

Recruitment in randomly varying environments

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The dominant role of environmental variability in the recruitment dynamics of exploited marine populations has long been recognized. However, studies of the structural features of recruitment variability and its implications for management are comparatively recent. The objective of the present study is to develop stochastic analogues of several stock-recruitment models in an attempt to characterize the expected form of recruitment fluctuations. Approximate expressions for the mean and variance of recruitment are first developed for several models including generalized Ricker and Beverton–Holt models. The mean recruitment is higher under stochastic variation in mortality rates than for the corresponding deterministic case. The approximate variance of recruitment increases with increasing population fecundity (initial cohort size), duration of the pre-recruit phase, and variability in mortality rates, but decreases as mortality rates increase. Extension of these results to multistage recruitment processes is also considered.

Conditional probability density functions of recruitment are next developed for models under the assumption of normally distributed density-independent mortality rates. The general conclusions of the approximate analysis are shown to hold under more specific assumptions regarding the probability distribution of mortality rates. The implication of autocorrelated random variability in mortality rates is also explored. These models provide a general context for interpretation of empirical recruitment distributions.

Key words: recruitment, variability, compensation, density-dependence, environmental stochasticity.

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Introduction

Ricker (1954) and Beverton and Holt (1957) established a general theoretical framework for modelling recruitment dynamics. This approach has been extended to include additional forms of compensatory control during the early life stages (Paulik, 1973; Harris, 1975; Deriso, 1980; Ware, 1980; DeAngelis and Christensen, 1980; Shepherd and Cushing, 1980; Shepherd, 1982; Beyer, 1989; MacCall, 1990). These deterministic models provide important insights into the stability and resilience of fish and invertebrate populations to sustained perturbations such as exploitation. Traditional stock-recruitment models address mechanisms of population regulation but do not include exogenous sources of variability, nor are they intended to provide short-term predictions.

Recruitment variability is a pervasive feature of the dynamics of many marine fish and invertebrate populations (Sissenwine, 1984). Random variation in demographic rates and processes results in the marked recruitment fluctuations characteristic of many exploited marine populations. In variable environments, the relatively low

energetic and behavioral investment in individual progeny of these species virtually assures high variability in survival rates during the early life stages. Here, it is argued that a stochastic representation provides the most realistic approach to modelling recruitment processes for these species (see also Laurence, 1990). The high dimensionality of the biotic and abiotic environment (Rothschild, 1986) complicates any attempt to partition the variance in recruitment into definable sources except in the simplest systems. No attempt is made in the present analysis to model explicitly the linkages between environmental factors and recruitment. Rather, variability in environmental factors in general is assumed to translate into random variation in demographic rates with direct consequences for expected levels of recruitment variability.

Recruitment variability has typically been viewed as an impediment to understanding regulatory processes in exploited fish and invertebrate stocks. Here, an alternative view is adopted which recognizes the intrinsic importance of variability in general, and occasional strong pulses of recruitment in particular, for persistence of populations in stochastic environments (Chesson and Warner, 1981; Sale,

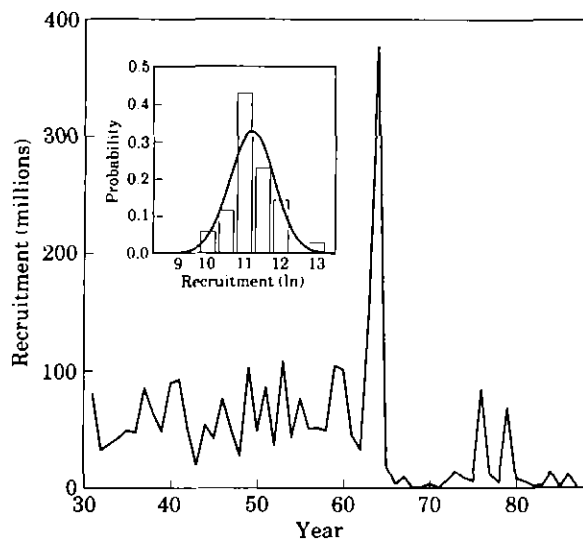


Figure 1. Recruitment estimates for the period 1931–1988 for Georges Bank haddock. The inset shows the empirical probability distribution of \ln -transformed recruit estimates for the period of relative stability in the population (1931–1965). The solid curve is the fitted normal distribution for these estimates.

1982; Chesson, 1983, 1984; Warner and Chesson, 1985). For iteroparous species characterized by high and variable juvenile mortality rates but comparatively low adult mortality, this "storage" mechanism (Chesson, 1983) can play a central role in population and community dynamics (see also Murphy, 1967, 1968; Goodman, 1984). The recruitment strategy of many exploited marine populations conforms to this general pattern. Shepherd and Cushing (1990) proposed a stochastic regulatory mechanism in which increased variance in mortality rates at low population levels results in increased mean levels of recruitment without the mediation of a traditional compensatory process. These studies have collectively led to an increased appreciation of the potential importance of variability, in itself, as a factor in recruitment processes.

Hennemuth *et al.* (1980) described empirical recruitment distributions for marine fish populations. Log-normal distributions were found to provide useful descriptors of recruitment patterns (e.g. Fig. 1). Related developments have been explored by Peterman (1981), Garrod (1982, 1983), Beddington and Cook (1983), Rothschild (1986), Myers *et al.* (1990), Koslow (1992), and Shelton (1992). The objective of the present study is to define the relationship between recruitment variability and population fecundity, mortality rates, and the duration of the pre-recruit phase, and to describe recruitment probability distributions for several stochastic models under certain assumptions regarding the probability distribution of density-independent mortality rates.

Deterministic case

In this section, generalized stock-recruitment models are described and contrasted with a density-independent (null) recruitment model. The solutions of these deterministic models provide the basis for the subsequent development of stochastic models. For economy of notation, density-independent mortality rates are designated μ throughout this paper. For models incorporating compensatory mechanisms, κ represents a threshold cohort size above which compensation dominates (Shepherd and Cushing, 1980), and γ is a shape parameter. It is appreciated that these parameters do have different interpretations in the alternative models.

The appropriate null model for comparison with compensatory recruitment functions is a density-independent model (Fogarty *et al.*, 1992). Rothschild (1986; pp. 110–112) provides an overview of this model in the context of recruitment dynamics. Sissenwine and Shepherd (1987) base their development of a replacement-level concept for indeterminate stock-recruitment relationships on a density-independent recruitment model (see also Shepherd and Cushing, 1990). The rate of change of cohort size for the density-independent model is:

$$\frac{dN}{dt} = -\mu N, \quad (1)$$

where μ is the density-independent mortality rate and N is cohort size. The solution is given by:

$$N_t = R = N_0 e^{-\mu t}, \quad (2)$$

where N_t is the number surviving to recruitment (hereafter designated R), N_0 is the initial number in the cohort (total egg production), and t is the duration of the pre-recruit phase ($t = t_r - t_0$). This expression describes a linear stock-recruitment function through the origin with slope equal to the survival rate. Models of this general form are basic to much of demographic theory and illustrate the linkage between elemental considerations in stock-recruitment theory and demography.

The classical Ricker and Beverton–Holt models can be derived as extensions of the density-independent model to include compensatory sources of mortality (see Rothschild, 1986, for a recent review). The Ricker model assumes an over-compensatory or stock-dependent (*sensu* Harris, 1975) response, while the Beverton–Holt model assumes a density-dependent mechanism. Here, generalizations of both models are employed which include the original forms as special cases (see also Paulik, 1973; Harris, 1975; MacCall, 1990). These generalized models remove the constraint of a linear *per capita* compensatory response and allow greater flexibility in describing recruitment dynamics.

The rate of change of cohort size for the generalized Ricker model can be expressed:

$$\frac{dN}{dt} = -\mu(1 + N_0^\gamma/\kappa)N, \tag{3}$$

where all terms are defined as before and N_0 is a constant. When N_0^γ is greater than κ , compensatory mortality is considered to dominate. The solution can be written:

$$R = N_0 e^{-\mu(1 + N_0^\gamma/\kappa)t}, \tag{4}$$

This functional form gives the well known dome-shaped recruitment function of Ricker (1954) when $\gamma=1$. Examples of the shape of the curve for several values of γ are provided in Fig. 2. The model can be written in more compact form as:

$$R = \alpha N_0 e^{-\beta N_0^\gamma}, \tag{5}$$

where $\alpha = \exp[-\mu t]$ and $\beta = (\mu/\kappa)t$. The expression (μ/κ) represents the compensatory effect. Paulik (1973) introduced a similar expression based on an asymptotic exponential model and MacCall (1990) provided an interesting analysis of a generalized Ricker model of this form with an explicit interpretation of the shape parameter in terms of density-dependent habitat selection.

The rate of change of cohort size for the generalized Beverton–Holt model can be written:

$$\frac{dN}{dt} = -\mu(1 + N^\gamma/\kappa)N \tag{6}$$

and the solution is given by:

$$R = \left\{ \frac{1}{N_0^\gamma} [e^{\mu\gamma t}] + \frac{1}{\kappa} [e^{\mu\gamma t} - 1] \right\}^{-1/\gamma} \tag{7}$$

(examples for several values of γ are provided in Fig. 2). As noted previously by Harris (1975), this family of curves is asymptotic and an over-compensatory response is not possible. This model can be simplified to:

$$R = \{(\alpha'/N_0^\gamma) + \beta'\}^{-1/\gamma}, \tag{8}$$

where $\alpha' = \exp[\mu\gamma t]$ and $\beta' = \{(\mu/\kappa)[\exp(\mu\gamma t) - 1]\}$.

In the following, the original solutions for the generalized Ricker and Beverton–Holt models will be retained to allow a direct interpretation of the effects of the individual parameters. Further, no attempt is made to express the models in terms of spawning stock size by assuming a specific relationship between total egg production and spawning biomass (see Rothschild and Fogarty, 1989, for further discussion on this point).

Stochastic case

Approximate mean and variance

Approximate estimators for the mean and variance of the three recruitment models are developed below for the case where the density-independent mortality coefficient is a time-varying random variable (here designated μ_t). The

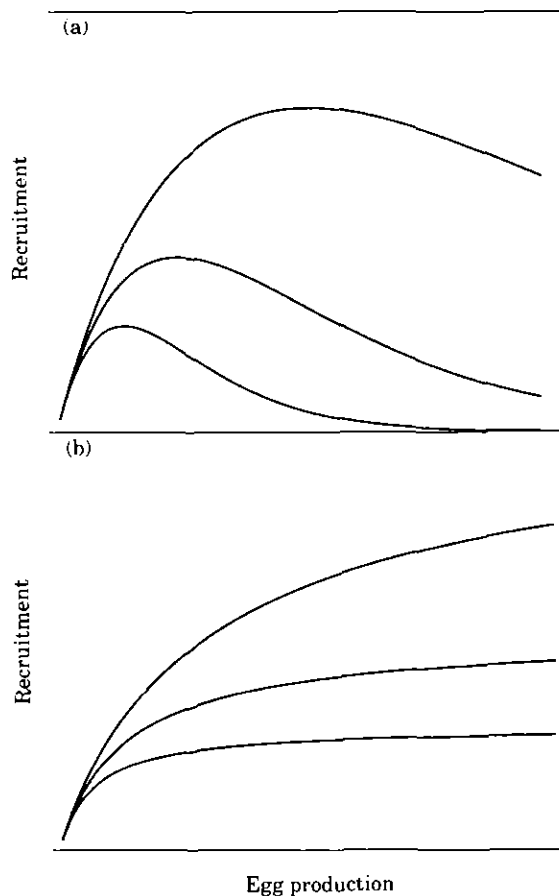


Figure 2. Examples of the Ricker (a) and Beverton–Holt (b) type generalized recruitment curves for three values of the shape parameter $\gamma < 1$ (upper curve), $\gamma = 1$ (middle curve), and $\gamma > 1$ (lower curve).

approximate means and variances are derived using the Delta method (see Kendall and Stuart, 1977, pp. 246–248; Oehlert, 1992) assuming that the variance of the mortality coefficient is relatively small so that higher-order terms in the Taylor series expansion can be ignored (see Reed, 1983, for an application to a full age-structured model). The advantage of this general approach is that no distributional assumptions about the mortality coefficient need be made. Fogarty *et al.* (1991) provide approximate variance estimators for the more traditional forms of the Ricker and Beverton–Holt models (note that for the functional forms used in the present analysis, random variation is introduced into the model in a more complicated fashion). The objective of this analysis is to describe the basic structural relationships between the mean and variance of recruitment and factors such as initial cohort size (egg production), duration of the pre-recruit stage, and the model parameters and not to provide mean and variance estimates *per se*. Inclusion of higher-order terms in

the series expansions may be desirable if estimation is the principal objective. Additional variance results are provided in Appendix A for the case where all model parameters have associated variance and covariance terms.

The mean for the null model is approximately:

$$E(R) \approx N_0 e^{-\bar{\mu}t} [1 + (\sigma_\mu^2/2)t^2], \quad (9)$$

where $\bar{\mu}$ is the mean of μ , and σ_μ^2 is its variance. The variance of recruitment is:

$$V(R) \approx N_0^2 e^{-2\bar{\mu}t} \sigma_\mu^2 t^2 \quad (10)$$

to a first approximation. The variance of recruitment increases geometrically as the initial egg production increases for this model (Fig. 3).

The mean recruitment for the generalized Ricker model is approximately:

$$E(R) \approx N_0 e^{-\bar{\mu}t + N_0^{\gamma}/\kappa} [1 + (\sigma_\mu^2/2) ((1 + N_0^{\gamma}/\kappa)t)^2] \quad (11)$$

and the variance is:

$$V(R) \approx N_0^2 e^{-2\bar{\mu}t + 2N_0^{\gamma}/\kappa} [1 + (N_0^{\gamma}/\kappa)^2 \sigma_\mu^2 t^2]. \quad (12)$$

The approximate variance in recruitment is highest at intermediate levels of initial cohort size (Fig. 3). The variance is lowest at very low and high initial cohort sizes. Strong (1986a,b) has described this type of pattern as "density-vague".

The mean recruitment for the generalized Beverton-Holt model is approximately:

$$E(R) \approx \bar{R} \left\{ 1 + \frac{\sigma_\mu^2}{2\gamma} \left[\frac{\gamma + 1}{\gamma} \bar{R}^{2\gamma} \left[\frac{N_0^{\gamma} + \kappa}{N_0^{\gamma} \kappa} e^{\bar{\mu}\gamma t} \right]^2 - \bar{R}^{\gamma} \left[\frac{N_0^{\gamma} + \kappa}{N_0^{\gamma} \kappa} e^{\bar{\mu}\gamma t} \right] \gamma t \right] \right\}, \quad (13)$$

where \bar{R} is the expression for the deterministic recruitment for this model [Equation (7)]. The variance is:

$$V(R) \approx \bar{R}^{2\gamma+1} \left[\frac{N_0^{\gamma} + \kappa}{N_0^{\gamma} \kappa} e^{\bar{\mu}\gamma t} \right]^2 \sigma_\mu^2 t^2 \quad (14)$$

to a first approximation. The variance of recruitment increases from low initial cohort levels and approaches an asymptote (Fig. 3).

For all three models, the mean recruitment under stochastic variation in the density-independent mortality rate is higher than for the deterministic case. The initial cohort size contributes strongly to the absolute variance of recruitment; the variance increases as the square of the initial number in the cohort and of the duration of the pre-recruit phase. Conversely, the variance declines as mortality rates increase. The higher the combined effects of density-independent and compensatory mortality, the lower the variance of recruitment. The mortality terms therefore effectively serve to counter the effects of high

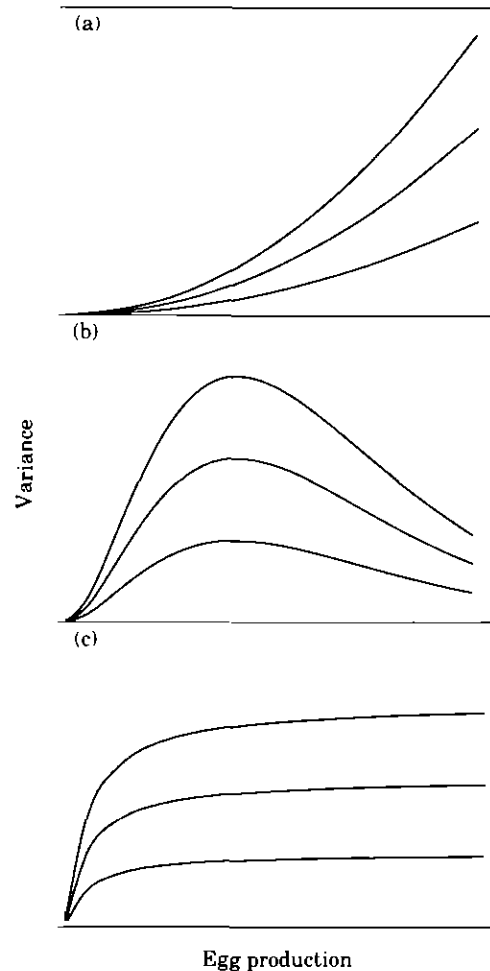


Figure 3. Changes in the approximate variance of recruitment at different initial cohort sizes for the null recruitment model (a), the Ricker model (b), and the Beverton-Holt model (c). For each recruitment model, three levels of variability in the density-independent mortality coefficient are illustrated corresponding to coefficients of variation of 10, 20, and 30%. For clarity, the curves have been drawn to different scales and only an indication of general form is intended.

population fecundity. High mortality rates *per se* clearly do not contribute to recruitment variability. High mortality rates during the early life stages do *indirectly* contribute to high recruitment variability, however, because even a modest coefficient of variation for the mortality term will result in a large absolute variance in mortality. Note that the recruitment variance increases monotonically as the variance of the mortality rate increases (Fig. 3). These general conclusions are shown to hold for size-based recruitment models (e.g. Shepherd and Cushing, 1980; Beyer, 1989) in Appendix B.

The coefficient of variation of recruitment is dominated by the variance of the mortality coefficient (exclusively so for the null model). Accordingly, general statements about the expected levels of relative recruitment variability

cannot be framed in terms of population fecundity or the magnitude of mortality rates, but rather must be considered in the context of factors affecting the variance of the mortality rates including the degree of environmental stochasticity and the life-history characteristics determining the response to exogenous variability.

Multistage models

The implications of complex life-history patterns (*sensu* Wilbur, 1980) for the development of stock-recruitment theory was first explored by Beverton and Holt (1957, pp. 65–66). Paulik (1973) developed the concept of multistage recruitment models in considerable detail (see also Rothschild, 1986). The models described earlier implicitly treat the pre-recruit period as a single life-history stage. However, differences in ecological characteristics for various life-history stages (egg, larva, post-larva, etc.) during this period may require separate treatment of each individual stage to address fully sources of recruitment variability. There has been considerable interest in the question of when during this period recruitment is “fixed” (Sissenwine, 1984). Further, compensatory population regulation can potentially occur at one or more points during the pre-recruit phase and different life stages are subject to different sources of density-independent and compensatory mortality.

Consider a general two-stage recruitment model:

$$R = N_2 = f_2\{f_1(N_0)\}, \tag{15}$$

where R is the number at the end of the second stanza (i.e. recruitment), $f_1(N_0)$ and $f_2(N_1)$ represent the functional forms of the relationships between successive life stages [$N_1 = f_1(N_0)$; $R = f_2(N_1)$]. If it is assumed that the density-independent mortality rate during the first stanza is a random variable ($\mu_{1,t}$) and that the initial number (N_0) is fixed, the variance in the number surviving to the end of the first stage is approximately:

$$V(N_1) \approx \left[\frac{\partial f_1(N_0)}{\partial \mu_{1,t}} \right]^2 \sigma_{\mu_{1,t}}^2, \tag{16}$$

where $\sigma_{\mu_{1,t}}^2$ is the variance of $\mu_{1,t}$. If the density-independent mortality during the second stage is also a random variable ($\mu_{2,t}$), the approximate variance in recruitment will then be:

$$V(R) \approx \left[\frac{\partial f_2(N_1)}{\partial (N_1)} \right]^2 V(N_1) + \left[\frac{\partial f_2(N_1)}{\partial (\mu_{2,t})} \right]^2 \sigma_{\mu_{2,t}}^2, \tag{17}$$

where $\sigma_{\mu_{2,t}}^2$ is the variance of $\mu_{2,t}$, assuming that the covariance between $\mu_{2,t}$ and N_1 is zero. It is clear that the variability in the first stage is translated through to the second stage.

Variability in the mortality rates in either of the two life stages has the potential to contribute strongly to recruit-

ment variability. To see this, consider the simplest possible case where only density-independent mortality rates operate during the two life stages. The mean recruitment is then:

$$E(R) \approx N_0 e^{-\bar{\mu}_{1,t_1} + \bar{\mu}_{2,t_2}} [1 + (1/2)(\sigma_{\mu_{1,t_1}}^2 t_1^2 + \sigma_{\mu_{2,t_2}}^2 t_2^2)] \tag{18}$$

and the variance is:

$$V(R) \approx N_0^2 e^{-2\bar{\mu}_{1,t_1} + 2\bar{\mu}_{2,t_2}} [\sigma_{\mu_{1,t_1}}^2 t_1^2 + \sigma_{\mu_{2,t_2}}^2 t_2^2] \tag{19}$$

to a first approximation if all covariance terms are zero. It is readily verified that both stages contribute equally to the variance in recruitment for the case where $\mu_1 = \mu_2$, $\sigma_{\mu_1}^2 = \sigma_{\mu_2}^2$, and $t_1 = t_2$. These results support the contention of Cohen *et al.* (1988) that the dominant sources of recruitment variability need not occur in the earliest life-history stages. Peterman *et al.* (1988) provide an example of substantial variability occurring in the later larval stages of northern anchovy. Results are provided in Appendix C for more complex two-stage life-history patterns.

In general, the contribution to recruitment variability of the two stages will depend on the cumulative mortality rates, their variances during each stage, the form of the relationship between the success life stages, and the duration of each stage. The methods used here can be readily extended to include the case of variable stage durations. Pepin and Myers (1991) provide empirical evidence for a linkage between larval stage duration and recruitment variability.

Recruitment distributions

Further insight into the structural features of recruitment variability cannot be gained without specification of the full probability distributions of model parameters. Stochastic recruitment models are described below for the case where the density-independent mortality term is assumed to be a Gaussian random variable. The variance of the density-independent mortality rate is taken to be sufficiently small to prevent the occurrence of a change in sign of the mortality rate. In general, this restriction is not limiting within the range of realistic variability levels for the mortality coefficient.

If the mortality coefficient varies randomly during the pre-cult phase, then the overall mortality can be viewed as a sum of random variables. For the case of independent mortality rates and for a relatively large number of such intervals, the overall mortality rate will be normally distributed. However, the central limit theorem also holds for the more general case of certain non-independent stationary processes (e.g. Feller, 1957, p. 374; Loeve, 1963; Anderson, 1971, p. 427; cf. Shelton, 1992) and the assumption of normality is robust under a broad range of conditions (Feller, 1957, p. 240).

The conditional probability density function of recruitment for the density-independent model is lognormal:

$$P(R|N_0) = \frac{R^{-1}}{\sqrt{2\pi\sigma_\mu t}} \exp \left\{ - \frac{[\log_e(R/N_0) + \bar{\mu}t]^2}{2\sigma_\mu^2 t^2} \right\}, \quad (20)$$

where again $\bar{\mu}$ is the mean of the time-varying density-independent mortality rate μ , and σ_μ^2 is the variance of μ . The shape of the distribution for several levels of initial cohort size is illustrated in Fig. 4. The mean recruitment for this model is given by:

$$E(R) = N_0 e^{-\bar{\mu}t + (\sigma_\mu^2/2)t^2} \quad (21)$$

and its variance is:

$$V(R) = N_0^2 e^{-2\bar{\mu}t + \sigma_\mu^2 t^2} [e^{\sigma_\mu^2 t^2} - 1]. \quad (22)$$

The mean recruitment level is higher for the stochastic model than for the corresponding deterministic case by the factor $\exp[\sigma_\mu^2/2)t^2]$; note, however, that the modal recruitment is lower by the factor $\exp[-\sigma_\mu^2 t^2]$ for each level of egg production. The risk of reducing the population to low levels therefore increases with increasing stochasticity. See Horwood (1984) and Tuljapurkar (1989) for related results in full age-structured models.

It is clear that the relative roles of population fecundity, mortality, and the variance of the mortality coefficient are similar in defining the variance of recruitment for the null stochastic model relative to the approximate form described earlier. The coefficient of variation of recruitment for the null model $[CV(R) = \{\exp(\sigma_\mu^2 t^2) - 1\}^{1/2}]$ depends solely on the variance of the mortality coefficient and the duration of the pre-recruit phase.

For the generalized Ricker model, the number of recruits for a given initial cohort size has the distribution:

$$P(R|N_0) = \frac{[R(1 + N_0^2/\kappa)]^{-1}}{\sqrt{2\pi\sigma_\mu t}} \exp \left\{ - \frac{[\log_e(R/N_0) + \bar{\mu}(1 + N_0^2/\kappa)t]^2}{2\sigma_\mu^2(1 + N_0^2/\kappa)^2 t^2} \right\}, \quad (23)$$

where all terms are defined as before. The mean recruitment is given by:

$$E(R) = N_0 e^{-\bar{\mu}(1 + N_0^2/\kappa)t + (\sigma_\mu^2/2)(1 + N_0^2/\kappa)^2 t^2} \quad (24)$$

and its variance is:

$$V(R) = N_0^2 e^{-2\bar{\mu}(1 + N_0^2/\kappa)t + \sigma_\mu^2(1 + N_0^2/\kappa)^2 t^2} [e^{\sigma_\mu^2(1 + N_0^2/\kappa)^2 t^2} - 1]. \quad (25)$$

The form of the recruitment distribution for the case where $\gamma = 1$ is illustrated in Fig. 4. Again, the general conclusions regarding the relative role of initial cohort size, mortality rates, and their variances are supported for the full stochastic model. Results for an alternative specification of the generalized Ricker model are provided in Appendix D.

For the generalized Beverton-Holt model with identical assumptions regarding the density-independent mortality term, the probability density of recruitment is:

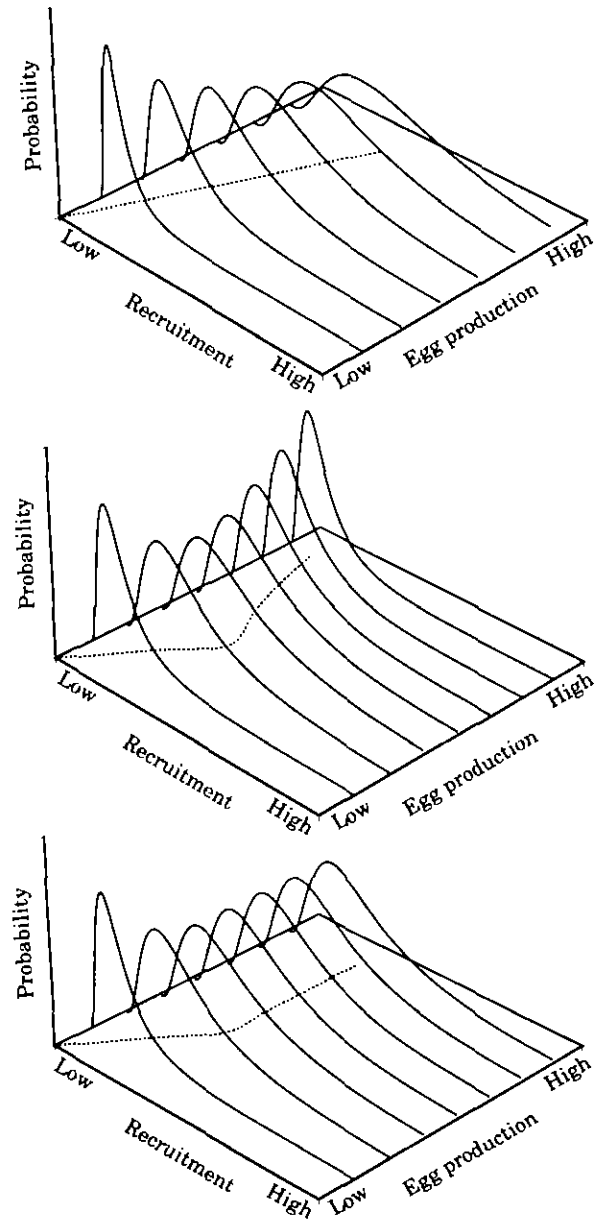


Figure 4. Probability density functions of recruitment for varying initial cohort sizes for the null (density-independent) (a), Ricker-type (b) and Beverton-Holt type (c) stochastic models. For clarity, the curves have been drawn to different scales and only an indication of the general form is intended.

$$P(R|N_0) = \frac{[R(1 + R^2/\kappa)]^{-1}}{\sqrt{2\pi\gamma\sigma_\mu t}} \exp \left[- \frac{[\log_e \left(\frac{R^2(\kappa + N_0^2)}{N_0^2(\kappa + R^2)} \right) + \gamma\bar{\mu}t]^2}{2\gamma^2\sigma_\mu^2 t^2} \right] \quad (26)$$

where all terms are defined as before. Examples of the recruitment distributions for varying levels of initial cohort size are provided in Fig. 4. Analytical expressions for the mean and variance do not appear to be possible for this model. However, the approximate estimators for the mean and variance derived earlier [Equations (13) and (14)] can be used in this case with the inclusion of higher-order terms if necessary for estimation purposes.

Multistage models

These general principles extend to the case of multistage life-history patterns. For the simple two-stage model considered earlier with only density-independent mortality in the two stages, the probability density function of recruitment is:

$$P(R|N_0) = \frac{R^{-1}}{\sqrt{2\pi(\sigma_{\mu_1}^2 t_1 + \sigma_{\mu_2}^2 t_2)}} \exp \left\{ - \frac{[(\log_e(R/N_0) + \tilde{\mu}_1 t_1 + \tilde{\mu}_2 t_2)]^2}{2(\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2)} \right\} \quad (27)$$

where $\tilde{\mu}_1$ and $\tilde{\mu}_2$ are the means of $\mu_{1,t}$ and $\mu_{2,t}$ with variances $\sigma_{\mu_1}^2$ and $\sigma_{\mu_2}^2$, respectively. Then mean recruitment is:

$$E(R) = N_0 e^{-[\tilde{\mu}_1 t_1 + \tilde{\mu}_2 t_2] + 1/2(\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2)} \quad (28)$$

and the variance is given by:

$$V(R) = N_0^2 e^{-2[\tilde{\mu}_1 t_1 + \tilde{\mu}_2 t_2] + (\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2)} [e^{\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2} - 1]. \quad (29)$$

Again, the general conclusions based on the approximate estimators hold for the exact case when the full probability distribution of mortality rates is specified.

Autocorrelated random variability

Environmental variables affecting recruitment are often autocorrelated (Sissenwine, 1984). Steele and Henderson (1984) emphasize the potential importance of autocorrelated random variability in the dynamics of marine populations. To explore the implications of autocorrelated random variability in mortality rates on recruitment levels on an inter-annual (or other appropriate time scale), numerical studies were undertaken assuming that the density-independent mortality rate follows a first-order autoregressive process. Random mortality coefficients were drawn from a bivariate normal distribution according to:

$$\mu_t = \tilde{\mu} + Z_t \sigma_\mu (1 - \rho^2)^{1/2} + \rho Z_{t-1} \quad (30)$$

where μ_t is the density-independent mortality rate for time period t , $\tilde{\mu}$ is the mean mortality rate, Z_t is the standard normal deviate for time period t , σ_μ is the standard devi-

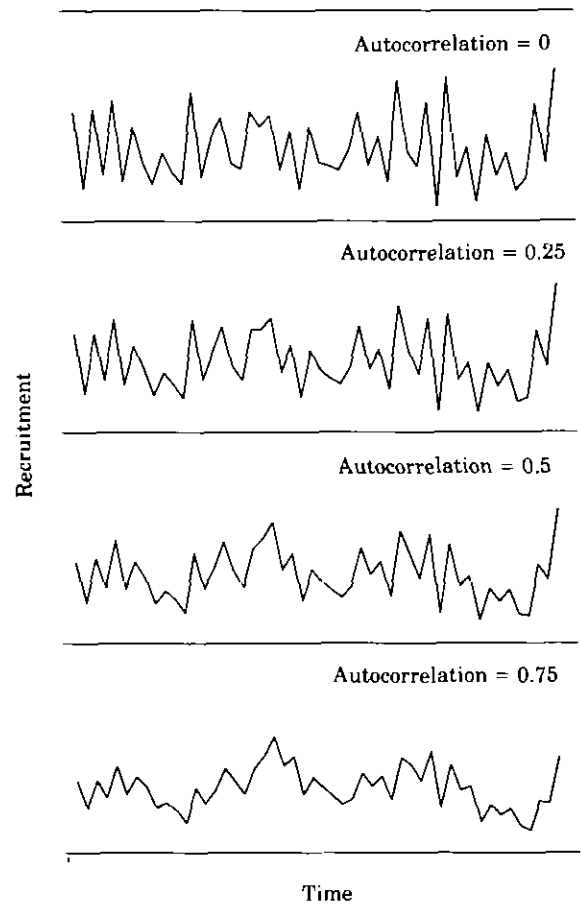


Figure 5. Examples of simulated recruitment trajectories for several levels of autocorrelation in the density-independent mortality rate. The first 50 time steps used in the analysis are shown.

ation of the mortality process, and ρ is the first-order autocorrelation coefficient. The same seed number was used in generation of the pseudorandom numbers in each simulation. Recruitment was evaluated for 600 iterations of the model at four levels of autocorrelation in the density-independent mortality coefficient ($\rho=0, 0.25, 0.50, \text{ and } 0.75$). The first 100 iterations were discarded to prevent any effect of the initial conditions. For the purposes of this exercise, a Ricker-type model was employed with a coefficient of variation in the density-independent mortality coefficient of 25%.

Examples of recruitment trajectories for the four levels of autocorrelation in the density-independent mortality coefficient are provided in Fig. 5 for the first 50 time steps used in the analysis. Autocorrelation in the mortality coefficient translates, of course, into autocorrelation in the sequence of recruitment values where the smoothing effect of the serial correlation is evident (Fig. 5). The empirical probability distribution of recruitment for these

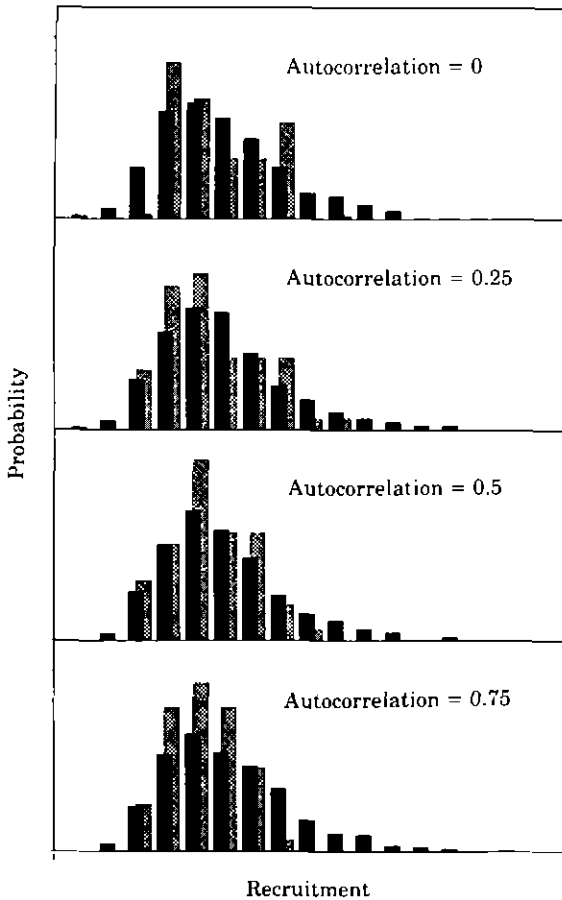


Figure 6. Examples of probability distributions of recruitment levels for the simulations described in Figure 5 based on the first 50 iterations used in the analysis (identical to those depicted in Figure 5) (shaded bars) and for a sample of 500 observations (solid bars) at several levels of autocorrelation in the density-independent mortality rate.

50 observations for each level of autocorrelation is depicted in Fig. 6. Note that in this particular example for a relatively short series of observations, a concentration of the probability mass is evident at higher levels of autocorrelation. As expected, however, for the longer series of 500 time steps, the probability distribution of recruitment is identical for all levels of autocorrelation (Fig. 6). Autocorrelation affects the sequence in which the various recruitment "states" are visited but not their relative frequency for sufficiently large sample sizes. For shorter observation series, chance sequences or runs for the autocorrelated series results in deviations from the underlying recruitment distribution. The shorter series also demonstrates the effect of chance recruitment events on the shape of the observed recruitment distribution. It is clear that a series of 50 observations, which is long by ecological standards, is still sensitive to chance recruitment sequences, creating difficulties in characterizing the underlying distribution.

Discussion

Recruitment variability is an inescapable consequence of the reproductive strategy of most marine teleosts and invertebrates. Survival through the pre-recruit phase is dependent on the probability of an individual encountering prey items of appropriate size, species composition, and density to support adequate growth and nutrition, avoiding predation and disease and avoiding advective transport to unfavourable areas. Random storm events can disrupt the vertical distribution of fish larvae and their prey, affecting feeding success (Lasker, 1975, 1981; Buckley and Lough, 1986; Peterman and Bradford, 1987). Turbulence can also affect encounter rates between predators and their prey (Rothschild and Osborn, 1988; Rothschild *et al.*, 1989). Losses due to predation are dependent on chance encounters with predators and the probability of a successful attack (Vlymen, 1977; Beyer and Laurence, 1980, 1981). Offshore transport of larvae in random advective events (e.g. entrainment in warm or cold core rings, wind generated currents, upwelling, etc.) can also potentially affect survival rates (e.g. Nelson *et al.*, 1977; Flierl and Wroblewski, 1985; Myers and Drinkwater, 1989). These considerations underscore the probabilistic nature of mortality during the pre-recruit phase and the need for explicit recognition of environmental-driven variability.

Recruitment variability has often been characterized as the central problem of fish population dynamics (Sissenwine, 1984). Further, high levels of recruitment variability have been cited as evidence against the existence of a relationship between stock and recruitment (e.g. Hall, 1988). Here, it is argued that: (1) there is necessarily a relationship between the adult population (or more specifically egg production) and recruitment and that the appropriate null model is a density-independent model; and (2) potentially high levels of recruitment variability can be expected in populations subject to stochasticity in demographic parameters (particularly growth and mortality) and should not be interpreted as evidence for the lack of a stock-recruitment relationship. With respect to the first point, there can be no recruitment without egg production; stock and recruitment are therefore functionally related. The central issue is whether the relationship is linear (density-independent) or non-linear (compensatory) and not whether there is a structural relationship. A population with no little or no compensatory capacity will be particularly vulnerable to exploitation. Accordingly, it is extremely important to specify the null model correctly (Fogarty *et al.*, 1992). With respect to the second point, consider a population characterized by a purely density-independent recruitment process with normally distributed instantaneous mortality rate μ , with $\bar{\mu} = 10.0$ and $\sigma_{\mu}^2 = 1.0$ and an age of recruitment of 1 year. The coefficient of variation of the mortality rate is only 10% but this translates into a coefficient of variation of recruitment

of 131% [$CV(R) = 100\{\exp(1.0) - 1\}^{1/2}$]. These values are within the ranges expected for the mortality coefficient and for the expected range of recruitment variability (e.g. Sissenwine, 1984; Koslow, 1992). Relatively small changes in demographic parameters can have large effects on recruitment (see also Houde, 1987; Underwood and Fairweather, 1989). In this case, there is an underlying linear relationship between stock and recruitment which is highly variable because of small relative variation in mortality.

The stochastic models described above provide a theoretical setting for interpretation of empirical recruitment distributions. The conditional probability density function of recruitment is of the lognormal type when the density-independent mortality rate is normally distributed (for a comprehensive review of ecological applications of the lognormal distribution, see Dennis and Patil, 1991). Although the assumption of normally distributed mortality rates is sufficiently robust to provide useful general results, application to any particular population should carefully be evaluated. Lognormality implies that recruitment levels for a given initial cohort size will generally be low to moderate with occasional large year-classes (representing the right-hand tail of the distributions). The mean recruitment is higher for the stochastic case than the recruitment under the corresponding deterministic model as a result of the dominant effect of these strong year-classes.

The full stochastic models described here represent the probability density functions of recruitment for each level of initial cohort size (egg production). Empirical recruitment distributions drawn from varying initial cohort sizes will, in general, consist of distribution mixtures. Accordingly, there should be no expectation that any simple density function will necessarily apply to recruitment estimates unless they are partitioned to represent restricted ranges of egg production levels.

In principle, the roles of different life-history characteristics as determinants of recruitment variability can be examined in comparative studies among taxa and across environmental gradients. However, comparisons of recruitment variability among taxonomic groups differing with respect to basic life-history features should not focus on factors such as fecundity and mortality rates *per se*, but rather on the biological, behavioural, and environmental attributes that affect the variance of mortality rates or other relevant demographic parameters. There are clear tradeoffs between clutch size and individual egg size for many organisms (Godfray *et al.*, 1991), including teleosts (Elgar, 1990). Species characterized by low fecundity and extensive energetic or behavioural investment in individual progeny may be expected to have lower relative variance in recruitment not because of low reproductive output (and low mortality rates) *per se* but because of the mechanisms that serve to reduce the variance in mortality. To the extent that larger egg or larval size reduces the

variance in mortality *in a given environment* by reducing the variability in vulnerability to predation, periods of food deprivation (Miller *et al.*, 1988), or advective loss, the relative variance in recruitment will be reduced.

Pepin and Myers (1991) found no significant relationship between recruitment variability and either egg size or length at hatch in marine teleosts. However, the problem may be brought into sharper relief by considering additional taxonomic groups (e.g. elasmobranchs) which offer a broader contrast in progeny size. It is also necessary to consider the general environmental setting. Within the framework proposed here, the appropriate comparisons would be for populations with different life-history characteristics subjected to the same levels of environmental stochasticity and not those drawn from differing environments. Myers (1991) has demonstrated that recruitment variability is higher for populations at the extremes of the range for three species of marine teleosts. The problem of comparing different species in widely differing environments greatly compounds the difficulty in examining the implications of alternative reproductive strategies.

It may be difficult or impossible to partition the variance in recruitment into its component sources except in systems dominated by strong environmental signals. The numbers of covarying environmental variables that can affect recruitment is potentially very large and it may be difficult or impossible to disentangle the population signal from the environmental noise in these systems (however, see Nelson *et al.*, 1977; Penn and Caputi, 1985; Reisch *et al.*, 1985; Stocker *et al.*, 1985; Tang, 1985; and Crecco *et al.*, 1986, for examples where empirical recruitment-environmental models have been successfully developed). Because our capacity to predict the environmental variables themselves is limited, the development of long-term predictors of recruitment is necessarily limited even if all the environmental interactions could be specified (Walters and Collie, 1988).

Variable recruitment should not be taken as evidence of a lack of compensatory population controls. Indeed, it is clear that much higher variability is possible than is generally observed (Ursin, 1982; Gulland, 1982; Beverton *et al.*, 1984; Beyer, 1989; Jones, 1989). Compensatory mortality and/or growth rates provide one class of mechanisms that can dampen recruitment variability. Variability in mortality rates obscures the functional form of the relationship between population egg production and recruitment. For short time series, in particular, it will be extremely difficult to determine the underlying form of the stock-recruitment relationship (e.g. Koslow, 1992). This problem is exacerbated by measurement error in the recruitment and egg production (or spawning biomass) estimates (Walters and Ludwig, 1981). These observations suggest that the role of empirical stock-recruitment diagrams in understanding recruitment processes is inherently limited. Alternative methods of estimation of the parameters of

stock-recruitment models are needed. The focus should be on testing specific mechanisms and not on curve-fitting exercises.

Renewed emphasis has been placed on the potential role of certain compensatory mechanisms, including size-dependent processes affecting recruitment (Shepherd and Cushing, 1980; Werner and Gilliam, 1984; Houde, 1987, 1989; Anderson, 1988; Beyer, 1989). Examination of the interaction of growth and mortality rates and its implications for recruitment dynamics is feasible in field and laboratory observations and experiments. This important class of compensatory mechanisms should be examined in detail. It is clear that very subtle interactions between growth rates (which are particularly dependent on variation in temperature and food supplies) and predation can have important effects on recruitment. Other compensatory mechanisms that are amenable to detailed study include changes in maturation rates and fecundity, cannibalism, and density-dependent predation. Process-oriented studies designed to test for density-dependent mortality rates over a range of cohort sizes can be undertaken (see Beverton and Iles, 1992a,b, for a synthesis of results for certain flatfish species). The focus of these studies should be on directed observational and experimental studies designed to test specific hypotheses regarding modes of population regulation.

The occurrence of dominant year-classes may allow persistence of iteroparous species through periods of unfavourable environmental conditions if adult survival rates are relatively high. The stochastic models described above are consistent with a mechanism of this type. The potential importance of storage mechanisms in fishery dynamics has been appreciated qualitatively since Hjort's (1914) classic studies. A species may be able to persist by producing occasional strong cohorts and "overwhelming" competitors or predators. An intensive fishery reduces the mean life expectancy of a cohort. If the life expectancy is substantially reduced, the probability of decreased population size or extinction is increased. Chesson (1985) has advanced similar arguments with respect to the maintenance of genetic diversity. Selection for different genotypes under different environmental conditions, coupled with random variation in survival rates, could favour the maintenance of genetic variation in the population if dominant year-classes are comprised of different genotypes under differing environmental conditions. Harvesting may therefore have direct implications for the reproductive strategies and genetic structure of marine fish and invertebrates in a way that could not be foreseen based on a deterministic view of the system. The central lesson of recruitment dynamics may lie not in uncovering the manifold mechanisms that contribute to variability but rather in understanding the ways in which the variance is important in itself and its implications for devising appropriate management strategies.

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Appendix A

The Delta method (see Kendall and Stuart, 1973) provides a useful technique for estimating the moments of an expression as a function of the variance of input parameters. It is assumed here that the variance of the input parameters is relatively small so that higher-order terms can be ignored. Results are provided below for the approximate variance when all of the model parameters are random variables for the Ricker and Beverton-Holt models. For simplicity, μ , γ , and κ will be used to designate the time-varying coefficients and will not be subscripted but it should be understood that these symbols represent time-varying coefficients. For the recruitment model:

$$R = f\{N_0, \mu, \kappa, \gamma\}, \quad (A.1.1)$$

assuming a fixed initial cohort size N_0 , the variance in recruitment is approximately:

$$V(R) \approx \left\{ \frac{\partial f(N_0)}{\partial \mu} \right\}^2 V(\mu) + \left\{ \frac{\partial f(N_0)}{\partial \kappa} \right\}^2 V(\kappa) + \left\{ \frac{\partial f(N_0)}{\partial \gamma} \right\}^2 V(\gamma)$$

$$\begin{aligned}
 &+ 2 \left\{ \frac{\partial f(N_0)}{\partial \mu} \right\} \left\{ \frac{\partial f(N_0)}{\partial \kappa} \right\} \text{COV}(\mu, \kappa) \\
 &+ 2 \left\{ \frac{\partial f(N_0)}{\partial \mu} \right\} \left\{ \frac{\partial f(N_0)}{\partial \gamma} \right\} \text{COV}(\mu, \gamma) \\
 &+ 2 \left\{ \frac{\partial f(N_0)}{\partial \kappa} \right\} \left\{ \frac{\partial f(N_0)}{\partial \gamma} \right\} \text{COV}(\kappa, \gamma).
 \end{aligned} \tag{A.1.2}$$

where COV indicates the covariance between parameters and all other terms are defined as before. The results provided earlier for the null model are complete if N_0 is fixed. Results are provided below for compensatory models of the Ricker and Beverton-Holt types.

For the generalized Ricker model, the appropriate partial derivatives for substitution in the above equation are:

$$\frac{\partial f(N_0)}{\partial \mu} = -\bar{R} \{ (1 + N_0^\gamma / \kappa) \}, \tag{A.1.3}$$

(where \bar{R} is the deterministic recruitment for a given level of egg production for this model)

$$\frac{\partial f(N_0)}{\partial \kappa} = N_0^{1+\gamma} e^{-\mu t + N_0^\gamma / \kappa} \kappa^{-2} \mu t \tag{A.1.4}$$

and

$$\frac{\partial f(N_0)}{\partial \gamma} = -N_0^{1+\gamma} \log_e N_0 e^{-\mu t + N_0^\gamma / \kappa} \kappa^{-1} \mu t \tag{A.1.5}$$

For the generalized Beverton-Holt model, the partial derivatives are:

$$\frac{\partial f(N_0)}{\partial \mu} = -\bar{R}^{\gamma+1} e^{(\gamma \mu t)} \frac{N_0^\gamma + \kappa}{N_0^\gamma \kappa} \tag{A.1.6}$$

$$\frac{\partial f(N_0)}{\partial \kappa} = \bar{R}^{\gamma+1} \kappa^{-2} \gamma^{-1} [e^{\gamma \mu t} - 1] \tag{A.1.7}$$

and

$$\begin{aligned}
 \frac{\partial f(N_0)}{\partial \gamma} = & -\bar{R}^{\gamma+1} \gamma^{-1} \exp^{\gamma \mu t} \left[\frac{N_0^\gamma + \kappa}{N_0^\gamma \kappa} - \frac{\log_e N_0}{N_0^\gamma \mu t} \right] \mu t \\
 & + \log_e \bar{R}^{-\gamma} \gamma^{-2} \left\{ \frac{1}{N_0^\gamma} e^{\gamma \mu t} + \frac{1}{\kappa} [e^{\gamma \mu t} - 1] \right\}^{-1/\gamma}
 \end{aligned} \tag{A.1.8}$$

where again, in all cases, \bar{R} is the deterministic recruitment for a given initial cohort size for the Beverton-Holt type model.

Appendix B

Recruitment models based on density-dependent growth during the early life stages have been described by

Beverton and Holt (1957), Shepherd and Cushing (1980), and Logan (1985). Beyer (1989) presented a generalized framework for consideration of size-based recruitment models. These models are predicted on the premise that mortality rates decrease with increasing size (Ware, 1975) and that individual growth is stock- or density-dependent. The role of size dependent predation, in particular, has been implicated as a specific regulatory mechanism. These size-based models link an expression for individual growth rate (here taken to be exponential) with the cohort model. The following development is based on the Shepherd-Cushing approach. Because of space limitations, only results for the variance of recruitment will be given although the expected values can be easily obtained using the Delta method and are readily shown to be similar to the age-based models.

The null size based recruitment model is:

$$\frac{dW}{W} = -\frac{G}{\mu} \frac{dN}{N}, \tag{A.2.1}$$

where G represents the individual growth rate. The solution is:

$$R = N_0 e^{-\mu T_0}, \tag{A.2.2}$$

where $T_0 = \{ (1/G) \ln(W_1/W_0) \}$ (Shepherd and Cushing, 1980), W_1 is the weight (size) at recruitment, and W_0 is the initial size. T_0 is the time required to grow through the pre-recruit phase.

Random variation in the size-specific mortality rates can be expected as a result of variability in predator fields or in physical conditions. The maximum growth rate will also vary randomly with changes in temperature and prey availability. If both the density-independent mortality term and the growth rate are random variables, the variance of recruitment will be approximately:

$$V(R) \approx N_0^2 e^{-2\mu T_0} V(c), \tag{A.2.3}$$

where $c = \mu T_0$ and

$$V(c) \approx c^2 \left[\frac{V(\mu)}{\mu^2} + \frac{V(G)}{G^2} - \frac{2\text{COV}(\mu, G)}{\mu G} \right]. \tag{A.2.4}$$

The case where either the mortality coefficient or the maximum growth rate alone varies can be easily determined.

Next consider a size-based Ricker-type model:

$$\frac{dW}{W} = -\frac{G^*}{\mu} \frac{dN}{(1 + N_0^\gamma / \kappa) N}, \tag{A.2.5}$$

where G^* represents the maximum individual growth rate (Shepherd and Cushing, 1980) and all other terms are defined as before. The solution is:

$$R = N_0 e^{-\mu(1 + N_0^\gamma / \kappa) T_0}, \tag{A.2.6}$$

where $T'_0 = \{(1/G^*)\ln(W_1/W_0)\}$ (the time required to grow through the pre-recruit phase at the maximum growth rate). This result is, of course, similar to the generalized Ricker model described earlier but embodies a completely different compensatory mechanism. The approximate variance is:

$$V(R) \approx N_0^2 e^{-2[\mu(1 + N_0^{\gamma}/\kappa)T'_0]} [1 + N_0^{\gamma}/\kappa]^2 V(c), \quad (\text{A.2.7})$$

where $c' = \mu T'_0$ and

$$V(c') \approx (c')^2 \left[\frac{V(\mu)}{\mu^2} + \frac{V(G^*)}{G^{*2}} - \frac{2\text{COV}(\mu, G^*)}{\mu G^*} \right]. \quad (\text{A.2.8})$$

Finally, the generalization of the size-based model of Shepherd and Cushing (1980) is:

$$\frac{dW}{W} = -\frac{G^*}{\mu} \frac{dN}{(1 + N^{\gamma}/\kappa)N}, \quad (\text{A.2.9})$$

where all terms are defined as before. The solution can be written:

$$R = \left\{ \frac{\kappa + N_0^{\gamma}}{\kappa N_0^{\gamma}} e^{\gamma \mu T_0} - \frac{1}{\kappa} \right\}^{-1/\gamma}, \quad (\text{A.2.10})$$

where again $T'_0 = \{(1/G^*)\ln(W_1/W_0)\}$. The approximate variance is:

$$V(R) = R^{2(1+\gamma)} \left[\frac{\kappa + N_0^{\gamma}}{\kappa N_0^{\gamma}} e^{\gamma \mu T_0} \right]^2 V(c), \quad (\text{A.2.11})$$

where $c = \mu T'_0$ and $V(c)$ is defined as above.

Appendix C

A simple, density-independent multistage model was described earlier. Consider a more complex model in which the first stage follows a Ricker-type formulation and the second stage is density-independent. The mean recruitment is approximately:

$$E(R) \approx N_0 e^{-(\bar{\mu}_1(1 + N_0^{\gamma}/\kappa_1)\bar{\mu}_1 + \bar{\mu}_2 t_2)} \{1 + (1/2)[\sigma_{\mu_1}^2(1 + N_0^{\gamma}/\kappa_1)^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2]\} \quad (\text{A.3.1})$$

using the Delta method where $\bar{\mu}_1$ and $\bar{\mu}_2$ are the means of $\mu_{1,t}$ and $\mu_{2,t}$ for stages 1 and 2 and $\sigma_{\mu_1}^2$ and $\sigma_{\mu_2}^2$ are their variances. The variance of recruitment is:

$$V(R) \approx N_0^2 e^{-2[\bar{\mu}_1(1 + N_0^{\gamma}/\kappa_1)\bar{\mu}_1 + \bar{\mu}_2 t_2]} [\sigma_{\mu_1}^2(1 + N_0^{\gamma}/\kappa_1)^2 t_1^2 + \sigma_{\mu_2}^2 t_2^2] \quad (\text{A.3.2})$$

to a first approximation if all covariance terms are zero.

Conversely, if the first stage is density-independent and the second stage follows a Ricker-type model, we have:

$$E(R) \approx N_0 e^{-(\bar{\mu}_1 t_1 + \bar{\mu}_2(1 + N_1^{\gamma}/\kappa_2)t_2)} \{1 + (1/2)[\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2(1 + N_1^{\gamma}/\kappa_2)^2 t_2^2]\} \quad (\text{A.3.3})$$

with approximate variance:

$$V(R) \approx N_0^2 e^{-2[\bar{\mu}_1 t_1 + \bar{\mu}_2(1 + N_1^{\gamma}/\kappa_2)t_2]} [\sigma_{\mu_1}^2 t_1^2 + \sigma_{\mu_2}^2(1 + N_1^{\gamma}/\kappa_2)^2 t_2^2] \quad (\text{A.3.4})$$

if all covariance terms are zero.

An assessment of the magnitude of the variance when a density-dependent stage follows a density-independent stage relative to the converse requires specification of the coefficients and their variances.

Appendix D

An alternative specification of the generalized Ricker model can be developed as:

$$\frac{1}{N} \frac{dN}{dt} = -(\mu + \mu' N_0^{\gamma}), \quad (\text{A.4.1})$$

where μ' is the stock-dependent mortality rate. The solution of this deterministic equation is:

$$R = N_0 e^{-(\mu + \mu' N_0^{\gamma})t}. \quad (\text{A.4.2})$$

If we now take the density-independent mortality rate to be a normally distributed random variable μ , the conditional probability density function of recruitment for a given initial cohort size is:

$$P(R|N_0) = \frac{R^{-1}}{\sqrt{2\pi\sigma_{\mu}^2 t}} e^{-\frac{[\log_e(R/N_0) + (\mu + \mu' N_0^{\gamma})t]^2}{2\sigma_{\mu}^2 t^2}}. \quad (\text{A.4.3})$$

where all terms are defined as before. The mean recruitment is:

$$E(R) = N_0 e^{-(\bar{\mu} + \mu' N_0^{\gamma})t + (1/2)\sigma_{\mu}^2 t^2} \quad (\text{A.4.4})$$

and the variance is:

$$V(R) = N_0^2 e^{-2[\bar{\mu} + \mu' N_0^{\gamma})t + \sigma_{\mu}^2 t^2]} [e^{\sigma_{\mu}^2 t^2} - 1]. \quad (\text{A.4.5})$$

Note that the variance of the density-independent mortality coefficient enters the model in a much simpler fashion than in the alternative version of the generalized Ricker model described in the text where the variance of the mortality coefficient also affects the overall compensatory coefficient (μ/κ).