Abstract. – To test the hypothesis that year-class strength in marine fishes is determined in the early-larval stages, and that these stages can be used to predict recruitment, I modeled the recruitment process using a modified form of key-factor analysis. Using data compiled from the fish literature, I found a significant relationship (R^2 0.90, $P \ll 0.001$, n 97) between the mean and interannual variance of stage-specific mortality rates that provided variance estimates for the model. The R^2 values for the true correlation between abundances of small larvae and subsequent recruitment for four example species of marine fish were predicted to lie between 0.10 and 0.57, depending on the assumptions of the model. I therefore suggest that recruitment levels are fixed after the early-larval period. However, the precision of sample correlations are too low (10-yr data series) to empirically test whether abundances or mortality rates of early larvae are in reality strongly or poorly correlated with recruitment. After metamorphosis, the strength of the true relationship and the precision of sample correlations increase sufficiently to permit precise forecasting of recruitment. Recruitment is a complex process in which variation in all life stages contributes substantially to the variability in final abundance; therefore, researchers should recognize the importance of the later prerecruit stages and the interactions among all stages.

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Precision of recruitment predictions from early life stages of marine fishes

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A major problem in the management of marine fisheries is the unpredictable fluctuations in stock size resulting from variable recruitment. Hjort (1913) first recognized this recruitment variability and proposed a number of hypotheses that linked the survival of small first-feeding larvae and subsequent year-class strength (reviewed by Wooster and Bailey 1989). These hypotheses have formed the basis of much research on the early life history of fishes, research which has been largely focused on the 'critical period' during the transition from endogenous to exogenous modes of feeding. While much has been learned about the biology of larval fish, the evidence for a critical period of increased mortality and a link between the larval stage and recruitment remains equivocal (May 1974, Ware and Lambert 1985, Peterman et al. 1988, Campana et al. 1989). Explanations for this failure have ranged from sampling and technical difficulties, such as inappropriate scales of sampling (Leggett 1986, Taggart and Leggett 1987, McGurk 1989), to the suggestion that no such critical period exists, and that all prerecruit stages contribute to some degree to variability in year-class strength (Sissenwine 1984, Anderson 1988, Peterman et al. 1988).

There have been few attempts to model the recruitment process to assess the likelihood that early-larval mortality is a dominant feature of year-class variability. Manipulations of life tables have shown that small changes in larval mortality have the potential to cause great variation in recruitment (Smith 1985, Houde 1987 and 1989, Pepin and Myers 1991); however, the influence of the larval stages in a fully dynamic model incorporating variability in all stages has not been investigated. In particular, the role of postlarval mortality in causing recruitment variability is unclear and has been the cause of some controversy (Sissenwine 1984, Peterman et al. 1988, Taggart and Frank 1990, Wooster and Bailey 1989).

An often-stated justification for research on the early life history of fish is to provide short-term forecasts of recruitment, thereby allowing managers to adjust fishing regulations in response to changes in stock size (Gulland 1989). While it is obvious that the stages very close to recruitment will give the most accurate predictions, sampling these stages is often difficult and expensive (Smith 1985), unless they are caught incidentally in other fisheries. Rather, efforts have usually been concentrated on finding a predictive relationship between recruitment and the abundance or some measure of survival of larvae and recruits, on the working assumption that Hjort's hypothesis of year-class determination at this early stage is valid (Peterman et al. 1988, Cushing 1990).

The utility of short-term (i.e., annual) predictors of recruitment in the management of fish stocks has recently been challenged by Walters and Collie (1988) and Walters (1989). In simulated management examples, Walters (1989) finds that only extremely accurate forecasts of recruitment can offer significant improvements over using the long-term mean recruitment in stock assessment models. Thus, while studies of the early stages of marine fish may reveal insights into their ecology, it is unclear whether sufficiently accurate forecasts of recruitment will ever be possible from these early stages.

In this paper I first pose the question, "How strong are the correlations between abundances or mortality rates of the early life stages and recruitment likely to be?" I develop a simple analytical model based on key-factor analysis (Varley and Gradwell 1960, Manly 1977). I use parameter estimates compiled from a literature survey to calculate the expected correlations between life stages for the prediction of fish recruitment. I suggest that the assertion that year-class strength is fixed in the early-larval stages is not general, and, furthermore, under likely field conditions it will be difficult to quantitatively test this hypothesis.

The model

I developed a simple model to simulate the variability in population numbers and the strength of correlations between life stages. In brief, the model generated annual abundances and mortality rates over a specified number of years from which correlations between early-life-history stages and recruitment were calculated. This process was repeated in a Monte Carlo fashion to estimate the sampling distribution of the correlation coefficients.

I divided the egg-recruit period into four intervals: (1) egg-yolksac larvae, (2) early-feeding larvae, (3) late-feeding larvae, and (4) juveniles from metamorphosis to age 1, which I assumed to be the age of recruitment. I assumed that populations would be sampled at five distinct times that divide the egg-recruit period into four intervals. Sampling points were: eggs spawned (N_e), first-feeding larvae (N_f), young larvae (N_l), metamorphs (N_m), and recruits (N_r). First-feeding larvae were operationally defined as larvae that have just begun to feed, while young larvae were defined as having an age of 10 days after the onset of feeding.

In any year, the number of recruits is the product of the number of eggs spawned and the survival rates of the prerecruit stages:

$$\text{Recruitment} = \text{Eggs} \cdot S_{ys} \cdot S_{el} \cdot S_{ll} \cdot S_j,$$

where the subscripts refer to the egg-yolksac, early-larval, late-larval, and juvenile periods outlined above. Expressing survival rates as instantaneous mortalities, $M = -\ln(S)$, and taking logs of the abundances give the usual equation of key-factor analysis (Varley and Gradwell 1960):

$$N_r = N_e - M_{ys} - M_{el} - M_{ll} - M_j, \qquad (1)$$

where N_r and N_e are log abundances of recruits and eggs of a particular cohort, and the M_i values are interval-specific instantaneous mortalities for four intervals defined above. I assume, following Hennemuth et al. (1980) and Peterman (1981), that log abundances and instantaneous mortality rates are normally distributed with stage-specific variances described below. This multiplicative process results in lognormally distributed recruitment, consistent with empirical results (Hennemuth et al. 1980). All subsequent references to abundance made in this paper are to log-transformed values.

Since I am interested in short-term forecasting, I assumed that stock size and, therefore, mean egg production are stationary in time and that variation in egg production is independent of recruitment. Thus, in the absence of density-dependent processes, recruitment is linearly related to egg production.

To introduce stochastic variation in the model, the abundance of eggs, N_e, and the interval-specific mortality rates were simulated as normal random variables. As the time-series of egg production was stationary and my interest is in correlations rather than abundances, the abundance of eggs and the mortality rates all had a mean of 0.

To start the sequence of calculations in a given model year, the initial abundance of eggs was randomly chosen. In the simplest version of the model, which assumes mortality in each interval is independent of the others and is density-independent, the following equation was then used to calculate the numbers of each subsequent stage:

$$N_{k+1} = N_k - m_k, \qquad (1)$$

where N_k is the abundance of stage k, and m is a normal random deviate that simulates random interannual variability in mortality of interval k.

The complete independence of mortality of one stage with that of a subsequent stage is probably an unrealistic assumption because, for example, years which are good for yolksac larval survival may also be good for the survival of older larvae. This can be modeled by introducing covariances between the interval-specific mortality rates (Gerrodette et al. 1984). Covariation between interval-specific mortality rates was modeled by assuming that there was a positive correlation between the mortality rate of adjacent intervals across years. The mortality of a given interval in any model year then depends partially on the mortality of the previous period in that same year. With ρ equal to the correlation between adjacent interval-specific mortality rates, I used the following equation to calculate the mortality rate of successive intervals:

$$M_{k+1} = \rho \left\{ \frac{SD(M_{k+1})}{SD(M_k)} \right\} M_k + (1-\rho^2)^{1/2} M_{k+1}.$$

In this equation, the actual mortality for stage k + 1 is a linear combination of the random variables simulating the variability in stages k and k + 1. The correlation coefficient determines how much mortality in stage k + 1 is similar to that of stage k. The ratio of standard deviations in the first term scales the contribution of the mortality of the previous interval to the appropriate variance. To simplify, I assumed throughout this paper that there was no covariance between the number of eggs spawned and mortality in subsequent intervals.

Finally, density-dependent mortality was incorporated in some versions of the model. Density-dependent mortality was added to the juvenile period, following suggestions of Houde (1987) and Smith (1985) that this is the most likely interval for density effects. While a number of formulations are possible, I chose a power function (Peterman 1982):

$$Y = aX^b,$$

where in this case X and Y are the abundances of juveniles and recruits, respectively. For density-independent mortality, b = 1; b is <1 for density-dependent cases. The parameter a is thus the density-independent survival rate. After taking logs, the log of the abundance of recruits is now a function of the log of the number of metamorphs, N_m, and the density-independent mortality, M_j:

$$N_r = bN_m - M_j. \qquad (2)$$

In the stochastic simulations, this equation was used to calculate recruitment with a random normal deviate substituted for M_j.

The full model was run for 1000 10-yr trials in SAS (1987), and a matrix of abundances and mortality rates for each stage was built up. For each 10-yr trial, correlation coefficients were calculated between the various predictors of recruitment (i.e., abundances and mortality rates of each of the prerecruit stages), and the numbers of recruits and summary statistics of the distributions of correlation coefficients were derived.

Table 1

Daily mortality rates (M) and interval durations (t, in days) for four species used as examples in the analysis. Egg mortality includes the yolksac period up to first feeding; larval periods explained in text. Values were adapted from Houde (1987; cod *Gadus morhua*, and herring *Clupea harengus*), Smith (1985; anchovy *Engraulis mordax*), and Zijlstra and Witte (1985; plaice *Pleuronectes platessa*).

	Egg		Early larvae		Late larvae		Juveniles	
Species	M	t	M	t	M	t	M	t
Cod	0.061	18	0.160	10	0.063	46	0.010	291
Herring	0.050	21	0.080	10	0.034	70	0.015	264
Anchovy	0.250	7	0.160	10	0.050	79	0.012	269
Plaice	0.068	38	0.104	10	0.045	77	0.008	245

Model parameters

To generalize the results, I used four fish species as examples (Table 1). These were not chosen to be representative of a specific stock or situation, but rather to indicate the effect of different life histories on our ability to forecast recruitment. To parameterize the model for a specific species, the interannual variance of the number of eggs laid and the mortality of each prerecruit stage was required.

I obtained estimates of the variance in the number of eggs spawned from published reconstructions of stock abundances (Table 2). Except for cod, I used the residuals of linear regressions of log(eggs) on time to estimate the variance, since time trends existed for some stocks.

Estimates of the variability in mortality rates for all prerecruit stages are unavailable; I therefore sought a predictive relationship between interannual variance and the mean of daily mortality rates. This allowed estimation of the variances of mortality rates of the early life stages from mean daily rates. I surveyed the literature for papers containing 2 or more years of estimates of age- or stage-specific mortality for the same population or stock. All stages from egg to adult were used, for marine, freshwater, and anadramous fish species. No screening of the data was done except for estimates from adult fish, where only estimates using methods independent of catch-data analysis were used (i.e., tagging). Most adult estimates were from lightly or unfished stocks. In some cases I estimated mortality from annual estimates of abundance or from regressions of log abundance on time. All estimates were converted to daily values using annual estimates of stage duration if available, or the long-term average stage duration. Daily mortalities were then averaged over the number of years of data available, and the variance calculated. Both variates were log-transformed, and a least-squares regression was fitted to the data.

I used the variance-mean relationship to calculate the interannual variance in mortality from mean daily mortality rates extracted from published life tables (Table 1). I split the larval period and defined the first 10 days of feeding as the early stage. This period corresponds to the usual definition of the 'critical period' for first-feeding larvae (Leggett 1986): few marine larvae can survive more than 10 days without feeding (Miller et al. 1988). Except for anchovy, where values were taken directly from Smith (1985), the daily mortality rate for the early period was set at twice the average rate for the whole larval period. Mortality rates for the late period were adjusted so that the mortality for the total larval period matched the published life tables. The result of these calculations was that the daily mortality rates of the early-larval interval were about 2.5 times those for the late-larval period. It is difficult to assess whether this decline is realistic, because there is considerable variability in the decline in mortality over time in empirical studies; in many cases mortality has been found to be nearly constant over much of the larval period (Dahlberg 1979), while there are other cases where significant declines have been observed (i.e., Savoy and Crecco 1988). Declines in mortality with larval age may be accentuated by a possible bias due to sampling interval (Taggart and Frank 1990). The variance in mortality over the duration of a particular interval was then calculated as the product of the square of the interval's duration (in days), and the variance of the daily mortality rate predicted from the variance-mean relationship.

Covariation in mortality rates

Two scenarios were developed concerning the effects of covariation between mortality rates. In the independent case, all mortality rates were varied independently of one another, while for the 'covariance' version, mortality rates of adjacent stages were assumed to be correlated across years. Few data are available to estimate the strength of these correlations, so I assumed ρ values for the correlations between adjacent M_k based on the likelihood of common agents of mortality. I assigned a relatively low ρ value of 0.25 for the correlation between the egg/yolksac period and the early-larval mortality because early-larval mortality is thought to be strongly affected by feeding success, which does not affect egg survival. Nonetheless, predation pressures are probably similar for both stages, causing some covariation in mortality rates. A ρ value of 0.5 was used between the early- and late-larval intervals because of the similarity of habitat between these two periods. For the pelagic species, anchovy and herring, $\rho = 0.25$ was used for the correlation between the late-larval and juvenile intervals, while for the demersal species, cod and plaice, I set $\rho = 0$, reflecting the major habitat shifts associated with metamorphosis.

Table 2

Interannual variability in log-transformed egg production and recruitment, compiled from literature values. All egg estimates are residuals from linear regressions of log abundance on time, except for cod where an intermediate value between herring and plaice was used.

Species	$\mathrm{Var}(N_e)$	$\mathrm{Var}(N_r)$
Cod	0.075	0.40
Herring	0.081	1.92
Anchovy	0.282	1.91
Plaice	0.055	0.14

Data sources

Cod: mean of 5 northwest Atlantic stocks in Koslow et al. (1987).

Herring: mean of 7 northwest Atlantic stocks in Winters and Wheeler (1987).

Anchovy: eggs—Peterman et al. (1988), recruitment—Methot (1989).

Plaice: Bannister (1978).

Density-dependence

To explore the effects of density-dependence on correlations, I ran the model with b = 1.0, the density-independent case, or b = 0.7, simulating moderately strong density-dependent mortality. The variance of juvenile mortality predicted from Figure 1 is in fact the sum of both the density-independent and density-dependent sources of mortality. To estimate the density-independent component of mortality (M_j) required for Eq. (2), I had to remove the density-dependent mortality from the total juvenile mortality predicted by Figure 1. Rearranging Eq. (2) and solving for the total juvenile mortality (M_{jtot}) yields

$$M_{jtot} = N_m - N_r = (1 - b)N_m + M_j.$$

In the models without covariances between mortality rates, and in the covariance model for cod and plaice where there is no covariation in mortality across metamorphosis, taking variances yields

$$\mathrm{Var}(M_j) = \mathrm{Var}(M_{jtot}) - (1 - b)^2\mathrm{Var}(N_m).$$

In these cases, to find $\mathrm{Var}(M_j)$ I ran the stochastic model up to the metamorph stage and calculated the median Var(N_m). Var(M_j) was then found by subtraction using Var(M_{jtot}) predicted from Figure 1 (Table 3). For herring and anchovy in the covariance model, the equation above should include a term for the covariance between M_{jtot} and N_m. In these cases, Var(M_j) was found by trial by running the model with different values of Var(M_j) and matching the median M_{jtot} with the value predicted from the regression equation of Figure 1.

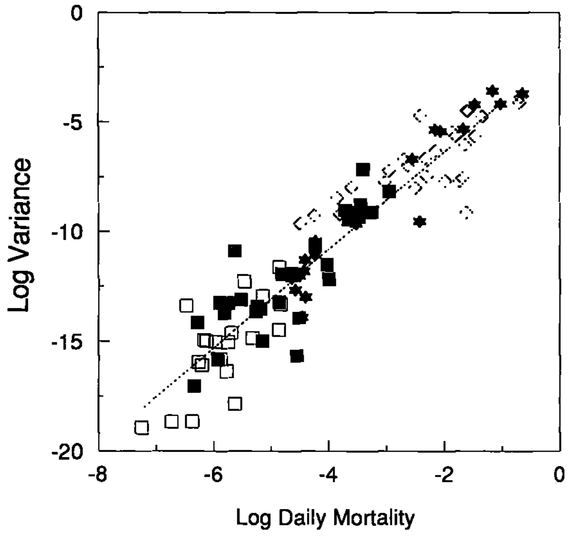

Figure 1

Relationship between interannual variance in daily mortality rates and mean daily mortality from published values. Symbols indicate eggs (*), larvae (◇), juveniles (■), and adults (□). Equation of the line: $\ln\{\mathrm{Var(M)}\} = 2.231 \ln(\mathrm{M}) - 1.893$ (R^2 0.90, $P<0.0001$). Regression uses the square root of number of years comprising each data point as weights.

Table 3

Variances of juvenile mortality rates V(M_j) used in the four versions of the model and the variance of log recruitment, V(N_r), generated by the model. Model versions include density-dependent (DD) or independent (DI) juvenile mortality and, in some cases, covariance between stage-specific mortality rates (COV). Variances for M_j in the DD models are for the density-independent component only, and were found by simulation.

	DI		DI-COV		DD		DD-COV	
Species	V(M_j)	V(N_r)	V(M_j)	V(N_r)	V(M_j)	V(N_r)	V(M_j)	V(N_r)
Cod	0.45	1.49	0.45	2.04	0.35	0.87	0.34	1.15
Herring	0.91	1.49	0.91	2.08	0.85	1.14	0.92	1.59
Anchovy	0.58	2.54	0.58	3.91	0.40	1.36	0.45	2.16
Plaice	0.22	1.64	0.22	2.46	0.09	0.79	0.09	1.04

To provide objective criteria for evaluating recruitment hypotheses, I defined two performance criteria for the correlations with recruitment. Recruitment research is commonly cast as a search for the stage when "year-class strength is determined" or "recruitment is fixed." I define such a stage as having an $R^2>0.50$ with recruitment, i.e., being able to account for at least half of the variability in year-class strength. A more rigorous standard of $R^2>0.80$ was set for correlations to be used for management purposes (Walters 1989).

Results

Variance-mean relationship

There was a highly significant relationship (R^2 0.90, $P<0.0001$, n 97) between the log of mean daily stage-specific mortality and the log of the interannual variance in the daily mortality rate (Fig. 1). The variance in mortality rate was independent of the number of years of data comprising each point (multiple regression with mean mortality, P 0.81 for sample size). The square root of sample size was used as a weight in all analyses. There was no significant effect of life history (freshwater, marine, or anadramous) on the variance-mean relationship (ANCOVAR; for slopes and adjusted means, all $P>0.20$). There was no difference in the relationship between the variance and mean of mortality among the egg, juvenile, and adult stages ($P>0.5$), but the slope for the larval stage was significantly different from the other three stages (intercept P 0.10, slope P 0.010). Because there were a number of studies on the same species, I also averaged the data across both species and stage to decrease the non-independence of the data due to common phylogeny. The variance-mean regression for this averaged dataset was almost identical to the full set (R^2 0.92, $P<0.0001$, n 53); the regression parameters differed by <2%. In this case, the regression for the larvae was not different than for the other three stages (intercept P 0.28, slope P 0.11), suggesting the significant effect found for the full dataset may have been due to the overrepresentation of some species. I therefore used the overall regression (Fig. 1) to predict the variance of mortality of all stages, rather than using a separate regression for larvae. This is a conservative procedure for rejecting Hjort's hypothesis, because the single regression predicts a more variable mortality for the early-larval stage than does the separate larval regression; the single regression produces stronger correlations between abundance of early larvae and recruitment than the separate larval regression.

Correlations between early life history and recruitment

Correlations between abundances at early life stages and recruitment increased in strength as the interval between the two stages decreased (Figs. 2, 3). Overall, covariances in mortality rates across stages increased R^2 values between early abundances and recruitment by 0.01–0.25, while density-dependent juvenile mortality had only a small and usually negative effect on R^2 values.

Correlations between egg or first-feeding larvae and recruitment were weak; the average R^2 over all species and models was 0.05 for eggs and 0.20 for first-feeding larvae. None of the values exceeded 0.50, indicating that these early stages have little predictive capability. At the end of the early-larval stage, R^2 values increased; and in 4 of 16 cases in Figures 2 and 3 the R^2 values exceeded 0.50. However, no values exceeded 0.80, the suggested requirement for recruitment forecasting to be beneficial for management (Walters 1989).

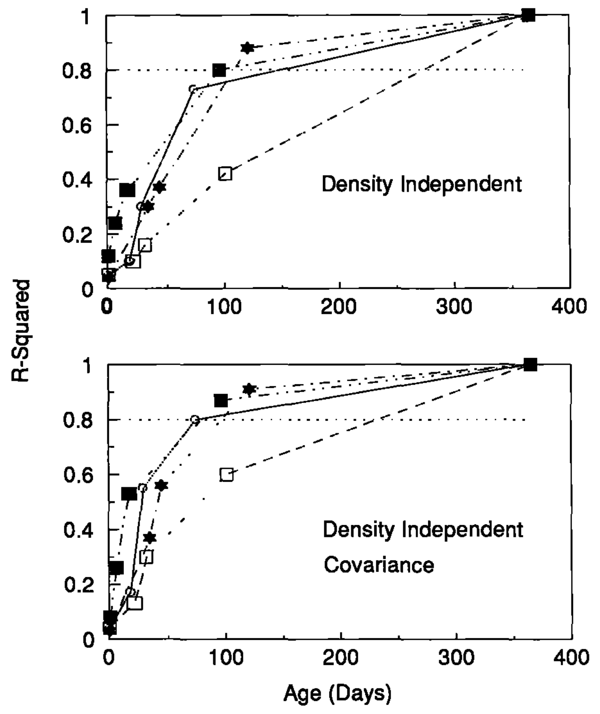

Figure 2

Predicted R^2 values for correlations between recruitment and early life stages for cod (O), anchovy (■), plaice (*), and herring (□). For each species, symbols represent, from left to right: abundance of eggs (at $t = 0$), first-feeding larvae, 10-d larvae, and metamorphs. Dotted line indicates the strength of correlations required for recruitment prediction (Walters 1989). Both examples include density-independent juvenile mortality; lower panel also incorporates covariance between interval-specific mortality rates.

In nearly all cases, the majority (R^2>0.50) of recruitment variation was predictable at the age of metamorphosis. The exception was the herring example, which gave low correlations because of high variability in the juvenile mortality rate. Half the correlations met the forecasting requirement of R^2>0.80 by the age of metamorphosis; these cases occurred in species with the lowest juvenile mortality rates.

The success of larval mortality rates in predicting recruitment was lower than for larval abundance estimates. The correlation between the mortality rate of the early-larval period and recruitment was strongly affected by the presence of covariation between stage-specific mortality rates; without these covariances the average R^2 was 0.12; the largest value was 0.18. When the covariances were incorporated, these correlations are increased, although none exceed 0.5 (Fig. 4). Ten of 16 R^2 values exceeded 0.50 for the much

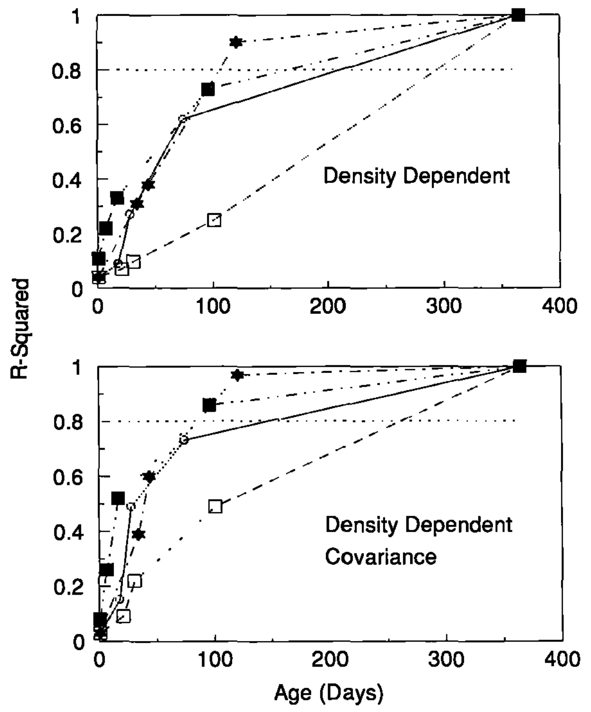

Figure 3

As in Figure 2, except both versions include density-dependent juvenile mortality; lower panel also incorporates mortality covariances.

longer late-larval period. The recruitment-forecasting threshold of 0.8 was never reached for correlations between recruitment and any larval mortality rate.

A wide range of R^2 values can result from a short time-series. For example, the 95% range of R^2 values for the correlation of early cod larvae with recruitment (10-yr time-series) in the density-independent model that includes covariance in mortality rates extended from 0.07 to 0.86 (Fig. 5). The 95% range decreases if the true relationship between the variables is stronger; for cod metamorphs the conclusion that this stage can be used to describe the majority of recruitment variation will nearly always be reached (Fig. 5).

Sensitivity analysis

Two sensitivity analyses were conducted to assess dependence of the results on input parameters. First, stage-specific variances in mortality were recalculated with the slope of the variance-mean regression set at its 95% confidence limits; the intercept was derived by constraining the line through the mean of both variables. For the cod-DI model, increasing the slope to the upper confidence limit increased the R^2 for the correlations between the abundance of recruits and early larvae or metamorphs by about 0.05; decreasing the slope lowered R^2 values by similar amounts. There was little effect on correlations involving the egg or first-feeding stages. I also recalculated the correlations with the intercept of the variance-mean regression at its 95% confidence limits. With the intercept at its lower limit, R^2 values increased by 0.01–0.04, and at the upper limit the correlations decreased by a similar amount. Thus, the overall results are not particularly sensitive to the sampling error associated with the data in Figure 1.

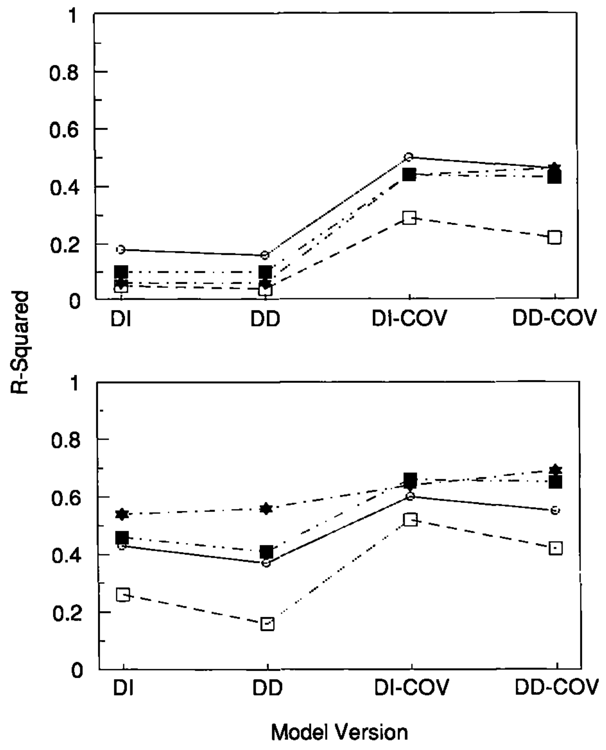

Figure 4

Predicted R^2 values for correlations between recruitment and early- and late-larval mortality rates for cod (O), anchovy (■), plaice (*), and herring (☐). Axis labels refer to four versions of the model, incorporating density-independent (DI) or -dependent (DD) juvenile mortality and covariances between mortalities (COV).

I also varied the length of the early-larval period. In the life tables (Table 2), I fixed the early-larval period at 10 days and set the daily mortality rate at twice the average for the whole larval period. In sensitivity runs I varied this period from 5 to 15 days; duration and mortality rate of the late-larval period were recalculated to keep the total mortality for the larval period constant. The duration of this period of high larval mortality had a strong effect on the strength of the correlation between abundance of larvae sampled at the end of the early period and recruitment. When the early-larval period was increased by 5 days, the R^2 in the cod-DI model increased by 0.21 (Fig. 6).

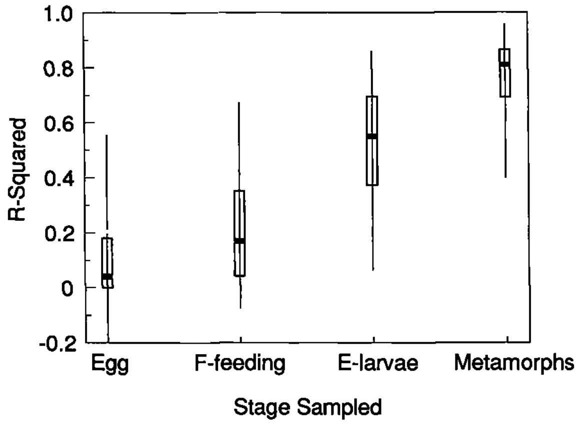

Figure 5

Variability in sample R^2 values (10-yr series) for the correlation between recruitment and abundances of early stages for cod in the model, with density-independent juvenile mortality and mortality covariances. Shown are the median (bar), interquartile (rectangle), and 95% ranges (line). Data are from 1000 runs; note that the criterion for significance ($R^2 > 0$, α 0.05) is 0.40.

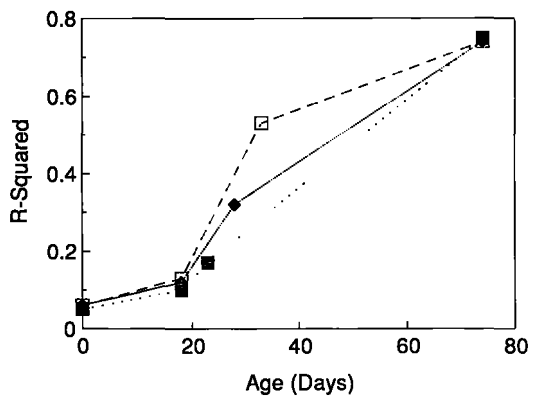

Figure 6

Effects of altering length of the early-larval stage on recruitment correlation for the cod DI-COV model. Early stage is defined as having twice the daily mortality rate of the total larval period. Shown are results with the early stage set at 5 (■), 10 (◆), and 15 (□) days. Symbols represent, from left to right: egg, yolk-sac larvae, early larvae, and metamorph stages.

Discussion

My results indicate that only predictions of recruitment based on abundances of postmetamorphic fish are likely to be useful for the management of marine fishes. The contribution to recruitment variation made by egg number (and, therefore, stock biomass) is very small, a prediction confirmed by most stock-recruit data (Parrish 1973). Correlations involving the abundance of early larvae are stronger, but are still too weak for forecasting. The model R^2 values for correlations involving early larvae are similar to the range, extending from 0.01 to 0.66, for published values compiled by Peterman et al. (1988). Accurate recruitment forecasting may be possible by sampling during the late-larval period (Graham and Sherman 1987). However, this is highly dependent on parameters and the dynamics of the particular species; only for cases with low variability in juvenile mortality or with mortality rates correlated across stages are the abundances of late larvae likely to be useful for recruitment forecasting.

Research on recruitment variability has been oriented to the early-larval stages largely as the result of Hjort's (1913) hypotheses and the observation that most of the individuals of a year-class die during the first few weeks of life (Wooster and Bailey 1989). In my four example species, the average cumulative mortality on the cohort to the 10-d larval stage is 93% (Table 1), yet the variation in abundance of these larvae explains more than 50% of recruitment variability in less than half of the cases. Variability in the late-larval and juvenile stages is still large enough to influence the strength of correlations of recruitment with larval abundances. My results suggest that the stage 'when year-class strength is determined' (defined here as $R^2 > 0.5$) occurs after this early critical period. However, the sensitivity analysis indicates that the strength of the correlation between the abundance of larvae and recruitment will depend strongly on the rate at which mortality declines during the larval period, and at what age the larvae are being sampled.

Strong linkages in mortality rates across intervals also render the definition of a 'critical period' less concise. Correlations between early life stages and recruitment were stronger when there were linkages, because survival to the age of sampling will be correlated to survival in the future. An estimate of mortality or abundance in one stage will be an index of mortality in all early life stages. This may be especially true for the early-larval stages (the classical 'critical period') because small larvae are probably subjected to a similar source of mortality as older larvae, especially if spawning occurs over a protracted period, mixing larvae of different ages together in the same body of water. In addition, environmental conditions during an early stage may affect survival of the cohort in the future. Poor feeding conditions of early larvae, for example, may have a long-term effect on growth and survival (Frank and McRuer 1989). In these cases, recruitment will be somewhat predictable from the early-larval stages, but this is not support for a strict interpretation of Hjort's hypothesis that an early critical period determines recruitment because mortality is correlated across all prerecruit stages.

The difficulty and expense of obtaining accurate estimates of abundances of eggs and larval fish have led to increased interest in finding indirect estimates of mortality rates that may be simpler to collect and could provide an index of year-class strength. Such measures include estimates of growth (Houde 1987), condition, lipid content (Theilacker 1986), and RNA/DNA ratios (Buckley and Lough 1987) as well as oceanographic variables such as upwelling and wind events (Peterman and Bradford 1987). My results show that such mortality estimates made on small larvae are not likely to be strongly correlated with recruitment (Fig. 4). Mortality estimates on older larvae will have stronger correlations, potentially closer to a value of 0.50. Note that the correlations in Figure 4 are for direct estimates of mortality, indirect indices will be more poorly related to recruitment. A combination of larval abundances and mortality rate estimates may allow more precise prediction of recruitment (Graham and Sherman 1987, Frank and McRuer 1989); if estimates are accurate and are based on older larvae, correlations nearly as strong as those predicted for metamorphs might be possible.

The correlations will be weaker if sampling errors are included in the estimates of abundance. Preliminary simulations with random sampling errors with a coefficient of variation of 50% (untransformed abundances) decreased R^2 values in Figures 2 and 3 by 0.10–0.15 (Bradford unpubl.). Biased estimates, e.g., due to gear avoidance (Lo et al. 1989), will not affect correlations between an early stage and recruitment, unless the magnitude of the bias is correlated with the estimate. Precision, through the use of consistent technique across years, is more important for the purposes of forecasting. Large-scale surveys of abundance of late larvae or juveniles may be sufficiently accurate for the forecasting of recruitment (Lo et al. 1989) if the stage sampled is likely to be strongly correlated with recruitment (Fig. 5).

An implicit, though infrequently stated, assumption of research on early-life-history influences on recruitment is that the mean and the interannual variance of mortality rates are correlated. High mortality alone will not cause recruitment variation; it must also be coupled with high interannual variability. The data compiled in Figure 1 provide evidence that this is generally true, and that the interannual variability in the larval period is proportionately no greater than that found for other stages. In addition, my sensitivity analysis suggests that the general conclusions of this paper are robust to the sampling variability of this relationship. However, detailed investigation of the recruitment dynamics of an individual species will require estimation of the variance of stage-specific mortality rates, because the predictive power of Figure 1 is still relatively low for any particular case, and the biology of an individual species may not result in rates that follow the overall average pattern. Examples are provided by species which spawn during periods of extreme climatic events such as wind storms (e.g., capelin *Mallotus villosus* or red drum *Sciaenops ocellatus*, reviewed by Taggart and Frank 1990). In these cases, interannual variability in the mortality of the earliest stages is probably larger than predicted by the regression of Figure 1, and the correlation between the early stages and recruitment is likely to be stronger than I have predicted. In contrast, for the North Sea plaice a relationship (R^2 0.7) was found between egg abundance and recruitment (Zijlstra and Witte 1985), which is higher than my model predicts for this species (although just within the 95% range). This species has relatively low recruitment variation, suggesting that larval and juvenile survival rates are not as variable as predicted by Figure 1, or that density-dependent mortality might be important in regulating recruitment (Zijlstra and Witte 1985).

The recruitment variances generated by various versions of the model tend to be higher than published values (Tables 2, 3). These literature estimates will likely be underestimates of the true variability in recruitment, because errors in catch sampling and ageing can greatly reduce recruitment variability estimated from sequential population analysis (Rivard 1989, Bradford 1991). Alternatively, my recruitment variances could be too high because I have either overestimated the variances of mortality rates or underestimated the severity of density-dependent mortality. Since the data in Figure 1 include sampling error, all of the variances in Tables 2 and 3 will be somewhat inflated. If sampling error is proportional to the rate of mortality, the sensitivity analysis suggests that removing sampling error (i.e., lowering the intercept of Fig. 1) will have only a slight effect on recruitment correlations.

One additional source of variability not explicitly considered in my analysis is the effect of varying stage duration, due to interannual variability in growth rates. Houde (1987, 1989) has demonstrated through life-table manipulation that small variations in larval growth may have large effects on the number of metamorphs produced. The effect on recruitment will be buffered somewhat as shortening the larval period will increase the length and, therefore, the total mortality of the juvenile stage. However, if the variation in growth rates is due to temperature, Pepin (1991) suggests that the offsetting effects of temperature on development and mortality will result in no net effect of temperature variation on cumulative mortality over the egg and larval stages. In this case, by not including variation in growth rates I will have overestimated the variability in larval mortality. However, to some extent the effects of growth-rate variation are already included in my model because many of the estimates in Figure 1 are based on total stage length and will, therefore, include the effects of varying stage duration caused by variation in growth rates in the calculation of the average daily mortality rate.

The sampling variability of correlations from short datasets makes it difficult to draw inferences about the causes of recruitment variability. This low precision suggests that confidence limits around the sample estimates, r or R^2, should always be supplied, much in the same way that standard errors are given for sample means. A population correlation from Figures 2 and 3 is a value that would be obtained from a very long time-series of data, and is a true measure (in the context of the model) of the contribution of an early life stage to recruitment variation. However, there is a good chance (e.g., >30% for early larvae in Fig. 5) that a sample correlation between the abundance of an early stage and recruitment may not be significantly different from 0. Even if the correlation is significant, statements about whether the relationship is, in reality, weak or strong cannot be made because the 95% confidence limits around the sample correlation are wide (Fig. 5). Published correlations between early life stages and recruitment vary greatly in strength (e.g., Peterman et al. 1988, Stevenson et al. 1989, Cushing 1990); unfortunately with short data series, true differences in the biology of these species cannot be distinguished from sampling error. The correlations between early larval abundances and recruitment compiled by Peterman et al. (1988) also illustrate this point: in only 1 of 7 cases do the 95% confidence limits around R^2 not include both 0.2 and 0.8. This problem of low precision is less serious when the true correlation is likely to be fairly high (Fig. 5, metamorphs).

The precision of correlations is also relevant to analyses involving oceanographic or climatic variables and recruitment. These studies usually invoke hypotheses that the environmental variables are agents of larval mortality, either through transport or their effects on the production or concentration of larval food (Shepherd et al. 1984, Hollowed and Bailey 1989); therefore, their true correlations with recruitment can be no stronger than the correlations for mortality rates directly (Fig. 4). Yet the sampling variability of R^2 for a short series of data suggests that there will be a good chance of finding at least one strong sample correlation among a group of 4–5 predictors that may be, in reality, only weakly related to recruitment. Adding more data will result in the sample correlation declining towards ρ; this frequently results in the sample correlation becoming nonsignificant (Koslow et al. 1987, Walters and Collie 1988, Prager and Hoenig 1989). My model results suggest environmental variables will be strongly correlated with recruitment only if the environmental factor is related to mortality across all prerecruit stages (e.g., Fig. 4; covariance models).

In summary, my analysis indicates that it is unlikely that estimates of abundance of survival rates of the egg and early-larval stages of marine fish will lead to useful predictions of recruitment. Although mortality in the earliest life stages is a major source of recruitment variability, the late-larval and juvenile periods are also important. Peterman et al. (1988), Fritz et al. (1990), and Pepin and Myers (1991) argue for the need for coordinated research on all prerecruit stages, rather than focusing only on the early stages, and my results support this view. The modeling approach I have developed here can be easily modified for any particular species to estimate *a priori* the likelihood of success of proposed recruitment research and to suggest particularly fruitful avenues of investigation.

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Citations

Ahlstrom, E.H.
1954 Distribution and abundance of egg and larval populations of the Pacific sardine. Fish. Bull., U.S. 56:83–140.

Alexander, G.R., and D.S. Shetter
1969 Trout production and angling success from matched plantings of brook trout and rainbow trout in East Fish Lake, Michigan. J. Wildl. Manage. 33:682–692.

Al-Hossaini, M., Q. Lui, and T.J. Pitcher
1989 Otolith microstructure indicating growth and mortality among plaice, *Pleuronectes platessa*, post-larval sub-cohorts. J. Fish. Biol. 35(Suppl. A):81–90.

Allen, R.L.
1977 Status of the upper Columbia river salmon and steelhead runs. *In* Schwiebert, E. (ed.), Columbia river salmon and steelhead, p. 23–30. Am. Fish. Soc. Spec. Publ. 10, Bethesda.

Anderson, J.T.
1984 Early life history of redfish (*Sebastes* spp.) on Flemish Cap. Can. J. Fish. Aquat. Sci. 41:1106–1116.
1988 A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J. Northwest Atl. Fish. Sci. 8:55–66.

Bannister, R.C.A.
1978 Changes in plaice stocks and plaice fisheries in the North Sea. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 172:86–101.

Bannister, R.C.A., D. Harding, and S.J. Lockwood
1974 Larval mortality and subsequent year-class strength in the plaice (*Pleuronectes platessa*). *In* Blaxter, J.H.S. (ed.), The early life history of fish, p. 21–37. Springer-Verlag, NY.

Barnaby, J.T.
1944 Fluctuations in abundance of red salmon, *Oncorhynchus nerka*, of the Karluk River, Alaska. Fish. Bull., U.S. 50: 237–295.

Bradford, M.J.
1991 Effects of ageing errors on recruitment time series estimated from sequential population analysis. Can. J. Fish. Aquat. Sci. 48:555–558.

Buckley, L.J., and R.G. Lough
1987 Recent growth, biochemical composition, and prey field on larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) of Georges Bank. Can. J. Fish. Aquat. Sci. 44:14–25.

Campana, S.E., K.T. Frank, P.C.F. Hurley, P.A. Koeller, F.H. Page, and P.C. Smith

1989 Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. 46 (Suppl. 1):171-182.

Chadwick, E.M.P.

1982 Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Can. J. Fish. Aquat. Sci. 39: 1496-1501.

1987 Causes of variable recruitment in a small Atlantic salmon stock. *In* Dadswell, M.J., et al. (eds.), Common strategies of anadromous and catadromous fishes, p. 390-401. Am. Fish. Soc. Symp. 1, Bethesda.

Clady, M.D.

1975 Early survival and recruitment of smallmouth bass in northern Michigan. J. Wildl. Manage. 39:194-200.

Cushing, D.H.

1990 Plankton production and year-class strength in fish populations: An update of the match/mismatch hypothesis. Adv. Mar. Biol. 26:250-294.

Dahlberg, M.D.

1979 A review of survival rates of fish eggs and larvae in relation to impact assessments. Mar. Fish. Rev. 41(3):1-12.

Dey, W.P.

1981 Mortality and growth of young-of-year striped bass in the Hudson river estuary. Trans. Am. Fish. Soc. 110:151-157.

Dragesund, O., and O. Nakken

1973 Relationship between parent stock size and year class strength in Norwegian spring spawning herring. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164:15-29.

Farris, D.A.

1960 Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). Fish. Bull., U.S. 61:247-279.

Foerster, R.E.

1968 The sockeye salmon (*Oncorhynchus nerka*). Fish. Res. Board Can. Bull. 162, 422 p.

Forney, J.L.

1971 Development of dominant year classes in a yellow perch population. Trans. Am. Fish. Soc. 100:739-749.

Frank, K.T., and J.K. McRuer

1989 Nutritional status of field-collected haddock (*Melanogrammus aeglefinus*) larvae from southwestern Nova Scotia: An assessment based on morphometric and vertical distribution data. Can. J. Fish. Aquat. Sci. 46(Suppl. 1):125-133.

Franklin, D.R., and L.L. Smith

1963 Early life history of the northern pike with special reference to the factors influencing the numerical strength of year classes. Trans. Am. Fish. Soc. 92:91-110.

Freeburg, M.H., W.W. Taylor, and R.W. Brown

1990 Effect of egg and larval survival on year-class strength of lake whitefish in Grand Traverse Bay, Lake Michigan. Trans. Am. Fish. Soc. 119:92-100.

Fritz, E.S., L.B. Crowder, and R.C. Francis

1990 The National Oceanic and Atmospheric Administration plan for recruitment fisheries oceanography research. Fisheries (Bethesda) 15:25-31.

Gerrodette, T., D. Goodman, and J. Barlow

1984 Confidence limits for population projections when vital rates vary randomly. Fish. Bull, U.S. 83:207-215.

Graham, J.J., and K.M. Sherman

1987 Recruitment mechanisms of 2-year-old atlantic herring to the Maine fishery: The larval stage. *In* Hoyt, R.D. (ed.), 10th annual larval fish conference, p. 61-68. Am. Fish. Soc. Symp. 2, Bethesda.

Gulland, J.A.

1989 Fish populations and their management. J. Fish. Biol. 35A:1-9.

Harding, D., J.H. Nichols, and D.S. Tungate

1978 The spawning of plaice (*Pleuronectes platessa*) in the southern North Sea and English Channel. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 172:102-113.

Hatch, J.T., and J.C. Underhill

1988 Abundance, distribution, and mortality of larval lake herring in western Lake Superior. *In* Hoyt, R.D. (ed.), 11th annual larval fish conference, p. 95-103. Am. Fish. Soc. Symp. 5, Bethesda.

Heessen, H.J.L., and A.D. Rijnsdorp

1989 Investigations on egg production and mortality of cod (*Gadus morhua*) and plaice (*Pleuronectes platessa*) in the southern and eastern North Sea in 1987 and 1988. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:15-20.

Hennemuth, R.C., J.E. Palmer, and B.E. Brown

1980 A statistical description of recruitment in eighteen selected fish stocks. J. Northwest Atl. Fish. Sci. 1:101-111.

Hjort, J.

1913 Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 19:1-228.

Hollowed, A.B., and K.M. Bailey

1989 New perspective on the relationship between recruitment of Pacific hake (*Merlucius productus*) and the ocean environment. *In* Beamish, R.J., and G.A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 207-220. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Houde, E.D.

1987 Fish early life dynamics and recruitment variability. *In* Hoyt, R.D. (ed.), 10th annual larval fish conference, p. 17-29. Am. Fish. Soc. Symp. 2, Bethesda.

1989 Subtleties and episodes in the early life of fishes. J. Fish. Biol. 35A:29-38.

Howe, A.B., P.G. Coates, and D.E. Pierce

1976 Winter flounder estuarine year-class abundance, mortality, and recruitment. Trans. Am. Fish. Soc. 105:647-657.

Johannessen, A.

1986 Recruitment studies of herring in Lindaaspollene, western Norway, 1-3. Fiskeridir. Skr. Ser. Havunders. 18: 139-240.

Jonsson, B., S. Skulason, S.S. Snorrason, O.T. Sandlund, H.J. Malmquist, P.M. Jonasson, R. Gydemo, and T. Lindem

1988 Life history variation of polymorphic Arctic charr (*Salvelinus alpinus*) in Thingvallavatn, Iceland. Can. J. Fish. Aquat. Sci. 45:1537-1547.

Kawanabe, H.

1969 The significance of social structure in production of the ayu, *Plectoglossus altivelis*. *In* Northcote, T.G. (ed.), Symposium on salmon and trout in streams, p. 243-265. H.R. MacMillan Lect. Fish., Univ. Brit. Col., Vancouver.

Koslow, J.A., K.R. Thompson, and W. Silvert

1987 Recruitment to northwest Atlantic cod (*Gadus mordua*) and haddock (*Melanogrammus aeglefinus*) stocks: The influence of stock size and climate. Can. J. Fish. Aquat. Sci. 44:22-39.

Kramer, R.H., and L.L. Smith

1962 Formation of year classes in largemouth bass. Trans. Am. Fish. Soc. 91:29-41.

Leggett, W.C.
1986 The dependence of fish larval survival on food and predator densities. *In* Skreslet, S. (ed.), The role of freshwater outflows in coastal marine systems, p. 117–137. Springer-Verlag, Berlin.

Lo, N.C.H., J.R. Hunter, and R.P. Hewitt
1989 Precision and bias in estimates of larval mortality. Fish. Bull., U.S. 87:399–416.

Lockwood, S.J.
1980 Density-dependent mortality in 0-group plaice (*Pleuronectes platessa*) populations. J. Cons. Cons. Int. Explor. Mer 39:148–153.

Manly, B.J.F.
1977 The determination of key factors from life table data. Oecologia 31:111–117.

Manooch, C.S., and G.R. Huntsman
1977 Age, growth, and mortality of the reg porgy, *Pagrus pargrus*. Trans. Am. Fish. Soc. 106:26–35.

Mansfield, P.J., and J.D. Jude
1986 Alewife (*Alosa pseudoharengus*) survival during the first growth season in southeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 43:1318–1326.

Mathews, S.B.
1984 Variability of marine survival of Pacific salmonids: A review. *In* Pearcy, W.G. (ed.), The influence of ocean conditions on the production of salmonids in the north Pacific, p. 161–182. Oreg. State Univ., Corvallis.

Mathews, S.B., and F.W. Olson
1980 Factors affecting Puget Sound coho salmon (*Oncorhynchus kisutch*) runs. Can. J. Fish. Aquat. Sci. 37:1373–1378.

May, R.C.
1974 Larval mortality in marine fishes and the critical period concept. *In* Blaxter, J.H.S. (ed.), The early life history of fish, p. 3–19. Springer-Verlag, Berlin.

McDonald, J., and J.M. Hume
1984 Babine Lake sockeye salmon (*Oncorhynchus nerka*) enhancement program: Testing some of the major assumptions. Can. J. Fish. Aquat. Sci. 41:70–92.

McGurk, M.D.
1989 Advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasi* in Bamfield Inlet, British Columbia. Mar. Ecol. Prog. Ser. 51:1–18.

McNeil, W.J.
1969 Survival of pink and chum salmon eggs and alevins. *In* Northcote, T.G. (ed.), Symposium on salmon and trout in streams, p. 101–117. H.R. MacMillan Lect. Fish., Univ. Brit. Col., Vancouver.

Methot, R.D.
1989 Synthetic estimates of historical abundance and mortality for the northern anchovy. *In* Edwards, E.F., and B.A. Megrey (eds.), Mathematical analysis of fish stock dynamics, p. 66-82. Am. Fish. Soc. Symp. 6, Bethesda.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marshall
1988 Larval size and recruitment mechanisms in fishes: Towards a conceptual framework. Can. J. Fish. Aquat. Sci. 45:1657–1670.

Nickelson, T.E.
1986 Influences of upwelling, ocean temperature, and smolt abundance on marine survival of coho salmon (*Oncorhynchus kisutch*) in the Oregon production area. Can. J. Fish. Aquat. Sci. 43:527–535.

Nielson, L.A.
1980 Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Can. J. Fish. Aquat. Sci. 37:11–19.

Palomera, I., and J. Lleonart
1989 Field mortality estimates of anchovy larvae, *Engraulis encrasicolus*, in the western Mediterranean. J. Fish. Biol. 35(Suppl. A):133–138.

Parker, R.R.
1968 Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25:757–794.

Parrish, B.B. (editor)
1973 Fish stocks and recruitment. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164.

Pearcy, W.G.
1962 Ecology of an estuarine population of winter flounder, *Pseudopleuronectes americanus*. III. Distribution, abundance, growth, and production of juveniles; survival of larvae and juveniles. Bull. Bingham Oceanogr. Collect. Yale Univ. 18: 39–64.

Pepin, P.
1991 Effect of temperature and size on development, mortality and survival rates of the pelagic early life stages of marine fish. Can. J. Fish. Aquat. Sci. 48:503–518.

Pepin, P., and R.A. Myers
1991 Significance of egg and larval size to recruitment variability of temperate marine fish. Can. J. Fish. Aquat. Sci. 48:1820–1828.

Peterman, R.M.
1981 Form of random variation in salmon smolt-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38:1113–1119.
1982 Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39: 904–913.

Peterman, R.M., and M.J. Bradford
1987 Wind speed and mortality rate of a marine fish, the northern anchovy, *Engraulis mordax*. Science (Wash. DC) 235:354–356.

Peterman, R.M., M.J. Bradford, N.C.H. Lo, and R.D. Methot
1988 Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45:8–16.

Poole, J.C.
1969 A study of winter flounder mortality rates in Great South Bay, New York. Trans. Am. Fish. Soc. 98:611–616.

Prager, M.H., and J.H. Hoenig
1989 Superposed epoch analysis: A randomization test of environmental effects on recruitment with application to chub mackerel. Trans. Am. Fish. Soc. 118:608–618.

Pritchard, A.L.
1948 Efficiency of natural propagation of the pink salmon (*Oncorhynchus gorbuscha*) in McClinton Creek, B.C. J. Fish. Res. Board Can. 7:224–236.

Rivard, D.
1989 Overview of the systematic, structural, and sampling errors in cohort analysis. *In* Edwards, E.F., and B.A. Megrey (eds.), Mathematical analysis of fish stock dynamics, p. 49–65. Am. Fish. Soc. Symp. 6, Bethesda.

Roberson, K., and R.H. Holder
1987 Development and evaluation of a streamside sockeye salmon (*Oncorhynchus nerka*) incubation facility, Gulkana River, Alaska. *In* Smith, H.D., L. Margolis, and C.C. Wood (eds.), Sockeye salmon (*Oncorhynchus nerka*) population biology and future management, p. 191–197. Can. Spec. Publ. Aquat. Sci. 96.

SAS

1987 SAS/STAT guide for personal computers, version 6. SAS Inst. Inc., Cary, NC.

Savoy, T.F., and V.A. Crecco

1988 The timing and significance of density-dependent and density-independent mortality of American shad, *Alosa sapidissima*. Fish. Bull., U.S. 86:467–488.

Seelbach, P.W.

1987 Effect of winter severity on steelhead smolt yield in Michigan: An example of the importance of environmental factors in determining smolt yield. *In* Dadswell, M.J., et al. (eds.), Common strategies of anadromous and catadromous fishes, p. 441–450. Am. Fish. Soc. Symp. 1, Bethesda.

Shepherd, J.G., J.G. Pope, and R.D. Cousens

1984 Variations in fish stocks and hypotheses concerning their links with climate. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 185:255–267.

Shetter, D.S.

1961 Survival of brook trout from egg to fingerling stage in two Michigan trout streams. Trans. Am. Fish. Soc. 90: 252–258.

Sissenwine, M.P.

1984 Why do fish populations vary? *In* May, R.M., (ed.), Exploitation of marine communities, p. 59–94. Springer-Verlag, Berlin.

Smith, P.E.

1985 Year-class strength and survival of 0-group clupeoids. Can. J. Fish. Aquat. Sci. 42(Suppl. 1):69–82.

Stevenson, D.K., K.M. Sherman, and J.J. Graham

1989 Abundance and population dynamics of the 1986 year class of herring along the Maine coast. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:345–350.

Sunby, S., H. Bjorke, A.V. Soldal, and S. Olsen

1989 Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua*). Rapp. P.-V. Reun. Cons. Int. Explor. Mer 191:351–358.

Taggart, C.T., and K.T. Frank

1990 Perspectives on larval fish ecology and recruitment processes: Probing the scales of relationships. *In* Sherman, K., C.M. Alexander, and B.D. Gold (eds.), Large ecosystems: Patterns, processes and yields, p. 151–164. Am. Assoc. Adv. Sci., Wash. DC.

Taggart, C.T., and W.C. Leggett

1987 Short-term mortality in post-emergent larval capelin *Mallotus villosus*. I. Analysis of multiple *in situ* estimates. Mar. Ecol. Prog. Ser. 41:205–217.

Taylor, W.W., M.A. Smale, and M.H. Freeberg

1987 Biotic and abiotic determinants of lake whitefish (*Coregonus clupeaformis*) recruitment in northeastern Lake Michigan. Can. J. Fish. Aquat. Sci. 44(Suppl. 2):313–323.

Theilacker, G.H.

1986 Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods. Fish. Bull., U.S. 84:1–17.

Thorne, R.E., and J.J. Ames

1987 A note on variability of marine survival of sockeye salmon (*Oncorhynchus nerka*) and effects of flooding on spawning success. Can. J. Fish. Aquat. Sci. 44:1791–1795.

Turner, J.L., and H.K. Chadwick

1972 Distribution and abundance of young-of-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento–San Joaquin estuary. Trans. Am. Fish. Soc. 101:442–452.

Uphoff, J.H.

1989 Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. Trans. Am. Fish. Soc. 118:251–263.

Van Woert, W.F.

1980 Exploitation, natural mortality, and survival of smallmouth bass and largemouth bass in Shasta Lake, California. Calif. Fish Game 66:163–171.

Varley, G.C., and G.R. Gradwell

1960 Key factors in population studies. J. Anim. Ecol. 29: 399–401.

Walters, C.J.

1989 Value of short-term forecasts of recruitment variation for harvest management. Can. J. Fish. Aquat. Sci. 46: 1969–1976.

Walters, C.J., and J.S. Collie

1988 Is research on environmental factors useful to fisheries management? Can. J. Fish. Aquat. Sci. 45:1848–1854.

Walton, C.J.

1987 Parent-progeny relationships for an established population of anadramous alewives in a Maine lake. *In* Dadswell, M.J., et al. (eds.), Common strategies of anadromous and catadromous fishes, p. 451–454. Am. Fish. Soc. Symp. 1, Bethesda.

Ward, B.R., and P.A. Slaney

1988 Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. Can. J. Fish. Aquat. Sci. 45:1110–1122.

Ware, D.M., and T.C. Lambert

1985 Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42:577–592.

Watanabe, Y., and N.C.H. Lo

1989 Larval production and mortality of Pacific saury, *Cololabis saira*, in the northwestern Pacific Ocean. Fish. Bull., U.S. 78:601–613.

Winters, G.H., and J.P. Wheeler

1987 Recruitment dynamics of spring-spawning herring in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 44:882–900.

Wooster, W.W., and K.M. Bailey

1989 Recruitment of marine fishes revisited. *In* Beamish, R.J., and G.A. McFarlane (eds.), Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, p. 153–159. Can. Spec. Publ. Fish. Aquat. Sci. 108.

Zijlstra, J.J., and J. IJ. Witte

1985 On the recruitment of 0-group plaice in the North Sea. Neth. J. Zool. 35:360–376.

Zijlstra, J.J., R. Dapper, and J. IJ. Witte

1982 Settlement, growth and mortality of post-larval plaice (*Pleuronectes platessa*) in the western Wadden Sea. Neth. J. Sea. Res. 15:250–272.

Appendix

Daily mortality rates and interannual variances plotted in Figure 1. Stage refers to egg (E), larval (L), juvenile (J), or adult (A) periods. For anadromous salmon, fry-smolt and smolt-adult mortality were classified as juvenile and adult mortality, respectively. *N* is the number of years of data in each study.

Species	Stage	M	var(M)	*N*	Study
Alosa pseudoharengus	L	0.0490	4.31E-04	9	Mansfield and Jude 1986
	L	0.1980	1.07E-04	8	Walton 1987
A. sapidissima	L	0.0524	2.96E-04	8	Savoy and Crecco 1988
	L	0.0978	1.28E-03	8	
	L	0.2290	3.50E-03	8	
	J	0.0027	1.30E-07	8	
	J	0.0185	5.08E-06	8	
Clupea harengus	E	0.3135	2.80E-02	2	Dragesund and Nakken 1973
	L	0.2060	1.10E-02	2	
	L	0.0275	3.38E-04	11	Graham and Sherman 1987
	L	0.1168	1.83E-03	4	Johannessen 1986
	L	0.0900	8.98E-03	2	McGurk 1989
Cololabis saira	L	0.0726	9.19E-04	14	Watanabe and Lo 1989
Coregonus artedii	L	0.5000	1.63E-02	2	Hatch and Underhill 1988
C. clupeaformis	E	0.0299	6.40E-05	2	Taylor et al. 1987
	L	0.0143	9.30E-05	2	
	L	0.0216	2.10E-04	2	Freeberg et al. 1990
Engraulis encrasicolis	L	0.2000	1.11E-02	3	Palomera and Lleonart 1989
E. mordax	E	0.3600	1.53E-02	13	Peterman et al. 1988
	L	0.1860	5.52E-04	13	
	J	0.0180	9.77E-06	13	
Esox lucius	L	0.1650	3.60E-03	3	Franklin and Smith 1963
Gadus morhua	E	0.1890	4.84E-03	3	Campana et al. 1989
	L	0.1940	2.37E-03	3	
	E	0.2304	1.48E-02	7	Heessen and Rijnsdorp 1989
	L	0.1010	5.63E-04	8	Sunby et al. 1989
	J	0.0312	8.90E-05	7	
Melanogrammus aeglefinus	E	0.1270	4.43E-03	3	Campana et al. 1989
	L	0.2630	8.56E-03	3	
Micropterous dolomieui	E	0.0890	7.12E-05	3	Clady 1975
	L	0.0310	7.74E-05	3	
	A	0.0007	6.00E-09	2	Van Woert 1980
M. salmoides	L	0.0224	9.90E-05	3	Kramer and Smith 1962
	J	0.0078	1.80E-06	4	
Morone saxatilis	L	0.1770	4.50E-04	2	Dey 1981
	J	0.0040	2.00E-06	2	
	L	0.1550	4.30E-03	6	Uphoff 1989
	J	0.0530	2.80E-04	10	Turner and Chadwick 1972
Oncorhynchus gorbuscha	E	0.0097	5.32E-06	6	Pritchard 1948
	J	0.0260	7.80E-05	3	Parker 1968
	A	0.0080	1.65E-06	3	
O. kisutch	A	0.0028	1.37E-07	8	Mathews 1984
	A	0.0078	5.15E-07	17	Mathews and Olson 1980
	A	0.0049	3.51E-07	22	Nickelson 1986
O. mykiss	J	0.0036	1.85E-05	3	Seelbach 1987
	A	0.0020	1.02E-07	4	Allen 1977
	A	0.0022	3.08E-07	7	Ward and Slaney 1988

Appendix (continued)

Species	Stage	M	var(M)	*N*	Study
Oncorhynchus nerka					
Sixmile Creek	E	0.0103	3.15E-06	2	Foerster 1968
Scully Creek	E	0.0116	8.82E-07	6	
Williams Creek	E	0.0111	5.91E-06	3	
Chilko Creek	E	0.0123	2.24E-06	7	
Tally Creek	E	0.0146	1.53E-05	11	
Port John Lake	E	0.0123	1.20E-05	9	
Karymai Spring	E	0.0120	7.23E-06	8	
Chilko Lake	J	0.0018	3.96E-08	7	
Karymai Spring	J	0.0056	1.31E-06	8	
Cultus Lake	J	0.0053	1.47E-06	10	
Port John Lake	J	0.0028	1.77E-06	8	
Babine Lake	J	0.0052	1.17E-06	10	
	J	0.0032	1.72E-06	14	McDonald and Hume 1984
	A	0.0026	2.98E-07	7	Foerster 1968
	A	0.0021	3.26E-07	24	Peterman 1982
Karluk River	A	0.0017	7.86E-09	6	Barnaby 1944
Summit Lake	A	0.0036	1.73E-08	3	Roberson and Holder 1987
Ten Mile Lake	A	0.0032	2.88E-07	6	
Gulkana Hatchery	A	0.0031	7.65E-08	9	
Lake Washington	A	0.0034	4.42E-07	11	Thorne and Ames 1987
Oncorhynchus spp.	E	0.0147	2.90E-05	23	McNeil 1969
Pagrus pagrus	A	0.0012	7.76E-09	3	Manooch and Huntsman 1977
Perca flavescans	J	0.0146	2.36E-05	6	Forney 1971
	J	0.0320	1.53E-04	8	
	A	0.0079	8.90E-06	12	Nielson 1980
Plecoglossus altivelis	J	0.0097	6.70E-06	3	Kawanabe 1969
Pleuronectes platessa	E	0.0783	1.24E-03	11	Harding et al. 1978
	E	0.1165	4.70E-03	2	Heessen and Rijnsdorp 1989
	L	0.0525	7.24E-04	4	Bannister et al. 1974
	L	0.0112	6.46E-05	7	Zijlstra et al. 1982
	J	0.0336	7.69E-04	2	Al-Hossaini et al. 1989
Firemore	J	0.0303	1.07E-04	4	Lockwood 1980
Filey Bay	J	0.0245	1.18E-04	4	
	J	0.0030	1.08E-06	5	Zijlstra et al. 1982
Pseudopleuronectes americanus	J	0.0389	1.09E-04	3	Howe et al. 1976
	J	0.0058	3.04E-07	2	Pearcy 1962
	A	0.0019	1.18E-07	5	Poole 1969
Salmo salar	J	0.0019	7.07E-07	7	Chadwick 1982
	J	0.0027	1.38E-07	10	Chadwick 1987
	A	0.0058	2.36E-06	9	
Salvelinus alpinus	A	0.0015	1.53E-06	2	Jonsson et al. 1988
S. frontinalis	J	0.0082	6.47E-06	6	Shetter 1961
	J	0.0110	8.76E-07	9	
	J	0.0106	1.55E-07	3	
S. salvelinus	A	0.0042	4.59E-06	5	Alexander and Shetter 1969
Sardinops caerulea	L	0.0831	3.32E-04	2	Ahlstrom 1954
Scomber scomber	E	0.5260	2.50E-02	4	Ware and Lambert 1985
	L	0.5110	2.12E-02	3	
Sebastes spp.	L	0.0680	1.25E-03	2	Anderson 1984
Trachurus symmetrichus	L	0.1387	4.62E-04	3	Farris 1960