



# Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis

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## Abstract

The uncertainty of the biological basis of fisheries management can be greatly reduced by examining many data sets and combining the results by various statistical methods. A major cause of uncertainty in the population biology of exploited species is the lack of very long time-series; this can be overcome by examining data on many populations (over 500 are examined here). We describe how meta-analysis can be used to address the fundamental problems of population biology and management, e.g. the relationship between spawner abundance and recruitment, the existence of depensation, the estimation of the limits of fishing. We conclude that meta-analysis, and related techniques, can considerably reduce the biological basis of uncertainty in fisheries management. © 1998 Elsevier Science B.V. All rights reserved.

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## 1. Introduction

The point of view of this paper is that the uncertainty of the biology of exploited species is much less than that commonly assumed, and that a systematic, comprehensive examination of the available data would demonstrate this. Here we will review attempts to reduce the uncertainty in fishery management by applying meta-analysis to population dynamics data.

The need for comparative analysis has long been recognized in fisheries research (Beverton and Holt, 1959; Pauly, 1980; Brander, 1994) and pioneering work on the relationship between spawner abundance and recruitment was based upon analysis of many data

sets (Ricker, 1954; Cushing, 1971). Here we describe how newer statistical and analytical methods, coupled with much more extensive data compilations, can greatly extend these earlier analyses.

Meta-analysis is the term used to describe quantitative methods for combining evidence across studies. In the work we describe here, results are combined across populations instead of experiments. That is, we treat the time-series of each population as a realization of a natural experiment, and combine the results across populations.

An alternative approach to meta-analysis, empirical Bayesian analysis, has certain advantages, particularly in a decision analysis framework. We will concentrate on the meta-analytic approach because Bayesian methods in fisheries have recently been reviewed in detail by Punt and Hilborn (1997) and Hilborn and Liermann (1998). There are strong similarities

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<sup>1</sup>My good friend Gordon Mertz tragically died the week this manuscript was being finished; his intelligence, humor and charm will be greatly missed – R.A. Myers.

between a meta-analytic or an empirical Bayes approach, and both approaches should lead to similar conclusions. In particular, when a empirical Bayes or mixed model approach is used, the results should be virtually identical (Robinson, 1991, with comments and a rejoinder by the author).

The use of meta-analysis or empirical Bayes methods is motivated by the lack of long term data for any one population. We may never have data on over 100 generations for a natural fish population, and yet this is what we need 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 to combine data from many populations. There are many subtle pitfalls if multiple studies are combined in a naive fashion. For example, when studies are being reviewed, it is often examined how often a given hypothesis is statistically significant. This can be very misleading. For example, if the reviewer simply examines how often an outcome is statistically significant, then there will be a strong bias towards the conclusion that the process or treatment has no effect because the proportion of a large number of studies that yield statistically significant results is approximately the average power of the test used (Hedges and Olkin, 1985). That is, a reviewer of research studies 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. Furthermore, this bias is not reduced as the number of studies increases. This is a severe problem in fisheries research because many studies have very low statistical power.

Although meta-analysis can greatly reduce uncertainty of the biology of exploited species, it is of very little help in reducing the inherent uncertainty associated with inter-annual variability in recruitment. There is good theoretical and empirical evidence that it is virtually impossible to usefully predict year to year recruitment. (Bradford, 1992; Mertz and Myers, 1995).

We review some of the conclusions that we have arrived at with co-workers by using these techniques. We have spent over a decade compiling a database of over 500 multivariate time-series of spawner, recruitment, catch and fishing mortality (Myers et al., 1990, 1995b). This database is available from the author to any researcher. We are expanding the database by about 100 stocks a year.

## 2. Meta-analysis and the reduction of biological uncertainty

Meta-analysis is usually used in reviews and synthesis of experimental data. Typically, meta-analysis is used to combine estimates of treatment effects from different research studies that examine identical or similar treatments. Thus, the basic unit of analysis in this case is the published experiment, and meta-analysis uses the published summary statistics to provide a broader base for conclusions than is possible from a single study. The key to using meta-analysis in the study of population dynamics is to find a way of comparing many experiments or multivariate time-series using a common scale.

The simplest approach to meta-analysis is to combine tests of statistical significance. Methods for combining tests of significance, sometimes called omnibus or non-parametric tests, are widely used because they do not depend upon the type of data, test, or statistical assumption, as long as the  $p$ -values are given or can be calculated. The most commonly used omnibus test is based upon combining the probability levels from one-sided significance tests (Fisher, 1954; Hedges and Olkin, 1985). Although these tests are useful, they cannot tell the magnitude of the effects being considered, i.e. we cannot tell the importance of the process being considered. This approach has been used to combine data on recruitment variability across populations (Myers and Drinkwater, 1989; Myers, 1991).

A preferable approach to meta-analysis is to combine estimates of effect size. In meta-analysis, the effect size or the standardized mean difference between treatment groups is  $(\mu_1 - \mu_2) / \sigma$ , where  $\sigma$  is the within-group standard deviation, is most frequently used to compare research studies. Although the standardized mean difference is convenient for experimental studies, it is less so for ecological studies. The crucial need is for a parameter that describes an ecological effect that can be compared across populations, and an estimate of its sampling variance. Below we will describe how to use the methods of meta-analysis to combine estimates of delayed density-dependent mortality rates across populations.

Methods also exist for combining estimates of correlation coefficients. The correlation coefficient is a scale-free measure of the linear relationship

between two variables, and thus can be used as an effect magnitude for cumulation across studies. Combining correlation coefficients is useful in the study of the relationship between environmental variables and recruitment (Myers, 1997b).

One of the main difficulties in using meta-analysis in population biology is constructing a population parameter that can be combined across studies. One solution is to construct a non-dimensional parameter. For example, a ratio of two parameters or a power term in an equation can be used. An example of the latter is the  $\delta$  in the sigmoid Beverton–Holt spawner-recruitment functions:

$$R = \frac{\alpha S^\delta}{1 + S^\delta/K}, \quad (1)$$

where  $S$  is the quantity of spawners,  $R$  the subsequent recruitment,  $\alpha$  the slope at the origin, and  $K$  is related to the carrying capacity. The parameter  $\delta$  in the sigmoid Beverton–Holt function controls the degree of depensation (Thompson, 1993). If  $\delta=1$ , the function reduces to the Beverton–Holt function; if  $\delta>1$ , the function displays depensation; if  $0<\delta<1$ , the initial increase of the function will be greater than that of the Beverton–Holt function. The parameter  $\delta$  is dimensionless and can be compared across populations.

Another approach is to combine parameters that have units that are compatible across populations. Below, we will show how the slope at the origin of the spawner-recruitment function,  $\alpha$ , can be modified and compared among populations.

A statistical issue that has to be addressed in the use of any statistical method to combine data, is that nearby populations of fish are not independent in the sense that recruitment is correlated among regions (Myers et al., 1995c). This can be dealt with by modelling the degree of correlation among stocks, and then weighting the different estimates appropriately (Myers et al., 1997a).

### 3. Implementing

The philosophy here is to exploit commonalities of populations (say) within a species to reduce uncertainties in parameters describing individual populations. For example, density-dependence parameters usually carry “units” of one-upon-spawners (or

spawning biomass) and it follows that the scaling of the parameters with the number of spawners (or spawning biomass) should yield a normalized parameter with a very small spread of values compared to the raw estimates. It may be that the distribution of parameters is compatible with a distribution representing a grand mean plus estimation errors (with no true inter-population variation). In this simplest of all cases, the grand mean, which is well determined, provides a reliable estimate of the density-dependence parameter for any particular population, whereas the actual estimate for that population may be extremely unreliable (owing to estimation error).

At the next level of complexity, the scaled parameter may be drawn from a distribution representing a grand mean, plus true inter-population variation, plus estimation error. In this case, obtaining the variance of the true inter-population variability provides information on the reliability of any particular estimate (as assessed by the number of standard deviations it lies from the grand mean).

It is in this vein that we proceed. By identifying the proper scaling, we can form a normalized population parameter which has, in effect, been drawn from an underlying distribution characterizing (say) the species. Thus, an estimate of the parameter for any particular population provides information about the true value of the parameter for all the other populations included in the analysis. By capitalizing on this joint information, the uncertainty in the estimate for any particular population can be reduced.

## 4. Results of meta-analytic studies

### 4.1. Spawners and recruitment

Although the relationship between spawner abundance and recruitment is perhaps the most fundamental question in fisheries biology, there is a great difference in opinion about the importance of spawner abundance. The reason for this lack of consensus is that each biologist tends to examine a very small number of data sets with little or no understanding of the statistical power of his analysis, i.e. there is a great lack of synthesis of research. To overcome this problem, Myers and Barrowman (1996) asked the following three questions:

1. Does the largest recruitment occur when spawner abundance is high?
2. Does the smallest recruitment occur when spawner abundance is low?
3. Is the mean recruitment higher if spawner abundance is above the median rather than below?

In that paper, we demonstrated how non-parametric methods can be used to address these three questions. We were able to address these questions definitively because we were able to combine the results on the analysis of a compilation of data on over 300 fish stocks (Myers et al., 1995b).

In all the three cases the results were clear. If the range of observed spawner abundance was large, the largest recruitment tended to occur when the spawner abundance was large; the lowest recruitment tended to occur when the spawner abundance was low; and the ratio of the mean recruitment above the median level of spawners to that below, was greater than for all the families if the range of observed spawners was large.

Gilbert (1997) used an earlier version of Myers' database to reach the same conclusion for salmonoids, but different conclusions for marine fish. However, Myers (1997a) demonstrated that although Gilbert's methods are highly inefficient, they can be used to reject his own conclusions, and strongly support the analysis of Myers and Barrowman (1996): recruitment is a function of the spawner abundance. The key is to understand that not all time-series are equally reliable. If time-series are separated on the criterion of potential reliability, then we can reject Gilbert's suggestion, among stocks, among families, and among stocks within families. However, we believe that we share a common ground with Gilbert in the idea that autocorrelation in recruitment and/or juvenile survival is real, and creates very difficult statistical problems. By not realizing that his idea necessarily implies autocorrelation, Gilbert fails to relate his idea to other work that attempts to address the same problem. For example, Myers and Barrowman (1996) attempted to deal with the problem by eliminating stocks from an analysis with moderate and high autocorrelation and by extensive simulations (Myers and Barrowman, 1995). The difficulties of adequately understanding autocorrelated data are great; particularly when long-distance correlations are present and are not adequately described by traditional models. Myers' com-

parison of spawner recruitment data is available to anyone who is interested in exploring this, or any other problem.

#### 4.2. Depensation

Theoretical studies show that 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 for 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 and a population has been reduced by harvesting to a lower abundance level, 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 estimates of spawner abundance and recruitment for 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  $\delta$  as a free parameter and the same model with  $\delta$  fixed at 1 (the standard Beverton–Holt model). In this case, the dimensionless parameter,  $\delta$ , was used in the analysis because it can be compared across populations.

For 9 of the 129 stocks, the model with  $\delta$  as a free parameter gave a significantly better fit at the 0.05 level. Only three of these populations showed significant depensation ( $\delta > 1$ ), approximately the number that would be expected by a chance alone. Even if we examine the most convincing example of depensation, Icelandic spring spawning herring, environmental change may be a better explanation than depensation for the observations because survival was low for the last 15 years of the time-series.

Estimates of the statistical power of the tests strengthen our conclusion that depensatory dynamics in the relationship between spawner abundance and subsequent recruitment are unlikely for most exploited populations (Myers et al., 1995a). We concluded that the effects of overfishing are, in general, reversible, and that fish stocks collapse because of overfishing or environmental change. Despite much speculation and

many theoretical models, increased depensation per capita mortality at low densities, is at best a very rare phenomenon.

Liermann and Hilborn (1997) used an empirical Bayes hierarchical model on the same data set. Their approach has several advantages over the approach in Myers et al. (1995a). They used an alternative standardization, and provided empirical prior distributions, instead of relying on a hypothesis testing approach. Liermann and Hilborn (1997) concluded that although there was not a strong evidence for many populations, the possible range of depensation levels that was consistent with the data was broad. They also suggested that the possibility should be incorporated into spawner recruitment models.

#### 4.3. Estimating delayed density-dependent mortality

If several populations share a common pattern of delayed density-dependence, then we can apply meta-analytic techniques. Myers et al. (1997a) 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 the spawner abundance at lag 0, 1, and 2. This results in the model

$$R_t = \alpha S_t e^{-\beta S_t - \phi S_{t-1} - \gamma S_{t-2} + \epsilon_t}, \quad (2)$$

where  $\beta S_t$ ,  $\phi S_{t-1}$  and  $\gamma S_{t-2}$  are the density-dependent mortality due to the number of spawners with lags of 0, 1, and 2. A standardization is required so that the delayed density-dependent parameters can be compared among populations. From Eq. (2), a natural scaling is  $\phi' = \phi$ ,  $\gamma' = \gamma/\beta$ . This simple scaling allows a meta-analysis among populations to be carried out.

Using this approach, we have found the evidence of moderate delayed density-dependent mortality at lag one for sockeye and pink salmon populations. However, for sockeye delayed density-dependent mortality at lags greater than one year was estimated to be at most weak and not statistically significant.

The results are very important for the management of sockeye populations because they reduce the uncertainty of the biological basis for the extreme cyclic behaviour of some sockeye populations. Uncertainty in the cause of the cycling resulted in management that increased fishing mortality on populations at the low parts of the run (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.

#### 4.4. The maximum annual reproductive rate

The maximum annual reproductive rate – which we define as the average number of replacement spawners which are produced per spawner per year at low abundance (after a time delay for the age at maturity) with no fishing mortality – 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 the estimation of the population growth rate, often denoted as “ $r_m$ ”, to estimate the limits to overfishing (Mace, 1994; Myers et al., 1994), and to understand the dynamic behaviour of the population, i.e. whether the population has oscillatory or chaotic behaviour. We will demonstrate the usefulness of estimates of the maximum annual reproductive rate in each of the following sections.

For the semelparous species in which  $R$  and  $S$  are in the same units, the slope at the origin,  $\alpha$ , for the Ricker or Beverton–Holt models can be directly interpreted as the maximum annual reproductive rate. For other species,  $\alpha$  must be standardized. First consider

$$\hat{\alpha} = \alpha \cdot \text{SPR}_{F=0}, \quad (3)$$

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,  $\hat{\alpha}$ , represents the number of spawners produced by each spawner over its lifetime at a very low spawner abundance. The quantity,  $\tilde{\alpha}$ , required for our calculations 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 the adult survival is  $p_s$ , then  $\hat{\alpha} = \sum_{i=0}^{\infty} p_s^i \tilde{\alpha}$ , or summing the geometric series

$$\tilde{\alpha} = \hat{\alpha}(1 - p_s) = \alpha \cdot \text{SPR}_{F=0}(1 - p_s). \quad (4)$$

This quantity,  $\tilde{\alpha}$  is the maximum annual reproductive rate.

To estimate  $\tilde{\alpha}$ , we convert recruits into units compatible to that of the spawners. That is, we multiply the number of recruits by  $\alpha \cdot \text{SPR}_{F=0}(1 - p_s)$ . For this analysis, we wish to consider  $p$  populations, subscripted by  $i$ , simultaneously. This requires recruitment and

spawners to be doublesubscripted. If the Ricker spawner recruitment model is assumed, then we estimate a model of the form

$$\log \frac{R_{i,t}}{S_{i,t}} = \log \tilde{\alpha}_i + \beta_i S_{i,t} + \epsilon_{it}, \quad (5)$$

where we assume that  $\tilde{\alpha}_i$  is a normal random variable, i.e. a random effect,  $\beta_i$  is a fixed effect that depends upon the carrying capacity of population  $i$ , and  $\epsilon_{it}$  is a normal, possibly autocorrelated, residual. In the above 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 to easily carry out the estimation (Searle et al., 1992). It is possible to obtain best linear unbiased predictors (BLUPs) of the  $\tilde{\alpha}_i$  in which the data on the individual population and the data from all the populations

considered are optimally combined (Myers et al., 1996). The estimates of the true underlying variability in the parameters is much less than the individual estimates would suggest (Fig. 1).

The analysis presented in Myers et al. (1996) suggests a new and unsuspected finding: The maximum annual reproductive rate for any of the species examined is typically between 2 and 5. This number may be less for some species and more for others, but the relative constancy of the annual reproductive rate is an unanticipated finding.

There are other approaches to this problem, particularly Bayes or empirical Bayes hierarchical models (Efron, 1996). McAllister et al. (1994) implemented an empirical Bayes approach to estimate a parameter functionally related to the slope at the origin, e.g. the steepness parameter, using an earlier version of the

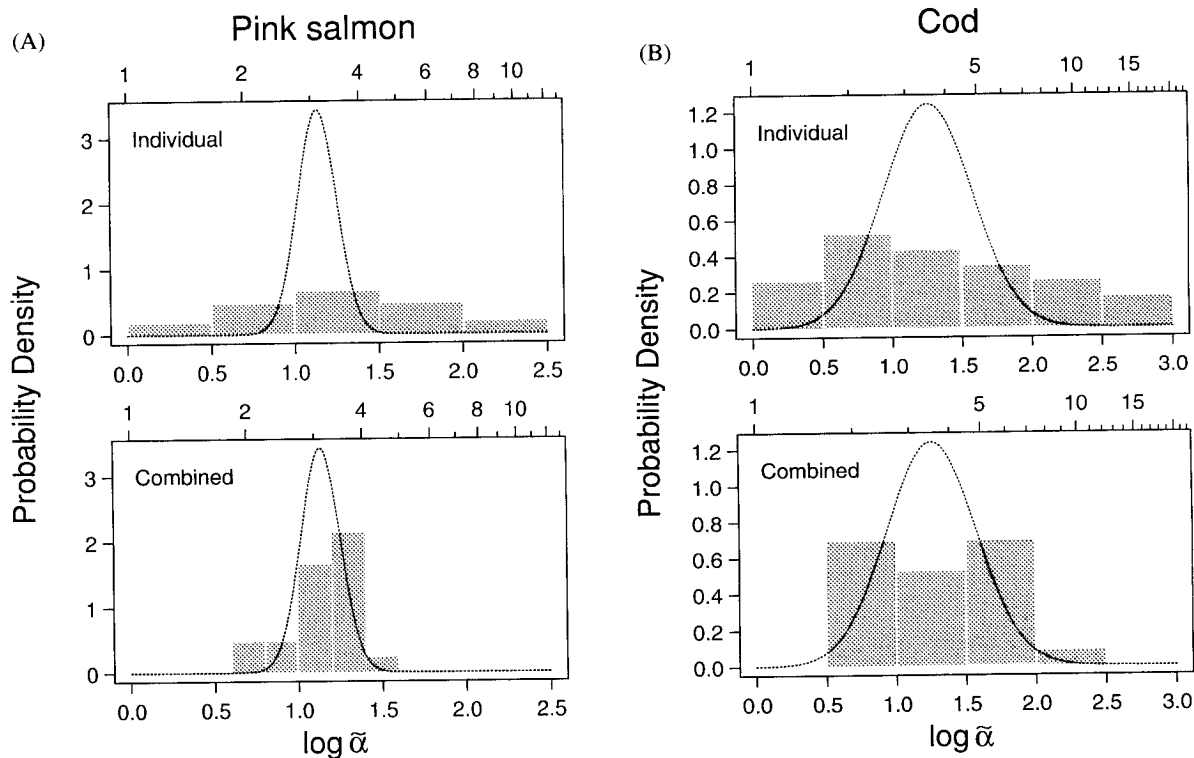


Fig. 1. (A) Histograms of the estimates and predictions of the log of the annual reproductive rate,  $\log(\tilde{\alpha})$  for pink salmon (*Oncorhynchus gorbuscha*). The top panel shows the estimates if each population is considered separately (i.e. the results from a standard Ricker fit for each population), while the bottom panel shows the predicted values from the best linear unbiased predictor from the mixed model. The dashed line shows the estimate of the underlying true variability in  $\log(\tilde{\alpha})$  from the mixed model, i.e. the best linear unbiased predictor (BLUP). Note that the top axis of the plots shows the untransformed annual reproductive rate. (B) Same as (A) except for cod (*Gadus morhua*).

data set used here. It will be of considerable interest if alternative techniques lead to the same generalization for the relative constancy of the maximum reproductive rate.

#### 4.5. Estimating the limits of fishing

It is well known that 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 et al. (1998) formulated a simple model which permits a ready approximation of the influence of the age of first harvest on the sustainable fishing mortality. It will be assumed that the selectivity is knife-edge, but the age of entry into the fishery will be allowed to vary (Beverton and Holt, 1957). The model will be used to calculate the limiting (maximum sustainable) fishing mortality  $F_\tau$  (Mace and Sissenwine, 1993; Mace, 1994).

The limiting fishing mortality is the maximum possible that can be imposed on a stock without causing extinction, designated as  $F_\tau$ . If knife-edge fishing mortality begins at age  $a_{\text{sel}}$ , and age at maturity for all females is  $a_{\text{mat}}$  and  $a_{\text{sel}} < a_{\text{mat}}$ , then Myers et al. (1998) demonstrated that the limiting fishing mortality is given implicitly by

$$\hat{\alpha} = e^{F_\tau(a_{\text{mat}} - a_{\text{sel}} + 1)} \left( 1 - e^{-(M + F_\tau)} \right), \quad (6)$$

where  $M$  is the natural mortality. That is, the biological limit of fishing is a function of the scaled slope at the origin,  $\hat{\alpha}$ , or in ecological terms, the maximum annual reproductive rate; see Myers et al. (1998) for details. Thus, armed with an approximate estimate of maximum annual reproductive rate, the limits to fishing can easily be approximated. The result of this analysis is shown for the Northern cod, i.e. the cod stock off Labrador and the Northeast coast of Newfoundland (Fig. 2). 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 reproducing, i.e.  $a_{\text{sel}} > a_{\text{mat}}$ . 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

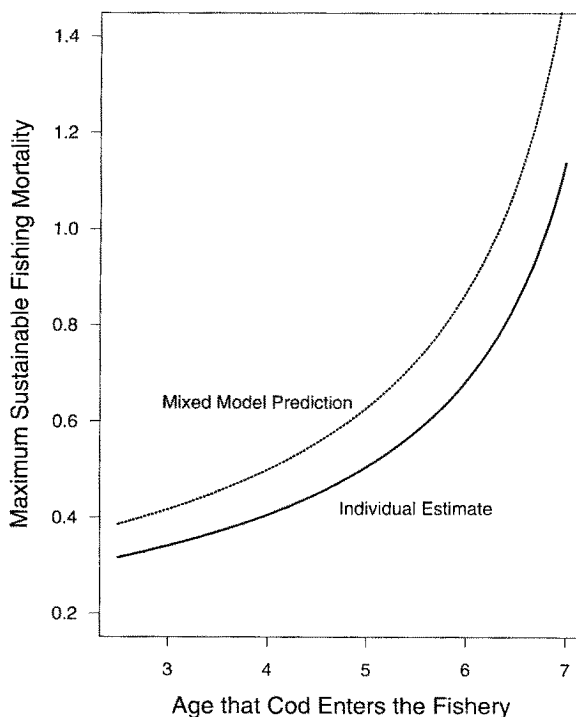


Fig. 2. The biological limit of fishing mortality,  $F_\tau$ , versus the age at selection to the fishery ( $a_{\text{sel}}$ ) for two levels of  $\hat{\alpha}$  (short dashes,  $\hat{\alpha} = 2.3$ ; the maximum likelihood estimate) and solid line  $\hat{\alpha} = 3.7$ , the BLUP from the mixed model. Data are for the “northern” cod stock (NAFO Div. 2J3KL) off the coast of Labrador and Newfoundland. We have assumed that the age at maturity is seven years, which is the approximate age of full maturity for cod stocks in colder water.

the stock if fishing mortality targets are exceeded (Myers et al., 1998). (A spawn-at-least-once policy requires that fish becomes vulnerable to the commercial gear only after having spawned once.)

#### 4.6. Implications of maximum replacement rate for estimating population growth and recovery rates

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 with no fishing. Myers et al. (1997c) demonstrated that the maximum annual reproductive rate, estimated as described above, could be used to simply 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 for cod, and there is evidence that population variability increases as these extremes are approached (Myers, 1991). The increase in population variability at the limits of the range of cod could impose constraints on  $r_m$  that would mask the simple dependence of  $r_m$  on the metabolic rate or the somatic growth rate apparent in cross species comparisons. In fact, an unanticipated result, even for a within-species comparison, is that there is a strong coupling between  $r_m$  and metabolic rate or somatic growth rate (as represented by age at maturity or temperature) (Myers et al., 1997c). Our results have implications for the recovery rates of a number of recently collapsed Atlantic cod populations (Hutchings and Myers, 1994). We showed that  $r_m$  was about 0.2 for the cod in cold conditions, but around 0.8 at the warmest portions of its range. The relatively low population growth rate for the cod in the colder part of its range, implies that the recovery of severely overexploited populations may take very long.

An implicit formula for approximately estimating  $r_m$  is

$$(e^{r_m})^{a_{\text{mat}}} - e^{r_m(a_{\text{mat}}-1)-M} - \tilde{\alpha} = 0, \quad (7)$$

where  $a_{\text{mat}}$  is the age at maturity (Goodman, 1984; Myers et al., 1997c). If  $p_s=0$ , then we have the simple expression

$$r_m = (1/a_{\text{mat}})\log \tilde{\alpha}. \quad (8)$$

Such simple approximations are crucial for the management of fish stocks. Hutchings et al. (1997) described how the maximum growth rate of “Northern” cod was overestimated, with great economic consequences.

#### 4.7. Thresholds for recruitment overfishing

For management purposes, it is often desirable to estimate a minimum biomass reference level at which recruitment to a fish stock is seriously reduced. Myers et al. (1994) took an empirical, comparative approach to the problem by examining observations on a wide range of fish stocks. Eight methods for estimating spawning stock biomass thresholds for recruitment overfishing were investigated. Their behaviour was

tested using spawner and recruitment data for 72 finfish populations each with at least 20 years of data. We considered three classes of thresholds defined by

1. the stock size corresponding to 50% of the maximum predicted average recruitment,
2. the minimum stock size that would produce a good year class when environmental conditions are favourable, and
3. the stock size corresponding to 20% of various estimates of virgin stock size.

The estimators of the first type (“1” above) are generally preferable because they are easily understood, relatively robust if only data at low stock sizes are available, and almost always result in higher levels of recruitment above the threshold.

The major limitation for employing thresholds for recruitment overfishing based upon the spawner biomass that results in a 50% reduction in recruitment, is the difficulty of estimating a reliable spawner recruitment function (Myers et al., 1994), particularly the slope at the origin. By using the meta-analytic methods described above, data from many stocks can be combined to yield a much more reliable estimate of the threshold for recruitment overfishing.

#### 4.8. Did low recruitment cause the collapse of the Canadian cod stocks?

We have concentrated on general biological issues; however, meta-analysis can also be applied to specific management issues. The collapse of six cod stocks in Eastern Canada has been studied by applying meta-analysis on the results of the research surveys of these stocks (Myers et al., 1997b). We tested the hypothesis that these collapses were caused by poor recruitment of cod to the fishery by combining the results for a total of 10 surveys; there was a very strong evidence that the collapses was not caused by poor recruitment. Meta-analysis was then used to show that the trends in recruitment estimated from virtual population analysis (VPA) were inconsistent with the trends estimated from research surveys. This led us to the hypothesis that the discarding of young fish increased with increased fishing mortality and that this could explain the significant differences that exist between survey and VPA indices of abundance. In each of the six stocks, high juvenile mortality was associated with

high adult mortality, which is consistent with the hypothesis of discarding.

In each of these analyses, the results for any one stock were not convincing; however, the consistency of the results across six stocks and 10 surveys allowed us to reach firm conclusions with great power: the cod stocks in eastern Canada collapsed because of over-fishing on juveniles.

We can now interpret the analysis for the maximum fishing rate that a population can withstand in the context of the collapse of the cod stocks in Eastern Canada. We have seen that the collapse was associated with a shift of fishing mortality to younger fish; as we have seen earlier, this has a disastrous effect on the ability of cod stocks to withstand fishing pressure (Fig. 2).

## 5. Limitations of meta-analytic techniques

We have concentrated on the advantages of meta-analytic approaches to reduce uncertainty. Any user should be aware of the inherent trade-offs in such an approach; the most fundamental of which is the mean-variance trade-off. That is, by using data from other populations, there is a risk of obtaining a biased result even though the result may be on an average closer to the truth.

The user should also be aware that meta-analysis does not eliminate inherent biases or fundamental problems with the data.

## 6. Conclusions

The uncertainty of the biological processes underlying the population dynamics of exploited species can be greatly reduced by combining data from many studies. Perhaps the most important result of this review is that it is critical to consider the spawner abundance in fisheries management, and that the relative constancy of the maximum reproductive rate allows for simple, broad conclusions to be reached on the management of fish stocks. That the maximum reproductive rate is typically around 2–5 replacement spawners per spawner per year is a powerful tool for the management of fish stocks. It allows the maximum exploitation rate to be quickly estimated, and the

recovery rates of exploited fish populations to be calculated.

Fisheries management needs to become more reliable. Fisheries biologists should be able to use simple approximations, such as Eq. (6) and Eq. (7), to estimate the critical parameters needed for the management of any fish stock. For example, Eq. (7) gives an approximate formula for estimating the maximum population growth rate and Eq. (6) gives a quick approximation to the maximum sustainable level of fishing mortality. All that is required to use these approximations is the data on the natural mortality, age at maturity, and the maximum reproductive rate. These approximate formulas will require testing and verification, but this approach should allow progress to be made on critical issues.

## References

- Beverton, R.J., Holt, S.J., 1957. On the dynamics of exploited fish populations. MAFF Fisheries Investigations Series II 19, 533.
- Beverton, R.J.H., Holt, S.J., 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: Wolstenholme, G.E.W., O'Connor, M. (Eds.), CIBA Foundation Colloquia on Ageing, vol. 5, pp. 142–174.
- Bradford, M.J., 1992. Precision of recruitment estimates from early life stages of marine fishes. *Fish. Bull.* 90, 439–453.
- Brander, K., 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: The utility of inter-regional comparisons. *ICES Mar. Sci. Symp.* 198, 406–413.
- Clark, C.W., 1990. *Mathematical Bioeconomics*, 2nd ed. Wiley/Interscience, New York.
- Cole, L.C., 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* 29, 103–137.
- Cushing, D.H., 1971. The dependence of recruitment on parent stock in different groups of fishes. *J. Cons. Int. Explor. Mer.* 33, 340–362.
- Efron, B., 1996. Empirical Bayes methods for combining likelihoods. *J. Am. Stat. Assoc.* 91, 538–565.
- Fisher, R.A., 1954. *Statistical Methods for Research Workers*, 12th ed. Oliver & Boyd, Edinburgh.
- Gilbert, D., 1997. Towards a new recruitment paradigm for fish stocks. *Can. J. Fish. Aquat. Sci.* 54, 969–977.
- Goodman, D., 1984. Statistics of reproductive rate estimates, and their implications for population projection. *Rep. Int. Whaling Comm. Spec. Issue* 6, 161–173.
- Hedges, L.V., Olkin, I., 1985. *Statistical Methods for Meta-analysis*. Academic Press, San Diego.
- Hilborn, R., Liermann, M., 1998. Standing on the shoulders of giants: Learning from experience in fisheries. *Rev. Fish. Biol. Fisheries* 8, 1–11.

- Hutchings, J.A., Myers, R.A., 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. *Can. J. Fish. Aquat. Sci.* 51, 2126–2146.
- Hutchings, J.A., Walters, C., Haedrich, R.L., 1997. Is scientific inquiry compatible with government information control? *Can. J. Fish. Aquat. Sci.* 54, 1198–1210.
- Levy, D.A., Wood, C.C., 1992. Review of proposed mechanisms for sockeye salmon, population cycles in the Fraser River. *Bull. Math. Biol.* 54, 241–261.
- Liermann, M., Hilborn, R., 1997. Depensation in fish stocks: A hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.* 54, 1976–1985.
- Mace, P.M., 1994. Relationships between common biological reference points used as threshold and targets of fisheries management strategies. *Can. J. Fish. Aquat. Sci.* 51, 110–122.
- Mace, P.M., Sissenwine, M.P., 1993. How much spawning per recruit is enough? In: Smith, S.J., Hunt, J.J., Rivard, D. (Eds.), *Risk Evaluation and Biological Reference Points for Fisheries Management*. *Can. Spec. Publ. Fish. Aquat. Sci.* 120, 101–118.
- McAllister, M.K., Pikitch, E.K., Punt, A.E., Hilborn, R., 1994. A Bayesian approach to stock assessment and harvest decisions using the sampling/importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* 51, 2673–2688.
- Mertz, G., Myers, R.A., 1995. Estimating the predictability of recruitment. *Fish. Bull.* 93, 439–453.
- Myers, R.A., 1991. Recruitment variability and range of three fish species. *NAFO Sci. Council. Stud.* 16, 21–24.
- Myers, R.A., 1997a. Comment and reanalysis: Paradigms for recruitment studies. *Can. J. Fish. Aquat. Sci.* 54, 978–981.
- Myers, R.A., 1997b. The role of meta-analysis in the study of recruitment variation in fish populations. In: Chambers, R.C., Trippel, E.A. (Eds.), *Early Life History and Recruitment in Fish Populations*. Chapman & Hall, London, pp. 575–596.
- Myers, R.A., Barrowman, N.J., 1995. Time series bias in the estimation of density-dependent mortality in stock-recruitment models. *Can. J. Fish. Aquat. Sci.* 52, 223–232.
- Myers, R.A., Barrowman, N.J., 1996. Is fish recruitment related to spawner abundance? *Fish. Bull.* 9, 707–724.
- Myers, R.A., Barrowman, N.J., Hutchings, J.A., Rosenberg, A.A., 1995a. Population dynamics of exploited fish stocks at low population levels. *Science* 269, 1106–1108.
- Myers, R.A., Blanchard, W., Thompson, K.R., 1990. Summary of north atlantic fish recruitment 1942–1987. *Can. Tech. Rep. Fish. Aquat. Sci.* 1743.
- Myers, R.A., Bradford, M.J., Mertz, G., Bridson, J.M., 1997a. Estimating delayed density-dependent mortality in sockeye salmon, *Oncorhynchus nerka*: A meta-analytic approach. *Can. J. Fish. Aquat. Sci.* 54, 2449–2463.
- Myers, R.A., Bridson, J., Barrowman, N.J., 1995b. Summary of worldwide stock and recruitment data. *Can. Tech. Rep. Fish. Aquat. Sci.* 2024.
- Myers, R.A., Drinkwater, K.F., 1989. The influence of Gulf Stream warm core rings on recruitment of fish in the northwest Atlantic. *J. Mar. Res.* 47, 635–656.
- Myers, R.A., Hutchings, J.A., Barrowman, N.J., 1997b. Why do fish stocks collapse? The example of cod in eastern Canada. *Ecol. Appl.* 7, 91–106.
- Myers, J.A., Mertz, G., Barrowman, N.J., 1995c. Spatial scales of variability in cod recruitment in the North Atlantic. *Can. J. Fish. Aquat. Sci.* 52, 1849–1862.
- Myers, J.A., Mertz, G., Barrowman, N.J., 1996. Invariants of spawner-recruitment relationships for marine, anadromous, and freshwater species. *ICES CM 1996/D: 11*.
- Myers, J.A., Mertz, G., Bridson, J.M., 1998. Spatial scales of interannual recruitment variations of marine, anadromous, and freshwater fish. *Can. J. Fish. Aquat. Sci.* 54, 1400–1407.
- Myers, R.A., Mertz, G., Fowles, S., 1997c. The maximum population growth rates and recovery times of Atlantic cod, *Gadus morhua*. *Fish. Bull.* 95, 762–772.
- Myers, R.A., Rosenberg, A.A., Mace, P.M., Barrowman, N.J., Restrepo, V.R., 1994. In search of thresholds for recruitment overfishing. *ICES J. Mar. Res.* 51, 191–205.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. *J. Cons. Int. Explor. Mer.* 39, 175–193.
- Pimm, S.L., 1991. *The Balance of Nature*. The University of Chicago Press, Chicago.
- Punt, A., Hilborn, R., 1997. Fisheries stock assessment and decision analysis: the Bayesian approach. *Rev. Fish Biology Fish.* 7, 35–65.
- Ricker, W.E., 1954. Stock and recruitment. *J. Fish. Res. Bd. Can.* 11, 559–623.
- Robinson, G.K., 1991. That BLUP is a good thing: The estimation of random effects. *Statist. Sci.* 6(1), 15–51.
- Searle, S.R., Casella, G., McCulloch, C.E., 1992. *Variance Components*. Wiley, New York.
- Thompson, G.G., 1993. A proposal for a threshold stock size and maximum fishing mortality rate. In: Smith, S.J., Hunt, J.J., Rivard, D. (Eds.), *Risk Evaluation and Biological Reference Points for Fisheries Management*, vol. 120. *Can. Spec. Publ. Fish. Aquat. Sci.* 120, 303–320.