# S E D A R

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# Life-History Based Estimates of Natural Mortality for Atlantic Menhaden

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## Natural Mortality

### Introduction

Age-structured models attempt to reconstruct the fish population and fishing mortality rates by age and year, where total instantaneous mortality rate ($Z$) is the sum of instantaneous rates of fishing ($F$) and natural ($M$) mortality. Historically, natural mortality has been assumed to be constant over ages and years. In many stock assessments, constant values for $M$ have been obtained from life history analogies (e.g. maximum age, growth rate parameters, etc.). Because it is thought that younger fish are more vulnerable to predation, natural mortality may decline with size or age. Several approaches have been considered to provide such size-varying estimates of natural mortality. For purposes of stock assessments, sizes are related to age to provide age-varying estimates of natural mortality.

First, we provide an overview of natural mortality. Because menhaden are abundant in coastal waters and are a common prey species to many predatory fishes, sea birds and marine mammals, predation mortality is probably the greatest component of natural mortality. This high rate of mortality is particularly acute among the youngest age classes, due to mouth gape limitation of most piscivorous fishes. Menhaden are preyed upon by a variety of predators such as bluefish, striped bass, king mackerel, Spanish mackerel, pollock, cod, weakfish, silver hake, tunas, swordfish, bonito, tarpon, and a variety of sharks (ASMFC 2001). In turn, menhaden are valuable forage for many commercial and recreationally important East Coast fishes. Given the importance of menhaden as a forage species and the assumed high predation that presumably occurs on young of the year and juvenile fish, age-varying natural mortality rates maybe more appropriate for this species.

Coastal pollution and habitat degradation threaten marine fish species, such as Atlantic menhaden, which spend their first year of life in estuarine waters and the rest of their life in both ocean and estuarine waters. Other poorly understood sources of natural mortality for Atlantic menhaden are diseases and parasites. A partial list of parasites was given in Reintjes (1969), but there is no information available concerning the extent of parasitism or its possible effect on survival. Ahrenholz et al. (1987a) described the incidence of ulcerative mycosis (UM), a fungal infestation that was observed in menhaden over much of their range in 1984 and 1985 and in a more restricted area in 1986. A large fish kill in Pamlico Sound, North Carolina in November 1984 was associated with UM, but its primary effect may be to weaken fish, making them more susceptible to other causes of mortality, such as predation, parasites, other diseases, and low dissolved oxygen concentrations. The overall impact of UM on the 1984 and 1985 year classes could not be assessed, but it was not believed to be significant (Ahrenholz et al. 1987a). Vaughan et al. (1986) believed that the mortality effects of a disease or other event must be "truly catastrophic" to be detectable.

Another source of natural mortality for Atlantic menhaden (and many other species) may be "red tide." The term refers to the color of water caused by the rapid multiplication, or "bloom", of single-celled planktonic organisms called dinoflagellates, which produce a toxic compound. The toxin accumulates in the tissues of filter-feeding animals, which ingest the dinoflagellate. An outbreak of red tide occurred along the coast of the Carolinas during November 1987 - April 1988 when Gulf Stream water containing the dinoflagellates was transported into coastal waters. Menhaden recruitment in Beaufort Inlet during this period was severely reduced (S. Warlen, NMFS, Beaufort N.C., pers. comm. as cited in ASMFC 1992). A new species of toxic dinoflagellate was identified as the causative agent in a major menhaden kill in the Pamlico River, North Carolina, in May 1991. Problems with toxic phytoplankton organisms may increase in the future since their appearance has been correlated with increasing nutrient enrichment in estuarine and coastal waters that are subject to increasing organic pollution (Smayda 1989).

An additional source of mortality are fish "kills", which occur when schools of menhaden enter enclosed inshore bodies of water in such large numbers that they consume all available oxygen and suffocate. The mean lethal dissolved oxygen concentration for menhaden has been reported to be 0.4 mg/l (Burton et al. 1980). Bluefish are known to follow (or even chase) schools of menhaden inshore, feeding on them, and may contribute to their mortality by preventing them from leaving an area before the oxygen supply is depleted. High water temperatures, which increase the metabolic rate of the fish, accelerate oxygen depletion. Concurrently, oxygen is less soluble in warm water. Menhaden that die from low oxygen stress can immediately be recognized by the red coloration on their heads caused by bursting blood capillaries. Just before death, the fish can be seen swimming very slowly in a disoriented manner just below the surface of the water. This is a common phenomenon that has been observed throughout the range of the species. Menhaden spotter pilots have reported menhaden "boiling up" from the middle of dense schools and washing up on the beach, apparently from oxygen depletion within the school. This phenomenon was observed during December 1979 in the ocean off Atlantic Beach, North Carolina (M. Street, NC DMF, pers. comm. as cited in ASMFC 1992). Smith (1999) reported a similar event off Core Banks, North Carolina, in December 1997. Other species are not nearly as susceptible simply because they do not enter enclosed inshore waters in such large numbers.

## Life-History Based Approaches

While methods that relate life history traits with natural mortality were reviewed in Vetter (1987) newer methods have been developed since that land mark paper. A variety of methods have been explored during past menhaden SEDAR data workshops, and the results of some of these methods are summarized in this section. Often *M* is related to the parameters from the von Bertalanffy growth equation (K, $L_\infty$), or as an inverse function of size at age, so

consideration of growth of Atlantic menhaden is relevant to this section. More recently, age-varying estimates of natural mortality due to predation has been developed through ASMFC (MSVPA-X).

This preliminary version was developed prior to the SEDAR 18 Data Workshop as *S20DW03*.

*Age-Constant M Approaches*

There are several methods for determining an age-constant *M* based on life history characteristics, notably maximum age ($t_{max}$), von Bertalanffy growth parameters (k, $L_\infty$), and average water temperature ($T^oC$). Results from the following approaches are summarized in **Table 1**.

| Source | Equation |
|---|---|
| Alverson and Carney (1975) | $M = 3K/(exp(0.38*t_{max}*K)-1)$ |
| Hoenig (1983; F ~ 0) | $M = exp(1.46 - 1.01*ln(t_{max}))$ |
| Jensen (1996) | $M = 1.5*K$ |
| Pauly (1980) | $M = exp(-0.0152+0.6543*ln(K)-0.279*ln(L_\infty, cm) +0.4634*ln(T^oC))$ |
| "Rule of thumb" (Hewitt & Hoenig 2005) | $M = 3/t_{max}$ |

Mean environmental temperature ($T^oC$), or mean annual temperature where the fish is caught, used here was $19^oC$ [from Williams et al. (1973) for North Carolina]. Quinn and Deriso (1999) have converted Pauly's equation from base 10 to natural logarithms as presented above. The "rule of thumb" method has a long history in fisheries science, but it is difficult to pin down its source. Hewitt and Hoenig (2005), recently compare this approach to that of Hoenig (1983) and noted that the Hoenig (1983) method provides an estimate of *M* only when fishing mortality can be assumed small (*F* ~ 0) otherwise it was suggested to be an upper bound on *M*. It is believed that with sufficient age sampling over a long period of time, as in the case of Atlantic menhaden, a useful tool for determining *M* can be utilized. We have calculated annual values of M for those equations above for which we have annual values of input parameters; e.g., Alverson and Carney (1975), Jensen (1996) and Pauly (1980) (**Figure 1**).

Estimates of *M* in the early literature on Atlantic menhaden vary, though not widely (Ahrenholz 1991). Schaaf and Huntsman (1972) estimated $M = 0.37\ yr^{-1}$ based on an *ad hoc* approach regressing total mortality rate (*Z*) on fishing effort. Estimates were $M = 0.52\ yr^{-1}$ from a preliminary tag-recovery analysis (Dryfoos et al. 1973) and $M = 0.50\ yr^{-1}$ from a more extensive tag-recovery analysis (Reish et al. 1985). The mean of the range ($M = 0.45\ yr^{-1}$) has been used routinely in Atlantic menhaden assessments beginning with Ahrenholz et al. (1987b).

During the course of the SEDAR 20 Data Workshop, we discussed these approaches, but recognized that the MSVPA-X results with age-varying *M* and potentially year-varying *M* would be the favored approach.

*Age-Varying M Approaches*

Several approaches have been developed to provide age-varying estimates of *M* (Peterson and Wroblewski 1984, Boudreau and Dickie 1989, Lorenzen 1996). All use an inverse relationship between size and natural mortality (*M*). To apply these methods, weight at age is calculated for the middle of the calendar year (July 1). Because fishing year begins on March 1, or 2 months into the calendar year, the fraction, 1/3 (4 months), is added to each age in the von Bertalanffy growth equation to calculate corresponding length on July 1, and then converted to weight using a corresponding weight-length relationship.

The method of Peterson and Wroblewski (1984) recently was used to describe natural mortality for young-of-year Atlantic menhaden (Heimbuch et al. 2007), and uses a dry weight as its independent variable. The method of Boudreau and Dickie (1989) has been applied in several assessments, notably for gulf menhaden in Vaughan et al. (2007). However, the method of Lorenzen (1996) has gained favor in recent years, especially in the SEDAR arena (e.g., S10, S15, S17 and S18). When applying the method of Lorenzen (1996), estimates of age-varying *M* are scaled such that cumulative survival from age 1 through the maximum age is equal to 1.5%. This cumulative survival value comes from the fixed *M* method of Hoenig (1983) as described in Hewitt and Hoenig (2005). When scaled, the resulting M from Peterson and Wroblewski (1984), Boudreau and Dickie (1989) and Lorenzen (1996) provide very similar results (**Figure 2**).

Unscaled and scaled estimates of *M* based on the approaches of Lorenzen (1996) were developed from von Bertalanffy growth parameters using the von Bertalanffy growth equation applied to ages 1 through maximum age separately. Additionally, a range in Hoenig-based estimates of *M* can be used to rescale the Lorenzen estimates of M so as to provide a range of age-varying *M* for use by the SEDAR 20 Assessment Workshop.

The Hoenig-based estimate of *M* is 0.42, which produces a scaling to 1.5% survival from age 1 through age 10. Corresponding percentages can be developed to scale *M* ranging from *M* = 0.37 to 0.52 (or 2.5% and 0.6% survival, respectively). Unscaled age-varying estimates of M are summarized for ages 0-10 (**Table 2**).

During the course of the SEDAR 20 Data Workshop, we discussed the need for using age-varying estimates of *M*, recognizing higher natural mortality for the youngest ages.

**Natural Morality from Multi-Species VPA**

Using a Multi-Species Virtual Population Analysis model (MSVPA-X) allows further decomposition of natural mortality (*M*) into predation mortality, $M_2$, and other sources of natural mortality, $M_1$. $M_2$ is more appropriately described as natural mortality due to predators. Total instantaneous mortality rate, *Z*, can then be formulated as:

$$Z = F + M_1 + M_2$$

Examinations of age variable predation mortality rates suggest greater mortality on the youngest age classes and subsequently lower predation mortality on older age classes, in keeping with the life history of short lived forage species. Incorporation of age variable mortality rates into age-structured population models usually results in increased abundance in younger age classes to offset this increase in natural mortality; particularly when the bulk of the increased natural mortality comes before full recruitment to the fishery. It should be noted that whether using age-variable and/or multi-species derived *M*, some component of the natural mortality is normally assumed, rather than empirically derived.

To address the concerns of menhaden as an important forage species and explore the role of $M_2$ in the population dynamics of this stock, the Commission began developing a Multispecies Virtual Population Assessment model (MSVPA-X) in 2001. The MSVPA-X model initially focused on the effects of predation by bluefish, striped bass, and weakfish on the Atlantic menhaden population, and has since been extended to adjust for the population estimates of the predators and alternative prey species. The Commission also hosted several workshops to verify the data used in the model and obtain feedback from various technical committees on features to include in the model. Early versions of the MSVPA-X model were used by the Atlantic Menhaden Technical Committee to explore some basic questions about the abundance of age 0 and 1 menhaden, as well as effects on reference points. Additionally, an age-varying natural mortality was derived in some part by that version of the MSVPA-X. As with the scaling for age-varying *M* (previous section), scaling of M at age is carried out for ages 1-10 (maximum age observed). *M* for ages 6+ are assumed constant. These results were then used as a vector in the single species formulation for menhaden during the most recent bench mark assessment (ASMFC 2004).

A subsequent revision of the MSVPA-X was reviewed by the 42nd SAW (Stock Assessment Working-group; http://www.nefsc.noaa.gov/nefsc/publications/crd/crd0609) in December 2005 (NEFSC 2006a, 2006b). At that meeting the SAW suggested improvements to the model; however, overall the SAW- approved model formation, inputs, and its use in providing ancillary management advice on the predator prey interactions of these stocks. More recently, this model and data input have undergone an additional update as part of the ASMFC Multi-Species Technical Committee during 2008-2009.

While the model only explicitly models menhaden, bluefish (as a biomass predator), weakfish, and striped bass interactions and population dynamics, other prey items have been included to produce a more realistic ecosystem picture across the predators' size and spatial ranges. These include:

Sciaenids (spot, croaker)
Bay anchovy
Medium Forage species (butterfish, squid)
Other clupeids (Atlantic herring, Atlantic thread herring, and others)
Benthic invertebrates (worms)
Benthic crustaceans (lobsters, blue crabs, rock and Jonah crabs)
Macrozooplankton (shrimps, mysids, and amphipods)

For the MSVPA-X, estimates of M decline with increasing age, similar in pattern to that obtained from the inverse growth pattern described in the previous section (**Figure 2**). In the last peer reviewed assessment (ASMFC 2004), an average vector of age-specific M from an earlier version of MSVPA-X was scaled within the model. This approach failed to produce reasonable scaling in the subsequent update (ASMFC 2006). In that assessment, the age-specific vector of M was scaled to historical estimates of M from tagging studies. Different potential scalings for MSVPA-X age-varying *M* are compared in **Figure 3**. The average age-varying estimates of *M* from MSVPA-X are computed for 1982-2006 (**Table 3**) to minimally provide input for a continuity model run. However, the SASC is very much interested in pursuing year-varying (and age-varying) *M* for this assessment.

Because the age- and year-varying estimates of *M* from MSVPA-X are only available for 1982-2006 and the menhaden assessment typically includes at the least years 1955-2008, it will be necessary to develop approaches to develop age- and year-varying estimates of *M* for the remaining years (i.e., 1955-1981 and 2007-2008). Values for 2007-2008 were obtained from the projection component of MSVPA-X. For this assessment, projections were made assuming constant (terminal year) fishery mortality rates and stock sizes of "other prey items" within the MSVPA-X (ASMFC 2008) The simplest approach for filling in for 1955-1981 is to use the vector for 1982 and apply it to all previous years (1955-1981). This approach is summarized in **Table 3**.

Annual age-averaged estimates of *M* from MSVPA-X are compared with both the fixed estimates of *M* (**Figure 1**) but annually varying estimates of *M* (e.g., Alverson and Carney, Jensen, and Pauly) and the annually varying estimates of *M* (**Figure 4**) from the age-varying (inverse weight) approaches (e.g., Peterson and Wroblewski, Boudreau and Dickie, and Lorenzen). The most promising approach seems to be relating MSVPA-X estimates of $M_X$ (collapsed across ages 1-10) with that of Alverson and Carney ($M_{AC}$). This relationship produced

a correlation coefficient of 0.72 (Pr < 0.0001). The $R^2$ value implies that about 51% of the variation is explained by the linear regression having the following form:

$$M_X = 0.4007 + 0.2667*M_{AC} + \varepsilon,$$

where ε is NID(0,$\sigma^2$). Annual predicted values of *M* ($M_X$) are compared with the observed values of averaged *M* from the MSVPA-X and with *M* ($M_{AC}$) from the Alverson and Carney (1975) approach (**Figure 5**). We then rescale these annual estimates of $M_X$ to age-varying estimates of *M* using one of two approaches. We use the average vector of *M* at age from the MSVPA-X for the period 1982-1989, and applied this vector to the unknown years (1955-1981). As before, projected values from the MSVPA-X were used for 2007-2008. Age- and year-varying estimates of M are summarized from this approach are presented in **Table 4**.

During the course of the SEDAR 20 Data Workshop, the following topics were discussed:

- Given the availability of MSVPA-X, the group favored this approach over that of age-varying natural mortality based on inverse relation to weight at age.

- We considered using the average age-vector for *M* from the MSVPA-X and scale to tagging as in the last assessment (2006 update), but the SASC prefers to explore using year- and age-varying estimates of *M*.

- The average age-varying estimates of *M* (1982-2006) from the MSVPA-X is provided as at least continuity with previous assessments, but the SASC wishes to pursue year-varying *M* as well.

- Two approaches were considered for developing year-varying estimates of M from the MSVPA-X estimates which are only available for 1982-2008 (including projected values of M for 2007-2008).

    - The favored method was to use the age-varying vector of *M* for 1982 from the MSVPA-X for all earlier years (1955-1981).

    - The relationship with Alverson and Carney (1975) outlined above provides an alternative to using a constant vector across years prior to 1982 (and age vector based on average across 1982-1989).

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**Table 1.** Constant *M* from life history approaches, using K & $L_\infty$ averaged across annual values, either full period of 1955-2008 or recent period of 2000-2008. Maximum age, $t_{max}$, is 10 years, and water temperature, $T^oC$, is 19. For comparison, we have included the average estimates of *M* from age-varying approaches for ages 1-10.

| **Life History** | **Parameters** | **Recent (2000-2008)** | **Overall (1955-2008)** |
|---|---|---|---|
| ***Fixed M Approaches:*** | $t_{max}$ = 10<br>T = 19$^o$C | $L_\infty$ = 33.47 cm,<br>K = 0.455 | $L_\infty$ = 36.75 cm,<br>K = 0.362 |
| Alverson & Carney | K, $t_{max}$ | 0.30 | 0.37 |
| Hoenig | $t_{max}$ | 0.42 | 0.42 |
| Jensen | K | 0.68 | 0.53 |
| Pauly | K, $L_\infty$, $T^oC$ | 0.86 | 0.72 |
| Rule of thumb | $t_{max}$ | 0.30 | 0.30 |
| ***Age Varying Approaches:*** | | ***M Averaged over Ages 1-10 and then over years*** | |
| Peterson & Wroblewski | $W_a^{-1}$ | 0.64 | 0.63 |
| Boudreau & Dickie | $W_a^{-1}$ | 0.52 | 0.51 |
| Lorenzen | $W_a^{-1}$ | 0.59 | 0.58 |
| MSVPA-X (1982-2006) | MSVPA-X | 0.49 | 0.50 |

**Table 2.** Summaries of various age-specific estimates of *M* including those as inverse function of size at age [Petersen and Wroblewski (1984), Boudreau and Dickie (1989), and Lorenzen (1996)], and the predator-prey approach used in MSVPA-X.

| Age | Peterson & Wroblewski | Boudreau & Dickie | Lorenzen | MSVPA-X |
|---|---|---|---|---|
| 0 | 1.187 | 1.173 | 1.257 | 1.065 |
| 1 | 0.904 | 0.819 | 0.902 | 0.805 |
| 2 | 0.745 | 0.633 | 0.711 | 0.614 |
| 3 | 0.665 | 0.546 | 0.620 | 0.521 |
| 4 | 0.620 | 0.497 | 0.569 | 0.476 |
| 5 | 0.591 | 0.467 | 0.537 | 0.446 |
| 6 | 0.573 | 0.448 | 0.516 | 0.425 |
| 7 | 0.560 | 0.435 | 0.502 | 0.425 |
| 8 | 0.551 | 0.426 | 0.493 | 0.425 |
| 9 | 0.544 | 0.419 | 0.486 | 0.425 |
| 10 | 0.540 | 0.414 | 0.481 | 0.425 |

**Table 3.** Observed year- and age-varying estimates of *M* from MSVPA-X for 1982-2006, projected values from MSVPA-X for 2007-2008, and age-varying values for 1982 repeated for 1955-1981. Average age-varying M from MSVPA-X for 1982-2006 shown at bottom.

| Year | 0 | 1 | 2 | 3 | 4 | 5 | 6+ |
|---|---|---|---|---|---|---|---|
| 1955 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1956 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1957 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1958 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1959 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1960 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1961 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1962 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1963 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1964 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1965 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1966 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1967 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1968 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1969 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1970 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1971 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1972 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1973 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1974 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1975 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1976 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1977 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1978 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1979 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1980 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1981 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |

**Table 3.** (cont.)

| Year | 0 | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|---|
| 1982 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1983 | 1.335 | 1.100 | 0.822 | 0.649 | 0.555 | 0.489 | 0.436 |
| 1984 | 1.219 | 0.992 | 0.737 | 0.591 | 0.517 | 0.468 | 0.434 |
| 1985 | 1.274 | 1.016 | 0.756 | 0.604 | 0.524 | 0.468 | 0.433 |
| 1986 | 1.291 | 1.014 | 0.769 | 0.618 | 0.534 | 0.471 | 0.432 |
| 1987 | 1.181 | 0.902 | 0.690 | 0.569 | 0.503 | 0.456 | 0.422 |
| 1988 | 1.081 | 0.859 | 0.661 | 0.549 | 0.490 | 0.446 | 0.419 |
| 1989 | 0.935 | 0.742 | 0.602 | 0.527 | 0.487 | 0.460 | 0.424 |
| 1990 | 0.888 | 0.687 | 0.557 | 0.499 | 0.471 | 0.451 | 0.439 |
| 1991 | 0.896 | 0.686 | 0.559 | 0.501 | 0.473 | 0.456 | 0.435 |
| 1992 | 0.791 | 0.629 | 0.522 | 0.476 | 0.455 | 0.441 | 0.432 |
| 1993 | 0.823 | 0.648 | 0.533 | 0.481 | 0.456 | 0.440 | 0.427 |
| 1994 | 0.879 | 0.653 | 0.522 | 0.470 | 0.448 | 0.436 | 0.424 |
| 1995 | 0.944 | 0.670 | 0.517 | 0.465 | 0.445 | 0.434 | 0.426 |
| 1996 | 0.945 | 0.668 | 0.514 | 0.460 | 0.439 | 0.427 | 0.420 |
| 1997 | 0.920 | 0.667 | 0.518 | 0.458 | 0.433 | 0.417 | 0.411 |
| 1998 | 0.938 | 0.683 | 0.533 | 0.468 | 0.438 | 0.421 | 0.408 |
| 1999 | 1.023 | 0.687 | 0.527 | 0.468 | 0.443 | 0.430 | 0.416 |
| 2000 | 1.023 | 0.677 | 0.511 | 0.459 | 0.439 | 0.429 | 0.422 |
| 2001 | 1.063 | 0.686 | 0.521 | 0.468 | 0.448 | 0.437 | 0.426 |
| 2002 | 1.185 | 0.760 | 0.540 | 0.472 | 0.447 | 0.432 | 0.426 |
| 2003 | 1.132 | 0.812 | 0.575 | 0.482 | 0.445 | 0.423 | 0.413 |
| 2004 | 1.224 | 0.951 | 0.669 | 0.534 | 0.475 | 0.442 | 0.417 |
| 2005 | 1.214 | 0.938 | 0.668 | 0.537 | 0.481 | 0.446 | 0.425 |
| 2006 | 1.044 | 0.826 | 0.629 | 0.525 | 0.474 | 0.442 | 0.420 |
| 2007 | 1.180 | 1.028 | 0.748 | 0.588 | 0.512 | 0.475 | 0.456 |
| 2008 | 1.344 | 1.078 | 0.745 | 0.582 | 0.508 | 0.473 | 0.454 |
| Average (1982-2006) | 1.066 | 0.806 | 0.614 | 0.521 | 0.476 | 0.446 | 0.425 |

**Table 4.** Year- and age-varying estimates of *M* from MSVPA-X as expanded to the early time period 1955-1981 based on Alverson and Carney (1975). Age-expansion based on average vector for 1982-1989. Observed age-varying *M* from MSVPA-X available for 1982-2006, and projected values for 2007-2008 as in **Table 3**.

| Year | A&C | MSVPA Obs | MSVPA Pred | 0 | 1 | 2 | 3 | 4 | 5 | 6+ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1955 | 0.328 | | 0.489 | 1.090 | 0.875 | 0.665 | 0.539 | 0.470 | 0.420 | 0.384 |
| 1956 | 0.237 | | 0.464 | 1.034 | 0.830 | 0.631 | 0.511 | 0.446 | 0.399 | 0.364 |
| 1957 | 0.305 | | 0.483 | 1.076 | 0.864 | 0.657 | 0.532 | 0.464 | 0.415 | 0.379 |
| 1958 | 0.268 | | 0.472 | 1.053 | 0.846 | 0.643 | 0.521 | 0.454 | 0.406 | 0.371 |
| 1959 | 0.406 | | 0.510 | 1.137 | 0.913 | 0.694 | 0.562 | 0.490 | 0.438 | 0.401 |
| 1960 | 0.349 | | 0.494 | 1.103 | 0.885 | 0.673 | 0.545 | 0.475 | 0.425 | 0.388 |
| 1961 | 0.408 | | 0.511 | 1.139 | 0.914 | 0.695 | 0.563 | 0.491 | 0.439 | 0.401 |
| 1962 | 0.394 | | 0.507 | 1.130 | 0.907 | 0.690 | 0.559 | 0.487 | 0.436 | 0.398 |
| 1963 | 0.410 | | 0.511 | 1.140 | 0.915 | 0.696 | 0.563 | 0.491 | 0.439 | 0.401 |
| 1964 | 0.403 | | 0.509 | 1.136 | 0.912 | 0.693 | 0.561 | 0.489 | 0.438 | 0.400 |
| 1965 | 0.410 | | 0.511 | 1.140 | 0.915 | 0.696 | 0.564 | 0.491 | 0.440 | 0.402 |
| 1966 | 0.410 | | 0.511 | 1.140 | 0.915 | 0.696 | 0.563 | 0.491 | 0.439 | 0.401 |
| 1967 | 0.298 | | 0.480 | 1.071 | 0.860 | 0.654 | 0.529 | 0.462 | 0.413 | 0.377 |
| 1968 | 0.368 | | 0.500 | 1.114 | 0.895 | 0.680 | 0.551 | 0.480 | 0.430 | 0.392 |
| 1969 | 0.533 | | 0.545 | 1.215 | 0.976 | 0.742 | 0.601 | 0.523 | 0.468 | 0.428 |
| 1970 | 0.504 | | 0.537 | 1.197 | 0.961 | 0.731 | 0.592 | 0.516 | 0.462 | 0.422 |
| 1971 | 0.257 | | 0.469 | 1.046 | 0.840 | 0.639 | 0.517 | 0.451 | 0.403 | 0.369 |
| 1972 | 0.234 | | 0.463 | 1.032 | 0.829 | 0.630 | 0.510 | 0.445 | 0.398 | 0.364 |
| 1973 | 0.448 | | 0.522 | 1.163 | 0.934 | 0.710 | 0.575 | 0.501 | 0.448 | 0.410 |
| 1974 | 0.544 | | 0.548 | 1.222 | 0.981 | 0.746 | 0.604 | 0.526 | 0.471 | 0.430 |
| 1975 | 0.434 | | 0.518 | 1.155 | 0.927 | 0.705 | 0.571 | 0.497 | 0.445 | 0.407 |
| 1976 | 0.639 | | 0.574 | 1.280 | 1.027 | 0.781 | 0.632 | 0.551 | 0.493 | 0.451 |
| 1977 | 0.494 | | 0.534 | 1.191 | 0.956 | 0.727 | 0.589 | 0.513 | 0.459 | 0.420 |
| 1978 | 0.632 | | 0.572 | 1.276 | 1.024 | 0.779 | 0.631 | 0.550 | 0.492 | 0.449 |
| 1979 | 0.441 | | 0.520 | 1.159 | 0.930 | 0.707 | 0.573 | 0.499 | 0.447 | 0.408 |
| 1980 | 0.437 | | 0.519 | 1.156 | 0.928 | 0.706 | 0.571 | 0.498 | 0.446 | 0.407 |
| 1981 | 0.504 | | 0.537 | 1.197 | 0.961 | 0.731 | 0.592 | 0.516 | 0.462 | 0.422 |

**Table 4.** (cont.)

| Year | A&C | MSVPA Obs | MSVPA Pred | 0 | 1 | 2 | 3 | 4 | 5 | 6+ |
|---|---|---|---|---|---|---|---|---|---|---|
| 1982 | 0.585 | 0.599 | 0.559 | 1.412 | 1.185 | 0.902 | 0.701 | 0.581 | 0.492 | 0.426 |
| 1983 | 0.486 | 0.580 | 0.532 | 1.335 | 1.100 | 0.822 | 0.649 | 0.555 | 0.489 | 0.436 |
| 1984 | 0.411 | 0.548 | 0.512 | 1.219 | 0.992 | 0.737 | 0.591 | 0.517 | 0.468 | 0.434 |
| 1985 | 0.407 | 0.553 | 0.510 | 1.274 | 1.016 | 0.756 | 0.604 | 0.524 | 0.468 | 0.433 |
| 1986 | 0.457 | 0.557 | 0.524 | 1.291 | 1.014 | 0.769 | 0.618 | 0.534 | 0.471 | 0.432 |
| 1987 | 0.498 | 0.523 | 0.535 | 1.181 | 0.902 | 0.690 | 0.569 | 0.503 | 0.456 | 0.422 |
| 1988 | 0.462 | 0.510 | 0.525 | 1.081 | 0.859 | 0.661 | 0.549 | 0.490 | 0.446 | 0.419 |
| 1989 | 0.519 | 0.494 | 0.541 | 0.935 | 0.742 | 0.602 | 0.527 | 0.487 | 0.460 | 0.424 |
| 1990 | 0.271 | 0.486 | 0.473 | 0.888 | 0.687 | 0.557 | 0.499 | 0.471 | 0.451 | 0.439 |
| 1991 | 0.376 | 0.485 | 0.502 | 0.896 | 0.686 | 0.559 | 0.501 | 0.473 | 0.456 | 0.435 |
| 1992 | 0.244 | 0.468 | 0.466 | 0.791 | 0.629 | 0.522 | 0.476 | 0.455 | 0.441 | 0.432 |
| 1993 | 0.343 | 0.469 | 0.493 | 0.823 | 0.648 | 0.533 | 0.481 | 0.456 | 0.440 | 0.427 |
| 1994 | 0.297 | 0.465 | 0.480 | 0.879 | 0.653 | 0.522 | 0.470 | 0.448 | 0.436 | 0.424 |
| 1995 | 0.229 | 0.466 | 0.462 | 0.944 | 0.670 | 0.517 | 0.465 | 0.445 | 0.434 | 0.426 |
| 1996 | 0.222 | 0.461 | 0.460 | 0.945 | 0.668 | 0.514 | 0.460 | 0.439 | 0.427 | 0.420 |
| 1997 | 0.295 | 0.455 | 0.480 | 0.920 | 0.667 | 0.518 | 0.458 | 0.433 | 0.417 | 0.411 |
| 1998 | 0.462 | 0.458 | 0.525 | 0.938 | 0.683 | 0.533 | 0.468 | 0.438 | 0.421 | 0.408 |
| 1999 | 0.360 | 0.464 | 0.497 | 1.023 | 0.687 | 0.527 | 0.468 | 0.443 | 0.430 | 0.416 |
| 2000 | 0.221 | 0.463 | 0.460 | 1.023 | 0.677 | 0.511 | 0.459 | 0.439 | 0.429 | 0.422 |
| 2001 | 0.264 | 0.469 | 0.471 | 1.063 | 0.686 | 0.521 | 0.468 | 0.448 | 0.437 | 0.426 |
| 2002 | 0.193 | 0.478 | 0.452 | 1.185 | 0.760 | 0.540 | 0.472 | 0.447 | 0.432 | 0.426 |
| 2003 | 0.322 | 0.480 | 0.487 | 1.132 | 0.812 | 0.575 | 0.482 | 0.445 | 0.423 | 0.413 |
| 2004 | 0.421 | 0.516 | 0.514 | 1.224 | 0.951 | 0.669 | 0.534 | 0.475 | 0.442 | 0.417 |
| 2005 | 0.350 | 0.520 | 0.495 | 1.214 | 0.938 | 0.668 | 0.537 | 0.481 | 0.446 | 0.425 |
| 2006 | 0.400 | 0.500 | 0.509 | 1.044 | 0.826 | 0.629 | 0.525 | 0.474 | 0.442 | 0.420 |
| 2007 | 0.250 | 0.563 | 0.467 | 1.180 | 1.028 | 0.748 | 0.588 | 0.512 | 0.475 | 0.456 |
| 2008 | 0.321 | 0.566 | 0.487 | 1.344 | 1.078 | 0.745 | 0.582 | 0.508 | 0.473 | 0.454 |

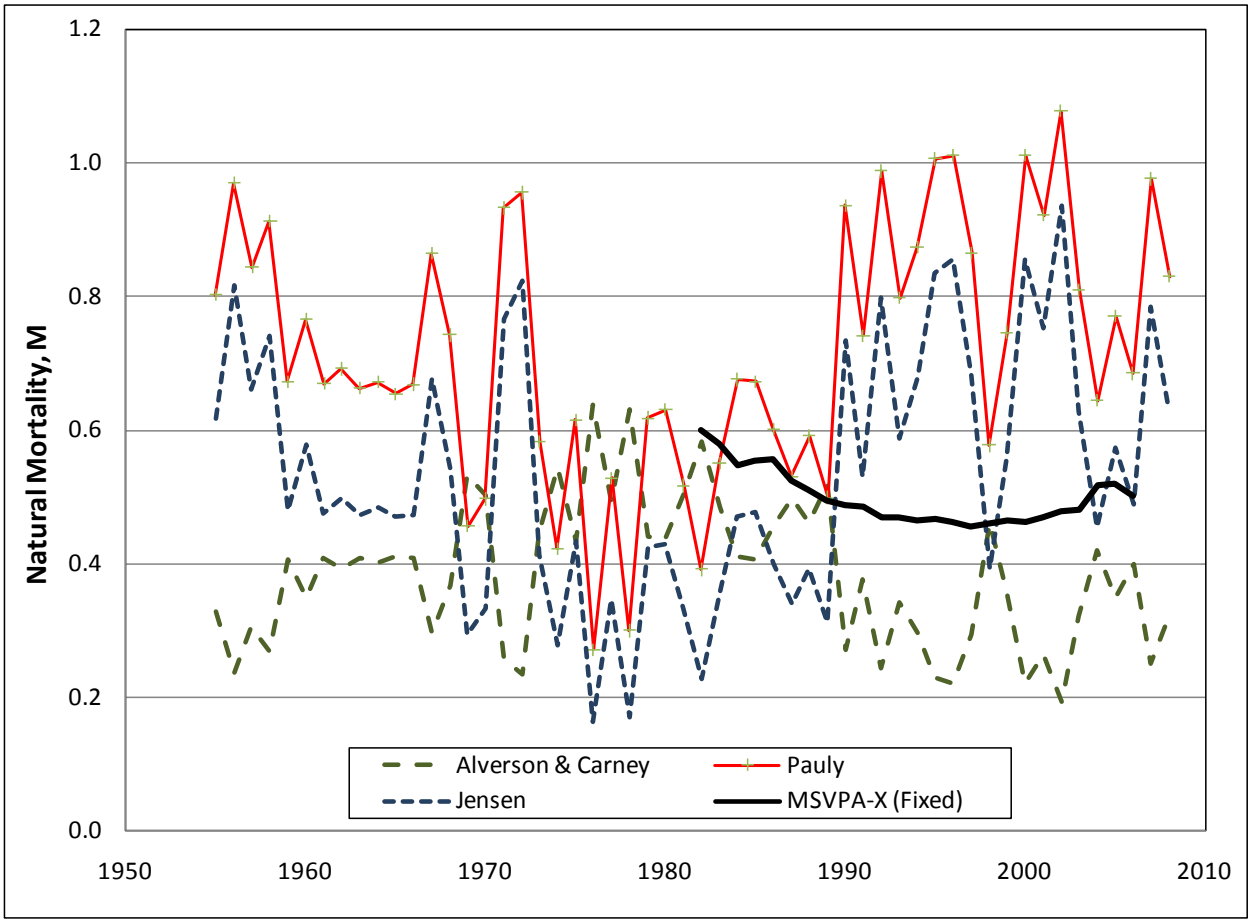


**Figure 1**. Annual calculated values of *M* from age-constant *M* approaches and average *M* across ages 1-10 (constant for 6+) of MSVPA-X.

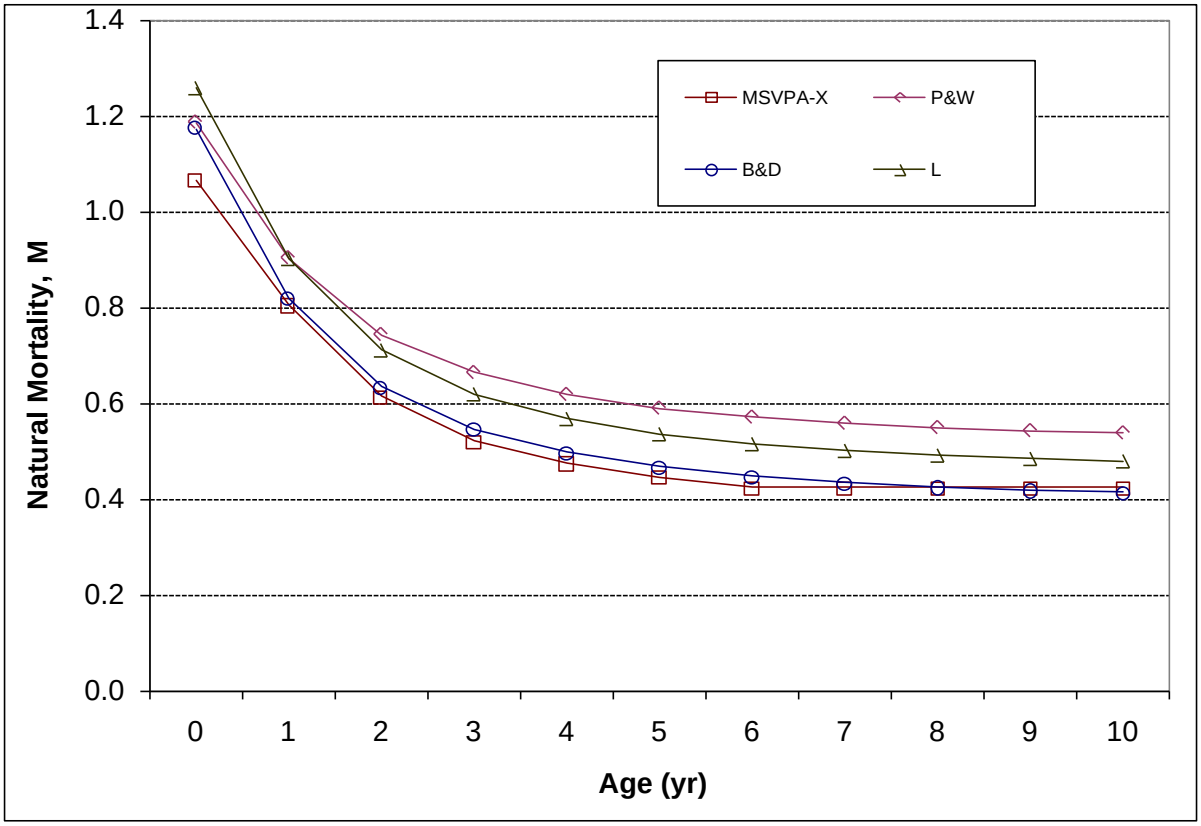


**Figure 2**. Age-varying estimates of *M* averaged across all available years for three age-varying methods based on weight at age (Boudreau & Dickie, Peterson & Wroblewski, and Lorenzen) and MSVPA-X.

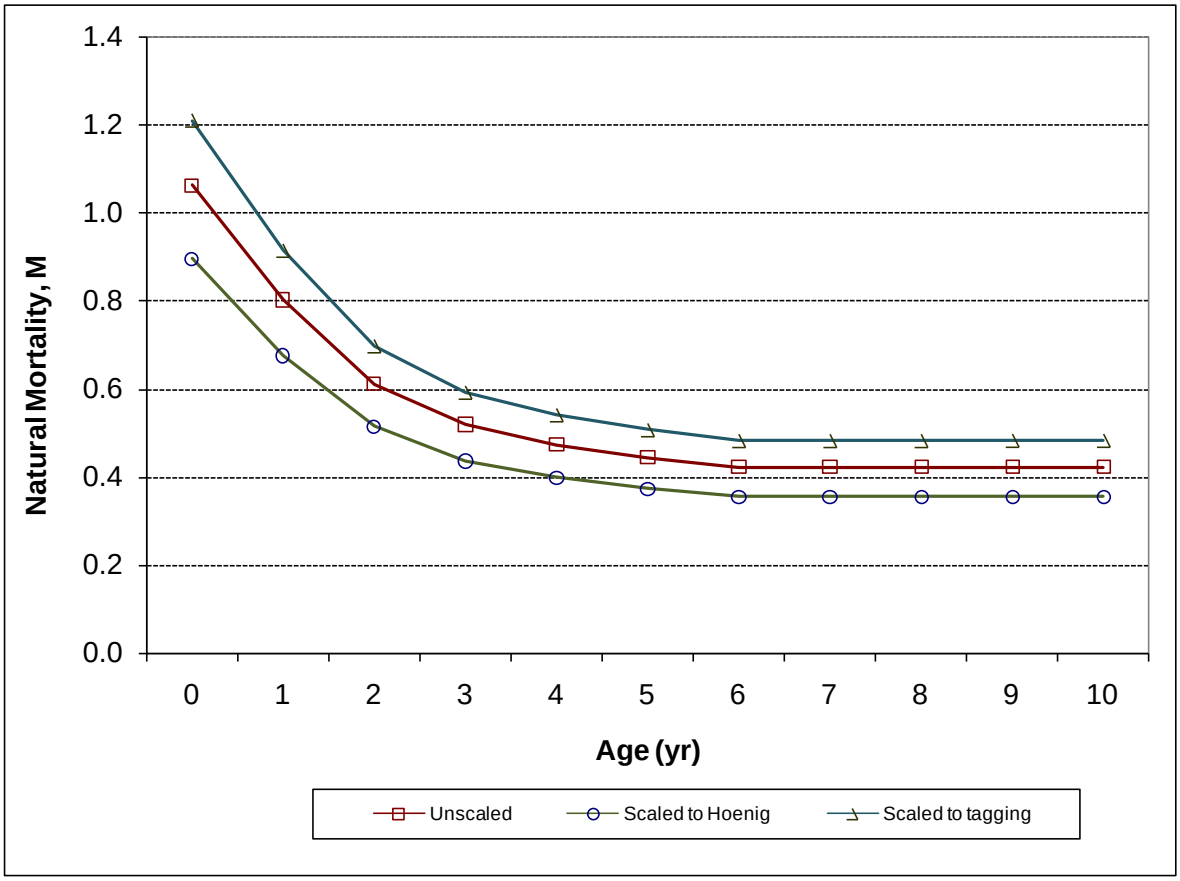


**Figure 3.** Different potential scalings for MSVPA-X age-varying *M*.

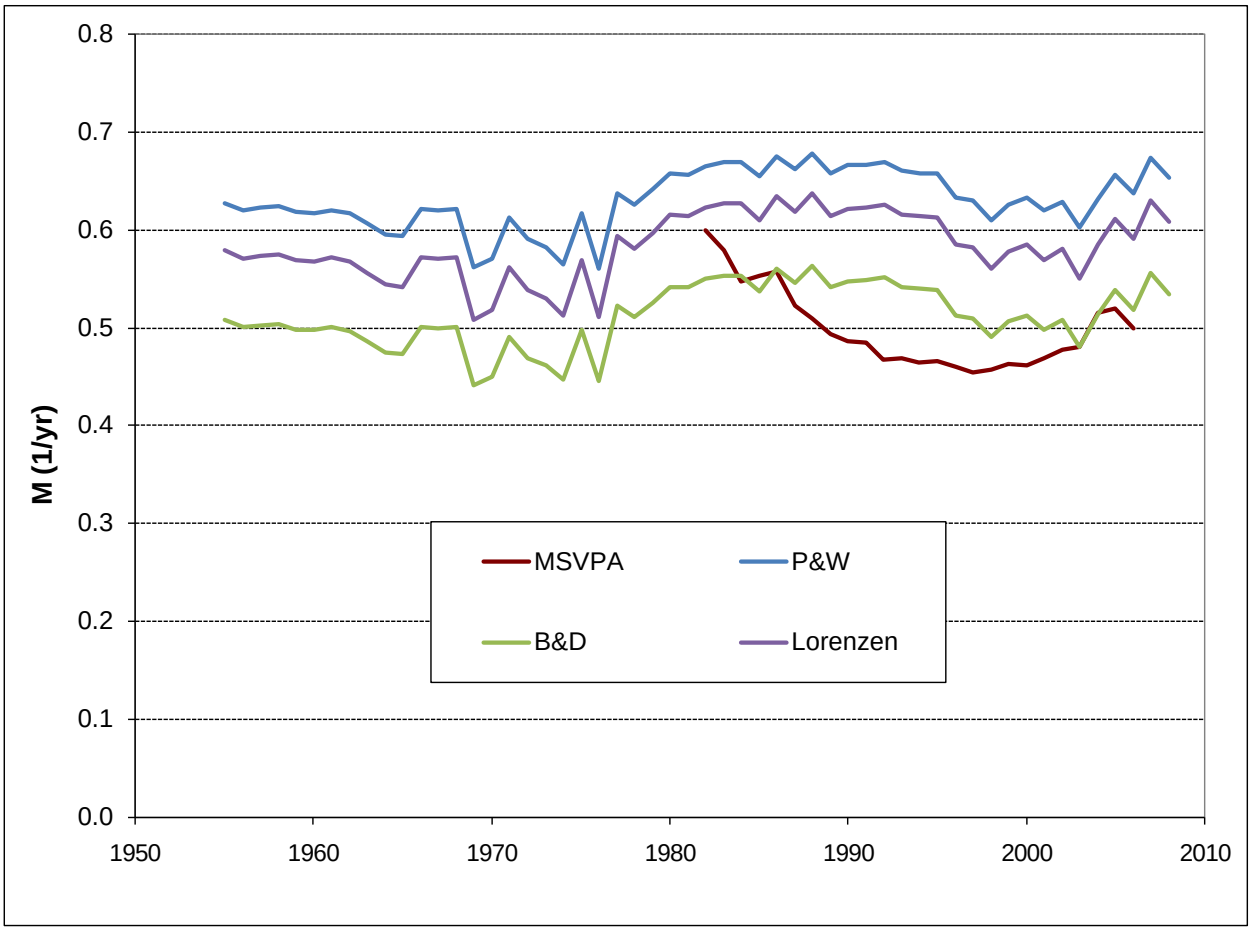


**Figure 4.** Comparison of several age-varying methods for estimating *M* scaled to average *M* over ages.

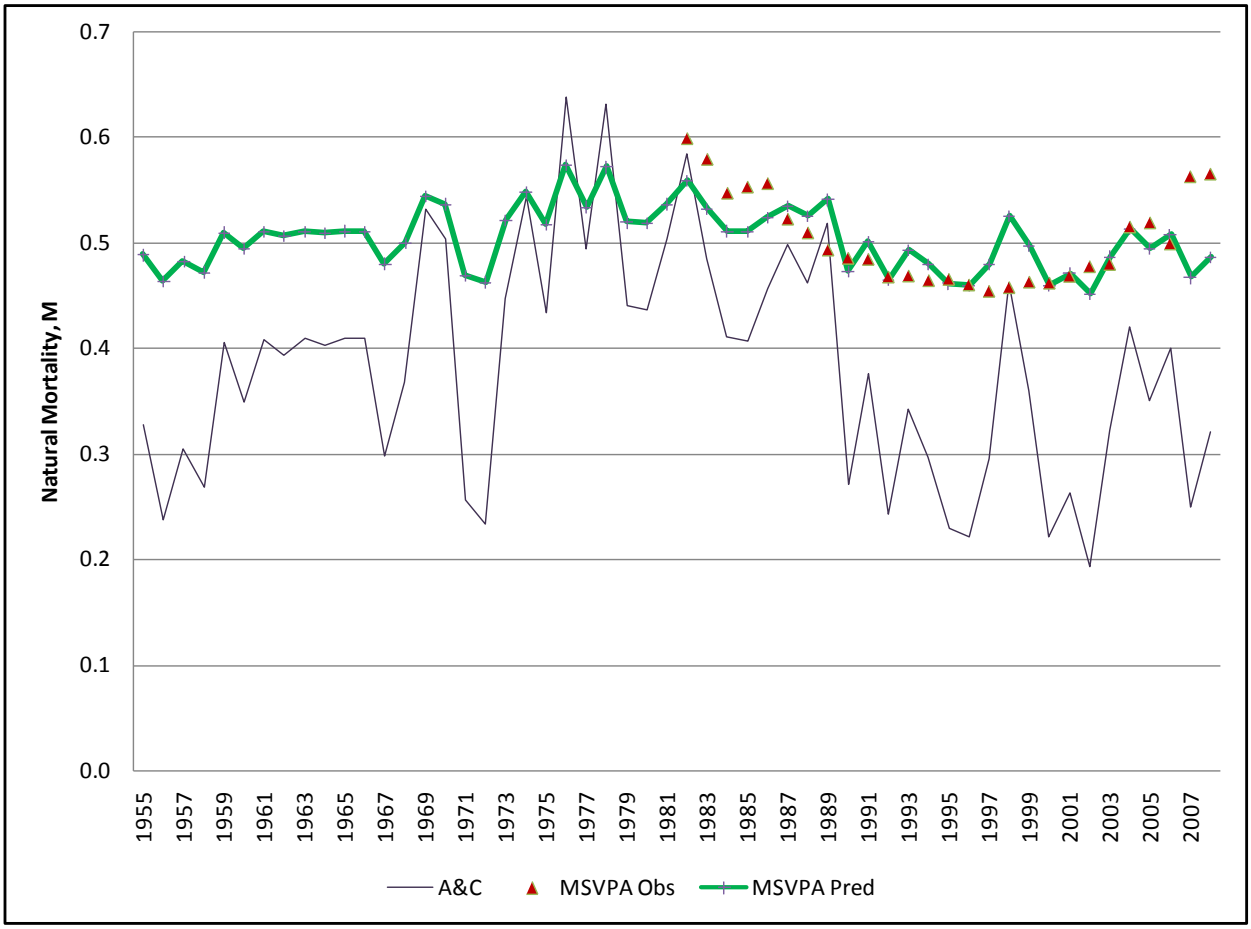


**Figure 5.** Observed and predicted annual average *M* (across ages) for MSVPA-X from the Alverson and Carney (1975) estimator.