as in the Beverton and Holt form but do show some small (but admittedly not visually obvious) evidence of the non-linearity which one would hope to see in the data for stocks that have collapsed; and (ii) that for Group 3, although there is no evidence of non-linearity, the compensation coefficient is greater than 1, i.e., the data do not conform to the asymptotic Beverton and Holt model.

The estimates for β, ln K and ln $(1/a)$ for the grouped data have been summarised at the bottom of Table 2 on the same basis as for the individual stock estimates. Apart from stocks in Group 3, where the estimate could be expected not to represent the asymptotic value of β, the Group estimates of ln K and β fall within the range indicated by the individual stock analyses. These two have then been used to re-estimate algebraically ln $(1/a)$ using the individual stock mean ln E and mean ln (E/R), to remove the density independent scaling factor from the grouped data. The individual stock parameters are given in Table 3 and illustrated in Figure 4.

4. Discussion

It will be immediately obvious from the steps in analysis that the data used either as individual stocks, or in the grouped form, still do not allow a convincing estimation of the appropriate parameters of stock and recruitment curves. It can only be argued that the data available do give a faintly detectable indication of non-linearity where the density dependent process dominates the density independent effect in the region ln $E > 30$, and that the compensation coefficient lies at or slightly below 1 in Group 2 stocks, and slightly above 1 in Group 3, though the value for the largest single stock (St Lawrence mackerel) appears to be somewhat higher, perhaps by reason of that stock's larger size in terms of egg production. The analysis also provides a broad order of magnitude of ln $(1/a)$. There are variations, but it is to be noted that the lowest values occur in stocks laying demersal eggs, which is perhaps indicative of a selective advantage in the strategy, and that the highest values occur in stocks known to occupy habitats towards the limit of their range of environmental tolerance.

There is a further point arising from the aggregation procedure. The observed stock sizes for each stock overlap over a wide range of *absolute* values, and there is no obvious topographical constraint on the dispersion of eggs and larvae, so the absolute stock size has been taken as being synonymous with egg and larval density. This may not always be so. There are stocks which are small in absolute terms and which spawn in restricted areas where, perhaps as a result of the behaviour of the stocks concerned, the spawning products occur at a density comparable to that of larger stocks spawning in larger areas. In that event the generalisation of density dependent mortality with absolute stock size would break down and a similar analysis would show compensation coefficients at small stock sizes which are comparable with those of the larger stocks. Evidence of this can be seen in Irish Sea stocks, although the time series of data are too short to justify extensive analysis (Anon, 1980). Table 4 summarises the comparison between estimates of β by linear regression from cod, plaice and sole stocks in the Irish Sea, and larger stocks of the same species elsewhere. In each case the compensation coefficient for the Irish Sea stocks is higher, and significantly so for cod and sole. The generalization used earlier concerning the density dependent process must therefore be used with caution, with due regard to the ecological circumstances of each stock.

Table 3 Final estimates of individual stock parameters.

Group	Stock	$\ln (1/a)$	$\ln K$	β	$\Delta \ln (E/R)$ σ
1	California sardine	9.7	28.3	0.08	0.54
2	Norwegian spring spawning herring	8.3	30.5	0.95	1.26
	North Sea hering	8.1	30.5	0.95	0.59
	Greenland cod	12.2	30.5	0.95	1.12
	St Lawrence cod	11.9	30.5	0.95	0.36
3	Arcto-Norwegian cod	8.6	30.0	1.25	0.72
	North-east Arctic haddock	10.2	30.0	1.25	1.04
	North Sea haddock	9.5	30.0	1.25	1.01
	Georges Bank haddock	11.4	30.0	1.25	0.56
	North Sea sole	11.1	30.0	1.25	0.75
	North Sea plaice	9.7	30.0	1.25	0.36
	St Lawrence mackerel	7.1	30.5	1.50	0.38

Table 4 Comparison of parameter estimates of Irish Sea with other stocks of cod, plaice and sole.

Species	Stock	n	$\ln E$	$\ln (E/R)$	β	r
Cod:	St Lawrence	25	31.84	13.37	0.69	0.68
	Irish Sea	11	28.82	13.32	1.82	0.70
Plaice:	North Sea	30	31.27	11.44	0.88	0.47
	Irish Sea	15	28.01	11.51	0.96	0.89
Sole:	North Sea	20	30.96	12.54	0.79	0.40
	Irish Sea	8	28.37	12.41	2.67	0.78

5. Stock and recruitment curves

The Shepherd model, Equation (1) was originally defined as

$$R = \frac{aS}{1 + (S/K)^{\beta}}$$

where the nomenclature is as before except that S is the biomass of the spawning stock rather than eggs, used here to investigate the form of the relationship. Recruitment is usually expressed in units of the order 10^6 and biomass as tonnes x 10^3 (i.e., g x 10^9).

Then, to reconstitute the Shepherd model in which spawning stock is expressed in units of thousand tonnes of both sexes

$$K = 2 \quad \frac{\exp (\ln K)}{e \times 10^9}$$

where e defines the fecundity as eggs per gram female; the integer 2 allows for the sex ratio (here taken as 1:1); and

$$a = (\exp (\ln 1/a) \times 0.5\, e)\, 10^3 .$$

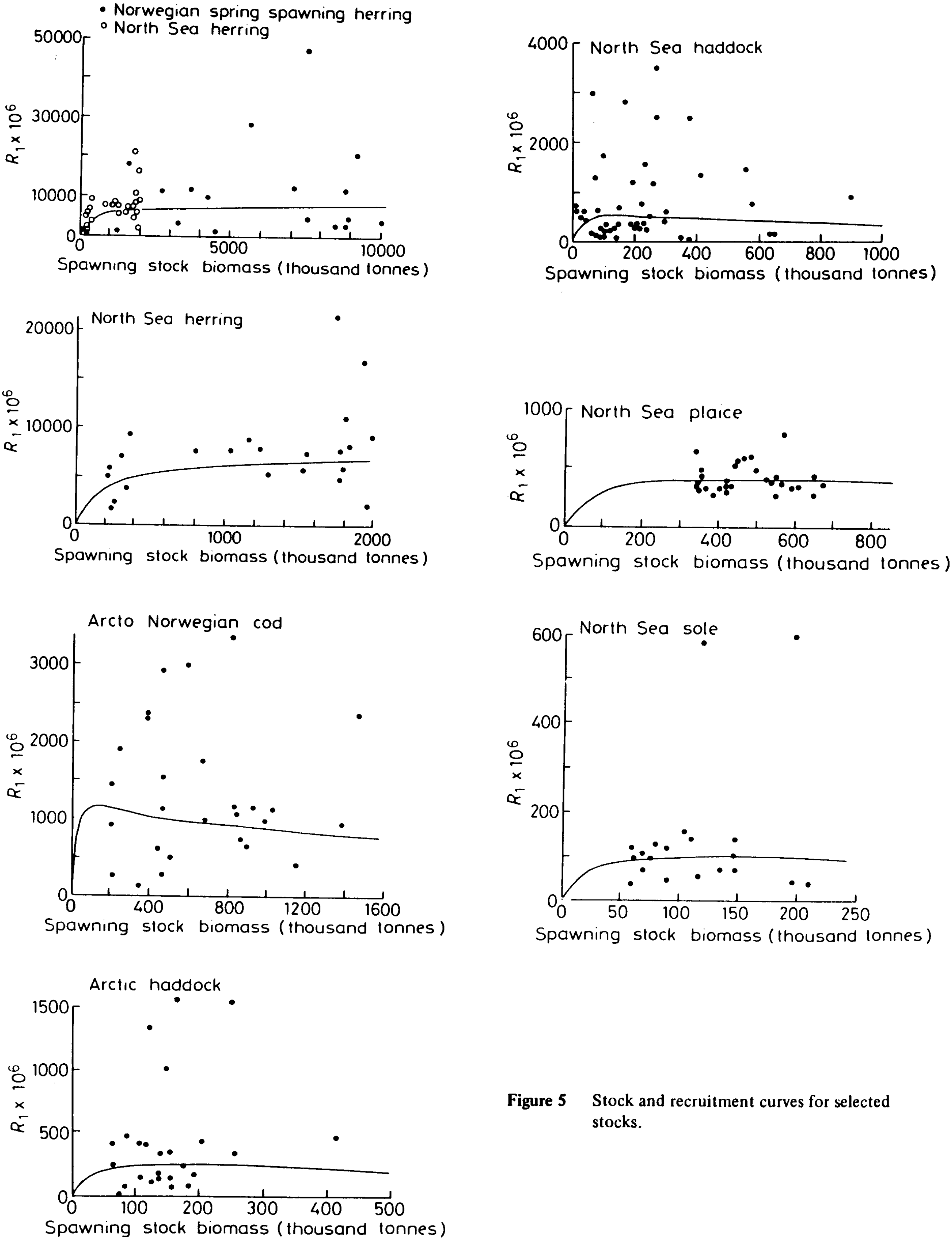

Figure 5 Stock and recruitment curves for selected stocks.

Table 5 Transformation of logarithmic to arithmetic parameters of the Shepherd model

Group	Stock	Fecundity eggs/gram female	ln (1/a) (from Table 3)	ln K (from Table 3)	a^1	K^2	β
1	California sardine	400	9.7	28.3	12.3	9.8	0.08
2	Norwegian spring spawning herring	300	8.3	30.5	37.3	159	0.95
	North Sea herring	300	8.1	30.5	45.5	143	0.95
	Greenland cod	360	12.2	30.5	0.9	120	0.95
	St Lawrence cod	500	11.9	30.5	1.7	78	0.95
3	Arcto-Norwegian cod	500	8.6	30.0	46.0	43	1.25
	North-east Arctic haddock	500	10.2	30.0	9.3	43	1.25
	North Sea haddock	500	9.5	30.0	18.7	43	1.25
	Georges Bank haddock	500	11.4	30.0	2.8	43	1.25
	North Sea sole	528	11.1	30.0	4.0	40	1.25
	North Sea Plaice	164	9.7	30.0	5.0	130	1.25
	St Lawrence mackerel	450	7.1	30.5	185.6	78	1.50

[1] Millions of R^1 recruits per thousand tonnes spawning stock biomass

[2] Thousand tonnes

The two alternatives for the stocks analysed in this paper are listed in Table 5. The resulting stock and recruitment curves for North-east Atlantic stocks are shown in Figure 5. These present the usual visual ambiguities but on the analysis presented here there is no reason to suppose that they reflect anything other than a family of closely related curves scaled by the density independent mortality of each stock and the particular biological characteristics of growth and fecundity required to generate comparable levels of egg production. Most of the relationships are similar to those presented by other authors but it is instructive to make the comparison between the various stocks and perhaps most interesting to see the close similarity of the curves for North Sea and Norwegian spring spawning herring. They are sufficiently similar to suggest that those two stocks are responding on different segments of the same overall relationship by virtue of their differing life history strategies (growth and age at maturity) in relation to the age and level of exploitation by the commercial fisheries.

The curves of total yield against fishing mortality and spawning stock biomass for the two herring stocks and for North Sea haddock are shown in Figure 6 to illustrate the consequences of combining these stock and recruitment relationships with the yield per recruit characteristics of each stock. The exact form of the relationship is, of course, dependent *inter alia* upon the partial exploitation patterns used. In the examples used these have been taken as:

North Sea herring	50% 0-group, 100% 1-group and older;
Norwegian spring spawning herring	50% 1-group, 100% older age groups;
North Sea haddock	70% 1-group, 100% older age groups.

It is not claimed that such partial exploitation patterns represent the historic or recent fisheries for these stocks – they are merely used as realistic examples of the form of the relationships. The yield curves for the two herring stocks are very similar, as would be expected from the stock and recruitment relationship: they are in effect simply scaled by the growth potential and exploitation patterns for the two stocks. There must also be some doubt whether the ultimate levels of spawning stock size at low levels of exploitation could be achieved, but the locations of the maximum yield and associated level of fishing mortality are consistent with experience and, as always, stress the need to take account of the stock and recruitment relationship in estimating prospective yield, even though the estimates of parameters are not as statistically justifiable as one could wish in a perfect world.

6. Summary

The 'Shepherd Model', a simple and versatile form of the stock and recruitment relationship, has been used to analyse time series of data from a selection of stocks. The analysis remains limited by the characteristic variability of the data but estimates are given of the likely magnitudes of the compensation coefficient and the density independent mortality. Comparison of the parameters between stocks suggests that the levels of density independent and density dependent mortality are less different than is sometimes supposed on the basis of individual stocks analysed in 'isolation' and when the stock is expressed in terms of its biomass rather than potential egg production. Of the stocks examined here, California sardine appears to have shown very little density dependent variation in mortality as the stock declined; the stock and recruitment relationship of two herring stocks is close to the asymptotic Beverton and Holt form, but for several demersal groundfish stocks the relationship may be weakly domed.

The parameter estimates are used to define the stock and recruitment curves of the various species and to illustrate how they may be used to generate yield rather than yield per recruit curves as a basis for management advice.

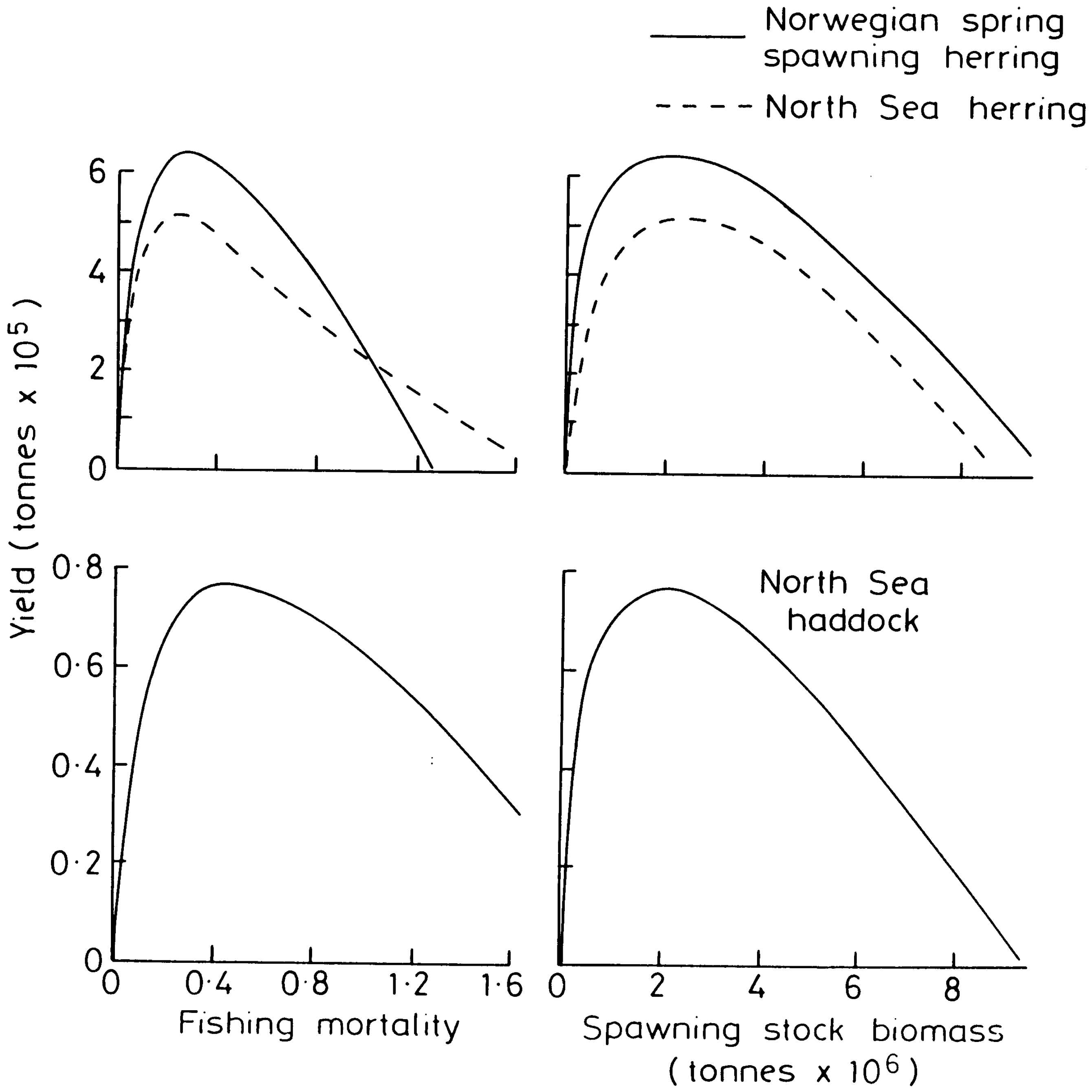

Figure 6 Relationship between potential yield and spawning stock biomass for Norwegian spring spawning herring, North Sea herring and North Sea haddock.

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Appendix 1: Table 1. Basic stock and recruitment data (eggs x 10^{12}, R_1 x 10^6)

	California sardine		Norwegian spring spawning herring		North Sea herring		St Lawrence mackerel	
Eggs/gram female.	400		300		300		450	
First year	1932		1950		1952		1966	
References	10, 16, 22, 23, 30 P. E. Smith (personal communication)		8, 11, 19, 25		1, 2, 25		20	
	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6
	705.6	5939	1410	78300	297	9100	186.6	2906
	684.7	12949	1365	20700	276	8070	239.6	7514
	727.0	21187	1320	11300	267	7700	445.4	2848
	566.2	6113	1065	12600	267	4760	853.2	3309
	366.6	4208	1140	4700	262	21370	1073.8	1710
	242.0	8030	1320	3100	229	5640	981.4	1834
	239.6	10353	1335	4600	184	7820	836.3	1345
	320.2	10089	1500	3700	294	1980	787.6	2379
	350.4	17615	1275	2900	289	16720	527.9	3923
	492.2	21545	1125	47400	232	7330	533.2	1798
	411.2	9178	840	28600	172	8730		
	336.6	4875	630	9900	271	10950		
	251.9	5550	495	2800	279	5710		
	143.9	3558	240	18000	193	5290		
	113.2	2424	555	11400	156	7580		
	81.4	2487	675	900	120	7620		
	148.3	5781	405	11200	51	3820		
	159.0	6357	195	700	54	9060		
	155.9	5505	36	600	46	7110		
	55.6	433	12	1200	33	5010		
	27.1	592			39	2240		
	40.4	1450			34	5900		
	47.9	1786			36	1040		
	34.1	570						
	21.5	394						
	18.0	877						
	35.5	2366						
	24.5	1350						
	17.6	430						
	10.8	166						
	5.4	110						

Appendix 1: Table 1 (continued)

	Arcto-Norwegian cod		North-East Arctic haddock		Greenland cod		St Lawrence cod	
Eggs/gram female.	500		500		360		500	
First year	1950		1950		1958		1950	
References	3, 25		3		14, 25, 26		20, 21	
	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6
	365	2370	62.1	1530	391	603	82	161
	345	950	34.5	190	429	245	95	117
	287	400	20.7	70	441	145	107	104
	225	650	16.1	250	325	631	121	125
	207	1190	41.4	70	289	718	108	159
	217	740	36.8	1040	349	298	136	165
	247	1010	108.1	470	262	322	132	214
	232	1170	73.6	350	186	101	122	201
	255	1370	46.0	160	234	115	106	69
	210	1090	36.8	350	320	91	90	90
	150	710	29.9	410	254	51	82	62
	127	510	23.0	470	199	128	86	91
	117	1160	34.5	140	131	24	81	78
	95	2360	35.3	350	101	19	64	91
	60	1930	16.1	420	70	21	47	158
	52	250	18.4	30	40	24	44	142
	85	170	32.2	30	43	216	38	86
	115	290	43.7	250	29	37	36	80
	110	620	39.1	140	16	61	46	114
	117	1540	41.4	1540	10	7	45	46
	117	2920	50.6	430			50	78
	170	1030	39.1	70			46	91
	167	1780	32.2	120			43	63
	95	2300					31	115
	52	940	27.6	140			30	119
	50	1450	27.6	410				
			30.6	1340				

Appendix 1: Table 1 (continued)

	North Sea haddock		Georges Bank haddock		North Sea plaice		North Sea sole	
Eggs/gram female.	500		500		164		528	
First year	1920		1936		1947		1957	
References	5, 17, 18, 24		9, 12, 13		4, 6, 7, 27		4, 15, 28, 29	
	Ex10^{12}	R_1 x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6	Ex10^{12}	R_1x10^6
	66	3549	15	99	29	424	29	148
	51	340	15	74	29	324	31	582
	85	71	12	65	29	356	36	72
	93	2523	13	112	28	342	39	134
	48	1197	17	110	32	273	55	37
	57	785	18	58	33	328	52	43
	129	1496	17	23	34	337	53	598
	52	338	20	55	34	400	21	125
	43	2851	25	49	34	249	18	67
	27	556	23	79	36	341	38	67
	49	333	19	50	37	565	38	106
	57	1563	16	29	38	582	31	52
	36	384	13	110	39	588	28	155
	37	707	13	49	41	478	25	46
	32	282	12	98	43	394	20	92
	24	1755	10	43	46	403	23	118
	10	402	14	133	46	1310	18	106
	23	247	13	49	44	376	16	38
	26	306	18	80	47	365	16	97
	29	249	19	63	49	333	16	119
	24	280	25	63	53	273		
	17	190	23	65	55	353		
	7	549	26	121	53	423		
	2	714	27	120	50	332		
	4	616	26	53	45	268		
	10	617	31	38	46	811		
	18	1290	43	149	36	524		
	22	66	52	283	30	323		
	37	55			29	484		
	47	368			28	640		
	25	229						
	20	142						
	20	632						
	17	3004						
	24	68						
	91	63						
	158	147						
	143	767						
	76	6297						
	55	385						
	161	109						
	225	899						
	103	1324						
	58	254						
	62	1298						
	67	2541						
	61	552						
	74	457						

Note: Estimates of R_1 for North Sea haddock exclude recent adjustments for haddock discarded or caught in industrial fisheries for other species.

Appendix 2: The reproductive potential of a stock.

Following Garrod and Knights (1979)

$$R_{t+1} = R_t E_R e^{-Mo} \qquad (1)$$

where R_{t+1} = is the average number of one-year-olds,

R_t is the average recruitment of year-classes in the stock, again as one-year-olds,

E_R is the average number of eggs per recruit (R_t) in the unexploited stock, irrespective of sex, and

e^{-Mo} is the survival in the first year of life.

At replacement in the unexploited stock $R_{t+1}/R_t = 1$ and $e^{Mo} = E_R$. The number of eggs per recruit is therefore the best available estimate of the reproductive rate that must be achieved to offset mortality in the first year, and its inverse, the recruits per egg estimates the mortality in the first year to which the stock has become adapted over evolutionary time.

Eggs per recruit of an unexploited stock can be readily determined from the survival of a cohort under natural mortality together with estimates of sex ratio, maturity, weight at age and fecundity. Text Table 3 summarises the estimates for the stocks listed. The calculations assume current estimates of the biological parameters and therefore exclude the effect of density dependent processes. But note that in the logarithmic form as an estimate of mortality, errors of a factor of 2 will not invalidate the value of the parameter at the order of magnitude involved: the estimate is fairly robust.

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