Recruitment models: diagnosis and prognosis

Coby L. Needle
FRS Marine Laboratory, PO Box 101, Victoria Road Aberdeen, AB11 9DB Scotland
(E-mail: c.needle@marlab.ac.uk)

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Abstract

Probabilistic projections of future fish population dynamics and the determination of many management reference points are both driven by fishery recruitment models. In turn, these projections and reference points largely govern perceptions of the likely response of a population to fishery management action. Hence, recruitment modeling is a vital component of stock assessment as carried out for the purposes of strategic fisheries management. This review presents a synopsis of the types of recruitment model that are currently utilised in stock assessments, the reasons that certain models are habitually selected and the problems inherent in their use, and some of the key ongoing research efforts that are attempting to improve the validity of recruitment models. The need for increased multidisciplinary symbiosis in the development of recruitment models is emphasized.

Recruitment modeling

"The most important and generally most difficult problem in biological assessment of fisheries is the relationship between stock and recruitment . . . Fisheries managers simply cannot ignore the fact that if you fish hard enough on any stock, you will reduce recruitment" (Hilborn and Walters, 1992, p. 241).

Fish are a finite resource. Unlike farmers or foresters, marine fishermen can do little to replace or rejuvenate the stock that has been removed by fishing, and must rely on the natural ability of the fish population to replace itself. Whether it is able to do so or not, and whether recruitment (that is, the number of young entering the fished population) will be enough to meet the demands of the fishery in the medium- to long-term, are the subjects of recruitment modeling.

One facet of such modeling is to try to understand what causes the large and often seemingly random variation in the number of recruits to fish populations. Another is to attempt to model the variation in a probabilistic manner, in such a way as to inform perceptions by fisheries managers of the likely future performance of the population under a range of exploitation rates. Many different approaches have been used in the past, but without conspicuous success and the effective prediction of the likely values and variability of future recruitment is still a major challenge for fisheries stock assessment. Despite this, recruitment models are widely used because strategic fishery management *demands* an assessment of the likely future response of fish populations to exploitation.

This paper considers the functions that are currently fulfilled by recruitment models, associated problems, ongoing research efforts to alleviate or circumvent these problems, and future directions which recruitment modeling might take. Attention is focused on the north-east Atlantic context with which the author has most experience, although contrasts with practice elsewhere are also presented. It is hoped that such a synopsis might serve as a useful reminder of how important recruitment modeling is to fisheries science and management, and how much is still to be achieved.

Uses and abuses of recruitment models

The purpose of recruitment modeling

Recruitment models do not exist in isolation. Current incentives to develop them lie in the probabilistic forecast of future catches, and the scientific formulation of realistic management options. In these circumstances, a recruitment model should seek to achieve two main aims: (1) minimization of some biological risk, for example the risk of fishery collapse due to over-exploitation; and (2) minimization of management variations in inputs (such as fishing effort) or outputs (such as fishing quotas), thereby lessening adverse socio-economic impacts. A third aim might be the optimization of longer-term economic or biological goals, although these can be unrealistic and should be made conditional on aims (1) and (2) once levels of acceptable risk have been agreed to between fisheries managers and the fishing industry. Given variations in inputs according to appropriate harvest control rules, and upper and lower bounds on the impacts of conceivable environmental change, managers need appropriate advice in order to meet these aims. Such advice will be based on population projections utilising estimates of the expected values (and variability) of recruitments over short- to medium-term timescales (1–10 years, depending on the longevity of the species concerned).

Good recruitment models greatly improve the ability of managers to make informed policy decisions on these questions, but the determination of the suitability of a particular model is difficult. To be appropriate, a model should be a good statistical fit to the given data, it should encapsulate adequately the biological processes thought to apply to the stock in question, and it should behave sensibly in probabilistic projections (for example, the model should predict stock collapse if an intense fishery is postulated on an already weak adult population). Above all, it should be based on data of good quality. Models deficient in any of these areas may conceivably lead to inappropriate management decisions.

This section discusses the several ways in which recruitment models are used in current fisheries stock assessment around the world. The derivations and formulations of the models mentioned (see Table 1 and Figure 1) are not discussed: the reader is referred to the reviews by Hilborn and Walters (1992) and Quinn II and Deriso (1999).

The uses of recruitment models in fisheries management

Recruitment models are closely linked with management procedures. Estimates of reproductive potential (S), often approximated by spawner biomass, and recruitment (R), on which stock-recruitment modeling is based, are usually derived from assessment models (Megrey, 1989), while external estimates of S and R can themselves be used as inputs to assessments. Reference points for stock dynamics derived from recruitment models can be used directly to drive management action under some form of harvest control rules. Recruitment indices and models are also essential for any form of projection of future stock dynamics.

It must be emphasised at the outset that the relative importance of recruitment modeling in an assessment is very much reliant on the institutional practice of the scientific organisation producing that assessment. Table 2 summarises the use made of recruitment
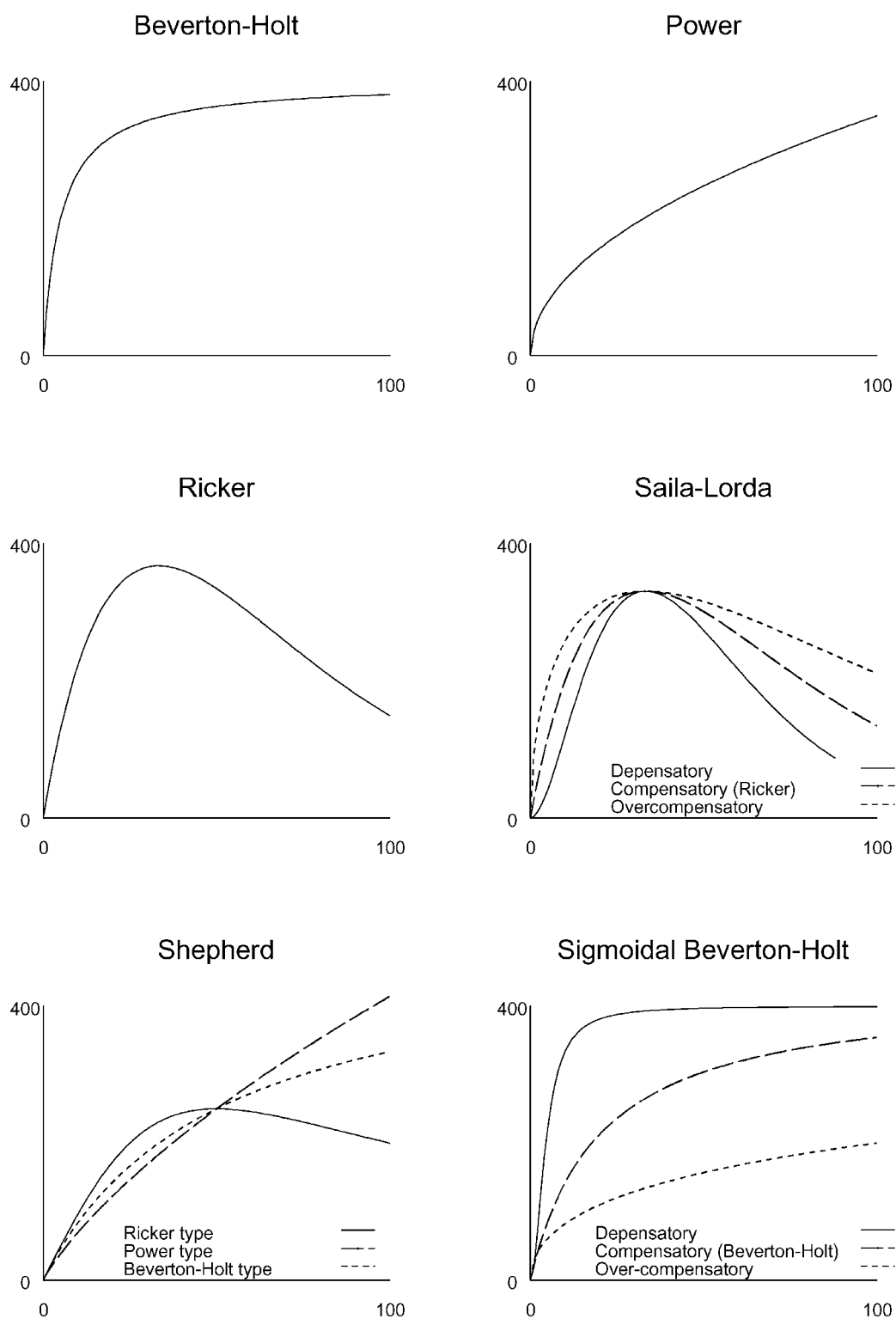
Beverton-Holt

Power

Ricker

Saila-Lorda

Depensatory ——
Compensatory (Ricker) —— —
Overcompensatory ---- -

Shepherd

Ricker type ——
Power type —— · —
Beverton-Holt type ---- -

Sigmoidal Beverton-Holt

Depensatory ——
Compensatory (Beverton-Holt) —— —
Over-compensatory ---- -

Figure 1. A selection of stock-recruit curves from widely-used parametric recruitment models. Estimated recruitment R is plotted on the vertical axis in each case, reproductive-potential index S on the horizontal.

Table 1. A selection of widely-used recruitment models. R denotes estimated recruitment, S denotes an index of reproductive potential, while α, β and γ are parameters to be estimated. S^* is defined to be the lowest desirable level of S, below which recruitment success may be compromised

Model name	Formulation	Principal reference(s)
Beverton-Holt	$R = \frac{\alpha S}{\beta + S}$	Beverton and Holt (1957)
Power	$R = \alpha S^{\beta}$	Cushing (1973)
Ricker	$R = \alpha S e^{-\beta S}$	Ricker (1954)
Saila-Lorda	$R = \alpha S^{\gamma} e^{-\beta S}$	Iles (1994)
Shepherd	$R = \frac{\alpha S}{1 + (S/\beta)^{\gamma}}$	Shepherd (1982)
Sigmoidal Beverton-Holt	$R = \frac{\alpha S^{\gamma}}{\beta + S^{\gamma}}$	Myers et al. (1995)
Piecewise linear	$R = \begin{cases} \alpha S, & S < S^* \\ \alpha S^*, & S \geq S^* \end{cases}$	Butterworth and Bergh (1993), Barrowman and Myers (2000)
Lowess smoother	Locally-weighted regression	Cook (1998)
Markov transition matrices	Transition probabilities between S–R classes	Getz and Swartzmann (1981), Rothschild and Mullen (1985)

models in the four different aspects to be discussed below (inputs to assessments, estimates of management parameters, and short- and medium-term forecasts), by three different scientific organisations, and demonstrates the wide variation that exists in the degree to which recruitment models are employed.

Inputs to stock assessment models

Recruitment models can provide inputs to, or fix constraints on, stock assessment models. Assessment models can be divided into three broad categories. The first, exemplified by implementations of virtual population analysis (VPA; Gulland, 1973) such as XSA (Darby and Flatman, 1994), consists of approaches that make little use of recruitment models to generate year-class sizes as they usually calculate population numbers backwards through a cohort starting with the oldest age.

Statistical catch-at-age models comprise the second category, based on the formulations of Fournier and Archibald (1982) and Deriso et al. (1985), and these have the option to employ an auxiliary stock-recruit model to constrain fitted recruitment values. For example, the ICA model (see Patterson and Melvin, 1996), used for assessing pelagic stocks in the ICES (International Council for the Exploration of the Seas) region (ICES, 2000a), can be configured to make an initial assumption that stock and recruitment for the period being modeled are constrained by the Beverton-Holt model. Other assessment tools of this type, which can incorporate a stock-recruitment formulation, include the ADAPT (Gavaris, 1989) and Stock Synthesis (Methot, 1990) models.

The third category of assessment models contains many recent developments on, and departures from, these standard approaches. For example, an implementation of the Gudmundsson (1994) *Kalman filter* method, known as TSA (time-series analysis), is currently being used to address particular difficulties with assessments of demersal gadoid populations on the European northern shelf (ICES, 2000c), and has the option to constrain recruitment to follow a defined probabilistic stock-recruit model. The use of environmental and stock-structure models in assessment and forecasting is discussed in the Section entitled *Some current approaches.*

Estimates of management parameters

Once derived, stock-recruitment datasets can be used directly to decide on appropriate levels of fishing

Table 2. The use of recruitment models as inputs to fisheries stock assessments varies around the world. Such variability is demonstrated here by analyses of model use in the most recently available assessment reports from three scientific assessment organisations. Reports were mostly obtained from institutional websites. The organisations are the International Council for the Exploration of the Sea (ICES), the Northwest Atlantic Fisheries Organisation (NAFO), and the New Zealand Ministry of Fisheries (NZ MFish). Values in parentheses are the numbers of assessments/projections/reference points for a given organisation that utilise recruitment models: for example, 37 of the 49 ICES reference point estimations use recruitment models

Organisation	Stocks	Analytic assessments	Short-term projections	Reference points	Medium-term projections
ICES	73	57 (9)	46 (37)	49 (37)	29 (28)
NAFO	39	7 (0)	0 (0)	5 (3)	2 (1)
NZ MFish	60	14 (8)	2 (1)	41 (3)	5 (3)
Total	172	78 (17)	48 (38)	95 (43)	36 (32)

mortality for a given stock. Many management parameters can be derived from standard stock-recruitment models, although with due caveats about model suitability and fit. For example, Ludwig and Walters (1981) showed that extrapolations of the stock-recruit curve to high stock sizes are unjustifiable in the presence of measurement error.

Developments over the last 20 years have led to a more widespread adoption of the use of stock-recruitment plots, and the associated yield-per-recruit and SSB-per-recruit curves, to directly determine certain key fishing mortality rates which can be used by managers as reference points for management decisions (either limit points, to be avoided, or target points, to be sought). For example, the slope of the stock-recruitment curve at the origin defines the replacement line (G_{crash}), indicating the level of fishing mortality (F_{crash}) that would theoretically lead to stock extinction . However, F_{crash} is difficult to derive if there are few points near the origin on the stock-recruit scatterplot. As an alternative, the slope of a replacement line (on a stock-recruit plot) corresponding to the lowest observed spawning stock size (B_{loss}) is used: this leads to an estimate of the fishing mortality rate (F_{loss}) corresponding to B_{loss} which may be viewed as a lower bound on F_{crash} (Cook, 1998; O'Brien, 1999). The fishing mortality rate, which is hypothesised to result in maximum sustainable yield (F_{MSY}) can also be derived from a stock-recruitment curve, as can the corresponding biomass level (B_{MSY}). The utility of (F_{MSY}) is questionable: it is hard to estimate precisely, and its use as a target reference point can lead to rapid investment in fleets

and subsequent overcapacity when stock levels fall (Caddy and Mahon, 1995; ICES, 1998). However, it is still used as the basis of management on occasion and under the 1995 United Nations Straddling Fish Stocks Agreement is considered to represent the upper limit on fishing mortality.

Several reference points have been derived within the context of the precautionary approach. B_{lim} refers to a spawning-stock biomass below which there is a high probability of low recruitment (or, alternatively, below which there is no information regarding recruitment response), and may be estimated with reference to a scatterplot of recruitment (R) against spawning-stock biomass (S). Given B_{lim}, F_{lim} can be defined as a fishing mortality rate above which there is an unacceptable risk of stock size falling below B_{lim} in the foreseeable future. Furthermore, a lower mortality rate is often set so that there is a high probability that F_{lim} will be avoided. This rate is estimated differently by each regulatory body, and is referred to variously as F_{pa} (ICES), F_{buf} (NAFO; Northwest Atlantic Fisheries Organisation) or $F_{threshold}$ (ICCAT; International Commission for the Conservation of Atlantic Tunas). It can be defined, for example, as a fishing mortality rate at which there is a less than 10% likelihood that the implied equilibrium biomass will fall below a specified value in the future. This value (B_{pa}, B_{buf} or $B_{threshold}$) may be taken to be the lowest observed spawning-stock biomass (if the fitted stock-recruitment curve has a negative or zero slope over the whole SSB range), or some other point so defined as to reduce the likelihood of recruitment overfishing and minimise the risk of recruitment failure in areas

of unknown stock dynamics. The size of the buffer zone delimited by precautionary reference points will depend on the natural variability in the stock, the perceived precision of the assessment and the level of acceptable risk. Target biomass reference points will sometimes be defined (e.g., ICCAT B_{MSY}, NAFO B_{target}. Re-expression of the stock-recruit curve as a spawner-per-recruit (SPR) formulation allows the derivation of a wide range of additional potential reference points: these have been discussed in detail by Caddy and Mahon (1995) and Schnute and Richards (1998).

Recent research has concentrated on models which are designed to estimate particular aspects of a general stock-recruitment curve in the context of uncertainty. The G_{loss} algorithm (Cook, 1998) estimates the slope-at-origin by extrapolating from the left end-point of a smoothed locally-weighted sum-of-squares (LOWESS) fit down to the origin. Such approaches might be more successful at estimating this statistic than the use of parametric models, which are designed to fit all of the data points equally well and which may thus give biased values for the slope-at-origin. On the other hand, O'Brien (1999) argued that the uncertainty of the fishing mortality rate F_{loss} implied by the estimated value of G_{loss} is difficult to ascertain accurately and that the proposed distribution of F_{loss} can be misleading as a result, particularly in a declining stock.

Short-term forecasts
Various methods are used to produce short-term (1- to 2-year) forecasts of stock dynamics, which in turn are used as the basis of advice on TACs (total allowable catches) for the year following the assessment. Certain assessment methods (ICA and TSA of those mentioned above, for example) naturally produce a one-year forecast of population numbers given an in-year survey index. Another popular method is to calibrate pre-recruit survey indices of various life-history stage abundances and use current in-year surveys to predict year-class size one or two years hence: such an approach is embodied in the RCT3 program prevalent in ICES assessments (Shepherd, 1997). Failing this, the long-term geometric mean of past recruitments may be used to drive forecasts. In-year environmental information has been used in certain optimal cases: an example is the use of an index of upwelling to indicate the prospects of the Bay of Biscay anchovy (*Engraulis encrasicolus*) fishery

(Borja et al., 1998). The inclusion of a large number of different categories (both quantitative and qualitative) of potentially relevant environmental and biotic information in short-term forecasts is facilitated by the use of *neural networks*, which take account of data quality while developing recruitment models empirically. Fuzzy logic is used to determine the optimal network. For example, annual assessments by the US National Marine Fisheries Service of the status of several stocks off the west coast of North America are constrained by neural-network fuzzy-logic recruitment models which account for such factors as rainfall and water volume transport (Chen and Ware, 1999).

Medium-term forecasts
Medium-term (5- to 10-year) projections cannot be based solely on currently available data, but must rely on some model of recruitment. The key task for recruitment modeling is to characterize appropriately the probable variation in future recruitments and hence, the likely fluctuations in stock sizes under all feasible combinations of environmental conditions and fishing mortality. Precautionary reference points for fishing mortality are usually determined by analysis of such projections, which must be probabilistic in order to accommodate the apparently random environmental variations in marine ecosystems. Table 2 summarises the extent to which recruitment models are used in medium-term projections in three scientific assessment organisations. For example, the ICA software package (Patterson and Melvin, 1996) includes a module which produces medium-term probabilistic simulations of future stock dynamics for ICES pelagic stocks which can, if desired, be based on an underlying Beverton-Holt recruitment model: the WGMTERM program (ICES, unpublished data) fulfils the same function for demersal species with rather more flexibility over model choice.

While it is clear that apparently stochastic environmental fluctuations will be the principal determinant of future recruitment variation, it is not so obvious how environmental information should be incorporated into medium-term forecasts. In any case, such inclusion would only be desirable if there was a strong and predictable autoregressive signal in the environmental time series and there was a clear and demonstrable causal linkage between the environment and recruitment. Spawning-stock effects, whether through fecundity or direct density-dependent juvenile

mortality (cannibalism or competition for food), are the only mechanisms that can in theory be managed via fishery regulations. Using a simulation model of an entire fishery assessment system, Basson (1999) demonstrated that inclusion of environmental variables may actually degrade projections if either of the aforementioned prerequisites do not apply.

Choices and problems

In any recruitment analysis there are two key decisions to be made: which model to use, and how it should be fitted to data. At one extreme, both the model and its parameters can be chosen solely with reference to expert knowledge about the biological characteristics of the stock. At the other, competing models can be compared solely on the basis of goodness-of-fit measures arising from statistical parameter estimates, with no reference to biology at all. An intermediate and commonly-taken path is to base the choice of the shape of the curve on assumed biology, and to use statistical methods to estimate the parameters of the selected model. The ability of the chosen model to perform appropriately in a probabilistic medium-term projection framework must also be considered.

It is clear that, however it is achieved, the determination of an appropriate functional form must be complemented by accurate and efficient estimation of the component parameters. Only then can the annual variability about the expectation of recruitment, which is what the fishery manager actually needs to know, become apparent.

Model choice

Strict criteria for selecting the appropriate model are not generally available. Choice of model can be based on *a priori* biological considerations, given what is known of the stock in question, and a statistical measure of goodness-of-fit can be a useful guide. As part of a general Bayesian stock-assessment model, Patterson (1999) suggested that the choice of stock-recruit model could be based on the relative likelihoods of the general Bayesian fits that arose when different models were used. This application of Bayes' theorem is discussed further in McAllister and Kirkwood (1998). Models and model fits can be evaluated further using a variety of meta-analytic techniques (Myers et al., 1995).

It should be remembered that the "best" model (in a biological or statistical sense) is not always the most appropriate for management purposes. Consider the case of a flatfish population to which Beverton-Holt and Ricker curves have been fitted with similar goodness-of-fit statistics (Figure 2). Here the Beverton-Holt curve would be chosen on *a priori* biological grounds, as (for example) cannibalism is unlikely for flatfish for which juvenile and adult populations are geographically discrete. However, it does imply a good level of R until a very low level of S is reached, which may be over-optimistic. In this situation a careful consideration of the robustness of scientific advice (and subsequent management action) to the choice of model would be required. If management inputs (as determined according to harvest control rules) were found to be sensitive to model choice *and* the biological grounds for choosing a particular model were not compelling, the use of other recruitment paradigms (for example, non-parametric models) would have to be considered.

In ICES fishery assessments, combinations of survey recruit indices are routinely used to estimate the size of the incoming year-class (details of the method are given in Shepherd, 1997; see also Section *The uses of recruitment models in fisheries management*), whereas recruitment models are used to drive medium-term projections. The standard procedure is that fits for Beverton-Holt, Ricker and Shepherd curves are estimated and a determination is made of which is most appropriate (given that all fits tend to be poor and statistical diagnostics are generally unhelpful). The reason that these three models are pre-eminent is largely historical (that is, there is an institutional familiarity with them), but also practical: they are not over-complicated, can usually be fitted easily, and cover a broad range of expected curve shapes. The ICES advice to working groups (ICES, 1998) with regards to the precautionary approach is that the choice of model should be based on known biological characteristics: the precautionary approach is a consideration for management rather than assessment. In many other assessment regions, sufficient data are not available to allow for medium-term projections, or there may be institutionalised aversion to their use.

The validity of medium-term projections is starting to be questioned, given that they can be highly sensitive to small perturbations in input data and underlying assumptions, and misleading if no quantitative estimate is made of their inherent uncertainty.
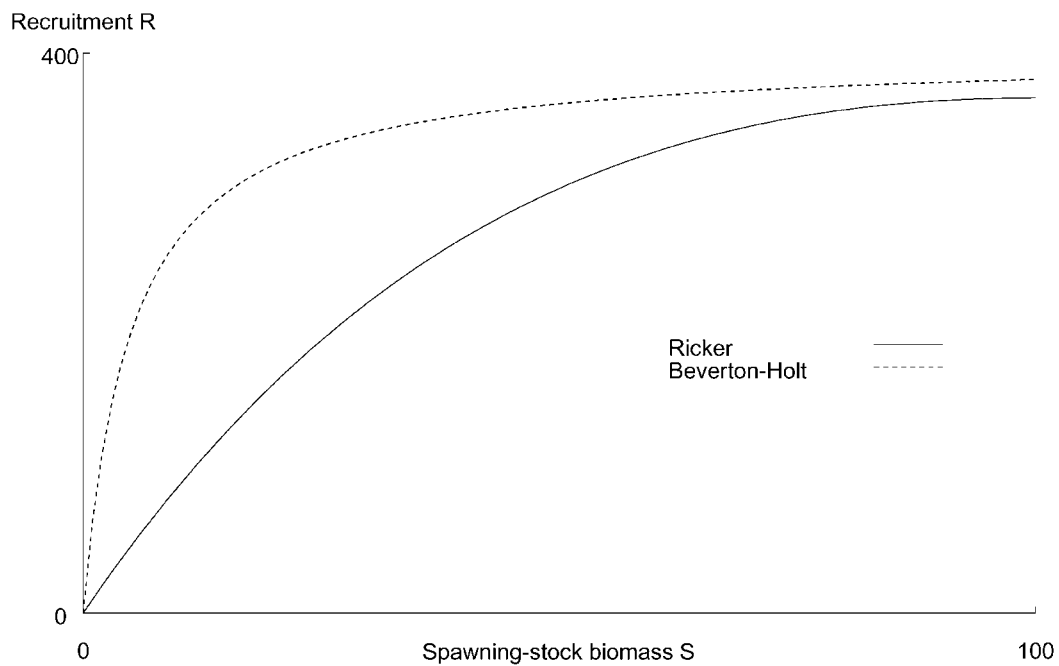
Recruitment R

Figure 2. Slopes of hypothetical Beverton-Holt and Ricker curves near the origin.

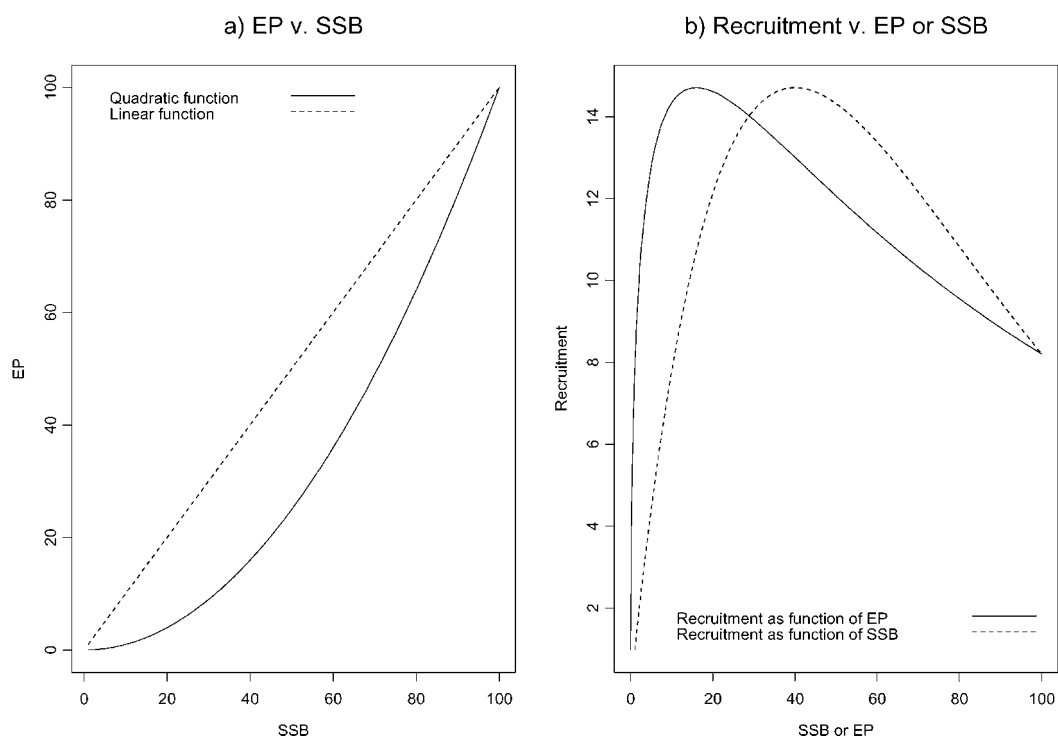a) EP v. SSB   b) Recruitment v. EP or SSB

Figure 3. a. Plot of hypothetical egg production (EP) against spawning stock biomass (SSB) for the commonly-used linear relationship (dotted line) and for the type of quadratic relationship observed for north-east Arctic cod (Marshall et al., 1998; solid line). b. Hypothetical Ricker stock-recruitment relationships when the dependent variable is EP (solid line) and SSB (dotted line).

Problems with stock-recruitment models

Variables

The models of Ricker and Beverton-Holt were originally developed with reference to egg production: "… the annual egg production (E) will be proportional to the annual mean biomass of the mature section of the population" (Beverton and Holt, 1956, p. 430). Over the years, spawning-stock biomass S (that is, Beverton and Holt's mean mature biomass) has become a convenient proxy for E. However, S has been shown to be a non-linear and potentially density-dependent function of E in many cases and is therefore not directly comparable (Rothschild and Fogarty, 1989; Iles and Beverton, 1998), and this reduces the utility of all parametric recruitment modeling. Marshall et al. (1998) showed that, for north-east Arctic cod, E is a quadratic function of S, with high S yielding higher and more variable egg production than would be anticipated if linear proportionality prevailed (due largely to a more diverse age-structure at high S). The corollary to this is that an assumption of linearity may lead to substantial changes in the form of the estimated stock-recruitment relationship, and an underestimate of reproductive potential if stock levels are low (Figure 3). Since eggs from large females are often larger themselves and therefore more likely to survive, S weighted by length or fish mass may be a more valid predictor of recruitment than S alone (Sparholt, 1996). Lowerre-Barbieri (1998) used individual-based simulation models to demonstrate that the population dynamics of multiple spawners (i.e., species that spawn several batches over a season) are governed by quite different processes to single spawners: egg production in such species is not limited by body-cavity size, and in these cases numbers of mature fish could be used as a proxy for production rather than S.

Despite these problems, S is used to model R because it is widely available. Furthermore, to ignore the influence of S altogether is to incite heavy overfishing and very imprudent management (Myers, 1997a). Hence, the widely-accepted approaches to recruitment modeling all involve some recognition of the influence of S. In the words of Fogarty (1993, p. 254): "Potentially high levels of recruitment variability can be expected in populations subject to stochasticity in demographic parameters … and should not be interpreted as evidence for the lack of a stock-recruitment relationship." Ludwig and Walters (1981, p. 716) argued that the study of the influence of stock size on recruitment is vital, for the simple reason that "it is [only] the spawning stock that can be controlled through management decisions." Myers and Barrowman (1996) offered a further validation of the assumption that stock size is influential. They used simple non-parametric tests to ask three key questions: (1) Does the highest recruitment occur when spawner abundance is high? (2) Does the lowest recruitment occur when spawner abundance is low? (3) Is the mean recruitment higher if spawner abundance is above rather than below the mean? They found that, in general, and given adequate ranges and contrasts of spawner abundance, the answers to all three questions were nearly always yes, although this conclusion is dependent to some extent on the degree of compensatory survival experienced by the stock and the life history stage at which recruitment is estimated.

Both stock and recruit data are commonly derived from the same catch-at-age analysis and cannot be viewed as independent variables. The significance of the relationship between stock and recruitment may be specious, particularly if there is little contrast in S. On the other hand it might not, and it would be unwise to assume (as does Gilbert, 1997) that low R always arises from factors other than low S. This point, and potential remedies, are discussed at length by Gilbert (1997) and Hilborn and Walters (1992).

Measurement error

Walters and Ludwig (1981) suggested that a data series which includes the early development stages of the fishery is much less sensitive to the effects of measurement errors than one which only encompasses a period of heavy exploitation, while Schnute and Richards (1995) argued that assessment models from which stock-recruit data are derived perform better when recruitment error is the dominant source of model variability. A simple example of the potential danger of measurement error in environmental variables is given by Walters and Ludwig (1981, p. 705): "High river flows may cause difficulties in counting Pacific salmon spawners: underestimates of spawning would then lead to overestimates of recruits per spawner, and high river flows at spawning time would thus appear to have positive effects on spawning success." The determination of the influence of such environmental factors is particularly problematic. It is often difficult to distinguish between environment and fishing as the principal causative factor behind

any recruitment failure, yet such an understanding is crucial since management decisions depend on which is perceived to be the greater threat to future stocks (Gulland, 1973).

Uncertainty in hyper-parameters (such as maturity ogives, natural mortalities, sex ratios, and fecundities) used in catch-at-age estimates can lead to errors in both S and R. Misreported landings will lead to underestimates of both S and R, causing diagonal shifts of stock-recruit pairs towards the origin. Large errors in estimates of S can make R appear to be independent of S when in fact it is not, and this can promote overexploitation. To examine this, Walters and Ludwig (1981) used a simulation model to generate data in which there was a close stock-recruitment relationship. They then imposed observational error on the data: either the relationship completely disappeared, or the slope of the final stock-recruit curve was heavily biased downwards, thus promoting overexploitation. Hilborn and Walters (1992) showed that the slope at the origin of a stock-recruitment relationship would be under-estimated if uncertainty in S was ignored. Hence estimates of stock and recruitment are only of real value if their accuracy is also assessed. Catch-at-age analyses can give suspect estimates of recruitment, especially if the underlying algorithm does not converge well, and in any case such estimates often represent the pooled contributions of different spawning stocks within a given area. The type, size and number of fish caught are dependent on changes in customer demand, changes in fishing effort and technology, and implementation or circumvention of conservation measures: so the catch data on which catch-at-age analyses (and therefore recruitment estimates) are based can be biased still further (Hislop, 1996).

Time-series bias and autocorrelation

Unless otherwise accounted for, time-series autocorrelation can be a severe problem with parametric stock-recruitment models. If environmental conditions are favourable for several years, it is likely that S and R will both rise. Density-dependent mortality will be overestimated, and a potentially spurious stock-recruitment relationship will appear (Hilborn and Walters, 1992). Such time-series bias is caused by "correlation between deviations and subsequent levels of the independent variables when these levels are not chosen through deliberate experimental design" (Walters, 1985). If this is present, it can be detected using the standard Durbin-Watson test, and Monte Carlo simulation may be used to estimate its magnitude: an example of such analysis is given in Sparholt (1996). Walters (1990) suggested a tractable means by which the influence of autocorrelated environmental effects may be partially reduced, namely a correction equation for the estimated regression parameters in a two-stage Ricker process. The effect of this is usually to make both estimated terms smaller in modulus (desirable as they are generally overestimated), although the correction will not reveal much about the autocorrelation patterns and will thus not provide better forecasts. Sissenwine et al. (1988) described how to incorporate autocorrelation into a parametric relationship by fitting a time-series model to the residuals from the parametric fit (recent developments of this methodology are discussed further in the Section entitled *Some current approaches*).

Myers and Barrowman (1995) tested the importance of time-series bias when a Ricker stock-recruitment model is applied to a variety of marine populations. The results of stochastic runs on simulated populations were used in conjunction with species information to give rough estimates of the time-series bias to be expected for each stock in question, and whether it was likely to be problematic. It was found that time-series bias is important for all semelparous (spawning once) species. For iteraparous species (spawning many times), the conclusion drawn depends on the value of the slope of the Ricker curve at the origin. If this is high (as with cod, for example), bias may not be a problem, while it may be so if the slope is low. Whatever the estimated value of the slope, time-series bias is likely to be present if the stock is over-exploited.

Biological processes

Process uncertainty in models arises from a lack of information about the biological processes affecting marine biota. An example of this is the potential effect of interactions between marine species and the environment, about which knowledge and data are scanty. The timing and *modus operandi* of density-dependent mortality are also areas in which hard evidence to support hypotheses is limited, although recent attempts (see, for example, Bjorkstedt, 2000) to characterize density-dependent processes acting on a series of life-history stages might serve to direct analysis and collation efforts.

In addition, particular aspects of the biology of a species may affect the ability of recruitment models to reflect its stock dynamics appropriately.

For example, Koslow (1992) showed that the high fecundity of many marine teleost species amplifies natural environmentally-induced variation in larval and juvenile mortality to such an extent that no stock-recruitment relationship is generally discernible, even in a simulated stock which is generated on the basis of an underlying relationship. Findings such as these diminish the relevance of parametric stock-recruitment models for highly fecund populations. On the other hand, Mertz and Myers (1996) argued that there was no general linear relationship between recruitment variability and fecundity in any of the 41 species for which sufficient data existed.

Statistical model-fitting problems

Difficulties with parameter estimation for stock-recruitment models include: misuse of common statistical methods and inaccurate parameter fitting; lack of data; lack of contrast in data which inhibits precision of parameter estimates; and extreme sensitivity of the shape of the curve to a small number of outliers. The given dataset often does not warrant the estimation of two or three parameters, and these may be highly correlated as a result. In addition, it should be noted that there are practical impediments to the fitting of three-parameter models to stock-recruitment data: quite apart from over-parameterisation, the formulation of many of these models gives no clearly-defined bounds to the parameters, which leads to very large and flat sum-of-squares surfaces and the strong likelihood of false minima. Thus parameter estimates for such models should be treated with caution. The fact that only one pair of values can be obtained for each year further limits the statistical robustness of any analyses. Fuzzy regression offers a possible solution to such difficulties (Saila and Ferson, 1998), but requires further investigation in the context of fisheries models.

The prevailing management practice can also hinder the analysis. Stock-recruitment relationships are particularly difficult to model when a constant-stock-size harvesting policy is in operation, as the level of contrast in data required for accurate parameter estimation is never allowed to develop (Hilborn and Walters, 1992). The fact that data are generally only available from exploited periods further limits understanding of relevant biological processes. Recent work (for example, Finney et al., 2000) has used biological and environmental indicators to extend backwards the historical time-series of abundance in Pacific salmon stocks and thereby re-evaluate the form of the stock-recruitment relationship for these stocks. This may yield new qualitative perceptions of historical population dynamics, but is reliant upon good auxiliary indicators and the applicability of this approach to marine iteraparous species is as yet unknown. In addition, the relevance of pre-exploitation population dynamics to current fisheries management (often dealing with extremely low spawning stock levels) is uncertain.

Incorrect model selection

The suggestion that a single curve can be used to describe highly-variable recruitment data series is often questionable. The validity of parametric equations has been criticized (for example, Wooster and Bailey, 1989), as little empirical evidence has been found to support them. That is, there has never been an observed case of a stock adhering to a stock-recruitment curve sufficiently closely for that curve to be viewed as a good representation of reality. Plots of recruitment against spawning stock size are usually inconclusive, and stock-recruitment curves may be of little use in a prescriptive sense. Reflecting this view, Schnute and Richards (2001) recently coined the term "fishmetic" to denote the uncertainty inherent in the conversion of the usual laws of arithmetic into fishery models.

In addition, it is incorrect to assume that a single model can be fitted to an entire historical stock-recruit time-series. In general, stock structure is heterogeneous, the timing and influence of external variables change, and stock-recruit parameters vary. This nonstationarity limits the potential applicability of models in projections.

Interpretation of parameters

The parameters of most stock-recruitment models (except for such explicit reparameterisations as given in Schnute and Kronlund, 1996; Schnute and Richards, 1998) do not have direct biological meanings, but are referred to by such euphemisms as "density-dependence" or "limitation": hence, the estimation of a given parameter generally gives little or no information about the underlying biological processes in operation. Bjorkstedt's (2000) work on concurrent density dependence has demonstrated how meaning can be assigned to such parameters, given sufficient process information.

Ongoing research directions

The need for improvement

We have seen that there are many potential pitfalls in recruitment modeling, and in particular the parametric or non-parametric modeling of the stock-recruitment relationship, which is the basis of so many fisheries assessments. Problems arise in the choice of functional form, in the estimation of parameters, and in the assumption that a single model is valid for all space and time. All these must be considered carefully and some measure of the amount of resultant error or bias should be included in any subsequent management advice. Care must be taken with statistical methodology. Parameter estimation can be hindered by uncertainty in the correct form of the relationships between the variables, imprecision in the stock-recruit data, incorrect choice of error distribution, or small sample size. Recent work (for example, Saila and Ferson, 1998) suggests that a possible solution to these problems may lie with fuzzy regression techniques, whereby it is a measure of "vagueness" in the dependent variable (recruitment) that is minimised, rather than a sum-of-squared residual metric. Further exploration of this and other related methodologies would be beneficial. Management advice should be tested for robustness to the choice of stock-recruitment model and fitting method employed, over as many suitable candidate models as feasible. The meta-analytic approach propounded by Ransom Myers and co-workers (summarised in Myers, 1997b; Liermann and Hilborn, 1997), in which the results of analyses on many stocks are combined to aid understanding, may often yield much information about underlying processes and should be investigated fully where possible, in tandem with operating-model simulations of the entire fishery system (for example, Basson, 1999).

Some current approaches

Time-series modeling

One immediate need for fisheries assessment is for an adequate specification of the likely future variability of recruitment. A tractable method might be to model the residuals to a parametric stock-recruit curve as an autoregressive moving-average (ARMA) process, and to use projections of this process as the basis for medium-term simulations (Sissenwine et al., 1988; Box et al., 1994; Needle et al., in press). When compared with a standard WGMTERM bootstrapped-residual approach this tends to reduce the uncertainty in projections of S in the short term, although if such projections are based on an incorrect stock-recruit model then this improved precision might only mean that projections are more precisely wrong. It is also likely that appropriate characterizations of the future development of weights-at-age and maturity ogives are at least as important to forecasting as the modeling of recruitment (Needle et al., 2001). Rather than being utilized directly, time-series structure can be ameliorated: the approach of Walters (1990) in correcting environmental time-series autocorrelation in salmonid stocks could be extended to the study of fisheries in general. Myers et al. (1997) highlighted the bias in stock reconstruction caused by a lack of knowledge of discarding and misreporting, particularly on juvenile fish, and work on this aspect would be opportune.

Non-parametric approaches

Due to the history of recruitment modeling in the ICES area with which the author is most familiar, this review has concentrated largely on parametric models. This is not to say that the parametric approach is universally applicable. The implementations of non-parametric recruitment estimation by Getz and Swartzmann (1981), Rothschild and Mullen (1985), and Evans and Rice (1988), along with more recent work on fuzzy logic (Mackinson et al., 1999) or fuzzy regression (Saila and Ferson, 1998), may be appropriate for certain stocks in which there is little demonstrable parametric stock-recruit relation or where statistical model-fitting problems are acute, and further comparative testing of such methods would be useful. Indeed, recent developments in approaches such as fuzzy logic may enable explicit modeling of the uncertainty inherent in stock-recruit data.

Environmental and process models

There is currently much interest in the incorporation of such models in the assessment process. This direction of effort has many detractors: Myers et al. (1996, p. 300) made the telling point that "environmental correlates are unlikely to be useful in predicting recruitment with sufficient accuracy to be useful in management," and suggested that "the strong emphasis on research into environmental causes of recruitment variability should be reconsidered." In the same vein, Walters and Collie (1988, p. 1848) wrote that "key uncertainties will not be resolved by continued correlative and biological process studies"

(although ecosystem modeling is viewed more favourably; Walters and Kitchell, 2001). However, no valid addition to knowledge of recruitment processes should be rejected just because it is "theoretical" or "practical" in nature. Perhaps such work should concentrate on the estimation of likely upper and lower bounds to environmental variables and the consequences if these positions are approached: it should be remembered that recruitment-environment correlations are more likely to persist over time at the edges of the geographic range of a species (Myers, 1998). Basson (1999) highlighted the need for clarity in both environmental time-series and linkages with recruitment for such an approach to be successful. Environmental influences on recruitment can be modelled as an integral part of the historical assessment method, although this approach is fraught with danger both from inconsistency in the recruitment-environment relationship, and from a lack of understanding of underlying physical mechanisms (Maunder, 1998; ICES, 2000b).

Alternatively, methods such as *birthdate back-calculation* (Methot, 1983; Heath and Gallego, 1998), in which the relative survivorship of different temporal components of annual production is estimated via otolith microstructure analyses and dispersion models, may allow the disaggregation of environmental and spawning-stock effects, thus allowing the underlying form of the latter to be evaluated more clearly. The use of egg production in place of spawning-stock biomass as an index of stock size (Marshall et al., 1998) would have a similar effect. The inclusion of indices of spawner age diversity in stock-recruitment models may go some way towards accounting for extraneous variation in the stock-recruit relationship, as would the use (where possible) of independent estimates of egg production as the predictor variable rather then spawning stock biomass. Larkin et al. (1964) and Paulik (1973) examined population dynamics in separate life-history stages, an approach which has been elaborated upon recently by Ulltang (1996), Nash (1998) and Bjorkstedt (2000), although such studies are hindered by an extreme paucity of data and a requirement for stages that are clearly delimited, either temporally or spatially. This work may also be utilized in the synthesis of environmentally-determined families of stock-recruit models: here a given stock is governed by a series of stock-recruit models, the choice of which is determined by environment. The key concept in these approaches is that of different individual fish

having different responses, driven by phenotypic variations, to the same environmental influences, and that those individuals which survive to recruiting age are probably unusual in some way. It is often argued that models of the population should be grounded on models of the individual (Elliot, 1994; Heath and Gallego, 1997). Work on such individual-based models is progressing (an example is simulation of fecundity in multiple-spawners; Lowerre-Barbieri et al., 1998), but is hindered by computational restrictions and the current lack of an appropriate compensatory density-dependent feedback mechanism.

New recruitment models

Model formulations appear with considerably less frequency now than was once the case. They are now generally tailored to answer particular problems, in contrast to the generalised approaches of the Ricker or Beverton-Holt type. A recent example is the CONCR model (Bravington et al., 2000), a nonparametric smoother fitted to the stock-recruitment scatterplot which is constrained to be always concave and which was designed with the express purpose of determining lower confidence bounds on estimates of F_{crash}. Much attention has been paid to the dynamics of populations as numbers decline, specifically to the possibility of *depensation* (that is, reduced recruits-per-spawner at low spawner numbers). Although statistical evidence of depensation is scarce, this may be a result of the aggregation of substocks into large management stock units or other statistical artefacts and should not be ignored (Myers et al., 1995; Frank and Brickman, 2000; Walters and Kitchell, 2001). An example of a depensatory curve is given by the Saila-Lorda model (Figure 1 and Table 1).

An attainable solution?

It would be a truism to state that much work remains to be done in the study of the stock-recruitment relationship. Johan Hjort showed foresight when he wrote: "A final solution to the problem of fluctuations in the fishery by any permanently valid formula must be regarded as an impossibility and all assertions as to the discovery of such a solution may safely be relegated to the sphere of pure imagination" (Hjort, 1914). If the "solution" referred to was exact prediction of year-class size and recruitment, then Hjort was probably right. However, while pertinent as framed, his bleak outlook may be circumvented by restating the search for a "solution" in terms of the *variability* of future

recruitments in the medium term, and the probable bounds thereof: that is the key task for recruitment modeling.

For models to be tractable, efficient, applicable over extended time periods and directly relevant to the assessment and management process, they should lie at an appropriate point on the continuum from the mathematician's goal of parsimony to the biologist's aim of scientific completeness. Inclusion of every conceivable influential biological factor is not necessary, as long as the given model predicts recruitment reasonably well; so a balance must be struck between multi-species meta-analyses and finely-detailed biological studies of particular stocks. Hutchings and Myers (1994) called for the development of better understanding of life history, population structure and community ecology; the only drawback with this laudable aim is that its attainment may be neither feasible (data-collection restrictions) nor helpful (increasing complexity rather than usefulness). These caveats apply equally well to the "spatially explicit theoretical framework" for ecosystem models advocated by, for example, Baumann (1998). One example of an approach which may be both feasible and useful is that due to Walters and Korman (1999). They developed a model based on the ratio of food supply to predator abundance, which arrives at a relationship very similar to the Beverton-Holt curve but by a different methodological route. At the other extreme, Walters and Collie (1988) called for biological process studies to be viewed as valuable only for hypothesis generation about processes rather than for direct management, and (along with Schnute and Richards, 1995) advocated the use of deliberate harvest policies aimed at varying stock size and thus giving information about the recruitment response to as wide a range of stock sizes as possible. This may be an effective analysis tool, but the risks inherent in such manipulation are enormous and would have to be carefully considered.

Fisheries science in general, and recruitment studies in particular, stand to benefit from the application of non-traditional analyses: the paradigms of Ricker and Beverton and Holt have changed little since their inception and are becoming increasingly inappropriate. It behoves fisheries scientists to look further afield for inspiration, as the appropriation of techniques from a wider field of scientific endeavour can only yield benefits. For example, comparisons of stock-recruitment models could be facilitated by the use of an operational model approach (e.g., Basson, 1999), which would allow testing of the robustness of any chosen management procedure to the particular stock-recruitment model employed and (more importantly) its uncertainty. The meta-analysis approach of Mertz and Myers (1994) and Myers (1997b) could be used to evaluate the validity of a variety of hypotheses, such as the existence of depensation. Meta-analysis can also facilitate the formulation of priors on Bayesian forecasts of recruitment. Hilborn and Liermann (1998) referred to this technique as "standing on the shoulders of giants": that is, making best use of knowledge already gained to improve current studies.

The need for greater cross-fertilization of ideas between fisheries biologists, oceanographers, climate modelers, economists, sociologists, fishermen and mathematicians cannot be overemphasised. Applied mathematical models, in this context, are only worthwhile if they can be used to solve some problem that is faced in the real world of fisheries management. Future work on recruitment modeling must be problem-led and assessment-driven. There should be a movement away from estimation of the parameters of a stock-recruitment curve, and towards an understanding and quantification of recruitment variability and the validity of different models. Robust management procedures should be developed in order to accommodate uncertainty in the stock-recruitment relationship which is unlikely ever to be alleviated.

To conclude: recruitment is not deterministic, and should not be viewed as such. In particular, its variability and the causes thereof are what need to be understood and quantified, rather than precise predictions of the year-class size arising from a given stock in a given year. Parsimonious mathematical models at the scale of the population must be complemented and strengthened by oceanographic studies of causal interactions at a finer level, and the joint pursuit of theoretical and practical strands is to be encouraged. Biological analyses and detailed hydrographic simulations are often interesting and informative, but must be directly relevant to the problem of fish stock assessment. Therefore, a key task must be the linkage of biological and oceanographic recruitment models with assessment procedures. It is the complexity of stock-recruitment models, rather than their predictive power, that has increased over time: the true nature of the causes of recruitment variation is as opaque as ever.

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