Estimating Natural Mortality in Stock Assessment Applications

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August 11–13, 2009
Alaska Fisheries Science Center, Seattle, WA

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EXECUTIVE SUMMARY

As part of the national program to improve and standardize stock assessment methods and to foster interaction among fisheries stock assessment scientists, the National Marine Fisheries Service (NMFS) Assessment Methods Working Group sponsored a three-day workshop on estimating natural mortality (*M*) for use in stock assessment applications. The workshop was held August 11–13, 2009, at the Alaska Fisheries Science Center in Seattle, Washington. A keynote presentation was delivered by Dr. Kai Lorenzen and 43 other scientists participated. The presentations and discussions covered biological aspects of mortality, methods for estimation of *M*, and best practices for use of *M* in assessment models. Below is a list of findings of this workshop.

- Empirical evidence and ecological theory indicate that the *M* of fish and invertebrate fishery resources scale with body mass or size. For a given species, early life history stages experience higher *M* than juvenile stages which, in turn, experience higher *M* than mature adults. Stress of reproduction and senescence may lead mortality rates to increase again in old fish.
- A pragmatic approach to modeling age-specific *M* was developed. The traditional assumption of a constant *M* may be appropriate when only mature fish are of explicit interest in the assessment. When juvenile fish need to be modeled explicitly (e.g. because these juveniles are targeted in a fishery or caught as bycatch), size dependence in *M* should be incorporated into the assessment application, for example, by means of a Lorenzen curve. The size-dependent mortality model for juveniles may be extended into the adult age groups, or combined with either a constant adult *M* or a more complex model for adults that allows for increasing *M* at age due to reproduction or senescence. It was noted that, while the size-dependent component of *M* appears to be general and well-quantified, reproductive and senescent effects on adult *M* may be more species-specific and are currently less predictable.
- Approaches to the estimation of *M* can be categorized into tiers based on available data, where higher tiers have more information available to estimate natural mortality. The lowest, Tier 1, comprises traditionally accepted values and those estimated from meta-analyses or life history theory. Tier 2 comprises direct, stock-specific estimates of *M*. Tier 3 comprises stock-specific estimates obtained from integrated assessment models. Tier 4 comprises estimates of *M* that account for temporal and/or spatial variation, including those derived from ecosystem models. In all tiers, constant or simple size/age–dependent *M* models may be used, but application of more complex size/age–dependent models may be limited to higher tiers. It is desirable to obtain multiple, separate estimates of *M* within tiers or involving multiple tiers where possible. Where multiple estimates of *M* are available, averaging the set of candidate estimates is considered good practice unless a single best value can be identified based on relative credibility or goodness of fit to observed data.
- It is important to characterize the variability of estimates of *M* for stock assessment applications. Using a point estimate of *M* will underestimate the uncertainty associated with assessment results. There was a consensus that it was important to propagate uncertainty in the estimate of *M* into assessment results where practicable.
- Best practices for implementing changes to the natural mortality rate in a stock assessment application require conducting a benchmark assessment with the new natural mortality rate. The benchmark assessment should be subject to full peer review. When estimating *M* within an integrated assessment model, it is recommended that a thorough exploration of model performance with respect to the estimation of *M* be conducted where practicable.
- It was recommended that research to investigate factors that cause *M* to vary in time and space be prioritized. Research into conceptual approaches to account for the effects of long-term changes in *M* on estimates of fishing mortality, spawner abundance, and biological reference points is strongly encouraged.
- An updated database of estimates of *M* by species, including a description of the method used to calculate *M*, would be a useful resource for future investigations into estimating natural mortality in stock assessment applications.

NATURAL MORTALITY WORKSHOP REPORT

INTRODUCTION

Importance of the Natural Mortality Rate

Natural mortality (*M*) is one of the most influential quantities in fisheries stock assessment and management. The magnitude of natural mortality relates directly to the productivity of the stock, the yields that can be obtained, optimal exploitation rates, management quantities, and reference points. Unfortunately, natural mortality is also one of the most difficult quantities to estimate. Commonly used methods—based on empirical relationships, life history theory, and maximum age—are notoriously problematic. In addition, many of the methods estimate only total mortality and, as a result, natural mortality must be separated from fishing mortality to quantify the relative effects of fishing versus natural mortality. Furthermore, there was no explicit consideration of the effects of density dependence in early life history mortality rates in this workshop because the workshop focused on stock assessment applications, which typically do not attempt to model mortality rates of eggs and larval fish but do include density-dependence as part of the spawner-recruitment relationship.

Terms of Reference

As part of the national program to improve and standardize stock assessment methods and to foster interaction among fisheries stock assessment scientists, the Assessment Methods Working Group of NOAA's National Marine Fisheries Service (NMFS) sponsored a three-day workshop on estimation of natural mortality. The proposed terms of reference included:

1) Identify and compare **alternative methods** of estimating natural mortality rates for conducting stock assessments. For example:
    a. **Empirical** methods
    b. **Life history** correlates
    c. *M* estimation performance using **integrated analysis** models
    d. Contribution of **predation** estimates from food web studies

2) Make recommendations for **best practices** for estimating natural mortality rates. Specifically consider:
    a. Evidence for **age-varying** *M*
    b. **Bayesian approaches** and prior elicitation
    c. Potential **inter-annual variability**
    d. **Assessment impact** versus best-fit to data given model assumptions

3) **Provide examples** of natural mortality rate estimation:
    a. Evaluated as a source of **retrospective** patterns?
    b. Evidence for **sex-specific** differences. Is estimating the ratio of rates enough?
    c. Confounding issues, e.g. between *M* and catchability coefficient
    d. Ability to estimate *M* under fishery **closures**

4) Prepare a **document** addressing these recommendations that can be used to guide future assessments by NMFS

This report summarizes workshop discussions and identifies recommendations in line with the Terms of Reference.

BIOLOGY OF NATURAL MORTALITY

On the first day of the natural mortality workshop, much of the discussion focused on the question, "What are the important factors driving *M*?" It was thought that the factors driving *M* could be dichotomized into intrinsic and extrinsic effects. Intrinsic factors included important correlations between life span, body size, and senescence, as well as between metabolic rate and body mass as adjusted for habitat temperature. These intrinsic factors can be linked to the development of a metabolic theory of ecology that relates metabolic rate to survival, growth, and reproduction (Brown et al., 2002). Extrinsic factors affecting natural mortality included disease, predation, and other exogenous sources of mortality that lead to death before expected life span was achieved. The relative importance of intrinsic versus extrinsic factors was thought to differ by species, although intrinsic factors have been observed to operate over a wide range of animal sizes and habitats (McCoy and Gillooly, 2008).

Intrinsic Factors

While intrinsic factors have an important impact on natural mortality rate, they may not be sufficient to explain differences in the value of *M* between species. For example, adult biomasses of some Pacific salmon and rockfishes are similar but these species have substantially different life spans and associated mortality rates. Pacific salmon are semelparous and die after a life span of a few years, while Pacific rockfishes are iteroparous and many rockfish species have life spans of several decades. In this comparison, body size does not explain the differences in life span and natural mortality rate across species because salmon and rockfish have evolved very different life history characteristics to maximize fitness within their habitats.

Lifetime mortality schedules of fish and aquatic invertebrates arise from a combination of size-dependent and life history stage/age-dependent processes. Strong size dependence of mortality rates is a well-established feature of aquatic ecosystems and communities. This basic size dependence is modulated, however, by additional age-dependent mortality associated with the survival costs of reproduction and senescence in adults and by density-dependent starvation and predation mortality in juveniles (Lorenzen, Abstract #7). The resulting lifetime patterns of natural mortality as a function of age tend to be L- or U-shaped, declining rapidly with age in early life stages and juveniles, stabilizing in adults, and possibly increasing again at old age.

Empirical evidence and ecological theory indicate that the *M* of fishes and invertebrates generally scale with body mass or size (Andersen et al., 2009; Brown et al., 2002; Gislason et al., 2010; Lorenzen, 1996; McCoy and Gillooly, 2008; McGurk, 1986; Peterson and Wroblewski, 1984). For a given species, one can expect that early life history stages experience higher *M* than juvenile stages which, in turn, experience higher *M* than adults. *M* may stabilize for adults in which increasing metabolic costs of reproduction at age (intrinsic *M*) counterbalance decreasing extrinsic *M* due to increased body mass. *M* during early life stages, especially pelagic eggs and larvae, are expected to be highly variable due to their susceptibility to fluctuating environmental conditions.

For some species, senescence may be an added source of natural mortality as fish survive to ages much greater than age at maturity. Senescence would tend to counteract the high fecundity, and possibly the higher survival rates of the offspring of older, larger spawners. On the other hand, senescence may not be an important population process to include in a stock assessment model if such older fish do not represent an abundant age group in the unfished population. Sexual dimorphism may also influence natural mortality rates and sex-specific rates may be needed where dimorphism is important.

Extrinsic Factors

Extrinsic factors influencing *M* include changes in food web interactions and other exogenous sources of mortality due to fluctuating environmental conditions. Gaichas et al. (Abstract #4) pointed out that high trophic level species are more likely to have mortality patterns consistent with single-species assessment assumptions. In comparison, stock assessments for mid trophic level species can probably be enhanced by including food web-derived predation information, because fishing mortality on such species is small compared with the high and variable natural mortality rates due to predation. Many natural populations experience short-term mortality events in the form of diseases or environmental episodes, such as red tide events, that may operate in addition to the baseline natural mortality (Walter et al., Abstract #15).

Compensation

The issue of compensatory density-dependence in mortality rates is relevant to both natural processes of population regulation and the impact of fishing on total mortality rates (additive or compensatory). Compensatory density dependence in mortality of fish appears to be strongest in the juvenile stage, rather than in early life history stages or in adults (Brooks et al., Abstract #3; Lorenzen, 2005; Myers and Cadigan, 1993). Compensatory mechanisms may involve, for example, the limitation of settlement sites for juveniles or the functional responses of predators to juvenile abundance. Fishing mortality rates for juveniles may be partially compensated by decreases in natural mortality rates, but this effect is unlikely to be strong in late juveniles or adults.

Modeling Natural Mortality

It was agreed that two aspects were needed to characterize *M*: 1) the shape of the natural mortality rate as a function of age, or length, and 2) the scale of the natural mortality rate relative to the population turnover rate, or the expected life span.

Age and Size Dependence

It was agreed that a flexible approach to modeling age-specific M was generally needed. The traditional assumption of a constant M may be appropriate when only mature fish are of explicit interest in the assessment. However, when juvenile fish need to be modeled explicitly (e.g. because these juveniles are targeted in a fishery or caught as bycatch), size dependence in M should be incorporated into the assessment application, for example, by means of the Lorenzen curve (Brooks et al., Abstract #3; Lorenzen, Abstract #7). The size-dependent mortality model for juveniles may be extended into the adult age groups, or combined with either a constant adult M or more complex adult models that allow for increasing M at age due to reproduction or senescence. It was noted that, while the size-dependent component of M appears to be general and well-quantified, reproductive and senescent effects on adult M may be more species-specific and are currently less predictable. Alternative models for adult natural mortality patterns should be considered in stock assessment applications, where relevant, in order to account for this uncertainty.

One simple model of age-specific M was developed to account for the likely differences in juvenile and adult M; this was deemed the "best ad hoc mortality model." This age-specific model of the expected M required information on length at age, age (or length) at maturity, and adult M. For fish younger than the age at maturity, the age-specific M was proportional to the ratio of length at maturity to juvenile body length at age. For fish older than the age at maturity, M was modeled as a constant rate based on the best estimate of adult M. Thus, the best ad hoc mortality model combined size-dependent juvenile with constant adult M to estimate age-specific M as

$$M(a) = \begin{cases} M_c \dfrac{L_{mat}}{L(a)} & for \quad a < a_{mat} \\ M_c & for \quad a \geq a_{mat} \end{cases}$$

where L_{mat} is the length at maturity and M_c is the natural mortality at L_{mat}. Alternatively, Maunder (Abstract #11) proposed a model of age-specific natural mortality rates based on combining Lorenzen's (2000) observation that natural mortality is inversely proportional to length for young fish and Lehodey et al.'s (2008) logistic model for older fish. One caveat to these approaches for estimating M as a function of age was that possible increases in adult M due to increased reproductive costs or senescence were not explicitly considered.

The effects of senescence were also considered to be difficult to predict, in part because the various factors affecting this process are interrelated and may be difficult to discern for individual species. It was noted that oxidative damage associated with senescence accumulates in all species, but that some species have the capacity to repair some oxidative damage. The question of whether senescence could be assessed through meta-analysis using evidence from tagging data or other sources was discussed. For example, some tagging data from Hampton (2000) suggested that the natural mortality rate as a function of age was U-shaped for yellowfin tuna in the Central Pacific. These data were consistent with a pattern of senescence in which natural mortality increases for older age groups. It was also pointed out that care should be taken in interpreting these data because high seas tuna tag reporting rates are low and this could affect the empirical results. Overall, it was thought that species-specific patterns of senescence would remain poorly known in the absence of new data collection programs.

The discussion of senescence also considered the example of southern bluefin tuna (SBT), which appears to exhibit a pattern of senescence (e.g. U-shaped natural mortality) around age 20. In general, it was noted that a dome-shaped pattern of fishery selectivity can be confounded with a pattern of increasing natural mortality rate at older ages (e.g. Thompson, 1994). In the case of SBT, it was observed that the fishery was catching very few big fish. This suggested that either fishery selectivity was asymptotic with an increasing M for older ages, or that fishery selectivity was dome-shaped with a constant M for older ages. Discerning between these two patterns was not thought to be resolvable in a modeling context. Regardless, it was suggested that there was low credence within the SBT working group for selectivity curves that decreased rapidly at older ages. Although it was also pointed out that a working group process may not achieve consensus based on data, in general, estimates of M based on the opinions of groups of individuals were considered to be less reliable than information based on data.

Overall, four general models for predicting age-dependent M were considered during the course of the workshop. These were, in order of increasing complexity: 1) constant M; 2) M declining with size (e.g. the "Lorenzen curve" with $M \sim L^{-1}$); 3) a combination of M declining with size in juveniles and constant M in recruited fish; and 4) a combination of M declining with size in juveniles and increasing again after maturation.

Compensatory Effects

The issue of compensatory natural mortality was considered to be an important factor for the estimation of *M*. The relative importance of compensatory versus additive natural and harvesting mortalities was thought to be measurable in some cases where there were sufficient observations (e.g. natural mortality rates of ducks and the tradeoff with harvest rates from duck hunters). In particular, when juvenile fish are exploited (or stocked) and thus must be assessed explicitly, it may be important to account for compensatory density dependence in mortality rates, which is typically strongest in juvenile stages (Brooks et al., Abstract #3; Lorenzen, Abstract #7). For example, Lorenzen (2005) describes an approach to formulating a size- and density-dependent juvenile mortality model by combining the length-inverse mortality curve with a multistage Beverton-Holt stock-recruitment model.

Other factors may influence the potential for modeling compensatory natural rates for the estimation of *M*. Time trends in natural mortality were thought to be a potentially confounding factor for compensatory mortality. The perception that *M* may increase due to increases in cryptic mortality was also discussed, as was the question of whether *M* estimated from unexploited populations were similar for exploited populations. While it was unknown whether ecosystem studies might be sufficient to show that changes in *M* had occurred, compensatory natural mortality processes and trends in environmental conditions were additional complicating factors for understanding patterns in *M*.

Spatial and Temporal Variability

Natural mortality rates were considered to have spatial and temporal dimensions of variability, reflecting fluctuations in the probability of survival in space and time or with age and size. It was not clear that a single estimation approach or methodology could account for more than a few of the possible dimensions. For example, movement rates and space-dependent natural mortality rates would be expected to be confounded and it was not clear what sources of data would be available to disentangle these factors for fish populations. In general, the nonhomogeneity of spatial patterns of fish stock structure was thought to provide a basis for assuming that spatial differences in *M* were appropriate. Spatial variation in *M* was thought to be potentially important, especially for assessing sessile stocks, but it was not clear that there were sufficient data in practice to quantify spatial differences in *M*.

While there were few documented cases of changes in natural mortality rates, the Gulf of St. Lawrence cod stock was mentioned as an example where there was strong evidence that natural *M* had increased since the 1980s based on long-term survey data (Sinclair, 2001). Other suggested cases of increased *M* were less definitive, however. In general, accounting for variability in *M* through measurements of how their predator field varies through time was thought to be more important for small pelagic forage species, such as herring. Starvation and disease were two other sources of changes in natural mortality that were considered to be difficult to measure in practice. It was also pointed out that misreported catch was typically not easy to separate from other potential sources of changes in natural mortality.

ESTIMATION OF NATURAL MORTALITY

Approaches to the estimation of *M* can be categorized into tiers (Table 1) where higher tiers correspond to having an increasing amount of information available to estimate natural mortality. The lowest information category, Tier 1, comprises traditionally accepted values of *M* and those estimated from meta-analyses or life history theory. Tier 2 comprises direct, stock-specific estimates of *M*. Tier 3 comprises stock-specific estimates obtained from integrated assessment models. Estimates of *M* for Tier 4 account for temporal or spatial variation, including those derived from ecosystem models. For example, information on the maximum expected age in an unfished population (T_{MAX}) can, in theory, provide a direct estimate of population turnover ($1/T_{MAX}$) within the first tier. However, such information on unfished age structure is not usually available for exploited populations, leading one to consider empirical estimators of *M* based on estimates of T_{MAX} (e.g. Hoenig, 1983) from fishery or survey sampling. Such empirical approaches are clearly useful but may have problems with obtaining representative samples of the population age structure and with choosing the best statistic (maximum, 95th percentile, 99th percentile, or others) to estimate the maximum expected age. On the other hand, while estimates of predation mortality derived from multispecies ecosystem models in Tier 4 have far greater data requirements, they may provide useful information on trends in *M* that would not be available from a simpler model. Overall, it was expected that there would be a trade off between bias due to model approximation and parameter variability due to effective sample size when estimating *M* in a model-based context. The best method for estimation of *M* also partly depends on the relative influence of intrinsic versus extrinsic factors. Life history correlates and the maximum age observed in

Table 1. Four tiers for estimating natural mortality rates.

Tier 1: Traditionally accepted values and those estimated from meta-analyses or life history theory

- Constant or age-dependent M based on past practices
- Constant or age-dependent M estimated from a life history correlate, such as the age at maturity
- Constant or age-dependent M estimated from the maximum expected age contingent on adequate sampling

Tier 2: Direct, stock-specific estimates

- Stock-specific constant or age-dependent estimate of M from surviving numbers-at-age regression curve
- Stock-specific constant or age-dependent estimate of M from $Z = M + q^{*}F$ regression contingent on contrast in fishing mortality (F)
- Stock-specific constant or age-dependent estimate of M from tag-recapture data contingent on random sampling
- Stock-specific constant or age-dependent estimates of M derived from auxiliary data such as no-fishing areas, counts of dead animals, etc.
- Life history correlates for estimating constant or age-dependent M that account for age or gender effects
- Probability distribution for constant or age-dependent M based on the variability of life history correlates

Tier 3: Estimates obtained from integrated assessment models

- Integrated analysis model estimate of M using size or age data, assuming at least one fleet has asymptotic selectivity, and assuming an informative prior for M
- Integrated analysis model estimate of M using tag-recapture or age-composition data with an informative prior for M based on life history along with a Lorenzen-type scaling for M as a function of body mass

Tier 4: Estimates that account for temporal and/or spatial variation

- Estimates of M derived from ecosystem model analyses
- Estimates of M that account for spatial variability in natural mortality processes

unfished populations (or in marine reserves) could provide good estimates of intrinsic factors affecting M, but could miss changes that occur in a fully exploited ecosystem due to extrinsic factors affecting M. Overall, it was thought that predator-prey modeling was a useful approach for identifying the magnitude and changes in extrinsic factors that influence M.

The application of more complex size- or age-dependent models of M will likely be restricted to higher tiers. The simplest size-dependent model, which assumes that M is proportional to the inverse of length, $M{\sim}L^{-1}$ (e.g. a Lorenzen curve), requires only one parameter similar to the traditional constant M assumption. Lorenzen (2000) suggested that the allometric scaling of mortality with body size is more consistent among populations than the overall level of mortality. This implies that an inverse relationship between M and length may be assumed to hold within populations, but the relationship should be rescaled to reflect population-specific levels of natural mortality. Porch (Abstract #12) discussed approaches to rescaling the Lorenzen curve using M estimates for the recruited stock (e.g. from Hoenig's method).

It was agreed that it is desirable to obtain multiple, separate estimates of M within tiers or involving multiple tiers where possible. Where multiple estimates are available, averaging the set of candidate estimates may be considered good practice unless best values can be identified based on relative credibility or goodness of fit to observed data.

Tier 1: Traditionally Accepted Values and Those Estimated From Meta-analyses or Life History Theory

Stockhausen (Abstract #14) compared indirect estimates of natural mortality for Alaskan flatfish stocks based on life history invariants and meta-analyses. Systematic differences were apparent with Lorenzen's method (M at L_{mat}) yielding the highest, and Hoenig's method (M from longevity) the lowest estimates of M for most stocks. These differences may, in part, reflect emphasis on late juvenile and early adult mortality in Lorenzen's method, and on mortality of larger and older fish (longevity) in Hoenig's method. Other estimates of *M* were intermediate to those based on life history invariants and were higher than those based on empirical models. In the absence of any specific reason to prefer one estimator over another, it may be best to use a measure of central tendency for a set of candidate estimates of *M*, such as the arithmetic mean, to set default *M* values for stock assessment applications and to explore uncertainty appropriately (Brodziak, Abstract #2).

In this context, there was some discussion of the work of Pauly (1980), which incorporated a number of intrinsic factors to predict natural mortality rates. These predictors included asymptotic body mass (or length), temperature, and Brody growth coefficient (*K*). There was some question about the accuracy of predicted *M* values from Pauly's and related studies because the variation in predicted survival rates was rather large. In support of Pauly's approach, it was argued that the contemporary strength of natural selection should lead to natural mortality rates that were consistent with life history theory.

How uncertain are estimates of *M* derived from meta-analyses, and how can this uncertainty be quantified? During the workshop it was noted that many of the early methods for estimating M were based on older methods of age determination (i.e. "surface reads" of otoliths) that are now known to underestimate age. This suggests that many older estimates of M may be too high, and consequently this bias may exist in the calibration of some of the older meta-analytical methodologies to estimate M. Participants suggested it may be worthwhile to re-examine the validity of the underlying data in those older studies. Hamel (Abstract #5) pointed out that a key issue for quantifying uncertainty is the ability to separate process from observation error. Confidence intervals would appropriately reflect uncertainty in *M* primarily due to observation error. Conversely, prediction intervals would reflect uncertainty in *M* due to process error (i.e. variation in true mortality rates). MacCall (Abstract #8) quantified uncertainty in estimates of *M* based on prediction intervals for the Hoenig and Pauly methods, and suggested that the expected coefficient of variation for *M* estimates derived from such methods was roughly CV = 0.5.

Tier 2: Direct, Stock-specific Estimates

Shepherd and Moser (Abstract #13) estimated natural and fishing mortality in black sea bass and concluded that *M* was likely to be higher than the value of 0.2 year^{-1} estimated from longevity. Again this suggested that estimates of *M* based on longevity may underestimate *M* for the younger, more abundant age groups (see also Porch, Abstract #12 and Stockhausen, Abstract #14).

Hart et al. (Abstract #6) discussed approaches for directly estimating natural mortality rates where additional, pertinent data were available (i.e. herring consumption, sea scallop clapper survey data, and squid age composition) or where stocks can be observed in the absence of fishing mortality (i.e. sea scallop closed areas and squid age composition). These studies emphasized the potential of combining data analysis with modeling. These examples used modeling approaches that may be applicable to other species but were not commonly used (herring consumption data as catch, surveys for dead animals such as sea scallop clappers, and the maturation-mortality model for shortfin squid).

There was a brief discussion of marine protected areas (MPAs) and the estimation of natural mortality. It was mentioned that MPAs could provide useful data for the estimation of *M* for some sessile species. However, it was also pointed out that, because MPA sites were not typically chosen at random, it might be difficult to get a representative data set to infer *M* for some species using MPA observations.

Some suggested that fieldwork may be a useful way to measure fishery selectivity in order to better understand whether natural mortality increased with age. Gear selectivity experiments were considered to be useful for understanding technical interactions in fisheries, but were also thought to be less powerful for measuring population effects because fishery selectivity depends on the spatial distribution of both fish and fishing effort.

Tier 3: Estimates Obtained From Integrated Assessment Models

Maunder et al. (Abstract #10) considered the estimation of *M* within an integrated assessment model through a simulation analysis of 12 stock assessments conducted using Stock Synthesis. The 12 stock assessments differed in their characteristics (number of fisheries, types of data and quality, number of genders, catch histories, selectivity assumptions [dome shape or asymptotic], and estimated parameters). The simulation results suggested that in most cases natural mortality can be estimated with high precision ($CV \leq 11\%$) and low bias ($< 12\%$) compared to the values of *M* used in the assessments. This was also true for assessments that had differences in natural mortality between males and females or between juveniles and adults. In several cases, the estimates of natural mortality from the original data fell outside the range of uncertainty from the simulations, and this was thought to indicate that either the assumed value for natural mortality was incorrect or the model assumptions (including model structure, fixed parameter values, and data assumptions) were incorrect. It was suggested that the misconception that natural mortality cannot be estimated in stock assessment models was due partly to the resulting estimates often being unrealistic. Consequently, if simulation analysis can demonstrate that natural mortality can be estimated with reasonable precision and accuracy, then unrealistic estimates of natural mortality are probably an indication of severe model mis-specification. Because contemporary stock assessment models integrate data that are also used in traditional approaches to estimate natural mortality, but make fewer assumptions about those data, it may be preferable to estimate natural mortality within the stock assessment model rather than to use the traditional approaches.

When one attempts to estimate *M* within an integrated assessment model, it was recommended that a thorough exploration of model performance with respect to *M* estimation be conducted where practicable (e.g. Aanes et al., 2007). For example, it is important to identify what data are driving the estimate of *M*, what model specifications are affecting the estimation of *M*, and what parameters are highly correlated with the estimate of *M*. Further, it is important to see whether the estimate of *M* becomes more stable as more data are added and also to investigate whether unreported catches were confounded with the estimate of *M*. Overall, it was thought that having an absolute abundance estimate from a survey would provide a stronger basis for estimating *M* within a model. It was also recognized that it may be difficult to objectively set weights or priors relative to data likelihoods when attempting to estimate *M* within an integrated assessment model.

There was also some discussion of the question, "What is a good performance metric for models to estimate *M*?" This was a challenging question that was difficult to address in an empirical manner because there are few situations where *M* was known and where alternative estimators could be applied to compute *M* for comparison with the known value. Comparing theoretical estimates of *M* with field-derived measurements of *M* was also a recommended approach where practical.

Tier 4: Estimates that Account for Spatial or Temporal Variation

Several presentations illustrated the potential for estimating temporal variation in mortality rates using auxiliary information. Walter et al. (Abstract #15) estimated the additional natural mortality on grouper stocks due to red tide events. Hart et al. (Abstract #6) described natural mortality estimates for herring based on predator consumption; these estimates were obtained by defining consumption by predators as an additional source of catch in the assessment model.

DEALING WITH UNCERTAINTY AND VARIATION IN *M* IN STOCK ASSESSMENTS

Uncertainty

It is important to characterize the uncertainty of estimates of natural mortality rates for stock assessment applications. Using a point estimate of *M* will generally underestimate the uncertainty associated with assessment results. It is important to characterize the full range of biological uncertainty for risk analyses and, in general, using the estimated distribution of *M* would provide a more accurate approximation of parametric uncertainty. In this context, there was a consensus that it was important to propagate uncertainty in the estimate of *M* into assessment results where practicable. For example, higher uncertainty in *M* could translate into a larger buffer between the allowable biological catch and the catch at the overfishing level, all else being equal.

It was suggested that it was important to evaluate alternative hypotheses about *M* in the context of assessment impacts. Evaluating several hypotheses about *M* was thought to be a good assessment practice, but it was also pointed out that it was important to eliminate poorly supported hypotheses a priori. Overall, quantifying the effects of using alternative values of *M* on assessment results was believed to be useful and important.

Best practices for implementing changes to *M* in a stock assessment application require conducting a benchmark stock assessment with the new *M*. The benchmark assessment should be subject to full peer review. In this context, it is recommended that the results of using the new *M* estimate in the previous stock assessment model be shown to provide a bridge between the new benchmark and the previous assessment.

MacCall (Abstract #9) pointed out that the delta method provides a simple and practical way of quantifying the effect of uncertainty in *M* on outputs of stock assessments including estimates of spawning biomass and fishing mortality.

Andrews et al. (Abstract #1) reported on simulation studies to investigate the use of constant *M*, to compare the abilities of different *M* models to produce the true natural mortality rate, and to examine the consequences of using different models to calculate natural mortality on the resulting biological reference points. The simulation results suggested that a constant *M* assumption may be reasonable under certain conditions, but not if there is a sufficient reason to consider size- or age-dependent factors.

Process Variability

Gaichas et al. (Abstract #4) suggested that it was important to incorporate trophic interactions within a Management Strategy Evaluation (MSE) for a commercially important species that was likely to suffer from substantial variation in predation mortality. This might be achieved by distilling information on likely changes in predation mortality from food web models in a streamlined format that minimized the additional computational complexity within the MSE (rather than attempting to run an entire ecosystem model within the MSE).

Many natural populations experience short-term mortality events in the form of diseases or environmental episodes that can operate in addition to the baseline *M*. Walter et al. (Abstract #15) showed that Gulf of Mexico red and gag groupers can suffer substantial additional mortality due to red tide events and that these extrinsic factors influencing natural mortality may need to be considered in future stock assessments.

Future Research

It was recommended that research to investigate factors that cause *M* to vary in space and time be given a higher priority. Research into conceptual approaches to account for the effects of long-term changes in *M* on estimates of fishing mortality, spawner abundance, and biological reference points were strongly encouraged. Episodic events that influence *M* were also thought to be important in some cases (e.g. toxic algal blooms). Similarly, research on the interrelationship between spatial structuring of habitat (both natural and man-made), fish movement, and spatial variation in *M* was encouraged. Overall, it was recognized that determining whether *M* was stationary in space or time was a difficult research topic that would benefit from further data collection and research. To address this issue, three research projects of practical importance were identified to improve the scientific basis for estimating natural mortality for stock assessment applications:

- Compile a database of independent estimates of *M* by species with an emphasis on identifying and documenting data quality.
- Pursue direct estimation of natural mortality rates where feasible (e.g. in connection with marine protected areas, no-fishing zones or tagging studies).
- Conduct management strategy evaluations to quantify the effects of changing *M* in space or time on important assessment outputs.

ABSTRACTS

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Abstract #1: Calculating natural mortality; convention, accuracy, and consequences

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A variety of models exist for deriving natural mortality, from the simplest methods that estimate a constant value to methods that calculate a variable mortality by age or weight (Chen and Watanabe, 1989; Lorenzen 1996, 2000; Peterson and Wroblewski, 1984). A constant value is often used for stock assessment purposes, and we investigate the accuracy of that choice in these studies. We carried out three simulation studies: one to investigate the use of constant *M*; one to compare the abilities of different *M* models to produce the true natural mortality rate; and one to examine the consequences of using different models to calculate natural mortality on the resulting biological reference points.

Calculating natural mortality, *M*, for long-lived fishes is often difficult. We rarely have a data set that is long enough to derive the parameter directly, in which case we depend on established models for estimating *M* that require life history or length data. A prime example of this dilemma is the stock assessment of California sheephead (*Semicossyphus pulcher*) undertaken by the California Department of Fish and Game in 2005, aided by researchers on the UC Santa Cruz campus. The researchers used Hoenig's method to estimate *M* proportional to the maximum age (53 years). Since there are other models available to calculate *M*, we compared those model results using data from the sheephead commercial fishery. We determined the estimates of *M*, using weight and life history-based methods. We found that the estimate of *M* converges to a constant if the fish recruit to the fishery in the model after age 2. Therefore it may be reasonable, under certain assumptions, to use a constant natural mortality for California sheephead and other long-lived species.

Our next study used blue shark (*Prionace glauca*) as a case study for a population. We used an age-structured model and parameters from Apostolaki et al. (2005). We designated a natural mortality equation with three inputs: intrinsic, size-based, and age-based. Then we used various models available in the literature to try and calculate *M*. Most of the estimated values underestimated the true natural mortality. Based on our results there are two published models that estimated natural mortality in our simulated population fairly well: the McGurk method (1986) and the method by Chen and Watanabe (1989).

The Chen and Watanabe method should be used if senescence is expected in the population being assessed. The McGurk method performs well in the absence of senescence. Our simulation shows that a constant is not appropriate for natural mortality if there is any reason to think there are size- or age-dependent factors to consider.

Finally, we conducted a simulation study where natural mortality was modeled according to several of the different methods available, and then evaluated the consequences on estimated biological reference points (MSY, F_{MSY}, SSB_{MSY}, SPR_{MSY}). This analysis sheds light on the assumptions within each method and the stability of each BRP estimate based on assumptions about this key life history trait, natural mortality. Status determination with respect to overfished and overfishing, and the associated thresholds and control rules, are also affected by the different methods applied.

Abstract #2: An investigation of potential natural mortality rates for North Pacific swordfish

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Natural mortality rates are key parameters for stock assessments that are generally not well determined. In this working paper, potential natural mortality rates for conducting a stock assessment of North Pacific swordfish (*Xiphias gladius*) by the Billfish Working Group (WG) of the International Scientific Committee (ISC) for Tuna and Tuna-like Species in the North Pacific were investigated. Natural mortality rates (M) were estimated using several empirical and theoretical approaches that depend on estimates of life history parameters of swordfish in the Central North Pacific Ocean. Sex-specific estimates of M were developed to account for sexual dimorphism in swordfish growth. Age-dependent estimates of M were evaluated to account for changes in survival rates as fish age.

Overall, the Hoenig (1983), Alverson and Carney (1975), Pauly (1980), and Beverton-Holt invariant 2 (Jensen, 1996) provided consistent estimates of M for female and male swordfish in the Central North Pacific with M ranging from roughly $M = 0.35$ to $M = 0.41$ year^{-1}. Of the variable M estimators, the Lorenzen (1996) tropical system estimator appeared to provide the most plausible results that were consistent with the central tendency of the constant M estimators. Together, these estimators were chosen by the WG to be the set of candidate models for estimating M and the consensus of the WG was to use a model averaged estimator of swordfish natural mortality by sex to account for uncertainty in model selection. Based on the concordance of the unfished survival curves of the set of candidate estimators and in the absence of any specific reason to prefer one estimator over another, the WG agreed to use a measure of the central tendency of the joint distribution of the candidate M estimators. In particular, the arithmetic mean of swordfish natural mortality estimates by age and sex was used for the development of a length-structured assessment model for swordfish.

Abstract #3: Estimates of natural mortality in juvenile red snapper from two trawl surveys

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In this paper, we explore the estimability of juvenile natural mortality of red snapper using density-independent and density-dependent random effects models. First, we use simulations to explore model performance with respect to various assumptions. Next, we attempt to estimate natural mortality from a series of fishery independent trawl surveys conducted annually in the summer and fall. Natural mortality rates for age 0 and age 1 red snapper are of critical assessment importance because their magnitudes have direct bearing on the estimated impact of shrimp trawl bycatch of juvenile snapper.

Individual fish captured by the trawl survey can be visually assigned to ages 0 or 1 by examining length frequencies, providing a means to track changes in cohort numbers over time. Assuming a closed system, total mortality rate can be measured from the decline in cohort numbers over time. Given the ratio of cohort numbers over time and a measure of fishing effort in that same time interval, one can attempt to estimate natural mortality. Applying a standard linear regression, or taking an errors-in-variables approach, may produce solutions but estimation performance may be poor when the regression is not well determined. Random effects models provide an alternative approach with more desirable statistical properties.

Simulation results indicated that the model parameters of interest (natural mortality, catchability, bycatch reduction device (BRD) effect) were identifiable and unbiased. Comparing simulations that assumed either normal or lognormal error structure, we found that assuming lognormal errors in the estimation routine was more robust to mis-specification. Density-independent models applied to red snapper catch rate data performed poorly for estimating age 0 natural mortality (Table 2). Estimates for the age 0 model hit the minimum bound on catchability, which effectively produces constant survival by negating any effect of bycatch mortality upon total mortality. This arose from the apparent lack of change in total mortality over the entire time series for age 0 red snapper, despite the 75% decline the shrimp fishing effort. For age 1 the slope of the regression is only slightly positive, indicating that total *Z* increases with shrimping effort. For age 0, total *Z* appears to decline with fishing effort, which is counterintuitive if survival is truly density-independent.

Examining the red snapper catch rate data and assuming density-dependence performed better than the density-independent model in that the catchability estimate did not hit the lower bound every time in the age 0 models, provided only data through 2005 was used. It is unclear at this point why the data for 2006-2008 caused the model to converge at the lower bound of catchability, once again forcing constant survival at age 0 over the time series. Estimates of *M* for age 1 did not have the same boundary conditions but nevertheless were poorly estimated as indicated by very high standard deviations (Table 2).

Given some of the convergence issues, and the model tendency to estimate a BRD effect > 1 (indicating that BRDs increase rather than decrease red snapper catchability), we feel that the results are best interpreted as bounding total mortality. Despite the large reduction in total shrimp effort in recent years, it is not possible with this data, or this approach, to separately estimate fishing and natural mortality. Thus, the overall magnitude of total mortality for age 0 is likely to be between 2–3, and between 1–2 for age 1; both of these ranges are higher than previously estimated or assumed in the assessment.

Table 2. Parameter estimates and standard deviations from random effects models of red snapper natural mortality. The runs labeled M0_estdelta to 2005 were run with data from 1987–2005 only, rather than the full dataset to 2008.

Model	Density Dep	*q*	std dev	*M* year^{1}	std dev	delta	std dev	*c*	*c*.std	AICc
M0_estdelta		0.10	0.26	3.26	0.58	2.0	0.04			18.8
M0_fixdelta		0.01	0.00	3.47	0.21	1.0				16.3
M0_estdelta	yes	0.11	0.22	3.24	0.51	2.0	0.00	0.22	0.14	19.8
M0_fixdelta	yes	0.01	0.00	3.47	0.21	1.0	0.00	0.21	0.14	17.2
M0_estdelta to 2005		0.24	0.32	2.89	0.69	2.0	0.41			21.4
M0_fixdelta to 2005		0.02	0.96	3.35	1.45	1.0				19.1
M0_estdelta to 2005	yes	0.45	0.89	2.58	1.39	0.5	0.10	0.21	0.15	23.0
M0_fixdelta to 2005	yes	0.29	0.89	2.95	1.35	1.0	0.00	0.20	0.15	20.7
M1_est_delta		0.68	0.48	0.76	1.60	1.4	0.41			6.8
M1_fixdelta		0.57	0.47	1.39	1.46	1.0				5.0
M1_est_delta	yes	0.72	0.43	0.63	1.45	1.4	0.34	0.17	0.17	8.8
M1_fixdelta	yes	0.60	0.43	1.29	1.35	1.0		0.15	0.17	7.1

fixed “best” AIC hit boundary

Abstract #4: Gulf of Alaska food web modeling and predation mortality estimates: information for single-species *M*

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Examining food web relationships for commercially important species enhances fisheries management by identifying potential sources of variability in mortality and production which are not included in standard single-species stock assessments. We use a static mass balance model to evaluate relationships between species in a large marine ecosystem, the coastal Gulf of Alaska. The model includes area- and time-specific biomass, production, consumption and diet composition parameters for 122 functional groups based on research surveys, stock assessments, and published literature. We focus on results for four case study species: Pacific halibut, longnose skate, walleye pollock, and squids. In each case study, we present the species' position within the food web, evaluate fishing mortality relative to predation mortality, and evaluate the diet compositions of each group. Food web modeling outlines general situations where simplifying assumptions are supported and where food web relationships should be considered; for example, high trophic level species, whether commercially valuable (halibut) or incidentally caught (skates), are more likely to have mortality patterns consistent with single-species assessment assumptions (i.e. fishing mortality dominates a relatively constant natural (predation) mortality). Conversely, assessments for mid-trophic level species, whether commercially valuable (pollock) or incidentally caught (squids), can be enhanced by including food web-derived predation information because fishing mortality is small compared with high and variable natural (predation) mortality. Finally, we outline food web relationships which suggest how production of species may change with diet composition or prey availability.

Information from the food web model can be used to incorporate trophic interactions within a Management Strategy Evaluation (MSE) for a commercially important single species, Gulf of Alaska pollock. Rather than run an entire ecosystem model, we can provide information on potential changes in pollock mortality under different ecosystem conditions in a streamlined format that minimizes computational complexity within the MSE. Results of thousands of Gulf of Alaska ecosystem model runs were converted into functional relationships between pollock mortality and predator biomass which considered different levels of pollock biomass and ecosystem-wide primary productivity. Preliminary results show fairly strong relationships between the biomass of a handful of key predators and total pollock mortality; the relationship is especially strong between juvenile pollock mortality and arrowtooth flounder biomass (Figure 1). In general, these distilled results suggest that pollock mortality increases with predator biomass more quickly and to a higher level when pollock biomass is relatively low (red lines), and that individual predators affect pollock mortality to a lesser extent when pollock biomass is high (green line). However, at low and intermediate pollock biomass (red and blue lines in Figure 1), ecosystem productivity can influence the relationship as well. For example, the thin blue line demonstrates that under conditions of low primary productivity, pollock mortality may increase quickly with predator biomass even though pollock biomass is at an intermediate level. Under conditions of higher ecosystem primary productivity, these distilled model results suggest that pollock mortality increases less quickly with increasing predator biomass (thick blue line).

Abstract #5: Prediction intervals and priors for natural mortality rates

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The natural mortality rate *M* is an extraordinarily difficult parameter to estimate for many fish species and stocks. The uncertainty associated with *M* translates into increased uncertainty in fishery stock assessments. Estimation of *M* within a stock assessment model is complicated by the confounding of this parameter with other life history and fishery parameters which are also uncertain and which may be estimated within the model.

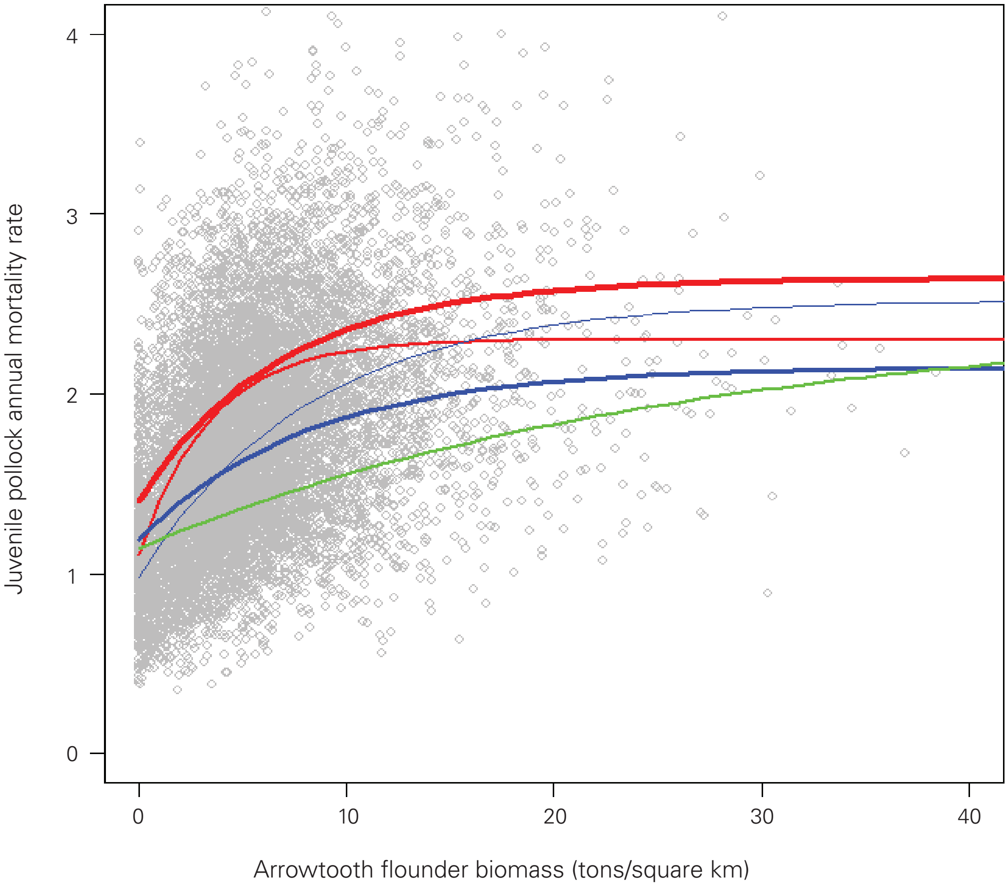

Figure 1. Relationship between arrowtooth flounder biomass and juvenile pollock mortality from 9,845 simulations with the Gulf of Alaska ecosystem model. Each open circle is the output of an individual model run; these model runs were conducted with parameters varying according to our uncertainty in the underlying information, so the whole spread of points represents a wide range of pollock and ecosystem conditions as well as our uncertainty in the underlying parameters. Each line represents the best fit relationship between flounder biomass and pollock mortality under different levels of pollock biomass and overall ecosystem production. Red lines indicate low pollock biomass (below the stock assessment reference point indicating 25% of unfished biomass), blue lines indicate intermediate pollock biomass, and the green line indicates high pollock biomass (above the stock assessment reference point indicating unfished biomass). Thickness of lines represents overall ecosystem production. Thinner red and blue lines indicate primary productivity at or lower than estimated current levels, and thicker lines indicate higher primary productivity than estimated current levels. Primary productivity had no impact on the relationship when pollock biomass was high (single green line).

To avoid the pitfalls of trying to estimate *M* either directly from data or within a model, a number of meta-analytical approaches have been developed over the years. These methods use empirical relationships between *M* and other life history parameters which are ostensibly easier to estimates. While these methods are generally empirical, they are rooted in life history and evolutionary theory. Often these approaches use single predictive parameters for the meta-analysis, although multiple regression has been applied as well (e.g. Pauly, 1980). Meta-analyses have found relationships between *M* and maximum age (A_{max}), the von Bertalanffy growth parameter *k* (e.g. Jensen, 1997), and the gonadosomatic index (GSI; Gunderson, 1997), a measure of reproductive effort, among others. Theoretical relationships have been suggested as well (e.g. McCoy and Gillooly, 2008), with subsequent empirical fits to the underlying theoretical relationship.

Generally, single point estimates from these meta-analyses have been used in assessments despite the generally fairly wide scatter of points around the regressions. While this wide scatter is due in part to observation error in both the covariate an in *M*, it is undoubtedly also true that a good deal is due to process error—i.e. an imperfect relationship between the parameters in question. While alternative values of *M* are often considered in sensitivity analyses, it is unlikely that these are capturing the full uncertainty associated with the meta-analysis, or that the meta-analytical estimate is therefore better than estimates that could be made within or outside of the model using available data. Here, the extent of uncertainty associated with the meta-analyses is analyzed and methods of creating prediction intervals and priors on *M* are described.

Gunderson et al. (2003) calculated confidence intervals for meta-analytical estimates of *M* from estimates of von Bertalanffy growth coefficient *k* and GSI. However, confidence intervals give a range for the mean value of *M*, rather than the range for *M* in individual species. Confidence intervals are only appropriate for estimating uncertainty in the predicted variable when all the variability about the regression line in the meta-analysis is due to observation error and the relationship is exact. Prediction intervals are commonly used for delineating the range for a new observation, in this case a new species or stock. These are quite a bit wider. Prediction intervals give an expected range for a new observation drawn from the same distribution (about the regression) as the original data. One should note, however, that this new observation would include as much observation error as the original data, and therefore the prediction interval is likely wider than the actual variation in *y* about the regression line. Neither confidence nor prediction intervals are perfect, but represent the boundaries of the possible intervals to measure the uncertainty of natural mortality. If all the variation around the regression is due to observation error, then the confidence interval provides the best estimate of uncertainty in *M* for a new stock given the covariate. If all of the variation around the regression is due to true variation in the relationship, then the prediction interval is the best representation of that uncertainty. The truth is undoubtedly in between these two extremes.

Hewitt et al. (2007) took another approach to providing ranges for *M* given a number of meta-analytical relationships and uncertainty about the meta-analytical covariates. Like Gunderson et al. (2003) the authors implicitly assume that the meta-analytical relationships are exact, and uncertainty is only due to uncertainty in either the covariate for the species in question, or the uncertainty in the relationship as provided by the confidence interval. Here I calculate prediction intervals based upon log-log regressions. Using prediction intervals implicitly implies that the meta-analytical relationships themselves are imprecise.

Along with prediction intervals, the analysis undertaken above provides log-normal distributions which can be taken as priors on *M* for the new species of interest. Strictly speaking, as described above with the prediction intervals, the prior is on a new measurement of *M* for this species, given all the error and bias in the original sample for each meta-analysis. However, we will take it to be a prior on *M*, noting that the meta-analyses should be taken up again and updated to reflect the best current understanding.

Given multiple such priors, the question is how to combine them. Under the assumption that each prior gives unique and orthogonal information from the others, the normal priors (in log space) can all be multiplied together and standardized to give a new log-normal prior. If, on the other hand, the assumption is that they all are giving the same information (i.e. all of the covariates are perfectly correlated and should predict *M* the same) and the difference is just error, they should all be averaged (via multiplying n normal priors together, all the to the power n^{-1}). Various intermediate weighting schemes are, of course, possible. In any particular case weighting should be done based upon overlap in data and covariates, knowledge about correlation of parameters, and confidence in the application of the prior to the species in question (i.e. does the relationship between the covariate(s) and *M* vary by taxonomic group, and is the meta-analysis representative of the taxon in question).

Abstract #6: Estimating natural mortality in Atlantic sea herring, Atlantic sea scallops and shortfin squid off the Northeastern USA

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The four presentations involved scientists at the Northeast Fisheries Science Center in Woods Hole, MA with several common themes. The first theme was data particularly suited to estimation of natural mortality (i.e. herring consumption, sea scallop clapper survey data and squid age composition). The second common theme was estimation of natural mortality in the absence of fishing (sea scallop closed areas and squid age composition). The third theme emphasizes the importance of modeling in addition to data. Most of the examples used modeling approaches that may be applicable to other species but are not commonly used (herring consumption data as catch, surveys for dead animals such as sea scallop clappers, and the maturation-mortality model for shortfin squid).

Atlantic sea herring

Times varying natural mortality rates were estimated for herring using estimates of herring consumed by demersal and pelagic fishes, marine mammals and sea birds. Consumption estimates for fish predators were from stomach sampling during spring and fall bottom trawl surveys. Consumption estimates for sea birds and marine mammals were from published studies. A wide range of uncertainty was considered in estimating consumption. The consumption estimates were used in an assessment model as if they were catch data for a separate "fleet." Mortality due to predation by other species, disease and senescence was assumed negligible. Estimated mortality due to predators was related to abundance of both herring and predators. It was relatively low during the 1960s while herring were abundant and high in the late 1970s and early 1980s while herring abundance declined. Predator induced mortality declined in the 1990s as herring abundance increased. Biological reference points for herring indicated that MSY was lower when predation effects were included.

Atlantic sea scallop in closed areas

The stock assessment for Atlantic sea scallops was modified to handle closed areas where no fishing is allowed (see http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0716/). Demonstration data for closed areas on Georges Bank during 1982–2009 included six years since 1994 with no fishing. Relatively precise estimates of natural mortality (CV < 10%) were obtained in the stock assessment model, probably because of substantial changes in abundance and length composition during years with no fishing and because fishing mortality and natural mortality were not confounded. Sea scallop are an ideal case because they are sessile, closed areas are relatively large and because the stock is "data rich." Nevertheless, it seems reasonable that periods with no fishing should enhance estimation of natural mortality for other species.

Atlantic scallop clappers and time-varying mortality

Clappers are the two valves of a dead sea scallop that are still connected by the hinge ligament after mortality by predators like starfish. Clappers are taken along with live sea scallops during routine sea scallop surveys. Clapper-live scallop ratios vary substantially over time based on survey catch data indicating time dependent natural mortality rates. The CASA stock assessment model was modified to accommodate shell height composition and survey "abundance" data for clappers (see http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0716/). Briefly, predicted survey data for clappers in the model was assumed proportional to the average number that died during a relatively short interval prior to the survey. The survey catchability coefficient for clappers is aliased in modeling with separation time and estimated survey size selectivity for clappers is aliased with actual selectivity, size-based variability in separation time and breakage of hinge ligaments. It was possible to estimate average and time varying natural mortality rates in experimental CASA runs with closed area data for Georges Bank. However, fit to other data degraded when clappers were included in the model. Additional work on selectivity patterns appears warranted and predation (e.g. by lobsters) that does not result in clapper formation may be important.

Natural mortality rate estimation for spawning and non-spawning female squid

Most cephalopod stock assessment models assume a constant natural mortality rate that does not account for post-spawning mortality, even though older individuals are more likely to spawn so that natural mortality is likely to increase with age. Squid are short-lived, important prey species which are generally semelparous. We provide a method of estimating the mortality and maturation rates of female cephalopods, using data from a stratified, random bottom trawl survey for unfished Northern shortfin squid, *Illex illecebrosus*, as an example. Natural mortality rate estimates were much higher than typically assumed, particularly for spawners. Estimated maturation and spawning mortality rates were incorporated into per-recruit models to estimate biological reference points. Mortality and reference point estimates were plausible and the modeling approaches should be applicable to a wide range of semelparous stocks.

Abstract #7: Age- and size-varying natural mortality rates: biological causes and consequences for fisheries assessment

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Natural mortality rates in most fish and marine invertebrate populations vary over the life cycle, often by orders of magnitude. Driven by physiological (internal) and ecological (external) processes, lifetime mortality schedules show strong patterns of regularity but are also influenced by environmental factors and density-dependence, particularly in early life stages and juveniles. Traditionally, fisheries models and stock assessment methods have adopted a highly simplified representation of the life cycle, with a recruited stage where natural mortality is described explicitly as a constant rate, and a stock recruitment relationship that implicitly accounts for juvenile mortality (and the environmental and density-dependent influences upon it). Limitations of this representation and the 'constant *M*' paradigm for the recruited stock are becoming increasingly apparent from practical and theoretical considerations. Many fisheries now exert heavy, targeted and incidental fishing mortality on juveniles which must be explicitly considered in assessments. At the same time, due to the proliferation of marine reserves, populations where truly 'old' fish are well represented are bound to become more common and consideration of senescence effects more relevant. Last but not least, current interest in size-based population dynamics and the evolutionary ecology of aging challenge the 'constant *M*' paradigm from a scientific perspective.

Biology of age- and size-dependent mortality

Lifetime mortality schedules in fish and aquatic invertebrates arise from a combination of size-dependent and life history stage/age-dependent processes. Strong size dependence of mortality rates is a well established feature of aquatic ecosystems and communities. The same basic size-dependence is reflected in lifetime mortality schedules of organisms where it is, however, modulated by additional age-dependent mortality associated with survival costs of reproduction/senescence in adults and by density-dependence in juveniles (Figure 2). The resulting lifetime patterns of natural mortality tend to be 'L' or 'U' shaped, declining rapidly with age in early life stages and juveniles, stabilizing in adults and possibly increasing again at old age.

The size-dependent component of natural mortality is subject to a broadly consistent scaling at fish population, species and community level, with all major empirical studies showing allometric weight exponents between -0.28 and -0.37. A more moderate exponent of -0.25 has been predicted in some theoretical studies, but enjoys little empirical support. Multiple, alternative or related biological explanations for this scaling pattern can be found in physiological, population and community ecology. Predation probably accounts for a large share of natural mortality in fish communities and is often seen as the primary driver of size-dependence. However, many other sources of mortality are also size-dependent. Mortality rates in aquaculture systems, where predation is minimized, are more strongly size-dependent (if lower overall) than in natural fish communities (Lorenzen, 1996).

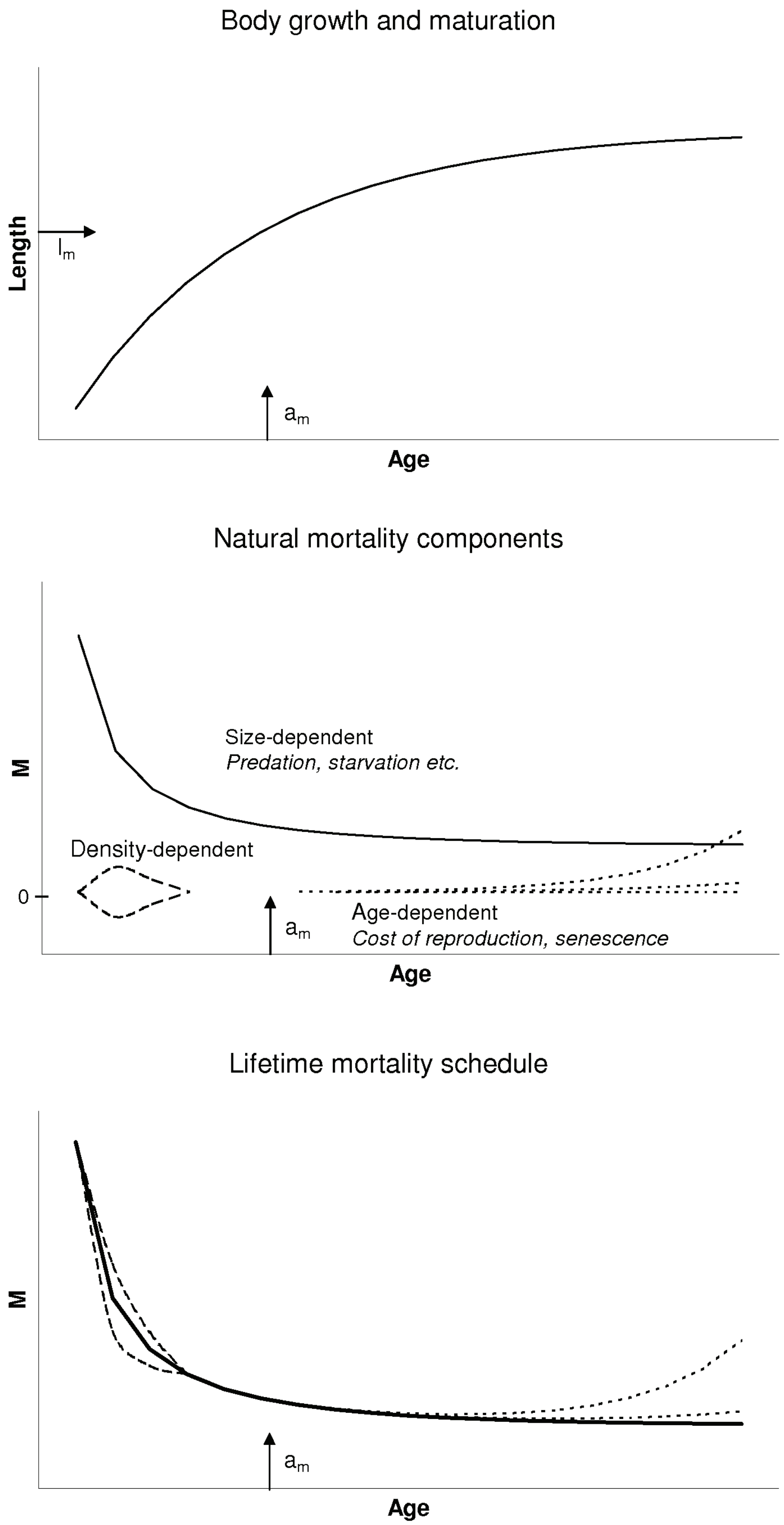

Figure 2. Components of natural mortality and the resulting lifetime mortality schedule.

The age/stage-dependent cost-of-reproduction/senescence component of mortality is less well understood than the size-dependent component and appears to be far more variable among species. There is empirical evidence for both, survival costs of reproduction (e.g. due to depletion of reserves or exposure to predation at spawning sites) and senescence (metabolic damage) in certain species. Whilst some fish species show clear increases in mortality associated with maturation or old age, others do not and may indeed be subject to almost negligible senescence. Life history theory and ageing research suggest that appreciable senescence is most likely to be found in fast-growing, early maturing animals.

Natural mortality may be strongly density-dependent in prerecruit fish, as is reflected in stock-recruitment relationships. Density-dependent mortality appears to be centered on the juvenile stage, rather than early life stages or adults, in all fish populations regardless of maximum body size (Leggett and Deblois, 1994; Lorenzen, Pers. obs.; Myers and Cadigan, 1993). The density-dependent phase therefore represents a life history- rather than size-based feature of the mortality schedule. Density-dependent juvenile mortality confers the greatest share of compensatory reserve in many fish populations, but may be supplemented in this role by other mechanisms such density-dependent growth in the recruited phase (Lorenzen, 2008).

Using age- and size-dependent mortality models in fisheries assessments

The lifetime mortality pattern sketched out in Figure 2 suggests that the traditional assumption of constant M is appropriate for assessments where harvesting is concentrated on mature or almost-mature fish and truly 'old' fish are rare even under unexploited conditions.

The constant M assumption is clearly inappropriate for assessments where fishing or other human impacts on juveniles need to be considered. Juvenile mortality is governed primarily by size-dependent processes and described well by a simple length-inverse model (Lorenzen, 2000):

$$M(l) = M_r \frac{l_r}{l}$$

where M_r is the natural mortality rate at reference length l_r. The model implies consistent allometric scaling of mortality (at a weight exponent of -0.33) among populations, regardless of the overall level of mortality. This assumption is supported empirically by analyses of post-release mortality in hatchery fish (Lorenzen, 2000). The reference length may be fixed at an arbitrary value (e.g. where mortality rates are to be compared between studies involving different species) or set to a stock-specific life history endpoint such as asymptotic length l_∞ or length at maturity l_m. Lorenzen (2000) provides age-dependent survival equations based on this model for different growth curves.

The parameter M_r may be estimated directly in integrated assessment models, from mark-recapture studies (e.g. Coggins et al., 2006; Lorenzen, 2006) or from catch curves. Often however, M_r is obtained by rescaling the length-inverse mortality curve to approximate a constant M value used in previous assessments and/or derived from empirical models. Constant M values reported in the literature tend to reflect mortality in the most abundant, fully selected age groups: typically late juveniles and young adults, rather than very old fish. When rescaling the mortality curve it is therefore best to match $M(l_m)$, not $M(l_\infty)$ to the constant M value. This is confirmed empirically by scaling curves to the M values collated in Pauly's (1980) data set: scaling curves such that $M(l_m)$ matches the constant M values results in a predicted mean $M(l)$ for small ($l = 5$ cm, $w = 1$ g) fish of 2.95 (95% CI [2.59, 3.36]) year $^{-1}$, almost exactly equal to the mean M for this size estimated independently from mortality-weight data in Lorenzen (1996). Scaling the curves by matching $M(l_\infty)$ to M over-predicts average $M(l)$ in small fish by about 50%.

Should the length-inverse mortality curve be applied to the adult phase of the life cycle? The influence of cost-of-reproduction and senescence on mortality rates appears to be highly variable, but often low. Indeed, exploratory analyses on population- and species-level data from Lorenzen (1996) suggest that the length-inverse model enjoys more empirical support than alternative models involving constant or increasing mortality-at-age in adults. It may therefore be best to use the length-inverse model as default, but consider alternatives where increasing M in adults is expected on biological grounds or evident from data. Simulation should be used to explore implications of alternative adult mortality models where substantial structural uncertainty is perceived to exist. More often than not, this is likely to show low sensitivity of key outputs to assumptions about mortality in old fish.

Where the dynamics of younger juveniles are to be considered explicitly in assessments, it may become necessary to consider density-dependence in mortality rates. Lorenzen (2005) describes an approach to formulating a size- and density-dependent juvenile mortality model by combining the length-inverse mortality curve with a multistage Beverton-Holt stock-recruitment model. The approach allows combining empirical information on size dependence (from the length-inverse curve) and density dependence (from the stock-recruitment relationship) of mortality rates into a model that represents juvenile dynamics explicitly, yet collapses into a simple Beverton-Holt SRR outside the prerecruit stage. Originally developed to facilitate assessment of hatchery releases and implemented in the EnhanceFish model (Medley and Lorenzen, 2006), the approach is easily adapted to dealing with juvenile harvesting issues.

The greatest structural uncertainties with respect to lifetime mortality schedules in fish now relate to 1) the influence of costs of reproduction and senescence on adult mortality patterns, and 2) the 'distribution' of density dependence within the juvenile mortality pattern. Both issues may benefit from meta-analytical approaches.

Abstract #8: What is the precision of M?

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A variety of methods exist to estimate the natural mortality rate (M) from limited data sources. Less attention has been given to estimating the precision of those estimates, perhaps because M is usually treated as a fixed parameter in fisheries models. Estimated precision of M may nonetheless be needed for use in specifying a Bayesian prior or for use in calculations of the precision of assessment outputs (see MacCall, Abstract #9).

One of the most widely used methods is that proposed by Hoenig (1983), who derived a log-log linear regression of total mortality rate (Z) on maximum observed age (T_{MAX}), $\ln(Z) = a - b^*\ln(T_{MAX}) + \varepsilon$. Because most of the cases were unexploited stocks, Hoenig's regression is commonly used to estimate natural mortality rate. Unfortunately, Hoenig did not report detailed statistics on the precision of his regression, but these can be obtained from re-analysis of his original data. Hoenig (1982) contains values for 82 of the 84 points used in his regression for fish. The re-analysis comes close to the original estimates ($a = 1.51$ vs. original 1.46, and $b = -1.02$ vs. original 1.01, $r^2 = 0.71$ vs. original 0.68). The RMSE of the residuals (ε) has a value of $\sigma = 0.508$, which can be taken as the basis of a prediction interval. If the precision needs to be expressed as a coefficient of variation (CV) about the back-transformed value, lognormality provides that $CV = \text{sqrt}\{(\exp(\sigma^2) - 1)\}$, or $CV = 0.54$. Also back-transformation from the log-transform has an estimated geometric mean bias of $\exp(\sigma^2/2)$ or about -14%.

[Note: Hoenig (Pers. comm.) does not consider the prediction interval to be the best precision statistic for his regression. Because the Z estimates were based on catch-curve analysis, there is a substantial component of estimation error in the observed Z values. On average, the true Z values should tend to lie closer to the regression line than the observed data indicate. Consequently, for estimating a new value of Z or M, the error statistic should be smaller than the value of σ given above. The magnitude of this bias correction would also be smaller under Hoenig's interpretation.]

Another widely used method is that of Pauly (1980), who used a multiple log-log linear regression to estimate $\log_{10}(M)$ as a function of von Bertalanffy growth parameters k and L_∞, and mean water temperature. Converting Pauly's estimate from $\log_{10}$ to $\log_e$ gives $\sigma = 0.564$ (CV = 0.61; GM bias correction is -17%) which is only slightly less precise than the Hoenig estimate.

It appears that a general "default" level of precision of data-limited estimates of *M* is about CV = 0.5. Higher precision requires multiple independent estimates or use of more extensive data, such as in a full likelihood-based stock assessment model.

Abstract #9: Accounting for the uncertainty associated with fixed *M* (and other parameters) by means of the delta method

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Using constant values of poorly-known parameters (a.k.a. "fixing" parameters) is a widespread practice in stock assessment. Although the natural mortality rate (*M*) is almost universally treated as a fixed parameter, many other influential parameters such as steepness (*h*) of the stock-recruitment relationship (SRR) and the error variability about the SRR (σ_R) are frequently fixed. Contrary to common sense, the statistical implication is that these parameters are known without error, and the conventionally-reported precision (usually based on bootstrap analysis of VPA, or on asymptotic properties of likelihood matrices) of these assessments is overstated. Attempts to address precision by means of Bayesian Markov Chain Monte Carlo exploration have seldom achieved a full exploration. The delta method provides an easily calculated alternative, and is a useful tool for fully estimating precision of status quantities (e.g. current abundance, current fishing mortality rate) and management reference points (e.g. target abundance, target fishing mortality rate), and is especially useful in the context of specifying Annual Catch Limits.

The delta method is a means of estimating probability distributions based on asymptotic properties of its component functions and variances, and has a well-established history of use in econometrics, engineering and quantum physics (many useful links exist on the web, e.g. http://en.wikipedia.org/wiki/Delta_method). The delta method also has a history of use in population assessment, where it was popularized by Seber (1973). More recently, the delta method seems to have been lost from the standard stock assessment toolkit. Prager and MacCall (1988) used the delta method to comprehensively describe the precision of a time series of VPA abundance estimates. However, application of the delta method to estimating variances of current status quantities and management reference points is simpler than it might appear from Prager and MacCall's paper.

Slightly modifying Seber's notation, the delta method estimate of the variance of a function $g(\theta)$ is given by

$$V[g(x)] \approx E[\{g(x) - g(\boldsymbol{\Theta}\}^2]$$

$$V[g(x)] \approx V[g(\bullet)] + \sum_{i=1}^{n} V[x_i]\left(\frac{\partial g}{\partial x_i}\right)^2 + 2\sum_{i<j}\sum \mathrm{cov}[x_i, x_j]\left(\frac{\partial g}{\partial x_i}\right)\left(\frac{\partial g}{\partial x_j}\right)$$

where *g* is an assessment output quantity such as current biomass ($B_{current}$), a management reference point such as B_{MSY}, or a relative measure such as $B_{current}/B_{MSY}$, and *x* is the list of fixed parameters, such as *M*. The conventionally reported variance (in which values of parameters *x* are fixed) is $V[g(\bullet)]$.

The partial derivatives are easily estimated numerically by means of small changes in the value of the fixed parameters. The variances of the fixed parameters, $V[x_i]$ can sometimes be obtained from meta-analyses, e.g. Dorn (2002), otherwise they may require a reasonable guess. The variance of *M* is addressed in other abstracts in this collection. Myers et al. (2002) examined the relationship between *M* and steepness, and concluded that they covary only for fishes with a reproductive lifespan less than five years.

The following example (Table 3) is based on a VPA of Georges Bank haddock conducted by Liz Brooks (Pers. comm., Northeast Fisheries Science Center). The assessment was subsequently revised, so these values are not official.

Table 3. VPA of Georges Bank haddock conducted by Liz Brooks (Pers. comm., Northeast Fisheries Science Center). Values are not official.

	Assessment Result		Management Reference Point	Status Determination
Quantity (g)	SSB_{2007}	F_{2007}	SSB_{MSY}	SSB_{2007}/SSB_{MSY}
CV Base	0.1987	0.1647		0.1987
Base Variance $V[g(\bullet)]$	3.942E+09	1.435E-03		1.562E-01
Variance due to M				
M = 0.18	297518	0.2390	132567	2.2443
M = 0.20 (Base)	315975	0.2300	158873	1.9889
M = 0.22	336727	0.2187	159287	2.1140
Partial Derivative	980225	-0.5075	668000	-3.258
$V(M)$	0.01136	0.01136	0.01136	0.01136
Delta Method $V[g(M)]$	1.092E+10	2.926E-03	5.070E+09	1.206E-01
Total Variance				
Sum of Variances	1.486E+10	4.361E-03	5.070E+09	2.768E-01
CV Total	0.386	0.287	0.448	0.265
% Variance from Base	27%	33%		56%
% Variance from M	73%	67%	100%	44%

Abstract #10: Estimating natural mortality within a stock assessment model: an evaluation using simulation analysis based on twelve stock assessments

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Natural mortality is one of the most influential quantities in fisheries stock assessment and management. The magnitude of natural mortality relates directly to the productivity of the stock, the yields that can be obtained, optimal exploitation rates, management quantities, and reference points. Unfortunately, natural mortality is also one of the most difficult quantities to estimate. Commonly used methods, based on empirical relationships, life history theory, and maximum age, are notoriously problematic. In addition, many of the methods estimate only total mortality, so natural mortality must be separated from fishing mortality. Maximum age-based methods are one of the most commonly used approaches to estimate natural mortality. However, the maximum age of fish in a sample is dependent on the sampling design, including the effective sample size, and the sampling design is often unknown. If the sampling design is known, then catch-curve or integrated analysis may be better choices. Life history-based methods provide insight into the relationship between natural mortality and other life history parameters. However, as estimation tools, they must be validated with empirical data. There are numerous studies that have developed relationships with life-history parameters, maximum age, and other quantities to estimate natural mortality based on regressing estimates of natural mortality with these quantities. Unfortunately, the variation in the predictions from these relationships is so large that they are generally not useful for stock assessment. Predation-based estimates provide useful insight into how natural mortality is related to species interactions and how it may change over time. However, predation mortality generally occurs on small individuals that may not be highly vulnerable to the fishery and therefore not impact the stock assessment. In addition, natural mortality not caused by predation still must be estimated. Analysis of tagging data is probably the most promising direct method to estimate natural mortality. However, it is difficult and expensive to design and implement a tagging study that addresses all the issues (mortality due to handling and tagging, reporting rate, tag loss, nonmixing, etc.) that can bias the results. Catch curve analysis is crude and relies on many assumptions that are likely to be violated. However, catch-at-age data may be the only historical data that are available from when the stock was unexploited or lightly exploited. The success of estimating natural mortality within a stock assessment model has been variable and is probably dependent on the amount and type of data that are available, other structural features of the assessment model, and the age-specific pattern of the natural mortality that is modeled. Data used in other approaches (e.g. catch curve and tagging analyses) to estimate natural mortality can be included in stock assessment models and the stock assessment model more appropriately identifies and deals with model assumptions.

We use simulation analysis based on twelve peer-reviewed stock assessments (arrowtooth flounder, black rockfish north, black rockfish south, blue rockfish, canary rockfish, chilipepper rockfish, darkblotched rockfish, english sole, hake, sablefish, shortbelly rockfish, and yelloweye rockfish), conducted using Stock Synthesis, to determine whether, given the model assumptions and data, natural mortality can be reliably estimated. The stocks assessments differed in their characteristics (number of fisheries, data type, quality, and amount, number of genders, catch histories, selectivity assumptions (dome shape or asymptotic), and parameters estimated). The results suggested that in most cases natural mortality can be estimated with high precision (CV ≤ 11%) and low bias (< 12%). This was also true for applications that have differences in natural mortality between males and females or juveniles and adults. The exceptions were darkblotched rockfish (CV = 15%), black rockfish north old (bias = -17%), and sablefish (bias = -28). In several cases (arrowtooth flounder, black rockfish south young, english sole, and hake), the estimates of natural mortality from the original data were outside the range of uncertainty from the simulations, indicating that the assumed value for natural mortality is incorrect or the model assumptions (including model structure, fixed parameter values, and data assumptions) are incorrect. We argue that the misconception that natural mortality cannot be estimated in stock assessment models is due partly to the resulting estimates often being unrealistic. We suggest that the unrealistic estimates are due to model mis-specification, rather than inability to estimate natural mortality. Consequently, if simulation analysis shows that natural mortality can be estimated with reasonable precision and accuracy, unrealistic estimates of natural mortality are a good indication of severe model misspecification. We recommend that life history theory and empirical relationships always be calculated to compare with the estimates from stock assessment models as a way of evaluating the estimates of natural mortality from the stock assessment model. However, the maximum age based rule of thumb tended to be too low and the life history relationships too high for these species. We also argue that because contemporary stock assessment models integrate data that are used in traditional approaches to estimate natural mortality, but make fewer assumptions, it is preferable to estimate natural mortality within the stock assessment model rather than to use the traditional approaches.

Abstract #11: Proposed formulation for age-specific patterns in natural mortality

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We develop a model for representing age- and sex-specific natural mortality based on the following assumptions:

1) Natural mortality for younger fish is due mainly to processes (e.g. predation) that are functions of the size of the individuals.
2) Natural mortality increases after individuals become reproductively mature.
3) Maturity follows the logistic curve.
4) Natural mortality due to reproduction may differ between males and females, but juvenile mortality is independent

of sex.

5) Natural mortality due to senescence over and above that caused by reproduction is either small or occurs at an age for which there are few fish alive, so that it does not significantly influence the results.

The model is based on combining Lorenzen's (2000) observation that natural mortality is inversely proportional to length for young fish and Lehodey et al.'s (2008) logistic model for older fish. The logistic curve is used to represent the proportion of fish mature at age.

$$M_{s,a} = M_{juv}\left(\frac{L_{mat,s}}{L_{s,a}}\right)^{\lambda} + \frac{M_{mat,s} - M_{juv}}{1 + \exp\left[\beta_s\left(L_{s,a} - L_{50,s}\right)\right]}$$

With possible defaults: $\lambda = 1$, β_s and $L_{50,s}$ from the maturity curve, $M_{mat,s}$ from Jensen (1996) and $M_{juv} = 3W_{mat}^{-0.288}$ from Lorenzen (1996).

Where $L_{mat,s}$ is the length and W_{mat} the weight at which individuals first become mature, a = age and s = gender.

The predation term and the maturity terms interact, so that if the length at age changes substantially after L_{mat}, the natural mortality may reduce below M_{juv} for ages for which only a proportion of the individuals are mature or M_{mat} for ages for which all individuals are mature. The equation could be separated, but this would not be differentiable if the growth parameters are estimated unless a fixed age at first maturity is used for separating the equations.

$$M_{s,a} = \begin{cases} M_{juv}\left(\dfrac{L_{mat,s}}{L_{s,a}}\right)^{\lambda} & a < a_{mat,s} \\ M_{juv} + \dfrac{M_{mat,s} - M_{juv}}{1 + \exp\left[\beta_s\left(L_{s,a} - L_{50,s}\right)\right]} & a \geq a_{mat,s} \end{cases}$$

The first equation may be appropriate for fish that are still prey as adults (e.g. anchovy) and the second for fish that are not preyed on in substantial amounts as adults (e.g. most species of tuna). If the size or age at maturity differs between males and females, the equations could be parameterized using L_{mat} or a_{mat} from the gender that matures first. The models can also be simplified by assuming that reduced mortality due to increased size does not provide additional benefits so the individuals become mature and $M_{mat} = M_{juv}$ (perhaps using the age at 50% maturity, rather than the age at which individuals first become mature). In this case, the first model is equivalent to Lorenzen (1996) and the second model a combination of Lorenzen (1996) and constant mortality for mature individuals. In both cases, using the default leaves only a single parameter, M_{juv}, to be estimated.

Abstract #12: Rescaling the Lorenzen natural mortality curve: issues from the Southeast Data Assessment and Review

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Lorenzen (1996) compiled evidence to suggest that the natural mortality rate of fish decreases as a power function of weight, e.g. for oceanic species the estimated relationship was $M = 3.69W^{-0.305}$. There is, however, substantial variation among species with similar weights. For this reason, the Lorenzen curve is believed to represent relative mortality at size better than the absolute mortality. The question then becomes how best to rescale the Lorenzen curve to the appropriate magnitude for a given species. A straightforward way to do this is to set the multiplicative parameter equal to the value that best matches the size distribution of the unexploited population. A similar approach may be employed for exploited populations provided there is sufficient contrast in fishing mortality. In practice, however, the data may be too noisy or the contrast too low to afford precise estimation.

Several assessments done through the Southeast Data, Assessment and Review (SEDAR) process have adopted an alternative approach whereby the Lorenzen curve is rescaled such that the average mortality rate matches a target value over the relevant life history phase. This is typically accomplished in three steps: 1) the Lorenzen curve is converted to a function of age by use of a growth equation, 2) the target value of M is determined external to the assessment model, and 3) the Lorenzen curve is rescaled such that

$$M(t) = M_{target} \frac{nL(t)}{\Sigma_{t_c}^{t_{max}} L(t)}$$

where t is age, $L(t)$ is the age-converted Lorenzen curve, t_c is the first fully exploited age class, t_{max} is the oldest age class, and n is the number of exploited age classes. The results of this rescaling approach are sensitive to the value of t_c when it falls within the age range where growth is rapid (Figure 3). The approach is also sensitive, of course, to the value of the target *M*.

Most SEDAR participants have agreed that the natural mortality rate likely decreases with age and that assuming the Lorenzen curve is probably more appropriate than assuming a constant value for all ages. There has been some discussion regard-

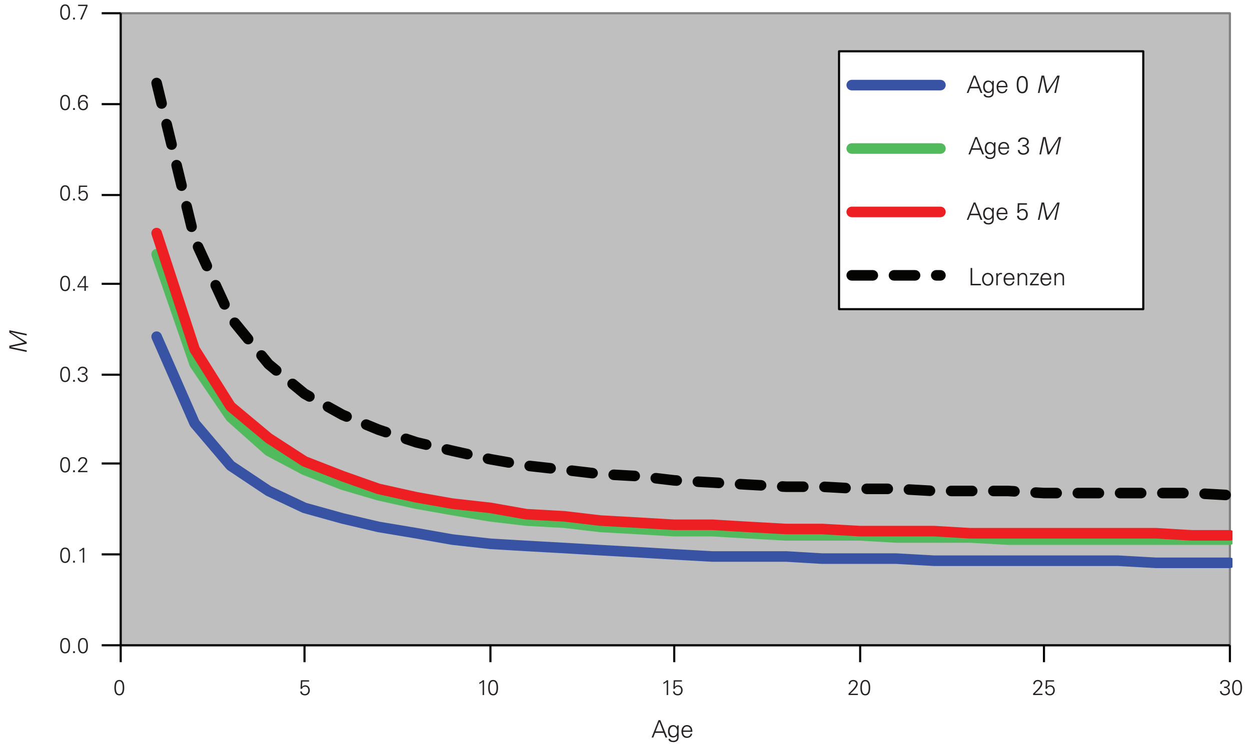

Figure 3. Examples of the Lorenzen curves (converted to functions of age) used for Gulf of Mexico gag grouper. The dashed line represents the curve obtained by direct conversion of the Lorenzen curve for oceanic fish. The solid lines represent curves that have been rescaled such that the average natural mortality rate equals a value of 0.15 for ages 5 to 30, 3 to 30 and 0 to 30 (from top to bottom, respectively).

ing senescence and the U-shaped mortality rate pattern it would imply, but in most cases it was felt that the affected age classes were too rare to matter. Most of the concern has centered on the value of the target *M*. For example, several SEDAR applications have based M_{target} on Hoenig's (1983) maximum age method, in which case concerns have been expressed that the observed maximum ages have come from exploited populations and therefore the values of *M* may be overestimated. Others have suggested that Hoenig's (1983) method may be biased low as it often produces *M* values that are lower than other common empirical methods (e.g. Pauly, 1980). Concern has been expressed that *M* may vary substantially in time and space owing to changes in predator abundance, episodic diseases and other factors. To date, the data have been insufficient to shed much light on the issue.

Abstract #13: Estimates of fishing and natural mortality of black sea bass, *Centropristis striata*, in the Mid-Atlantic based on a release-recapture experiment

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Black sea bass in the Mid-Atlantic Bight are exploited by recreational and commercial fisheries. To evaluate mortality rates, a tag release/recapture study was conducted with 13,794 tagged black sea bass (12,310 legal-size) released between Massachusetts and Cape Hatteras, NC from 2002 to 2004. Of these legal-size releases, 1,683 were recaptured during 2002 to 2007. An instantaneous rates configuration of a Brownie band recovery model was used to estimate both fishing and natural mortality. A seasonal model of fishing mortality, adjusted for nonmixing, and a constant natural mortality best explained the tag recoveries. Fishing mortality estimates were between 0.3 and 0.4 whereas the natural mortality estimate was greater than 1.0. The estimate of natural mortality includes the effects of all unaccounted tag losses, however the results suggest that natural mortality is likely greater than 0.2 which has been assumed based on a maximum age of 15. Higher overall rates of natural mortality could result from increased vulnerability at sexual transition in this hermaphroditic species.

Abstract #14: A comparison of natural mortality estimates for Alaskan flatfish stocks using a variety of methods

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A variety of simple relationships have been developed between (more easily measured) life history traits associated with a species or population and its rate of natural mortality, *M*. Consequently, measurement of these associated life history traits allows one to obtain estimates of *M* for a given species or population. Most of the resulting methods for estimating *M* are semi-empirical: based on a combination of life history optimization theory and statistical fitting of free parameters over many species and populations where *M* was known from other means. A few methods, however, have no free parameters and are completely based on theoretical "invariants". Here, I used measured life history characteristics from nine flatfish species found in the eastern Bering Sea and/or Gulf of Alaska (13 stocks total) to calculate sex-specific values of *M* based on 11 different estimation methods: Hoenig's (1983) method based on maximum age (three varieties); Pauly's (1980) method based on von Bertalanffy growth parameters (L_∞ and *K*) and mean environmental temperature (*T*); Jensen's (1996) re-analysis of Pauly's data, Gunderson's (1997) method based on GSI (two varieties), the so-called life history invariants (LHI: three methods) based on *K* and age at maturity, and Lorenzen's (1996) relationship for a "bulk" *M* (based on age at maturity).

Natural mortality estimates for these Alaskan flatfish stocks vary in range from 0.043 year^{-1} (Gulf of Alaska rex sole, Gunderson's method) to 0.71 year^{-1} (Bering Sea Alaska plaice, Lorenzen's method), while the range of estimates within a stock is scarcely smaller if results from Lorenzen's method are included (Figure 4). Overall, Lorenzen's method yields the highest estimates of *M* for all stocks. These estimates were based on female size at 50% maturity and would be expected to decrease if

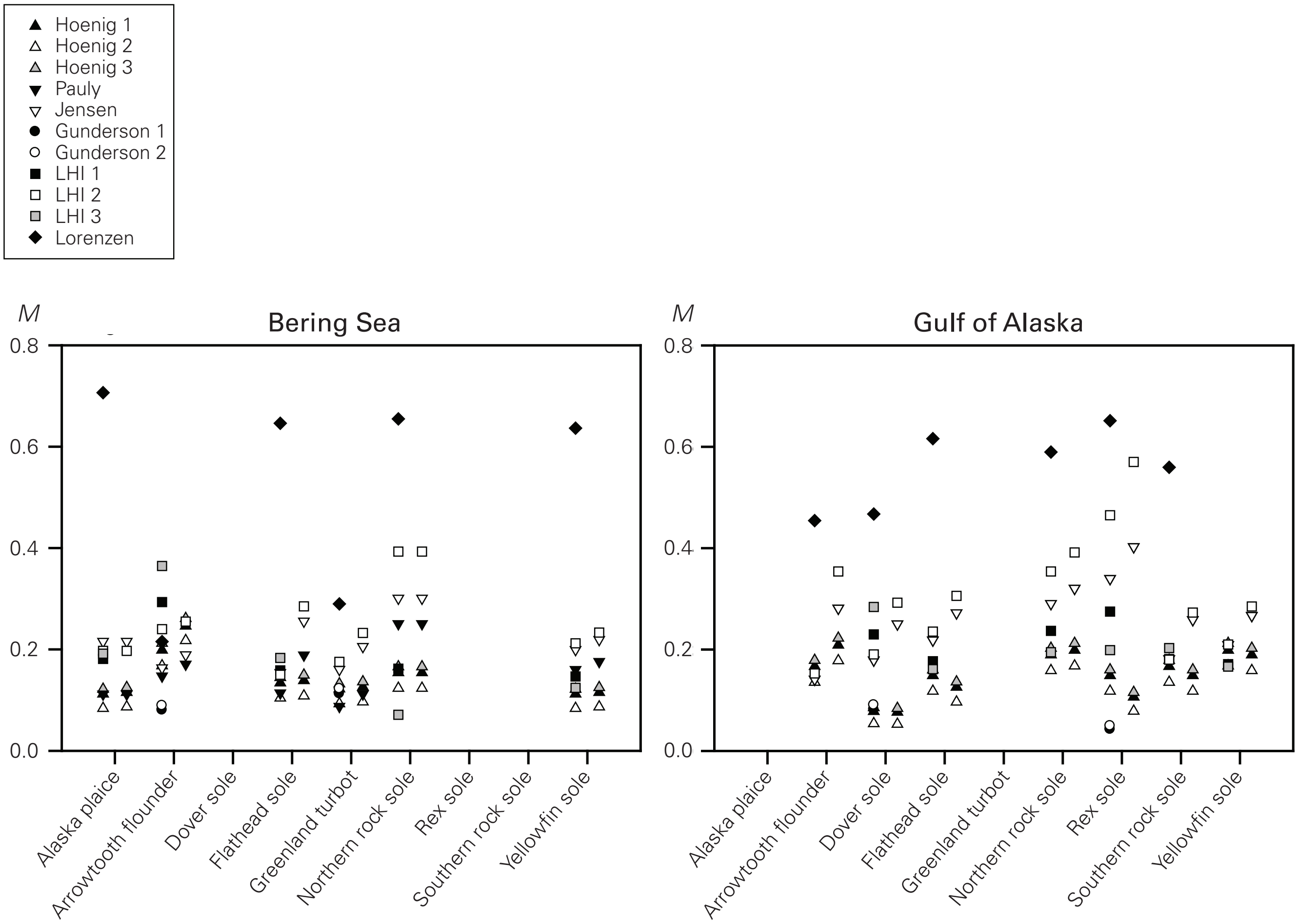

Figure 4. Sex-specific estimates of *M* for nine flatfish species (13 stocks) in the eastern Bering Sea and Gulf of Alaska. For each species, estimates for females are in the leftward column and males are in the right. Methods based on GSI and age at maturity were not applied to males.

mean size at maturity were used instead (Lorenzen suggests both, but favors the latter). Estimates based on the 2nd Life History Invariant ($M/K = C$) tended to yield the next highest values for *M*. Estimates based on Hoenig's method tended to be the lowest. Even if one ignores the estimates based on Lorenzen's method, there is little suggestion of sex-specific differences in natural mortality for any stock except arrowtooth flounder in the Gulf of Alaska.

The disparate estimates of natural mortality obtained here, both across species and within species, illustrate that the between-model uncertainty for *M* can be quite large. This suggests caution in using any single method to estimate *M*, the need to consider the within-model variability associated with each estimate of *M*, and the need to develop methods to combine different estimates of *M*.

Abstract #15: Episodic red tide mortality in Gulf of Mexico red and gag grouper

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Many natural populations experience short-term mortality events in the form of diseases or environmental episodes that may operate in addition to the baseline natural mortality (M). Even with clear visual evidence, it is quite difficult to determine the population level impacts of these events. Stock assessments generally do not consider short-term mortality events, other than assuming them to be part of the baseline M, the assessment framework represents an extremely powerful tool for assessing their population-level impacts. Further, in situations where the impact appears demonstrably extraordinary to the assumed M, stock assessments may have to account for such episodes. In this paper we describe the modeling and assessment of the impact of a severe red tide event on grouper populations in the Gulf of Mexico.

In two recent stock assessments of red (*Epinephelus morio*) and gag (*Myctoperca microlepis*) groupers in the Gulf of Mexico, every index of population abundance, both fishery dependent and fishery independent, showed an approximately 50% or greater decline between the years 2005 and 2006 (Figures 5 and 6). At no other time in the 23 year time series for both species had a similarly large, synchronous, single-year decline been observed. The time period over which the abundance indices declined coincided with a severe outbreak of red tide (*Karenia brevis*) in 2005 which blanketed the habitat of both red and gag groupers. Though red tide events are common in the Gulf of Mexico, the 2005 event was the most severe on record since 1971, leading to a record number of fish kill reports, and extensive areas of extremely poor or toxic water quality.

For both species, forward-projecting statistical catch at age models were used for assessment; the Age-Structured Assessment Program (ASAP; Legault and Restrepo, 1998) for red grouper and C++ Algorithmic Stock Assessment Laboratory (CASAL; Bull et al., 2005) for gag. In both programs an additional mortality term (M_{epi}) was estimated for 2005. This mortality term was additive to the baseline M and F and was modeled to occur throughout the year and equally for all ages for both species. Incorporation of M_{epi} provided a much improved fit to the CPUE indices for both species as well as

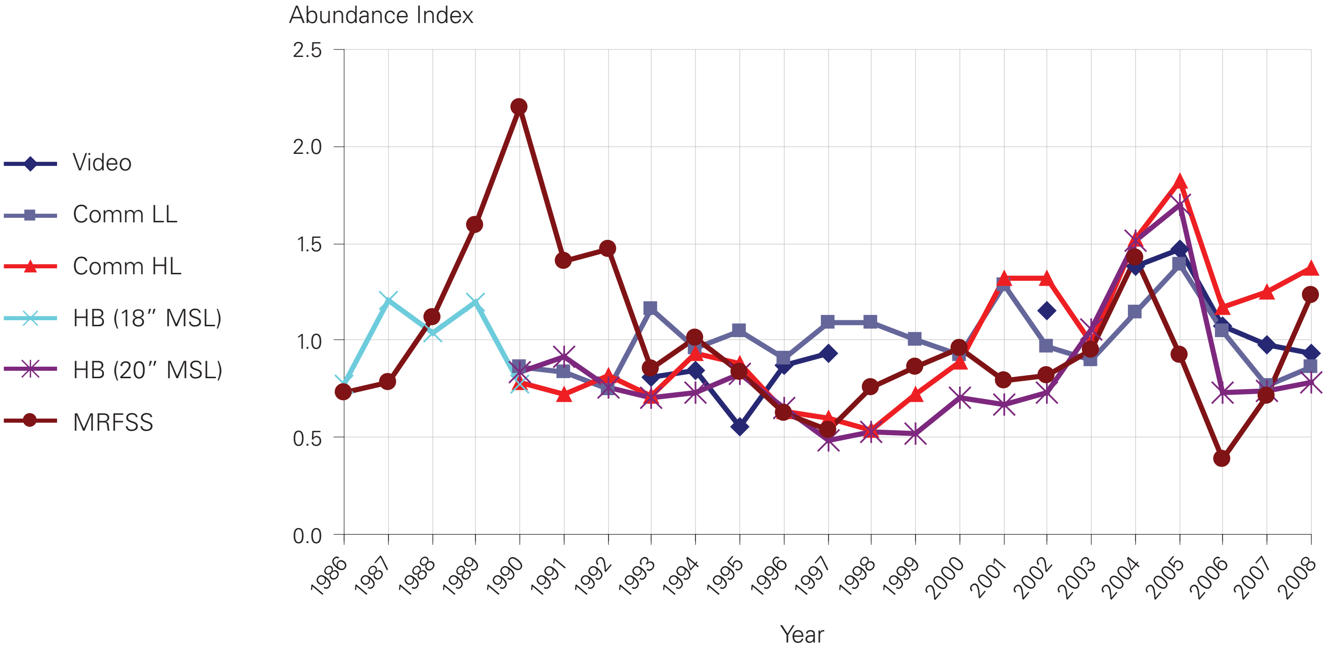

Figure 5. Standardized indices of abundance of Gulf of Mexico red grouper.

substantially improved overall model fit (Figure 7 [fits shown only for red grouper]). M_{epi} was estimated to be 0.27 for gag, representing a kill of 1.25 out of 6.83 million fish in 2005 or 18% of the total population. For red grouper, a similarly high M_{epi} of 0.32 was estimated, representing 8.4 out of 37 million (21%) of the population. For red grouper the model was run to estimate M_{epi} in each year of time series but one year at a time (Figure 8). Only for the first year 1986 and for 2005 and 2006 was M_{epi} estimated to be above a very low level of 0.05 and for most years it was estimated to be at or near the lower bound, indicating that there was very little evidence of substantial additional mortality in other years.

In conclusion, it appears that there was strong evidence for substantial additional mortality in 2005 as well as strong evidence for a causative mechanism in the red tide event. Assessment advice was promulgated using this additional M_{epi} and it is likely that significant red tide events may need to be considered in future assessments.

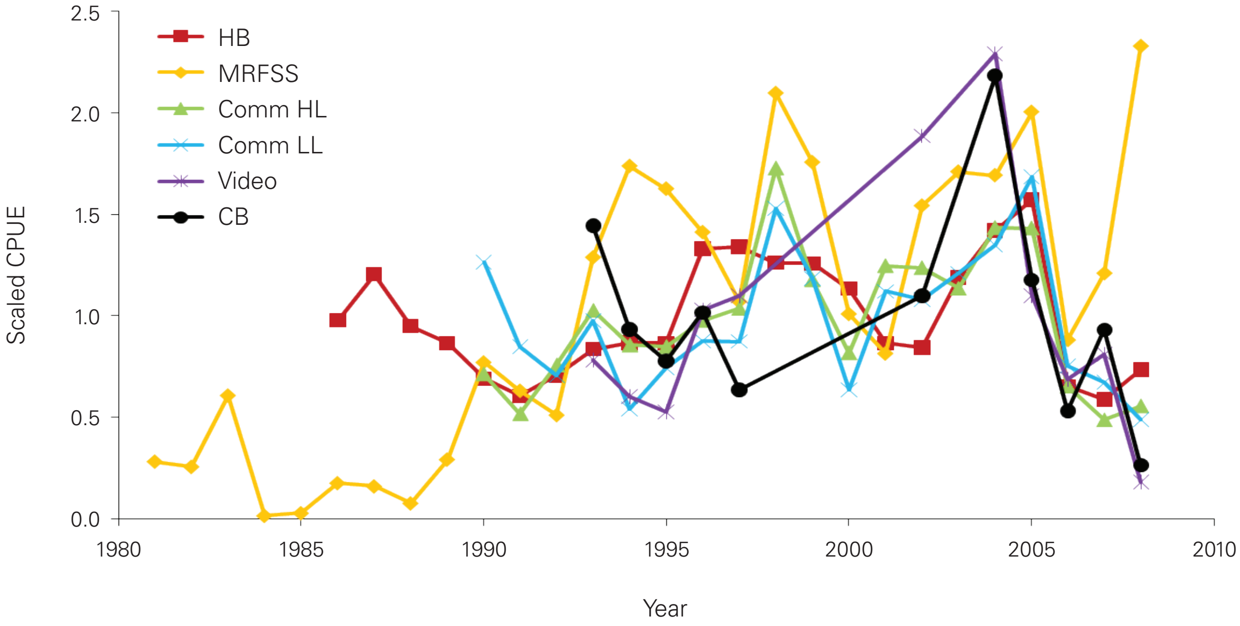

Figure 6. Standardized indices of abundance of Gulf of Mexico gag grouper.

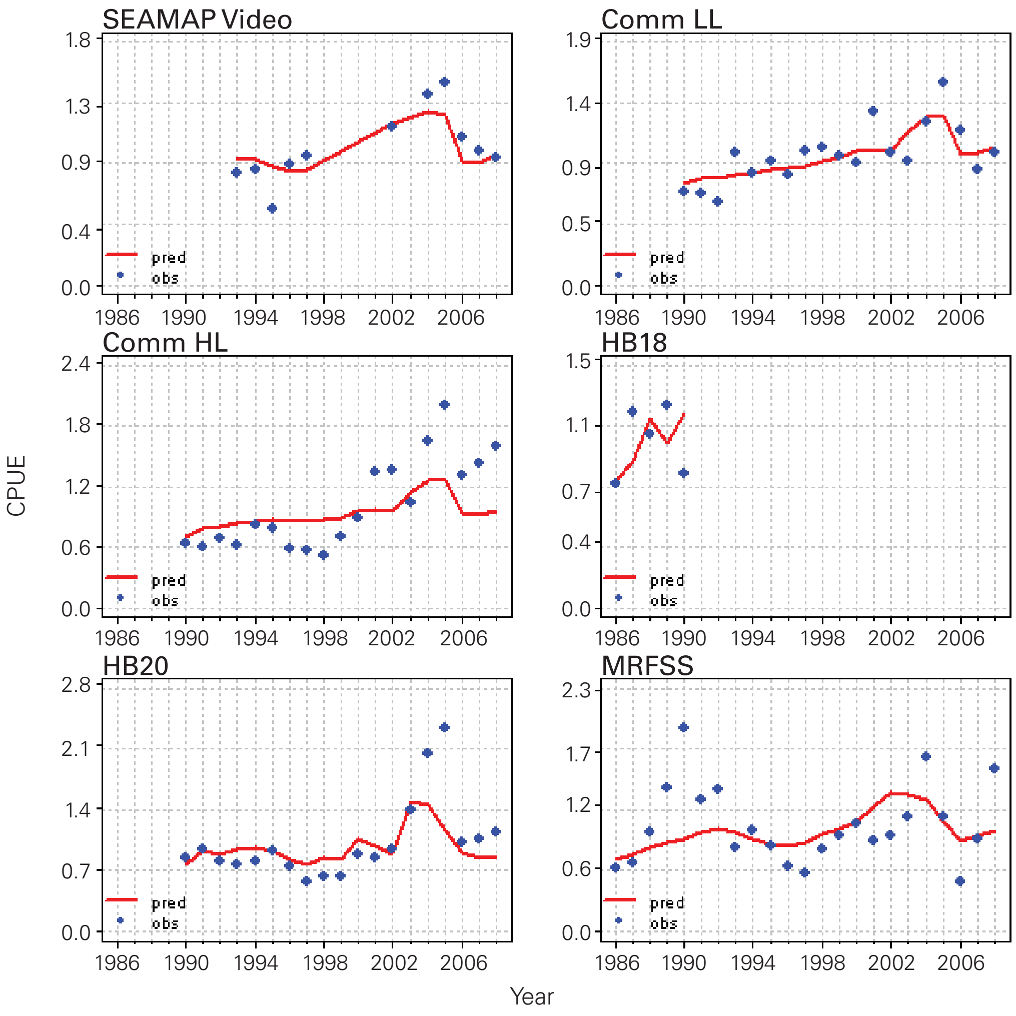

Figure 7. Model fits to CPUE indices for red grouper with episodic *M* in 2005.

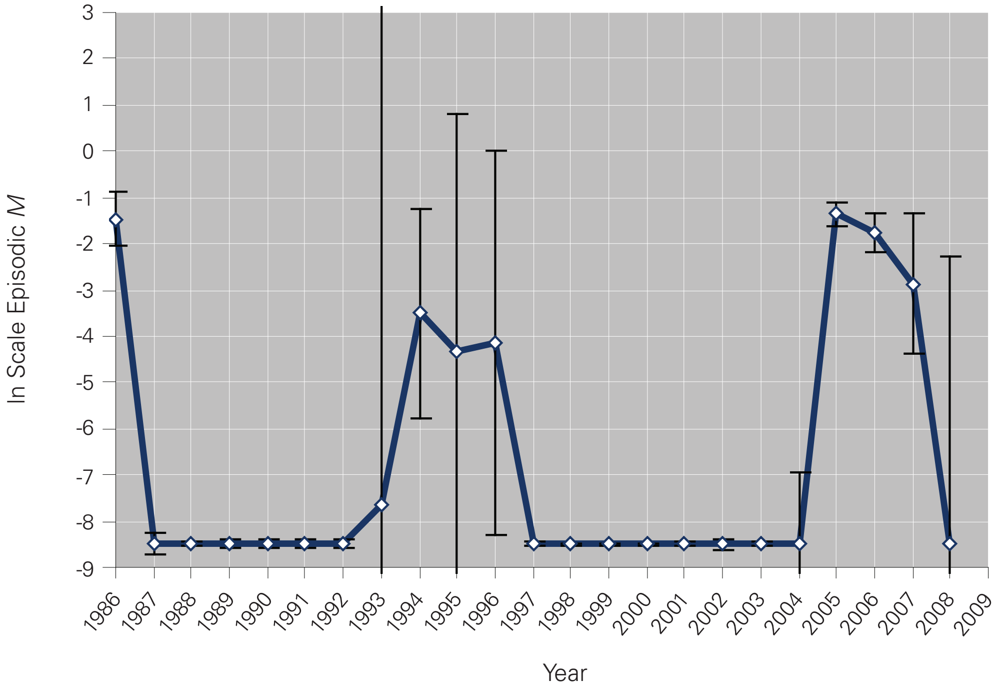

Figure 8. Log-scale estimated episodic *M* of red grouper for each year singly.

Acknowledgements

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APPENDIX 1: WORKSHOP AGENDA

*denotes presenting author

Tuesday, August 11 2009

8:30–11:30 AM

Welcome, Introductions, Approval of Agenda

Theme: BIOLOGY, ECOLOGY, and CONSEQUENCES of M

- Age- and size-varying natural mortality rates: biological causes and consequences for fisheries management (*Lorenzen*)
- Gulf of Alaska food web modeling and predation mortality estimates: information for single-species *M* (*Gaichas*)
- An ecosystem approach for assessment advice and biological reference points for the Gulf of Maine—Georges Bank Atlantic herring complex (*Overholtz, Jacobson*, and Link*)
- Modeling natural mortality and the effects on biological reference points (*Andrews*)

Discussion

- How do fish die? Starvation, Predation, Disease, Epizootics, Senescence
- Temporal, ontogenetic and spatial patterns in *M*
  - Long-term trends and patterns
  - Episodic: epizootics, predator invasions, etc.
- Is *M* in today's fully exploited ecosystems the same as *M* in yesterday's lightly exploited systems from which we have observed the oldest fish?

1–5 PM

Theme: ESTIMATION of M

- Estimating *M* for young red snapper from shrimp trawl catches (*John Walters*)
- What is the precision of *M*? (*MacCall*)
- Episodic mortality due to red tide on grouper (*Porch*)
- Estimates of fishing and natural mortality of black sea bass in the Mid-Atlantic based on tag release/recapture (*Shepherd and Joshua Moser, Sosebee presenting*)
- A comparison of natural mortality estimates using a variety of methods for Alaska flatfish (*Stockhausen*)

Discussion

- What kinds of data are most informative about *M*
- Potential new field studies for *M* relevant data
- Role of tag-recapture studies (more mini-presentations encouraged here)

Wednesday, August 12 2009

8:30–11:30 AM

Discussion - Continued

Wednesday, August 12 2009 (continued)

1–5 PM

Theme: MODEL-BASED and META-ANALYTIC APPROACHES

- Estimating M for sea scallops off the northeast coast in a size-specific assessment model and in closed areas (*Hart and Jacobson**)
- Scaling age-specific mortality curves (*Porch*)
- Model averaging to estimate natural mortality rates (*Brodziak*)
- Development of prediction intervals and priors for M using meta-analyses (*Hamel*)
- Delta method for assessment variance when M is fixed (*MacCall*)
- Estimating natural mortality within a stock assessment model: an evaluation using simulation analysis based on twelve stock assessments (*Maunder*)

Thursday, August 13 2009

8:30 AM–12 PM

Discussion

- Model based approaches to estimating M and its uncertainty
- Compare: bottom-up approaches (food web), empirical approaches (age composition, mark-recapture), correlative (life history meta-analysis), integrated analysis
- Overall conclusions

Appendix 2: List of Participants

Name	**Affiliation**
NOAA Participants	
Kate Andrews	Southeast Fisheries Science Center
Jon Brodziak	Pacific Islands Fisheries Science Center
Ray Conser	Southwest Fisheries Science Center
Jason Cope	Northwest Fisheries Science Center
E.J. Dick	Southwest Fisheries Science Center
Jeff Fujioka	Alaska Fisheries Science Center
Sarah Gaichas	Alaska Fisheries Science Center
Vladlena Gertseva	Northwest Fisheries Science Center
Owen Hamel	Northwest Fisheries Science Center
Xi He	Southwest Fisheries Science Center
Jim Ianelli	Alaska Fisheries Science Center
Walter Ingram	Southeast Fisheries Science Center
Larry Jacobson	Northeast Fisheries Science Center
Hui-hua Lee	Southwest Fisheries Science Center
Sandra Lowe	Alaska Fisheries Science Center
Alec MacCall	Southwest Fisheries Science Center
Richard Methot	Office of Science & Technology
Michael O'Farrell	Southwest Fisheries Science Center
Kevin Piner	Southwest Fisheries Science Center
Clay Porch	Southeast Fisheries Science Center
Kathy Sosebee	Northeast Fisheries Science Center
William Stockhausen	Alaska Fisheries Science Center
John F Walter	Southeast Fisheries Science Center
Chantell Wetzel	Northwest Fisheries Science Center
Tom Wilderbuer	Alaska Fisheries Science Center
Stephani Zador	Alaska Fisheries Science Center
Non-NOAA Participants	
Cameron Ainsworth	Northwest Fisheries Science Center Postdoc
Teresa A'Mar	University of Washington
Luiz Barbieri	South Atlantic Fishery Management Council Scientific and Statistical Committee
Valerie Brown	University of California Santa Cruz
Joanne Fergin	AmGen
Claudia Friess	Ocean Conservancy
Tommy Garrison	University of Washington
Steven Hare	International Pacific Halibut Commission

Name	**Affiliation**
Non-NOAA Participants, continued	
Melissa Hedges	Sea Grant (student)
Daniel Hively	University of California Santa Cruz
Momoko Ichinokawa	National Research Institute of Far Seas Fisheries
Kai Lorenzen	Invited speaker, Imperial College London (now University of Florida)
Mark Maunder	Inter-American Tropical Tuna Commission
Julie Neer	Southeast Data, Assessment, and Review
William Patterson	Gulf of Mexico Fishery Management Council
Kate Richerson	University of California Santa Cruz
Alex da Silva	Inter-American Tropical Tuna Commission
Yukio Takeuchi	National Research Institute of Far Seas Fisheries
Not Attending; E-mail Participation Only	
Gerard Dinardo	Pacific Islands Fisheries Science Center
Trevor J. Kenchington	gadus@istar.ca
Cindy Tribuzio	Alaska Fisheries Science Center