# The Natural Mortality Rate of Gag Grouper:
# A Review of Estimators for Data-Limited Fisheries

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## Introduction

The SEDAR 10 assessment of Gulf of Mexico gag grouper, as revised through September 2007, produced a picture of the past history of the fishery that showed prolonged recruitment failure in the 1960s and early 1970s, which led to a steep decline in biomass despite the near absence of fishing mortality. Thereafter and especially post-1989 (according to the assessment), recruitment increased more or less steadily, causing biomass to first stabilize despite increasing fishing effort and then (after 1995) to increase sharply despite fishing mortality rates that hovered around 0.35. Those trends were so pronounced that acceptance of the assessment implies acceptance that the gag resource is primarily driven by unknown, non-fishing factors that cause marked inter-decadal changes in recruitment levels. Since the controlling factors remain unknown, they are necessarily unpredictable and hence biomasses cannot be projected more than a few years into the future with any pretence at accuracy. Management by catch controls (whether bag limits, IFQs or the now-required ACLs) would thus lack any rational foundation – if the assessment is accepted as it stands.

However, the extreme changes in recruitment levels appear implausible and call the assessment itself into question. Its model of the gag resource was fit to data showing a sharp rise in CPUE in recent years, despite high and on-going catches, while an assumption of constant catchability meant that model interpreted the increasing catch rates as a reflection of increasing biomass. That model also incorporated an assumption, in its estimate of the natural mortality rate (M = 0.15)[1], that gag are a long-lived and

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[1] The assessment used 0.15 as the value of an "overall" natural mortality rate. It used age-specific values of M, following a Lorenzen curve (Lorenzen 1996), that was scaled such that the average of the M-at-age over a selected range of ages (3 to 30 years in the final

hence low-productivity species. It appears possible that the optimal model fit, with its pattern of recruitment failure (during the "burn in" period for which data are sparse) followed by a rebound supporting the rise in CPUE, was some computer's best attempt to explain the apparent paradox of the biomass of a resource assumed to be inherently unproductive increasing sharply while supporting high catches. If so, and if the estimate of M was unreasonably low, the entire assessment output would be not merely questionable but wrong.

It is therefore appropriate to reconsider the value of M used by SEDAR 10. That is not a new observation: In 2007, the review panel of the SEDAR Grouper Review expressed its uneasiness with the value being used for M and recommended that a national or international workshop be held to examine methods for estimating natural mortality rates – though it did not withhold approval of the assessment pending such a workshop. In April 2008, the GMFMC (seeing that projections prepared in September 2007 showed that overfishing of Gulf of Mexico gag had ended between 2005 and 2006 but warned by NMFS that some indicators suggested that those projections might be overly optimistic) referred the status of the gag resource back to its SSC. That Committee was also charged (partly at the urging of the current writer) with examining the question of the natural mortality rate, albeit not with the role of conducting the workshop envisioned by the SEDAR review panel.

This document has been prepared in support of the SSC's discussion of natural mortality rate estimates and estimators. It begins with an examination of the estimate of the "overall" rate of natural mortality (M = 0.15) used in the SEDAR 10 assessment and its revisions through September 2007. I argue that that estimate is implausibly low and is not consistent with what is known of the population dynamics of gag grouper. In the process, I illustrate the use of a numerical approach for informal examination of mortality rates which, while far from ideal, avoids the pitfalls in some published estimators. Thereafter, I review various mortality-rate estimators of that have been suggested in the primary literature for use in data-limited situations. Estimates of gag grouper mortality rates derived using most of those methods are presented in Table 1. I conclude that none of the available methods can provide adequate precision to support an analytical stock assessment but that the rate of natural mortality in gag grouper (averaged over late-juvenile and adult age-classes) is very likely in the range 0.2 to 0.3. Hence, the scientific advice to fisheries management concerning the gag grouper resource should be generated as alternative outputs, using input estimates of M of 0.20, 0.25 and 0.30.

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version) was equal to the "overall" rate. In practice, the M-at-age for all ages greater than about 10 years was somewhat less than 0.15, while the values for young gag were much higher (e.g. 0.3 for 3 year-olds).

# Mortality Rate & Longevity: A Numerical approach Applied to Gag Grouper

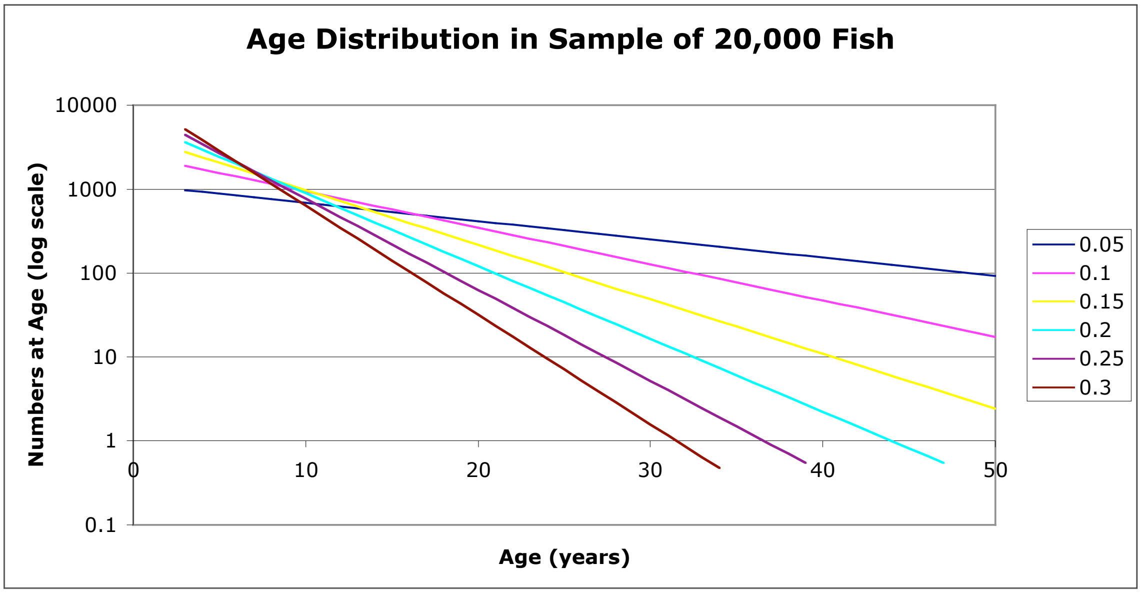
In an unexploited population, numbers-at-age in late-juvenile and adult age-classes of a particular year-class are conventionally modelled as:

$$N_t = N_0 \, e^{-Mt}$$

where $N_0$ is the number of individuals of zero age that would have produced the observed number of young adults if the natural mortality rate were truly constant from spawning onwards (which it clearly is not). If, for the purposes of illustration, it is assumed that recruitment is constant and continuous, the population will have a stable age distribution and the above equation describes not only the numbers of individuals in one year-class over time but also the numbers of individuals at one time across many year-classes. M is usually assumed constant across ages and across time, largely for lack of any reliable means of quantifying any variations.

The SEDAR 10 gag assessment did incorporate variation in M-at-age through its use of Lorenzen curves (Lorenzen 1996). However, rather than using the mortality-rate vectors generated by the Lorenzen Method itself (see below), the curves were scaled such that an average of the M-at-age over ages 3 to 30 (in the final version) equalled a fixed “overall” natural mortality rate, here denoted simply as M. Thus modelled, the cumulative mortality rate of fish from ages 3 to 30 (i.e. the sum of 27 different values of M-at-age) is equal to 27 M. When fitted to the growth parameters of gag grouper, Lorenzen curves are rather flat for ages greater than about 10 years and hence that equivalence can be extended to ages higher than 30 as an approximation and an overestimate (the Lorenzen M-at-age for ages older than 30 years being somewhat lower than the “overall” M). For present purposes, it is therefore sufficient to consider only alternative values for M and to disregard the complications of the Lorenzen curve for gag of Age 3 and older.

If it were possible to collect a sample of fish for ageing, such that the number of individuals in each age-class (above some minimum age, here taken to be 3 years, to avoid the higher mortality rates of very young age-classes) in the sample is proportional to the number in that age-class in the population, the observed age distribution would depend on only two variables: the natural mortality rate and the size of the aged sample. A simple numerical simulation, prepared on a spreadsheet, is sufficient to show that, for a sample size of 20,000 (approximately the total of gag grouper ages available to SEDAR 10) and a range of values of M between 0.05 and 0.30, the distributions (when plotted on a log scale and truncated to a maximum age of 50 years) would be:



Each line is shown extending from Age 3 to the age at which the calculated number of individuals in a sample of 20,000 drops to 0.5, which is to say the expected maximum observed age. Since the curves as shown were drawn using constant values of M, they are less steep at younger ages, and somewhat steeper at ages above about 10, than had they been drawn using M-at-age from a Lorenzen curve.

It can be seen that, if the “overall” value of M used in the assessment, 0.15, were correct, an ageing sample of 20,000 fish should included about 50 individuals of Age 30, a similar number in their forties and indeed a dozen or so of ages 50 and greater. The expected maximum observed age would be 60 years. In contrast, the oldest gag known to the SEDAR 10 data workshop was 31 years old when caught. There have been no reports of individuals as old as 40, let alone 50 or 60 – not in the ageing sample but also not from the early years of the fishery. It seems very unlikely that M is as low as 0.15.

A direct comparison of the above figure with the observed age distribution of gag would suggest a mortality rate of about 0.30. However, such a reading would have obvious weaknesses. The difference between the constant-M model and the Lorenzen-based M-at-age approach would alter the numbers somewhat but only inconsequentially.

Much more seriously, recruitment to the gag resource is clearly not constant. Had there been a prolonged period of depressed recruitment, extending over three decades and commencing 60 years before the age sampling, the observed age distribution could be consistent with M = 0.15. Such a major change in the production of juvenile gag would be inherently improbable but shorter-term fluctuations in recruitment may well have caused the observed maximum age to be 31 (rather than, say, 28 or 34), if a strong year-class was spawned 31 years before the last year of intensive age sampling. Any estimates read from the diagram are necessarily imprecise and uncertain.

Next, it is unlikely that the aged sample was collected in such a way as to include numbers-at-age proportional to those in the population. The full range of biases was not documented by SEDAR 10. However, the principal one appears to have been towards collecting more samples from commercial fleets than from the recreational fishery, while the former tend to fish further from shore, in deeper waters, where they tend to catch larger fish. Hence, the ageing sample appears to have been biased towards larger and older fish, driving up the maximum observed age and making the mortality rate appear lower than it truly was.

Fourthly, models of natural mortality used in stock assessments are only required to represent non-fishing deaths of age-classes that occur in reasonable abundance in an exploited population. Should there be marked senescence at ages greater than, say, 20 or 25 years (i.e. a substantial increase in M-at-age for older fish), an assumption of $M = 0.15$ could be fully adequate for assessment purposes and yet fish older than about 30 could be extremely scarce. Significant levels of senescence do not seem to have ever been suggested for gag grouper and I know of no evidence supporting the idea but it remains a possibility. So also does “reverse senescence”, with M-at-age dropping as higher ages – potentially at a faster rate than is suggested by Lorenzen curves.

Those substantial sources of uncertainty notwithstanding, the principal deficiencies in a simple reading of the above diagram are that it assumes a total mortality rate, Z, that is constant over time and, if used to estimate M, further assumes that fishing mortality, F, is negligible. Yet the bulk of the aged gag were collected from 1978 onwards. Thus, the observed distribution of their ages was the end result not of M alone but also of the variable amounts of fishing effort over the decades from approximately 1930 to date. Unfortunately, it is not now possible to hindcast the changing value of F independently of some estimate of M[2]. Nor is there any simple way to prepare a diagram equivalent to that presented above incorporating both time-varying F and age sampling spread over a number of years. All that can be said is that M is likely lower (perhaps substantially lower) than the mortality rate, approximately 0.30, suggested above. However, that figure cannot be taken as a firm upper bound since the extent of the bias in the aging sample towards larger and older fish is unknown. Its effects on the estimate might exceed those that arise from ignoring F through the decades preceding the sampling – for much of which time fishing effort seems to have been low.

In summary, a comparison of the conventional mortality model, which is effectively the one used in the SEDAR 10 gag assessment, with observed ages of the fish strongly suggests that M is not as low as 0.15 but could lie anywhere between, perhaps, 0.2 and 0.3.

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[2] Except perhaps through an assessment model that estimates both F and M (cf. Zheng *et al.* 1995), an option discussed below.

That is clearly a vague, imprecise and uncertain conclusion. I would argue that the clarity of its weakness is a great advantage. All estimates of M derived from the simple methods suited to data-limited situations are highly uncertain (as are many derived using copious data), yet too often the weaknesses in the methods are hidden behind a veil of mathematics that offers estimates with implied precisions of three or more decimal places, encouraging far more trust in the resulting assessments than can be warranted. In contrast, the simple numerical simulation approach remains close to the mortality model used in the assessment, while drawing attention to its own assumptions and facilitating judgements of the fit of alternative values of M to the available data.

## Estimators for Data-Rich Situations

The focus of this paper is on the estimation of M in data-limited settings. Before exploring those, however, some note of the alternatives that can be used when high-quality data are abundant is appropriate – not least because there seems to be a great amount of age data on gag grouper that might well permit the use of some of those approaches.

### *Catch Curves*

Given abundant age data, as appears to be available for gag, the classic way to estimate Z is by preparing a catch curve. M is then estimated by regressing Z against fishing effort to find Z when F = 0.

For that approach, it is not sufficient to have aged a large sample of fish. It is also necessary to have selected that sample in such a way that the distribution of ages in the population can be reconstructed, with acceptable accuracy. While that is an obvious requirement for the preparation of catch curves, it is no less required if mortality rates are to be estimated from some simpler measure of the age distribution, such as the maximum observed age used above and by the methods of Bayliff (1967) or Hoenig (1983). Simplicity in the estimator does not reduce the requirement for the age distribution to reflect that in the population if the resulting estimate is to reflect the population mortality rate.

In the case of gag grouper, if the available age data cannot support preparation of catch curves, it is unlikely that should be used in estimating mortality rates by other means, save perhaps in generating very broad indications of plausible rates, such as those offered above.

## Beverton & Holt Length-Based Method

Founded only on an assumption of growth following a von Bertalanffy curve and mortality (with constant Z) following the conventional exponential model, Beverton & Holt (1956) showed that:

$$Z = K\,(L_\infty - \bar{L}) / (\bar{L} - L_c)$$

where the mean length is determined between some selected $L_c$, usually the lowest length that is fully represented in the available length frequencies, and $L_\infty$. Strictly speaking, the relationship requires the average length of the fish in a single year class, considered over their entire lives, or else recruitment must be assumed to be constant and continuous. However, the method has long been used, with length data drawn from a few years and across many year-classes, to estimate the total mortality rate (or failing that at least the Z / K ratio) in situations where catch curves cannot be prepared.

Application of the method does, of course, require that a length frequency representative of the population and extending to the asymptotic length can be prepared. It also assumes that the dynamics pf the population are adequately described by the von Bertalanffy and exponential-mortality models. The greater limitation on the method's use is likely the assumption of constant Z. Except in cases where F can be assumed to be zero and M can be taken as constant, substantial variations in Z are to be expected and those invalidate Beverton & Holt's (1956) equation. The method is potentially useful in cases of unexploited resources or those subject to only light exploitation, when it can serve to estimate M, but it may then be difficult to obtain an adequate length frequency and even harder to accumulate sufficient knowledge of the resource to ensure that that length frequency is indeed representative of the population and not simply of one age-specific component.

It seems unlikely that this "Beverton & Holt Method" would be useful with gag grouper, given the species' ontogenetic movement onto offshore reefs and the behaviourally-induced variations in catchability-at-size typical of vertical-line fisheries for predatory fish. Modern sampling might circumvent those complications and generate a representative length frequency but fluctuations in F over recent decades would invalidate application of the method. Length data may be available from periods when it could be assumed that Z = M but it is unlikely that a credible figure for the mean length in the population at such times could be derived.

## Mark & Recapture

The methodology for analysis of tagging data has been refined to a very high level, with estimates of mortality rates being one potential output. However, developing reliable estimates of those rates places extreme demands on data quality. It seems unlikely that any of the gag tagging programs yet conducted has yielded data suitable for such analysis and this alternative will not be explored further here.

### Estimation Within Assessment Model

When using "forward calculating" assessment models (the general type employed in the SEDAR 10 gag assessments), it is possible to treat M as a parameter to be estimated during fitting of the model, rather than as an input to be determined *a priori* (Zheng 2005). That approach to the estimation of natural mortality rates appears to have first been used by Zheng *et al.* (1995) in an assessment of Bristol Bay king crab. In a data-rich setting, it might be the best approach of all but for reef fish, which are almost-necessarily data-limited, there is a serious risk of the assessment model becoming overparameterized, if indeed it can be fit to data at all.

The extreme, and implausible, long-term changes in recruitment suggested by the SEDAR 10 gag assessment are a warning that its model already allows too much flexibility, given the amount of data available to tie the output to reality. Allowing the model to also estimate M does not appear to be a sensible alternative for the resource of present interest.

### Estimation Within Ecosystem Model

Reasoning that most fish died, ultimately, as victims of predation, there have been various attempts to estimate M using some form of ecosystem model – formerly perhaps multispecies VPA, now more likely Ecopath. The demands on the data and existing knowledge are high, while the state of current understanding of most marine ecosystems suggests that the models typically have more utility in ecological research than in parameter estimation for stock assessments. The complex ecosystems of warm-water reefs seem particularly unsuited to the approach and it will not be discussed further here.

## Estimators Based on Age Data

Turning to methods suggested for use in data-limited situations, it is well to start with those that use age data, firstly because one such method (here termed the "Hoenig First Method") was used to estimate "overall" M in the SEDAR 10 gag grouper assessments and secondly because the direct influence of mortality rates on numbers-at-age holds out the promise of a closer link between estimates of those rates and data on age distributions than could be obtained with most other classes of estimators.

Unlike some of the methods considered in the previous section, the ones presented from here onwards were originally developed as ways of generating very approximate, initial estimates in data-limited situations, such as when previously-unexploited resources are first brought under fishing and fisheries management. It is doubtful that any of the them can produce an estimate of M with sufficient precision for use in an analytical stock assessment and they should be considered in light of that.

## *Bayliff Method*

Since the total mortality rate, Z, is simply the converse of survival rate, the lower Z may be, the higher the survival of the fish and the longer each individual may be expected to live. That was already recognized by Beverton & Holt (1959), while Beverton (1963) noted a linear relationship between Z and the inverse of the maximum observed age (here denoted as $T_{MAX}$), with slopes of 4.3 to 10.4 for various clupeids. It seems to have been Bayliff (1967) who first proposed using such a relationship to estimate the mortality rate. His regression-based estimator:

$$Z = 6.384 / T_{MAX}$$

was intended specifically for the Engraulidae.

This “Bayliff Method” incorporates all of the severe weaknesses of the numerical-simulation approach outlined above. In addition, it is based exclusively on observations of the maximum age. Yet, if the deaths of the fish approximate to the exponential model, fish of the oldest age class will always be scarce, resulting in considerable sampling error in estimates of $T_{MAX}$. Even with very extensive sampling, the observed maximum age will be unstable: Thirty years after a strong year-class was spawned, it is much more likely that the highest observed age will be 30 than either 28, 29, 31 or 32. The following year, the observation would more likely be of a fish aged 31.

For some species, there may also be a lack of validated ageing methods extending to high ages, making the true age of the oldest fish captured uncertain. There have been cases of species with low maximum ages that, with further research, have been re-aged to decades older than had been supposed (Beamish & McFarlane 1983).

There is, however, a greater weakness that can result in severe biases which make the Bayliff Method unsuitable, in most circumstances, even as a crude initial estimator of Z: Because older age classes are necessarily scarce, and (inter-annual variability in year-class strengths aside) the older they are the scarcer, larger ageing samples can be expected to yield single individuals with higher ages than the maximum observed in smaller samples. Yet the Bayliff Method ignores sample size. It should return approximately-correct values, at least for anchovies, when the size of the ageing sample is approximately the same as those in the prior studies that Bayliff (1967) used in estimating his slope parameter. However, the Method will seriously underestimate Z if the estimate of $T_{MAX}$ is drawn from a much larger ageing sample.

The importance of sample size must also draw attention to the representativeness of the ageing sample. A true random sample of a few thousand individuals from a typical teleost population would contain little but eggs and larvae, resulting in a very low estimate of $T_{MAX}$. Conversely, a sample of only dozens of fish might generate a very high estimate if it contained specimens selected for their very large sizes and hence their “suitability” for determining the maximum age. A useful mortality-rate estimator of Bayliff’s (1967) type requires the same assumptions about ages representative of those in the population above some minimum that are discussed above in relation to the numerical-simulation approach. To apply the Bayliff Method itself, however, it would be necessary to have an ageing sample that mimicked the biases in those used in the studies from which Bayliff (1967) derived his parameter value.

Considering all of the above, the Bayliff Method is not appropriate for generating estimates of M or Z for use in analytical stock assessments.

## *Hoenig First Method*

Hoenig's (1983) primary method for estimating the total mortality rate is of particular interest because it was the one used in the SEDAR 10 gag grouper assessments to provide a value for "overall" M. That was itself curious since Hoenig (1983) was clear and consistent in presenting his method as an estimator of Z, which it is, and the ageing sample for gag was mostly collected after a number of years with not-insignificant levels of fishing effort. The confusion may have arisen with Hewitt & Hoenig (2005), who represented the method as an estimator of M, though they did note that it can only be taken so if fishing mortality is light or if some individuals in refuge areas escape exposure to fishing[3].

Ignoring the causal relationship between mortality rates and observed ages, Hoenig (1983) followed Bayliff's (1967) regression approach in developing his estimator, though he included one additional parameter. Like Bayliff (1967), he disregarded the effects of sample size on estimates of $T_{MAX}$. Using data on 84 fish populations, drawn from a variety of prior studies, he thereby obtained the estimator:

$$Z = 4.31\ T_{MAX}^{-1.01}$$

which is to say:

$$Z \approx 4.3\ /\ T_{MAX}$$

In an addendum to his published note, Hoenig (1983) considered that his regression analysis might better have used a geometric mean regression, rather than the conventional arithmetic mean approach. Since both Z and $T_{MAX}$ are observed with great uncertainty, the GM regression would seem to be more appropriate. It would change the expression for fish to:

$$Z = 2.214\ T_{MAX}^{-0.767}$$

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[3] The latter idea, while attractive at first sight, would greatly complicate the estimation of effective sample size, since the observed $T_{MAX}$ could only be associated with that portion of the ageing sample which had not experienced significant fishing pressure through its lifetime.

Despite its broader foundation in prior studies and its slight increase in complexity, this "Hoenig First Method" shares the same severe weaknesses as the Bayliff Method. Neither can generate mortality estimates suitable for use in analytical assessments. Hoenig (1983) himself admitted to the sample-size problem and addressed it to some extent in an appendix which is considered below under the "Hoenig Second Method". Other errors aside, the Hoenig First Method returns approximately-correct results only if the ageing sample was comprised of some 125 to 250 fish (if Z is in the range 0.15 to 0.30), presumably reflecting typical sample sizes in the prior studies used by Hoenig (1983).

## *Sekharan Method*

Many smaller tropical species have short and perhaps determinate lifespans. It is far from certain that the conventional exponential mortality model is appropriate to such species but it is often applied nonetheless. Without laying out his methodology in any formal way, for two such populations, Sekharan (1975) assumed that, in the absence of exploitation, only 1% of the fish would reach the known maximum age. Hence:

$$N_{T\,[MAX]} / N_0 = 1 / 100 = e^{-T\,[MAX]\,M}$$

$$M \approx 4.6 / T_{MAX}$$

That estimator, which may have been used even earlier and just as informally, was formalized and generalized by Alagaraja (1984). It appears to have already been in widespread use by then, particularly in assessing fisheries in the developing world.

For unexploited resources, this "Sekharan Method" returns results almost identical to those of the Hoenig First Method, though the underlying logic is quite different.

Sekharan (1975) assumed that the exponential model could be applied to short-lived species and could be applied over their entire lifecycles. While those assumptions are questionable, his approach could be used for groupers if the younger age classes were ignored. However, in such an application, there would be no basis for the assumption that 1% of fish reach the maximum observed age – a point stressed by Hewitt & Hoenig (2005). A more realistic assumption would require information on sample size, which is as lacking from the Sekharan Method as it is from the Hoenig First Method.

Variants of the Sekharan Method appear to have been independently derived on multiple occasions, some of which may predate Sekharan's (1975) own work. Some have emerged using assumptions that the survivors to maximum age are some other proportion of the recruits than 1%. Hence, the estimator:

$$M = -\ln (P) / T_{MAX}$$

where P is the proportion surviving, has appeared in standard textbooks. With $P = 0.05$ (meaning $M \approx 3 / T_{MAX}$), that version has been used in assessments of the Chesapeake blue crab resource. Hewitt & Hoenig (2005) have correctly criticized that estimator (which they called the "rule-of-thumb approach") for its necessarily-arbitrary selection of a value of P. Unfortunately, they went on to recommend what is here termed the Hoenig First Method as an alternative when that approach merely abdicates the same decision to the sample sizes in the prior data sets that Hoenig (1983) used in developing his regression equations. In the event, those data sets gave him an estimator almost indistinguishable from an assumption of $P = 0.01$[4].

## *Alverson & Carney Method*

Starting from the similar assumptions to those of Beverton & Holt (1956), specifically that growth follows a von Bertalanffy curve, with $t_0 = 0$, that natural mortality follows the conventional exponential model, and adding an assumption that growth is isometric, Alverson & Carney (1975) showed that:

$$t_{mb} = (1 / K) \ln [(M + 3K) / M]$$

where $t_{mb}$ is that age at which a year-class achieves its maximum biomass, in the absence of any fishing, and K is the constant from the von Bertalanffy growth model. While their paper dealt broadly with fisheries population dynamics, Alverson & Carney (1975) noted that they had employed the above relationship to estimate M. To do so, they estimated $t_{mb} = 0.38\ T_{,MAX}$, using prior data on 63 fish populations. They did not explicitly provide an estimator of M but their expression can be recast as:

$$M = 3\ K / (e^{K\ 0.38\ T[MAX]} - 1)$$

That has appeared in textbooks and has been termed the "Alverson & Carney Method", by which name it will be known here.

It may be noted that this method generates estimates of M, not Z, but to do so must have an estimate of $T_{MAX}$ in the unfished condition. If the ageing sample was drawn from an exploited population, the maximum observed age will be less than in the virgin state, leading to an underestimate of $t_{mb}$ (all else being equal), inflating the estimate of M.

This method suffers from much the same deficiencies as the Bayliff and Hoenig First methods, the correct scaling of $T_{MAX}$ to $t_{mb}$ being dependent on sample size, while the constant 0.38 is approximately correct only if the observed maximum age is drawn from a sample of similar size to those in the 63 prior studies used by Alverson & Carney (1975). Their method also assumes von Bertalanffy growth, which is an unnecessary constraint, and requires an estimate of the K parameter. It seems to have no advantages over the Hoenig First Method, while being somewhat more awkward to apply.

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[4] For gag grouper specifically, McGovern *et al.* (2005) used $M = 2.98 / T$, which they supported with a citation of Hoenig (1983). Their estimator was in reality one variant of the very "rule-of-thumb" that Hewitt & Hoenig (2005) rejected in favour of the Hoenig First Method.

This method is no more suitable for generating mortality-rate estimates for use in analytical assessments than are the alternatives previously considered.

## *Zhang & Megrey Method*

Zhang & Megrey (2006) have recently revisited the Alverson & Carney Method and explored the consequences of relaxing the assumptions that $t_0 = 0$ and that growth is isometric, while also re-examining the constant 0.38. The presented a generalized estimator:

$$M = \beta K / (e^{K\,(t_{mb} - t_0)} - 1)$$

where $\beta$ is the exponent of the length / weight relationship. Zhang & Megrey (2006) suggested $t_{mb} = 0.44\ T_{MAX}$ for demersal fish and $t_{mb} = 0.302\ T_{MAX}$ for pelagics, based on data from 91 fish species drawn from the FishBase database, which also supported a constant of 0.393 [close to Alverson & Carney's (1975) 0.38] when pelagics and demersals were combined.

Zhang & Megrey (2006) proceeded to evaluate both their and the Alverson & Carney Method using estimates for those same 91 species. The two methods differed little across the realistic range of values of $\beta$ and $t_0$, through altering the relationship between $t_{mb}$ and $T_{MAX}$ not surprisingly did change estimated M. In consequence, while the Zhang & Megrey (2006) method returned estimates of M that conformed to those provided by FishBase, the Alverson & Carney Method only did so for pelagics. That test, however, depended on circular reasoning: Zhang & Megrey (2006) scaled their estimator so that it would return estimates that accorded with those in FishBase and it did so.

It remains unclear whether the Zhang & Megrey Method offers any appreciable advance over the Alverson & Carney Method to compensate for its increased complexity. It certainly fails to address the major deficiencies in the older method.

## *Hoenig Second Method and Holt Method*

The only author who has addressed the effects of sample size on the maximum observed age and hence on estimates of mortality rates is Hoenig (1983). In the main body of his published note, he skated over this issue and even proposed that his method could be applied when only the largest individuals are selected for ageing, as though such a bias would have no effect on the results. However, he also included an appendix in which he explored the issue of sample size. While he did not propose the outcome of that exploration as a method for estimation of Z, it is here treated as the "Hoenig Second Method".

Hoenig's (1983) appendix started with a declaration that the expected maximum age in a sample of size N individuals (assuming constant and continuous recruitment, giving a stable age distribution) is:

$$E(T_{MAX}) = (1 / Z) \sum^{N} (1 / i) + t_c$$

where $t_c$ is the youngest age fully represented in the catch. That expression, which was drawn from Johnson & Kotz (1970), Hoenig (1983) approximated with:

$$E(T_{MAX}) \approx [\ln (2N + 1) / Z] + t_c$$

Hoenig (1983) only used that relationship to explore the effects of sample size on the maximum observed age for a given mortality rate. He suggested that the consequences of larger ageing samples are limited if N exceeds about 200. That is true for linear increases but not for geometric ones. Example calculations will swiftly show that doubling N increases the estimate of Z, for a given $T_{MAX}$, by enough to have management significance, even when many thousands of individuals have been aged.

Holt (1965) had previously offered a similar expression:

$$E(T_{MAX}) \approx [(\ln N + 0.577) / Z] + t_c$$

that he characterized in the same way as Hoenig (1983) did much later. Either expression can readily be recast into an estimator of Z. In that form, they are here termed the "Hoenig Second Method" and the "Holt Method" respectively. The two versions give closely similar, but not quite the same, numerical results.

Unfortunately, Hoenig (1983) misinterpreted Johnson & Kotz (1970), whose concern was not with the size of a sample representing the age distribution in a population but rather with the size of a sample of lives – an appropriate focus in life-table studies and equivalent in fisheries symbology to $N_0$ or, in the particular case of the Hoenig Second Method, to $N_{t[c]}$. It is not certain that Holt (1965) made the same mistake but, in a worked example, he did use his N as the number of recruits in a population.

## *Corrected Hoenig Second Method*

To correct the Hoenig Second Method, it is necessary to determine the size of a population that would emerge, under a constant mortality of Z, given constant recruitment of $N_{t[c]}$. The definite integral (from zero to infinity) with respect to time of the conventional mortality model:

$$N_t = N_0 e^{-Zt}$$

is simply:

$$N_0 / Z$$

Hence, the size of a sample population, between the ages $t_c$ and $T_{MAX}$, where TMAX is the age at which the expected frequency of numbers-at-age is 0.5, is:

$$N = (N_{t[c]} - N_{T[MAX]}) / Z = (N_{t[c]} - 0.5) / Z$$

$$N_{t[c]} = Z\,N + 0.5$$

Hence the corrected expression is:

$$E(T_{MAX}) \approx [\ln \{2(Z\,N + 1)\} / Z] + t_c$$

That can readily be solved iteratively for any given values of N and $T_{MAX}$ to generate an estimate of Z.

This "Corrected Hoenig Second Method", presented for the first time in this paper, is the only mortality-rate estimator yet suggested that is based on $T_{MAX}$ and correctly accounts for sample size. As such, it is the first method for data-limited situations examined here that can be regarded as valid. However, while it avoids the single greatest deficiency of the Hoenig First Method, it does not escape the others, save for the First Method's reliance on a regression approach and hence on the validity of the estimates made by prior studies.

When compared to the numerical simulation approach with which this paper begins, the Corrected Hoenig Second Method returns a very similar best estimate of Z, which should be no surprise as the two approaches use identical logic (differing only in the one relying on integral calculus when the other uses iterative calculation). Both methods share identical assumptions and weaknesses, though the Corrected Hoenig Second Method relies exclusively on the observed maximum age, with all of its variability, where the numerical simulation approach allows consideration of the dozen or hundred greatest recorded ages (should data on those be compiled, which they have not yet been for gag grouper). There may be a further disadvantage to the Corrected Hoenig Second Method in that its presentation as a simple mathematical expression tends to imply a precision and reliability that the method does not have. The numerical simulation approach, in contrast, tends to draw attention to the weaknesses that are common to both alternatives.

## *Rikhter & Efanov First and Second Methods*

At much the same time as Alverson & Carney (1975) reported the first use of their method, Rikhter & Efanov (1976) noted the same basic relationships, including the form later developed by Zhang & Megrey (2006) for species with allometric growth. They, however, suggested that $t_{mb}$ could be estimated as equal to the age at 50% maturity, rather than using some proportion of $T_{MAX}$:

$$M = \beta K / (e^{K\,(t_m - t_0)} - 1)$$

where $t_m$ is the age at 50% maturity.

Alternatively, and based on a regression using prior data on only 14 fish populations, Rikhter & Efanov (1976) derived:

$$M = (1.521 / t_m^{0.720})$$

These “Rikhter & Efanov First” and “Rikhter & Efanov Second” methods are of dubious relevance to protogynous hermaphrodites and, when applied to gag grouper, yield mortality rates that are far too high to be credible. That is unfortunate since those estimates are independent of the size of the ageing sample and are of M, rather than Z.

## Estimators Based on Life History Correlates

The causal relationship between mortality rates and observed ages gives age-based estimators an obvious attraction, though any credible variant would have to place considerable demands on the quality and quantity of data if there were to be reliance on the precision of the resulting mortality estimates. Data of such quality might better be analyzed using catch curves.

The alternative approach is to estimate M from other life-history parameters using regression equations, sometimes supported by logic founded in evolutionary theory. Most such estimators can be criticized for lacking mechanistic foundations, though the relationships between growth patterns and death rates are not matters of mere chance: there are linkages through lifetime fecundities and the need for replacement of dead individuals in stable, unexploited populations.

More seriously, all mortality-rate estimators based on life-history correlates are necessarily regression estimators. They are therefore heavily dependent on the quality of the data used in developing the regression equation – as indeed are some of the age-based estimators. Since there are few good ways of estimating M, even in data-rich situations, major doubts necessarily surround all of the regressions.

### *Alagaraja Method*

Alagaraja (1984) suggested a variant of the Sekharan Method which avoided any dependence on age data. He replaced $T_{MAX}$, the maximum observed age, with $T_\infty$, the age at which an individual fish would be expected to reach the asymptotic length for the population in question, following a von Bertalanffy growth curve. While he did not admit the problem, Alagaraja (1984) avoided the awkward complication that $T_\infty$ is, by definition, infinite by substituting the age at which a fish would reach a length 5 mm shorter than $L_\infty$. He made allowance for the $t_0$ parameter, though that was probably a superfluous detail, given the general imprecision of his method.

Alagaraja (1984) then arbitrarily assumed that 5% of individuals would survive to his $T_\infty$ – which is entirely contrary to common observation of many fish species. It would remain an untenable assumption even if $N_0$ were taken to mean the number of zero-age fish that would have existed if the adult mortality rate applied from spawning onwards, rather than the actual number of zero-age animals. Without that interpretation, any assumption that 5% of individuals survived even one month after spawning would be farcical for most marine teleosts.

Alagaraja (1984) thus suggested that:

$$M \approx 3.0 / T_\infty$$

This "Alagaraja Method" does not merit serious consideration as a mortality-rate estimator.

## *Ralston Method*

Beverton & Holt (1959) noted that M is related to the K parameter of the von Bertalanffy growth equation. K is not a measure of growth rate but rather of the rate at which fish grow towards their asymptotic size. Approaching that size faster suggests a shorter lifespan and hence higher M, while the faster approach also argues for adaptation towards earlier sexual maturity (with the slowing in somatic growth that accompanies redirection of energy into gonad development), which is consistent with a shorter life expectancy. Perhaps the first attempt to quantify the relationship was Beverton's (1963). He found that the ratio M / K had values of 0.6 to 1.0 in various clupeoids.

Many years later, Ralston (1987) developed an M estimator based on K, specifically for snappers and groupers. Using prior data from 19 populations in an arithmetic mean regression, he found:

$$M = 0.0189 + 2.06\ K$$

$$M \approx 2\ K$$

Ralston (1987), however, preferred a geometric mean regression – correctly so as the prior values of M were estimated with considerable uncertainty. The estimator then became:

$$M = -0.0666 + 2.52\ K$$

$$M \approx 2.5\ K$$

Subsequently, Pauly & Binohlan (1996) offered an updated version of Ralston's (1987) estimator, based on data from 29 populations of snappers and groupers. The resulting "Ralston Method II", to use its authors' numbering, estimates M as:

$$M = -0.1778 + 3.1687\ K$$

Pauly & Binohlan's (1996) focus was on extolling the virtues of FishBase as a source of data for comparative studies of population dynamics and they did not discuss the development or properties of their version of the Ralston Method in any detail.

A particular weakness of each of these estimators, and of some to be discussed below, is that they rely on values of K, which itself often cannot be estimated with much precision. The problem arises because most fish age and length datasets contain data on many small fish (which serve to show that the growth curve passes near zero length at zero age) and on many medium-sized fish of moderate age but insufficient data on large, old fish to tie down the asymptotic size with much certainty. It becomes difficult to judge whether the medium-sized fish have grown swiftly towards a rather low $L_\infty$ or are only growing slowly towards a much larger one. It is then possible to estimate the ratio $K / L_\infty$ with confidence but not to generate precise estimates of either parameter alone. Confidence limits drawn around the two parameters together become "banana shaped" – stretched out along a hyperbola but quite narrow perpendicular to it.

The estimates in Table 1 illustrate the problem very clearly. Although the gag grouper of the Gulf of Mexico likely have dynamics little different from those in the South Atlantic Bight(and indeed a number of individuals pass between the two areas), the SEDAR 10 Data Workshop's estimates of von Bertalanffy parameters show higher $L_\infty$ and lower K in the Gulf of Mexico (131 cm, 0.14) than off the Atlantic coast (105.1 cm, 0.24). The Alverson & Carney, Zhang & Megrey and Rikhter & Efanov methods all use K in both a numerator and a divisor, which moderates the effects of those divergent estimates of the parameter. The Ralston Method, in contrast, does not. Its estimates of M for the South Atlantic thus become implausibly high. The estimates for the Gulf of Mexico can be no more certain, even though they appear more reasonable.

## *Jensen Method*

Jensen (1996) produced an estimator of M that is closely similar to Ralston's (1987), though founded on evolutionary theory rather than regression analysis. Jensen (1996) argued that the age of reproductive maturity in a fish was also approximately the age of the inflexion point in a von Bertalanffy curve of growth in weight and the age of maximum biomass of a year-class in the absence of fishing. The latter in particular is a questionable contention but, building on both assumptions, Jensen (1996) developed an argument that M is necessarily related to K by:

$$M = 1.5\ K$$

It is unclear whether that estimator is applicable to a protogynous hermaphrodite such as gag grouper. Some support for its more general application was generated by Jensen (1996) showing that the 175 prior studies amassed by Pauly (1980b) indicated a regression relationship:

$$M = 1.6\ K$$

This "Jensen Method" is as vulnerable to uncertainties in the estimate of K as are the various versions of the Ralston Method.

## *Pauly Method*

Further elaboration of the general approach was provided by Pauly (1978, 1980a, b), who produced an M estimator using multiple regression with the independent variables including not only K but also the asymptotic length and the water temperature inhabited by the fish – though he found that K had the greatest influence and $L_\infty$ the least. The effect of temperature was considerable even if secondary, Pauly (1980b) offering examples of two fish with the same growth curve, the one in cold-temperate waters having, by the estimators below, M = 0.32 while that in the tropics would have M = 0.68.

The first published version of the method (Pauly 1978, 1980a) was based on prior data on 122 populations and led to the estimators:

$$\log M = 0.1228 - 0.1912 \log L_\infty + 0.7485 \log K + 0.2391 \log \tau$$

$$M = 1.327\, L_\infty^{-0.1912}\, K^{0.7485}\, \tau^{0.2391}$$

$$\log M = 0.1091 - 0.1017 \log W_\infty + 0.5912 \log K + 0.3598 \log \tau$$

$$M = 1.286\, W_\infty^{-0.1017}\, K^{0.5912}\, \tau^{0.3598}$$

where $L_\infty$ is the asymptotic <u>total</u> length in centimetres, $W_\infty$ the asymptotic live weight in grams, and $\tau$ is the mean environmental temperature at the location of capture of the fish and in the depth range inhabited, in Celsius. Pauly (1980a,b) extracted mean annual sea-surface temperature data corresponding to prior studies of growth and mortality of pelagic species from oceanographic atlases and hence atlas data are the most appropriate to use in applying his estimator to such species, even when they are not the best available information on the temperatures actually encountered by the fish. For deeper-living demersal species, he relied on temperature estimates provided by an oceanographer. [Pauly (1980b) added an adjustment to $\tau$ when observed temperatures were below 4°C. That can be ignored here.]

The definitive versions of the estimator, presented by Pauly (1980b) were based on prior data from 175 populations and were:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log \tau$$

$$M = 0.9849\, L_\infty^{-0.279}\, K^{0.6543}\, \tau^{0.4634}$$

$$\log M = -0.2107 - 0.0824 \log W_\infty + 0.6757 \log K + 0.4627 \log \tau$$

$$M = 0.6156\, W_\infty^{-0.0824}\, K^{0.6757}\, \tau^{0.4627}$$

with the same parameter definitions as for the preliminary version. Pauly (1980b) also offered, "for practical purposes":

$$\log M \approx -0.28 \log L_\infty + 0.654 \log K + 0.463 \log \tau$$

$$M = L_\infty^{-0.28} K^{0.654} \tau^{0.463}$$

though that version does not seem to have seen much use in practice and is not further considered in this paper.

Those various estimators will here be termed the "Pauly Method" distinguished respectively as the "Pauly Method 0" and "Pauly Method I", the latter being the definitive form that has been widely used, particularly in the developing world, over the past three decades.

Later, Pauly & Binohlan (1996) offered a variant of the Method (which in deference to their numbering will here be called the "Pauly Method II") specific to snappers and groupers, based on data from the same 29 populations as they had used in developing the Ralston Method II (see above). They retained the same exponents as in the Pauly Method I and only adjusted the intercept, thus generating the estimator:

$$\log M = -0.0636 - 0.279 \log L_\infty + 0.6543 \log K + 0.4634 \log \tau$$

$$M = 0.8638\, L_\infty^{-0.279} K^{0.6543} \tau^{0.4634}$$

The Pauly Method II necessarily produces estimates of M that are 88% of those produced by the Pauly Method I. Whether that is a realistic adjustment to a genuine greater life expectancy among snappers and groupers than for fish in general, given similar growth curves and temperatures, is unclear. Considering the difficulties in generating any estimates of M, the common perception that groupers are "long lived" could easily have introduced a subconscious downward bias in the 29 prior estimates of M sufficient to scale the estimator down by 12%.

Based on high values of correlation coefficients (R = 0.8 for Pauly Model 0, R = 0.85 for Pauly Model I), Pauly (1980a) considered that his method would produce estimates that "should be very reliable". Those coefficients are, however, a poor indicator of predictive power in such regression estimators (Pascual & Iribarne 1993) and the Pauly Method should not be seen as more than indicative. The Method has also been questioned for its reliance on prior estimates of M that are themselves of dubious validity (a complaint that could equally be levelled at other regression estimators of mortality rates) and for ignoring differences among species with similar growth patterns inhabiting similar waters. One might suspect, for example, that epipelagic and reef-dwelling species would differ in mortality rates, as might live-bearers, spawners of bottom-attached eggs and species with planktonic eggs, even if growth rates and temperatures were identical.

No less seriously, the Pauly Method fails to escape from the effects of misestimating K that render the Ralston and Jensen methods so uncertain. Although the Pauly Method includes $L_\infty$ as an input, it is given a negative exponent such that the effect of a low estimate of asymptotic length is added to that of a correspondingly-high estimate of K, rather than the two errors compensating for one another. When applied to gag grouper in

Table 1, the various alternative forms of the Pauly Method do produce estimates of M for the Gulf of Mexico and the South Atlantic Bight that are less divergent than those generated by the Ralston or Jensen methods but apparently only because the use of a constant value for environmental temperature provides some stability.

## Peterson & Wroblewski Method

In parallel to fisheries scientists' recognition that M is correlated with growth patterns, marine ecologists have noted that mortality rates are inversely related to body size across a wide variety of pelagic animals. Peterson & Wroblewski (1984) may have been the first to quantify that relationship, working from the ecological theory of size spectra in pelagic systems and an assumption that all deaths in such systems are the result of predation. Their estimator:

$$M = 1.92\ W^{-0.25}$$

was for dry weights. Converting to the wet weights more familiar in fisheries assessments leads to:

$$M = 2.87\ W^{-0.25}$$

where W is the individual weight in grams.

Peterson & Wroblewski (1984) showed that the resulting estimates were consistent with prior values of M for a range of fish species, including some demersals. However, their equation returns mortality rates that seem rather too high for commercial-sized individuals, at least for those of bottom-oriented species like groupers: A 5 kg fish would have a natural mortality rate of 0.34, while M for a 10 kg fish would be 0.29. The problem may lie in the exponent, -0.25, which was selected on no better grounds than that it was an average of unpublished estimates of the upper and lower bounds of possible values: 0.1 and 0.4, respectively.

This "Peterson & Wroblewski Method" might be better regarded as a useful step in the development of ecological understanding than as a practical estimator of mortality rates to be used in fisheries assessments.

## Lorenzen Method

Gulland (1987) suggested that the appearance of a single relationship spanning many taxa from small zooplankton to whales, such as Peterson & Wroblewski's (1984), results from a false combination of data drawn from the different M-to-weight relationships of various groups, a suggestion supported by later analyses by McGurk (1987). Hence, a fish-specific relationship should yield more useful estimates of natural mortality rates. One such was later provided by Lorenzen (1996).

In the SEDAR 10 gag assessments, Lorenzen's (1996) work was only used to define the shape of the M-at-age curve, while the values of the natural mortality rate were scaled against a separate estimate of "overall" M. Lorenzen (1996), however, used a regression approach to develop not simply a shape of curve but an entire model of M:

$$M = 3.00\ W^{-0.288}$$

for weights in grams and for fish in natural (i.e.: non-aquaculture) systems. That equation returns more reasonable mortality rates for exploitable sizes of fish than does the Peterson & Wroblewski Method: 0.26 for a 5 kg fish and 0.21 for one of 10 kg, for example.

Lorenzen's (1996) parameter estimation used the Theil estimator, which avoided various limitations of the linear-regression methods applied by other authors, though it remained vulnerable to other weaknesses, such as the reliance on questionable prior estimates of M[5].

# Estimators Based on Evolutionary-Ecology Theory

Progressing beyond mere correlates, even if they can be expected to be related to M if the fitness of fish life histories are optimized, some authors have derived estimators of natural mortality rates based explicitly on aspects of evolutionary ecology.

## *Gunderson Method*

Gunderson (1980) reasoned, from r–K selection theory, that life expectancy should be related to the gonosomatic index and duly found that M was correlated to GSI in a small selection of fish populations, the regression equation being: $M = 4.64\ GSI - 0.37$. Gunderson & Dygert (1988) examined the relationship in more detail, using data from 20 populations, and derived the estimator:

$$M = 1.68\ GSI + 0.03$$

with GSI rigorously defined as gonad wet weight divided by somatic wet weight (gonads removed and stomach empty), calculated from gonads in the final stage of maturation but

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[5] It may be noted that whereas Lorenzen (1996) recommended an exponent of –0.29 (based on a non-parametric regression approach) to shape his eponymous curves for fish, Peterson & Wroblewski (1984) used –0.25, based on ecological theory and spanning all taxa. In other studies which stopped short of presenting mortality-rate estimators, Gulland (1987) suggested, following examination of data compiled by McGurk (1986), that the exponent might be as high as –0.5 for fish specifically. McGurk (1987) subsequently found exponents as low as –0.26 across taxa and as high as –0.40 for fish alone, depending on the type of regression used. Clearly, the pattern of change in M with size and age of the individual remains uncertain, though that issue is not considered in this paper.

before egg hydration, with the value adjusted to the mean length of fish in an unexploited population to allow for allometric development of gonad size. For batch spawners, further adjustment is needed to give an equivalent GSI supposing that the entire annual egg production were generated in a single spawning.

Gunderson & Dygert (1988) found that their estimator explained 81% of the variation in their data, while GSI had a closer linear fit to M than did other variables that they considered, including the age at which abundance dropped to 1% of that at the age of reproductive maturity. However, unless there were deficiencies in the data or else the exponential model of mortality is inappropriate for the species in question, a curvilinear relationship between M and the difference in ages across which abundance falls 99% must explain 100% of the variation.

Subsequently, Gunderson (1997) further extended the foundation of the method to include data on 28 populations. The estimator was revised to:

$$M = 1.64\ GSI + 0.041$$

or:

$$M = 1.871\ GSI + 0.005$$

using a GM regression. Gunderson (1997) showed that the relationship between M and GSI did not differ significantly between oviparous and viviparous fish species. The three estimators are here termed the “Gunderson Method I”, “Gunderson Method II” and “Gunderson Method III” respectively.

They are all of questionable practical utility, partly because GSI shows notable inter-annual variability (driven by feeding conditions), as Gunderson & Dygert (1988) acknowledged, but more because of the demands of selecting fish with gonads in the final stage of their maturation for determination of GSI. As with other spawning-related estimators, it is also questionable whether these methods are directly applicable to the protogynous groupers.

## *Myers & Doyle Method*

Myers & Doyle (1983) worked from an assumption that a fish’s life history strategy is evolutionarily stable, which required them to suppose that life-history data gathered from an exploited population was representative of the same species before it was fished, while the values of M generated were estimates of the mortality rate in a virgin population, rather than the non-fishing mortality in an exploited condition – which latter is the “natural mortality” of fisheries dynamics. The theoretical modelling led to an equation that is unstable with the post-maturational growth typical of fish, while Myers & Doyle (1983) could only suggest two constraints that would provide the required evolutionary stability: One was that the energy cost per egg spawned increases as more energy is devoted to reproduction, the other that the mortality associated with reproduction increases as a convex function of the proportion of energy devoted to reproduction. Based on the parameters of those constraints, it was possible to produce an estimator of M.

The "Myers & Doyle Method" required data on growth rates, fecundity-at-age, the energy content of eggs and the size and age at reproductive maturity, among others. It also required iterative solution of an equation that its authors did not clearly present. After examining its sensitivity to errors in various inputs and comparing estimates of M with prior values, Myers & Doyle (1983) concluded that their method was useful as a check on other approaches, which it may well be. However, whether because of the overt statement of assumptions that the authors of other estimators left implicit, the lingering suspicion that there may be quite other reasons for post-maturational growth in fishes, or simply because Myers & Doyle (1983) never offered their method in a practical form facilitating its use, this approach does not appear to have ever been used in support of stock assessments since its publication.

### *Roff Method*

Roff (1984) reasoned along similar lines to Alverson & Carney (1975), in a paper concerned with broader issues of fish life histories. He was led to two estimators of the natural mortality rate:

$$M \approx 3 / t_m$$

$$M = 3\,K\,L_\infty\,(1 - l_m/L_\infty) / l_m$$

where $t_m$ and $l_m$ are respectively the age and the length at reproductive maturity. As with the Gunderson Method, those estimators are of questionable validity for protogynous hermaphrodites, such as gag grouper.

## Estimator Based on Abundance Data

### *Somerton Ratio Method*

Zheng (2005), in a general review of methods for estimating natural mortality rates in data-limited situations, drew attention to an approach apparently first advanced by D.A. Somerton[6] and only occasionally used since. In a seasonally-restricted fishery with natural mortality operating throughout the year:

$$N_{t+1} = N_t\,e^{-M} - C_t\,e^{-yM} + R_t$$

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[6] Somerton, D.A. (1981) Life history nd population dynamics of two species of tanner crab, *Chionoecetes bairdi* and *C. opilio*, in the eastern Bering Sea with implications for the management of the commercial harvest. *Ph.D. dissertation, University of Washington, Seattle*: 220 p. [Cited by Zheng (2005)]

where $N_t$ is the number of individuals in the population at the start of year t, $C_t$ is the catch (in numbers) during that year, $R_t$ is the number of recruits in the same year and y is the period from the mid-point of the fishery to the end of the year. Given annual abundance surveys outside the fishing season, a year defined as starting at the time of the surveys and deleting the recruiting year-class from the estimate of $N_{t=1}$ leads to an estimator:

$$M = -\ln[N_{t+1} / (N_t - C_t e^{-y})]$$

While that may be useful under special circumstances, it does require annual surveys that generate high-precision estimates of absolute abundance, as well as reliable catch data. As stated, it is also applicable only to fisheries with restricted seasons, though it could be generalized to other temporal distributions of fishing and natural mortalities.

Lacking suitable abundance surveys, the method cannot be applied to gag grouper.

## Discussion

Examination of the published methods for estimating M and Z in data-limited situations has shown that many are methodologically invalid, either for all fish or for protogynous hermaphrodites, such as gag grouper. Of the eight methods that merit some closer attention, six are dependent on prior estimates of K and are badly affected by the anomalously-high estimate of that parameter for the South Atlantic Bight gag management unit, producing values that are not credible (Table 1). The remaining ten estimates of gag mortality rates cover a range from 0.19 to 0.34, the latter being an estimate of Z, rather than M. Hence, the full suite of available methods is consistent with the conclusion presented above, and built on examination of numerical simulations, that gag M is probably in the range 0.2 to 0.3. There does not seem to be any compelling evidence that would narrow the range: Methods as similar as Jensen and Ralston suggest values of 0.21 and 0.29, respectively. The long-established Pauly Method suggests that M is in the middle or upper portion of the range but the compelling idea of linking M-at-age to body weight leads to a Lorenzen Method estimate that “overall” M should be around 0.20.

This degree of uncertainty is not unexpected. Pascual & Iribarne (1993) explored the limited predictive power of some of these same methods and warned that the resulting uncertainties were sufficient, and the effects of errors in M so serious, that there was a “high risk of completely misjudging the dynamics of the stock under study”. They recommended that scientific advice to fisheries managers should reflect the uncertainty. Zhang & Megrey (2006) likewise, though more specifically, called for stock assessments to use alternative values of M, spanning the plausible range, rather than a single value. In the absence of any credible method for estimating M with useful precision, that seems the only viable option. Such uncertain advice should, of course, be accompanied by an explanation for management decision-makers of the risks of alternative responses to the uncertainty.

The SEDAR 10 reports are silent as to the reasons for choosing to use a data-limited approach to the estimation of M. With some 20,000 aged fish and extensive length-frequency information, it would appear that some of the data-intensive approaches might reduce uncertainty concerning this key input to the assessment. In the longer term, it would be well to investigate such alternatives.

More immediately, it is clear (from examination of numerical simulations, if nothing else) that the value used for "overall" M in the SEDAR 10 assessment, 0.15, is far too low. It was derived using the Hoenig First Method, which fails to allow for the size of the ageing sample and produces grossly-erroneous estimates (of Z, not M) when used with the maximum observed age in a large sample. Hence the estimate lacks any credible foundation, as well as being itself implausible.

The very low value of M = 0.15 may have seriously distorted the assessment. It would therefore be well to re-run the calculations, while following Zhang & Megrey's (2006) recommendation of using alternative values of M spanning the plausible range. Advice based on parallel calculations using M = 0.20, 0.25 and 0.30 would, collectively, provide management decision-makers with a better understanding both of the state of the resource and of current scientific uncertainty concerning that state.

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**Table 1 : Estimates of Z or M Derived Using Various Estimators**
Estimates are rounded to 2 decimal places.

Table entries for estimation methods that are deemed invalid (either for fish generally or specifically for protogynous hermaphrodites) are shown in normal type. Entries in bold face are for estimators deemed to be methodologically valid, even if highly imprecise. Some estimates of gag grouper M shown in bold face fall outside the plausible range.

| Estimator | Gulf of Mexico | Combined | South Atlantic |
|---|---|---|---|
| Bayliff Method | 0.21 | 0.21 | 0.21 |
| Hoenig First Method | 0.13 | 0.13 | 0.14 |
| Hoenig First Method: Approximation | 0.14 | 0.14 | 0.14 |
| Hoenig First Method: GM regression | 0.16 | 0.16 | 0.16 |
| Sekharan Method | 0.15 | 0.15 | 0.15 |
| “Rule-of-Thumb”, with P = 0.05 | 0.10 | 0.10 | 0.10 |
| Alverson & Carney Method | 0.10 |  | 0.05 |
| Zhang & Megrey Method | 0.07 |  | 0.03 |
| Hoenig Second Method | 0.37 | 0.38 | 0.35 |
| Holt Method | 0.37 | 0.38 | 0.34 |
| **Corrected Hoenig Second Method** | **0.33** | **0.34** | **0.29** |
| Rikhter & Efanov First Method | 0.55 |  | 0.54 |
| Rikhter & Efanov Second Method | 0.59 |  | 0.69 |
| Alagaraja Method | 0.08 |  | 0.14 |
| Ralston Method I: AM regression | 0.31 |  | 0.51 |
| **Ralston Method I: GM regression** | **0.29** |  | **0.54** |
| **Ralston Method II** | **0.27** |  | **0.58** |

| | | | |
|---|---|---|---|
| **Jensen Method** | **0.21** | | **0.36** |
| **Pauly Method 0: Length-based** | **0.25** | | **0.38** |
| **Pauly Method I: Length-based** | **0.28** | | **0.42** |
| **Pauly Method II: Length-based** | **0.25** | | **0.37** |
| Peterson & Wroblewski Method | 0.27 | | 0.28 |
| **Lorenzen Method** | **0.19** | | **0.21** |

The estimates presented in the table were prepared using the estimators described in the main text and the parameter values in Table 2, all of which were drawn from the report of the SEDAR 10 Data Workshop, except for the mean environmental temperature. That was estimated as 20°C for purposes of illustration.

The values of M presented for the Peterson & Wroblewski and Lorenzen methods are averages of the M-at-age for Ages 3 through 30 inclusive. All other tabulated values are for "overall" mortality rates.

**Table 2 : Parameter Values Used in Estimating Mortality Rates**

Values drawn from report of the SEDAR 10 Data Workshop

| ***Parameter*** | **Gulf of Mexico** | **Combined** | **South Atlantic** |
|---|---|---|---|
| Maximum observed age (years) | 31 | 31 | 30 |
| $t_c$ | 3 | 3 | 3 |
| $t_m$ | 3.7 | | 3.0 |
| N in ageing sample | 16,000 | 22,000 | 6,000 |
| $L_\infty$ (Total Length, cm) | 131 | | 105 |
| K | 0.14 | | 0.24 |
| $t_0$ | –0.37 | | –0.48 |
| Exponent of weight allometry | 3.03 | | 2.94 |
| $\beta$ (Total Length in mm, Wet Weight in g) | 1.0 x $10^{-5}$ | | 1.8 x $10^{-5}$ |
| Mean environmental temperature (Celsius) | 20 | 20 | 20 |