

Abstract.—A simple analytical technique is developed for estimating the predictability of recruitment, that is, correlations between recruitment and stage-specific mortalities or abundances. The method requires the input of estimates of the variability of stage-specific mortalities, which may be calculated from mean stage-specific mortalities by applying a published regression. It is shown that modification of this regression to compensate for sampling error in field measurements of abundance significantly reduces the estimated standard deviation of log-recruitment, which is an important factor in the predictability calculations. It is concluded that the prospects for predicting recruitment from egg or larval surveys or from environmental variables are quite poor for fish stocks showing the typical distribution of mortality across stages.

Estimating the predictability of recruitment

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The problem of predicting recruitment remains central to fisheries science (e.g. Bradford, 1992). Approaches to this task may involve finding environmental correlates of recruitment or the field sampling of prerecruit life history stages. In this study we present simple analytical formulae that permit one to estimate the potential explainable variance of recruitment without the use of detailed, specific data.

Certain environmental factors may be correlated with recruitment. Wind speed has been proposed as a determinant of recruitment because storm-driven mixing can disperse larvae and their prey, reducing food availability (Lasker, 1975, 1981; Buckley and Lough, 1987; Peterman and Bradford, 1987). Larval food supply may also be influenced by the lag between appearance of larvae and the peak abundance of their prey (Cushing, 1990). The intensity of turbulence may control the frequency of contact between larvae and their prey (Rothschild and Osborn, 1988). Larvae may be exported to inhospitable waters by the action of wind driven currents (Nelson et al., 1977) or by the incursion of Gulf Stream rings (Flierl and Wroblewski, 1985; Myers and Drinkwater, 1989). (For thorough discussions of environmental influences on recruitment see Fogarty [1993] or Wooster and Bailey [1989].) In each example noted

above, some measurable physical quantity may be plausibly postulated to be a proxy for (say) larval mortality, in a qualitative sense; it is our aim to quantify the expected predictive power of an environmental variable. Alternatively, but much more expensively, larval mortality could be estimated from field studies (Butler, 1991). We calculate the likely strengths of the correlations between mortality for an early life history stage and recruitment. A related problem that is addressed is the correlation between recruitment and abundance in an early life history stage, which can be determined from field studies (Peterman et al., 1988; Bradford, 1992). This treatment is an analytical complement to the simulation studies presented in Bradford (1992).

In the analysis to follow we first show how variability of mortality may be estimated from mean mortality while accounting for the effect of sampling error in the field measurements. We then proceed to formulate simple relationships permitting the calculation of the correlation coefficients between log-transformed or raw recruitment and stage-specific mortality or abundance, using only estimates of variability in stage-specific mortality. These two sets of analyses are then combined to provide estimates of the predictability of recruitment for a number of fish species.

Methods and analysis

Variability of mortality

To calculate correlations between stage-specific mortalities (or abundances) and recruitment, we required estimates of variability of mortality for each stage. Bradford (1992) compiled from the literature a large set of data on mortality rates and their interannual variabilities for the prerecruit stages of marine fishes. From this consolidation of data, Bradford regressed the interannual variance of daily mortality on its mean (averaged over years). We adopt the following notation: \hat{M} represents an estimate of M from a single year's survey (often only two abundance estimates are used to calculate \hat{M}); \bar{M} represents the average over a number of years of \hat{M} values; $\text{Var}(\hat{M})$ is the estimate of the variance of the mortality calculated from a number of years of \hat{M} data. Note that $\text{Var}(\hat{M})$ is not equal to the true variance, $\text{Var}(M)$, an issue dealt with below. Bradford found the following fit, holding across both stages and species: $\ln[\text{Var}(\hat{M})] = 2.231 \ln \bar{M} - 1.893$ ($r^2 = 0.90$; $P < 0.0001$). We can rewrite this relation as

$$\text{Var}(\hat{M}) = 0.15 \bar{M}^{2.2}. \quad (1)$$

This very appealing relationship specifies an almost constant CV for mortality; however, it is unclear if it is affected by measurement error.

When mortality is calculated from the difference of two field estimates of log abundance each with error ϵ , the following relationships hold:

$$\hat{M} = (1/T)[\ln N(t_2) - \ln N(t_1) + \epsilon(t_2) - \epsilon(t_1)], \quad (2)$$

$$\text{Var}(\hat{M}) = \text{Var}(M) + (2/T^2)\sigma_\epsilon^2, \quad (3)$$

where N represents the true abundance, σ_ϵ is the standard deviation of the estimation error ϵ , and $T = t_2 - t_1$. Approximately 70% of the mortality estimates in Bradford (1992) were obtained as the difference of two abundance estimates.

When mortality is estimated from a regression equation, by using a slope of log numbers versus time with n observations equally spread over time interval T , then we can use the standard formula in regression for the variance of the estimate of a slope to obtain

$$\frac{\sigma_\epsilon^2}{\sum_{i=1}^n (t_i - \bar{t})^2} = \frac{\sigma_\epsilon^2}{\frac{T^2 n(n+1)}{(n-1)^2} \left(\frac{2n+1}{6} - \frac{n+1}{4} \right)}, \quad (4)$$

where t_i is the time of the i th observation. This reduces to the right-hand side of Equation 3 when $n=2$, and decreases asymptotically as $1/n$ for large n . For 10 evenly spaced observations, the estimation error variance will be approximately reduced by one-half, compared with the case of two observations. To a good approximation, Equation 3 will provide a good estimate of the estimation error variance because only a few percent of the data used by Bradford had n larger than 10.

Predictability of recruitment: no density dependence

We can write recruitment as

$$R(t) = E(t) \exp[-(C_1(t) + C_2(t) + \dots)], \quad (5)$$

where t refers to a specific year, E is the total number of eggs produced, and C_i is the cumulative mortality in stage i . To be specific, we designate $i = 1$ for the egg stage, $i = 2$ for early larvae, $i = 3$ for late larvae, and $i = 4$ for juveniles. In accord with Equation 5, the abundance of prerecruits, N_i , at the end of stage i , is

$$N_i(t) = E(t) \exp[-(C_1(t) + C_2(t) + \dots + C_i(t))]. \quad (6)$$

These equations form the basis of the forthcoming analysis.

Let $C_i(t) = \bar{C}_i + \Delta C_i(t)$, and

$$\ln E(t) = \overline{\ln E} + \Delta \ln E(t),$$

then $\ln R(t) = \overline{\ln R} + \Delta \ln E - (\Delta C_1(t) + \dots + \Delta C_4(t))$. (7)

It follows from Equation 6 that

$$\ln N_i(t) = \overline{\ln N_i} + \Delta \ln E - (\Delta C_1(t) + \dots + \Delta C_4(t)). \quad (8)$$

Equations 7 and 8 are general, they hold whether or not correlations are present between stages. We make immediate use of these equations to examine the predictability of recruitment in the absence of interstage correlations, a simple case which serves well to illustrate the technique.

In the following calculations we concentrate on environmentally induced recruitment variations and neglect the contribution of interannual variations in egg production. Accordingly, we remove the stock effect from data-based estimates of recruitment variability before comparison with model-based values. Only trivial modifications are necessary to include the egg production factor should this be desired. In the absence of interstage correlations of mortality, it is easily shown that

$$(\sigma_{\ln(ni)})^2 = (\sigma_{c1})^2 + \dots + (\sigma_{ci})^2, \tag{9}$$

where $\sigma_{\ln(ni)}$ is the standard deviation of $\ln N_i$, and σ_{ci} is the standard deviation of C_i . Correspondingly,

$$(\sigma_{\ln R})^2 = (\sigma_{c1})^2 + \dots + (\sigma_{c4})^2. \tag{10}$$

We designate the correlation coefficient relating log recruitment and log abundance in stage i to be r_{ni} , and the corresponding coefficient relating log recruitment and stage-specific mortality to be r_{ci} . With Equations 7, 8, 9, and 10, it is easily demonstrated that

$$r_{ni} = \frac{\sigma_{\ln(ni)}}{\sigma_{\ln R}}; \tag{11}$$

this relation holds for $i = 1,2,3$; for $i = 4$, one has a correlation coefficient of 1.0, because we have stipulated that abundances are evaluated at the end of a given stage. Corresponding to Equation 11 we have

$$r_{ci} = \frac{\sigma_{ci}}{\sigma_{\ln R}}. \tag{12}$$

Predictability of recruitment: density dependence

We prescribe density dependence of the form discussed by Myers and Cadigan (1993, a and b), which is the same form as that used in key factor analysis (Varley and Gradwell, 1960; Manly, 1990; Bradford, 1992). In this formulation, mortality during the juvenile stage is increased (decreased) for years in which larval abundance is high (low). Specifically,

$$\Delta C_4 = \alpha \Delta \ln N_3 + \varepsilon, \tag{13}$$

where α gauges the strength of the density-dependence and ε (which should not be identified with the ε introduced in section 2) represents the portion of juvenile mortality uncorrelated with late-larval abundance. It follows that

$$\sigma_{c4}^2 = \alpha^2 (\sigma_{\ln(n3)})^2 + \sigma_{\varepsilon}^2, \tag{14}$$

where σ_{ε} is the standard deviation of ε . With this formulation the quantities of interest can be readily calculated.

The quantities $\sigma_{\ln(ni)}$ remain as given in Equation 9, for $i = 1,2,3$; for $i = 4$, again, $\sigma_{\ln(ni)} = \sigma_{\ln R}$, which is now given by

$$(\sigma_{\ln R})^2 = (1 - 2\alpha) [(\sigma_{c1})^2 + (\sigma_{c2})^2 + (\sigma_{c3})^2] + (\sigma_{c4})^2. \tag{15}$$

The correlation coefficients of interest may also be calculated:

$$r_{ci} = -(1 - \alpha) \frac{\sigma_{ci}}{\sigma_{\ln R}} \quad (i = 1,2,3) \tag{16}$$

$$r_{c4} = -\frac{-\alpha [(\sigma_{c1})^2 + (\sigma_{c2})^2 + (\sigma_{c3})^2] + (\sigma_{c4})^2}{\sigma_{\ln R} \sigma_{c4}}.$$

The coefficients r_{ni} are given by

$$r_{ni} = (1 - \alpha) \frac{\sigma_{\ln(ni)}}{\sigma_{\ln R}} \quad (i = 1,2,3), \tag{17}$$

and, again, $r_{n4} = 1$.

This treatment may be generalized to any case in which there exists a linear relation, analogous to Equation 13, among the stage-specific mortalities and log abundances. One could easily examine the case where two or more stage-specific mortalities are positively correlated, an effect that would enhance predictability. However, a relationship of this sort will also increase $\sigma_{\ln R}$, an outcome which is undesirable, as we show in the results section, when calculated values of $\sigma_{\ln R}$ are compared with those estimated from fisheries data.

Predictability of raw recruitment

Thus far, we have formulated relationships bearing on the predictability, from prerecruit mortalities or abundances, of log-transformed recruitment. It seems intuitively likely that raw recruitment will be considerably less predictable, which is unfortunate, because it is the untransformed recruitment which is sought for fisheries management purposes. In this section we undertake a quantitative investigation of the predictability of recruitment. The results that follow do not depend on the presence or absence of density dependence (or other interstage correlations).

Let r'_{ci} be the coefficient for the correlation between R and C_i . We wish to find a relationship between this quantity and the coefficient for the correlation between $\ln R$ and C_i , r_{ci} . This quantity, r'_{ci} , is calculated from

$$r'_{ci} = (\sigma_{ci} \sigma_R)^{-1} \left[\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} p(R, C_i) dR dC_i - \bar{C}_i \bar{R} \right]. \tag{18}$$

The joint probability $p(R, C_i)$ is obtained through

$$p(R, C_i) = p(\ln R, C_i) \frac{d(\ln R)}{dR}, \tag{19}$$

and, by assuming that $\ln R$ and C are normal, $p(\ln R, C_i)$ may be obtained from standard texts:

$$p(\ln R, C_i) = \frac{1}{2\pi\sigma_{\ln R}\sigma_{C_i}(1-r_{ci}^2)^{1/2}} \times \tag{20}$$

$$\exp\left[\frac{-1}{2(1-r_{ci}^2)}\left(\frac{(\Delta C_i)^2}{\sigma_{C_i}^2} - \frac{2r_{ci}\Delta C_i\Delta R}{\sigma_{C_i}\sigma_{\ln R}} + \frac{(\Delta \ln R)^2}{\sigma_{\ln R}^2}\right)\right].$$

Equations 20 and 19 may be substituted into Equation 18 to obtain an expression for r'_{ci} .

The integrations in Equation 18 can be straightforwardly executed to show that

$$r'_{ci} = r_{ci} \times \frac{\sigma_{\ln R}}{[\exp(\sigma_{\ln R}^2) - 1]^{1/2}}. \tag{21}$$

It is evident from this expression that if $\sigma_{\ln R}$ is small, then $r'_{ci} = r_{ci}$.

An identical result holds for the coefficient of correlation between R and $\ln N_i$, designated r'_{ni} ; it is given by

$$r'_{ni} = r_{ni} \times \frac{\sigma_{\ln R}}{[\exp(\sigma_{\ln R}^2) - 1]^{1/2}}. \tag{22}$$

The coefficient of correlation between R and N_i , designated r''_{ni} , can be found through a procedure analogous to that employed in the calculation of r'_{ci} . The result is

$$r''_{ni} = \frac{\exp(r_{ni}\sigma_{\ln R}\sigma_{\ln(ni)}) - 1}{[\exp(\sigma_{\ln R}^2) - 1]^{1/2} [\exp(\sigma_{\ln(ni)}^2) - 1]^{1/2}}. \tag{23}$$

In the limit that $\sigma_{\ln(ni)} \ll 1$, Equation 23 reduces to $r''_{ni} = r'_{ni}$.

Results

Variability of mortality

To obtain a relationship between the true variance of mortality, $\text{Var}(M)$, and mean mortality we can substitute Equation 3 into Equation 1. However, it must be borne in mind that there is likely to be a relationship between \bar{M} and T (Taggart and Frank, 1990). To address this problem, we extracted, from the

sources cited in Bradford (1992), the sampling period for the surveys providing mortality estimates and then plotted $\ln \bar{M}$ versus $\ln T$ in order to test for the existence of a power law relationship between these two variables (Fig. 1). The regression (Fig. 1) yields $\ln \bar{M} = -0.991 \ln T + 0.776$, or, equivalently

$$\bar{M} = 2.17T^{-1}. \tag{24}$$

This apparent tendency of \bar{M} and T^{-1} to covary may stem from the existence of excluded regions of the \bar{M}, T^{-1} plane. If \bar{M} is small, mortality will be detectable only if sampling times are well separated, implying that small \bar{M} corresponds to large T . Similarly, if \bar{M} is large, the interval between samples cannot be great, because the abundance will possibly decline rapidly below the threshold of detectability; thus, large \bar{M} corresponds to small T .

We can now use Equation 24 to obtain a relation for the true variance of M , $\text{Var}(M)$, by substituting Equations 1 and 3 and then substituting Equation 24 into the result, with the outcome

$$\text{Var}(M) = (0.15\bar{M}^{0.2} - 0.42\sigma_e^2)\bar{M}^2. \tag{25}$$

Even for a given life history stage, there can be great differences in the estimation error for abundance. For the Peterman (1981) salmon smolt study, $\sigma_e \approx 0.08$, whereas for the juvenile groundfish surveys examined in Myers and Cadigan (1993, a and b), σ_e

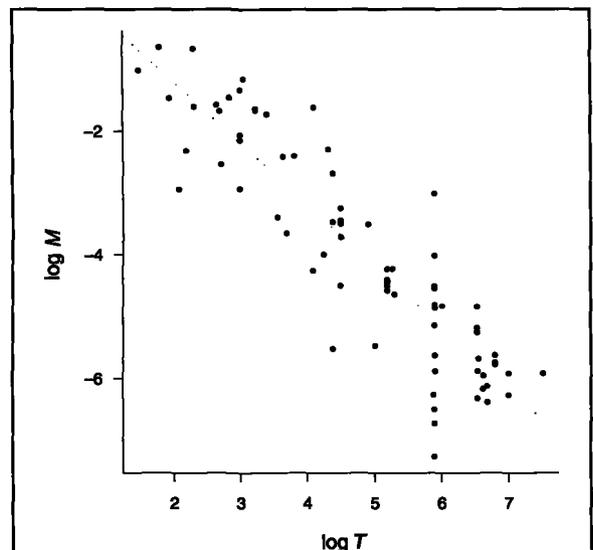
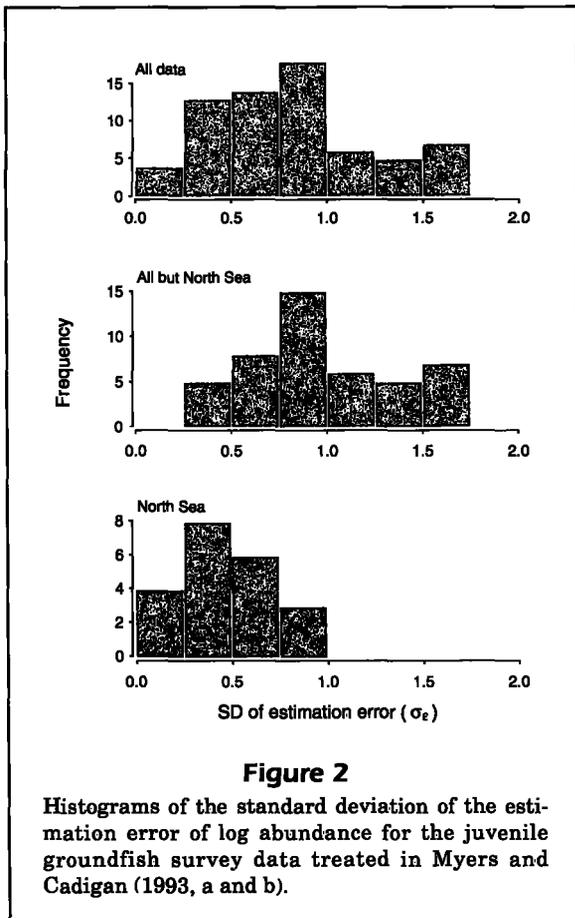


Figure 1

The natural logarithm of the daily mortality rate versus the natural logarithm of the sampling duration for prerecruit stages of marine fish, based on sources listed in Bradford (1992).



has a median value of about 0.75 (Fig. 2). Of necessity, the discussion of the importance of measurement error cannot be precise. We examine the effect of σ_ϵ in the interval 0.3 to 0.5, a range about midway between 0.08 and 0.75, on the variance of M estimates.

If the error in the log-transformed survey abundances is characterized by $\sigma_\epsilon = 0.3$ (corresponding to a CV of approximately 30% in the untransformed abundances), then for the range of mortalities in Bradford's regression, $\hat{M} \approx 10^{-4}$ to $0.4d^{-1}$, Equation 25 shows that estimation error accounts for 30% (upper end of range) to 100% (lower end of range) of the variance in M . In other words, the true variance in M amounts to between 0% (lower end of range) and 70% (upper end of range) of the variance of M . If $\sigma_\epsilon = 0.5$, then the true variance represents 0% (lower end of range) to 20% of the estimated variance of M . Of more interest is the range of mortalities for major fish species, entered in Table 1 of Bradford (1992), $\hat{M} \approx 10^{-2}$ to $10^{-1} d^{-1}$. For this range, with $\sigma_\epsilon = 0.3$, we find that the true variance constitutes about one-half of the estimated variance of M . If $\sigma_\epsilon = 0.5$, then the true variance is estimated to make no contribution to the estimated variance. On the basis of these num-

bers, but somewhat arbitrarily, we assume, for the range $\hat{M} \approx 10^{-2}$ to $10^{-1} d^{-1}$, that the true variance represents 25% of the estimated variance of M , so that $\text{Var}(M) \approx 0.04 \bar{M}^2$ or

$$\sigma_m \approx 0.2\bar{M}, \quad (26)$$

where σ_m is the standard deviation of M .

Finally, we wish to utilize Equation 26 to obtain a relationship between the interannual variability in cumulative mortality in a given stage and the mean cumulative mortality. Since the M values in Bradford's data base are largely stage averages, the cumulative mortality is just $C = M t_s$, where t_s is the stage duration. It also follows that the standard deviation of cumulative mortality σ_c , is given by $\sigma_c = \sigma_m t_s$. Applying these relations to Equation 26, we arrive at $\sigma_c = 0.2\bar{C}$, where we have placed a bar over the C to indicate that we are relating the interannual variability of C (represented by σ_c) to its mean value (\bar{C}). We can be more specific, since Bradford's regression applies across stages, and make the standard deviation and mean specific to each stage i :

$$\sigma_{ci} = 0.2\bar{C}_i. \quad (27)$$

The coefficient in Equation 27 is only half as large as that in Bradford's regression (i.e. the square root of the factor 0.15 which appears in Equation 1). This adjustment of slope, arising from correction for estimation error, could be too severe (Bradford and Cabana, in press; Bradford¹); nevertheless, we take Equation 27 at face value, use it to predict σ_{lnR} , and compare the derived values to data. In the discussion we comment on the influence of the slope parameter in Equation 27 on the predictability calculations.

Predictability of recruitment: no density dependence

In Table 1 we present the estimates of the correlation coefficients derived from Equations 11 and 12; in the final column the calculated σ_{lnR} , from Equation 10, appears. If we had used relation (Equation 1) in the calculation of σ_{lnR} , without adjusting for measurement error, then the calculated values of σ_{lnR} would be one and a half times as large. It is evident that (Fig. 3) σ_{lnR} is overestimated for cod, anchovies, and plaice. Myers and Cadigan (1993, a and b) have shown that density-dependent juvenile mortality can be expected to appreciably attenuate larval variability in cod and plaice.

¹ Bradford, M. Dept. 1994. Fisheries and Oceans, West Vancouver Laboratory, 4160 Marine Dr., West Vancouver, B.C. V7V 1NG, Canada. Personal commun.

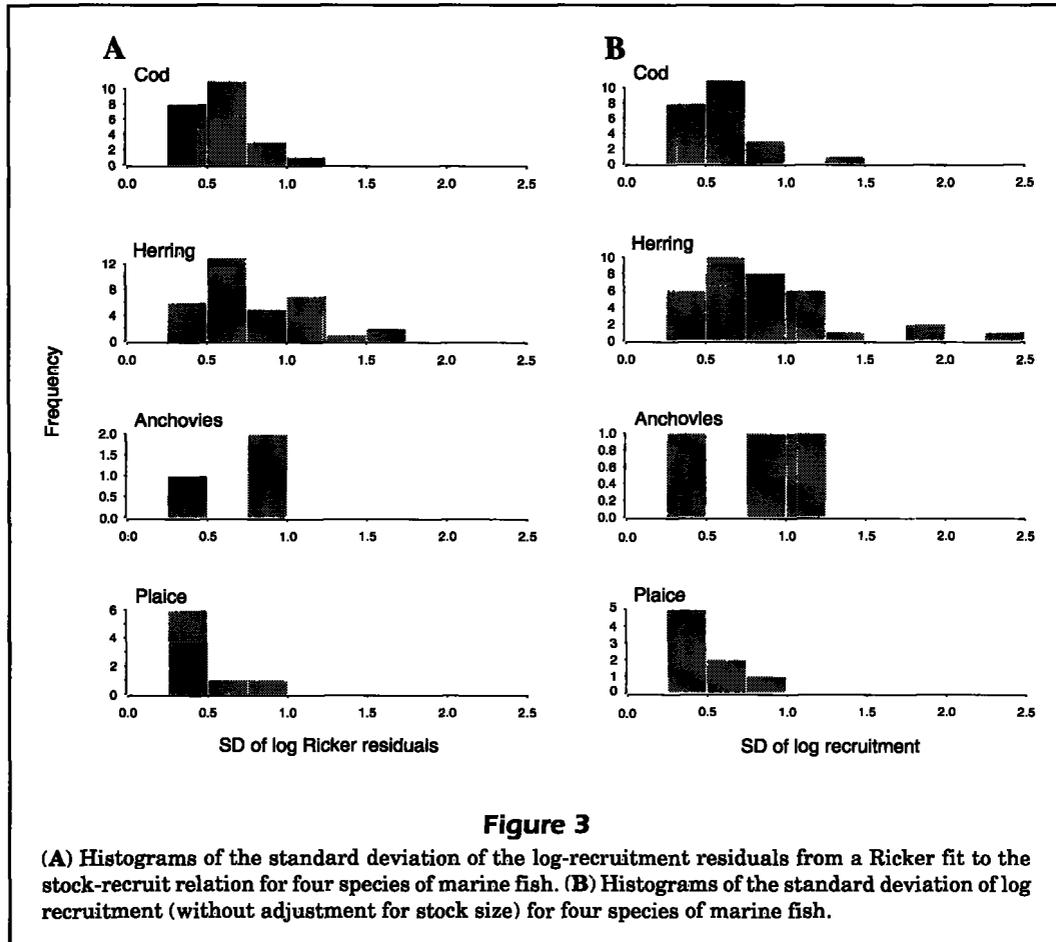


Figure 3

(A) Histograms of the standard deviation of the log-recruitment residuals from a Ricker fit to the stock-recruit relation for four species of marine fish. (B) Histograms of the standard deviation of log recruitment (without adjustment for stock size) for four species of marine fish.

Predictability of recruitment: density dependence

It is evident from Equation 15 that the effect of positive α is to reduce $\sigma_{\ln R}$, which is desirable here, because the formulation with $\alpha = 0$ overestimated $\sigma_{\ln R}$ for cod and plaice (Table 1).

We now select cod for closer examination, since there are reliable estimates for the strength of density dependence in this species (Myers and Cadigan [1993a]). Our parameter α corresponds to $1-\lambda$ in Myers and Cadigan (1993a). They found that λ was typically about 0.5 for a cod stock, suggesting $\alpha = 0.5$. With this specification we find from Equation 15 that $\sigma_{\ln R} = 0.58$, which is in good agreement with Figure 3A. For this case, $\alpha = 0.5$, the correlation between ΔC_4 and $\Delta \ln N_3$ is 0.6, so that about 36% of the variance in juvenile mortality is related to larval abundance (see Eq. 13).

With α fixed we have recalculated, r_{ci} and r_{ni} , for cod using the equations above, and have displayed them in Table 2 along with their counterparts calcu-

lated for Table 1 (for which $\alpha = 0$ was assumed). It is apparent that the prescribed density dependence has appreciably lowered the correlation coefficients. There is a particularly large reduction in r_{c4} , stemming from the fact that the juvenile mortality has two components which tend to offset one another (in the limit $\varepsilon = 0$, in Equation 13, juvenile mortality will actually be *positively* correlated with recruitment). Thus, realistic levels of density dependence (Myers and Cadigan, 1993a) have the effect of substantially reducing the predictability of log-recruitment from prerecruit mortalities or abundances.

Predictability of raw recruitment

For $\sigma_{\ln R} = 0.5$ we find from Equation 21, $r'_{ci}/r_{ci} = 0.94$ and for $\sigma_{\ln R} = 1.0$ we have $r'_{ci}/r_{ci} = 0.76$. It is evident that the predictability of raw recruitment (r'_{ci}) declines relative to the predictability of log recruitment (r_{ci}) as $\sigma_{\ln R}$ increases.

In Table 3 we have completed the presentation for the cod case, showing the $r'_{ci}, r'_{ni}, r''_{ni}$ in comparison to

Table 1

Calculated parameters relevant to the predictability of recruitment analysis, for four fish species: σ_{ci} is the standard deviation of total mortality for stage i ; $\sigma_{\ln(ni)}$ is the standard deviation of log abundance in stage i ; $\sigma_{\ln R}$ is the standard deviation of the log recruitment; r_{ci} is the coefficient of correlation between log recruitment and mortality for stage i ; r_{ni} is the coefficient of correlation between log recruitment and log abundance in stage i . The quantities $\sigma_{\ln R}$, r_{ci} , and r_{ni} were calculated by assuming no inter-stage correlations.

	Egg	Early larvae	Late larvae	Juveniles	
Cod					
σ_{ci}	0.22	0.32	0.58	0.58	$\sigma_{\ln R} = 0.91$
$\sigma_{\ln(ni)}$	0.22	0.39	0.70	0.91	
$ r_{ci} $	0.24	0.35	0.64	0.64	
r_{ni}	0.24	0.43	0.77	1.0	
Herring					
σ_{ci}	0.21	0.16	0.48	0.79	$\sigma_{\ln R} = 0.96$
$\sigma_{\ln(ni)}$	0.21	0.26	0.55	0.96	
$ r_{ci} $	0.22	0.17	0.49	0.82	
r_{ni}	0.22	0.28	0.57	1.0	
Anchovy					
σ_{ci}	0.35	0.32	0.79	0.65	$\sigma_{\ln R} = 1.13$
$\sigma_{\ln(ni)}$	0.35	0.47	0.92	1.13	
$ r_{ci} $	0.31	0.28	0.70	0.57	
r_{ni}	0.31	0.42	0.82	1.0	
Plaice					
σ_{ci}	0.52	0.21	0.70	0.39	$\sigma_{\ln R} = 0.97$
$\sigma_{\ln(ni)}$	0.52	0.56	0.90	0.97	
$ r_{ci} $	0.53	0.22	0.72	0.40	
r_{ni}	0.53	0.57	0.92	1.0	

the r_{ci} , r_{ni} . It is clear in these examples that predictability is lost when one works with the untransformed recruitment or abundance.

Peterman et al. (1988) have investigated the predictability of recruitment from surveys of prerecruit abundances. Equations 22 and 23 shed some light on how predictability is influenced by log transforming the prerecruit abundances. Recall that when $\sigma_{\ln(ni)} \ll 1$, then $r_{ni}'' = r_{ni}'$, i.e. the raw recruitment is predicted equally well by abundance or log abundance. However, if $\sigma_{\ln(ni)}$ is considerably larger than $\sigma_{\ln R}$, then $r_{ni}' > r_{ni}''$ (e.g. for $\sigma_{\ln R} = 1.0$, $\sigma_{\ln(ni)} = 2.0$, $r_{ni} = 0.5$, then $r_{ni}' = 0.38$, whereas $r_{ni}'' = 0.18$). Conversely, if $\sigma_{\ln R}$ is considerably larger than $\sigma_{\ln(ni)}$, then, $r_{ni}'' > r_{ni}'$ (e.g. for $\sigma_{\ln R} = 2.0$, $\sigma_{\ln(ni)} = 1.0$, $r_{ni} = 0.5$, then $r_{ni}' = 0.14$ and $r_{ni}'' = 0.18$). This implies that whether or not one will achieve a better correlation between recruitment and log abundance (of prerecruits) than between recruitment and abundance depends on the relative magnitudes of $\sigma_{\ln R}$ and $\sigma_{\ln(ni)}$.

Discussion

CV for mortality

The incorporation of estimates of measurement error into the relationship between variability of mortality and mean mortality indicates that the slope coefficient (see Eq. 27), which is the mortality CV, may be substantially altered by measurement error. However, removal of the error component does not destroy the intuitively appealing approximate proportionality between variability of mortality and its mean.

In the presence or absence of density dependence the slope parameter in Equation 27 does not affect the predictability of log recruitment; see Equations 11, 12, 16, and 17. Increasing this parameter inflates $\sigma_{\ln(ni)}$ and σ_{ci} but it also increases $\sigma_{\ln R}$ by the same proportion, leaving the correlation coefficients r_{ni} and r_{ci} unchanged. This invariance of the correlation coefficients with respect to the mortality CV is a useful result stemming from our treatment of the predictability problem. The predictability of raw recruitment is influenced by the mortality CV, because $\sigma_{\ln R}$ depends on this CV and because $\sigma_{\ln R}$ affects the correlation coefficients for raw recruitment (Eqs. 21 and 22).

The true size of the mortality CV cannot be determined with certainty, because the degree of inflation of the true CV by measurement error cannot be accurately ascertained. However, Equation 27, which specifies a mortality CV of only 0.2, gives reasonable estimates for the magnitude of the recruitment variability ($\sigma_{\ln R}$). Comparison of Table 1 and Figure 3A shows that Equation 27 (with Equation 10) overpredicts the median $\sigma_{\ln R}$ in three cases (cod, anchovies, and plaice). Underestimation of recruitment variability due to ageing errors by 20–30% (Bradford, 1991; Bradford¹) could rectify this discrepancy. For cod and plaice it is likely that density dependence is in part responsible for the discrepancy between calculated (from Equation 27) and empirical values of $\sigma_{\ln R}$ (see Myers and Cadigan, 1993, a and b). In any case, the approximate agreement between calculated and observed values of $\sigma_{\ln R}$ is powerful verification for the general validity of Bradford's (1992) regressions.

Table 2

The coefficients of correlation for log recruitment of cod (see Table 1) versus stage-specific mortality, r_{ci} , and for log recruitment versus stage-specific log abundance, r_{ni} . The label "no d.d." implies absence of density dependence; the label "d.d." signifies that the parameters were calculated for the density-dependent case.

	Egg	Early larvae	Late larvae	Juveniles
$ r_{ci} $ (no d.d.)	0.24	0.35	0.64	0.64
$ r_{ci} $ (d.d.)	0.19	0.28	0.50	0.28
$ r_{ni} $ (no d.d.)	0.24	0.43	0.77	1.0
$ r_{ni} $ (d.d.)	0.19	0.33	0.60	1.0

Research needs

For research purposes one may seek correlations between recruitment and an environmental variable assumed to be a proxy for mortality during some prerecruit stage. It is apparent that there is no meaningful distinction between log recruitment and raw recruitment for the purposes of correlation analysis provided $\sigma_{\ln R} \leq 0.4$. For the optimal case of minimal density dependence, correlations between log recruitment and mortality seldom exceed 0.6 to 0.7 (Table 1). This implies that any environmental variable that is to serve as a proxy for mortality must be very tightly correlated with mortality if there is to be a significant correlation between the proxy variable and recruitment. Similar results were found by Bradford (1992).

Management needs

The criterion for successful recruitment prediction for stock management suggested by Walters (1989) requires that the proxy should explain 80% of the variance in log recruitment, or, equivalently, r_{ci} , $r_{ni} \approx 0.9$. Equations 11 and 12 allow a ready appraisal of the likelihood of meeting this criterion; the application of these equations yields the results in Table 1, indicating that this criterion is never fulfilled unless one samples late in the juvenile phase. The inclusion of density dependence (Eqs. 16 and 17) generally reduces the correlation coefficients r_{ci} and r_{ni} . These findings agree with those of Bradford (1992).

A management strategy requiring predictions of recruitment (rather than log recruitment) is not likely to be viable if the stock under consideration has high recruitment variability. For a stock with $\sigma_{\ln R} = 1.0$, if 80% of the log recruitment variance can be explained by a proxy, only 46% (Eq. 21 or 22) of

Table 3

The coefficients of correlation for log recruitment of cod versus stage-specific mortality, r_{ci} ; for recruitment versus stage-specific mortality, r'_{ci} ; for log recruitment versus stage-specific log abundance, r_{ni} ; for recruitment versus stage-specific log abundance, r'_{ni} ; and for recruitment versus stage-specific abundance, r''_{ni} . All examples shown are calculated for the density-dependent mortality case.

	Egg	Early larvae	Late larvae	Juveniles
$ r_{ci} $	0.19	0.28	0.50	0.28
$ r'_{ci} $	0.17	0.26	0.46	0.26
$ r_{ni} $	0.19	0.33	0.60	1.0
$ r'_{ni} $	0.17	0.30	0.55	0.92
$ r_{ni} $	0.19	0.33	0.60	1.0
$ r''_{ni} $	0.17	0.30	0.55	1.0

the variance of recruitment itself will be explained by this proxy. For a $\sigma_{\ln R}$ of 1.5, appropriate to some herring stocks, only 21% of recruitment variance could be explained by a proxy accounting for 80% of log recruitment variance. These calculations bear on the question of whether or not large year classes can be predicted (Bradford and Cabana, in press; Anderson, 1988). Capturing the size of a large year class requires an estimate of raw (rather than log-transformed) recruitment; however, those stocks which produce the most notable year classes (those with large $\sigma_{\ln R}$) are the least predictable.

Summary

The analysis presented here complements that of Bradford (1992). We have shown that correction for measurement error can appreciably reduce the CV for mortality, while not destroying the appealing proportionality between variability of mortality and mean mortality. We have demonstrated that in many cases the predictability of recruitment can be determined analytically. It is evident from our treatment that raw recruitment is considerably less predictable than log recruitment for stocks with high recruitment variability. Our results concur with those of Bradford, suggesting that the prospects of predicting recruitment from egg or larval surveys or from environmental variables are quite poor. However, it must be borne in mind that some fish stocks will deviate from the general pattern, and thus it is quite conceivable that there will be fish stocks for which a critical stage exists, allowing recruitment predictions from (say) larval abundances.

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