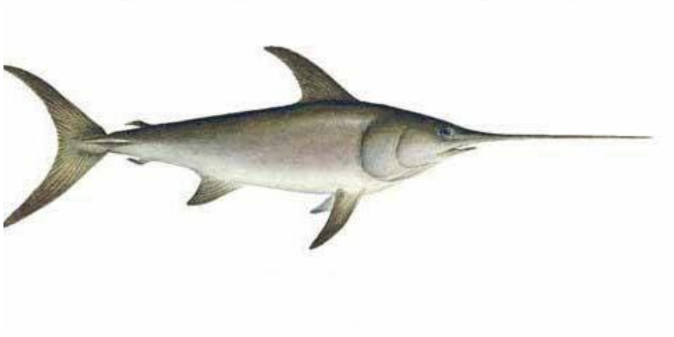
Age-structured Natural Mortality for Pacific Blue Marlin Based on Meta-analysis and an Ad Hoc Model[1]

Hui-Hua Lee and Yi-Jay Chang
Joint Institute for Marine and Atmospheric Research
University of Hawaii
Honolulu, Hawaii, USA



---

[1] Working document submitted to the ISC Billfish Working Group Workshop, 16-23 January 2013, Honolulu, Hawaii, USA. Document not to be cited without author's written permission.

Age-structured natural mortality for Pacific blue marlin based on meta-analysis and an ad hoc mortality model

Hui-Hua Lee and Yi-Jay Chang

University of Hawaii, Joint Institute for Marine and Atmospheric Research
2570 Dole St., Honolulu, HI 96822

Abstract

Recent growth and reproduction studies indicated the sex-dimorphism for Pacific blue marlin after first age 1 in which male has faster growth rate and shorter longevity. Growth for both female and male are rapid in the first year where males reach fully mature size. To account for life history trait of blue marlin, age- and sex- specific natural mortality estimates were developed. Estimates of adult M were based on a random effects meta-analysis to synthesize M estimates from a range of estimators. An ad hoc mortality model based on the Lorenzen's relationship was used to rescale juvenile M (age 0) for males to account for size-dependent processes. Mortality is assumed to be the same for females and males at age 0 and age 1 and female M is assumed to decline linearly from age 1 to fully mature age. In the absent of well-designed tagging study and good catch-at-age or catch-at-size data for each gender, natural mortality for adult estimates were derived from night estimators based on life history and evolutionary-ecology theory after a thorough evaluation of exiting methods. Estimates of uncertainty are also generated using a range of plausible biological and environmental factors based on the best available information. The adult M estimates derived from a random effects inverse variance weighting of each method were 0.22 yr^{-1} (95% CI: 0.13-0.30) for female and 0.37 yr^{-1} (95% CI: 0.28-0.46) for male. M for both males and females was 0.42 yr^{-1} at age 0 and 0.37 yr^{-1} at age 1. M for adult males at age 1+ maintained at 0.37 yr^{-1} and female M decline linearly to 0.22 yr^{-1} at fully mature age 4 and maintained at this level afterward.

Introduction

Natural mortality (M) is one measure of the productivity of the stock and has a large impact on the management quantities (e.g. maximum sustainable yield (MSY)) and reference points (e.g. the fishing mortality corresponding to MSY) used in fisheries management (Clark 1999; Williams 2002). It is one of the most difficult quantities to estimate, in particular, of exploited fish populations. Commonly used direct (e.g. based on catch curve, mark-recapture data) and indirect methods (e.g. based on maximum age, life history correlates, and evolutionary-ecology theory) have their benefits and deficiencies and there is no generally accepted approach for selecting values from different methods.

The highly simplified assumptions about M to be constant over time, age, and gender are notoriously problematic for many fish species (Vetter 1988). During early life stage, individuals experience higher natural mortality than juvenile stages due to disease, predation, and other exogenous sources of mortality. After an initial loss of density-dependent death that stabilizes recruitment, mortality rate declines with increasing body size due to the gain in biomass of a cohort through growth is greater than the losses due to M. As individuals mature, the growth rate decreases because of the initiation of allocation to reproduction. During this stage, mortality rate is less well known. The mortality rates appear to be stabilized for adults in which balance increasing costs of reproduction (increasing M) with increased body size (decreasing M). Senescence may exhibit in the later stage of life. Life history theory and ageing research suggest that senescence is most likely to be found in fast-growing, early maturing animals. Sexual dimorphism may also influence natural mortality rates and sex-specific rates may be needed where dimorphism is important. Often, the gender differences in M are apparent in growth (e.g. maximum age observed) and reproduction (e.g. age at maturity).

Pacific blue marlin exhibit sexual dimorphism in growth (Skillman and Yong 1976; Hill *et al.* 1989; Wilson *et al.* 1991) and reproduction (Shimose *et al.* 2009; Sun *et al.* 2009) resulting in the sexual differences in natural mortality estimates (Boggs 1989; Hinton 2001). Males appear to grow steadily to a smaller size than female indicating a faster growth rate for young fish and younger maximum observed size. With shorter longevity and faster growth rate, males tend to experience higher M than females. The otolith-based age estimates of age 0-1 year fish suggest the extremely rapid growth (146 cm EFL at age 1 year in the Shimose's unpublished study). Males also mature early age than females. The estimated length-at-50%maturity is 130 cm and 180 cm EFL for males and females, respectively, implying that males probably mature at very young age and experience high M. Moreover, most studies ignore sex the size-/age- structure of natural mortality leading to a constant M estimated. The magnitude of natural morality has varied considerably (Sun *et al.* 2012 Table 5), ranging from levels indicating a relatively unproductive stock (M=0.08) to levels of productive stock (M=0.81) for the Pacific Ocean stock. There is clearly a need to reconcile the apparent difference between the findings of the empirical studies, and develop a size-/age-specific mortality schedule for each gender. Fortunately, a number of recent studies contain size- or age-specific estimates of M (Lorenzen

1996; 2000; Gislason *et al.* 2010; Charnov *et al.* 2012) providing a possibility for improving our understanding of the parameters important for estimating M.

In this paper a random effects meta-analysis of M is used to synthesize a single M estimated from a range of M estimators for blue marlin in the Pacific Ocean. We assume this estimate represents adult M, and M at younger ages is based on a size-mortality relationship. Numerous estimators are thoroughly evaluated and night estimators are selected. Estimates of uncertainty are also generated using a range of plausible biological and environmental factors based on the best available information from extensive literature review.

Review of methods and selection among them for blue marlin

There are several direct and indirect methods that have been used to estimate natural mortality (Vetter 1988). Direct methods are referred to analyses using the actual data (e.g. catch data, tagging data) and indirect methods are referred to analyses conducted based on estimates of maximum age, life history correlates, and evolutionary-ecology theory. Estimation of natural mortality is feasible by integrating different types of data and assumptions in to stock the assessment models (Fournier *et al.* 1998; Maunder 1998; Hampton and Fournier 2001; Lee *et al.* 2011; Maunder and Wong 2011) and multispecies and ecosystem models (Pope 1989; Magnússon 1995).

Direct methods such as catch curve and mark-recapture analyses rely on many assumptions and representative sampling. Both analyses provide estimates of total mortality. If the data is from an unexploited population, the analysis provides an estimate of natural mortality. Separation is possible if fishing mortality can be estimated reliably. Common concerns with tagging analysis include non-reporting of tags, tag shedding, and tag induced mortality (either initial or long-term) and with catch curve analysis include double use of the catch-at-age data if estimates of M based on catch curves are then used into statistical assessment models.

Incorporating these data into a stock assessment model avoids the need to directly estimate fishing mortality and the double use data; however, the success of estimating natural mortality within a stock assessment model has been variable and is dependent on the amount and type of data that is available, the assumptions that are made in the assessment model, and the structure of the natural mortality that is modeled. Previous studies found that M is confounded from other model parameters estimates associated with productivity (growth and steepness) (Magnusson and Hilborn, 2007; Piner *et al.* 2011) or that describe the decline in observed proportions at older ages (selectivity) (Fu and Quinn, 2000; Thompson 1994). Also, the inclusion of length or age composition data is necessary to reliably estimate M (Magnusson and Hilborn 2007; Lee *et al.* 2011). The multispecies and ecosystem models demand more data and require more biological and ecological assumptions than single species assessment.

Although direct methods and estimation within an assessment model are promising with successful applications, it is not applicable for Pacific blue marlin without well-designed tagging study and good catch at age or catch at size data for each gender. In addition, indirect methods based on life-history theory and empirical relationships have been reviewed and re-evaluated in the massive literatures although criticism about the oversimplified values and large uncertainty exits. Nevertheless, various indirect methods are examined where sex-specific data and other scientific information are scarce for blue marlin.

Maximum age

Relationship between longevity and mortality rate can be observed since animals from a population with a high mortality rate would not survive long enough to reach old age (Beverton and Holt 1959). Estimator was developed based on the linear regression of mortality versus maximum age (Hoenig 1983). In addition, several approximations of mortality were derived from the survival rate (Hoenig 1983). In other words, the probability of a fish living to a given age under a given level of total mortality can be calculated from the standard exponential decay model of population dynamics. Once this arbitrary probability or representative sample size used to determine the maximum observed age is given, mortality can be estimated from estimators such as rule-of-thumb (Tanaka 1960; Sekharan 1975; Hewitt and Hoenig 2005; Quinn and Deriso 1999) and sample size correlate (Holt 1965; Hoenig 1983).

This method has been criticized for a number of reasons (Maunder and Wong 2011). First, method is dependent on the use of a validated ageing to determine the maximum age where aging studies have not been completed and validated. Second, fish of the oldest age classes is usually scare resulting in considerable sampling error in estimates of maximum age. Third, method is dependent on the recruitment and exploitation history of the fishery. In other words, this method does not account for the change in the recruitment event or the change in fishing pressure. For example, maximum aged fish more likely comes from the cohort represented by the large recruitment with less fishing pressure. Fourth, this method used to estimate natural mortality is based on similar arguments to those used for catch curve analysis, where provide estimate of total mortality. It can only estimate M if the samples come from an unexploited population or if the fishing mortality is known. Without reliable estimates of observed maximum age and fishing mortality, this method is not considered for Pacific blue marlin.

Life history correlates

Life history and evolutionary-ecology theory is based on the biological and evolutionary characteristics through tradeoffs among growth, reproduction, and survival (Beverton and Holt 1959; Alverson and Carney 1975; Roff 1984; Charnov 1993; Jensen 1996). Generally speaking, a species with high natural mortality has short lifespan, large gonads in relationship to body size, high fecundities, fast growth rates and small asymptotic sizes. Many estimators and relationships were developed based on this theory that can be used to estimate natural mortality (Pauly 1980; Charnov and Berrigan 1990; Jensen 1996; Gunderson 1997). For example, Beverton and Holt (1959), Alverson and Carney (1975), Roff (1984), Pauly (1980) and Jensen (1996) have demonstrated that the parameters of the von Bertalanffy growth equation and the natural mortality rate are correlated.

This method however, has been criticized for a number of reasons. First, estimators developed using regression methods are heavily dependent on the quality of data and predictions are generally imprecise (Pascial and Iribarne 1993). Second, this method requires accurate estimates of the life history evolution parameters. Third, this method does not consider uncertainty. For example, K is often confounded with the asymptotic length (L_∞) of the von Bertalanffy growth curve and there may be a large amount of uncertainty in the estimate of K and L_∞. Growth parameters (Chang *et al.* 2013) and maturity-at-length (Shimose *et al.* 2009; Sun *et al.* 2009) are available for Pacific blue marlin and hence, several estimators of this method are considered for Pacific blue marlin.

Age- and size- dependent mortality

Lifetime mortality schedules in fish arise from a combination of size-dependent and life history age-dependent processes (Lorenzen 2000). Predation probably accounts for a large share of natural mortality and is often seen as the primary driver of size-dependence. Theoretical and empirical studies (Peterson and Wroblewski 1984; McGurk 1986; Lorenzen 1996) indicate the existence of an allometric relationship between M and body weight.

The age-dependent cost-of-reproduction component of mortality is less well understood than the size dependent component. There is empirical evidence for survival costs of reproduction (e.g. exposure to predation at spawning sites), survival gain with increased body size, and senescence (metabolic damage) in certain species. Some fish species show clear increases in mortality associated with maturation or old age and others may be subject to almost negligible senescence. Life history theory and ageing research suggest that senescence is most likely to be found in fast-growing, early maturing animals. The resulting lifetime patterns of natural mortality tend to be ‘L’ or ‘U’ shaped, declining rapidly with age in early life stages and juveniles, stabilizing in adults and possibly increasing again at old age.

Ad hoc mortality models of age-specific M were developed to account for the transition between juvenile and adult M. Several relationships based on the proportion to body length-at-age (Lorenzen 2000) and weight-at-age (Lorenzen 1996) and empirical methods (e.g. Charnov *et al.* 2012) have been used to estimate relative M to inform the descending changes of M through age.

Since female Pacific blue marlin is not considered as fast-growing, early maturing animals, senescence is not considered in developing the lifetime patterns of natural mortality. If there is any senescence, male blue marlin is more likely than female because male tend to mature at early stage, grow faster, and disappear at certain size above based on the fishery-dependent data.

Methods

Estimating adult M

Night applicable methods based on the life history correlates were compiled to estimate adult M for female and male (Table 1). These methods relied on life history and environmental factors and plausible ranges of factor levels were used to estimate within method uncertainty in the magnitude of adult M (Table 2). Range of sex-specific growth parameters (L_∞, K, and t_0) were taken from the mean and ± 1 standard deviation based on the Bayesian meta-analysis of blue marlin from four studies (Chang *et al.* 2013). Range of maturity-at-length parameter (L_m) was taken from the smallest length at maturity to length-at-95%maturity (Shimose *et al.* 2009; Sun *et al.* 2009) for each gender. Range of maturity-at-age (t_m) was derived from the maturity-at-length and growth curves. The power parameter (β) for the length-weight relationship was based on the meta-analysis from 3-4 studies (Brodziak 2013). Range of maximum observed/assumed age (t_{max}) was derived from the growth curves. Range of temperature (T) was taken from the range of three studies (Nakamura 1985; Molony 2005; Su *et al.* 2008).

The final estimate of M was random effects inverse variance weighted mean across all methods. The methods of estimation of the weighted mean are based on Borenstein *et al.* (2010). In the random-effects models, mean of each method differs from the underlying population mean due to two components of errors, observation error of each method and the underlying population error. Observation error of each method arises from the deviation of the method's observed mean from the method's true mean and is assumed to follow a normal distribution with mean at zero and its observation variance (within-method variance, v_i). Underlying population error arises from the deviation of the method's true mean from the grand mean and is assumed to follow a normal distribution with mean at zero and overall variance (between methods variance, τ^2). A method's total variance under the random-effects model is the sum of v_i and τ^2.

Since the method's true mean is unknown, estimating τ^2 is then based on heterogeneity statistic Q using DerSimonian and Laird approach (1986) as follows.

$$\tau^2 = \begin{cases} \dfrac{Q - df}{C} & \text{if } Q > df \\ 0 & \text{if } Q \le df \end{cases}$$

where the heterogeneity statistic Q is calculated as a weighted sum of the squared deviation of each method mean (X_i) from the weighted mean across methods ($\bar{X}.$).

$$Q = \sum_{i=1}^{j} w_i (X_i - \bar{X}.)^2$$

$$df = j - 1$$

$$\mathrm{C} = \sum \mathrm{w_i} - \frac{\sum \mathrm{w_i^2}}{\sum \mathrm{w_i}}$$

where i is an index of the methods,

j is the number of methods,

w_i is the weight assigned to each method which is the inverse of that method's variance ie. $w_i = 1/v_i$,

$\bar{X}.$ is the weighted mean as follows,

$$\bar{X}. = \frac{\sum w_i X_i}{\sum w_i}$$

C is a scaling factor based on the within method weight, w_i and is

$$\mathrm{C} = \sum \mathrm{w_i} - \frac{\sum \mathrm{w_i^2}}{\sum \mathrm{w_i}}$$

Q is weighted in such a manner that assigns more weight to more precious method, and this also puts Q on a standardized metric. In this metric, the expected value of Q if all methods share a common mean is df. Therefore, $Q - df$ represents the excess (observed minus expected) variance between methods. Since $Q - df$ is on a standardized scale, scaling factor, C, puts this index back into the same metric that had been used to report the within-method variance. If τ^2 is less than zero, it is set to zero, since a variance cannot be negative.

Total variance of each method and its weight under the random-effects are then

$$V_i = v_i + \tau^2,\ W_i = 1/V_i$$

The weighted mean under the random-effects is calculated as:

$$M = \frac{\sum W_i X_i}{\sum W_i}$$

The variance (V_M) of the weighted mean (M) is also given by:

$$\mathrm{V_M} = 1/\sum \mathrm{W_i}$$

Estimating juvenile M

Juvenile natural mortality is governed primarily by size-dependent processes and assumed to decline through age. Growth is rapid in the first year where males reach fully mature size based on the growth and reproduction studies. After male fish are fully mature, M is assumed to be a constant. Male mortality in the first year is described by an ad hoc mortality model where a simple weight-based model (Lorenzen 1996) was used to calculate relative change of M between age 0 and age 1. Relative M for age 0 was calculated as M estimate at age 0 divided by M estimate at maturity-at-age. M at age 0 was the product of the relative M from the Lorenzen's relationship and adult M from meta-analysis for males.

Both female and male marlins are assumed to have little sexual dimorphism between age 0 and age 1 (Shimose's unpublished study). Mortality is the same for females and males at age 0 and age 1. Female mortality is assumed to decline linearly from age 1 to fully mature age to account for size-dependent processes and cost-of-reproduction. After female fish are fully mature, M is assumed to be a constant.

Results

The estimated M by method varied widely for female and male. Female M ranged from 0.12 yr^{-1} for Zhang and Megrey's method (2006) to 0.93 yr^{-1} for Roff (1984) and male M from 0.23 yr^{-1} for Zhang and Megrey (2006) to 0.96 yr^{-1} for Roff (1984) (Table 3).

Table 3 shows the estimates from each method and a random effects mean from meta-analysis. Estimates of mean and variance derived from t_m (Jensen t_m, empirical t_m, and Roff first) were higher than other estimators. These indicated that uncertainty exist in the maturity-at-length or in the growth curves used to convert maturity-at-length to maturity-at-age. Estimates of mean and variance derived from t_{max} (Zhang and Megrey) were lower than other estimators. This could be explained by the uncertainty of estimating t_{max} or underestimate of estimates from the method itself for the long-live stock.

The t_m for female is higher than male resulting a lower M in the estimators of Jensen t_m and empirical t_m. Lower *K* and larger L_∞ for female than male resulting in lower M in estimators of Jensen *K*, empirical *K*, Hoenig *K*, Roff second, and Pauly. Overall, lower estimates of M for female than male are consistent among estimators. The inverse weighted average M across all methods was 0.22 yr^{-1} (95% CI 0.13-0.30 yr^{-1}) and without weighting 0.37 yr^{-1} (95% CI 0-0.95 yr^{-1}) for female and was 0.37 yr^{-1} (95% CI 0.28-0.46 yr^{-1}) and without weighting 0.49 yr^{-1} (95% CI 0-1.01 yr^{-1}) for male.

Age-specific M is given in Table 4. Mortality is the same for females and males at age 0 and age 1 where there is little sexual dimorphism. Estimated M at age 0 derived from the rescaled adult M for male at age 1 based on the Lorenzen's weight-based model (Lorenzen 1996) was 0.42 yr^{-1}. M for adult male at age 1+ maintained at 0.37 yr^{-1} and female M decline linearly to 0.22 yr^{-1} at fully mature age 4 and maintained at this level afterward.

A review of the literature (Table 5) indicated that blue marlin stock assessments generally assumed M between 0.08 and 0.25 yr^{-1} with a mean of 0.17 yr^{-1} (95% CI 0.06-0.28 yr^{-1}) for female and between 0.38 and 0.81 yr^{-1} with a mean of 0.55 yr^{-1} (95% CI 0.21-0.90 yr^{-1}) for male. For combined gender, assumed M between 0.1 and 0.41 yr^{-1} with a mean of 0.25 yr^{-1} (95% CI 0-0.52 yr^{-1}). Our new weighted estimate of M is at the upper tails for female and at the lower end of this CI for male. Most published estimates previously used in population models were constant across age and only one was estimated by the assessment model.

Discussion

Given the choice of factor levels based on best available life history information for Pacific blue marlin, the estimates of adult M are most dependent on methods by Jensen *K* (Jensen 1996), empirical *K* (Jensen 1996), Hoenig *K* (Hoenig 1983), Roff second (Roff 1984), Pauly (Pauly 1980), and Zhang and Megrey (Zhang and Megrey 2006) for both female and male. Weights are more similar to one another under the random-effects model than under the fixed-effect model. In other words, less uncertain (smaller variance) estimators are assigned smaller relative weight under the random-effects model preventing that few estimators dominate the estimates of M. This leads to the combined mean is smaller under the fixed-effect model than the random-effects model where less uncertain estimators have more modest influence (e.g. Pauly method and Zhang and Megrey method). In addition, the simple un-weighted mean may be an inefficient statics (the mean has a large variance) when the variance differs substantially (an order of magnitude) from estimator to estimator. A weighted estimate is preferable to an un-weighted estimate. While the weighted estimate may be biased, it might still be more accurate in terms of having smaller mean-squared error than the un-weighted estimate (Borenstein *et al.* 2010).

In this paper, small number of estimators (9 methods) may dampen precision of the between-methods variance. Other methods of estimation for between- methods variance than the DerSimonian and Laird (1986) used in this paper are available such as maximum likelihood estimation and the iterative and computationally intensive restricted maximum likelihood (REML) estimation. A comparison among these models would help to better understand of reliability of estimates; however, with small number of estimators, no method can yield very precise estimates of between-methods variance.

All of information come from fishery data and Pacific blue marlin have been exploited for decades. When theoretical vital rates are needed, observed vital rates that are influenced by fishing were used to represent population vital rates. For example, maximum age was taken from meta-analysis of growth curve (Chang *et al.* 2013). We assumed that uncertainty in maximum age (regarding unfished population) would be one directional (older). Other estimators could also be influenced through fishery dependent data selection. In presence of size selective gears, the estimates of growth parameters therefore maturity-at-age are probably biased. The uncertainty would be both directions.

The effects of senescence were not considered, in part because the various factors affecting this process are interrelated and may be difficult to discern. Senescence could be assessed using evidence from tagging data or other sources. For example, Hampton (2000) suggested that the natural mortality rate as a function of age was U-shaped for yellowfin tuna in the central Pacific Ocean using tagging data. However, as for high seas tuna, high non-reporting of tags could affect the empirical results. It was thought that species-specific patterns of senescence would remain poorly known in the absence of other sources of data collection programs. The constant adult M assumed in this paper produces an average adult M. Although increasing M at the oldest ages is still possible, this is an area for future work.

This paper derived age- and sex- specific estimates of M that account for size-dependent mortality by gender. This is consistent with recommendations from a recent NOAA workshop on M and from recent growth and reproduction studies (Shimose *et al.* 2009; Sun *et al.* 2009; Chang *et al.* 2013) and modeling works (Su *et al.* 2011) for Pacific blue marlin.

Reference

Alverson, D.L. and Carney, M.J. 1975. A graphic review of the growth and decay of population cohorts. Journal du Conseil International pour l'Exploration de la Mer, 36: 133-143.

Anon. 2011. Report of the 2011 blue marlin stock assessment meeting and white marlin data preparatory meeting. Collect. Vol. Sci. Pap. ICCAT, 68(4): 1273-1386. SCRS/2011/013.

Beverton, R.J.H. and Holt, S.J. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In: CIBA Foundation Colloquia on Ageing, Vol. 5. The Lifespan of Animals (eds G.E.W. Wolstenholme and M. O'Connor) Churchill, London, 142-180.

Boggs, C.H. 1989 Vital rate statistics for billfish stock assessment. In: Planning the Future of Billfishes, Part 1. R.H. Stroud (ed.) Savannah, GA: National Coalition for Marine Conservation, pp. 225–233.

Borenstein, M., Hedges, L.V., Higgins, J. P. T., and Rothstein, H. R. 2010. A basic introduction to fixed effect and random effects models for meta-analysis. Research Synthesis Methods, 1: 97-111.

Brodziak, J. 2013. Combining information on length-weight relationships for Pacific blue marlin. . The ISC Billfish Working Group. Honolulu, Hawaii, January 16-23, 2013. ISC/13/BILLWG-1/XX.

Charnov, E.L. 1993. Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford: Oxford University Press.

Charnov, E.L. and Berrigan, D. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. Evolutionary Ecology. 4: 273–275.

Charnov, E.L., Gislason, H., and Pope, J.G. 2013. Evolutionary assembly rules for fish life histories. Fish and Fisheries (in press).

Chang, Y.J., Brodziak, J., Lee, H.H., DiNardo, G., and Sun, C.L. 2013. A Bayesian meta-analysis of blue marlin (*Makaira nigricans*) growth in the Pacific Ocean. The ISC Billfish Working Group. Honolulu, Hawaii, January 16-23, 2013. ISC/13/BILLWG-1/02.

Clark, W.G. 1999. Effects of an erroneous natural mortality rate on a simple age structured stock assessment. Canadian Journal of Fisheries and Aquatic Sciences, 56: 1721–1731.

Cox, S.P., Essington, T.E., Kithell, J.F., Martell, S. J.D., Walters, C.J., Boggs, C., and Kaplan, I. 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952-1998. II. A preliminary assessment of the tropic impacts of fishing and effects on tuna dynamics. Canadian Journal of Fisheries and Aquatic Sciences, 59:1736-1747.

DerSimonian, R. and Laird, N. 1986. Meta-analysis in clinical trials. Controlled Clinical Trials, 7: 177–188.

Fournier, D.A., Hampton, J., Sibert, J.R., 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. Canadian Journal of Fisheries and Aquatic Sciences, 55: 2105–2116.

Fu, C., Quinn II, T.J., 2000. Estimability of natural mortality and other population parameters in a length based model: Pandalus borealis in Kachemak Bay, Alaska. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2420–2432.

Gislason, H., Daan, N., Rice, J.C., and Pope, J.G. 2010. Size, growth, temperature, and the natural mortality of marine fish. Fish and Fisheries, 11: 149–158.

Gunderson, D.R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Canadian Journal of Fisheries and Aquatic Sciences, 54: 990-998.

Hampton, J. 2000. Natural mortality rates in tropical tunas: size really does matter. Canadian Journal of Fisheries and Aquatic Sciences, 57: 1002–1010.

Hampton, J. and Fournier, D.A. 2001. A spatially disaggregated, length-based, age-structured population model of yellowfin tuna (*Thunnus albacares*) in the western and central Pacific Ocean. Marine and Freshwater Research, 52: 937–963.

Hewitt, D.A. and Hoenig, J.M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fishery Bulletin, 103: 433–437.

Hill, K.T., Cailliet, G.M., and Radtke, R.L. 1989. A comparative analysis of growth zones in four calcified structures of Pacific blue marlin, *Makaira nigricans*. Fishery Bulletin, 87: 829–843.

Hinton, M.G. 2001. Status of blue marlin in the Pacific Ocean. In: Stock Assessment Report 1, Status of Tuna and Billfish Stocks in 1999. M.G. Hinton (ed.) La Jolla, CA: Inter-Am. Trop. Tuna Comm, pp. 284–319.

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

Holt, S.J. 1965. A note on the relation between the mortality rate and the duration of life in an exploited fish population. International Commission for the Northwest Atlantic Fisheries Research Bulletin, 2: 73-75.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal tradeoff of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences, 53: 820-822.

Kleiber, P., Hinton, M.G., and Uozumi, Y. 2003. Stock assessment of blue marlin (*Makaira nigricans*) in the Pacific using MULTIFAN-CL. Marine Freshwater Research, 54(4):349-360.

Lee, H.H., Maunder, M.N., Piner, K.R., and Methot, R.D. 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. Fisheries Research, 109: 89–94.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: A comparison of natural ecosystems and aquaculture. Journal of Fish Biology, 49: 627-647.

Lorenzen, K. 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. Canadian Journal of Fisheries and Aquatic Sciences, 57: 2374-2381.

Magnússon, K.G. 1995. An overview of the multispecies VPA – theory and applications. Reviews in Fish Biology and Fisheries, 5: 195-212.

Magnússon, A., Hilborn, R., 2007. What makes fisheries data informative? Fish and Fisheries, 8: 337–358.

Maunder, M.N. 1998. Integration of Tagging and Population Dynamics Models in Fisheries Stock Assessment. PhD thesis, University of Washington.

Maunder, M.N. and Wong, R.A. 2011. Approaches for estimating natural mortality: Application to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. Fisheries Research, 111: 92– 99.

McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Marine Ecology Progress Series, 34:227–242.

Molony, B. 2005. Summary of the Biology, Ecology and Stock Status of Billfishes in the WCPFC, with a Review of Major Variables Influencing Longline Fishery Performance. Working Paper EB-WP-2, 1st Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission (WCPFC-SC1), 8–19 August 2005, New Caledonia, Noumea, 67 pp.

Nakamura, I. 1985. Billfishes of the world. FAO Fisheries Synopsis 125, 65p.

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

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

Peterson, I., and Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences, 41: 1117–1120.

Piner, K.R., Lee, H-H., and Maunder, M.N. (2011) A Simulation-Based Method to Determine Model Misspecification: Examples Using Natural Mortality and Population Dynamics Models. Mar. Coast. Fish. 3(1): 336-343

Pope, J.G. 1989. Multispecies extensions to age-structured assessment models. American Fisheries Society Symposium, 6: 102-111.

Prager, M.H. and Goodyear, C.P. 2001. Effects of mixed metric data on production model estimation: simulation study of blue marlin like stock. Transactions of the American Fisheries Society, 130:927-39.

Quinn II, T.J., Deriso, R.B., 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. Canadian Journal of Fisheries and Aquatic Sciences, 41: 989-1000.

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 Journal of Fisheries, 21: 177-182.

Skillman, R.A. and Yong, M.Y.Y. 1976. Von Bertalanffy growth curves for striped marlin, *Tetrapturus audax*, and blue marlin, *Makaira nigricans*, in central north Pacific Ocean. Fishery Bulletin, 74(3):553-566.

Shimose, T., Fujita, M., Yokawa, K., Saito, H., and Tachihara, K. 2009. Reproductive biology of blue marlin *Makaira nigricans* around Yonaguni Island, southwestern Japan. Fisheries Science, 75(1):109-119.

Su, N.J., Sun, C.L., Punt, A.E., and Yeh, S.Z. 2008. Environmental and spatial effects on the distribution of blue marlin (*Makaira nigricans*) as inferred from data for longline fisheries in the Pacific Ocean. Fisheries Oceanography, 17:432–445.

Su N.J., Sun, C.L., Punt, A.E., Yeh, S.Z., and DiNardo, G. 2011. Evaluation of a spatially sex-specific assessment method incorporating a habitat preference model for blue marlin (*Makaira nigricans*) in the Pacific Ocean. Fisheries Oceanography, 20(5):415-433.

Sun, C.L., Chang, Y.J., Tszeng, C.C., Yeh, S.Z., and Su, N.J. 2009. Reproductive biology of blue marlin (*Makaira nigricans*) in the western Pacific Ocean. Fishery Bulletin, 107(4):420-432.

Sun, C.L., Chang, Y.J., Yeh, S.Z., and Su, N.J. 2012. A review of life history parameters of the Pacific blue marlin. The ISC Billfish Working Group. Shanghai, China, April 2-9, 2012. ISC/12/BILLWG-1/06.

Tanaka, S. 1960. Studies on the dynamics and the management of fish populations. Bulletin of the Tokai Regional Fisheries Research Laboratory 28, 200 pp. [In Japanese with English summary.]

Thompson, G.G., 1994. Confounding of gear selectivity and the natural mortality rate in cases where the former is a nonmonotone function of age. Canadian Journal of Fisheries and Aquatic Sciences, 51: 2654–2664.

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

Williams, E., 2002. The effects of unaccounted discards and misspecified natural mortality on harvest policies based on estimates of spawners per recruit. N. Am. J. Fish. Manage, 22: 311–325.

Wilson, C.A., Dean, J.M., Prince, E.D. and Lee, D.W. 1991. An examination of sexual dimorphism in Atlantic and Pacific blue marlin using body weight, sagittae weight, and age estimates. J. Exp. Mar. Biol. Ecol. 151:209–225.

Zhang, C.-I. and Megrey, B.A. 2006. A revised Alverson and Carney model for estimating the instantaneous rate of natural mortality. Transactions of the American Fisheries Society, 135: 620-633.

Table 1. Estimators of M and rescaling of juvenile M.

Name	Reference	Equation
Adult M, $\boldsymbol{M_m}$		
Jensen t_m	Jensen (1996)	$M_m = 1.65/t_m$
Empirical t_m	Charnov and Berrigan (1990)	$M_m = 2/t_m$
Jensen K	Jensen (1996)	$M = 1.5K$
Empirical K	Jensen (1996)	$M = 1.6K$
Hoenig K	Hoenig (1983)	$M = 1.8K$
Roff first	Roff (1984)	$M = \frac{3K}{\exp(t_m K) - 1}$
Roff second	Roff (1984)	$M = \frac{3KL_\infty(1 - {}^{L_m}/_{L_\infty})}{L_m}$
Pauly	Pauly (1980)	$\ln(M) = -0.0152 - 0.279\ln(L_\infty) + 0.6543\ln(K) + 0.4634\ln(T)$
Zhang and Megrey (Revised Alverson and Carney)	Zhang and Megrey (2006)	$M = \frac{\beta K}{\exp(K(0.302t_{max} - t_0)) - 1}$
Juvenile M (Size-dependent), $\boldsymbol{M_t}$		
Lorenzen	Lorenzen (1996)	$M_t = 3W_t^{-0.288}$

K: growth rate parameter of von Bertalanffy growth curve
L_∞ : asymptotic length parameter of von Bertalanffy growth curve
L_m : length at reproductive maturity
L_t : length at age t
W_t: weight at age t
t_m: age at reproductive maturity
t_{max}: maximum observed or assumed age
t_0: age at zero length parameter of von Bertalanffy growth curve
T: mean environmental temperature
β: power parameter of length-weight relationship

Table 2. Assumed levels of variability in key factors.

Factor	Range of level	Source
K	Female: 0.05 to 0.16 Male: 0.15 to 0.28	Chang *et al.* (2013) based on meta-analysis
L_∞ (EFL)	Female: 267 to 365 cm Male: 194 to 215 cm	Chang *et al.* (2013) based on meta-analysis
L_m (EFL)	Female: 180 to 194 cm Male: 130 to 140 cm	Shimose *et al.* (2009) Sun *et al.* (2009)
t_m	Female: 2 to 4 yr Male: 2 to 3 yr	Maturity-at-length: Shimose *et al.* (2009); Sun *et al.* (2009) Growth: Chang *et al.* (2013)
t_{max}	Female: 23 to 26 yr Male: 10-13 yr	Derived from Chang *et al.* (2013)
t_0	Female: -5.8 to -3.6 Male: -3.9 to -2.2	Chang *et al.* (2013) based on meta-analysis
temperature	24 to 27 °C	Nakamura (1985); Molony (2005); Su *et al.* (2008)
β	Female: 2.956 Male: 2.975	Brodziak (2013)

Table 3. Estimates of adult M, their variance, and weights for the variance for female and male Pacific blue marlin of each estimator based on the range given in Table 2. An un-weighted mean across estimators and inverse weighted mean using fixed effect and random effects meta-analyses are given below. Weights has been normalizes (0-1).

Method	Mean M		Within-method variance (relative weights)		Within-method and between methods variance (relative weights)	
	Female	Male	Female	Male	Female	Male
Jensen t_m	0.60	0.69	0.0441 (0.01)	0.0378 (0.02)	0.0510 (0.04)	0.0454 (0.04)
Empirical t_m	0.72	0.83	0.0648 (0.01)	0.0556 (0.01)	0.0717 (0.03)	0.0632 (0.03)
Jensen K	0.17	0.32	0.0051 (0.12)	0.0051 (0.15)	0.0119 (0.15)	0.0127 (0.15)
Empirical K	0.18	0.34	0.0058 (0.11)	0.0058 (0.13)	0.0126 (0.14)	0.0134 (0.14)
Hoenig K	0.20	0.38	0.0073 (0.09)	0.0073 (0.10)	0.0141 (0.13)	0.0149 (0.13)
Roff first	0.93	0.96	0.1058 (0.01)	0.0694 (0.01)	0.1126 (0.02)	0.0770 (0.02)
Roff second	0.23	0.33	0.0119 (0.05)	0.0067 (0.11)	0.0188 (0.10)	0.0143 (0.13)
Pauly	0.21	0.36	0.0030 (0.21)	0.0024 (0.31)	0.0099 (0.18)	0.0100 (0.19)
Zhang and Megrey	0.12	0.23	0.0016 (0.39)	0.0045 (0.16)	0.0085 (0.22)	0.0121 (0.16)

	Mean M		95% CI lower and upper bound	
	Female	Male	Female	Male
un-weighted mean	0.37	0.49	0 -0.95	0-1.01
inverse weighted mean (fixed-effect)	0.18	0.35	0.13-0.23	0.29-0.40
inverse weighted mean (random-effects)	0.22	0.37	0.13-0.30	0.28-0.46

Table 4. Estimates of M schedule for female and male Pacific blue marlin.

Age	Female M	Age	Male M
0	0.42	0	0.42
1	0.37	1+	0.37
2	0.32		
3	0.27		
4+	0.22		

Table 5. Overview of the estimates of M for blue marlin. The category age specific refers to if a constant M or age-specific M was used in the model. The category assumption refers to if the M was estimated or fixed at a specific value in the model. The bottom of the table gives the mean of the values and associated 95% CI.

Area	Source	Female	Male	Combined	Age specific	Assumption
Pacific	Boggs (1989)	0.21	0.53		No	assumption
Pacific	Hinton (2001)	0.18	0.38		No	assumption
Pacific	Hinton (2001)	0.14	0.81		No	assumption
Pacific	Hinton (2001)	0.19	0.41		No	assumption
Pacific	Hinton (2001)	0.25	0.63		No	assumption
Pacific	Hinton (2001)	0.08			No	assumption
Pacific	Hinton (2001)	0.14			No	assumption
Pacific	Kleiber *et al.* (2003)			0.38	No	estimated
Pacific	Pine *et al.* (2008)			0.41	No	assumption
Pacific	Cox *et al.* (2002)			0.2	No	assumption
Atlantic	Prager and Goodyear (2001)			0.1 for adult	Yes	assumption
Atlantic	ICCAT (2011)			0.139	No	assumption
Mean		0.17	0.55	0.25		
95% CI		0.06-0.28	0.21-0.9	0-0.52		