



Natural mortality estimators for information-limited fisheries

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Abstract

The 29 estimators of natural mortality (M) that have been proposed for 'information-limited' fisheries are reviewed, together with a new alternative presented here. Each is applied to 13 example populations for which well-founded estimates are available of both M and the estimators' parameters. None of the 30 can provide accurate estimates for every species, and none appears sufficiently precise for use in analytical stock assessments, while several perform so poorly as to have no practical utility. If the growth coefficient K has been reliably estimated, either $M = 1.5 K$ or Pauly's long-established estimator can provide useful estimates of M , but they fail with species that have long adult lives after swift juvenile growth, with those that never reach their asymptotic lengths and with species that otherwise deviate from archetypal teleost life histories. If a pre-exploitation maximum observed age (T_{\max}) can be established, M can be estimated for both teleosts and sharks using $M = 4.3/T_{\max}$ but that seriously underestimates when the effective sample size (n_e) is large and overestimates with species showing pronounced senescence. The new estimator presented here addresses n_e but is upset by even mild senescence. Some estimators of M -at-size, particularly ones recently advanced by Gislason *et al.* and Charnov *et al.*, also show promise but require further examination. It is recommended that fisheries scientists measure M by more advanced methods whenever possible. If 'information-limited' estimators must be used, their uncertainties should be acknowledged and their errors propagated into management advice.

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Introduction

One of the most important parameters in fisheries dynamics is the natural mortality rate, M , which is best defined by:

$$N_{t+1,j+1} = N_{t,j} e^{-Z} = N_{t,j} e^{-(F+M)}$$

where $N_{t,j}$ is the number of individuals in year class j of the population at time t , Z (the total mortality rate) is a measure of the overall death rate and F (the fishing mortality rate) is that portion of Z which varies proportionately to fishing effort. For the purposes of fisheries assessment and management, the time step is conventionally taken as 1 year. Thus defined, M is only equal to the death rate in the absence of fishing if fishery-induced population depletion does not alter the non-fishing mortality rate and if there are only negligible non-fishing anthropogenic deaths. Within a population, M is strongly age- and size-related, can be highly variable over time and may differ markedly between subpopulations. It is nevertheless common in stock assessments for M to

be assumed invariant across exploited age-classes, because deriving a single estimate with useful precision is challenging enough, without attempting to develop year- or age-specific values.

Fisheries conservation management seeks a balance between harvests and the productivity of the resource – the latter (in a stable, unexploited condition) equalling M . Stock-assessment outputs often show optimal F approximating to input M . Meanwhile, current F is commonly estimated by deducting M from an empirically based value for Z . It follows that the perceived status of the fishery, along with the scientific advice to fishery managers, is highly dependent on the chosen value of M .

Unfortunately, M is exceptionally difficult to estimate with useful accuracy. The classic approach requires multiple Z values from catch curves, one from each of several periods of stable but differing F . Regressing Z against fishing effort and extrapolating to $F = 0$ provides M (Ricker 1975), though a single-catch curve is sufficient in the special case of an unexploited resource. The requirement for

an extensive ageing programme can be evaded using Beverton and Holt's (1956) equation for length-based estimates of Z or one of its later derivatives, while Csirke and Caddy (1983) offered an alternative avoiding the need for an index of effort proportional to F by substituting the assumptions of the Graham-Schaeffer logistic production model. The prolonged collection of representative samples of the resource remains necessary.

Mark and recapture experiments provide a different approach to M estimation (e.g. Quinn and Deriso 1999), though developing reliable results places extreme demands on a tagging programme. Following individuals through telemetry can be effective in some cases. Alternatively, given comprehensive catch data and high-precision resource surveys, F can sometimes be estimated as the ratio of catch to fishable biomass, allowing M to be found from any estimate of Z . Few surveys are adequate for that approach but it has potential in particular cases (e.g. Xu *et al.* 1995). When adequate data are available, M can alternatively be estimated from the gonosomatic index, though that must be determined from fish with gonads in the final stage of their maturation, collected across multiple years and with complex corrections in cases of either allometric growth, batch spawning or both (Gunderson 1980, 1997; Gunderson and Dygert 1988). For some resources in the well-studied north-east Atlantic and its marginal seas, M is routinely estimated through multispecies VPA (Magnússon 1995; Anon 2007). In other assessment models, it is sometimes possible to treat M as a parameter to be estimated, rather than an input to be determined *a priori* (e.g. Maunder and Wong 2011). For data-rich fisheries, that may prove the best approach of all but the breadth of its applicability remains controversial (Lee *et al.* 2011, 2012; Francis 2012). Finally, unusual approaches to M estimation are available for some particular resources, such as the sea scallop (*Placopecten magellanicus*: Pectinidae: Dickie 1955; Merrill and Posgay 1964).

All of those estimation approaches are data-intensive. Most require advanced scientific capabilities, with supporting infrastructure and budgets. Worse, if M is to be estimated with useful accuracy, they all require extensive prior knowledge of resource biology. It is impossible, for example, to design a protocol for unbiased sampling across ages without first mapping the migrations of the

fish. Hence, the above methods are simply unavailable to most of the world's fisheries, especially with newly emerging harvesting of virgin resources or many fisheries under the jurisdiction of fishery-dependent nations, most of which are small island states that generally lack the required capacities.

Many authors, from Beverton (1963) onwards, have therefore sought simpler, less onerous and more pragmatic, though necessarily less reliable, estimators of M , using various combinations of point estimates of age, growth parameters, life-history theory and regressions of M in well-studied populations against measurable indices. There is no accepted label for such estimators. Some have been termed 'indirect' methods (e.g. Hewitt *et al.* 2007), but there are few approaches to M more direct than uniting the exponential mortality model with an estimate of the maximum age in an unexploited population. Cubillos *et al.* (1999) preferred the term 'empirical methods', yet some pragmatic estimators are based solely on life-history theory with no appeal to empiricism. Brodziak *et al.* (2011) grouped the simple methods within their 'Tier 1' but also included there mere 'traditionally accepted values', which need have no foundation in science. I will therefore divide the universe of approaches for estimating M into the onerous, information-intensive ones available to few fisheries and the pragmatic alternatives suited to information-limited situations.

When proper estimation of a parameter is challenging, it would be naïve to expect that a simple approach could yield precise results. Yet the ease of use of some M estimators intended for information-limited fisheries has encouraged uncritical acceptance of their numerical outputs, with damaging consequences if M of an overfished resource is overestimated or that in a well-managed fishery is underestimated. Such misuse has not been confined to the developing world but is increasingly seen in the assessment of fisheries in the most advanced nations, such as estimates of M for several dozen resources in the Pacific waters of the U.S.A. (Gunderson *et al.* 2003; Dick and MacCall 2010). Estimators built on regressions of teleost data have been applied not only to sharks, including for no better reason than widespread prior use (Simpfendorfer 1999a,b), but also to shellfish (e.g. Groeneveld 2000; Hewitt *et al.* 2007).

Unfortunately, while some individual applications of each 'information-limited' M estimator

can chance to return accurate estimates, if only through fortuitous cancellation of errors, the overall performance of most is so poor that it is remarkable that they have been given any credence at all. Yet, few of the original authors who offered an estimator tested their proposed method against empirical data. Those who developed regression-based approaches did not use a jack-knife approach. There have been subsequent empirical trials of some estimators, though mostly with reference to particular resources, not leading to general conclusions. Hence, I here offer the first review of all known M estimators suited to information-limited fisheries. I then illustrate their performance by applying them to thirteen example resource populations, for each of which M is known with reasonable confidence. From the results of those limited trials, I provide recommendations for application of the estimators.

Estimators of M for information-limited fisheries

Thirty different estimators are recognized here, some in two or more variants. For convenience of presentation, they are grouped into four loose

families, though, other classifications could be equally appropriate. Each estimator has its own set of weaknesses or challenges to be faced in its application, some of which are common to multiple estimators. To minimize repetition, those are explained in the text under only the first estimator to which they apply. Figure 1 offers a summary of the limitations and hence a reference to where each is discussed. Throughout, I use an internally consistent symbology (Table 1), which has required some modification of equations from those in original publications.

Estimators based on maximum observed ages

As numbers-at-age are directly influenced by Z , that rate must control longevity (cf. Beverton and Holt 1959), suggesting that it can be estimated from maximum observed ages. The approach has been explored by multiple authors, although it is not as useful as it may at first appear. For one thing, T_{\max} can only be used to estimate Z , not M . One important class of information-limited fisheries comprises those for newly exploited resources, such that $Z \approx M$. For other fisheries, care is needed over what is being estimated.

Estimator:	Bayliff's	Hoening's	Sekharan's	Tanaka's	Kenchington's	Alverson & Carney's	Zhang & Megrey's	Rikhter & Efanov's First	Rikhter & Efanov's Second	Roff's First	Chen & Watanabe's	Charnov & Berrigan's	Jensen's First	Alagaraja's	Ralston's	Pauly's	Djabali's	Jensen's Third	Griffiths & Harrod's	Frisk's	Gislason's First and Second	Cubillos'	Jensen's Second	Peterson & Wroblewski's	Lorenzen's	Ursin's	Jennings & Dulvy's	Roff's Second	Groeneveld's
Dependent on regression																													
Estimates Z over years																													
Dependent on single maximal age																													
Affected by senescence																													
Requires validated ageing protocol																													
Ignores sample size																													
Requires extreme assumptions																													
Requires estimate of effective n																													
Requires data from unexploited era																													
Dependent on estimate of K																													
Requires other growth parameters																													
Requires validated age at maturity																													
Requires length at maturity																													
Requires temperature value																													

Figure 1 Summary of some limitations of, and challenges confronting application of, the M estimators. The fourteen limitations and challenges are explained in the text, primarily under the first of the estimators concerned. Shading indicates that a named estimator is affected by the specified issue.

Table 1 Standard symbols used in this review.

α	Parameter of the length/weight relationship
β	Exponent of the length/weight relationship
τ	Mean environmental temperature
F	Fishing mortality rate
K	Parameter of von Bertalanffy growth curve
L_{∞}	Asymptotic fish length
l	Individual fish length
l_m	Length at reproductive maturity
M	Natural mortality rate
M_l	Natural mortality rate at length l
M_t	Natural mortality rate at age t
M_w	Natural mortality rate at weight w
N_i	Number of individuals in a population at time i or age i
$N_{i,j}$	Number of individuals in a year-class j at time i
N_0	Number of individuals in a year class at age zero
n	Number of individuals in a sample
n_e	Effective sample size, as defined for use in Kenchington's Estimator
P	Proportion of fish in a population surviving to age T_{\max}
T_{\max}	Maximum observed or assumed age
T_{∞}	Age at which fish are expected to reach a length of $L_{\infty} - 5$ mm
$T_{95\%}$	Age at which fish are expected to reach a length of $0.95 L_{\infty}$
t_a	Average female adult lifespan
t_c	Youngest age fully represented in the catch or, in Kenchington's Estimator, the minimum fish age considered in n_e
t_m	Age at reproductive maturity
t_{mb}	Age at which year-class achieves its maximum biomass in the absence of fishing
t_s	Age at onset of senescence
t_0	Parameter of the von Bertalanffy growth curve
W_{∞}	Asymptotic fish weight
w	Fish weight
Z	Total mortality rate

Bayliff's and Hoenig's Estimators

Beverton (1963) noted a linear relationship between Z and the inverse of T_{\max} , with slopes of 4.3 to 10.4 for various clupeids, and Bayliff (1967) used such a relationship to estimate mortality rates – an idea anticipated by Tauchi (1956) and Tanaka (1960) writing in Japanese. They all, however, ignored the causative linkage between Z and T_{\max} , opting instead for regression-based estimators. Bayliff's (1967) was specifically for the Engraulidae and founded on only six prior data points:

$$Z = 6.384/T_{\max}$$

That is here termed 'Bayliff's Estimator', although its author only used it as a last resort when other approaches were unavailable. Ohsumi (1979) later developed a similar estimator for cetaceans, as well as one based on adult length. As those were never

intended for use with fish, they are not considered further here.

The approach was taken up by Hoenig (1982, 1983), who offered four variants of an estimator, based on prior data drawn from studies of, respectively, 84 fish populations (80 of them teleosts), 28 molluscs (primarily bivalves), 22 cetaceans and the combined set. Other than their broader foundation, Hoenig's (1983) regressions differed from Bayliff's (1967) in adding an additional parameter, viz.:

$$Z = 4.31T_{\max}^{-1.01} \approx 4.3/T_{\max} \text{ for fish}$$

$$Z = 3.42T_{\max}^{-0.832} \text{ for molluscs}$$

$$Z = 2.56T_{\max}^{-0.873} \text{ for cetaceans, and}$$

$$Z = 4.22T_{\max}^{-0.982} \approx 4.2/T_{\max} \text{ for all three taxa combined.}$$

As both Z and T_{\max} were observed with great uncertainty, however, Hoenig's (1983) analysis might better have used a geometric mean regression. He considered that in an addendum, changing the four expressions to:

$$Z = 6.99T_{\max}^{-1.22} \text{ for fish,}$$

$$Z = 4.49T_{\max}^{-0.94} \text{ for molluscs}$$

$$Z = 5.20T_{\max}^{-1.04} \text{ for cetaceans, and}$$

$$Z = 5.52T_{\max}^{-1.08} \text{ for the combined data set.}$$

The eight are here collectively termed 'Hoenig's Estimator'.

Although these estimators have been widely used, they are burdened with several challenges. Most obviously, as regression-based estimators, they cannot be any more accurate than the prior values of Z and T_{\max} used in deriving the expressions, some of which were very doubtful. Next, both estimators rely on maximal observed ages, which are often difficult to determine accurately and usually require a validated ageing protocol. They are liable to yield wildly erroneous values for Z if an unvalidated ring count is substituted for a known age (cf. Beamish and McFarlane 1983). Further, the focus on a single old fish, ignoring all other observed ages, introduces both extreme sampling error and instability. Thirty years after a strong year class was spawned, it is more likely that observed T_{\max} would be 30 than 29. The

following year, T_{\max} would likely be 31. More subtly, mortality models in stock assessments need only represent deaths among the abundant age-classes in an exploited population. Should the species show marked senescence at higher ages, T_{\max} would be reduced relative to expectations from the exponential model, increasing estimated Z . Meanwhile, gear selection and fishery targeting can bias observed T_{\max} in either direction. The estimators incorporate these complications to the extent that they affected the populations represented by the prior data used in the regressions, but they are apt to severe errors if applied to resources that are differently affected.

When Hewitt and Hoenig (2005) renewed attention to the latter's Estimator, they treated its output as M , an interpretation that Hewitt *et al.* (2007) sought to justify on the grounds that the data used in Hoenig's (1983) regressions came from lightly exploited populations. Those regressions, however, merely scaled the effects of the exponential mortality model relative to observed T_{\max} . The Estimator's output depends on the input T_{\max} , which varies with Z , not M . Indeed, with non-zero and temporally variable F , the output Z is an amalgam of annual Z s over the lifespan of the oldest individual observed – not necessarily a useful quantity for stock-assessment purposes.

Finally, these estimators will yield biased estimates unless the size of the sample from which T_{\max} was drawn approximates those in the prior studies underlying the regressions – meaning a few hundred individuals for Hoenig's Estimator. As Hoenig (1983) recognized, because the oldest age classes are necessarily scarce, larger samples tend to contain single individuals with higher ages, depressing estimated Z . Hoenig (1983) claimed that the consequences are limited if n exceeds about 200 but that is only true of linear increases in n , not of geometric ones. Although Hoenig (1983) claimed that his Estimator can be applied when only the ages of a few of the largest (and hence oldest) individuals are known, the relevant n is the number of individuals from which the largest were selected for ageing. In many fisheries that can total tens of thousands, sufficient for Z to be severely underestimated by Hoenig's Estimator.

Sekharan's and Tanaka's Estimators

Many smaller tropical species have short and perhaps determinate lifespans. The exponential mortality model is poorly suited to such species,

but it is often applied nonetheless. For two such populations, Sekharan (1975) assumed that, in the absence of exploitation, 1% of individuals would reach the known T_{\max} . Hence:

$$\begin{aligned} N_{T_{\max}}/N_0 &= 1/100 = e^{-T_{\max}M} \\ M &\approx 4.6/T_{\max} \end{aligned}$$

That relationship, which has subsequently been independently developed for multiple stock assessments, was formalized by Alagaraja (1984). It has sometimes been identified with his name but is here termed 'Sekharan's Estimator'. It has seen widespread use, particularly in assessing fisheries in the developing world. Although their derivations were very different, for unexploited resources it returns results just 7% higher than those of Hoenig's Estimator – the numerical similarity linked to the latter's expectation of a sample size corresponding to about 1% survival to observed T_{\max} .

Variants of Sekharan's Estimator have emerged using assumptions about other proportions surviving to maximum age. Hence:

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

where P is the proportion surviving to T_{\max} , has appeared in standard textbooks (e.g. Quinn and Deriso 1999; Cadima 2003). It is sometimes credited to Tanaka (1960) and is here given his name, though others have called it the 'Rule of Thumb' (e.g. Hewitt and Hoenig 2005). It has been applied, most often with $P = 0.05$, not only in information-poor situations but even for comparatively data-rich fisheries (e.g. Hewitt and Hoenig 2005; McGovern *et al.* 2005).

If these estimators are used with an observed T_{\max} , rather than one drawn from the known biology of the species, the output will only be M if the observations were made on an unexploited population. Otherwise, they yield the same form of Z as do the previous estimators.

Sekharan's and Tanaka's estimators escape the reliance on regressions which weakens Bayliff's and Hoenig's but they do so by relying on a purely arbitrary (and generally untenable) assumption of the proportion of individuals surviving to T_{\max} . In all other respects, the weaknesses of these first four estimators are identical.

Kenchington's Estimator

Holt (1965) and Hoenig (1983) both considered sample size in relation to T_{\max} , though neither

proceeded as far as a Z estimator. The former derived an expression for the expected maximum observed age in a population, based only on assumptions of the exponential mortality model and a stable age distribution, viz.:

$$T_{\max} = \frac{\ln n + 0.577}{Z} + t_c$$

In that, Holt (1965) took n to be the annual number of recruits, not the number of individuals in an ageing sample. Hoenig (1983) developed a similar expression that, as noted above, he used to examine the effects of n on observed T_{\max} . He started from Johnson and Kotz's (1970) expression for the expected maximum age in a sample under a stable age distribution:

$$T_{\max} = \frac{1}{Z} \sum_{i=1}^n \frac{1}{i} + t_c$$

which Hoenig (1983) approximated as:

$$T_{\max} \approx \frac{\ln(2n + 1)}{Z} + t_c$$

That returns the same values as Holt's (1965) expression when sample sizes are large but slightly overestimates when they are small. Johnson and Kotz's (1970) concern, however, was not with a representative sample of a population, as implied by Hoenig (1983), but with a sample of lives – a focus of life tables. Thus, both Holt's (1965) and Hoenig's (1983) expressions use an n which is unknowable when estimating Z .

To correctly allow for sample size in such estimation would likely require modelling based on statistical Extreme Value Theory, while allowing for the typically large and skewed variability of year-class strengths. No such sophisticated estimator has yet been attempted and the effort would hardly be justified, when the many uncertainties would reduce its outputs to mere crude first estimates. A simple approximation can, however, be advanced, as much to illustrate the challenges facing estimation of Z from T_{\max} as for practical application.

Given constant mortality, Z , in a population with constant recruitment, N_{t_c} at some age of recruitment, t_c , the abundances-at-age in the population, at ages greater than t_c , can be represented by the conventional:

$$N_t = N_{t_c} e^{-Z(t-t_c)}$$

If a sample could be withdrawn from that population without sampling error, it would have the

same relative abundances-at-age as the population, though N_{t_c} would be proportionately smaller. Within such a sample, the expected value of T_{\max} can be approximated as the age at which $N_t = 0.5$, as about half of all trials should return higher values and half lower. The definite integral from zero to infinity with respect to time of:

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

is simply N_0/Z . Hence, the size of the sample, between ages t_c and the expected value of T_{\max} can be approximated as:

$$n = \frac{N_{t_c}}{Z} - \frac{N_{T_{\max}}}{Z} = \frac{N_{t_c} - 0.5}{Z}$$

$$N_{t_c} = Zn + 0.5$$

In practice, samples are almost always taken using gears that are, to some degree, size- and age-selective, while the least age in a sample, t_c , may be low enough that the requirement for constancy of Z across ages is seriously violated. Hence, it is convenient to replace n , the actual sample size, with an 'effective sample size', n_e , that is the size a sample would have had to be to match the observed T_{\max} while conforming to the assumptions of constant Z and N_{t_c} at some chosen t_c .

Substituting into the exponential mortality model then gives:

$$\frac{0.5}{(Zn_e + 0.5)} = \frac{1}{(2Zn_e + 1)} = e^{-Z(T_{\max} - t_c)}$$

$$\frac{-\ln(2Zn_e + 1)}{-Z} = T_{\max} - t_c$$

$$T_{\max} = \frac{\ln(2Zn_e + 1)}{Z} + t_c$$

which assumes both sampling throughout the year and age treated as a continuous variable. If the sampling is conducted over a short season and age is recorded as an integer, the expression becomes:

$$T_{\max} = \frac{\ln\{2n_e(1 - e^{-Z}) + 1\}}{Z} + t_c$$

with a pocket calculator, either variant can readily be solved iteratively for any given values of n_e , T_{\max} and t_c to generate an estimate of Z . With high T_{\max} , both expressions yield essentially the same values but they can differ markedly when applied to short-lived species.

Those expressions, which may be termed ‘Kenchington’s Estimator’ for present purposes, constitute the only Z estimator based on T_{\max} yet suggested that accounts for sample size. However, while it avoids one deficiency of the previous estimators, this one does not escape the need for a validated ageing protocol, the dangers of relying on a single observation of T_{\max} nor the potential for errors caused by senescence, while it returns estimates of the same multiyear Z as do the other methods, rather than the desired M . Beside those challenges, the biases arising from its simplified derivation may be inconsequential but they should not be forgotten.

Moreover, to allow for sample size, Kenchington’s Estimator requires an estimate of n_e . It is not necessary to gather a random sample of individuals older than t_c , still less to age all those fish, but application of the Estimator requires *a posteriori* determination of an effective sample size. Choice of an appropriate value can only be situation-specific, but it could involve some adjustment of the actual sample size by the fraction of the oldest fish that were aged, as any subsampling for ageing might mean that the observed T_{\max} amongst the aged individuals was not the highest age in an overall sample. More often, sample size should be adjusted by applying the inverse of the age-selectivity of the sampling protocol, including the effects of both gear selectivity and the distribution of sampling across any differential distributions of fish age-classes, to the age composition of the sample. In practice, it may be necessary to make that adjustment by size-class rather than by ages or to forego it simply for lack of information on the applicable selectivities, accepting the inevitable increase in uncertainty surrounding the estimate of Z .

Including the t_c parameter in the Estimator means that early juveniles, with their high abundances and high mortality rates, can be ignored when determining n_e , simplifying that process. The value chosen for t_c is less critical than the adjustment of n_e to match both that value and the assumed constancy of Z -at-age. Indeed, it will sometimes be most convenient to set $t_c = 0$ and estimate n_e by projecting an initial estimate of Z backwards to zero age.

Clearly, it will rarely be possible to estimate n_e for an information-limited resource with even moderate precision but ranges of plausible values could be determined, given knowledge of the

distribution of sampling across the population, of selection by the sampling gear and of protocols used to pick old individuals for ageing. Thus, while Kenchington’s Estimator must be more demanding to apply than others, it would commonly yield only unsatisfactory estimates of Z . The alternatives cannot, however, evade the complications surrounding n_e . Rather, they substitute unjustifiable and often implicit assumptions for the overt examination of the sampling that is demanded by Kenchington’s. No T_{\max} -based estimates of M should be given much credence but the deficiencies of this last one are perhaps more obvious than those of others.

Other age-based estimators

A variety of other estimators have been suggested which are based on age information but not directly on T_{\max} .

Alverson & Carney’s and Zhang & Megrey’s Estimators

Starting from assumptions that growth is isometric and follows a von Bertalanffy curve, with $t_0 = 0$, while natural mortality follows the exponential model, Alverson and Carney (1975) showed that:

$$t_{mb} = \frac{1}{K} \ln \left[\frac{M + 3K}{M} \right]$$

Although their paper was broader, they used that relationship to estimate M , having previously 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:

$$M = \frac{3K}{e^{K \cdot 0.38 T_{\max}} - 1}$$

That has been termed the ‘Alverson and Carney Method’ (Zhang and Megrey 2006) and is credited to those authors here.

Their estimator generates values of M , not Z , but requires an estimate of T_{\max} in the unfished condition. Otherwise, it has the same deficiencies as Bayliff’s and Hoenig’s, the correct scaling of observed 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 prior studies used by Alverson and Carney (1975).

The assumption of von Bertalanffy growth is an unnecessary constraint, while the use of the K parameter introduces a further difficulty: most fish length-at-age data sets drawn from exploited populations contain insufficient data on large, old fish to provide confident estimates of asymptotic size. Such data sets allow reasonably precise estimation of the product of K and L_∞ but not of the value of either parameter alone.

Zhang and Megrey (2006) revisited Alverson and Carney's Estimator, exploring the consequences of relaxing the assumptions of isometric growth and $t_0 = 0$, while re-examining the constant 0.38. They presented a generalized version:

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

which is here termed 'Zhang and Megrey's Estimator'. They further suggested $t_{mb} = 0.440 T_{\max}$ for demersal fish and $t_{mb} = 0.302 T_{\max}$ for pelagics, based on data from 91 fish species, which also supported a constant of 0.393 [close to Alverson and Carney's (1975) 0.38] when pelagics and demersals were combined.

Zhang and Megrey (2006) proceeded to evaluate both their and Alverson and Carney's estimators against the 91 species used in their regressions. The two methods differed little across realistic ranges of β and t_0 , although altering the relationship between t_{mb} and T_{\max} necessarily changed the estimated M . It remains unclear whether Zhang and Megrey's Estimator offers any appreciable advance over Alverson and Carney's. It certainly fails to address the major deficiencies in the older alternative.

Rikhter and Efanov's First and Second Estimators

At much the same time as Alverson and Carney (1975), Rikhter and Efanov (1976) noted the same basic relationships, including the form later developed by Zhang and Megrey (2006) for species with allometric growth. They, however, suggested that t_{mb} could be approximated as the age at 50% maturity, rather than using some proportion of T_{\max} , which implies:

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

Alternatively, and based on a regression using prior data on only 14 fish populations, they derived:

$$M = \frac{1.521}{t_m^{0.720}} - 0.155$$

Those expressions are here termed 'Rikhter and Efanov's First' and 'Second' estimators, respectively.

The resulting estimates are independent of the size of the ageing sample and are of M , not Z . They do, however, require information on maturation as well as age – and in the case of Rikhter and Efanov's First Estimator also the parameters of a growth curve and a length/weight relationship. Their Second Estimator is additionally vulnerable to the deficiencies of regression-based approaches.

Roff's First Estimator

Roff (1984) reasoned along similar lines to Alverson and Carney (1975) and Rikhter and Efanov (1976), in a paper concerned with broader issues of fish life histories. He was led to an expression for an upper bound to M :

$$M \leq \frac{3 K e^{-K t_m}}{1 - e^{-K t_m}}$$

$$M \leq \frac{3 K}{e^{K t_m} - 1}$$

which is here termed 'Roff's First Estimator'. When $K t_m$ is small, it reduces to:

$$M \approx 3/t_m$$

Roff (1984) cautioned that small errors in t_m could have large effects on estimates of M for early-maturing species but he nevertheless presented this relationship as an estimator for practical application.

Chen and Watanabe's Estimator

Chen and Watanabe (1989) independently developed an estimator for age-specific M that has some similarity to Rikhter and Efanov's First. They sought a model that, in addition to the expected high mortality early in life, would also show senescence at high ages. They did not, however build their model on either theory or empirical observation but merely assumed that M_t is inversely proportional to a 'growth measure', with the constant of proportionality being K . Hence:

$$M_t = \frac{K}{1 - e^{-K(t-t_0)}}, \quad t \leq t_s$$

$$M_t = K / \left[1 - e^{-K(t_s - t_0)} \left[1 - K(t - t_s) + 0.5K^2(t - t_s)^2 \right] \right],$$

$$t \geq t_s$$

where t_s , the age at which senescence commences, is:

$$t_s = -\frac{1}{K} \ln |1 - e^{K t_0}| + t_0$$

This complex ‘Chen and Watanabe’s Estimator’ has seen little practical application. Its value of t_s is very sensitive to the input value of t_0 , a mere correction factor that adapts the von Bertalanffy curve to the realities of juvenile fish growth, and is undefined when t_0 is set at zero. Small values of t_0 produce estimates of t_s that can exceed T_{\max} . The estimator of M_t then generates a curve showing high juvenile mortality but no senescence. With moderate t_0 , this Estimator does produce the U-shaped curves that its authors desired but, with some parameter estimates, M_t increases to infinity at ages well below the observed T_{\max} . At still higher ages, the estimator then returns negative values.

Charnov and Berrigan’s and Jensen’s First Estimators
Charnov and Berrigan (1990) briefly examined the properties of the dimensionless number $t_m M$. From regression analysis, they estimated that average female adult lifespan, t_a , averages 45% of t_m in fish and shrimp, while suggesting that $t_a = 1/M$. They did not explicitly combine those two relationships nor suggest their application in estimating M . Hewitt *et al.* (2007) have, however, used:

$$M = 2.2/t_m$$

which is here termed ‘Charnov and Berrigan’s Estimator’.

Jensen (1996) further explored such relationships, while noting that for many fish t_m is approximately equal to both t_{mb} and the age of the inflexion point in a von Bertalanffy curve of growth in weight. Building on those observations, he argued that M should equal $1.65/t_m$. That is here termed ‘Jensen’s First Estimator’.

Alagaraja’s Estimator

Alagaraja (1984) suggested a variant of Tanaka’s Estimator, which avoids the need for age data if a growth curve can be developed by other means. He replaced the observed T_{\max} with T_{∞} , the age at which a fish would reach its asymptotic length – which is, by definition, infinite. Alagaraja (1984) evaded that problem by arbitrarily substituting the

age at a length 5 mm shorter than L_{∞} . He then assumed that either 1% or 5% of individuals would survive to his T_{∞} – which is contrary to common observation of many fish species, even if the youngest age-classes are ignored.

‘Alagaraja’s Estimator’ is thus either:

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

or

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

Considering its dubious assumptions that Estimator cannot be recommended but, for purposes of illustration, it is here considered in the first of its forms, which can be expanded as:

$$M \approx 3 / \left(t_0 - \frac{\ln(0.5/L_{\infty})}{K} \right)$$

Estimators based on life-history correlates

While observed ages are the obvious foundation for mortality rate estimation, an alternative is to estimate M from other life-history parameters using regression equations, sometimes supported by logic founded in theory. Most such estimators can be criticized for lacking explicit mechanistic foundations, though the linkages between growth patterns and death rates are fundamental to population dynamics. More seriously, all estimators based on life-history correlates are necessarily dependent on regressions and hence on the quality of (often questionable) prior estimates.

Ralston’s Estimator

Beverton and Holt (1959) noted that M is related to the K parameter of the von Bertalanffy growth equation, a measure of the rate at which fish grow towards their asymptotic size. Beverton (1963) made the first attempt to quantify the relationship, finding M/K in various clupeoids to be 0.6 to 1.0. Gulland (1969) suggested that it could be used to provide imprecise estimates of M , though he emphasized the variations in the constant both among and within groups of fish, M usually lying between K and $2K$ in clupeoids but between $2K$ and $3K$ in gadoids. Neither of those authors noted the frequent difficulty in estimating K with adequate precision.

Much later, Ralston (1987) developed a K -based M estimator specifically for Lutjanid snappers and Seranid groupers. Using prior data from 19 populations in an arithmetic mean regression, he found:

$$M = 0.0189 + 2.06K$$

$$M \approx 2K$$

Ralston (1987), however, preferred a geometric mean regression, rendering the estimator as:

$$M = -0.0666 + 2.52K$$

$$M \approx 2.5K$$

Both are here termed 'Ralston's Estimator I', distinguished as the AM and GM forms.

Subsequently, Pauly and Binohlan (1996) offered an updated version, which they termed the 'Ralston Method II', based on data from 29 populations of snappers and groupers:

$$M = -0.1778 + 3.1687K$$

Their focus was on the merits of FishBase as a source of data for comparative studies of population dynamics and they did not discuss the development or properties of their estimator in detail.

Pauly's Estimator

A more complex version of the same general approach was advanced by Pauly (1978a,b, 1980a,b), who produced an M estimator through multiple regression, with the independent variables including not only K but also L_∞ or W_∞ and the water temperature inhabited by the fish – though he found that K had the greatest influence and asymptotic size the least. The effect of temperature was considerable, though secondary.

The first published version of the method (Pauly 1978a, 1980a), here termed 'Pauly's Estimator O' was based on prior data on 122 populations:

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

$$+ 0.2391 \log \tau$$

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

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

$$+ 0.3598 \log \tau$$

$$M = 0.7779W_\infty^{-0.1017}K^{0.5912}\tau^{0.3598}$$

'Pauly's Estimator I', the definitive version which has been widely used over the past three decades, was based on data from 175 populations (almost all teleosts):

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

$$+ 0.4634 \log \tau$$

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

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

$$+ 0.4627 \log \tau$$

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

For members of the Clupeidae, Pauly (1980b) recommended estimating M as 60% of the value calculated from the above expressions – a surprisingly large adjustment for that one family if M for all others was adequately described by a generalized estimator. Pauly (1980b) also offered, 'for practical purposes':

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

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

though that version has not seen much use and is not further considered here.

Throughout those variants, L_∞ is measured in centimetres, W_∞ in grams, and τ , nominally the mean environmental temperature at the location and depth range inhabited by the fish, in Celsius. For pelagic and shallow-dwelling demersal species, Pauly (1980a,b) used mean annual sea-surface temperatures from oceanographic atlases and hence that source is the most appropriate when applying his estimator to such species, even if better information on the temperatures actually encountered by the fish is available. For deeper-living demersal species, Pauly (1980a,b) relied on temperature estimates provided by an oceanographer, which are hard to replicate. The influence of temperature on M appears to reverse below 4 °C and Pauly (1978a, b, 1980a,b) substituted an 'effective physiological temperature' to be used as τ for cold-water populations, providing tabular and graphical conversions between 'environmental' and 'physiological' scales.

Later, Pauly and Binohlan (1996) offered another length-based variant (which in deference to their numbering is here called 'Pauly's Estimator II'), specific to snappers and groupers, based on data from the same populations used in developing Ralston's Estimator II. They retained the same exponents as in the definitive version and only adjusted the intercept:

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

$$+ 0.4634 \log \tau$$

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

That necessarily produces values of M that are 88% of those produced by Pauly's Estimator I.

Along with Pauly's (1980a) adjustment for the Clupeidae, it is a valuable reminder that mortality rates vary with body form and ecology, themselves linked to taxonomy.

Based on high values of correlation coefficients, Pauly (1980a) suggested that the results from his equations 'should be very reliable'. Those coefficients are, however, a poor indicator of predictive power in such estimators (Pascual and Iribarne 1993). Further, Griffiths and Harrod (2007) have noted statistical non-independence in Pauly's (1980b) regressions. His estimator has also been questioned for ignoring differences among species with similar growth patterns inhabiting similar waters – a complaint that could equally be levelled at other estimators reviewed here. Moreover, Pauly's is at risk from the effects of mis-estimated K and from errors in the prior estimates used in his regressions.

Djabali's Estimator

For Mediterranean Sea fish, Djabali *et al.* (1993) presented an alternative version of Pauly's Estimator, based on prior data for 56 teleost populations – though 48 of the M values had been generated by Tanaka's Estimator, a most unreliable source. There were editorial errors in the original publication and when those were corrected by Djabali *et al.* (1994), the temperature term was dropped as it proved non-significant across the narrow range in Mediterranean surface waters. Hence, 'Djabali's Estimator' is:

$$\log M = 0.0278 - 0.1172 \log L_{\infty} + 0.5092 \log K$$

$$M = 1.0661 L_{\infty}^{-0.1172} K^{0.5092}$$

$$\log M = -0.0656 - 0.0302 \log W_{\infty} + 0.5280 \log K$$

$$M = 0.8598 W_{\infty}^{-0.0302} K^{0.5280}$$

with the parameters defined as for Pauly's.

In 15°C water, near the centre of the range considered by Djabali *et al.* (1993), this Estimator returns similar results to Pauly's only for large ($L_{\infty} \approx 2$ m), slow-growing ($K \approx 0.1$) non-clupeid fish. For those that are smaller or faster growing, it generates lower estimates of M ; 50% lower for a species with $L_{\infty} = 30$ cm, $K = 1.5$. That is the expected consequence of using Tanaka's Estimator as a foundation for regression analysis.

Jensen's Third Estimator

Jensen (2001) re-examined Pauly's Estimator in the light of advances in life-history theory. He

claimed that one of Pauly's (1980b) data points was erroneous. Eliminating that and repeating the regression analysis led to:

$$\log M = 0.66 \log K + 0.45 \log \tau$$

$$M = K^{0.66} \tau^{0.45}$$

the other terms being non-significant. To maintain chronology, that is here termed 'Jensen's Third Estimator', despite the sequence in which it is presented. While a minor improvement, it shares all of the weaknesses of Pauly's version. Jensen (2001) also developed more advanced regression analyses of Pauly's (1980b) data but found that they did not improve on the predictive ability of the above expression.

Griffiths and Harrod's Estimator

Griffiths and Harrod (2007) also returned to Pauly's Estimator, with more advanced regression analyses and an expanded set of M estimates. Those were extracted from the FishBase database, apparently without applying such rigorous selection criteria as Gislason *et al.* (2010) later used, though estimates derived from regression-based estimators were excluded. Griffiths and Harrod (2007) confirmed that K is the dominant predictor of M but also found notable ecological and phylogenetic effects on mortality rates. The effect of temperature was significant but it was dropped from the estimator that they offered, viz.:

$$\log M = 0.148 - 0.616 \log W_{\infty} + 0.780 \phi,$$

where $\phi = \log K + \frac{2}{3} \log W_{\infty}$ and hence:

$$M = 1.406 W_{\infty}^{-0.096} K^{0.780}$$

for perciform fishes,

$$\log M = 0.2300 - 0.499 \log W_{\infty} + 0.567 \phi$$

$$M = 1.698 W_{\infty}^{-0.121} K^{0.567}$$

for non-perciform, non-reef dwelling demersal species living above 200 m depth,

$$\log M = 0.586 - 0.499 \log W_{\infty} + 0.567 \phi$$

$$M = 3.855 W_{\infty}^{-0.121} K^{0.567}$$

for non-perciform, reef dwelling fishes, and

$$\log M = 0.367 - 0.499 \log W_{\infty} + 0.567 \phi$$

$$M = 2.328W_{\infty}^{-0.121}K^{0.567}$$

for non-perciform pelagics. Weights were measured in grams throughout.

For a species with an asymptotic weight of 2 kg and a low $K = 0.1$, this 'Griffiths and Harrod's Estimator' returns M estimates of 0.11 for perciforms, 0.42 for other reef species, 0.18 for other demersals and 0.25 for pelagics, when Pauly's Estimator I would yield 0.20 for most fish and 0.12 for clupeids. Thus, the two estimators generate broadly similar results overall but very different ones for particular species.

Frisk's Estimator

Frisk *et al.* (2001) made a unique examination of similar relationships among the elasmobranchs, concluding that the link between M and K was significantly different from what is seen in teleosts. Through regression of data from 30 species in nine families, they arrived at an expression which, once corrected from the published version, was:

$$\ln M = 0.42 \ln K - 0.83$$

$$M \approx 0.436K^{0.42}$$

though they also found that M/K in the Rajidae was statistically indistinguishable from the relationship in teleosts and indicated that some other families similarly resembled teleosts in this respect. Frisk *et al.* (2001) suggested that it is the longer lived sharks which have lower M/K than other fish but inspection of their data indicates that it was a group of fast-growing ($K \approx 0.8$) carcharhinids with moderate M (≈ 0.2) which deviated from the relationship typical of other fishes. Whether the anomalies are adaptations to live bearing or merely result from mis-estimations in prior studies is unclear. Frisk *et al.* (2001) did not explicitly recommend their expression as a means of estimating M but it has been so used (e.g. Quiroz *et al.* 2010) and thus is here termed 'Frisk's Estimator'.

Frisk *et al.* (2001) also found that $M_{T_{\max}}$ in those elasmobranchs for which they had data was 4.2, which closely accords with the expectations of Hoenig's Estimator, while M_{t_m} was 1.7 – close to the parameterization of Jensen's First Estimator.

Gislason's First and Second Estimators

Alone among the authors who have proposed regression-based M estimators, Gislason *et al.*

(2010) applied rigorous criteria in selecting prior estimates, finding only 168 that they judged suitable. They fitted a model, which allowed M to vary with individual length, as well as with L_{∞} and K . Analysis showed that including temperature offered no significant improvement in M estimates and their recommended estimator was:

$$\ln M_l = 0.55 - 1.61 \ln l + 1.44 \ln L_{\infty} + \ln K$$

$$M_l = 1.73 l^{-1.61} L_{\infty}^{1.44} K$$

for lengths in centimetres, which is here termed 'Gislason's First Estimator'. For a 50 cm fish of a species with L_{∞} of 100 cm and $K = 0.1$, that suggests M of 0.24 compared with 0.18 by Pauly's Estimator I. For larger fish of the same population, however, Gislason's First Estimator could generate values as low as 0.08. Indeed, Gislason's First Estimator generates M_l which decline markedly in larger animals – a form of reverse senescence. That seems realistic for some species but others show strong (positive) senescence at ages of concern to resource conservation (e.g. Hampton 2000; Tanasichuk 2000; Cook 2004).

Charnov *et al.* (2012) re-analysed the data set assembled by Gislason *et al.* (2010) and showed that the exponents of the l and L_{∞} terms do not differ significantly in their absolute values, either from one another or from 1.5, while the constant in the logarithmic form of the estimator does not significantly differ from zero. Thus, the regression equation can be reduced to the simpler:

$$M_l = K \left(\frac{l}{L_{\infty}} \right)^{-1.5} = K \left(\frac{L_{\infty}}{l} \right)^{1.5}$$

which also has the advantage of being more readily interpretable in terms of life-history theory. Charnov *et al.* (2012) suggested this equation as an M estimator and, because it is so closely linked to the work of Gislason *et al.* (2010), it is here termed 'Gislason's Second Estimator'.

While these two are, to date, the best founded of the regression-based M estimators, Gislason *et al.* (2010) warned that, from variation in the regression alone, 95% confidence intervals around the outputs of their First Estimator stretch from one quarter to four times the estimate. Mis-estimation of the growth parameters for the population of interest must add further uncertainty. The other estimators reviewed here are unlikely to perform much better.

Cubillos' Estimator

Cubillos *et al.* (1999) applied what they claimed to be Hoenig's Estimator but they substituted a calculated age at 95% L_{∞} for observed T_{\max} and, by doing so, radically changed the approach. The age in question can be found from:

$$T_{95\%} = t_0 - \ln(0.05)/K \approx t_0 + 3/K$$

Substituting into the approximate form of Hoenig's First Estimator for fish while ignoring t_0 would yield:

$$M \approx 4.3K/3 \approx 1.4K$$

which barely differs from some other estimators considered below. Cubillos *et al.* (1999), however, did not make those simplifications. Hence, 'Cubillos' Estimator' is:

$$M = 4.31 \left[t_0 - \frac{\ln(0.05)}{K} \right]^{-1.01}$$

That is vulnerable to uncertainties in the growth parameters, while it shares some of the defects of Hoenig's Estimator and incorporates a dubious assumption that T_{\max} can be approximated as $T_{95\%}$. It does, however, offer estimates of M , rather than Z .

Estimators based on ecological theory

Some of the above estimators drew on life-history theory. The remaining means of estimating M in information-limited fisheries were built more firmly on such logic.

Jensen's Second Estimator

Continuing from Jensen's First Estimator, Jensen (1996) produced a second that is closely similar to Ralston's, though founded on theory rather than regression analysis:

$$M = 1.5K$$

That is here termed 'Jensen's Second Estimator'. It shares his First Estimator's reliance on a questionable assumption, while adding a dependence on poorly-estimable K . Jensen (1996) generated some support for it by showing that regression of the 175 prior studies of M amassed by Pauly (1980b) indicated $M = 1.6 K$. The latter has been represented as an alternative parameterization of the Estimator (Simpfendorfer 1999a; Heupel and Simpfendorfer 2002) but Jensen (1996) did not present it as such and it is not considered further here.

Jensen's (1996) multiplier, 1.5, can be compared with the 1.4 of the simplified alternative to Cubillos' Estimator and to the 2 or 2.5 of the approximate forms of Ralston's Estimator I, the latter appearing to be considerable overestimates. More recently, Charnov *et al.* (2012) have argued that M_t at t_m typically equals 1.82 K for fish and reptiles that have growth patterns which can be adequately described by the von Bertalanffy function, though they did not propose that as an estimator. As Charnov *et al.* (2012) saw M declining with age and size, their multiplier is not inconsistent with Jensen's (1996) if the latter's estimates of M are seen as averages across exploited size classes, which in many fisheries include fish older than t_m .

Peterson and Wroblewski's and Lorenzen's Estimators

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

$$M_w = 1.92w^{-0.25}$$

was for dry weights but agreed reasonably well with prior estimates of M , when wet weights were adjusted by an assumed 5:1 ratio (Peterson and Wroblewski 1984). Its authors cautioned against its use as an estimator for fisheries assessments but it is nonetheless considered here in the form:

$$M_w = 1.28w^{-0.25}$$

where W is individual animal wet weight in grams.

Gulland (1987) suggested that the appearance of a single relationship, such as Peterson and Wroblewski's (1984), spanning many taxa from small zooplankton to whales results from a false combination of data drawn from the different M -to-weight relationships of various taxa, a suggestion later supported by McGurk's (1987) analyses. Hence, a fish-specific relationship should provide a more useful estimator. One such was provided by Lorenzen (1996), who used a regression approach to develop:

$$M_w = 3.00w^{-0.288}$$

for weights in grams and for fish outside of aquaculture systems. Lorenzen (1996) found no signifi-

cant differences among parameter values for river, lake and marine fishes.

Like Gislason's, both of these 'Peterson and Wroblewski's' and 'Lorenzen's' estimators generate M -at-size that shows reverse senescence, the magnitude of which depends on the exponent. Peterson and Wroblewski (1984) selected their value, -0.25, 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), but it has since been supported both theoretically and empirically (McCoy and Gillooly 2008). Lorenzen's exponent was regression-based but is unlikely to realistically represent the patterns of senescence in all species.

Lorenzen (2000) later developed a relationship linking M to length, rather than weight. It cannot estimate M independently, however, but merely creates a curve of M -at-length from an input M at some reference length. That method is not considered further here.

Ursin's Estimator

Peterson and Wroblewski's (1984) approach was novel but the form of both their Estimator and Lorenzen's was not. Ursin (1967) had previously developed an argument, based on catabolic and anabolic processes and what he termed the 'density of molecular interactions', which led him through some 'frank approximations' to:

$$M_w \approx w^{-0.333}$$

for weights in grams. By comparison with Petersen and Wroblewski's and Lorenzen's, this 'Ursin's Estimator' severely underestimates M . It does not appear to have seen much practical application.

Jennings and Dulvy's Estimator

Charnov and Gillooly (2004) explored the effects of both body size and temperature on fish life histories, proceeding as far as 'a preliminary test' of the links between M and the two drivers. Jennings and Dulvy (2008) took the earlier authors' model, provided a parameter value that Charnov and Gillooly (2004) did not and proposed their expression as an M estimator. Correcting one typographic error and giving all constants their numerical values, the resulting 'Jennings and Dulvy's Estimator' is:

$$M_w = w^{-0.25} e^{26.25 - 6960/(t+273)}$$

for weights (apparently) in grams and temperatures in Celsius. Where Charnov and Gillooly (2004) had built their model from an assumption of constant M through adult life and defined w as body weight at t_m , Jennings and Dulvy (2008) presented their estimator as one of M -at-size using w as individual weight. It is so interpreted here.

Within the range observed in the sea, the temperature term of this estimator scales the mortality estimated from body weight by 1.757, for fish living at -2 °C, up to 26.48, for those at 30 °C – a magnitude of the effect of temperature which McCoy and Gillooly (2008) suggested was generally true for animals but which causes Jennings and Dulvy's Estimator to return unreasonable estimates for warm-water species.

Roff's Second Estimator

Following his First Estimator, based on t_m , Roff (1984) also derived:

$$M = \frac{3 K L_{\infty} \left(1 - l_m/L_{\infty}\right)}{l_m}$$

as an analogue of Pauly's Estimator, though one built on mechanistic reasoning rather than empirical data. Its author found that this 'Roff's Second Estimator' performed better than Pauly's for some data sets but cautioned against the use of either as estimation errors could be large.

Roff (1984), like Jensen (1996) later, followed the common assumption in life-history theory that t_m approximates to the age at the inflexion point of the von Bertalanffy curve for growth in weight. If growth is isometric and $t_0 = 0$, the latter age corresponds to a length of $2/3 L_{\infty}$. Roff's Second Estimator then reduces to $M = 1.5 K$ and hence to Jensen's Second Estimator. Field estimates of l_m would, however, be most unlikely to exactly equal $2/3 L_{\infty}$, while few fish have exactly isometric growth. Thus, in practical applications, the two estimators would yield somewhat different values of M .

Groeneveld's Estimator

Groeneveld (2000) introduced the expression:

$$M = K \left(\frac{3L_{\infty}}{l_m - 3} \right)$$

which he claimed to have drawn from Beverton and Holt (1959), though those authors did not present

it. As published, this 'Groeneveld's Estimator' may contain an error, as Groeneveld's (2000) reported application of it generated estimates which cannot be replicated using his parameter values. It is nevertheless here considered as an estimator available in the literature. It must always produce $M > 3K$ and for many species will yield much higher values. Thus, it will usually severely overestimate M .

Uncertainties and confidence intervals

A final comment may be added, applicable to all of these estimators. That the M estimates which they yield are highly uncertain should be clear from this review, yet of their original authors, only Cubillos *et al.* (1999) and Gislason *et al.* (2010) attempted to generate confidence intervals around those estimates. Perhaps that was appropriate: Management systems that can utilize stochastic information on M should seek more reliable estimators than those considered here. Moreover, these crude approaches are subject to severe gross errors, arising from faulty model structure, failures of ageing protocols, unrecognized sampling biases and the like. Estimates of confidence intervals calculated from the more tractable sources of error are likely to severely underestimate the uncertainties in estimated M , misleading users. The absence of explicit confidence intervals should not, however, be taken as any indication of high precision in output values. None of the 30 estimators is capable of providing that.

Example applications

Approach

The performance of the estimators is here examined by applying each of them to a variety of example populations. The primary requirement in selecting the latter was an available well-founded estimate of M for individuals of exploitable sizes, based on one of the methods suited to data-rich fisheries, so that the trial applications would yield relatively unequivocal results. Gislason *et al.* (2010) have recently compiled all such estimates that are available for finfish and the examples used here were necessarily selected from their list, though that must bias the trials in favour of Gislason's First and Second estimators (and to a lesser extent also of Pauly's, a few values of M being common to the regression foundation of that Esti-

mator also). Of equal importance, each example population required available values of all twelve parameters demanded by the estimators, though $t_0 = 0$ was accepted, W_∞ was usually estimated from L_∞ and the length-weight relationship for the population, while t_m was sometimes calculated from l_m or *vice versa* using the growth curve. Where sex differences were reported, female values were used, since the life-history theory underlying some estimators is specific to that sex. The values of n_c and t_c required by Kenchington's Estimator were estimated as best they could be for each resource. In contrast to the M values, those of the parameters were not expected to be highly accurate but rather representative of what might be employed in stock-assessment work, thus providing trials of the practical application of each estimator, at the cost of sometimes condemning an estimator for the failure of a parameter estimate. It should be recognized, however, that the example populations are relatively intensively studied (else they would lack well-found M values), and thus the estimators may here average a better performance than in typical practical applications. Within the above constraints, the example populations were chosen to span the range of finfish taxonomy and ecology, with the addition of a single shellfish resource, though duplicate sebastinid and lutjanid populations were added to check the patterns seen in those taxa. The selected examples and their parameter values are presented in Table 2, while the sources of the values used are given in detail elsewhere (see Supporting Information).

Tanaka's Estimator was tested with the conventional $P = 0.05$. Those estimators that have particular forms for specific taxa or ecological forms were appropriately applied in each case, though estimators designed for one taxon exclusively were applied to all examples regardless, for purposes of illustration.

Thorough testing of the estimators of M -at-size would require 'known' values for particular fish sizes. That has not been attempted here. Instead, two lengths were selected for each example population with the intent of spanning the range of fish sizes seen in the studies that produced the 'known' M (Table 2). The higher of the two was, however, limited to a maximum immediately below L_∞ , as Chen and Watanabe's Estimator is unable to provide M estimates for greater lengths. Weights corresponding to those selected lengths were calculated using the length-weight relationship for

Table 2 Parameter values for the example populations (ages are in years, lengths in centimetres, weights in grams and temperatures in Celsius, all rounded to a maximum of four significant figures; parameters are identified by their symbols, l 1 and l 2 being the lengths for which M -at-size is calculated when applying appropriate estimators).

	Chesapeake	Norwegian	Pacific Ocean	Southern	Great Barrier	Pilbara	Shetland	Western	Grand Bank	Northwest	Australian	Georges Bank
	Bay	Fjord	Perch west of	California	Reef	Scarlet	Sandee	Pacific	American Plaice	Atlantic	Sharpnose	Sea Scallop
	Anchovy	Lanternfish	Gwaii Hannas	Rockfish	Sripey Bass	Seaperch	Sandee	Skipjack Tuna	Hippoglossoides	Porbeagle	Shark	Placopecten
	Anchoa	Benthosema	Sebastes	Sebastes	Lutjanus	Lutjanus	Ammodytes	Katsuwonus	Hippoglossoides	Lamna	Rhizoprionodon	Placopecten
	mitchilli	glaciale	alutus	elongatus	carponotatus	malabaricus	marinus	pelamis	platessoides	nasus	taylori	magellanicus
	Engraulidae	Myctophidae	Scorpaenidae	Scorpaenidae	Lutjanidae	Lutjanidae	Ammodytidae	Scombridae	Pleuronectidae	Lamnidae	Carcharhinidae	Pectinidae
T_{max}	3	8	98	54	18	31	9	12	32	»26	6.9	25
L_{∞}	12.93	8.306	42.6	37.26	27.31	58.58	20	65	73	325.9	86.1	14.7
W_{∞}	20.79	8.68	1133	650.5	45.99	2678	47.35	6026	3220	2696	2828	424.4
K	0.23	0.204	0.126	0.098	0.54	0.262	0.393	1.3	0.10	0.07	0.63	0.38
t_0	-1.23	-0.64	-5.22	-2.36	0	-0.09	0	0	0.37	-6.06	-1.07	0
α	0.005477	0.00873	0.0089	0.00793	0.0143	0.01855	0.00184	0.00654	0.002721	0.041	0.0019	0.157
β	3.22	3.26	3.133	3.127	3.08	2.919	3.39	3.29	3.259	2.713	3.19	2.94
l_m	4	4.75	34.6	19	18.9	38.3	11.5	47.9	47.7	212	78	11.4
t_m	0.83	2	8.6	9.2	2.4	1.4	2	1.02	13	14	1.8	4
τ	17	8	5	10	26	28	10	28	1	10	25	10
n_e	863	309	10 ⁴	-	111	150	6500	10 ⁷	500	600	76	10 ⁶
t_e	0	4	10	-	5	12	1	0	8	0	1	1
l_1	3	2	35	20	25	30	15	50	30	100	55	7.5
l_2	10	8	42	36	27	57	19	64	72	325	72	14

Table 3 Results from applying the estimators to the parameter values for the example populations (all rounded to two decimal places; dash indicates that no estimate could be calculated). 'Known M ' is a value from the literature based on an 'information-intensive' estimation approach but is nevertheless uncertain.

	Pacific Ocean														Georges Bank Sea Scallop																																																																																																								
	Chesapeake Bay							Norwegian Lantemfish							Pacific Ocean							Georges Bank Sea Scallop																																																																																																	
	Anchovy							Benthosema glaciale							Hippocampus guttulatus							Sebastes alutus							Sebastes elongatus							Lutjanus carponotatus							Lutjanus malabaricus							Shetland Ammodytes marinus							Skipjack Tuna							Kalsuwonus pelamis							Hippoglossoides platessoides							Porbeagle Lamna nasus							Rhizoprionodon taylori							Placopecten magellanicus																											
	mitchilli							glaciale							guttulatus							alutus							elongatus							carponotatus							malabaricus							marinus							pelamis							platessoides							nasus							taylori							magellanicus																																		
Known M	2.19-2.95							0.7							1.22							0.04							0.15							0.2							0.12							0.6							1.2-2.0							0.18							0.56							0.1																																									
Bayliff's	2.13							0.80							1.16							0.07							0.12							0.35							0.21							0.71							0.53							0.20							0.93							0.26																																									
Hoeng's	1.42							0.61							0.77							0.04							0.08							0.23							0.13							0.47							0.35							0.13							0.61							0.23																																									
Hoeng's	1.43							0.54							0.78							0.04							0.08							0.24							0.14							0.48							0.36							0.13							0.62							0.17																																									
approx.																																																																																																																							
Hoeng's	1.43							0.55							0.79							0.05							0.08							0.25							0.14							0.49							0.37							0.14							0.63							0.18																																									
combined																																																																																																																							
Taxa																																																																																																																							
Hoeng's	1.40							0.53							0.76							0.04							0.08							0.23							0.14							0.47							0.35							0.13							0.61							0.17																																									
combined																																																																																																																							
Taxa approx.																																																																																																																							
Hoeng's GM	1.83							0.64							0.87							0.03							0.05							0.21							0.11							0.48							0.34							0.10							0.66							0.22																																									
Hoeng's GM	1.69							0.58							0.88							0.04							0.07							0.24							0.14							0.51							0.38							0.13							0.69							0.17																																									
combined																																																																																																																							
Taxa																																																																																																																							
Sekharan's	1.53							0.58							0.84							0.05							0.09							0.26							0.15							0.51							0.38							0.14							0.67							0.18																																									
Tanaka's	1.00							0.37							0.54							0.03							0.06							0.17							0.10							0.33							0.25							0.09							0.43							0.12																																									
Kenington's	2.83							1.75							1.37							0.08							-							0.33							0.22							1.21							1.43							0.23							0.65							0.58																																									
continuous																																																																																																																							
Kenington's	2.45							1.55							1.23							0.08							-							0.32							0.21							1.14							1.38							0.22							0.60							0.57																																									
Integer																																																																																																																							
Alverson &	2.30							0.71							0.75							0.00							0.05							0.04							0.04							0.42							0.01							0.13							0.45							0.03																																									
Camey's																																																																																																																							
Zhang &	1.17							0.77							0.33							0.00							0.03							0.02							0.36							0.04							0.11							0.32							0.02																																																
Megrey's																																																																																																																							
Rikhter &	1.22							0.93							1.53							0.08							0.15							0.63							1.60							1.12							1.55							0.13							0.39							0.31																																									
Efanov's																																																																																																																							
First																																																																																																																							

Table 3 (Continued).

	Chesapeake Bay	Norwegian Fjord	Pacific Ocean Perch west of Hawaii	Southern California	Great Barrier Reef	Pilbara	Shetland	Western Pacific	Grand Bank	Northwest Atlantic	Australian Sharpnose	Georges Bank Sea Scallop
	Anchovy	Lanternfish	Gwaii Hannas	Rockfish	Bass	Seaperch	Sandeel	Tuna	Plaice	Porbeagle	Shark	Placopecten magellanicus
	<i>Anchoa mitchilli</i>	<i>Benthosema glaciale</i>	<i>Sebastes alutus</i>	<i>Sebastes elongatus</i>	<i>Lutjanus carponotatus</i>	<i>Lutjanus malabaricus</i>	<i>Anmodytes marinus</i>	<i>Kalsuonius pelamis</i>	<i>Hippoglossoides platessoides</i>	<i>Lamna nasus</i>	<i>Rhizopteronodon taylori</i>	
Rikhter & Efanov's Second	1.58	0.77	0.17	0.15	0.65	1.04	0.77	1.34	0.08	0.07	0.84	0.41
Roff's First	3.28	1.21	0.19	0.20	0.61	1.77	0.99	1.41	0.11	0.13	0.90	0.32
Chen & Watanabe's	0.33-0.28	0.31-0.22	0.19 to -0.07	0.11-0.13	-	0.40-0.27	-	-	0.10-0.10	0.13 to -0.03	0.87-1.50	-
Charnov & Berrigan's	2.65	1.10	0.26	0.24	0.92	1.57	1.10	2.16	0.17	0.16	1.22	0.55
Jensen's First	1.99	0.83	0.19	0.18	0.69	1.18	0.83	1.62	0.13	0.12	0.92	0.41
Alagaraja's	0.23	0.23	0.10	0.07	0.40	0.17	0.32	0.80	0.06	0.03	0.42	0.34
Ralston's I AM	0.49	0.44	0.28	0.22	1.13	0.56	0.83	2.70	0.22	0.16	1.32	0.80
Ralston's I GM	0.51	0.45	0.25	0.18	1.29	0.59	0.92	3.21	0.19	0.11	1.52	0.89
Ralston's II	0.55	0.47	0.22	0.13	1.53	0.65	1.07	3.94	0.14	0.04	1.82	1.03
Pauly's 0 by Length	0.53	0.44	0.20	0.20	0.97	0.50	0.65	1.61	0.17	0.10	0.86	0.67
Pauly's 0 by Weight	0.66	0.52	0.20	0.23	1.18	0.52	0.69	1.24	0.19	0.10	0.84	0.54
Pauly's I by Length	0.69	0.51	0.19	0.23	1.18	0.62	0.67	1.71	0.17	0.10	0.93	0.72
Pauly's I by Weight	0.66	0.46	0.18	0.22	1.34	0.61	0.69	1.67	0.17	0.11	1.04	0.56
Pauly's II	0.60	0.44	0.16	0.20	1.04	0.54	0.59	1.50	0.15	0.09	0.82	0.63
Djabail's by Length	0.37	0.37	0.24	0.21	0.53	0.33	0.47	0.75	0.20	0.14	0.50	0.48
Djabail's by Weight	0.36	0.35	0.23	0.21	0.55	0.33	0.47	0.76	0.20	0.14	0.53	0.43
Jensen's Third	1.36	0.89	0.53	0.61	2.88	1.85	1.52	5.33	0.22	0.49	3.14	1.49
Griffiths & Harrod's	0.70	0.73	0.51	0.47	1.71	0.69	0.47	0.94	0.39	0.11	0.68	1.07
Frisk's	0.24	0.22	0.18	0.16	0.34	0.25	0.29	0.49	0.17	0.14	0.36	0.29

Table 3 (Continued).

	Pacific Ocean																			
	Chesapeake Bay		Norwegian Fjord		Rio Formosa		Perch west of Hawaii		Southern California		Pilbara		Western Pacific		Northwest Atlantic		Australian Shark		Georges Bank Sea Scallop	
	Anchovy	Anchoa mitchilli	Benthosema glaciale	Benthosema glaciale	Seahorse	Hippocampus guttulatus	Sebastes alutus	Sebastes alutus	Sebastes elongatus	Lutjanus carponotatus	Scarlet Seaperch	Shelland Sandeel	Katsuwonus pelamis	Grand Bank American Plaice	Porbeagle	Shark	Rhizoprionodon taylori	Placopecten magellanicus		
Gislason's First	2.71-0.39		2.44-0.26		1.78-0.63		0.16-0.12		0.25-0.10	0.61-0.54	0.67-0.24	0.65-0.44	1.69-1.14	0.35-0.09	0.30-0.05	1.05-0.68	1.23-0.45			
Gislason's Second	2.06-0.34		1.73-0.22		1.59-0.61		0.17-0.13		0.25-0.10	0.62-0.55	0.71-0.27	0.61-0.42	1.93-1.33	0.38-0.10	0.41-0.07	1.23-0.82	1.04-0.41			
Cubillos'	0.36		0.30		0.98		0.23		0.15	0.76	0.37	0.55	1.85	0.14	0.11	1.15	0.54			
Jensen's Second	0.35		0.31		0.86		0.19		0.15	0.81	0.39	0.59	1.95	0.15	0.11	0.95	0.57			
Peterson & Wroblewski's	1.94-0.74		2.38-0.77		1.10-0.65		0.26-0.22		0.41-0.26	0.31-0.29	0.29-0.18	0.62-0.51	0.18-0.15	0.35-0.17	0.13-0.06	0.25-0.20	0.46-0.29			
Lorenzen's	4.85-1.59		6.13-1.67		2.51-1.37		0.47-0.40		0.81-0.48	0.59-0.55	0.54-0.32	1.31-1.04	0.31-0.25	0.68-0.30	0.21-0.08	0.46-0.36	0.93-0.55			
Ursin's	1.74-0.48		2.28-0.51		0.81-0.40		0.12-0.10		0.22-0.12	0.15-0.14	0.14-0.07	0.38-0.29	0.07-0.06	0.18-0.07	0.05-0.02	0.11-0.09	0.26-0.14			
Jennings & Dulvy's	14.40-5.46		8.18-2.64		9.58-5.66		0.68-0.59		1.69-1.07	4.74-4.47	5.17-3.23		2.55-2.09	3.21-2.62	0.64-0.31	0.51-0.23	3.54-2.86			
Roff's Second	1.54		0.46		1.38		0.09		0.28	0.72	0.42	0.87	1.40	0.16	0.11	0.20	0.33			
Groeneveld's	8.92		2.90		4.26		0.51		0.68	2.78	1.30	2.77	5.65	0.49	0.33	2.17	2.00			

the population and the estimators were applied to the two fish sizes. Such limited trials cannot establish the validity of any estimator of M -at-size but they are sufficient to cast doubt on half of those yet published, narrowing the number to be considered in future trials.

The results of applying the estimators to the parameter values for the example populations are shown in Table 3, where they are rounded to two decimal places, though the second implies a precision that none of these methods can support. Those results cannot be unambiguously interpreted because the 'known' values of M were not measured without error, while some parameter estimates could have been replaced by different but equally valid alternatives, altering the apparent performances of the estimators. Moreover, some estimators can return reliable results but only in specific cases. Sekharan's, for example, will generate the same values as Kenchington's (and hence match the expectations of the exponential mortality model) if $n_e = 49/Z$ but not with much larger or smaller samples. Worse, some estimators generated accurate outputs for certain populations through fortuitous combinations of errors. Thus, conclusions can be drawn from the Table but they require attention to broad patterns, not individual estimates.

Results

Despite its recognized deficiencies, Kenchington's Estimator was the most consistent as a general indicator of M (Table 3). Before rounding, ten of its eleven estimates for finfish fell between 50% and 200% of the corresponding 'known' values (except 202% for sandeel), while its estimate for the lanternfish did not exceed 250% of 'known'. Bayliff's, Hoenig's and Sekharan's estimators were similarly accurate for eleven finfish but each failed badly with the large n_e of skipjack, despite strong senescence in that species. No other estimator performed as well. Each produced at least one estimate within 50% to 200% of 'known' but some yielded other values that were wrong by more than an order of magnitude, Jennings and Dulvy's Estimator being especially deficient, while Chen and Watanabe's returned some negative values.

The standard of precision required for assessment purposes is ill-defined but one might demand that estimates of M , once rounded to one significant figure (or one decimal place if greater than

1.0), should not deviate from the 'known' value by more than 20%. Six of the estimators did not achieve that standard with any of the teleost examples, while seven others did so only for one or two populations each. No estimator met the requirement for more than five of the ten, though Pauly's only slightly missed with a sixth, the lanternfish. It was defeated by Pacific ocean perch, the lutjanid snappers and the bay anchovy. There was very little difference in the performances of the various versions of Pauly's Estimator and no apparent justification to use anything but the standard one. Some sebastinids are unusual in almost, if not completely, ceasing growth after reaching adult size (Beamish 1979). When a von Bertalanffy curve is fitted nonetheless, K is forced to a high value, unrelated to the longevity of the species, leading to failure of any M estimator that emphasizes the growth parameter. Beverton (1992) suggested that M approximates $0.3 K$ in Pacific *Sebastes*, in contrast to the $K \leq M \leq 2 K$ of typical teleosts. Scaling the outputs of Pauly's Estimator by the ratio of Beverton's (1992) constants would appropriately correct the estimate for Pacific ocean perch but would throw off that for greenstriped rockfish. The same problem was not expected with lutjanids but the two selected examples both show rapid initial growth, followed by a swift transition to slow growth, meaning that K is unusually (though not erroneously) high. The failure with bay anchovy came from an opposite cause: the species does not live long enough to approach L_∞ and hence K is depressed relative to life expectancy.

Cubillos' and Jensen's Second estimators performed nearly as well as Pauly's, each falling a little short with the seahorse and with American plaice, while being more seriously erroneous with the lanternfish. Cubillos' Estimator has no obvious advantages over Pauly's but Jensen's Second has the advantage of simplicity, not only being easier to apply but carrying less of a patina of rigorous science – and perhaps thereby reminding its users that its outputs are not highly reliable.

Those estimators that rely on ecological or life-history theory to generate single M values, including all those that build on ages other than T_{\max} , generally performed badly, confirming the warnings of Peterson and Wroblewski (1984) and Roff (1984). Among them and aside from Jensen's Second Estimator, only his First met the requirement for $\leq 20\%$ error after rounding for as many as

four of the teleost examples. It was again defeated by Pacific ocean perch and the lutjanids but also by the seahorse, though it should be no surprise that a species with such a unique life history has an unusual relationship between t_m and longevity.

The T_{\max} -based estimators performed well with the ten teleost examples, despite the many difficulties surrounding maximal ages. Kenchington's Estimator, which should be approximately correct for populations conforming to the exponential mortality model, produced results within the 20% limit for four. Some of its failures can be ascribed to uncertainties in T_{\max} or mis-estimation of n_e , but trials with alternative values suggest that some others resulted from pronounced senescence, lowering T_{\max} relative to M of younger adults. Hoenig's Estimator succeeded where Kenchington's failed (and *vice versa*), perhaps because its foundations in regressions incorporated mild senescence effects, as well as its tendency to underestimate when n_e is high – the latter fortuitously balancing greater senescence in sandeel. There was little difference among the outputs of the variant forms of Hoenig's Estimator nor reason to use any other than $M = 4.3/T_{\max}$. Bayliff's Estimator proved no less successful, though it performed well with a different set of examples. Notably, as an estimator intended for the Engraulidae alone, it was especially accurate when applied to bay anchovy.

The M -at-size estimators generally offered wide ranges of values, increasing the probability that 'known' M falls within those bounds. Even so, neither Chen and Watanabe's, Jennings and Dulvy's nor Lorenzen's estimators generated usefully accurate estimates of M . Gislason's First Estimator worked well for most example teleost populations but, relying heavily on K , it failed with Pacific ocean perch and the lutjanids. Gislason *et al.* (2010) showed that their Estimator tends to agree with Pauly's when K is moderate but diverges when it is high. In practical application, however, both estimators returned similar values for skipjack (as they did for most teleosts), likely because Pauly's temperature term serves to 'correct' the estimates. As might be expected, Gislason's Second Estimator performed similarly to the First. The two produced estimates for greenstriped rockfish that were identical but those generated for bay anchovy, the lanternfish and skipjack tuna differed by enough to have major implications for fisheries management, which may be

some indication of which species violate common assumptions of generalized life-history theory. Peterson and Wroblewski's Estimator performed surprisingly well across a range of examples, considering its origins in pelagic ecological theory and its original authors' reticence, as did Ursin's Estimator.

In their recent compilation, Gislason *et al.* (2010) found only two reliable estimates of M for elasmobranchs and for only one of those is there an estimate of pre-fishery T_{\max} . For the other, northwest Atlantic porbeagle, the only available value comes from a study undertaken after decades of supposed intensive fishing. Hence, no adequate examination of the performance of the estimators when applied to elasmobranchs is possible. Such as they are, the values in Table 3 indicate that those estimators which emphasize K performed poorly with the two example sharks, as might have been anticipated from the work of Frisk *et al.* (2001) considered above, though Frisk's Estimator performed no better than Pauly's, despite being designed for sharks. Gislason's First and Second and Lorenzen's estimators of M -at-size showed promise but, as with the teleosts, they require further and more appropriate trials. A number of other estimators appeared to work with one or the other shark but they can be set aside as chance congruences and the only estimators which, on the very limited available evidence, can be given much credence for application to the elasmobranchs are those based on T_{\max} , which could only really be tested against the sharpnose shark. All versions of Hoenig's Estimator, Sekharan's and both forms of Kenchington's performed adequately with that species, the small sample size and limited senescence likely facilitating those successes. With porbeagle, however, either they seriously underestimated Z or else F has been much lower over recent decades than is usually supposed.

Tables 2 and 3 contain data and estimates for a single example shellfish, the sea scallop. That species is well known to have low M at the sizes typically caught but a moderate maximum observed age, even when virgin beds are first exploited. MacDonald and Thompson (1986) suggested a pronounced link between M and size in this scallop, driving strong senescence. Thus, it is not surprising that almost all the estimators, including the molluscan version of Hoenig's, failed. Even the apparent 'successes' of Tanaka's and Ursin's can be

dismissed as chance results. More promising performances might be seen with other invertebrate resources but the trials with sea scallop confirm that none of the estimators developed for finfish can simply be assumed to work with other taxa.

Discussion

Performance of the estimators

While this review is the first to examine the full range of M estimators for information-limited fisheries or to apply them to a wide variety of example populations, less extensive trials have been published previously – Newburger and Houde (1995), Simpfendorfer (1999b), Newman *et al.* (2000) and Newman (2002) anticipating subsets of the results presented above. Roff (1984) applied both Pauly's and his own Second estimators to seventeen teleosts. Eight of the outputs of Pauly's Estimator fell within 20% of 'known' M after rounding but there was no obvious pattern to the taxa with which it succeeded or failed. Only for the hake *Merluccius merluccius* (Merlucciidae) and the stickleback *Pungitius pungitius* (Gasterosteidae) did that Estimator fail to generate a value within 50 to 200% of 'known'. Roff's Second Estimator produced outputs within 20% of known, after rounding, for seven populations but fell outside 50% to 200% with three. Newman *et al.* (1996) and Fischer *et al.* (2005) compared estimates of M in hussar, five-line and grey snappers (*Lutjanus adetii*, *L. quinque-lineatus* and *L. griseus*, Lutjanidae) from catch curves with those from Hoenig's, Pauly's and Ralston's estimators. For all three species, as for the lutjanids considered above, Hoenig's Estimator generated reasonable agreement with 'known' M , while the estimators that emphasize K produced higher values. Cubillos *et al.* (1999) applied Pauly's and Rikhter & Efanov's Second estimators, as well as their own, to Chilean hake (*Merluccius gayi*, Merlucciidae). Estimates from Pauly's and Cubillos' were in close agreement with a value from regression of Z on fishing effort, while Rikhter and Efanov's Second performed less well. Cubillos *et al.* (1999) also developed 95% confidence intervals. Despite their growth parameters being unusually well estimated, the confidence intervals around the Pauly estimates were 0.38 to 0.49 for males and 0.21 to 0.32 for females. When the uncertainty in the original regression model was considered, those intervals widened to 0.22–0.88

and 0.12–0.56 – such poor precision as to be of questionable utility for analytical stock assessments. Rikhter and Efanov's Second and Cubillos' estimators displayed a similarly poor performance. Tanasichuk (2000) applied Hoenig's Estimator to Pacific herring (*Clupea pallasii*, Clupeidae), obtaining a value for M of 0.28, compared with estimates based on survey abundances of 0.21–1.26 or those from Gunderson and Dygert's (1988) GSI-based approach of 0.61–0.71. The underestimation by Hoenig's Estimator is not unexpected, considering the very large n_e underlying observed T_{\max} in herring. Lorenzo *et al.* (2002) applied four estimators to striped seabream (*Lithognathus mormyrus*, Sparidae), but the corresponding values from two information-intensive approaches were so divergent that no conclusions can be drawn about the accuracy of the four. Gunderson *et al.* (2003) applied Jensen's Second and Hoenig's estimators to arrowtooth flounder (*Atheresthes stomias*, now *Reinhardtius stomias*, Pleuronectidae) and darkblotched rockfish (*Sebastes crameri*, Scorpaenidae). They also offered 95% confidence intervals for the first of those. With the rockfish, the output of Hoenig's was depressed by high n_e , while that from Jensen's was inflated by high K , but both estimators performed well with the flounder. Kovačić (2006) studied striped goby (*Gobius vittatus*, Gobiidae), which lives to a maximum of three (males) or four (females) years, finding $M = 0.99$ (males) or 0.94 (females) by catch curves – though his data showed a linear decline in numbers-at-age, implying prominent senescence. Kovačić (2006) also applied Hoenig's, Pauly's, and Djabali's estimators, plus one of Rikhter and Efanov's, while applying Sekharan's in reverse to compare the results of the other estimators to an observed T_{\max} – an unreliable approach which risks rejecting an accurate estimate of M . With sample sizes of a few hundred, Hoenig's Estimator performed well for females, while Djabali's did so for both sexes. The other approaches overestimated, Hoenig's estimate for males being the highest at 1.43. Finally, Maunder and Wong (2011) applied Hoenig's, Tanaka's (with $P = 0.05$), Jensen's First and Second and Pauly's estimators to summer flounder (*Paralichthys dentatus*, Paralichthyidae). Pauly's and Jensen's Second performed comparatively well but Tanaka's generated gross underestimates while Jensen's First massively overestimated. Hoenig's Estimator provided values of Z

similar to estimates of M from a stock-assessment model. The input value of T_{\max} was, however, observed after prolonged and intensive fishing and it was purely fortuitous that the Estimator's tendency to underestimate balanced the difference between Z and M . Maunder and Wong (2011) also offered confidence intervals around the estimate from Hoenig's which suggested extreme uncertainties, M of males lying between 0.13 and 1.01.

Cortés and Parsons (1996) found that Pauly's Estimator broadly agreed with an M for bonnethead shark (*Sphyrna tiburo*, Sphyrnidae) that was based on catch curves. They misapplied Hoenig's Estimator but when it is fitted to their observed T_{\max} , it too generally agreed. Heupel and Simpfendorfer (2002) compared values for M of juvenile blacktip sharks (*Carcharhinus limbatus*) from Peterson and Wroblewski's Estimator with results from a tagging experiment, finding that the former severely underestimated. They also applied Hoenig's, Pauly's and Jensen's First and Second estimators, obtaining results somewhat lower than those from tagging, but that may only reflect the expected reduction in M between juvenile and adult ages.

Groeneveld (2000) estimated M in the spiny lobster *Palinurus delagoae* (Palinuridae), using regression of Z on fishing effort, at about 0.10 and compared that with output from Pauly's, Rikhter and Efanov's Second, Sekharan's and Jensen's Second estimators, as well as his own. Despite the application of methods designed for finfish to a crustacean, he reported all estimators agreeing with the 'known' value when rounded to one decimal place, except for Groeneveld's, which produced its expected overestimate. It is not, however, clear how he obtained those results. In particular, he seems to have used an asymptotic carapace length, where Pauly's Estimator calls for L_{∞} measured as total fish length. Hewitt *et al.* (2007) applied seven of the estimators to Chesapeake Bay blue crab (*Callinectes sapidus*), while using a range of plausible values for each input parameter. The resulting estimates of M lay between 0.30 and 2.35, the maximum from any one estimator being 150% to 450% of its minimum. Analysis of mark-recapture and exploitation-rate data suggested temporally variable M of 0.42 to 0.87. The lower bounds of the estimates generated by Hoenig's, Roff's First, Jensen's Second, Pauly's weight-based and Lorenzen's estimators all fell within that wide range, while Alverson and Carney's was 0.30.

Pauly's Estimator, with asymptotic carapace width used in place of L_{∞} , yielded a lower bound of 0.91 and Jensen's First Estimator gave 0.99. The upper bound from each of the estimators was much greater than the 'known' M .

None of those prior studies conflicts with the results presented in Table 3, though some add depth to current understanding of the estimators. In particular, the work of Groeneveld (2000) and Hewitt *et al.* (2007) confirm that estimators designed for finfish can sometimes work with invertebrate resources, despite their failure with the sea scallop. Meanwhile, Roff's (1984) observations serve to remind that the relationship between estimation success and taxonomic group is not absolute. Otherwise, the relative effectiveness of estimators that rely on K or T_{\max} , the generally poor performance of those built on ecological or life-history theory and the questionable success of attempts to improve on Pauly's Estimator remain apparent.

Clearly, none of the estimators can be relied upon to provide usefully accurate estimates of M for every resource, while some perform hopelessly badly. Pascual and Iribarne (1993) warned that the uncertainties resulting from some of them 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', while Gislason *et al.* (2010) have noted that estimates of M for particular species 'will always be highly uncertain'. Attempts to determine confidence intervals (e.g. Cubillos *et al.* 1999; Gislason *et al.* 2010; Maunder and Wong 2011) have found them to be 50% to 200% of the estimate or worse. That is unremarkable. Determining M is difficult and any approach that purports to provide an answer at low cost is unlikely to deliver on its promise. Yet the errors are not simply random. Some of the estimators do provide useful first approximations to M for certain kinds of fish, particularly those with the population dynamics of archetypal exploited teleosts, while failing badly when confronted with pronounced senescence or a life history showing swift growth to adult size followed by prolonged survival. Even at their best, however, none of these estimators can be an adequate substitute for proper determination of M . Citing the outputs of even the best of them beyond the first significant figure or first decimal place is an exercise in self-deception at best.

Recommendations for practical applications

Whether such uncertain estimates of so important a parameter as M can ever be useful in analytical stock assessments must be doubtful. Building a complex model on the foundation of such an estimate seems a misdirection of resources better devoted to establishing a reliable value for M . Some of the estimators may nevertheless be useful when preparing cruder forms of scientific advice to fisheries management.

To address their deficiencies, Gunderson *et al.* (2003) suggested using several estimators to 'minimize bias in stock assessment and expose any misconceptions or errors'. Simpfendorfer *et al.* (2005) proposed using the results from multiple estimators to provide an understanding of their uncertainty and Hewitt *et al.* (2007) recommended emphasizing the range of estimates common to multiple estimators, though they did not provide any indication that consistency equated to accuracy. Zhang and Megrey (2006) recommended that stock assessments use alternative values of M , spanning the plausible range, while Brodziak *et al.* (2011) suggested averaging the outputs of multiple estimators. Those approaches, however, give equal weight to each estimator and they are clearly not of equal reliability. Thus, a more deliberative approach is recommended.

None of the estimators should be used unless its input parameters can be estimated with reasonable confidence. Estimation of K is particularly problematic in a long-exploited population lacking old fish, while unexploited T_{\max} will generally be unavailable unless otoliths or other ageing structures were collected in the first years of a fishery and a validated ageing protocol has since been developed. While those two parameters provide the primary foundations of the only broadly reliable M estimators, there will be resources for which they are unknown but some other parameter has been measured. In such cases, the performance of the more-questionable estimators might be examined, through Table 3 or further trials, to determine whether one is appropriate for the resource in question.

When a reliable estimate of K is available, the trials to date (both in the present work and in the cited literature) suggest that Pauly's and Jensen's Second estimators can work well for 'archetypal' teleosts but can produce severe errors

when applied to species that have other relationships between growth and survival. It would be wrong to read too much into the results shown in Table 3 for any one example resource but it seems that neither estimator should be used with those elasmobranchs, lutjanids, sebastinids or other fish with long adult lives following rapid early growth, nor should they be used with species (like bay anchovy) which do not live long enough to reach L_{∞} . There is no apparent advantage in using any variant of Pauly's Estimator other than the standard version (Pauly 1980b). Whether that or Jensen's Second Estimator should be preferred largely depends on the behaviour of scientists. Suggesting that M can be estimated as 150% of K does not carry the misleading impression of precision offered by Pauly's exponents, with their four decimal places. Conversely, Jensen's Second Estimator facilitates casual estimation of M , while Pauly's demands some thought, if only in estimating τ .

The only other broadly applicable option is to estimate M from pre-exploitation T_{\max} , when a reliable estimate of the latter is available. When it is, Hoenig's Estimator performs well if n_e is in the hundreds, provided that the resource does not show strong senescence. The various versions of that Estimator differ little when compared to the uncertainties in each of them and the 'approximate' $M = 4.3/T_{\max}$ is recommended for its simplicity. With larger samples, Hoenig's is prone to serious underestimation but that is counterbalanced by its tendencies to overestimate in the face of either pronounced senescence or non-negligible F . In some trials, the balance produces estimates approximating to M but, while such luck is doubtless useful in stock assessment, it is not a foundation for scientific estimation. Conversely, Kenchington's Estimator responds to sample size but assumes no senescence at all. The two alternatives might be seen as bounding M but what is really required is a new regression-based estimator that uses n_e as a covariate. It would still be unreliable when applied to species with stronger or weaker senescence than the norm.

None of these estimators should be used with invertebrates unless it can be shown that the one chosen is applicable to the species in question. Simply assuming that the dynamics of shellfish resources are those typical of teleosts (cf. Hewitt *et al.* 2007) will lead to severe errors in some cases.

Some of the estimators of M -at-size may be useful for bounding a population's average M . Gislason's First and Second estimators appear to fill that function for a wide variety of finfish, though they have failed with the lutjanids and sebastinids. Lorenzen's may serve a similar role for sharks. Whether either can be relied on for an average M weighted by the size frequency of the resource, or for M -at-size itself, remains to be determined by appropriate trials.

Even with every caution in their application, these estimators are apt to yield seriously misleading values for M . When they must be used, Pascual and Iribarne (1993) demanded that the uncertainty in M and its consequences be explored in advice to fisheries managers – a recommendation echoed by Cubillos *et al.* (1999), Fischer *et al.* (2005), Hewitt *et al.* (2007) and Brodziak *et al.* (2011). It cannot be acceptable to use a single estimator and the resulting estimate simply because nothing more reliable can be suggested. Nor should any method be applied uncritically, especially those which offer seductive simplicity. Before any of the estimators reviewed here is used in generating scientific advice, its strengths and weaknesses should be fully understood. The consequences of the inevitable high uncertainty in estimated M should be thoroughly explored and explained to fishery managers.

Future advances

Maunder and Wong (2011) have expressed surprise at the lack of serious efforts to estimate M and it does appear strange that so much effort should be devoted to advanced modelling for assessments of 'information-rich' fisheries when the results are too often conditioned upon crude estimates of the central parameter. Scientists fortunate enough to work with such fisheries should devote more attention to estimating not only an average M but also its variations – both for the refinement of their own assessments and as a foundation for improved, if still crude, estimators that will continue to be needed for the many 'information-poor' fisheries. Only when M is much better known in well-studied populations, especially including those in which large, old individuals can still be found, will it be possible to materially advance our ability to estimate the values for other resources. There is a particular need to better understand changes in M with the

increasing age and size of fish, both its general decline and the onset and rate of senescent increase, including variations in those patterns among taxa. Nor should it be forgotten that M is both temporally and spatially variable, though the extent of that variability is all but unknown through lack of study.

The main scope for improved estimators for 'information-poor' situations appears to lie not in refining the existing generic approaches, nor in geographically-limited estimators such as Djabali's, but in developing taxon-specific alternatives. Beverton and Holt (1959), Bayliff (1967), Pauly (1980b), Beverton (1992), Pascual and Iribarne (1993) and others have recognized that the relationships between M and various predictors differ between taxa but the dearth of well-founded prior estimates has pushed that reality aside, resulting in estimators that can be wildly erroneous. Many fish expend resources on defensive morphology or predator-avoidance behaviours and it is to be expected that those species enjoy lower M as a consequence. All such factors are, however, ignored by the currently available estimators. Nor can it simply be assumed that the taxonomic variability lies entirely between Families or even between Genera and there may be advantages in seeking estimators specific to particular ecological roles, as Griffiths and Harrod (2007) attempted.

The future role of estimators of M -at-size remains unsure. Gislason *et al.* (2010) have correctly stressed the need to consider the changes in mortality driven by growth but that may be too much to ask of simple estimators for 'information-limited' situations that often fail to provide useful values for even a single, size-generalized, adult M . Nor is it clear that the sort of simple, robust assessments that are suited to imprecise estimates of M can utilize size-specific inputs. Nevertheless, Peterson and Wroblewski's, Ursin's, Gislason's First and Gislason's Second estimators merit further consideration, including testing against 'known' M -at-size.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Reasons for selecting, and sources of parameter estimates for, example populations.