

Stock and recruitment: generalizations about maximum reproductive rate, density dependence, and variability using meta-analytic approaches

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I describe the development and application of meta-analytic techniques to understand population dynamics. These methods have been applied to a compilation of over 700 populations of fish, which includes multivariate time-series of egg production, population size, natural mortality, and anthropogenic mortality. The key requirements of this approach are to make all units comparable and to make all model parameters random variables that describe the variation among populations. Parameters are then estimated using hierarchical Bayesian or classical mixed models. This approach allows patterns to be determined that are not detected otherwise. For example, the maximum annual reproductive rate is relatively constant for all species examined: between 1 and 7 replacement spawners are produced per spawner per year at low population size. Using these approaches, I also show a 20-fold variation in carrying capacity per unit area for cod, and a decrease in carrying capacity with temperature. Recruitment variability generally increases at low population sizes, for species with higher fecundity, for populations at the edge of their range, and in regions with less oceanographic stability. The spatial scale of recruitment correlations for marine species is approximately 500 km, compared with less than 50 km for freshwater species; anadromous species fall between these two scales. Recruitment variability generally decreases with age for marine demersal fish, but often increases with age for some salmonids.

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Introduction

The understanding of the relationship between spawner abundance and subsequent recruitment is the most important issue in fisheries biology and management. I will describe my attack on this problem, and review what we know, and what we do not know about this central problem in fisheries. We are undergoing a revolution in our approach to the management of renewable resources. The old approach of attempting to derive understanding from the examination of single data sets as if they were unrelated to all other biological populations will soon be a thing of the past. New approaches based upon meta-analysis (Myers and Mertz, 1998), variance components models (Myers *et al.*, 1999), and Bayesian analysis (Punt and Hilborn, 1997; Hilborn and Liermann, 1998) are becoming the standard approaches to understanding population dynamics. Such a synthetic

approach allows us to address questions that in the past were simply beyond our grasp.

Although the need for a synthetic approach to the study of fish population dynamics has long been recognized (Beverton and Holt, 1959; Pauly, 1980; Brander, 1994; Ricker, 1954; Cushing, 1971), there are several reasons why a synthesis is possible now. First, assessment methods have allowed detailed analysis of many more stocks to be completed. Second, the widespread use of research surveys allows these assessments to be more accurate, at least in theory. Finally, and most importantly, new statistical and analytical methods allow analyses and computations that simply were not possible a few years ago. For example, the use of Markov chain Monte-Carlo methods allows Bayesian methods to be easily implemented. Similarly, the widespread availability of high quality computer programs for mixed and variance components models

allows these methods to be easily applied. In particular, the introduction of “Proc Mixed” in SAS and Lindstrom and Bates nonlinear mixed models in Splus are of great practical use.

Here, I will examine the following components of the stock and recruitment problem: (1) What is the rate at which spawners can produce replacement spawners at low population sizes on average, i.e. in the absence of density-dependent mortality? (2) What is the carrying capacity of the environment? (3) What is the behaviour at low population sizes, i.e. does depensation occur? (4) What is the variability of recruitment, e.g. does variability in recruitment or survival increase at low population sizes? (5) Is delayed density-dependent mortality important? (6) What is the role of the environment in determining recruitment? (7) At what life stage does density-dependent mortality occur?

My attack on the stock-recruitment problem entails: (1) compiling all the spawner-recruitment data in the world, (2) developing simple models to describe the data, and (3) using meta-analytic methods to combine results across many populations. Note that I use “spawner abundance” or simply “spawners” because the use of “stock” is confusing to a population biologist outside of fisheries. I only consider studies on many data sets, and do not attempt to review the many excellent studies on individual populations.

Material and methods

This review is largely based on the database from over 700 populations, in which we attempted to compile all spawner/recruitment data in the world (Myers *et al.*, 1995b and updates; see also <http://fish.dal.ca/>). Although each data set was checked as thoroughly as possible, problems inevitably remain with the data. Therefore, robust methods are used whenever possible. Different subsets of data were used in the analysis described here because not all data were available for all populations and the analyses were carried out at different times.

A meta-analytic approach is needed because spawner-recruitment data are much like Hobbes’ view of primitive man: nasty, brutish, and short: these data are nasty because they often contain outliers, brutish because they have many undesirable statistical properties (e.g. extreme skewness), and short because data have not been collected for hundreds of years.

Meta-analysis is the term used to describe quantitative methods for combining evidence across studies. Here, results will be combined across populations instead of experiments. That is, the time-series of each population will be treated as a realization of a natural experiment. The use of meta-analysis is motivated by the lack of long-term data for any one population. We may never

have reliable data on over 100 generations for a natural fish population, and yet this is what is needed to make progress. By combining estimates for many populations, we may be able to reach firm conclusions. It is critical that appropriate statistical methods be used in combining data because there are many subtle pitfalls if multiple studies are combined in a naive fashion. For example, in reviewing multiple studies a simple examination of how often a given hypothesis is statistically significant can be misleading. There will be a strong bias towards the conclusion that the process or treatment has no effect because the proportion of studies that yield statistically significant results is approximately the average power of the test used (Hedges and Olkin, 1985). This bias is not reduced as the number of studies increases. That is, a reviewer may assume that he is examining the importance of an ecological process, but may only be examining the power of the tests used to detect it. This is a severe problem in fisheries research because many studies have very low statistical power. The study of fish population dynamics needs to be more of a predictive and engineering science.

The relationship between spawner abundance and subsequent mean recruitment is most commonly described by the following models:

$$R = \alpha S e^{-\beta S} \text{ -- Ricker}$$

$$R = \alpha S / (1 + (S/K)) \text{ -- Beverton and Holt}$$

$$R = \alpha S^\delta / (1 + (S^\delta/K)) \text{ -- sigmoid Beverton and Holt (if } \delta > 1)$$

where R is recruitment and S is spawner abundance. The parameter α in the first two models has dimensions of recruitment per unit spawner abundance and gives the slope of the function at $S=0$. This slope at the origin needs to be converted into a form that is easily interpretable in terms of traditional population biology.

The parameter δ in the “sigmoid” Beverton-Holt controls the degree of depensation, also known as the Allee effect (Thompson, 1993). If $\delta=1$, the function reduces to the Beverton-Holt function; if $\delta>1$, the function displays depensation (Figure 1); if $0<\delta<1$, the initial increase will be greater than for the Beverton-Holt function. The parameter δ is dimensionless and can be compared across populations. Depensation will always occur for dioecious species at very low population size; however, usually population sizes are sufficiently large that it is not important.

The Beverton-Holt and the Ricker models display compensation at low population sizes (i.e. survival increases). At high spawner abundances, recruitment declines for the Ricker model, which is known as overcompensation (Figure 1).

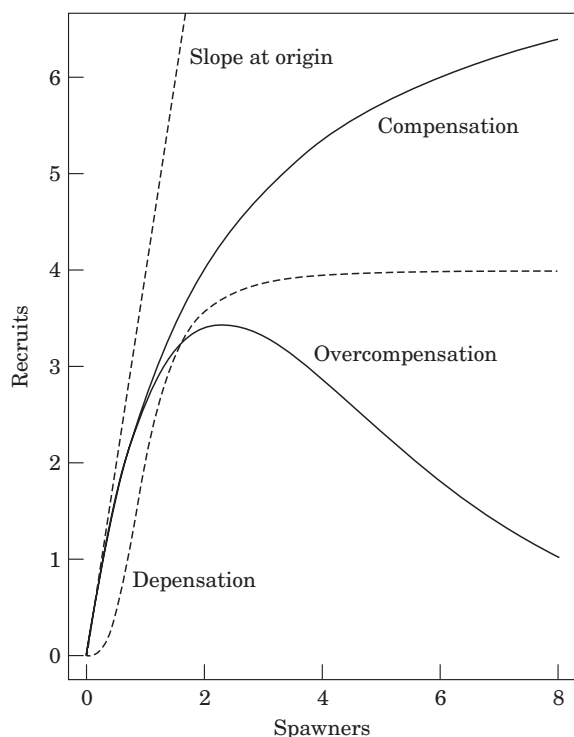


Figure 1. Depensation (sigmoid Beverton-Holt model), overcompensation (Ricker model), and compensation (Beverton-Holt model) for a spawner-recruitment relationship. Also shown is the slope at the origin for the latter two functions.

Maximum reproductive rate

The slope at the origin of the spawner-recruitment curve can be interpreted, after a suitable change in units, as the maximum reproductive rate. In the absence of depensation, the maximum annual reproductive rate can be defined as the average number of replacement spawners that are produced per spawner per year at low abundance (after a time delay for the age at maturity) with no fishing mortality. It is one of the most important parameters in population dynamics, and is critical in many problems in fisheries management. The maximum annual reproductive rate is central to estimating population growth rate (often denoted r_m ; Pimm, 1991), to estimating the limits to overfishing (Mace, 1994; Myers *et al.*, 1994), and to understanding the dynamic behaviour of the population (i.e. oscillatory or chaotic).

For semelparous species in which R and S are in the same units, the slope at the origin for the Beverton-Holt and Ricker models ($\hat{\alpha}$) can be directly interpreted as the maximum annual reproductive rate. For other species, α must be standardized. First, consider:

$$\tilde{\alpha} = \hat{\alpha} \text{SPR}_{F=0}$$

where $\text{SPR}_{F=0}$ is the spawning biomass resulting from each recruit (perhaps in units of kg-spawners per recruit)

in the limit of no fishing mortality ($F=0$). This quantity, $\tilde{\alpha}$, represents the number of spawners produced by each spawner over its lifetime, if there was no fishing mortality, at very low spawner abundance. The maximum annual reproductive rate in this case, $\tilde{\alpha}$, is the number of spawners produced by each spawner per year (after a lag of a years, where a is the age at maturity). If adult survival is p_s then:

$$\hat{\alpha} = \sum_{i=0} p_s^i \tilde{\alpha}$$

or summing the geometric series:

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s) = \alpha \text{SPR}_{F=0}(1 - p_s)$$

To estimate α over many populations of the same species, recruitment is first multiplied by $\text{SPR}_{F=0}(1 - p_s)$. Suppose we have M stocks and suppose that for stock i we have n_i observations, for $i=1, \dots, M$. The n_i observations are of the form (S_{ij}, R_{ij}) , where $j=1, \dots, n_i$, and, assuming the Ricker model, can be modelled as:

$$\log(S_{ij}, R_{ij}) = \log \tilde{\alpha}_i + \beta_i S_{ij} + \varepsilon_{ij}$$

where we assume that $\log \tilde{\alpha}_i$ is a normal random variable, i.e. a random effect, β_i is a fixed effect that depends upon equilibrium population size, and ε_{ij} is a normal, possibly autocorrelated, residual. In this formulation, the log transformation of the slope at the origin is an intercept term in a mixed effects linear model, and likelihood-based methods can be used for estimation (Searle *et al.*, 1992). Best Linear Unbiased Predictors (BLUP) of $\log \tilde{\alpha}_i$ can be obtained, in which the data on the individual population and the data from all the populations considered are optimally combined (Myers *et al.*, 1996). Using this approach, Myers *et al.* (1999) suggest that the maximum annual reproductive rate for most species examined is typically between 1 and 7. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate was an unanticipated finding.

There are other approaches to this problem, particularly Bayes or empirical Bayes hierarchical models (Efron, 1996). McAllister and coworkers (1994) implemented an empirical Bayes approach to estimating a "steepness" parameter functionally related to the slope at the origin, using an earlier version of the data set. It will be of considerable interest if alternative techniques lead to the same generalization for the relative constancy of the maximum reproductive rate.

The biological limit to the exploitation rate of a fish stock is determined by the maximum per capita reproductive rate and the age selectivity of the fishery (Mace, 1994; Myers *et al.*, 1994). Myers and Mertz (1998) formulated a simple model, which permits a

ready approximation of the limiting (maximum sustainable) fishing mortality that can be imposed on a stock without causing extinction (F_T ; Mace and Sissenwine, 1993; Mace, 1994). Selectivity was assumed to be knife-edge.

If knife-edge fishing mortality begins at age a_{sel} , and age at maturity is a_{mat} and $a_{\text{sel}} < a_{\text{mat}}$, then the limiting fishing mortality is given implicitly by:

$$\tilde{\alpha} = e^{F_T(a_{\text{mat}} - a_{\text{sel}} + 1)} (1 - e^{-(M + F_T)})$$

That is, the biological limit of fishing is given by the scaled slope at the origin or in ecological terms, the maximum annual reproductive rate. As the age of selection to the fishery decreases, the limiting fishing mortality drops very rapidly.

The results are different if fishing does not occur until after reproduction (i.e. $a_{\text{sel}} > a_{\text{mat}}$), for instance by using a mesh size that allows a species to spawn at least once. In this case, if the maximum annual reproductive rate is greater than 1, and it usually is, then it is impossible to collapse a stock by fishing (in the deterministic case). Thus, a spawn-at-least-once policy will prevent a collapse of the stock if fishing mortality targets are exceeded (Myers and Mertz, 1998).

The intrinsic rate of natural increase, r_m (Cole, 1954; Pimm, 1991) provides managers with an estimate of the average population growth rate of a severely depleted stock. Myers *et al.* (1997c) demonstrated that the maximum annual reproductive rate could be used to estimate the intrinsic rate of natural increase. We studied Atlantic cod because there is a wealth of good quality biological data collected for stock-management purposes. Moreover, cod populations occupy a broad span of latitudes, including regions, which are thought to represent the northern and southern limits of habitability. There is evidence that population variability increases as these extremes are approached (Myers, 1991), and this could impose constraints on population growth that would mask the simple dependence of r_m on metabolic rate or somatic growth rate apparent in cross-species comparisons. In fact, even for a within-species comparison, there is strong coupling between r_m and metabolic rate or somatic growth rate (as represented by age at maturity or temperature; Myers *et al.*, 1997c). These results have implications for the recovery rates of different recently collapsed Atlantic cod populations (Hutchings and Myers, 1994). We showed that r_m was about 0.2 for cod in cold conditions, but around 0.8 at the warmest portions of its range. This implies that the recovery of severely overexploited populations in the colder regions may take very long.

An implicit formula for approximately estimating r_m (Goodman, 1984; Myers *et al.*, 1997c) is:

$$e^{r_m \cdot a_{\text{mat}}} - e^{r_m(a_{\text{mat}} - 1) - M} - \tilde{\alpha} = 0$$

Such simple approximations provide an estimate of the average rate of increase. Although the real rate will vary with environmental conditions, the estimates are crucial for the rational management of fish stocks. For example, Hutchings *et al.* (1997) describe how the maximum growth rate of Northern cod was overestimated, which led managers to believe a recovery would occur much more quickly than could be expected even under average environmental conditions.

The maximum reproductive rate is also essential for estimates of the maximum sustainable yield.

Carrying capacity

For any non-trivial population model, parameters are required to describe behaviour at low population size, as well as density-dependent behaviour, which is typically related to carrying capacity. As for maximum reproductive rate, estimates of the carrying capacity (K or β) have to be standardized. The simplest approach is to divide both spawners and recruitment by some measure of the production that supports the species (recruitment should still be standardized as described above so that recruitment and spawners are in the same units). This might be spawning area for a salmonid, area of juvenile habitat for a flatfish (Rijnsdorp *et al.*, 1992), or the primary production for a filter-feeder. This approach of examining carrying capacity in terms of area of spawning gravel or area of rearing habitat has been widely used for salmonids (Bradford *et al.*, 1997). It allows for testing the importance of other factors (e.g., primary productivity or species interactions) in explaining differences in standardized carrying capacity within or among species. The first step, however, is a synthetic analysis of spawner-recruitment data that is standardized by habitat area.

Myers *et al.* (2001) assumed that both carrying capacity and maximum reproductive rate were joint random variables in a mixed model or Bayesian analysis, which has yielded some interesting results. From jointly modelling the cod stocks in the North Atlantic, and comparing the production among stocks, it appears that the most important limitation on many demersal fish is the strong density-dependent mortality during the juvenile phase, which may be caused by limited juvenile habitat. Juvenile habitat was estimated as the shelf area between zero and 300 meters' depth for each of the 20 major cod populations in the North Atlantic. Although this is a crude approximation, and could be refined, it does allow for standardization in the same units.

In this case, we define spawners S_{ij} in stock i in year j in units of tonnes km^{-2} and recruits R_{ij} as the resulting spawners km^{-2} in the absence of fishing. Assuming a Beverton-Holt model, we examine:

$$R_{ij} = [\hat{\alpha}_i S_{ij} / (1 + S_{ij}/K_i)] e^{c_{ij}}$$

Table 1. Results for the analysis demonstrating that variability in juvenile survival increases at low spawner abundance: numbers of populations (n), results of meta-analysis that combine the probability (p) levels from one-sided significance tests whether variance in log survival below the midpoint of observed adult abundance > variance above the midpoint, median values of the ratio of the two variances (Median 1), and median values of the ratio of mean R for SSB below and above the midpoint of observed adult abundance (Median 2).

Stock	n	p	Median 1	Median 2
CLUPEIFORMES	27	1.02×10^{-10}	2.32	0.84
Clupeidae	26	1.11×10^{-10}	2.38	0.87
Alewife (<i>Alosa pseudoharengus</i>)	1	0.01	12.2	0.53
Atlantic Menhaden (<i>Brevoortia tyrannus</i>)	1	0.37	1.71	0.89
Gulf Menhaden (<i>Brevoortia patronus</i>)	1	0.15	2.60	0.64
Herring (<i>Clupea harengus</i>)	19	2.36×10^{-10}	2.45	0.89
Sardine (<i>Sardinops sagax</i>)	2	0.52	1.16	0.65
Sprat (<i>Sprattus sprattus</i>)	2	0.10	3.06	0.88
Engraulidae	1	0.18	2.18	0.68
Peruvian anchoveta (<i>Engraulis ringens</i>)	1	0.18	2.18	0.68
GADIFORMES	24	3.29×10^{-8}	2.11	0.63
Gadidae	24	3.29×10^{-8}	2.11	0.63
Cod (<i>Gadus morhua</i>)	10	5.52×10^{-7}	3.38	0.62
Haddock (<i>Melanogrammus aeglefinus</i>)	6	0.04	1.64	0.61
Hake (<i>Merluccius capensis</i>)	1	0.10	5.00	0.60
Pollock or saithe (<i>Pollachius virens</i>)	2	0.26	1.52	0.77
Red hake (<i>Urophycis chuss</i>)	1	0.48	1.05	0.38
S.A. hake (<i>Merluccius capensis</i>)	1	0.24	1.73	0.89
Silver hake (<i>Merluccius bilinearis</i>)	2	0.01	3.37	0.32
Walleye pollock (<i>Theragra chalcogramma</i>)	1	0.11	2.09	1.21
PERCIFORMES	3	0.02	2.39	0.69
Percidae	1	0.66	0.74	1.32
Eurasian perch (<i>Perca fluviatilis</i>)	1	0.66	0.74	1.32
Scombridae	2	7.61×10^{-3}	4.92	0.58
Chub mackerel (<i>Scomber japonicus</i>)	1	0.17	2.39	0.47
Mackerel (<i>Scomber scombrus</i>)	1	5.72×10^{-3}	7.45	0.69
PLEURONECTIFORMES	6	0.62	0.86	0.85
Pleuronectidae	4	0.37	1.74	0.50
Petrale sole (<i>Eopsetta jordani</i>)	1	0.13	3.27	0.46
Plaice (<i>Pleuronectes platessa</i>)	1	0.64	0.80	0.52
Yellow flounder (<i>Limanda ferruginae</i>)	2	0.45	1.54	2.16
Soleidae	2	0.87	0.80	2.36
Sole (<i>Solea vulgaris</i>)	2	0.87	0.80	2.36
SALMONIFORMES	1	4.20×10^{-3}	1.43	0.58
Esocidae	1	0.26	1.43	0.81
Pike (<i>Esox lucius</i>)	1	0.26	1.43	0.81
Salmonidae	50	4.41×10^{-3}	1.37	0.57
Atlantic salmon (<i>Salmo salar</i>)	3	0.12	3.89	0.58
Chum salmon (<i>Oncorhynchus keta</i>)	3	0.13	2.09	0.94
Lake whitefish (<i>Coregonus clupeaformis</i>)	1	0.32	5.79	6.26
Pink salmon (<i>Oncorhynchus gorbuscha</i>)	15	6.04×10^{-3}	1.56	0.56
Sockeye salmon (<i>Oncorhynchus nerka</i>)	27	0.37	1.04	0.56
Whitefish (<i>Coregonus lavaretus</i>)	1	0.01	6.01	0.34
ALL SPECIES	111	3.3×10^{-16}	1.82	0.64

where $\hat{\alpha}_i$ and K_i are lognormal (to keep them positive) random variables, with a common mean for all stocks and variation among stocks. The errors are normally distributed (i.e., $\varepsilon_1, \dots, \varepsilon_{M_{NM}} \stackrel{iid}{\sim} N(0, \sigma_i^2)$; for details of the model and statistical procedures see Myers *et al.* (2001).

The analysis revealed clear and important differences in carrying capacity among cod populations (Figure 2). Because all stocks are on the same scale, it is clearly seen

that for example Iceland cod has a carrying capacity per unit area above the mean, while the Southwest Scotian Shelf stock has one below. The spawner biomass per unit area shows remarkably little variation for some populations (e.g. North Sea), while for others (e.g. Iceland) there has been a tenfold variation over historical time.

There appears to be great variation in the carrying capacity per unit area (more than 20-fold) that had

previously not been recognized. The method allows spawner-recruitment parameters to be fitted for a stock even when the data for that stock by itself give implausible estimates. The empirical Bayes estimates are clearly superior in these cases to the individual fits, but it is possible that they may shrink the estimates too close to the mean in some cases. In other words, too much weight may be given to the population estimate for the random effect, and not enough weight to the individual stock estimate. Nonetheless, this approach should be useful when designing management strategies for stocks whose population dynamics are too variable to allow reliable resolution of spawner-recruitment curves. [Hoenig et al. \(1994\)](#) provide an excellent example of a similar analysis of stock-production models.

There was also strong evidence that carrying capacity of cod declines at higher temperatures, which had not been previously suspected. The strong relationship between temperature and somatic growth rate and maximum population growth rate among populations ([Brander, 1994](#); [Myers et al., 1997c](#)) would indicate a positive effect and not the negative effect our analysis suggests. A possible explanation might be the greater number of competitors in warmer water, but this intriguing discrepancy bears further investigation.

Depensation

Many models of population dynamics in which the per capita reproductive success declines at low population levels, variously known as depensation in fish, the Allee effect in mammals, or positive density dependence in insects, can have multiple equilibria and may suddenly shift from one equilibrium to another ([Clark, 1990](#)). Predator saturation and the inability to find mates at low densities are the two most common explanations of this type of phenomena in fish. If such depensatory dynamics exist in a population that has been depleted by harvesting, reduced fishing may be insufficient to elicit stock recovery because the population may have also collapsed to a lower equilibrium level.

[Myers et al. \(1995a\)](#) analysed 129 fish stocks to test statistically for the presence of depensation in the relationship between spawner abundance and recruitment. Our test used the likelihood ratio between the sigmoid Beverton-Holt model with δ as a free parameter and the same model with δ fixed at 1 (the standard Beverton-Holt model). Because δ is dimensionless, it can be compared across populations.

For nine of the 129 stocks, the free model gave a significantly better fit at the 0.05 level. Only three of these showed significant depensation ($\delta > 1$), approximately the number that would be expected by chance alone. However, even in the most convincing example (Icelandic spring-spawning herring) environmental

change is a better explanation than depensation for the observations.

[Liermann and Hilborn \(1997\)](#) used a hierarchical Bayes model on the same data set that has several advantages over the approach in [Myers et al. \(1995a\)](#). They used an alternative standardization, and provided empirically derived predictive distributions, instead of relying on a hypothesis testing approach. However, both approaches can be greatly improved. To gain the full advantages of a mixed model or hierarchical Bayes model, all parameters need to be standardized. If recruitment and carrying capacity are standardized as described above, depensation in the Beverton-Holt model can be allowed to be a random variable:

$$R_{ij} = [\hat{\alpha}_i S_{ij}^{\delta_i} / (1 + S_{ij}^{\delta_i} / K_i)] e^{\epsilon_{ij}}$$

where $\hat{\alpha}_i$, K_i , and δ_i are lognormal random variables with a common mean for all stocks and variation among stocks. Using this formulation, [Barrowman \(2000\)](#) obtained much improved estimates of depensation, and the variability of depensation among populations. He showed that for coho salmon depensation did not occur unless fewer than one female per km of river returned to spawn.

Intercohort density-dependent mortality

Intercohort density-dependent mortality, or delayed density-dependent mortality, refers to a situation where survival of a cohort is affected by the abundance of fish in a previous cohort. [Helminen et al. \(1993\)](#) provide an excellent example for vendace in Finland. Asymmetrical competition between age classes results in strong biennial population oscillations in this heavily exploited species.

A similar mechanism has been proposed to account for the strong four-year oscillations in sockeye salmon ([Ricker, 1997](#)). However, detecting intercohort density-dependent mortality is difficult when time-series are relatively short. However, meta-analytic techniques may serve here as well. [Myers et al. \(1997\)](#) examined the hypothesis that survival from eggs produced by generation- t spawners that survive to return as recruits ($\log(R_t/S_t)$) is a linear function of spawner abundance at lag 0, 1, and 2. This results in the model:

$$R_t = \hat{\alpha} S_t e^{-\beta S_t - \phi S_{t-1} - \chi S_{t-2} + \epsilon_t}$$

where βS_t , ϕS_{t-1} and χS_{t-2} are the density-dependent mortalities owing to the number of spawners with lags of 0, 1, and 2. A standardization is required so that the parameters can be compared among populations. A natural scaling would be $\phi' = \phi/\beta$ and $\chi' = \chi/\beta$. Using this approach, [Myers et al. \(1997a\)](#) have found evidence of moderate intercohort density-dependent mortality at lag

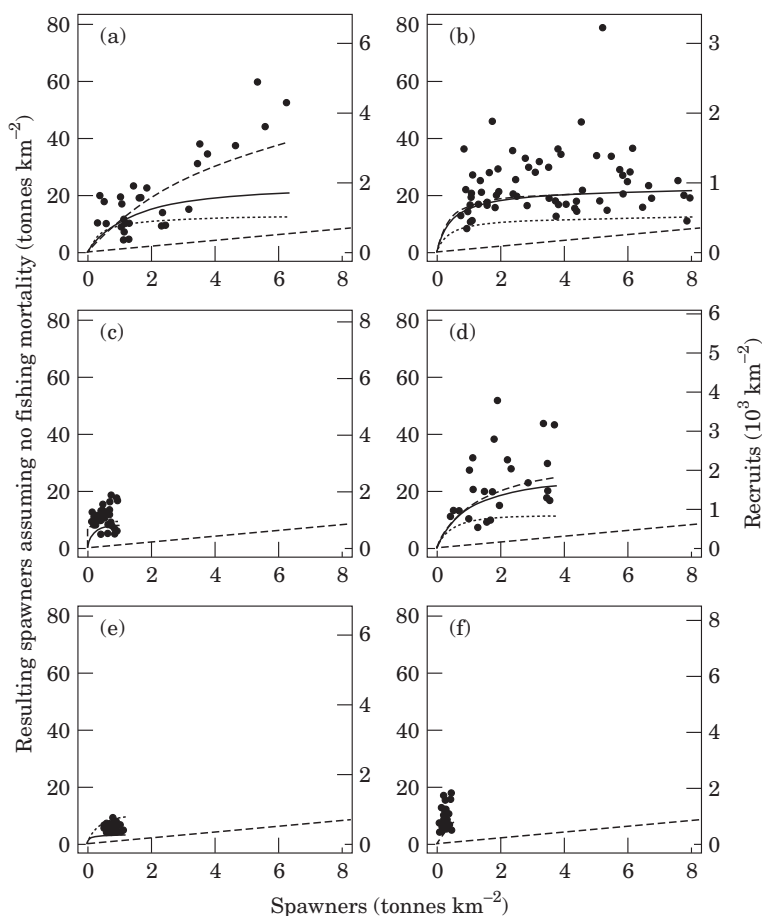


Figure 2. The relationship between recruits per km^2 and spawning-stock biomass per km^2 for three cod stocks in the northwest and three cod stocks in the Northeast Atlantic plotted on common scales on the two axes [(a): Labrador and Northeast Newfoundland; (b): Iceland; (c): Eastern Scotian Shelf; (d): Central Baltic; (e): Southwest Scotian Shelf; (f): North Sea]. Line symbolism: solid, empirical Bayes estimate for the individual stock; curvilinear dashed, single, stock maximum likelihood fit; dotted, mixed model estimate of species mean; straight dashed – 1:1 replacement line (see Myers *et al.*, 2001 for details).

one for sockeye salmon populations. For sockeye, inter-cohort density-dependent mortality at greater lags was at most weak and not significant.

The results are important for management because the uncertainty of the biological basis for the extreme cyclic behaviour of some sockeye populations has been reduced. This uncertainty has in the past resulted in increased fishing mortality on runs that were less abundant (Levy and Wood, 1992). Our results demonstrate the folly of this type of management: greater production of sockeye can be obtained by reducing fishing mortality when the sockeye populations are at their lowest.

This approach is not appropriate for many marine species assessed by virtual population analysis or similar methods because ageing error will create autocorrelation in recruitment time-series when none exists in reality (Bradford, 1991). However, if research surveys of juvenile abundance are available then models can be con-

structed that include estimation error to evaluate inter-cohort density-dependent mortality (Myers and Cadigan, 1993a). These authors found evidence of inter-cohort density-dependent mortality in cod.

Recruitment variability

Effects of spawner abundance

Does the variability in survival from egg production to recruitment change with spawner abundance? Survival until recruitment is proportional to R/S . The logarithm of this ratio has been termed the k -value or killing power (Varley *et al.*, 1973). Using a meta-analysis approach, I test if the variance of log survival above the midpoint of observed adult abundance (i.e. $S_{\min} + (S_{\min} + S_{\max})/2$) is greater than the variance below. For robustness, I made the same test for the variance above and below the median observed adult abundance. Fisher's method was

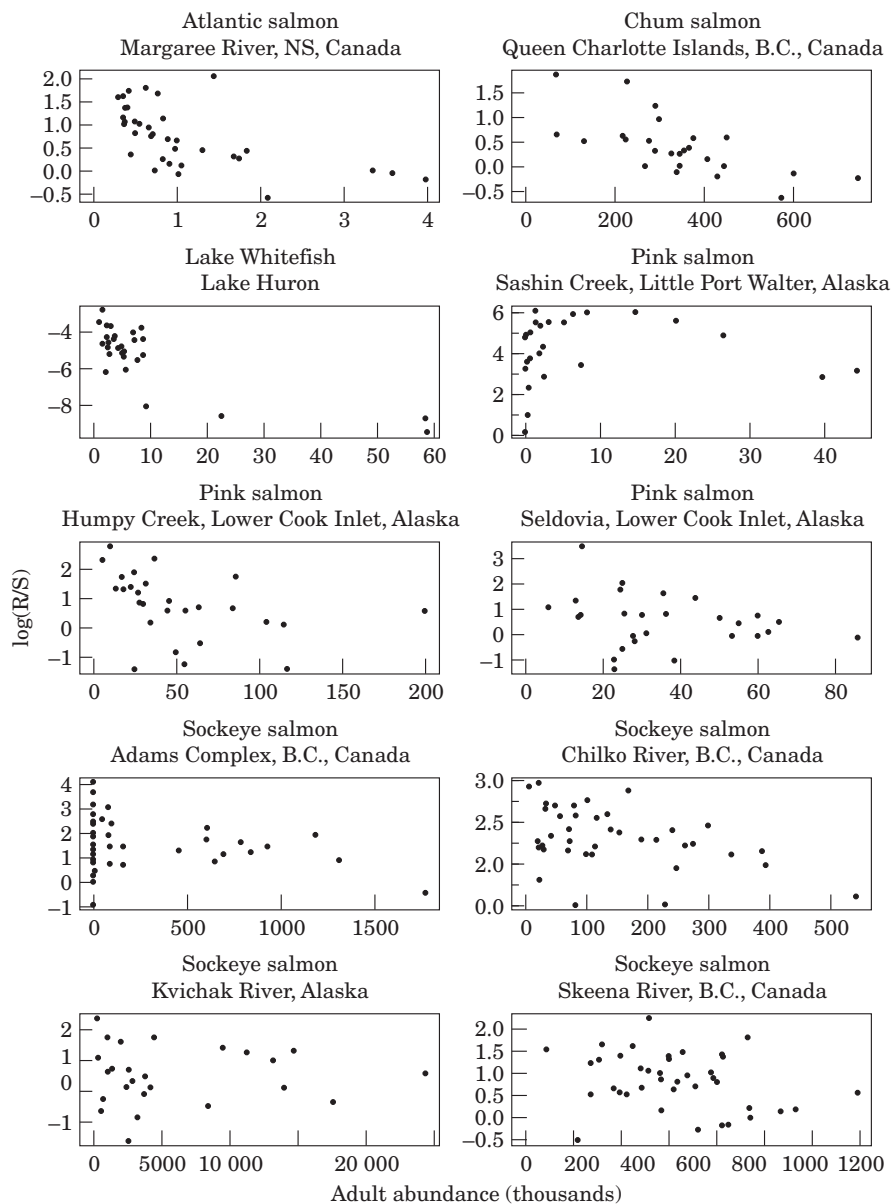


Figure 3(a).

Figure 3. Adult abundance versus log survival rate for (a) some representative salmonid populations (abundance in thousands; for lake whitefish of Lake Huron and pink salmon of Sashin Creek, recruitment units are relative year-class strength and number of fry, respectively, and abundance units are numbers of eggs and number of females, respectively). and (b) for some populations representative of the Clupeidae, Gadidae, Pleuronectidae, and Scombridae (abundance in thousand tonnes).

used to combine the probability levels from one-sided significance tests (Hedges and Olkin, 1985).

The variance in survival is generally higher at low adult abundance (Table 1; Figure 3). For all orders, except flatfish (Pleuronectiformes), the variance of survival below the midpoint of observed adult abundance was greater than the variance above, and the differences were statistically significant ($\alpha < 0.05$) with the same

exception. The difference was also statistically significant for most families and species if the number of populations included was not small. The median ratio for all species combined is 1.82. The slope of the relationship between survival and adult abundance is generally negative (as may be deduced from Table 1, last column), i.e. mortality is density-dependent as is commonly seen in fish populations (Myers and Cadigan, 1993a,b).

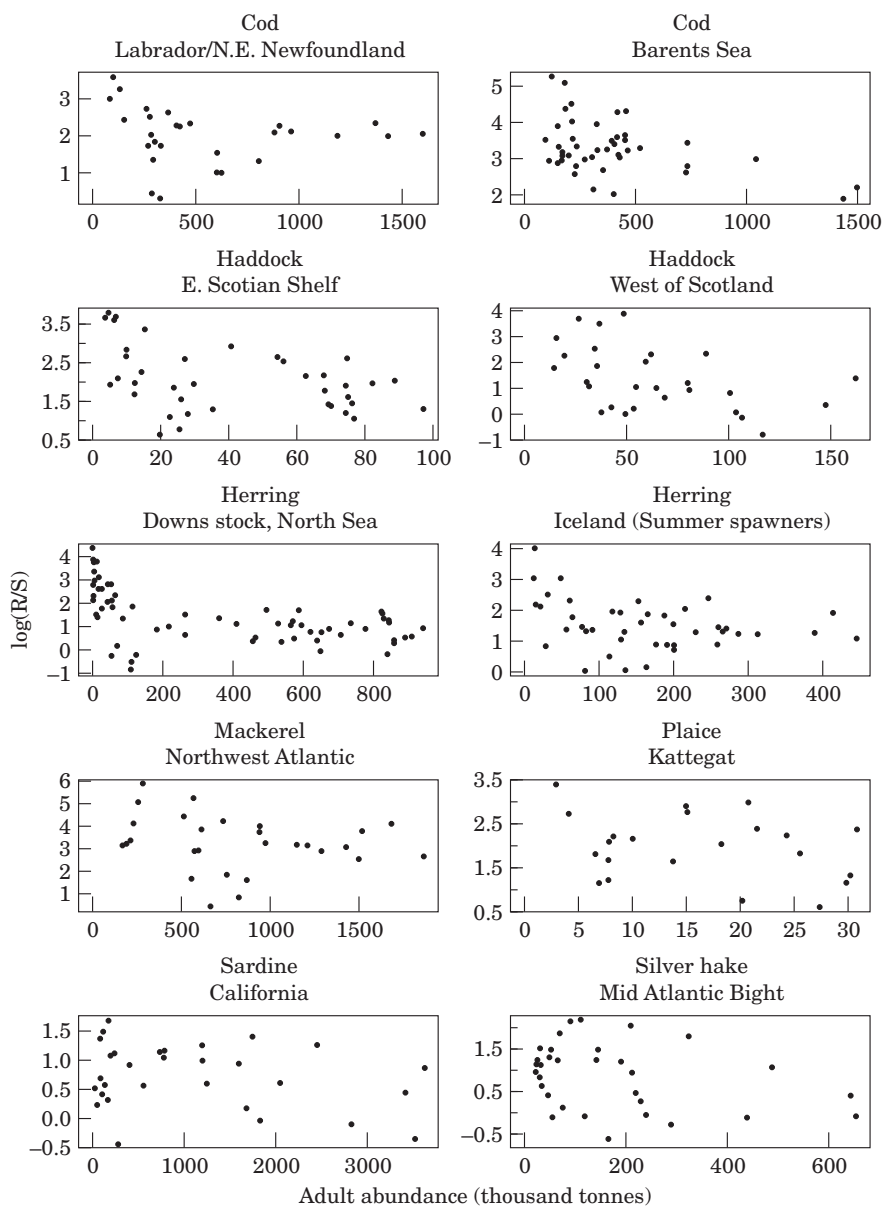


Figure 3(b).

The analysis was repeated using alternative selection criteria. The effect became stronger when only populations characterized by a wider range in adult abundance were included (the median ratio of the variance in 73 populations in which $S_{\max}/S_{\min} > 10$ is 2.17) and weaker when the observed range of adults was decreased (median ratio in 143 populations in which $S_{\max}/S_{\min} > 3$ is 1.62). In all cases, the differences were also highly significant when the median of adult abundance was used instead of the midpoint.

An examination of the individual plots shows that degree of variability is higher the lower population sizes

become. The greatest variability appears to occur in populations reduced to very low levels, such as Downs herring in the North Sea and Iceland spring-spawning herring, both of which were greatly overexploited. Pink salmon in Sashin Creek, Alaska, showed extreme variation in survival when the number of females spawning was reduced to below 300.

I suggest that the reason for the higher level of variability in survival at low abundance is that strong density-dependent mortality is operating at the juvenile stage, after the stochastic density-independent mortality operating in the egg and larval stage. The relative

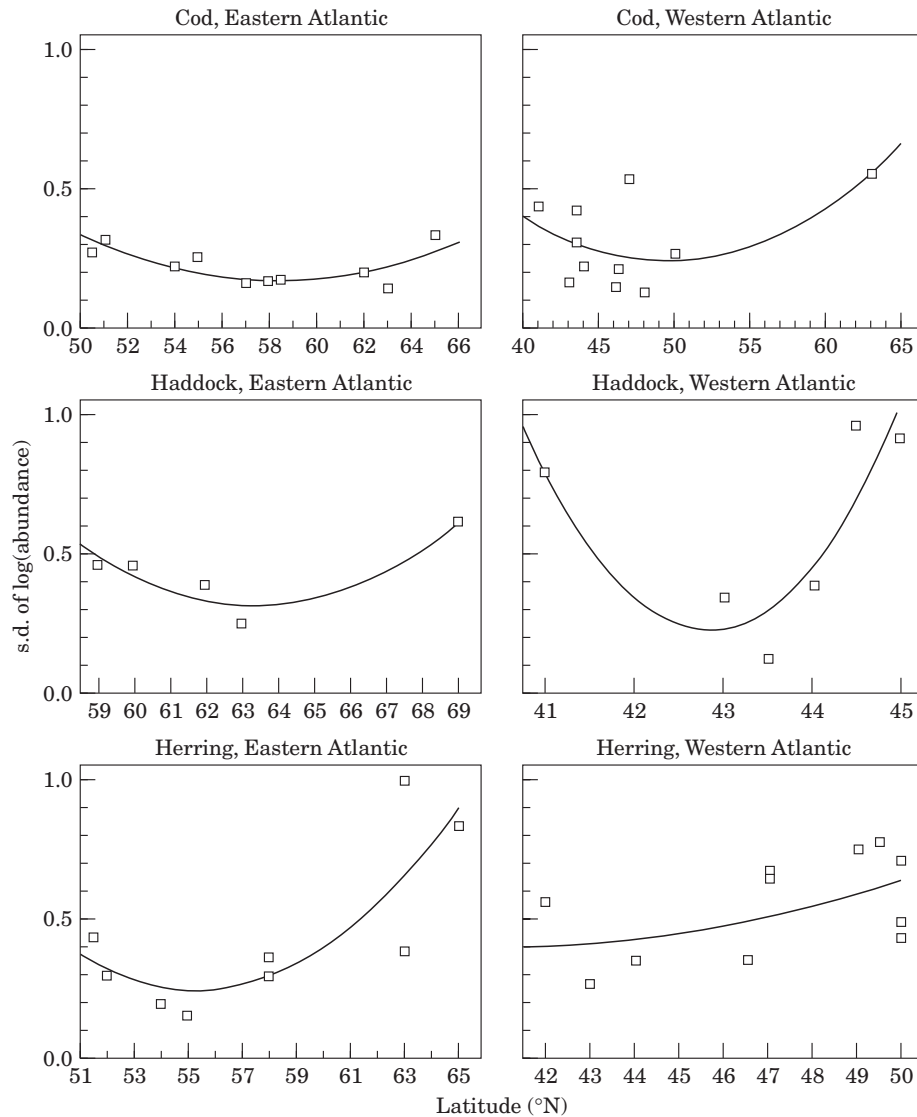


Figure 4. Standard deviation of logarithmically (base 10) transformed juvenile abundance(s) versus latitude of the spawning location. Also shown are the quadratic regression lines (see Myers, 1991).

importance of the two types of mortality at each life stage will determine the variability in survival at different population densities.

Effects of fecundity

It has often been contended that the strong recruitment variability in marine fish populations is a consequence of their large fecundities. To test this proposal, Mertz and Myers (1996) derived a simple model that predicted a linear relationship linking the standard deviation of log-recruitment for a species to its log-fecundity, and a specific slope coefficient. This result was tested using all available data for major marine fish stocks. Mertz and Myers (1996) found that the derived relationship

approximately predicts the ratio of recruitment variability to log-fecundity for the centroid of the cluster of data points, but the scatter about the centroid is so great that no significant relationship exists between recruitment variability and log-fecundity for any one species. However, if taxa are combined, then a slightly positive relationship emerges (Rickman *et al.*, 2000). We conclude that the standard deviation of log-recruitment does increase with log-fecundity, but the relationship is not a very important one.

Effects of spatial scale

A simple generalization can be made for the spatial scale of recruitment variability based on the spatial scale of

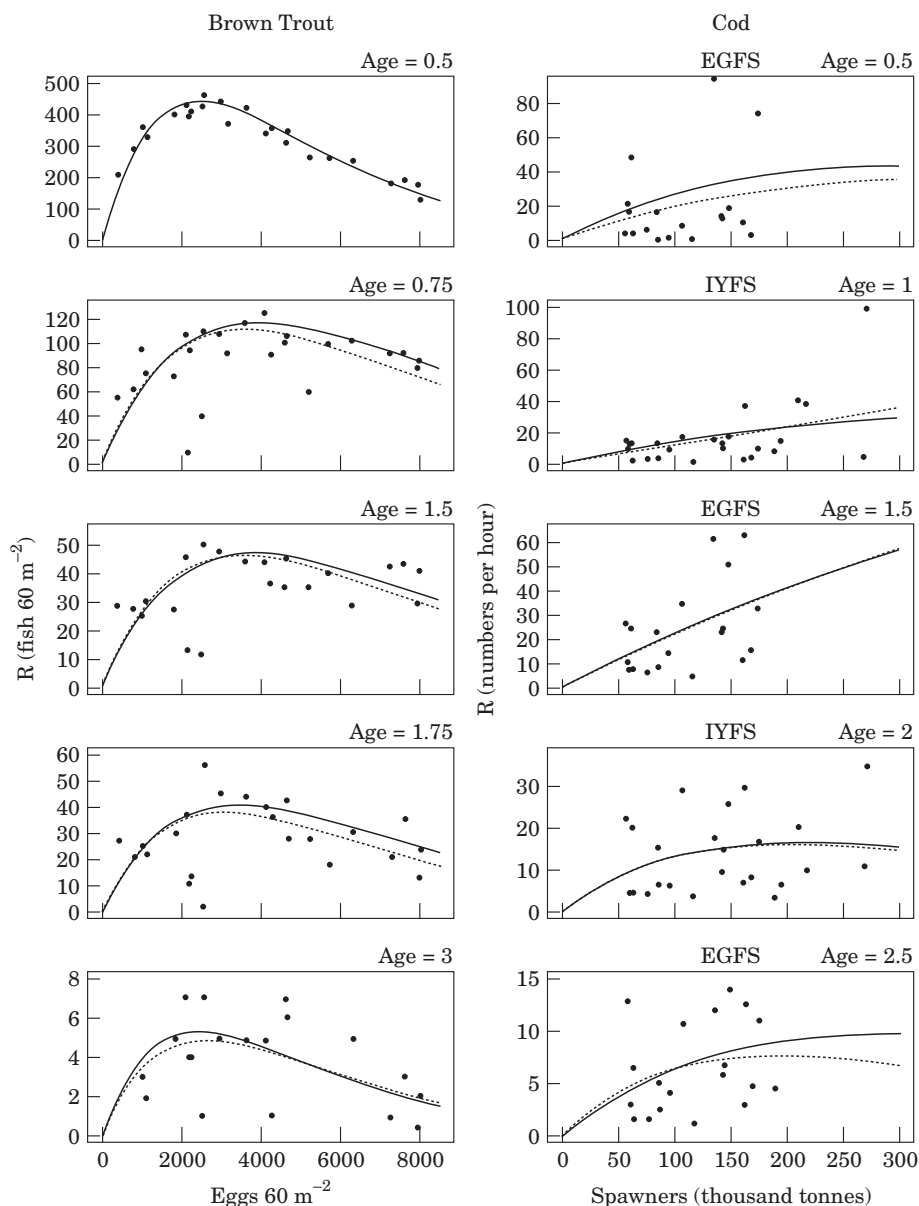


Figure 5. Recruitment versus spawner abundance at five ages for a brown trout population and North Sea cod (note that recruitment is estimated from two different surveys: EGFS, English groundfish survey; IYFS, International Young Fish Survey; the latter covers a longer period).

recruitment correlations for marine species of approximately 500 km, compared with less than 50 km for freshwater species (Myers *et al.*, 1995c, 1997). Anadromous species and species with estuarine nursery regions (e.g. plaice) fall between these two scales. These results are based upon the examination of multiple populations from 11 marine, three anadromous, and five freshwater species and have since been confirmed for coho salmon (Bradford, 1999).

In these studies, the estimate of the spatial scale is the distance over which the pairwise correlation between recruitment time-series is reduced by a factor e^{-1} i.e., the exponential decay rate or the e-folding scale. The scale for marine species is comparable to (but less than) that of the largest-scale environmental variables (and is compatible with the idea that large-scale environmental agents influence recruitment). The results are consistent with the hypothesis that predation is a more important

factor in determining recruitment in freshwater than it is in the marine environment.

Effects of spawning season

According to the match/mismatch hypothesis, larval fish survival and eventual recruitment is dependent on the offset time between the peaks of abundance of larvae and their planktonic prey. Mertz and Myers (1994) developed a larval food supply model to determine the dependence of food availability on the mismatch between peaks. The model predicts that recruitment variability should increase as spawning duration decreases, a result which is moderately supported by an analysis of Atlantic cod data.

Effects of oceanographic stability

Isolated offshore banks are presumably less stable environments than continental shelves. Myers and Pepin (1994) examined the hypothesis that recruitment is more variable in populations on isolated offshore banks than in nearby shelf populations. Recruitment of cod and American plaice on Flemish Cap was more variable than any comparable population. Recruitment of haddock on Rockall Bank was also more variable than that of surrounding populations. These results are confirmed by estimates obtained both by virtual population analysis and by research surveys. Recruitment of haddock and herring on Georges Bank was also more variable than in surrounding populations, but the results for two other groundfish populations, cod and yellowtail flounder, were ambiguous. Recruitment of marine fish populations on isolated banks appears to be more variable than those on nearby shelf regions, which would imply that recruitment variability and oceanographic stability co-vary.

Effects of species range

It has long been hypothesized that variability in abundance is greater at the edge of a species range, because populations at the edge of ranges may be more susceptible to density-independent factors than those at the centre (Haldane, 1956). I examined this prediction for cod, haddock, and herring recruitment in the North Atlantic (Myers, 1991).

The standard deviation of the log (base 10) transformed recruitment, denoted by s , was used here to measure temporal variability. The hypothesis of greater variability at the edge of the range was tested by determining the significance of the quadratic term in a quadratic regression of s versus the latitude of the spawning location for each population, i.e. $s = \beta_0 + \beta_1 L + \beta_2 L^2$, where L is the latitude of the spawning location. The *a priori* hypothesis is that $\beta_2 > 0$. Regressions were estimated separately for each species on each side of the Atlantic. Although the significance levels for each regression and rank correlation analysis were given

individually, I was concerned with the general hypothesis. I used Fisher's method to combine tests of significance (Hedges and Olkin, 1985).

Recruitment was more variable at the edges of the range. When the significance tests were combined, the overall results provide strong evidence for the hypothesis that the populations on the northern and southern ends of their range are more variable ($p < 0.001$). The results were consistent with the hypothesis that density-independent regulation is more important at the edge of a species range (Figure 4).

Effects of the environment

Most scientists who have tried to sort out the real effects of the environment on recruitment from phantom ones have had massive frustrations and become either chronically gullible or confirmed as skeptics. Some have suggested that the whole enterprise of finding environment-recruitment correlations should be abandoned (Smith, 1995).

I have recently completed a meta-analysis of over 50 studies where previously published environment recruitment correlations had been re-tested with new data (Myers, 1998). Although the proportion of published correlations that have been verified upon re-test was low, there are two generalizations that stand out. First, correlations for populations at the limit of a species' geographical range have often remained statistically significant when re-examined. In particular, all the temperature correlations that held up upon re-examination were associated with populations close to the northern limit (these were all in the northern hemisphere; with positive correlations) or at the southern limit (with negative correlations) of the species range. This general result has also been observed for cod (Planque and Frédou, 1999). And second, a dome-shaped relationship appears to exist between recruitment success of small pelagic fish in eastern boundary current upwelling systems (Bakun, 1996) and the upwelling intensity (the Optimal Environmental Window; Cury and Roy, 1989). Unfortunately, these environment-recruitment correlations do not appear to be very useful in practice. An examination of environment-recruitment correlations that were reviewed 13 years ago (Shepherd *et al.*, 1984) showed that the results for only one out of 47 reviewed studies is currently used for recruitment estimates in routine assessments.

An unresolved question

For most species, we do not know at what stage density-dependent mortality, and stochastic density-independent mortality occurs. This question was first addressed in terms of the critical-period hypothesis that states "the numerical value of a year class is apparently stated at a very early age, and continues in approxi-

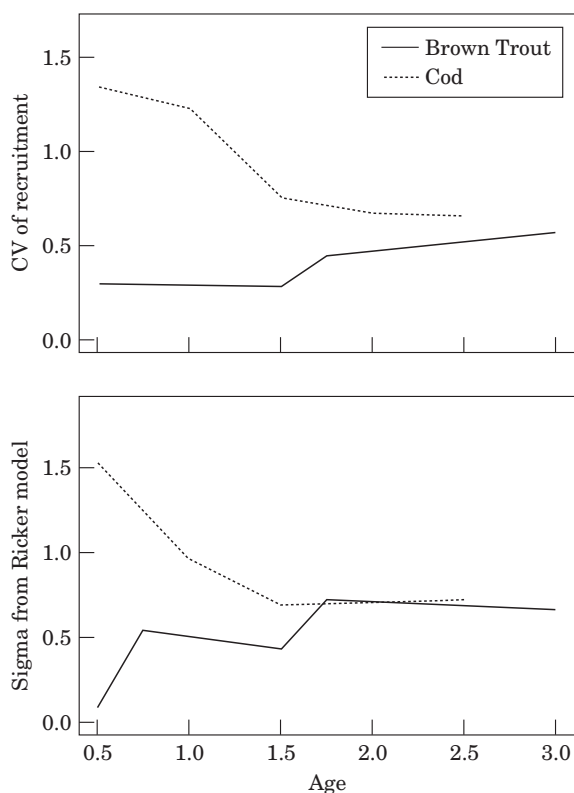


Figure 6. Changes in the coefficient of variation in recruitment and in the standard deviation of the log residuals of the recruitment from a Ricker model at five ages for brown trout and cod.

mately the same relation to that of other year classes throughout the life of the individuals" (Hjort, 1914). This is largely true but with the following limitation: relative abundance may change to some extent by a certain amount of stochastic mortality as well as density-dependent mortality. Nevertheless, good year classes remain good. For some populations, we can examine how interannual variability changes with age, and use models to examine when density-dependent and density-independent mortality occurs. Two contrasting situations are presented for brown trout from Black Brows Beck (Elliott, 1994) and North Sea cod (Figure 5). In brown trout, strong density-dependent mortality occurs during the first six months after eggs are deposited, while mortality varies largely independent of density among years until maturity at age 3. Recruitment variability increases with age (Figure 6).

The pattern is quite different for North Sea cod where recruitment variability decreases with age. The decrease is caused by strong density-dependent mortality during the demersal juvenile stage, as in the 17 populations of demersal fish studied by Myers and Cadigan (1993a,b). Several features should be noted: (1) year classes that are large soon after settlement remain relatively large for all

subsequent surveys, (2) variability decreases with age, and (3) spawner abundance is slightly positively correlated with recruitment. The first two features are apparent in virtually all population dynamics data on demersal fish with a planktonic life stage. The last feature is certainly weak for these data, but is a persistent feature of the vast bulk of spawner-recruit data (Myers and Barrowman, 1996). Note that both of these reliable data sets show similar levels of variation at age 3 (CV about 0.5) as have been commonly observed for many fish species (Myers, 2001).

While the result for demersal fish appears to hold for many populations (although variance is sometimes increased owing to stochastic density-independent mortality at later life-history stages; Myers and Cadigan, 1993b; Fromentin *et al.*, 2000), the result for trout may not be true for salmonids in general. For example, Bradford (1995) found that the variance in survival increased with age for many Pacific salmon species, and about half the variability in natural survival occurred after migration to the sea. It would be of great interest to apply the Myers and Cadigan (1993b) methods that include estimation error to examine the general question of the creation of variability in survival by density-independent mortality and the reduction in the variance by density-dependent mortality for salmonid data.

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