Stock, recruitment and moderating processes in flatfish

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Abstract

A difficulty that frequently arises when stock-recruitment relationships are fitted to historical data of fish populations is the high degree of variation in recruitment so that the relationship is difficult to identify with any precision. The purpose of this paper is to describe refinements that can be made to the model by incorporating information on parallel environmental factors that also affect recruitment. The identification of the stock-recruitment relationship can be made with greater precision because of the reduction in the unexplained variability. Many investigations on the effects of environmental changes on recruitment have been published in the fisheries literature. It is, however, comparatively rare for the simultaneous effects on recruitment of environmental factors and stock size to be analysed. Here we describe the formulation of an appropriate mathematical relationship to describe these effects. The framework of this formulation is F.E.J. Fry's classification of environmental factors into one of five kinds: controlling, limiting, lethal, masking and directive, following the work of Neill et al. (1994) [Neill, W.H., Miller, J.M., Van der Veer, H.W., Winemuller, K.D., 1994. Ecophysiology of marine fish recruitment: a conceptual framework for understanding interannual variability. Neth. J. Sea Res. 32, 135-152]. An examination of some of the theory underpinning stock-recruitment relationships indicates how independent experimental evidence on the effects of environmental factors on recruitment can be incorporated into the relationship in an appropriate mathematical form. A method is described for the graphical illustration of the relationship between, on the one hand, stock and recruitment allowing for the effects of environmental factors and, on the other hand, the relationship between environmental factors and recruitment allowing for changes in stock levels. The method is based on the idea of partial residuals (or adjusted variables) derived from statistical regression methodology. The scatter of the adjusted variables around the fitted relationship is often considerably less than that of the raw data. The method is illustrated by two examples of flatfish stocks, plaice (Pleuronectes platessa) in the North Sea and English sole (Pleuronectes vetulus) in the Hecate Strait off the coast of British Columbia. © 1998 Elsevier Science B.V. All rights reserved.

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1. Introduction

The effects of climate change and environmental influences on the ecology of fish populations have received much recent attention in the fisheries science community. Whole books and symposia have been devoted to the subject: Cushing (1982), Glantz (1992) and Laevastu (1993), the Canadian Special Publication edited by Beamish and McFarlane (1989), the symposia on cod and climate (ICES, 1994) and on stocks in the North Pacific (INPFC, 1986). With such a plethora of published work on
the subject, the value of a further contribution might be questioned. However, as longer and more reliable series of stock and recruitment data become available for study (Myers et al., 1990, 1995) the opportunity of improving the identification of stock–recruitment relationships becomes a practical proposition, and is investigated in some flatfish stocks in this paper.

Stock–recruitment relationships, or more generally relationships describing the numbers of fish in a population at some stage in their life history that are derived from numbers at some previous stage, are fundamental to the theory of fish population dynamics (Ricker, 1954, 1958; Beverton and Holt, 1957; Gulland, 1983). The identification of the nature of this relationship has considerable potential in the understanding of the mechanisms that regulate fish populations. Beverton (1995) made use of information from stock and recruitment investigations which gave some support to the concentration hypothesis that there are critical periods that are of primary importance in moderating fish numbers. Nash (1998) made use of a Paulik diagram to illustrate the relationship between four successive stages in the life history of plaice (Pleuronectes platessa) in the Irish Sea. His study is an example of the growing use of computer simulation models to represent the changes that occur in fish populations over time. Clearly such models depend on mathematical relationships between numbers at successive stages that are as accurate a representation of nature as can be achieved. In this paper we investigate the refinement of stock-recruitment models by the incorporation of additional variables representing environmental effects.

Stock and recruitment plots are notable for the degree of scatter that can be seen in a plot of recruitment $R$ against stock size $S$. Indeed this has led some authors, including Rothschild (1986), Pauly and Tsukayama (1987) and Wooton (1990), to cast doubt on the value of any attempt to fit a stock–recruitment relationship to data. Despite the large number of highly scattered stock–recruitment plots that have been published, it must be remembered that there are also examples in the literature in which some form of smooth curve representing a relationship between $R$ and $S$ is clearly evident (Elliott, 1984, 1985; Chadwick, 1985). It seems reasonable to suggest that, at least in some cases, the scatter around a stock–recruitment curve can be explained by additional factors that have affected recruitment. The graphical illustrations of Pauly and Tsukayama (1987), Svendsen et al. (1991) and Sparholt (1996) appear to us to be convincing evidence of this, though the former authors clearly expressed an opposing view in their article.

Although there have been many published studies describing the effects of environmental factors on the recruitment to fish stocks, the compounding effect on recruitment $R$ of parallel changes in spawning stock biomass $S$ is not always taken into account. Conversely, it is comparatively rare for a suggested functional relationship between $S$ and $R$ to make allowance for the additional effect of environmental factors $E$. Some recent articles that have included both $S$ and $E$ in a functional relationship to predict $R$ include those by Mills and Hurley (1990), Svendsen et al. (1991), Beverton and Iles (1992a), Da Silva (1993), Plikshs et al. (1993), Myers et al. (1993), Hutchings and Myers (1994), Iles (1994), Jacobson and MacCall (1995) and Sparholt (1996). In the majority of these articles the additional environmental factor included in the relationship to explain changes in $R$ is either temperature or salinity, or in the case of Plikshs et al. (1993) and Sparholt (1996), a combination of these two incorporated as a single variable measuring the volume of water available for spawning. Svendsen et al. (1991) is an exception; in their article it was variables related to wind speeds that were included, and one of the examples discussed by Iles (1994) made use of phosphate loadings as an additional explanatory variable. A somewhat similar approach to that of the stock–recruitment relationship together with an environmental variable is adopted by Fargo and McKinnell (1989) and Fargo (1994) but they incorporate $S$ and $E$ in the form of a response surface to investigate effects on $R$. Although this allows the shape of the relationship to be identified, and is indeed very flexible in allowing the surface to follow the mean of the scattered data closely, it does not identify a classical form of relationship between $R$ and $S$ such as the Beverton–Holt or Ricker curves.

Other approaches to the investigation of the relationship between $S$ and $R$ with account taken of $E$ include the non-parametric approaches of Rothschild and Mullen (1985), Prager and Hoenig (1989)
and Hoenig and Prager (1990). Tang et al. (1989) suggested that a family of Ricker stock-recruitment curves should be used according to environmental conditions. Welch (1986) used time-series methods to remove part of the environmental effects on $R$, but Stergiou (1989) used time-series methodology with the explicit intent of excluding changes in oceanographic and biological conditions from the prediction model.

In our preliminary investigation on the combined effects of $S$ and $E$ on $R$ (Beverton and Iles, 1992a), we stated two aims that are further pursued in this paper:

1. To determine the effect of $E$ on $R$ when allowance is made for $S$.
2. To find the form of the underlying stock-recruitment relationship that would have been identified had $E$ remained constant throughout the period covered by the data.

### 2. Formulation of the model

The predictive functional relationship between $R$, $S$ and $E$ advocated in this paper is of the general form:

$$R = f(S, E)$$

Ideally egg numbers should be used on the right-hand side of this equation and not the spawning stock biomass $S$. $S$ is generally assumed to be a proxy for egg numbers, relying on the conclusion derived from many studies of fecundity in teleost fish that egg numbers are, at least approximately, linearly related to biomass. However, there are other factors that affect egg production. Rijnsdorp (1994) reviewed some of the conditions that affect the production of eggs in flatfish and this demonstrates that the assumption that egg numbers are proportional to $S$ is merely an approximation. Thus refinements could be made to the model in the form of changes in the fecundity and condition of the spawning stock that may occur in time. Indeed such changes may themselves be influenced by environmental effects. It is beyond the scope of this present paper to attempt such refinements, and we will restrict attention to those factors that may be supposed to influence recruitment to the population.

The form of the relationship between $R$ and $S$ will be chosen from the range of standard stock-recruitment relationships. These were reviewed by Iles (1994), and methods were presented in that article for identifying the particular relationship that best describes the data, both with and without additional factors $E$ in the equation. Similar methods will be used in this paper, though for simplicity attention will be restricted to the two parameter models of Beverton–Holt, Cushing and Ricker. Three parameter models are undoubtedly more flexible, but they are also more difficult to justify for highly scattered data and are prone to the problems of inadmissibility described by Iles (1994). Their extra flexibility is gained at the expense of greater difficulty in the identification of parameter values. For similar reasons we shall restrict our attention to models in which at most two environmental factors $E$ are included in the model, and these will be included in a mathematically simple form.

There is a huge number of potentially influential environmental variables that might reasonably be incorporated in the prediction equation for $R$. The reviews by Bakun et al. (1982) and by Shepherd et al. (1984) together with the books by Cushing (1982), Glantz (1992) and Laevastu (1993) all contain sections discussing the possible environmental conditions that might influence recruitment. Amongst the factors that have emerged as particularly potent influences on recruitment are temperature, salinity, transport (currents and wind), and to a lesser extent the degree of ice cover and turbidity. These effects may themselves be related; temperature is often strongly related to salinity for example. Amongst biotic effects that strongly influence recruitment are the availability of prey and the presence of predators. It is, however, unwise to include as many environmental variables as can conveniently be measured into the prediction equation. Hilborn and Walters (1992) and Tyler (1992), amongst many others, have cautioned against this approach. No additional variable, when included as a new variable in a multiple regression equation, can increase the residual sum of squares. It is often possible to suggest a plausible relationship, finding a variable that apparently correlates significantly with recruitment by searching amongst a large number of environmental influences and discarding those that do not correlate well. It is less likely, however, that such relationships, carefully
tailored for a particular data set, will stand the test of subsequent investigations. Another criticism of investigations of this kind is that the environmental variables generally included in prediction equations are those for which data are readily available, perhaps from meteorological surveys. These data sets are not necessarily those that are most appropriate for a study of the effects on recruitment.

Whenever a statistical correlation is identified between variables there is always the possibility that the suggested relationship between the variables is false, and that it is generated by co-incidental trends in time. In addition to these problems of false correlations, there may be hidden relationships. It may be, for example, that a significant correlation can be shown to exist between sea surface temperature measured at the time that young fish are in their larval pelagic stages and ultimate recruitment. Sea temperatures, however, are often related to current speeds, and it could be transport that is actually the main influence on recruitment (see for example Van der Veer et al., 1998). The true nature of relationships may also be altered by the presence of other factors. Temperature is very likely to influence recruitment, but temperature may also affect the numbers of predators on the juvenile fish. If for some reason other than temperature, for example fishing pressure or disease, the predators are removed from the environment the apparent effect of temperature on recruitment may change substantially. Amongst all this caution it is heartening to remember that genuine causes and effects occur in nature, and it is only by investigative study that they can be scientifically proved.

"Theory and data complement one another and are both indispensable in order to arrive at a valid model" (Brown, 1993). With this in mind, some thought is necessary before a suitable model can be devised. It is certainly possible to investigate purely empirical prediction models. It is often convenient in investigations of the effect on recruitment to work with the logarithms of \( R \), and an empirical model of the form advocated by Hilborn and Walters (1992) and many other authors is readily formulated:

\[
\ln R = \ln f(S) + cE
\]

where \( f(S) \) is a suitably chosen stock recruitment model (e.g. Beverton–Holt). This corresponds to a model:

\[
R = f(S) e^{cE}
\]

and this is admissible as a prediction model. An empirical model of the form:

\[
R = f(S) + cE
\]

may for some data sets be shown to be statistically justifiable, but such a relationship is theoretically impossible since it admits of the possibility, with \( f(S) = 0 \), of a generation of recruitment by factors external to the parent population.

In many studies a preliminary exploratory study is made of the effects on recruitment before the final form for the prediction equation is derived. Although temperature is often selected as a variable to include in the equation, it is not always in the simple form of water temperature measurements at a specific time, or of averages over a suitable period. Mills and Hurley (1990) incorporated temperature together with their stock–recruitment relationship for perch (\textit{Perca fluviatilis}) in an English lake in the form of the number of degree days exceeding 14°C. Plikshs et al. (1993) and Sparholt (1996), following work of the ICES working group on demersal stocks in the Baltic, (ICES, 1991) showed that recruitment in cod (\textit{Gadus morhua}) in the Baltic was related to temperature and salinity in the form of the volume of water suitable for spawning by the fish (see also Beverton, 1992).

Suitable variables to include in the prediction equation, and the form in which they might be included, can often be deduced from exploratory work that is entirely separate from the samples and analysis that lead to the stock and recruitment series. Examples of such work include that of Pihl (1990), who showed that the abundance of 0-group plaice (\textit{Pleuronectes platessa}) in a Swedish bay was positively correlated with the strength of on-shore winds and negatively correlated with the severity of the winter preceding settlement of the fish. Boehlert and Mundy (1987) identified a significant positive association between sample numbers of juvenile English sole (\textit{Pleuronectes vetulus}) off the west coast of Canada and current speed. Other studies (Peterman and Bradford, 1987; Houde, 1989, 1990; Houde and Zastrow, 1993) have shown that juvenile mortality rates in fish are associated with environmental
effects, particularly temperature and wind speed. Pauly (1978) and Ursin (1984), in theoretical studies, showed that mortality rates were associated with temperature, together with other fundamental parameters of the species related to their growth rates. Relationships of this form are amongst those that will be suggested for inclusion into the theory of stock–recruitment equations in the next section.

The various theoretical forms of mathematical relationship that might be supposed to exist between various environmental factors and, respectively, individual fish, populations and communities of fish was extensively surveyed by Neil et al. (1994). They described five kinds of influence: controlling, limiting, lethal, masking and directive factors, basing their classification on the work of F.E.J. Fry. The incorporation of these different kinds of factors into a stock–recruitment relationship is discussed in more detail in the next section.

3. Incorporation of environmental factors in the stock–recruitment relationship

In this section we show how knowledge gained from experimental work or a knowledge of the nature of the effect might be incorporated into the theory of the inter-relationships between the parent stock and eventual recruitment to the population.

The first of the environmental influences described in Fry’s system of classification are controlling factors. These affect the population by altering the rate of change of numbers of young fish in time, most simply included in models of recruitment by changes in mortality rates. All three of the stock-recruitment relationships investigated in the present paper have as their basis a simple differential equation. Solution of this equation together with simple assumptions about the mortality rates and the relationship between spawning stock biomass and egg numbers gives the familiar form of the curves used in stock and recruitment studies, and shows how the effects of changing mortality rates can be incorporated into these equations.

In the case of the Ricker model, the rate of decrease in time \( \frac{dN}{dt} \) of the number of young fish \( N \) in the population, starting as eggs and progressing through successive life stages, is assumed to be limited by a density-dependent mortality directly proportional to the number of eggs \( N_0 \), thus:

\[
\frac{dN}{dt} = -N(\mu_1 + \mu_2 N_0)
\]

Here \( \mu_1 \) is a density-independent mortality, and \( \mu_2 \) the density-dependent component. Solution of this equation by integration gives:

\[
N_t = N_0 e^{-\mu_1 t} e^{-\mu_2 t N_0}
\]

Assuming then that \( t \) is chosen as the age at which fish are recruited, so that \( N_t = R \), and that \( \mu_1 \) and \( \mu_2 \) are both constants, then the assumption that \( N_0 \) is proportional to the spawning stock biomass gives the equation:

\[
R = \alpha S e^{-\beta S}
\]

which is the familiar Ricker stock–recruitment relationship. Exploring this link between the differential equation model and the resulting stock–recruitment model more generally, we might suppose that the density independent component of mortality \( \mu_1 \) is not constant, but related to a single exogenous environmental factor \( E \). (Exploration of relationships between \( \mu_2 \) and \( E \) lead to more complicated models that will not be pursued further in this study.) Following the work of Houde and Zastrow (1993), and also that of Pauly (1978), it appears possible, at least as a first approximation, that \( \mu_1 \) is directly proportional to \( E \), so instead of incorporating \( \mu_1 \) into the constants of the suggested relationship we obtain:

\[
R = \alpha S e^{-\beta S} e^{\beta E} \quad (1a)
\]

This model, in which the logarithm of recruitment is functionally related to \( S \) and \( E \) by a simple multilinear relationship, is the starting point for many empirical studies. Another simple assumption that might be made concerning the relationship between \( \mu_1 \) and \( E \) is that \( \mu_1 \) is proportional to the logarithm of \( E \). Then an equation of the form:

\[
R = \alpha S e^{-\beta S} E^c \quad (1b)
\]

is obtained.

The Cushing stock–recruitment relationship also has a basis in a differential equation model in which the density-dependent component of mortality is assumed to be related to the logarithm of population density (Beverton and Iles, 1992b):

\[
\frac{dN}{dt} = -N(\mu_1 + \mu_2 \ln N)
\]
The solution of this equation by integration is:

\[ N_t = \exp\left[\left(\exp(-\mu_2 t) - 1\right)\frac{\mu_1}{\mu_2}\right] N_0^{\exp(-\mu_2 t)} \]

As above with both \( \mu_1 \) and \( \mu_2 \) assumed to be constant, \( N_t = R \) and \( N_0 \) proportional to \( S \), Cushing’s stock recruitment equation is obtained:

\[ R = \alpha S' \]

With \( \mu_2 \) constant and \( \mu_1 \) assumed to be proportional first to \( E \) then to \( \ln E \), the equations:

\[ R = \alpha S' e^{cE} \quad (2a) \]

or

\[ R = \alpha S' E'' \quad (2b) \]

are obtained. As in the Ricker case, these are simple extensions of the Cushing stock–recruitment relationship that incorporate the additional environmental factor \( E \). Moreover, they are equations that on transformation by taking logarithms are linear in \( \ln S \) and \( E \) or \( \ln S \) and \( \ln E \), respectively, thus facilitating the simple fitting of the equations by multiple linear regression methods.

The differential equation for \( N \) assumed for the Beverton–Holt model is:

\[ \frac{dN}{dt} = -N(\mu_1 + \mu_2 N) \]

Integration of this equation with respect to \( t \) gives the solution:

\[ N_t = \frac{N_0 \mu_1 e^{-\mu_1 t}}{\mu_1 + \mu_2 N_0 (1 - e^{-\mu_1 t})} \]

Assuming as before that \( \mu_1 \) and \( \mu_2 \) are both constant, the Beverton–Holt stock–recruitment equation is obtained:

\[ R = S/(b + aS) \]

Both the functions \( (1-e^{cE})/E \) and \( (1-e^c)/\ln E \) are then approximately constant. It may be preferable, both to obviate this difficulty and for the sake of simplicity, to assume a model of the form:

\[ R = S e^{cE}/[b + aS] \quad (3a) \]

or

\[ R = S E''/[b + aS] \quad (3b) \]

The second of the environmental influences listed by Neill et al. (1994) are limiting factors. Such effects alter the carrying capacity of the habitat for recruits. The Beverton–Holt stock–recruitment relationship is the only one of the simple two-parameter models that incorporates a carrying capacity, an asymptotic upper limit to \( R \) for large \( S \). In the parameterisation used above this asymptote is \( 1/a \) so that if an environmental factor \( E \) is thought to affect the carrying capacity, it could be incorporated mathematically into the stock–recruitment model by replacing the constant \( a \) by a function of \( E \), for example:

\[ R = S/[b + a e^{cE} S] \quad (4a) \]

or

\[ R = S/[b + a E'' S] \quad (4b) \]

The third of Fry’s effects are lethal factors. Such factors, perhaps extreme concentrations of a toxin accidentally introduced into the habitat, or an epidemic disease, cause catastrophic and immediate recruitment failure. Once the lethal factor reaches a threshold value, recruitment effectively falls to zero whatever the current spawning stock size. A multiplication of the stock recruitment function by a step function that makes a sudden jump to zero as the level of the lethal factor passes through its threshold value would be the way to incorporate such an effect into the stock–recruitment model.

In Fry’s original context of environmental influence on metabolism, the fourth of his factors, masking effects, are those that load metabolism, determining the metabolic work needed for the maintenance of the individual. Translating this idea to the recruitment process, masking effects are those that control the stock size needed for a given recruitment. Thus a high environmental loading of a masking
Effect on the recruitment process would depress the average recruitment for any given stock size below that attained at a lower loading of the effect. Such a phenomenon can most easily be represented in the stock-recruitment relationships by changing the rate of increase of recruitment with respect to increases in stock size. Mathematically, this can be incorporated into the model by making the derivative \( \frac{dR}{dS} \) a function of \( E \). These derivatives are, for the Beverton–Holt, Cushing and Ricker equations, respectively:

\[
\frac{dR}{dS} = \frac{b}{(b + aS)^2} = b \left( \frac{R}{S} \right)^2
\]

\[
\frac{dR}{dS} = a \gamma S^{r-1} = \gamma \left( \frac{R}{S} \right)
\]

\[
\frac{dR}{dS} = \alpha e^{-\beta S} (1 - \beta S) = \frac{R}{S} (1 - \beta S)
\]

It is interesting to note in passing the simple relationship of the derivative \( \frac{dR}{dS} \) to the recruitment rate \( R/S \). Beverton and Iles (1992a) pointed out that this ratio is considered as a prime demographic parameter, though perhaps more often in the dynamics of populations of animals other than fish. Thus the simplest way of making \( \frac{dR}{dS} \) depend on \( E \) would be to replace the parameter \( b \), in the case of the Beverton–Holt model, \( g \) in the Cushing model or \( b \) in the Ricker model by a simple function of \( E \). Possible formulations of such models are:

\[
R = \frac{S}{b e^{cE} + aS}
\]

\[
R = \frac{S}{b E^c + aS}
\]

in place of the simple Beverton–Holt equation, or:

\[
R = aS^{k+cE}
\]

replacing the Cushing equation. A model such as:

\[
R = aS e^{-bS(1+cE)}
\]

is a possible extension of the Ricker model.

Directive factors, the final of Fry’s classification, play a central role in the theory of the effects of the environment on fish physiology. Unfortunately they would seem to be the most difficult of the factors to identify by a statistical analysis. Temperature, for example, is a controlling factor but also a directive factor, influencing the behaviour of the spawning stock itself. Purely as a controlling factor, temperature influences recruitment via the mortality rates amongst larvae and young fish. However, adult fish react to changes in temperature at spawning time, presumably so as to exploit to the maximum the habitat for their own spawning success. In especially cold years fish may, in the Northern Hemisphere, spawn further south than is usual. Thus the effect of temperature on recruitment is modified by this behaviour. The observed effect of a directive environmental factor on the stock-recruitment relationship cannot be assumed to be the same as the controlling effect of the same factor.

However, the model to describe the effects of stock size and environmental influences on recruitment is chosen, it is important that these should be incorporated simultaneously in the model. It is possible that \( S \) and \( E \) are statistically related, and then the stock-recruitment relationship that best describes recruitment may differ from the relationship when \( E \) is included in the model. Conversely, the apparent effect of \( E \) on \( R \) may be different from its effect when allowance is made for changing \( S \). Iles (1994) gives an example of an apparent relationship between phosphate concentrations and recruitment in plaice (Pleuronectes platessa) in the North Sea that could equally be explained by a concomitant change of stock size and phosphate concentrations.

4. Methodology

However well the additional environmental variable reduces the unexplained scatter about a stock-recruitment relationship, there is still likely to be some residual unexplained variation. This is incorporated into the model in the form of a random component that may be assumed to be additive in \( R \):

\[
R = f(S, E) + \varepsilon
\]

or alternatively in the logarithm of \( R \):

\[
\ln R = \ln [f(S, E)] + \varepsilon
\]

The fitting of such models, the selection of the best-fitting form of the stock-recruitment relationship and the diagnostic checking to justify the assumptions of the random component have all been described elsewhere (Iles, 1994) and will not be further discussed here.
In addressing the twin aims stated in the introduction of this paper, we will describe a method of adjusting $R$ for the effect of $E$ so that the adjusted variable can be plotted against $S$ to illustrate the relationship between stock and recruitment that would have been observed had the factor $E$ remained constant. Conversely we will show how $R$ may be adjusted for the effect of $S$ so as to demonstrate the underlying relationship between $R$ and $E$ independent of the effects of changing stock size.

Where a model of the form:

$$\ln R = \ln f_1(S) + \ln f_2(E) + \varepsilon$$

is assumed, a suitable adjustment is easily devised. Parameters of the model are estimated and a new adjusted variable:

$$\ln R_{E\text{adj}} = R - \ln \hat{f}_1(E)$$

is defined. Here the " over the second term on the right-hand side indicates that the function $f_2$ is calculated numerically using estimates of the parameters derived from a statistical analysis of data. Similarly $R$ adjusted for $S$ is defined as:

$$\ln R_{S\text{adj}} = R - \ln \hat{f}_1(S)$$

We will illustrate the use of these variables by one of the equations suggested in the previous section. We first describe the extended Cushing model, Eqs. 2a and 2b, since this is the simplest to describe mathematically.

Suppose then it is assumed that the random component of the model should be incorporated in the form that is linear in the logarithm of $R$. The full model:

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

is fitted to the data, conveniently as it turns out in this case by multiple linear regression, and parameters $\hat{\alpha}$, $\hat{\gamma}$ and $\hat{c}$ of the best-fitting equation are obtained. A new variable, $R$ adjusted for the effect of $E$ is then defined as:

$$\ln R_{E\text{adj}} = \ln R - \hat{c}E.$$  

This variable when plotted against $S$ exhibits the scatter derived from the residuals of the full model, including the environmental factor $E$ as well as stock size $S$, about the stock recruitment relationship. It is plots similar to these that were used by Pauly and Tsuchayama (1987), Beverton and Iles (1992a) and Sparholt (1996). Plots such as these are described in the statistical literature of regression diagnostics (for example Cook and Weisberg, 1982; Atkinson, 1985) and are known as partial residual plots. The scatter of the adjusted $R$ around the stock-recruitment relationship reflects the variability in $R$ that remains unexplained when both $\ln S$ and $E$ are incorporated in the prediction equation. It is this that has led to the criticism of partial residual plots by some authors since they may give a false impression of the strength of the relationship between $R$ and $S$. Such plots must always be interpreted in the knowledge that they are derived from a multiple variable equation, and that therefore a factor not directly plotted on the graph has been used to reduce the apparent variability of the data.

A disadvantage of the simple form of adjusted variable defined above is that the adjustment for $E$ alters the centre of the adjusted variable $R_{E\text{adj}}$ from the raw values of $R$. It is more convenient for graphical presentation to leave this centre unchanged, and this can be achieved by centring the environmental variable $E$ before making the adjustment. Thus we define the new variable, adjusted for $E$, as:

$$\ln R_{E\text{adj}} = \ln R - \hat{c}(E - \bar{E})$$

where $\bar{E}$ is the mean of the data available for $E$. If there are more than one environmental variable, then multiples of each one of their centred values are subtracted on the right-hand side. A plot of $\ln R_{E\text{adj}}$ against $S$ answers the second of our aims, representing the scatter of data that might have been expected had the environmental effect $E$ remained constant throughout the period when data were collected.

Similarly we define the new variable, adjusted for $S$, as:

$$\ln R_{S\text{adj}} = \ln R - \hat{\gamma} (\ln S - \ln \bar{S})$$

where $\ln \bar{S}$ represents the mean of the logarithms of the data on $S$. A plot of $\ln R_{S\text{adj}}$ against $E$ answers our other aim, that of identifying the underlying scatter of the data around a relationship between $R$ and $E$ when allowance is made for different contemporary values of $S$.

A simple linear regression of $\ln R_{E\text{adj}}$ recovers as the regression coefficient the estimate $\hat{\gamma}$ from the full multiple regression model. Similarly a simple linear
regression of $\ln R_{E, \text{adj}}$ on $E$ recovers the estimate $\hat{c}$ from the full multiple regression model.

The raw residuals from the full multiple regression equation are defined as:

$$ (\ln R)_{\text{res}} = (\ln R - \bar{\ln R} - \hat{\gamma}(E - \bar{E})) $$

$$ - \hat{\gamma}(\ln S - \bar{\ln S}) $$

Comparison of this equation with the definition of the adjusted variables given above gives the equation:

$$ \ln R_{E, \text{adj}} = (\ln R)_{\text{res}} + \hat{\gamma}(\ln S - \bar{\ln S}) + \bar{\ln R} $$

In words, this equation states:

$E$ ADJUSTED $\ln R = \text{RESIDUAL} + \ln(\text{CUSHING CURVE}) + \text{MEAN} \ln R$

In practice this simple formula for calculating the adjusted variables is the most convenient general definition, and can be used in contexts other than linear regression. Similarly:

$$ \ln R_{S, \text{adj}} = (\ln R)_{\text{res}} + \hat{\gamma}(E - \bar{E}) + \bar{\ln S} $$

$S$ ADJUSTED $\ln R = \text{RESIDUAL} + \ln(\text{ENVIRONMENTAL FACTOR}) + \text{MEAN} \ln R$

If instead of a Cushing stock-recruitment equation the Ricker equation is used, a similar procedure to that outlined above can be used. A regression of $\ln(R/S)$ on $S$ and $E$ provides the correct least-squares estimates of the parameters $\beta$ and $c$ of Eq. 2a. (A regression of $\ln(R/S)$ on $S$ and $\ln E$ should be used if Eq. 2b is to be fitted to the data.) The residuals from this equation are also the correct least-squares residuals. Care should be exercised in the interpretation of the usual $F$ and $R^2$ statistics, however. These represent a test of the Ricker model together with the environmental factor against a null model of a proportional line, and not a test against a null model of constant recruitment. Further information on this point is given in Iles (1994). Having obtained the estimates of the parameters of the fitted equation, and the raw residuals from the model, Eq. 9 above can be used to calculate the adjusted variable $\ln R_{S, \text{adj}}$. Eq. 8 has to be modified to incorporate the Ricker equation in place of the Cushing:

$$ \ln R_{E, \text{adj}} = (\ln R)_{\text{res}} + (\ln S - \bar{\ln S}) $$

$$ - \hat{\beta}(S - \bar{S}) + \bar{\ln R} $$

Eq. 9, with the residuals from the model incorporating both the Ricker equation and the environmental variable, gives $\ln R_{S, \text{adj}}$.

A model including an environmental variable together with a Beverton–Holt type of stock-recruitment relationship is more difficult to handle technically since, even in the $\ln$ domain, it is non-linear in the parameters. Fitting of the equation to the data therefore needs the use of a non-linear regression package. Eq. 3a, on taking logarithms, becomes:

$$ \ln R = \ln[S/(\hat{b} + \hat{a}S)] + cE $$

Once the parameters $a$, $b$ and $c$ are estimated the process of calculation of the adjusted variables follows similar lines to those outlined for the Cushing and Ricker cases. The adjustment for $E$ is effected by the following equation:

$$ \ln R_{E, \text{adj}} = (\ln R)_{\text{res}} + \ln[S/(\hat{b} + \hat{a}S)] $$

$$ - \ln[S/(\hat{b} + \hat{a}S)] + \bar{\ln R} $$

Here $(\ln R)_{\text{res}}$ are the residuals from the fitting of the full model to the data and the horizontal bars over the terms on the right-hand side indicate the arithmetic averages. The equation for $\ln R_{S, \text{adj}}$ is the same as Eq. 9 for the Cushing case.

There is little published work in the statistical literature on an equivalent of partial residual plots in non-linear regression applications (see, however, Loynes, 1987). The equations derived earlier for linear regression can be extended to cover these cases. However, the initial definition of adjusted variables (partial residuals) in which the environmental variable, multiplied by the partial regression coefficient $\hat{c}$, is subtracted from the raw $R$ values does not carry over to the non-linear case. The alternative formula in which the residuals from the full model are added to the part of the equation giving the stock-recruitment relationship does give an adjusted variable that has similar properties to the partial residuals of linear regression, and it is this adjusted variable that we suggest can be used to represent the stock-recruitment relationship adjusted for the environmental variable. As is the case in linear regression, it may be convenient for presentational purposes first to define the adjusted variable in such a way that the adjusted variable has a similar mean to the raw $R$ values. Where the relationship for predicting $R$ is of
the form:

\[ R - f_1(S) f_2(E) \]  

(11)

the equation for recruitment adjusted for the environmental variable is:

\[ R_{E\text{adj}} = k_1 f_1(S) + R_{\text{res}} \]

in which \( R_{\text{res}} \) are the residuals from the fitting of the full model, including the environmental variable, \( f_1(S) \) is the stock–recruitment relationship, with the * indicating that the parameters of this model have been estimated from the data, and \( k_1 \) is a constant chosen to match the mean of \( f_1(S) \) to the same mean as the raw values of \( R \). Notice that this adjustment for the mean, if it is made at all, should be done before the residuals are added. If it is done afterwards the scatter of data around the fitted curve will be distorted by the arbitrary adjustment. The centring of the adjusted variables cannot be done by addition or subtraction of constants, as is done in the linear case, unless the assumed model of Eq. 11 contains an additive constant. None of the models suggested in Section 3 contain an additive constant unless they are transformed by taking logarithms. The multiplication of \( f_1(S) \) by \( k_1 \) amounts to setting \( f_2(E) \) equal to a constant in Eq. 11, and this is equivalent to setting \( E \) to an arbitrary average value, simply for presentational purposes so that the adjusted \( R \) matches the original data.

In a similar way \( R \) can be adjusted for the effects of stock-size to represent the relationship that might have been observed between \( R \) and \( E \) had stock sizes remained constant:

\[ R_{S\text{adj}} = k_2 f_2(E) + R_{\text{res}} \]

Where the equation to predict \( R \) is of the form:

\[ R = f(S, E) \]

and \( f \) cannot be divided into a product of a function of \( S \) and a function of \( E \), this adjustment procedure requires a careful choice to be made of a suitable average value of \( E \), at \( E_{\text{mid}} \) say, so as to match the adjusted variable to the raw \( R \) values. This matching cannot be done by multiplication of \( f(S) \) by a factor:

\[ R_{E\text{adj}} = f(S, E_{\text{mid}}) + R_{\text{res}} \]

5. Examples

In this section the methodology outlined above is applied to two different flatfish stocks to illustrate the steps in calculation that have to be done in order to derive the adjusted variables. The first of these examples illustrates the simple case in which linear regression methods are used throughout. In a previous article (Iles, 1994) one of us described an analysis of some data on stock and recruitment in plaice (\emph{Pleuronectes platessa}) in the North Sea over the period 1958–1990. The right-hand limb of a Ricker stock–recruitment relationship was identified as a statistically significant explanation of the slight decrease in recruitment observed over this period as stock sizes were at their highest (Fig. 1). It was also shown that the model could be significantly improved by incorporating a measure of temperature, the average February sea surface temperature at Den Helder, located near the entrance of the Dutch Wadden Sea. Data from this stock have been extensively analysed; it is commercially a most important resource. Amongst many authors who have suggested possible reasons for variation in recruitment are Rijnsdorp and Millner (1996) and Rijnsdorp and Van Leeuwen (1996). They identified several contributory effects on recruitment and here we have selected from their work the growth of fish in the size range 35–39.9 cm, i.e. those aged between 5 and 6 years,
as a third variable $G$ (together with spawning stock biomass $S$ and temperature $T$) to include in an equation to predict $R$. The data are fitted to the logarithms of $R$, so the full model to represent recruitment is the linear one:

$$\ln R = \ln \alpha + \ln S - \beta S + cT + dG + \varepsilon$$

The steps in calculating the adjusted variables are as follows:

1. Fit the full model given above by multiple linear regression and estimate the parameters $a$, $b$, $c$ and $d$. At this stage calculations were done to test the statistical hypothesis that these parameters are zero, to determine if stock size, temperature and growth should all be incorporated in the prediction equation. These are standard methods discussed by Iles (1994) and will not be further discussed here.

2. Calculate the raw residuals, $(\ln R)_{\text{res}}$, from this fitted equation.

3. $R$ adjusted for temperature and growth is calculated as:

$$\ln R_{\text{adj}} = \ln R + (\ln S - \ln \bar{S}) - \hat{\beta}(S - \bar{S}) + (\ln R)_{\text{res}}$$

4. $R$ adjusted for stock size and temperature is calculated as:

$$\ln R_{\text{adj}} = \ln R + \hat{\alpha}(G - \bar{G}) + (\ln R)_{\text{res}}$$

Plots of these adjusted variables superimposed on the original data are given in Figs. 1 and 2. The fitted curves are also drawn on these figures. It is evident that the adjustment for temperature and growth tightens up the scatter of the stock–recruitment plot (Fig. 1). Moreover some suggestions can now be made that may explain the outliers in these data. The years of maximum recruitment over the period 1958–1990 were 1963, 1981 and 1985. An explanation that is often given for the good year classes of 1963 and 1985 is that the preceding winters were cold. However, 1981 was not a cold winter, yet recruitment was high. From this analysis a possible explanation has emerged. 1981 was the year when growth amongst 5–6 year old fish was the second highest in the series, indicating that the spawning stock in that year may have been in exceptionally good condition. A possible explanation for the low recruitment observed in 1967 (the point at the extreme right-hand edge of Fig. 1) may also be given. In that year growth of 5–6 year old fish was very low, the third lowest in the series.

Fig. 2 is the companion to Fig. 1, and shows the scatter plot of $\ln R$ against $G$, together with $\ln R$ adjusted for both $T$ and $S$. It is evident that, on average, recruitment is higher in those years when growth in 5–6 year old fish is high. Again the scatter in the plot is very much reduced by the additional explanatory variables, but the most striking feature of this figure is that the relationship between $R$ and $G$ is scarcely changed when account is taken of changing $S$ and $T$. In Fig. 1, on the other hand, the stock–recruitment relationship is somewhat flattened by the adjustment for $T$ and $G$.

In our second illustrative example we have explored the possibility that growth $G$ acts in the role of a masking variable, incorporating it in the Ricker stock–recruitment relationship in the form of Eq. 7. On taking logarithms the following equation is obtained:

$$\ln R = \ln a + \ln S - b(1 + dG)S + cT + \varepsilon$$

This equation is fitted to the data by multiple linear regression, regressing $\ln(R/S)$ on the three predictor variables $S$, $T$ and the product $S \times G$. Apart from the substitution of the product $S \times G$ for $G$, the calculation of $\ln R$ adjusted for $G$ and $T$ follows similar lines to the previous example, the only point to note being that in the centring process
Fig. 3. Stock and recruitment plot for North Sea plaice 1958–1990. Stock size in tonnes $10^{12}$. Recruitment in numbers of fish $10^{6}$. o, original data; +, data adjusted for temperature and growth. Ricker curves are fitted to the original data (solid line) and the adjusted data (dotted line).

$G$ was fixed at a suitable average value to match the mean of the adjusted In $R$ values to the raw values of $R$. These adjusted values, together with the raw data, are plotted in Fig. 3. Statistically there is very little to choose between this model and the previous one for the same data, though it can be seen from the figure that the stock–recruitment relationship adjusted for $G$ and $T$ (the dotted curve) is somewhat flatter than the corresponding curve in Fig. 1, and noticeably flatter than the curve fitted to the unadjusted data.

For our third illustrative example we have taken data on stock and recruitment together with measurements of Ekman transport in English sole ($Pleuronectes vetulus$) in Hecate strait, British Columbia. These are tabulated by Fargo (1994). We have selected this data set for illustration here for two reasons. The first is that the study of Boehlert and Mundy (1987) showed an association between numbers of juveniles of this species and current speed, an association further explored by Fargo (1994). The second reason is that the study of Boehlert and Mundy (1987) showed an association between numbers of juveniles of this species and current speed, an association further explored by Fargo (1994). The full model, incorporating the Ekman transport measurement $E$, is:

$$R = \frac{SE^c}{(b + aS)} + \epsilon$$

The stages in calculating the adjusted variables are as follows:

1. Fit the full model given above using non-linear regression methods, estimating the parameters $a$, $b$ and $c$ of the model.

2. Calculate the raw residuals from the fitted equation:

$$R_{res} = R - \frac{SE^c}{(b + aS)}$$

3. Calculate $R$, adjusted for $E$, by adding these residuals to the Beverton–Holt component $S/(b + \hat{aS})$ of the fitted model. These adjusted values will not have the same mean as the original $R$ data, but can simply be modified for presentation purposes so that they do match up. One way of doing this is to divide the calculated values of $S/(b + \hat{aS})$ by their mean and multiply the results by the mean of $R$. A second way is to select an arbitrary middle value for $E$ and substitute this in the equation $SE^c/(b + \hat{aS})$. Finally, add the residuals:

$$R_{adj} = R_{adj} + \frac{S}{(b + \hat{aS})} \cdot \frac{SE^c}{(b + \hat{aS})} + R_{res}$$

4. In similar fashion $R$ adjusted for stock size is defined as:

$$R_{Sadj} = \frac{SE^c}{SE^c} + R_{res}$$

Fig. 4 shows the stock–recruitment plot and fitted Beverton–Holt equation together with the superimposed adjusted variables and the modified Beverton–Holt equation (the dotted line). There is very little change in the stock–recruitment relationship when $E$ is included in the model, although again some of the variation in $R$ around the stock–recruitment function is clearly explained by differences in Ekman transport. Fig. 5 is the plot of recruitment against
Ekman transport. Here there is a somewhat more marked change in the nature of the suggested relationship between $R$ and $E$. It is not intended to suggest here that the curve in Fig. 5 can in any way be distinguished as a statistically better fit to the data than a simple straight line. The relationship is curved because of the assumed model of the form of Eq. 3b.

The conclusion from our work on these adjusted variable (partial residual) plots is that they are a most helpful graphical device that can be used to disentangle the inter-relationships, sometimes complex, that often complicate regression analysis. Graphical methods have much to commend them. An excellent introduction to some novel methods is Chambers et al. (1983). Although the examples that we have presented here have all been rooted in stock and recruitment investigations, the methodology is clearly capable of transfer to other applications.

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