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[Article]

A Revised Alverson and Carney Model for Estimating the Instantaneous Rate of Natural Mortality

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Abstract.—The Alverson and Carney (AC) model for estimating the instantaneous rate of natural mortality (M) was reformulated to include β and t_0 parameters. The revised Zhang and Megrey (ZM) model could be used for the estimation of M instead of the AC model since von Bertalanffy and allometric growth parameters are readily available for most exploited fish stocks. It was determined from the new formulation that the ratios of the age at maximum biomass (t_{mb}) to the maximum age (t_{max}) for pelagic and demersal species were significantly different from 0.38, the value originally proposed by Alverson and Carney. The ratios for these two ecological groups were 0.302 and 0.440, respectively, and were significantly different. We examined the sensitivity and bias in M from the new formulation relative to those from the AC model, which assumed that $\beta = 3.0$ and $t_0 = 0$. Estimates of M from the AC model are most sensitive to the assumption that growth starts at $t_0 = 0$ when growth rates are high as well as to the β and t_{mb} assumptions. The performance of the revised ZM model was evaluated by comparing calculated M values from the two models based on a paired-sample t-test. The results of the two statistical analyses showed that the ZM model produced values of M closer to published estimates than did the AC model. Thus, the ratio t_{mb}/t_{max} for specific ecological groups should be used rather than Alverson and Carney's constant 0.38. Analyses of exploited stock dynamics might be conducted using the possible range of M instead of the constant value. The range could be estimated from the ZM model using the mean ratio t_{mb}/t_{max} ± SD to get the t_{mb} for each subgroup or by explicit variance calculations.

The instantaneous rate of natural mortality (M) in exploited fish stocks is defined as the mortality created by all causes other than fishing. These include deaths from predation, cannibalism, disease, spawning stress, starvation, and senescence (Beverton and Holt 1957).

The value of M is considered one of the two critical aspects of the dynamics of a single species, which, together with the relation between recruitment and adult stock, produces significant uncertainties in long-term stock assessment and the strategic advice given to managers using traditional approaches. The significance of the value of M for management advice (e.g., on target values of fishing mortality, F) is well known to stock assessment scientists (Clark 1999) but has received less attention from the general fishery research community. One reason for this is that the degree of uncertainty in the values of M currently being used is not always obvious. Many assessment techniques, such as virtual population assessments, require setting the value of M early in the analysis, and the values used by assessment groups often become institutionalized mainly from customary use. Another reason is that it is difficult to identify lines of research that offer good prospects for coming up with better estimates of M (Gulland 1983). Therefore, at present, M is considered an important but poorly quantified parameter in most mathematical models of fish stock dynamics (Vetter 1988; Quinn and Deriso 1999).

Direct measurements of M are often difficult to obtain. Consequently, there have been many attempts to identify quantities that can be directly or indirectly related to M and that are easier to estimate (Sparre et al. 1989). Several attempts along these lines have been made to estimate M indirectly using reproduction indices (Rikhter and Efanov 1976; Gunderson and Dygert 1988; Gunderson 1997) or life history parameters (Alverson and Carney 1975; Pauly 1980).

Both the instantaneous rate of natural mortality and the curvature of growth on age are fundamental population-dynamic measures of fish. Growth and mortality may be correlated in an empirically useful way, namely, fast-growing fish tend to have higher mortality rates. The von Bertalanffy curvature parameter, K, which describes the rate at which the maximum size is approached, is linked to the longevity of the fish (Beverton and Holt 1959; Beverton 1992), and longevity is related to mortality (Tanaka 1960; Holt 1965; Saville 1977; Hoenig 1983; Alagaraja 1984). Ralston (1987) argued that M can simply be predicted

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with K, the former being roughly twice the latter, based on a review of the snapper (Lutjanidae) and grouper (Serranidae) literature. More recently, Jensen (1996) concluded that K alone was adequate for prediction. He proposed the formula $M = 1.60K$ based on the data for K and M on 175 different species provided by Pauly (1980). As a rough generalization, a long-lived fish approaches its limiting size relatively slowly, whereas a short-lived fish grows rapidly. Thus, fish species with high K values usually have high M values, and vice versa. A slowly growing species cannot bear high natural mortality, because if it did, it would never reach maturity and would soon go extinct.

Alverson and Carney (1975) assumed populations that had an exponential decay function describing their abundance through time and a von Bertalanffy growth schedule. They derived an empirical equation relating M to the maximum age and the growth parameter K. They solved the relationship between maximum age and critical age (the age at which the biomass of the cohort is maximum) using 63 reported stocks. However, they assumed that fish length was zero at age zero (i.e., eliminating the parameter t_0). Alverson and Carney (1975) stated that their empirical relationship would require future adjustments to accommodate negative values of t_0. Alverson and Carney (1975) also assumed isometric growth, that is, that weight is proportional to the cube of length. Quinn and Deriso (1999) indicate that the cubic relationship does not usually fit actual data well, and they also explicitly caution that the Alverson and Carney approach has not been strictly reevaluated in terms of the allometric growth model.

In spite of the simplifying assumptions, the Alverson and Carney model is still widely used to estimate M, and most population dynamics textbooks introduce this model as one of the standard methods (Sparre et al. 1989; Zhang 1991; Quinn and Deriso 1999). Moreover, a number of applied studies continue to rely on this model to estimate M (Efimov 1984; Megrey et al. 1990; Wakabayashi and Watanabe 1990; Quinn and Szarzi 1993; Zhang et al. 1998a; Wilderbuer and Zhang 1999).

In this paper, we have three objectives: (1) to reformulate the Alverson and Carney empirical relationship for estimating M to include the β and t_0 parameters; (2) to examine the sensitivity and bias of M to the assumptions that $\beta = 3.0$ and $t_0 = 0$; and (3) to reexamine Alverson and Carney's use of a constant 0.38 in relating the maximum age to the critical age and test whether the 0.38 multiplier is generally applicable for ecologically different groups of fishes, since the more r-strategic pelagic species could have different life history characteristics from the more K-strategic demersal species.

Methods

Derivation of the reformulation.—The exponential decay curve of Baranov (1918), which describes the decrease in abundance through time due to mortality, is given by

$$N_t = N_0 e^{-Mt}, \tag{1}$$

where N_t is the abundance at time t, N_0 is the abundance at $t = 0$, and M is the rate of natural mortality.

The growth of an animal, in length, can be represented by the von Bertalanffy model (von Bertalanffy 1938),

$$L_t = L_\infty[1 - e^{-K(t-t_0)}], \tag{2}$$

where L_t is the mean length of the fish at age t, L_∞ is the mean asymptotic length (i.e., the length it would ultimately reach at an infinitely old age), K is the Brody growth rate per unit of time, and t_0 is the theoretical age at which the fish would have length zero if it had always grown as described by equation (2). Theoretically, t_0 is rarely equal to zero, and it is usually less than zero (Quinn and Deriso 1999).

Fish growth can be expressed in terms of length or weight since the three dimensions making up a fish's body—length, width, and depth—all change over time. Under isometric assumptions, weight at age can be written as

$$W_t = \alpha L_t^3, \tag{3}$$

where L_t represents length and W_t represents weight, both at age t. With fish, the isometric relationship typically does not hold (Quinn and Deriso 1999), so equation (3) needs to be generalized to the allometric model, written as

$$W_t = \alpha L_t^\beta, \tag{4}$$

which assumes that growth in weight is proportional to some power of length. Equations (2) and (4) can be combined to express growth in weight through time as follows:

$$W_t = W_\infty[1 - e^{-K(t-t_0)}]^\beta, \tag{5}$$

where W_t is the mean weight of the fish at age t and W_∞ is the mean asymptotic weight.

Biomass at age t, B_t, is obtained by multiplying equation (1) by equation (5),

$$B_t = N_t W_t = N_0 W_\infty e^{-Mt}[1 - e^{-K(t-t_0)}]^\beta. \tag{6}$$

The instantaneous change in biomass with respect to age t is the time derivative of equation (6), namely,

$$\begin{aligned}\frac{dB_t}{dt} = {} & \beta K e^{Kt_0} N_0 W_\infty e^{-(M+K)t}[1 - e^{-K(t-t_0)}]^{\beta-1} \\ & - M N_0 W_\infty e^{-Mt}[1 - e^{-K(t-t_0)}]^\beta. \end{aligned} \tag{7}$$

By setting equation (7) to zero and $t = t_{\text{mb}}$, the critical age (the time that the cohort achieves its maximum biomass) is

$$\hat{M}_{\mathrm{ZM}} = \frac{\beta K}{e^{K(t_{\mathrm{mb}}-t_0)} - 1}, \tag{8}$$

where $t_{\mathrm{mb}} = C_i{\cdot}t_{\max}$. Here, $t_{\max}$ is the maximum age observed in the population (Beverton and Holt 1959; Alagaraja 1984). Since the ratio of the critical age to the maximum age could be different from a constant 0.38 for different ecological groups (especially for pelagic versus demersal species), the constant for each specific ecological group i, $C_{i,}$ is defined. In this study, i represents either the pelagic group or the demersal group. Equation (8) (hereafter referred to as the Zhang and Megrey model, or ZM model) indicates that natural mortality M can be expressed as a function of the growth rate (K), the power parameter of the length –weight relationship (β), the time the growth curve begins (t_0), and the critical age (t_{mb}).

Equation (8) can be rearranged to provide an estimate of the time at which a cohort maximizes its weight and the animal has reached critical age, namely,

$$t_{\mathrm{mb}} = \frac{\log_e\left(\frac{\beta K e^{Kt_0}}{\hat{M}_{\mathrm{ZM}}} + e^{Kt_0}\right)}{K}. \tag{9}$$

Equation (8) is an extension to the formulation of Alverson and Carney (1975; hereafter referred to as the Alverson and Carney model, or AC model),

$$\hat{M}_{\mathrm{AC}} = \frac{3K}{e^{Kt_{\mathrm{mb}}} - 1}, \tag{10}$$

where Alverson and Carney assumed that the proportionality relating t_{mb} to $t_{\max}$ is constant for all species defined by $t_{\mathrm{mb}} = 0.38{\cdot}t_{\max}$.

The variance of M can be approximated from equation (8) using the delta method (Seber 1982), as follows:

$$\begin{aligned}\mathrm{var}(\hat{M}) &= \left(\frac{\partial\hat{M}}{\partial\beta}\right)^2\cdot\mathrm{var}(\beta) + \left(\frac{\partial\hat{M}}{\partial K}\right)^2\cdot\mathrm{var}(K)\\ &+ \left(\frac{\partial\hat{M}}{\partial t_0}\right)^2\cdot\mathrm{var}(t_0) + \left(\frac{\partial\hat{M}}{\partial t_{\mathrm{mb}}}\right)^2\cdot\mathrm{var}(t_{\mathrm{mb}})\\ &+ 2\,\mathrm{cov}(\beta,K)\frac{\partial\hat{M}}{\partial\beta}\frac{\partial\hat{M}}{\partial K} + 2\,\mathrm{cov}(\beta,t_0)\frac{\partial\hat{M}}{\partial\beta}\frac{\partial\hat{M}}{\partial t_0}\\ &+ 2\,\mathrm{cov}(\beta,t_{\mathrm{mb}})\frac{\partial\hat{M}}{\partial\beta}\frac{\partial\hat{M}}{\partial t_{\mathrm{mb}}} + 2\,\mathrm{cov}(K,t_0)\frac{\partial\hat{M}}{\partial K}\frac{\partial\hat{M}}{\partial t_0}\\ &+ 2\,\mathrm{cov}(K,t_{\mathrm{mb}})\frac{\partial\hat{M}}{\partial K}\frac{\partial\hat{M}}{\partial t_{\mathrm{mb}}} + 2\,\mathrm{cov}(t_0,t_{\mathrm{mb}})\frac{\partial\hat{M}}{\partial t_0}\frac{\partial\hat{M}}{\partial t_{\mathrm{mb}}}.\end{aligned} \tag{11}$$

This requires evaluating the partial derivatives of equation (8) with respect to t_0, t_{mb}, K, and β, namely,

$$\frac{\partial\hat{M}}{\partial t_0} = \frac{\beta K^2 e^{K(t_{\mathrm{mb}}-t_0)}}{\left[e^{K(t_{\mathrm{mb}}-t_0)} - 1\right]^2} \tag{11a}$$

$$\frac{\partial\hat{M}}{\partial t_{\mathrm{mb}}} = \frac{-\beta K^2 e^{K(t_{\mathrm{mb}}-t_0)}}{\left[e^{K(t_{\mathrm{mb}}-t_0)} - 1\right]^2} \tag{11b}$$

$$\frac{\partial\hat{M}}{\partial K} = \frac{\beta\left[e^{K(t_{\mathrm{mb}}-t_0)} - Kt_{\mathrm{mb}}e^{K(t_{\mathrm{mb}}-t_0)} + Kt_0e^{K(t_{\mathrm{mb}}-t_0)} - 1\right]}{\left[e^{K(t_{\mathrm{mb}}-t_0)} - 1\right]^2} \tag{11c}$$

$$\frac{\partial\hat{M}}{\partial\beta} = \frac{K}{e^{K(t_{\mathrm{mb}}-t_0)} - 1}. \tag{11d}$$

Sensitivity of estimates of M to β and t_0 assumptions.—Estimates of M were calculated according to the AC model ($\hat{M}_{\mathrm{AC}}$ from equation 10) and the ZM model ($\hat{M}_{\mathrm{ZM}}$ from equation 8) using values of $K = 0.1$ and $t_{\max} = 20$. The values of t_{mb} for both models were calculated from the formula $t_{\mathrm{mb}} = C_i{\cdot}t_{\max}$. For demersal species, values of $C_i = 0.38$ ($t_{\mathrm{mb}} = 7.6$) and $C_i = 0.44$ ($t_{\mathrm{mb}} = 8.8$) are used in the AC and ZM models, respectively. For pelagic species, values of $C_i = 0.38$ and $C_i = 0.302$ ($t_{\mathrm{mb}} = 6.04$) are used.

Sensitivity of estimates of M to β and t_{mb} assumptions.—Estimates of M were calculated according to the AC and ZM models using values of t_{mb} ranging from 5.0 to 20.0, β from 2.5 to 3.5, and t_0 from −3.0 to +3.0. The percent difference in the estimates of M from the AC and ZM models was computed according to the formula

$$\text{Percent difference} = \frac{\hat{M}_{\mathrm{ZM}} - \hat{M}_{\mathrm{AC}}}{\hat{M}_{\mathrm{AC}}} \times 100. \tag{12}$$

Two cases were considered. In the first, M values from the ZM and AC models were calculated as a function of β and t_{mb}, with t_0 fixed at 3.0 for a fast-growing ($K = 1.5$) and a slow-growing ($K = 0.1$) fish. In the second, M values from the ZM and AC models were calculated as a function of β and t_0, with t_{mb} fixed at 5.0 for a fast-growing and a slow-growing fish.

Data.—The data used to evaluate the relationships described earlier were based on a compilation of data extracted from the FishBase 98 database (Frose and Pauly 1998), those summarized by Ault et al. (1998) and Ault et al. (2005), and those from other data sources known to the authors (Table 1). In the following sections, estimated values of $\hat{M}_{\mathrm{AC}}$ and $\hat{M}_{\mathrm{ZM}}$ are compared with those reported in FishBase, which we refer to as the "true" values of M (M_{true}). Records from FishBase that contained all five values were extracted and screened by eliminating duplicate records. A total of 91 values of K, t_0, M_{true}, β, and maximum age ($t_{\max}$)

were assembled. There were not many fish stocks that had all of the parameters required for the calculations necessary in this study. Multiple length–weight conversion parameters and values of $t_{\max}$ were available from FishBase for each species, so the values of β and $t_{\max}$ reported in Table 1 represent the arithmetic average and the maximum value, respectively.

We consider data from FishBase suitable for our analysis since all of the life history parameters contained in FishBase are independent, that is, they were not estimated using rules of thumb or empirical models linking M to a predictor variable or variables such as those presented by Pauly (1980). Indeed, Frose and Pauly (1998) explicitly point out that the data in FishBase are appropriate for deriving new empirical models.

We use data for the Australian gemfish (Rowling 1999) to illustrate the utility of our new formulation. Detailed growth data on this species are shown in Table 1. Data on the variances of K, t_0, and β are from Rowling (1999), and those for $t_{\max}$ are from Rowling (1997). Even though we had only one observation of $t_{\max}$ for this example, we calculated a variance for this variable by assuming that its coefficient of variation was 10% and that its mean value was 16. We believe that this assumption is reasonable, as the maximum age of a fish should be known with great precision. Using the delta method, the variance of t_{mb} was calculated as

$$\mathrm{var}(t_{\mathrm{mb}}) = C_i^2 \mathrm{var}(t_{\max}).$$

Evaluation of the relationship of t_{mb} to the maximum age for different ecological groups.—For the estimation of t_{mb}, the data in Table 1 were disaggregated into two ecological subgroups defined as pelagic species (31 stocks) and demersal species (60 stocks). Using the values of K, M_{true}, β, and t_0 from Table 1, t_{mb} was estimated from equation (9) and then the ratio $t_{\mathrm{mb}}/t_{\max}$ was calculated. Statistical tests on the mean ratios for the pelagic and demersal groups were performed to assess whether they were statistically different for the two groups as well as different from 0.38, the value proposed by Alverson and Carney. In technical terms, a two-tailed t-test was used to test the null hypotheses that $\mu_{\mathrm{pelagic}} = \mu_{\mathrm{demersal}} = 0.38$.

To evaluate the performance of the ZM model, M values calculated from equations (8) and (10) were compared with M_{true} by means of a paired-sample t-test. A paired two-tailed t-test was used to test the null hypothesis that the difference between $\hat{M}_{\mathrm{AC}}$ or $\hat{M}_{\mathrm{ZM}}$ and M_{true} was zero.

Results

Sensitivity of Estimates of M to β and t_0 Assumptions

A comparison of the results from estimating M from the AC and ZM models is shown in Figure 1 for demersal and pelagic species. In the AC model, β = 3.0, $t_0 = 0$, and $\hat{M}_{\mathrm{AC}} = 0.2636$ over the entire range of β and t_0 and is shown as a plane. The variable $\hat{M}_{\mathrm{ZM}}$ is a nonlinear function of β and t_0 and is shown as a curvilinear response surface. Where the two surfaces intersect corresponds to values of β and t_0 where $\hat{M}_{\mathrm{AC}} = \hat{M}_{\mathrm{ZM}}$.

The AC model did not show any difference between pelagic and demersal species because the C_i value did not differ between these ecological groups. However, the ZM model showed that demersal species, which generally grow slowly, have lower mortalities than faster-growing pelagic species. The response surfaces from both models have the same shape for both ecological groups. The ZM model scales differently in the response of M because different values of C_i lead to different values of t_{mb}. For demersal species, the AC model generally produces higher values of M than the ZM model over a broad range of β and t_0, but for pelagic species, the AC model generally produces lower values of M.

Sensitivity of Estimates of M to β and t_{mb} Assumptions

A comparison of the percent difference (calculated from equation 12) in estimates of M from the two models is shown in Figure 2. The percent difference is shown as a function of β and t_{mb} given $t_0 = 3$ for a fast-growing ($K = 1.5$; panel A) and slow-growing fish ($K = 0.1$; panel B) and as a function of β and t_0 given $t_{\mathrm{mb}} = 5.0$ for a fast-growing (panel C) and slow-growing fish (panel D). Specific values of $\hat{M}_{\mathrm{ZM}}$, $\hat{M}_{\mathrm{AC}}$, and the percent difference given below are written as a function of the parameters (i.e., $\hat{M}_{\mathrm{ZM}}[t_{\mathrm{mb}}, β]$, $\hat{M}_{\mathrm{AC}}[t_{\mathrm{mb}}, β]$, and %diff[$t_{\mathrm{mb}}$, β]).

In most cases the ZM model produced higher values of M than the AC model. The percent differences were higher in the case of fast-growing fish (panels A, C). For example, when β and t_{mb} varied and K and t_0 were fixed at 1.5 and 3, respectively, $\hat{M}_{\mathrm{ZM}}(5, 3.5) = 0.2719$, $\hat{M}_{\mathrm{AC}}(5, 3.5) = 0.00249$, and %diff(5, 3.5) = 11,000. When $\hat{M}_{\mathrm{ZM}}(10, 2.5) = 0.0001219$, $\hat{M}_{\mathrm{AC}}(10, 2.5) = 1.5 \times 10^{-6}$, and %diff(10, 2.5) = 7,522. The ZM model generally produced higher values of M than the AC model. In the fast-growing case (panel A), $\hat{M}_{\mathrm{ZM}}$ was more responsive to changes in β and mildly responsive to changes in t_{mb}, resulting in large positive percent differences. In the slow-growing case (panel B), $\hat{M}_{\mathrm{ZM}}$ was responsive to both β and t_{mb}, still being more responsive to changes in β and generating lower values of percent difference.

In the situation where β and t_0 varied and K and t_{mb} were fixed (panels C, D), the AC model produced a simple plane with $\hat{M}_{\mathrm{AC}} = 0.0249$. Percent difference was very responsive to changes to t_0, especially for positive values of t_0. The response to β was minor at

TABLE 1.—Life history parameters used in this study (see text for definitions). Values of t_{mb} were calculated from equation 9 using M_{true} as the value of natural mortality. References are keyed to the numbered list that follows the table.

	Published values					Calculated values			Reference				
Species	t_{max}	K	t_0	M_{true}	β	t_{mb}	M_{ZM}	M_{AC}	t_{max}	K	T_0	M_{true}	β
Pelagic													
Atlantic herring *Clupea harengi*	25	0.33	−1.66	0.20	3.033	3.77	0.051	0.045	2	2	2	1	2
	25	0.44	−1.27	0.16	3.033	3.81	0.028	0.021	2	2	2	3	2
Pacific herring *Clupea pallasii*	15	0.16	−2.49	0.42	3.27	2.57	0.253	0.322	4	4	4	4	4
Blackfin tuna *Thunnus atlanticus*	5	0.33	−1.57	0.67	3.041	1.20	0.570	1.135	5	5	5	6	5
	5	0.330	−1.57	0.67	3.100	1.24	0.581	1.135	26	5	5	6	25
King mackerel *Scomberomorus cavalla*	14	0.14	−2.08	0.37	2.994	3.33	0.296	0.380	7	7	7	7	7
	14	0.28	−1.17	0.37	2.994	3.06	0.238	0.245	7	7	7	7	7
Yellowfin tuna *Thunnus albacares*	5	0.45	−0.75	0.80	2.881	1.39	0.736	0.999	8	8	8	8	8
	5	0.327	−1.02	0.80	2.981	1.42	0.758	1.139	8	29	28	27	27
Cutthroat trout *Oncorhynchus clarkii*	9	0.16	−0.38	0.30	3.032	5.63	0.757	0.659	9	9	9	9	9
Pacific sardine *Sardinops sagax caeruleus*	13	0.4	−0.59	0.15	3.00	4.90	0.237	0.193	10	10	10	10	10
	13	0.4	−2.1	0.45	3.00	1.15	0.119	0.193	10	10	10	10	10
Australian salmon *Arripis trutta*	26	0.38	−0.07	0.80	2.80	2.16	0.055	0.027	11	11	11	11	11
	26	0.3	−0.17	0.80	2.80	2.22	0.084	0.049	11	11	11	11	11
Atlantic thread herring *Opisthonema oglinum*	8	0.249	−1.07	0.55	3.14	2.48	0.567	0.660	12	13	13	12	13
South American pilchard[a] *Sardinops sagax sagax*	5.5	0.358	−0.24	0.79	2.83	2.07	1.041	0.965	14	14	14	14	15
European anchovy *Engraulis encrasicolus*	5	0.380	−0.93	0.81	3.41	1.58	0.850	1.077	16	16	16	16	16
European pilchard *Sardina pilchardus*	8	0.820	−0.129	0.50	3.27	2.13	0.381	0.222	20	18	18	17	19
Albacore *Thunnus alalunga*	6	0.262	−1.31	0.20	2.877	4.65	0.596	0.962	24	22	22	21	23
Skipjack tuna *Katsuwonus pelamis*	4	0.110	−1.97	0.65	3.150	1.91	0.829	1.813	28	5	5	6	25
Bluefin tuna *Thunnus thynnus*	13	0.162	−1.12	0.10	3.009	9.81	0.386	0.396	8	29	29	30	31
Bigeye tuna *Thunnus obesus*	11	0.106	−1.13	0.39	2.902	4.36	0.511	0.570	33	32	32	33	34
Japanese sardine *Sardinops melanostictus*	9	0.467	−0.09	0.49	3.615	3.10	0.624	0.356	35	36	36	35	37
Pacific saury *Cololabis saira*	2	0.340	−1.19	1.60	3.220	0.34	1.304	3.459	40	38	38	38	39
Atlantic salmon *Salmo salar*	6	0.288	−0.46	1.10	3.000	1.55	0.937	0.931	8	43	43	41	42
Pacific mackerel *Scomber japonicus*	12	0.490	0.40	0.50	3.394	3.39	0.433	0.176	47	44	44	45	46
Greenback horse mackerel *Trachurus declivis*	16	0.200	−0.87	0.67	3.050	2.37	0.287	0.253	49	48	48	48	49
Jack mackerel *Trachurus symmetricus*	30	0.093	−2.01	0.15	3.223	9.80	0.167	0.148	51	50	50	51	52
Narrowbarred mackerel *Scomberomorus commerson*	14	0.250	−1.72	0.44	2.89	2.17	0.211	0.270	52	52	52	52	52
Northern anchovy *Engraulis mordax*	7	0.349	−0.043	0.92	2.95	2.11	0.919	0.684	56	53	53	54	55
Japanese anchovy *Engraulis japonicus*	3	1.586	0.001	0.80	3.68	1.34	1.829	0.933	60	57	57	58	59
Demersal													
Atlantic cod *Gadus morhua*	23	0.19	−0.042	0.17	3.046	7.76	0.098	0.134	61	61	61	61	61
European hake *Merluccius merluccius*	10	0.19	−0.85	0.20	3.048	6.31	0.338	0.538	62	62	62	62	62
Crimson jobfish *Pristipomoides filamentosus*	18	0.15	−1.67	0.25	2.653	4.68	0.124	0.251	63	63	63	63	63
Red snapper *Lutjanus campechanus*	10	0.2	0.13	0.20	2.831	6.85	0.420	0.527	64	64	64	64	64
	16	0.162	−0.01	0.19	2.953	7.75	0.224	0.290	65	65	65	65	65
Black snapper *Apsilus dentatus*	10	0.097	−1.728	0.30	2.815	4.94	0.336	0.653	65	65	65	65	65
Blackfin snapper *Lutjanus buccanella*	9	0.084	−2.896	0.23	2.974	5.86	0.321	0.757	65	65	65	65	65
Cubera snapper *Lutjanus cyanopterus*	20	0.16	−0.30	0.15	3.06	8.76	0.149	0.202	65	65	65	65	65
Dog snapper *Lutjanus jocu*	9	0.1	−2.00	0.333	2.857	4.19	0.351	0.736	65	65	65	65	65
Gray snapper *Lutjanus griseus*	10	0.136	−0.863	0.30	2.881	5.28	0.375	0.603	65	65	65	65	65
Lane snapper *Lutjanus synagris*	10	0.097	−1.728	0.30	2.815	4.94	0.336	0.653	65	65	65	65	65
Mahogany snapper *Lutjanus mahogani*	10	0.097	−1.728	0.30	2.719	4.78	0.325	0.653	65	65	65	65	65
Mutton snapper *Lutjanus analis*	14	0.129	−0.738	0.214	3.011	7.29	0.271	0.392	65	65	65	65	65
Schoolmaster *Lutjanus apodus*	12	0.18	0.00	0.25	2.978	6.36	0.338	0.424	65	65	65	65	65
Silk snapper *Lutjanus vivanus*	9	0.092	−2.309	0.23	3.10	6.46	0.366	0.746	65	65	65	65	65
Vermilion snapper *Rhomboplites aurorubens*	10	0.206	0.111	0.23	2.946	6.38	0.428	0.520	65	65	65	65	65
Striped mullet *Mugil cephalus*	11	0.15	−2.64	0.25	2.966	4.18	0.215	0.516	65	65	65	65	65
Speckled hind *Epinephelus drummondhayi*	25	0.13	−1.01	0.20	3.073	7.43	0.106	0.160	66	66	66	66	66
Snowy grouper *Epinephelus niveatus*	27	0.09	−1.01	0.18	2.843	8.82	0.117	0.178	67	67	67	67	67
	15	0.113	−0.915	0.13	2.93	10.29	0.248	0.375	65	65	65	65	65
Black grouper *Mycteroperca bonaci*	20	0.16	−0.30	0.15	3.205	8.99	0.156	0.202	65	65	65	65	65
Coney *Cephalopholis fulva*	17	0.145	−1.08	0.18	2.57	6.66	0.152	0.280	65	65	65	65	65
Gag *Mycteroperca microlepis*	13	0.149	−0.802	0.20	3.031	7.13	0.275	0.411	65	65	65	65	65
Graysby *Cephalopholis cruentata*	15	0.13	−0.94	0.20	3.044	7.46	0.238	0.355	65	65	65	65	65
Goliath grouper *Epinephelus itajara*	37	0.054	−3.616	0.081	2.98	16.65	0.083	0.143	65	65	65	65	65
Nassau grouper *Epinephelus striatus*	17	0.145	−1.08	0.18	3.229	7.76	0.190	0.280	65	65	65	65	65
Red grouper *Epinephelus morio*	17	0.153	−0.099	0.18	3.035	8.24	0.212	0.272	65	65	65	65	65
Red hind *Epinephelus guttatus*	17	0.207	−0.831	0.18	2.614	5.87	0.118	0.221	65	65	65	65	65
Rock hind *Epinephelus adscensionis*	12	0.191	−2.16	0.25	3.019	4.10	0.184	0.412	65	65	65	65	65
Scamp *Mycteroperca phenax*	21	0.126	−1.357	0.143	2.993	8.89	0.135	0.218	65	65	65	65	65
Speckled hind	15	0.13	−1.01	0.20	3.073	7.43	0.237	0.355	65	65	65	65	65
Warsaw grouper *Epinephelus nigritus*	41	0.054	−3.616	0.08	2.98	16.80	0.073	0.123	65	65	65	65	65
Yellowedge grouper *Epinephelus flavolimbatus*	15	0.17	0.00	0.18	2.98	7.88	0.245	0.312	65	65	65	65	65
Yellowfin grouper *Mycteroperca venenosa*	15	0.17	0.00	0.18	2.98	7.88	0.245	0.312	65	65	65	65	65

TABLE 1.—Continued.

	Published values					Calculated values			Reference				
Species	t_{max}	K	t_0	M_{true}	β	t_{mb}	M_{ZM}	M_{AC}	t_{max}	K	T_0	M_{true}	β?
Pollock *Pollachius virens*	10	0.13	−0.90	0.30	3.01	5.52	0.395	0.610	68	68	68	68	68
Rough sculpin *Cottus asperrimus*	5	0.18	−1.42	0.56	3.01	2.34	0.590	1.324	69	69	69	69	69
Palefin threadfin bream *Nemipterus thosaporni*	5	0.42	−0.41	1.73	3.02	0.90	0.637	1.032	70	70	70	70	70
Greater lizardfish *Saurida tumbil*	7	0.29	−0.28	0.46	3.166	3.50	0.557	0.748	71	71	71	71	71
Spotfin hogfish *Bodianus pulchellus*	12	0.19	−0.776	0.25	2.97	5.44	0.261	0.414	65	65	65	65	65
Bluestriped grunt *Haemulon sciurus*	6	0.484	−0.011	0.50	2.99	2.80	0.555	0.721	65	65	65	65	65
Black margate *Anisotremus surinamensis*	8	0.174	−0.45	0.374	3.042	4.62	0.532	0.749	65	65	65	65	65
Sailors choice *Haemulon parra*	7	0.22	−0.355	0.428	2.993	3.88	0.583	0.830	65	65	65	65	65
Tomato grouper *Cephalopholis sonnerati*	9	0.091	−2.095	0.333	3.208	4.82	0.397	0.748	65	65	65	65	65
White grunt *Haemulon plumierii*	8	0.186	−0.776	0.375	3.161	4.29	0.481	0.734	65	65	65	65	65
Great barracuda *Sphytraena barracuda*	15	0.172	−0.461	0.20	3.083	7.07	0.224	0.310	65	65	65	65	65
Yellowtail snapper *Ocyurus chrysurus*	8	0.279	−0.36	0.45	2.805	3.25	0.401	0.627	72	72	72	72	72
European seabass *Dicentrarchus labrax*[b]	15	0.14	−0.20	0.10	3.045	11.66	0.268	0.344	73	73	73	73	73
Japanese threadfin bream *Nemipterus japonicus*	8	0.314	−1.11	0.52	2.991	2.18	0.286	0.590	75	75	75	74	75
Eurasian perch *Perca fluviatilis*	22	0.163	−0.14	0.12	3.19	10.13	0.131	0.168	76	76	76	76	76
Kamchatka flounder *Atheresthes evermanni*	15	0.302	−0.29	0.18	3.057	5.71	0.132	0.197	77	77	77	77	77
Pacific ocean perch *Sebastes alutus*	98	0.167	−0.907	0.05	3.03	13.52	0.000	0.001	79	78	78	78	78
Yellowfin sole *Limanda aspera*	34	0.165	2.035	0.12	3.083	12.07	0.068	0.067	79	80	80	80	80
Alaska plaice *Pleuronectes quadrituberculatus*	31	0.18	1.96	0.22	2.897	8.71	0.073	0.074	79	81	81	81	81
Atka mackerel *Pleurogrammus monopterygius*	15	0.439	−0.13	0.3	3.091	3.76	0.075	0.117	79	82	82	82	82
English sole *Parophrys vetulus*	22	0.31	−0.751	0.26	3.127	4.26	0.040	0.075	79	83	83	84	83
Pacific cod *Gadus macrocephalus*	7	0.33	−0.15	0.65	2.89	2.59	0.501	0.704	85	85	85	86	87
Spiny dogfish *Squalus acanthias*	66	0.06	−4.79	0.09	3.004	13.54	0.027	0.051	79	88	88	89	54
Arrowtooth flounder *Atheresthes stomias*	23	0.17	−0.50	0.20	3.103	7.10	0.104	0.149	79	90	90	90	90
Sablefish *Anoplopoma fimbria*	94	0.141	−6.05	0.10	3.19	6.04	0.001	0.003	79	82	82	82	82
Australian gemfish[c] *Rexea solandri*	16	0.196	−0.585	0.458	3.389	2.01	0.171	0.256	92	91	91	91	91

[a] Also known as Chilean sardine.

[b] Also known as European bass *Morone labrax.*

[c] Also known as silver gemfish.

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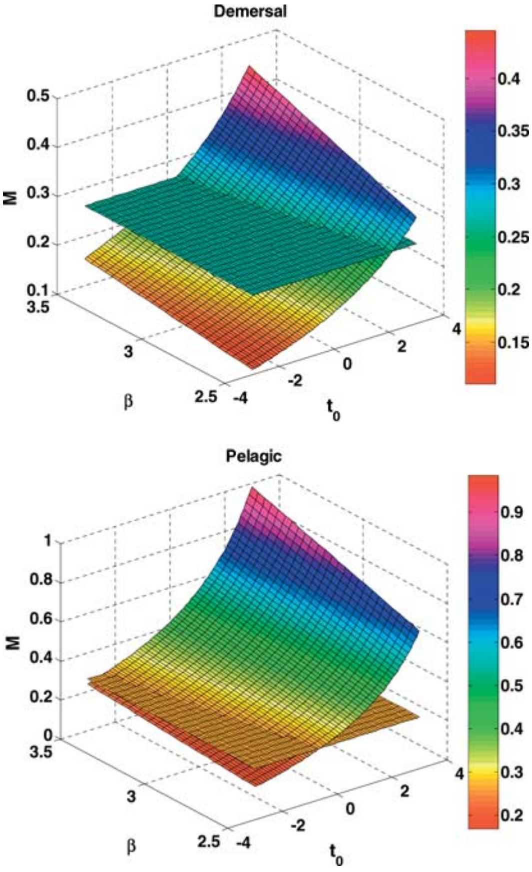

FIGURE 1.—Comparison of estimates of natural mortality (M) computed from the Zhang and Megrey (ZM) model (curvilinear response surface) and the Alverson and Carney (AC) model (linear plane) for demersal and pelagic species as functions of β and t_0. See text for additional details on these models. Values of $K = 0.1$ and $t_{\mathrm{max}} = 20$ were used in all calculations. The values of t_{mb} used in equations (8) (ZM model) and 10 (AC model) were calculated with the formula $t_{\mathrm{mb}} = C_i \cdot t_{\mathrm{max}}$. For demersal species, values of $C_i = 0.38$ ($t_{\mathrm{mb}} = 7.6$) and $C_i = 0.44$ ($t_{\mathrm{mb}} = 8.8$) are compared for the AC and ZM models, respectively. For pelagic species, values of $C_i = 0.38$ ($t_{\mathrm{mb}} = 7.6$) and $C_i = 0.302$ ($t_{\mathrm{mb}} = 6.04$) are compared.

negative values of t_0 and there was only a slight response at positive values of t_0. At low growth rates (panel D), the patterns were the same but the percent difference was much lower. For example, when $K = 1.5$ and $t_{\mathrm{mb}} = 5$, $\hat{M}_{\mathrm{ZM}}(t_0, \beta) = \hat{M}_{\mathrm{ZM}}(3.0, 3.5) = 0.2719$, $\hat{M}_{\mathrm{AC}}(3.0, 3.5) = 0.00249$, and %diff(3.0, 3.5) = 10,900, but when $K = 0.1$ and $t_{\mathrm{mb}} = 5$, $\hat{M}_{\mathrm{ZM}}(3.0, 3.5) = 1.581$, $\hat{M}_{\mathrm{AC}}(3.0, 3.5) = 0.4624$, and %diff(3.0, 3.5) = 241.8. Also, the percent difference response for the low-growth case was much less nonlinear.

Evaluation of Relationship of t_{mb} to Maximum Age for Different Ecological Groups

Table 1 shows the sources used in the evaluation of the relationship of t_{mb} to the maximum age. The value of the ratio $t_{\mathrm{mb}}/t_{\mathrm{max}}$ relating the maximum age to the age at maximum biomass was 0.302 for pelagic species and 0.440 for demersal species, respectively (Table 2). The mean ratios of both subgroups were significantly different from 0.38 ($P < 0.05$ for the pelagic subgroup; $P < 0.01$ for the demersal subgroup), although the pelagic subgroup had a higher sample variance than the demersal group. Moreover, the ratios between the two ecological groups showed a highly significant difference ($P < 0.0001$). Thus, the ratio for specific ecological groups should be used rather than Alverson and Carney's constant of 0.38. However, the overall grand mean (i.e., the mean obtained without splitting the data into two ecologically distinct groups) was 0.393, which is close to the 0.38 proposed by Alverson and Carney.

Table 3 shows the results of statistical analyses comparing the M values calculated from the ZM model (equation 8) and the AC model (equation 10). These results show that the M values from the revised formula were not significantly different from those of the true values for pelagic species ($P = 0.594$) and demersal species ($P = 0.570$). However, the M values from the AC model were highly significantly different from the true M values in the demersal subgroup ($P < 0.0001$), although they were not significantly different from those of the true values for demersal species ($P = 0.335$).

In the Australian gemfish example, we estimated the value of M from equation (8) as 0.171. The variance of M was then calculated from the data in Table 4 using equation (11); the calculated variance was 0.001187, and the 95% confidence interval was 0.171 ± 0.068.

Discussion

Estimates of M are critically necessary for the management of commercial fisheries. Standard population dynamics techniques requiring values of M are yield-per-recruit analysis, spawning-biomass-per-recruit analysis, virtual population analysis, and methods based on precautionary approaches. It is well known that these methods are extremely sensitive to errors in M. Two M-based biological reference points that are widely used to manage exploited fisheries are derived from the analyses of yield per recruit and spawning biomass per recruit (National Research Council 1998). The value of M, or some fraction of it, has been used in some fisheries to determine the level of fishing mortality (F) that would constitute overfishing. The

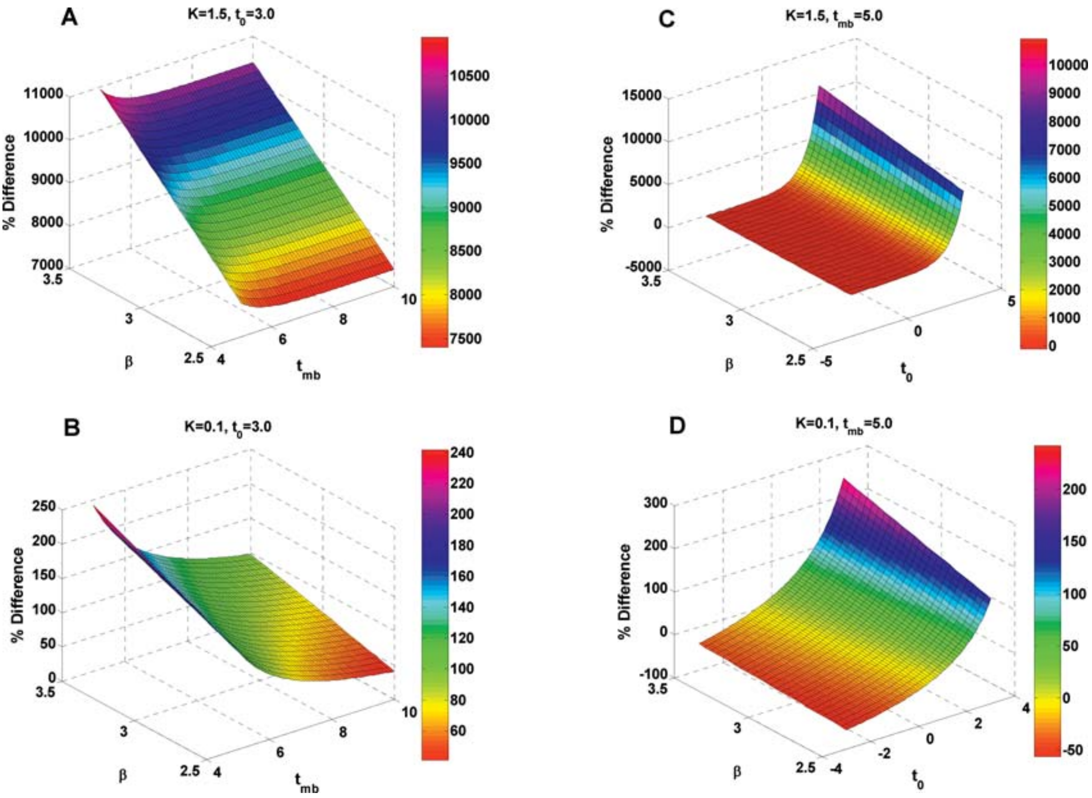

FIGURE 2.—Percent differences in estimates of M from the ZM model and the AC model calculated from equation (12). Shown are the percent differences as a function of β and t_{mb} given $t_0 = 3$ for **(A)** a fast-growing ($K = 1.5$) and **(B)** a slow-growing fish ($K = 0.1$) and those as a function of β and t_0 given $t_{mb} = 5$ for **(C)** a fast-growing and **(D)** a slow-growing fish.

rational for this approach is that short-lived species with high values of M should be able to sustain higher F levels than long-lived species with low values of M. Indeed, many fish stocks that have sustained fisheries for long periods have sustained levels of F near M (Mace 1994).

Unfortunately, M is difficult to estimate and it is not well known for most fish stocks. Since M is rarely estimated directly in fishery assessment models, estimates, guesses, or approximate values must be used in most stock assessment models. In a comprehensive examination of catch-at-age stock assessment models, Schnute and Richards (1995) found that natural mortality is extremely difficult to estimate from standard stock assessment data. Thus, it is introduced as an assumed and fixed value. Typically, F—the parameter managers are most interested in—is calculated by estimating total mortality (Z) and subtracting M (e.g., Ehrhardt and Ault 1992). Thus, any bias in M is transferred directly into estimates of F. An underestimate of M leads to an overestimate of F, and conversely for an overestimate of M.

Beverton and Holt (1959) and Beverton (1963) examined the utility of von Bertalanffy growth parameters in predicting M and found a positive correlation between K and M for some major fish species. Other researchers have also proposed methods for obtaining indirect estimates of M utilizing the

TABLE 2.—Mean ratio of age at maximum biomass to maximum age (t_{mb}/t_{max}), variance, null hypotheses, and results of two-tailed t-test for two ecological subgroups; n = sample size; μ = mean.

Subgroup	n	Mean t_{mb}/t_{max}	Variance	Null hypothesis	t-value	P-value
Pelagic	31	0.302	0.030	$\mu_{\text{pelagic}} = 0.38$	−2.530	<0.05
Demersal	60	0.440	0.021	$\mu_{\text{demersal}} = 0.38$	3.188	<0.01
Overall mean	91	0.393	0.028	$\mu_{\text{pelagic}} = \mu_{\text{demersal}}$	−4.030	<0.0001

TABLE 3.—Results of a paired-sample *t*-test under the null hypothesis that the Zhang and Megrey (ZM) model and the Alverson and Carney (AC) model are accurate in predicting the true value of natural mortality.

Subgroup	Statistic	ZM model	AC model
Pelagic	t	0.539	−0.979
	P	0.594	0.335
Demersal	t	0.571	−4.999
	P	0.570	<0.001

TABLE 5.—Summary statistics for model parameters. Data are from Table 1.

Statistic	t_{max}	K	t_0	β
Minimum	2.0	0.05	−6.05	2.57
Maximum	98.0	1.59	2.04	3.68
Median	13.00	0.18	−0.86	3.01
Mean	16.21	0.237	−0.99	3.03
Variance	232.96	0.037	1.32	0.032

growth parameters; these include Alverson and Carney (1975), who used maximum age and *K*; Pauly (1980), who used the von Bertalanffy growth parameters (K, L_∞) and average annual temperature; Roff (1984), who used those growth parameters and length at maturity; and Hoenig (1983), who used longevity, which is really a recasting of the Alagaraja (1984) estimator. The use of fishery-independent data will be useful to evaluate *M* estimates for stocks in the unexploited phase or unexploited species. For example, the Ehrhardt and Ault (1992) estimator of the total mortality rate *Z* is really estimating *M* when the size frequency distribution is obtained by fishery-independent methods for an unexploited population.

Usually, growth parameters are the best available information in population studies for most exploited and unexploited fish stocks (Gulland 1983; Zhang 1987). Among the methods utilizing growth parameters, the AC model uses simple growth information, while others require additional information. The AC model is widely used nowadays mainly because of its minimal information requirements.

Estimates of *M* from the AC model are most sensitive to the assumption that growth starts at $t_0 = 0$ when growth rates are high and to the β and t_{mb} assumptions (Figures 1, 2). It was generally true that the percent difference between the two methods increased as the value of β increased from 2.5 to 3.5 for fast- or slow-growing fishes when $t_0 = 3.0$. Figures 1 and 2 can be used to gauge the expected bias in the AC model against a particular suite of parameter values.

Frequency histograms for the model parameters were examined to see how the parameters were distributed, and summary statistics were calculated (Tables 5, 6). It can be seen that for all the species cataloged in this study t_0 is typically not zero but has a mean smaller than zero (−0.99) and values that range from −6.05 to +2.04. Similarly, β has a mean of 3.03 and ranges from 2.57 to 3.68. Relative to the results from using Alverson and Carney's assumptions that $t_0 = 0$ and $\beta = 3.0$, we can see that for the ensemble average of the data the estimate of *M* from the AC model is 15.5% higher for a long-lived, slow-growing fish and 62.5% higher for a short-lived, fast-growing fish. Also, our statistical analyses showed that the *M* values calculated from the ZM model (equation 8) were not significantly different from the true values, while the *M* values for the demersal subgroup calculated from the AC model were significantly different from the true values taken from the literature (Table 3). Therefore, the ZM model could be used instead of equation (10) for the estimation of *M* since von Bertalanffy and allometric growth data are readily available for most exploited fish stocks. Also, the values of t_{mb}/t_{max} for specific ecological groups could be used rather than the constant 0.38.

In our study, the constant relating the age at maximum biomass to the maximum age varied from 0.302 to 0.440, depending on the ecological subgroup. The variance of the constant for the pelagic subgroup

TABLE 4.—Data and parameter estimates required for the calculation of the variance of natural mortality for Australian gemfish.

Parameter	Value	Variance
K^{a}	0.196	0.000016
t^{a}_{0}	−0.585	0.002025
β^{b}	3.3895	0.0000084
t^{c}_{max}	16	2.56^{d}
Demersal t_{mb}/t_{max} ratio^{e}	0.440	0.02
Calculated t_{mb}	7.043	0.49^{f}

[a] Rowling (1999), Table 4.2.1 (mean of males + juveniles and females + juveniles).

[b] Rowling (1999), Table 4.7.

[c] Rowling (1997).

[d] Calculated by assuming a coefficient of variation of 10% for t_{max}.

[e] From Table 2.

[f] Calculated from the equation $\text{var}(t_{mb}) = C_i^2 \ \text{var}(t_{max})$, where $C_i = 0.44$.

TABLE 6.—Variance–covariance matrix for model parameters.

Parameter	t_{max}	K	t_0	β
t_{max}	232.37			
K	−0.70	0.04		
t_0	−6.71	0.06	1.31	
β	−0.03	0.015	0.008	0.031

was higher than that for the demersal group, revealing their higher variability (Table 2). Pauly (1980) also suggested the need to consider the life history features of separate ecological subgroups when estimating *M*. In particular, he suggested that the estimate of *M* for a schooling pelagic stock be calculated by multiplying the original value of *M* by 0.8.

Greater attention should be paid to including estimates of *M* in assessment models (National Research Council 1998). exploited stock dynamics can be more comprehensively analyzed by using a range of *M* values instead of a constant value. Many studies show that fishery models are sensitive to different choices for the value of *M*. Moreover, sensitivity is influenced not only by the values chosen for *M* but also by the interactions between *M* and the other parameters in the models (Gulland 1983; Vetter 1988). A plausible range for *M* could be estimated from equation (8) using the mean ratio of $t_{\mathrm{mb}}/t_{\max} \pm 1$ SD (from Table 2) multiplied by $t_{\max}$ for each subgroup. A range for *M* could also be obtained by calculating the variance using equation (11), though evaluation of that equation requires knowing the variances of four parameters and the covariances of six combinations of four parameters. The variance and covariance of the two von Bertalanffy growth parameters and the allometric length–weight parameter (K, t_0, and β) can be easily obtained from routine nonlinear regression fitting algorithms. However, care should be taken when calculating the variance of *M* using equation (11) since the delta method for approximating the variance of the function requires that the function be approximately linear (Rice 1995).

The precision of our estimate of *M* is acceptable mainly because it is based on growth parameters estimated from length–frequency sampling data. As these data sets typically reflect large sample sizes, the parameters estimated from them tend to have low variances and high precision. This underlying precision is transferred to the precision in the estimate of *M* through the variance equation. The value of *M* from this analysis differs from the value included in Table 1 ($M_{\mathrm{true}} = 0.458$), which came from a Bayesian stock assessment model (Rowling 1999). Variance estimates for *M* could be useful in a Bayesian analysis as a starting point for the description of prior distributions for *M*.

We realize that our estimate of the variance of *M* is an underestimate for two reasons. First, we assumed that all of the covariance terms in equation (11) were insignificant or zero. We know that this is not exactly the case and that departures from this assumption will add to the variance of *M* depending on the correlations between the model parameters. Second, our estimate does not include process error in estimating *M*. This could be particularly relevant, as it relates to the data taken from FishBase used in the analysis. Even with these caveats, we believe that we have shown the utility of our method of calculating variances for *M*, a feature not typically available from purely empirical approaches.

In summary, we have presented an extension of the original Alverson and Carney empirical estimate of natural mortality. Our new formulation (the ZM model) is less biased than the AC model and includes easily obtainable maximum age and von Bertalanffy and allometric growth parameters. We show that the relationship between the time a stock requires to maximize its biomass and its maximum age is dependent on the ecological group to which it belongs. We also present an easy way to calculate the variance of *M* using parameter variances usually obtainable from nonlinear regression computer algorithms.

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