Comparison of two approaches for estimating natural mortality based on longevity[*]

David A. Hewitt

John M. Hoenig

Virginia Institute of Marine Science
The College of William and Mary
P.O. Box 1346
Gloucester Point, Virginia 23062
E-mail address (for D. A. Hewitt): dhewitt@vims.edu

Vetter (1988) noted that her review of the estimation of the instantaneous natural mortality rate (M) was initiated by a discussion among colleagues that identified M as the single most important but least well-estimated parameter in fishery models. Although much has been accomplished in the intervening years, M remains one of the most difficult parameters to estimate in fishery stock assessments. A number of novel approaches using tagging and telemetry data provide promise for making reliable direct estimates of M for a given stock (Hearn et al., 1998; Frusher and Hoenig, 2001; Hightower et al., 2001; Latour et al., 2003; Pollock et al., 2004). However, such methods are often impracticable and fishery scientists must approximate M by using estimates made for other stocks of the same or similar species or by predicting M from features of the species' life history (Beverton and Holt, 1959; Beverton, 1963; Alverson and Carney, 1975; Pauly, 1980; Hoenig, 1983; Peterson and Wroblewski, 1984; Roff, 1984; Gunderson and Dygert, 1988; Chen and Watanabe, 1989; Charnov, 1993; Jensen, 1996; Lorenzen, 1996).

We are concerned with two approaches for predicting M based solely on the longevity of the members of a stock—an approach that can be used when data are not available to make direct estimates of the parameter. One is a linear regression model (Hoenig, 1983) and the other is a simple rule-of-thumb approach. Hoenig (1983) found that M was inversely correlated with longevity across a wide variety of taxa and recommended use of the following predictive equation relating the maximum age observed in the stock (t_{max}) to M:

$$\ln(\hat{M}) = 1.44 - 0.982 \times \ln(t_{max}). \quad (1)$$

The rule-of-thumb approach consists of determining the value of M such that $100(P)\%$ of the animals in the stock survive to the age t_{max}; thus,

$$\hat{M} = \frac{-\ln(P)}{t_{max}}. \quad (2)$$

The challenge in this approach is determining an appropriate value for the proportion P.

The rule-of-thumb approach has the potential to be used widely because it is presented in Quinn and Deriso (1999) and stock assessment manuals of the Food and Agriculture Organization of the United Nations (FAO; Sparre and Venema, 1998; Cadima, 2003). The approach has recently been used extensively, in the specific form $M \approx 3/t_{max}$, in work related to stock assessments for blue crab (*Callinectes sapidus*). In this note, we 1) show that the regression model and the rule-of-thumb approach can be compared directly; 2) illustrate the difference in the estimates of M generated by the two approaches; 3) discuss the origins and current use of the rule-of-thumb approach; and 4) recommend that the regression model be used instead of the rule-of-thumb approach.

Methods

With the rule-of-thumb approach, the fraction of a population that survives to a given age is used to estimate M. This approach is equivalent to a quantile estimator (Bury, 1975). Suppose the fraction surviving to age t is described by the negative exponential function

$$\frac{N_t}{N_0} = e^{-Zt}, \quad (3)$$

where Z is the total instantaneous mortality rate. The quantile estimator is of the form

$$P = e^{-Z\tau_P}, \quad (4)$$

where τ_P is the age at which $100(P)\%$ of the population remains. In the case where $P = 0.05$, the estimator, based on data from a sample of the population, is

$$0.05 = e^{-\hat{Z}t_{0.05}}, \quad (5)$$

where 5% of the animals in the sample are older than age $t_{0.05}$.

To estimate M, an empirical approach is usually taken where $t_{0.05}$ is replaced with t_{max}:
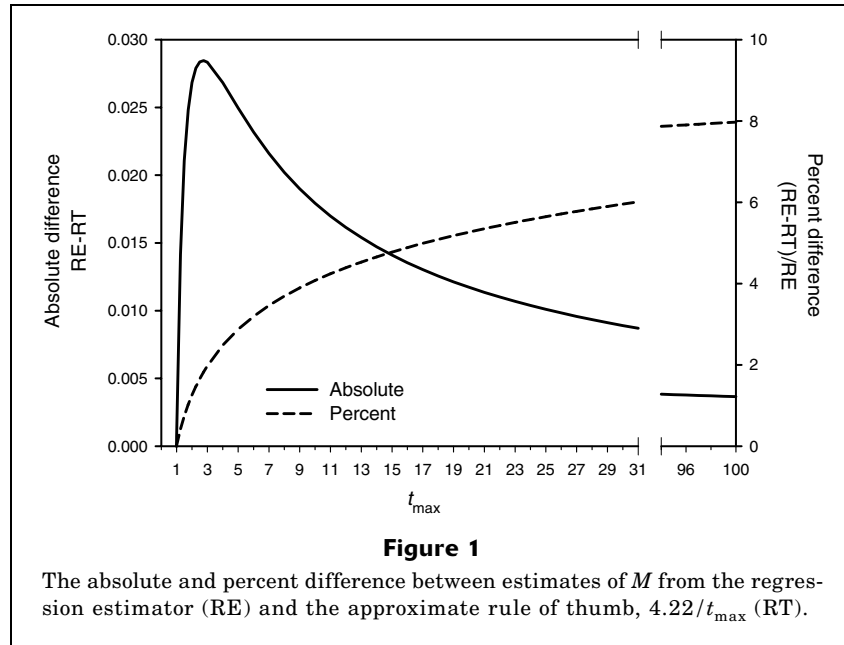
$$0.05 = e^{-\hat{M}t_{max}}, \quad (6)$$

where t_{max} is either the oldest age observed in the stock or the oldest age found in the literature for the species of interest. When age composition data are used from an exploited stock, Equation 6 will provide an estimate of M only if fishing mortality is reasonably close to zero ($M \approx Z$) or if there is a refuge where older animals can accumulate. If exploitation affects all

Figure 1

The absolute and percent difference between estimates of M from the regression estimator (RE) and the approximate rule of thumb, $4.22/t_{max}$ (RT).

animals in the stock, Equation 6 is unlikely to provide a reliable estimate of M.

The rule of thumb for approximating M follows directly from Equation 6:

$$-\ln(0.05) = \hat{M} \times t_{max}$$
$$\hat{M} = \frac{2.996}{t_{max}} \approx \frac{3}{t_{max}}. \tag{7}$$

Most importantly, note that the use of 0.05 or any other proportion in the equations is arbitrary because we have no reason to believe that t_{max} pertains to any particular quantile.

We show in the present study that this arbitrary rule of thumb for approximating M is unnecessary, as an empirical method (Hoenig, 1983) provides an analogous estimate based on a substantial data set. Equation 1 is based on the same model as that in Equation 3 and was developed from a regression of $\ln(M)$ on $\ln(t_{max})$ from data on 134 stocks of 79 species of fish, mollusks, and cetaceans. It can be shown to be of the same form as the rule-of-thumb approach as follows:

$$e^{\ln(\hat{M})} = e^{1.44 - 0.982 \times \ln(t_{max})}$$

$$\hat{M} = \frac{e^{1.44}}{e^{0.982 \times \ln(t_{max})}}$$

$$= \frac{4.22}{(t_{max})^{0.982}} \tag{8}$$

$$\approx \frac{4.22}{t_{max}}$$

Results

We substituted 1.0 for 0.982 in Equation 8 to allow the development of a simple, approximate rule of thumb for direct comparison with $3/t_{max}$. As a result, this rule of thumb strictly applies only to the case where $t_{max} = 1$. Estimates from the regression estimator in Equation 1 are always greater than estimates from Equation 8 for $t_{max} > 1$, although the difference is usually small (Fig. 1).
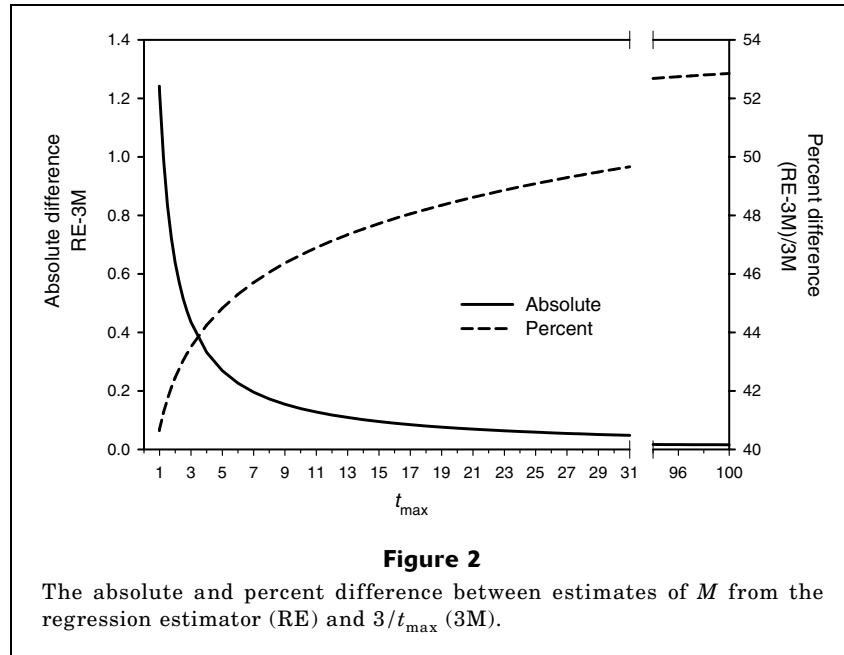
Estimates from the regression estimator are typically 40–50% greater than estimates from $3/t_{max}$ (Fig. 2). For example, if a maximum age of eight years is used for blue crab in Chesapeake Bay (Rugolo et al., 1998), $3/t_{max}$ gives an estimate for M of 0.375/yr and the regression estimator gives 0.548/yr.

Perhaps the most significant result is the finding that rearrangement of the regression model yields an estimate of an appropriate value for P in Equation 2. The value of 4.22 in Equation 8 approximately corresponds to $-\ln(0.015)$, indicating that the average longevity for stocks in the data set used by Hoenig (1983) is the age at which about 1.5% of the stock remains alive (versus 5% in $3/t_{max}$).

Discussion

Development of the rule-of-thumb approach

The rule-of-thumb approach appears to have arisen independently in four different places. Cadima (2003) supported the approach by citing the early work of Tanaka (1960). Sparre and Venema (1998) based their presen-

Figure 2

The absolute and percent difference between estimates of M from the regression estimator (RE) and $3/t_{max}$ (3M).

tation on the work of Alagaraja (1984), who provided the mathematics of a method that Sekharan (1975) used without description. Interestingly, Shepherd and Breen (1992) rearranged Equation 3 to obtain the rule of thumb based on the results of Hoenig (1983). This latter presentation is provided in Quinn and Deriso (1999). In all of these cases, the proportion of animals surviving to t_{max} is assumed to be some arbitrarily small value, typically 1% or 5%.

The development and use of the specific form $3/t_{max}$ in blue crab work occurred altogether separately. Its use began with an assessment for the Chesapeake Bay stock, in which Rugolo et al. (1998) used an estimate of M based on "the ICES [International Council for the Exploration of the Sea] convention; that is, 5% survivorship at maximum age following negative exponential depletion." The approach is more explicitly defined in their original document (Rugolo et al.[1]) as $M = (3/maximum\ age)$. The report also states that "this convention ... is widely used for many east coast finfish stocks (NMFS [National Marine Fisheries Service]/NEFSC [Northeast Fisheries Science Center], ASMFC [Atlantic States Marine Fisheries Commission])." Following its introduction by Rugolo et al. (Rugolo et al.[1]; Rugolo et al., 1998), the $3/t_{max}$ approach has been used in nearly all blue crab

stock assessment work conducted on the east coast of the United States (Miller and Houde[2]; Miller, 2001; Murphy et al.[3]; Helser et al., 2002; Kahn[4]).

The references used by Rugolo et al. (1998) in support of what they termed the "ICES convention" (Anthony[5]; Vetter, 1988) do not mention the $3/t_{max}$ approach. Rather than advocating a method for determining M, Anthony[5] called for standardization of the range of ages to include in the calculation of yield-per-recruit for a stock; this range of ages was termed the stock's "fishable life span." He proposed that the fishable life span should be defined such that the oldest age would be that

[1] Rugolo, L., K. Knotts, A. Lange, V. Crecco, M. Terceiro, C. Bonzek, C. Stagg, R. O'Reilly, and D. Vaughan. 1997. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus*), 267 p. Report of the Technical Subcommittee of the Chesapeake Bay Stock Assessment Committee of the National Marine Fisheries Service, NOAA (National Oceanic and Atmospheric Administration). NOAA Chesapeake Bay Office, 410 Severn Avenue, Suite 107, Annapolis, MD 21403.

[2] Miller, T. J., and E. D. Houde. 1999. Blue crab target setting, 167 p. Final report to the Living Resources Subcommittee of the Chesapeake Bay Program. University of Maryland Center for Environmental Science (UMCES) Technical Series No. TS-177-99. Chesapeake Bay Program, U.S. EPA (Environmental Protection Agency), 410 Severn Avenue, Annapolis, MD 21403.

[3] Murphy, M. D., C. A. Meyer, and A. L. McMillen-Jackson. 2001. A stock assessment for blue crab, *Callinectes sapidus*, in Florida waters, 56 p. FMRI (Florida Marine Research Institute) Inhouse Report Series IHR 2001-008. Florida Fish and Wildlife Conservation Commission, FMRI, 100 Eighth Avenue SE, St. Petersburg, FL 33701.

[4] Kahn, D. M. 2003. Stock assessment of Delaware Bay blue crab (*Callinectes sapidus*) for 2003, 52 p. Delaware Department of Natural Resources and Environmental Control, Division of Fish and Wildlife, P.O. Box 330, Little Creek, DE 19961.

[5] Anthony, V. C. 1982. The calculation of $F_{0.1}$: a plea for standardization, 16 p. Northwest Atlantic Fisheries Organization (NAFO) Serial Document N557, SCR 82/VI/64. NAFO Secretariat, P.O. Box 638, Dartmouth, Nova Scotia B2Y 3Y9, Canada.

at which 5% or less of the initial recruits survived. The use of Anthony's standard to approximate M makes the assumption that the fishable life span of an exploited stock is the same as the longevity of the members of the stock in an unexploited condition. It is unlikely that this assumption will be met unless the fishery is at an early stage in its development because fishing may alter the age structure of the stock (Hilborn and Walters, 1992). We note that although a limited number of scientists involved with ICES have used $3/t_{max}$ in a general way, the method has not been adopted as a convention within ICES (O'Brien[6]). Furthermore, we did not find evidence that the approach is currently in common use in stock assessments on the east coast of the United States, with the exception of those for blue crab. Nonetheless, the rule-of-thumb approach certainly has the potential to be used widely, given its repeated presentation in fishery literature and its accumulated momentum in blue crab work.

Recommendations

The power of empirical relationships for predicting natural mortality can be rather limited (Vetter, 1988; Pascual and Iribarne, 1993), and the uncertainty associated with parameter estimates should be taken into account whenever possible (Patterson et al., 2001). Furthermore, methods for directly estimating M are likely to be preferable to making predictions based on life history features. Nonetheless, such estimates may be needed when available data are inadequate for making a direct estimate. Given the results of our comparison, we recommend that the regression estimator be used instead of the rule-of-thumb approach when longevity is used to predict M. The regression estimator is based on a least squares fit to an extensive data set and thus matches experience better than a rule-of-thumb approach based on an arbitrary constant.

We recommend that use of the $3/t_{max}$ rule of thumb be abandoned, despite it being entrenched in blue crab literature. For a species like blue crab, for which t_{max} is less than 10 years, the differences in the estimates of M from the regression estimator and $3/t_{max}$ are not trivial (~45%). Although the regression estimator was based on data for fish, mollusks, and cetaceans (Hoenig, 1983) and may not be applicable to other exploited taxa, such as crustaceans, the model had a good fit to the data across widely disparate taxa. Finally, estimates of M for blue crab based on longevity are controversial because of continued difficulty in determining an appropriate t_{max}. In the absence of data to directly estimate M for this species, we suggest that the most prudent course

of action is a review and comparison of other methods for predicting M.

Acknowledgments

Literature cited

Alagaraja, K.
    1984. Simple methods for estimation of parameters for assessing exploited fish stocks. Indian J. Fish. 31:177–208.
Alverson, D. L., and M. J. Carney.
    1975. A graphic review of the growth and decay of population cohorts. J. Cons. Int. Explor. Mer 36:133–143.
Beverton, R. J. H.
    1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 154:44–67.
Beverton, R. J. H., and S. J. Holt.
    1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. *In* The lifespan of animals, CIBA Foundation colloquia on ageing, vol. 5 (G. E. W. Westenholme and M. O'Connor, eds.), p. 142–177. Little, Brown and Company, Boston, MA.
Bury, K. V.
    1975. Statistical models in applied science, 625 p. John Wiley and Sons, New York, NY.
Cadima, E. L.
    2003. Fish stock assessment manual. FAO Fish. Tech. Pap. 393, 161 p. FAO, Rome.
Charnov, E. L.
    1993. Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford Univ. Press, New York, NY.
Chen, S., and S. Watanabe.
    1989. Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55:205–208.
Frusher, S. D., and J. M. Hoenig.
    2001. Estimating natural and fishing mortality and tag reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear tagging model. Can. J. Fish. Aquat. Sci. 58:2490–2501.
Gunderson, D. R., and P. H. Dygert.
    1988. Reproductive effort as a predictor of natural mortality rate. J. Cons. Int. Explor. Mer 44:200–209.
Hearn, W. S., K. H. Pollock, and E. N. Brooks.
    1998. Pre- and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. Can. J. Fish. Aquat. Sci. 55:199–205.

---

[6] O'Brien, C. M. 2004. Personal commun. Chair of ICES Working Group on Methods of Fish Stock Assessments and ICES Resource Management Committee. CEFAS (Centre for Environment, Fisheries and Aquaculture Science) Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, England.

Helser, T. E., A. Sharov, and D. M. Kahn.
    2002.   A stochastic decision-based approach to assessing the status of the Delaware Bay blue crab stock.   *In* Incorporating uncertainty into fishery models (J. M. Berkson, L. L. Kline, and D. J. Orth, eds.), p. 63–82.   Am. Fish. Soc., Symposium 27, Bethesda, MD.

Hightower, J. E., J. R. Jackson, and K. H. Pollock.
    2001.   Use of telemetry methods to estimate natural and fishing mortality of striped bass in Lake Gaston, North Carolina.   Trans. Am. Fish. Soc. 130:557–567.

Hilborn, R., and C. J. Walters.
    1992.   Quantitative fisheries stock assessment: choice, dynamics and uncertainty, 570 p.   Chapman and Hall, New York, NY.

Hoenig, J. M.
    1983.   Empirical use of longevity data to estimate mortality rates.   Fish. Bull. 82:898–903.

Jensen, A. L.
    1996.   Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival.   Can. J. Fish. Aquat. Sci. 53:820–822.

Latour, R. J., J. M. Hoenig, D. A. Hepworth, and S. D. Frusher.
    2003.   A novel tag-recovery model with two size classes for estimating fishing and natural mortality, with implications for the southern rock lobster (*Jasus edwardsii*) in Tasmania, Australia.   ICES J. Mar. Sci. 60:1075–1085.

Lorenzen, K.
    1996.   The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture.   J. Fish Biol. 49:627–647.

Miller, T. J.
    2001.   Matrix-based modeling of blue crab population dynamics with applications to the Chesapeake Bay.   Estuaries 24:535–544.

Pascual, M. A., and O. O. Iribarne.
    1993.   How good are empirical predictions of natural mortality?   Fish. Res. 16:17–24.

Patterson, K., R. Cook, C. Darby, S. Gavaris, L. Kell, P. Lewy, B. Mesnil, A. Punt, V. Restrepo, D. W. Skagen, and G. Stefansson.
    2001.   Estimating uncertainty in fish stock assessment and forecasting.   Fish and Fisheries 2:125–157.

Pauly, D.
    1980.   On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks.   J. Cons. Int. Explor. Mer 39:175–192.

Peterson, I., and J. S. Wroblewski.
    1984.   Mortality rate of fishes in the pelagic ecosystem.   Can. J. Fish. Aquat. Sci. 41:1117–1120.

Pollock, K. H., H. Jiang, and J. E. Hightower.
    2004.   Combining telemetry and fisheries tagging models to estimate fishing and natural mortality rates.   Trans. Am. Fish. Soc. 133:639–648.

Quinn, T. J. II, and R. B. Deriso.
    1999.   Quantitative fish dynamics, 542 p.   Oxford Univ. Press, New York, NY.

Roff, D. A.
    1984.   The evolution of life history parameters in teleosts.   Can. J. Fish. Aquat. Sci. 41:989–1000.

Rugolo, L. J., K. S. Knotts, A. M. Lange, and V. A. Crecco.
    1998.   Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun).   J. Shellfish Res. 17: 493–517.

Sekharan, K. V.
    1975.   Estimates of the stocks of oil sardine and mackerel in the present fishing grounds off the west coast of India.   Indian J. Fish. 21:177–182.

Shepherd, S. A., and P. A. Breen.
    1992.   Mortality in abalone: its estimation, variability and causes.   *In* Abalone of the world: biology, fisheries and culture (S. A. Shepherd, M. J. Tegner, and S. A. Guzman del Proo, eds.), p. 276–304.   Fishing News Books, Cambridge, UK.

Sparre, P., and S. C. Venema.
    1998.   Introduction to tropical fish stock assessment, Part 1: manual.   FAO Fish. Tech. Pap. 306/1, rev. 2, 407 p.   FAO, Rome.

Tanaka, S.
    1960.   Studies on the dynamics and the management of fish populations.   Bull. Tokai Reg. Fish. Res. Lab. 28:1–200.

Vetter, E. F.
    1988.   Estimation of natural mortality in fish stocks: a review.   Fish. Bull. 86:25–43.