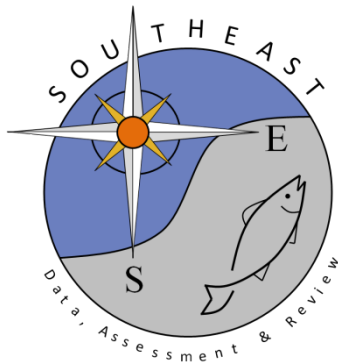


A Review for Estimating Natural Mortality in Fish Populations

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by

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Introduction

Natural mortality (M) is a parameter in most fish stock assessment models. For instance, the yield equation depends directly on M

$$Y(a, t, F, M) = (1 - e^{-F-M}) N(a, t) W(a) \left(\frac{F}{F + M} \right) \quad (1)$$

where a is an index for age, t is time, F is fishing mortality, and $W(a)$ is a function for weight at age a , and $N(a, t)$ is the number of individuals of age a at time t . Natural mortality can occur through predation or non-predation events such as senescence and disease. The von Bertalanffy growth equation (VBGE) is widely used to give estimates of growth parameters, but methods for estimating M are far less uniform within the discipline. It is also a difficult life history trait to measure in the laboratory or the field.

It is generally accepted that natural mortality is very high during the larval stages and decreases as the age of the fish increases, approaching a steady rate (Jennings et al. 2001). The rate then increases exponentially when the fish nears maximum age. A graphical representation looks like a vertical section of a bathtub, and was described by Chen and Watanabe as a Bathtub curve (Chen and Watanabe 1989). Natural mortality may also vary with size, sex, parasite load, density, food availability and predator numbers. However, in most cases, a single value—usually 0.2—for natural mortality is assumed for stock assessments, despite evidence to the contrary (Pope 1979, Quinn and Deriso 1999, Jennings et al. 2001).

When the same value of a parameter is used in almost all analyses, it may mean that there are no methods for obtaining a better estimate. There are, however, a variety of methods available for estimating natural mortality, and Vetter published a review of those methods (1988). Vetter reviewed catch-analysis methods, life history-based models, and predation models. Since her review, there have been a number of new models and model improvements.

In the following paper, I will review the methods available to estimate natural mortality since Vetter's review. I will describe a simulation study that tests the performance of most of the models I review when the parameters are known. Finally, I illustrate, through a case study on California sheephead, *Semicossyphus pulcher*, when it is appropriate to use a constant value for natural mortality.

Review of Methods to Estimate M

Life History Methods

The following is a table of the life history methods Vetter reviewed:

Life history-based methods for estimating natural mortality describe relationships between M and traits like age, growth rate, and weight. Table 1 illustrates the methods that Vetter (1988) reviewed.

Going beyond Myers and Doyle (Myers and Doyle 1983) and building on Gunderson (1980), Gunderson and Dygert (1988) use reproductive effort as such a trait:

$$M = 0.03 + 1.68GSI \quad (2)$$

where GSI is the gonadal-somatic-index. The GSI is a ratio of gonad mass to total body mass, and a high value indicates a large investment in reproduction.

Chen and Watanabe (1989) provide the first age-dependent model of natural mortality to our knowledge:

$$M(t) = \frac{k}{(1 - e^{-k(t-t_0)})} \quad \text{for } t < t_m \quad (3)$$

$$M(t) = \frac{k}{a_0} + a_1(t - t_m) + a_2(t - t_m)^2 \quad \text{for } t > t_m$$

$$a_0 = 1 - e^{-k(t_m - t_0)} \quad (4)$$

$$a_1 = ke^{-k(t_m - t_0)} \quad (5)$$

$$a_2 = -0.5k^2e^{-k(t_m - t_0)} \quad (6)$$

$$t_m = -\left(\frac{1}{k}\right)\log(1 - e^{kt_0}) + t_0 \quad (7)$$

where \bar{M} is average natural mortality, t_m is the age at maturity, t_0 is the theoretical age when size is zero, and k is the von Bertalanffy growth coefficient. This equation may be applied to data for which the von Bertalanffy growth parameters are known. Their results show strong coherence to results obtained using past methods, and they therefore deem their equations as “suitable for fish population dynamics”.

Hoening’s method is commonly used in fishery biology (Hoening 1983, Jennings et al. 2001, Hewitt and Hoening 2005)

$$M \approx \frac{3}{t_{\max}} \quad (8)$$

if approximately 5% of the population is still alive at the maximum age.

However, Hewitt and Hoenig (2005) expand on the earlier version with a larger data set.

The new empirically derived method is the following

$$M \approx \frac{4.22}{t_{\max}} \quad (9)$$

if approximately 1.5% of the population is still alive at the maximum age.

Jensen (1996) revisits the Beverton and Holt invariants

$$Mt_m \quad \text{and} \quad \frac{M}{k} \quad (10)$$

and relates them to constant values calculated by regressions across a variety of fish species. His results are the following:

$$M = \frac{1.65}{x_m} \quad (11)$$

$$\frac{M}{k} = 1.5 \quad (12)$$

He reasons that since the Beverton Holt invariants were derived independently from any growth model, these relations are applicable across fish regardless of their growth function. The parameter k , however, is the the vonBertalanffy growth coefficient. Therefore, there must be sufficient data to estimate k in order for one to use Jensen's equations.

Richter and Efanov (1977) used data from temperate stocks to relate natural mortality to the age at which 50% of the stock is mature

$$M = \left(\frac{1.52}{t_{mass}^{0.72}} \right) - 0.16 \quad (13)$$

where t_{mass} is the age in years when 50% of the stock is at mature.

Peterson and Wroblewski (1984) put forward an allometric model for M based on weight (see Vetter 1988). There is empirical evidence in fish populations that natural mortality is closely related to individual body weight (Post and Evans 1989). McGurk expands on the Peterson-Wroblewski model in his 1986 paper:

$$M_w = 0.00526W^{-0.25} \quad (14)$$

where M_w is natural mortality at weight W , and W is dry body mass. He believed an issue with previous models was the assumption that predation occurs everywhere randomly. As a result he included a measure of spatial patchiness using Lloyd's index (1967). He uses data from pelagic eggs and larvae to test his model output against the Peterson-Wroblewski estimates of M . His results show that the Peterson-Wroblewski model fits data for average-sized to large animals, but constantly underestimates the eggs and larvae of the same animals. However, his model represents eggs and larvae with relatively low mortality very well. He attributes the less good fit to eggs and larvae with higher mortality to real variation in time and space of patchiness and mortality.

Similarly, Lorenzen (1996a, 1996b) models natural mortality as a power function of weight:

$$M_w = M_u W^b \quad (15)$$

where M_w is natural mortality at weight W grams, M_u is mortality at unit weight, and b is the scaling factor. Natural mortality is measured as an annual rate. Lorenzen compared the results of M for fish in natural ecosystems and in aquaculture ponds. He found a higher mortality at unit weight for fish in natural ecosystems than for those in aquaculture ponds, even though they were held in the same latitudinal zone.

Growth coefficient

Since many of the life history models depend on the parameters of the von Bertalanffy growth equation (VBGE), we review some methods for estimating its parameters. Two commonly used methods for estimating k are ELEFAN and MULTIFAN. ELEFAN (Pauly and David 1981) is a computer-based method developed to analyze size-frequency distributions. The program “traces” the average of five age classes using the VBGE. ELEFAN is still used by the FAO to assess stocks in developing countries. MULTIFAN is a maximum likelihood method that assumes von Bertalanffy growth and normal distributions for mean lengths at age (Fournier et al. 1990, 1991). MULTIFAN can be used on multiple size-frequency data sets and is typically used to assess tuna stocks in the Eastern Tropical Pacific (Hampton 1997, Hampton 2000, Goodyear 2002).

Chapter ## in this thesis describes 2 Bayesian methods for estimating all parameters of the VBGE.

Predation Methods

These methods were developed to take into account the species interactions between predator and prey and translate that interaction to a mortality rate for the stock species. Multispecies virtual population analysis (MSVPA) was initiated by both Pope (1979) and Helgason & Gislason (1979). Vetter (1988) provides earlier references and a discussion of the application of MSVPA, and Magnusson (1995) provides a review.

Catch-Analysis Methods

Recently, Pine et al. (2003) published a review of tagging methods for estimating components of natural mortality. In the following section we review the key papers Pine et al. (2003) omitted.

Size-specific models of natural mortality are rarely used due to the difficulty of obtaining even a general estimate. It is recognized, however, that mortality is variable with age (Beverton and Holt 1957, Ricker 1975). There is a general consensus that mortality is higher in larval and juvenile stages, lowers at maturity, and increases again when the maximum age is approached (Vetter 1988). The Tag-attrition model (Kleiber et al. 1987; Hampton 1997) is a size aggregated capture-recapture model. Hampton (2000) builds upon the Tag-attrition model to estimate mortality in tropical tunas. In Hampton's model, the tagging data were classified based on the size at release. A VBGE was used to calculate growth while the tagged fish was at liberty. Then, using maximum

likelihood, natural and fishing mortality are estimated. Hampton (2000) found that natural mortality increased at the latest age classes.

Brooks et al. (1998) suggest generalizations of tagging models that produce estimates for natural mortality when both recreational and commercial fishing is present. Their method allows for the inclusion of data from fisheries that have been open for any length of time; normally, fishing is considered pulse or continuous. Brooks et al.'s (1998) method had good precision and will likely perform well in contentious situations with multiple user groups.

Beyer et al. (1999) present a size-specific method that assumes an inverse relationship between mortality and body size and a mortality that is approaching a minimum as fish grow to their maximum size. If there is no evidence that the species senesce or avoid fishing gear at older ages, this model will likely perform well.

Simulation Study

The number of models to estimate natural mortality is quite large, but which one should be used. Data will certainly limit the choice, but there will still be a number of options. In order to test the performance of these models, we conducted a population simulation.

We used literature values for life history parameters of the blue shark, *Prionace glauca*, from the Apostolaki et al. paper (2005). Individuals grow according to the von Bertalanffy growth equation

$$L(a) = L_{\infty} \left(1 - e^{-k(a-t_0)}\right) + \varepsilon_a \quad (16)$$

where L_{∞} is asymptotic size, k is the individual growth rate, a is an index of age, t_0 is

used to calculate size at birth, and ε_a is a random normal error with mean 0 and variance

5. Weight scales with length allometrically:

$$W(a) = 0.000000804L(a)^{3.2319} \quad (17)$$

where $W(a)$ is kilograms at age a in kilograms. Since blue sharks are livebearers, fecundity is in calculated in pup units

$$\Phi(a) = -91.97W(a)^{0.6052} \quad (18)$$

where $\Phi(a)$ is the number of pups each mother of age a produces. The previous equation doesn't account for whether the mother is mature, so we included a function that describes the proportion mature:

$$p_m(a) = \frac{1}{1 + e^{-c(a-A_{50})}} \quad (19)$$

where A_{50} is the age when 50% of the population is mature (5 years) and c is a shape parameter.

The stock-recruitment relationship follows a Beverton-Holt relationship

$$R(t) = \frac{\alpha E(t)}{1 + \beta E(t)} \quad (20)$$

where $R(t)$ is recruits in time t , α and β are Beverton-Holt parameters, and $E(t)$ is the number of pups in time t . Natural mortality is included in three forms: independent, size dependent, and age dependent. The population persists according to the following:

$$N(a+1, t+1) = N(a, t) e^{\left(-m_1 + \frac{m_2}{L(a)} + m_3 U(a)\right)} \quad (21)$$

where N is the number of individuals at time t and age a , m_1 is the size and age-independent mortality rate, m_2 is the size-based mortality rate, m_3 is the age-based component, and $U(a)$ is the function describing the bathtub curve

$$U(a) = c \left[e^{(-\lambda_d(a-d))} + e^{(\lambda_g(a-g))} \right] \quad (22)$$

where c is a scaling factor, d is the approximate age when constant mid-life mortality begins, and g is the approximate age when constant mid-life mortality ends. In our case, $d = 3$ and $g = 15$.

We run the simulation through 100 time steps 1000 times, which gives us an array of the stochastic population sizes through time and simulation runs. We allow the population to reach a stable age and size distribution (Figures 1 and 2) and we have 100 matrices for length, weight, and proportion mature at age (one example is given in Figure 3).

Application of the models to our simulated data

For our population simulation we used a combined mortality of 0.2, without considering the age-based mortality. Once the age-based component is included, the true mortality at age looks like the bathtub curve described earlier (See Figure 4, Chen and Watanabe 1989). We list our results in Table 2. McGurk's method fits very well until the oldest age classes, and the Chen and Watanabe method fits quite well throughout. The constant values derived from the life history methods average across periods of very high

mortality (early and late life). We argue that the McGurk method and the Chen and Watanabe method are far superior at estimating the true natural mortality. The difference between the two is the assumption that fish will senesce, but whether one's assumption is they do or they do not, both methods are available to apply to data.

When is a constant mortality appropriate? An application to California sheephead

Calculating key life history parameters for long-lived fishes is often difficult. We rarely have sufficient length-at-age or catch-at-age data to derive the parameters directly; in these cases we cannot depend on established growth models or methods for estimating natural mortality that require age data.

A prime example of this dilemma is the recent stock assessment of California sheephead, *Semicossyphus pulcher* (Alonzo et al. 2004). In the following section, I compare estimates of natural mortality for California sheephead using data from the commercial fishery compiled during the sheephead assessment. I find estimates of M , the natural mortality rate, using weight and life history-based methods. The estimate of constant mortality stabilizes if the fish recruit to the model after age two.

Methods and Results

We used a number of methods to calculate natural mortality that depend on the weight or the life history of the fish (Vetter 1988). The following length-weight relationship is used throughout the sheephead assessment:

$$W = 2.6935 \times 10^{-5} (FL^{2.857}) \quad (23)$$

where W is weight in kilograms and FL is fork length in centimeters. We used total length data for the estimate of asymptotic size, therefore we needed to convert to fork length to use Eqn. (23) for our estimates (Alonzo et al. 2004).

Given W , the Peterson and Wroblewski (1984) equation relating mortality to weight is

$$M_w = 1.29 \text{ year}^{-1} W^{-0.25} \quad (24)$$

where M_w is natural mortality at mass W .

Lorenzen (1996a) models natural mortality as a power function of weight in natural ecosystems

$$M_w = 3.00 \text{ year}^{-1} W^{-0.288} \quad (25)$$

where M_w is natural mortality, at W mass. The coefficient in Eqn. 6 is a joint estimate of fish in natural ecosystems based on Lorenzen's empirical work (Lorenzen 1996a).

Jensen (1996) derived two models to estimate M (Equations 7 and 8) We used $k = 0.0683$ and $x_m = 4-6$ years for our analysis, which is consistent with Alonzo et al.(2004).

The estimates of M using each of the models discussed are summarized in Table 3.

Since California sheephead are long-lived fish ($t_{\max} = 50$ years), calculating an average natural mortality across a population is also appropriate (Beverton and Holt 1959). Assuming individuals follow von Bertalanffy growth we can find weight at age using Eqn. (23). We can then relate this to the population using the following equations:

$$N(t) = N(0)e^{-\bar{M}(t)t} \quad (26)$$

$$\overline{M}(t_r) = \frac{1}{T} \sum_{t=t_r}^{T-1} M(W(t)) \quad (27)$$

where $N(t)$ is the population size at time t , $\overline{M}(t_r)$ is the estimate of average mortality when fish are recruited to the model at age t_r , T is the endpoint (50 in this case), and $M(W(t))$ is a weight-dependent mortality model (either Lorenzen's or Peterson and Wroblewski's). Simulating this population through 50 years, we use the population size at $T = 50$ and compare it to the population size at $t = 1$ using Eqn. (26) and Eqn. (27). Running the simulations twice, once for Lorenzen's equation and once for Peterson and Wroblewski's, we arrive at estimates of average natural mortality. In Figure 5 we show the population size as a function of time for both mortality models. Using Lorenzen's model for mortality, we calculated an average natural mortality rate of 0.54. Using Peterson and Wroblewski's mortality model, we calculated 0.60 as the average natural mortality rate.

Discussion

In most stock assessments, M is a fixed value. Our example shows that the age at which the fish recruit to the fishery can have a large impact on the estimate of a constant M . Assuming a weight-based mortality in fishes, Figure 5 shows that there is severe mortality in the first few years. Average natural mortality will change drastically—likely an order of magnitude or more—if those first few years are excluded from the calculation. In Figure 6, we plot $\overline{M}(t_r)$ as a function of the age the fish recruit to the model; after age two, the estimates of \overline{M} become more stable for California sheephead.

Alonzo et al. (2004) used an estimate of 0.2. As shown in Figure 6, our analysis supports their findings if the Peterson and Wroblewski mortality model is assumed.

Discussion

Natural mortality is a very important, yet illusive life history parameter. Errors in the estimation of mortality affect the outcome of various models used in stock assessments. Mertz and Myers (1997) show that an error in cohort reconstruction (cohort analysis) occurs when an inaccurate estimate of natural mortality is provided. Clark (1999) determines that an erroneous natural mortality estimate creates bias in the estimates of stock size provided by an age-structured model. Williams and Shertzer (2003) state that policy based on mortality is particularly sensitive to the estimation of model parameters. We demonstrate in Figure 7 the difference in yield when fishing mortality is fixed and M is allowed to vary.

We argue that the weight- and age-based method are most appropriate, and since many of the methods that estimate a constant value for M require growth data, the weight- and age-based methods are not data intensive.

Future Work

From our population simulation, we calculated mean weights at age and mean population sizes at age. For a future area of research, we propose using a distribution-based approach to estimating M . Using Bayesian statistics to find a posterior distribution for M given a model choice and a stochastic population simulation. Bayesian Model Averaging is an approach that would allow all or part of the relevant models to be

applied. More attention should be paid to estimating M , given it is a foundational parameter in stock assessment.

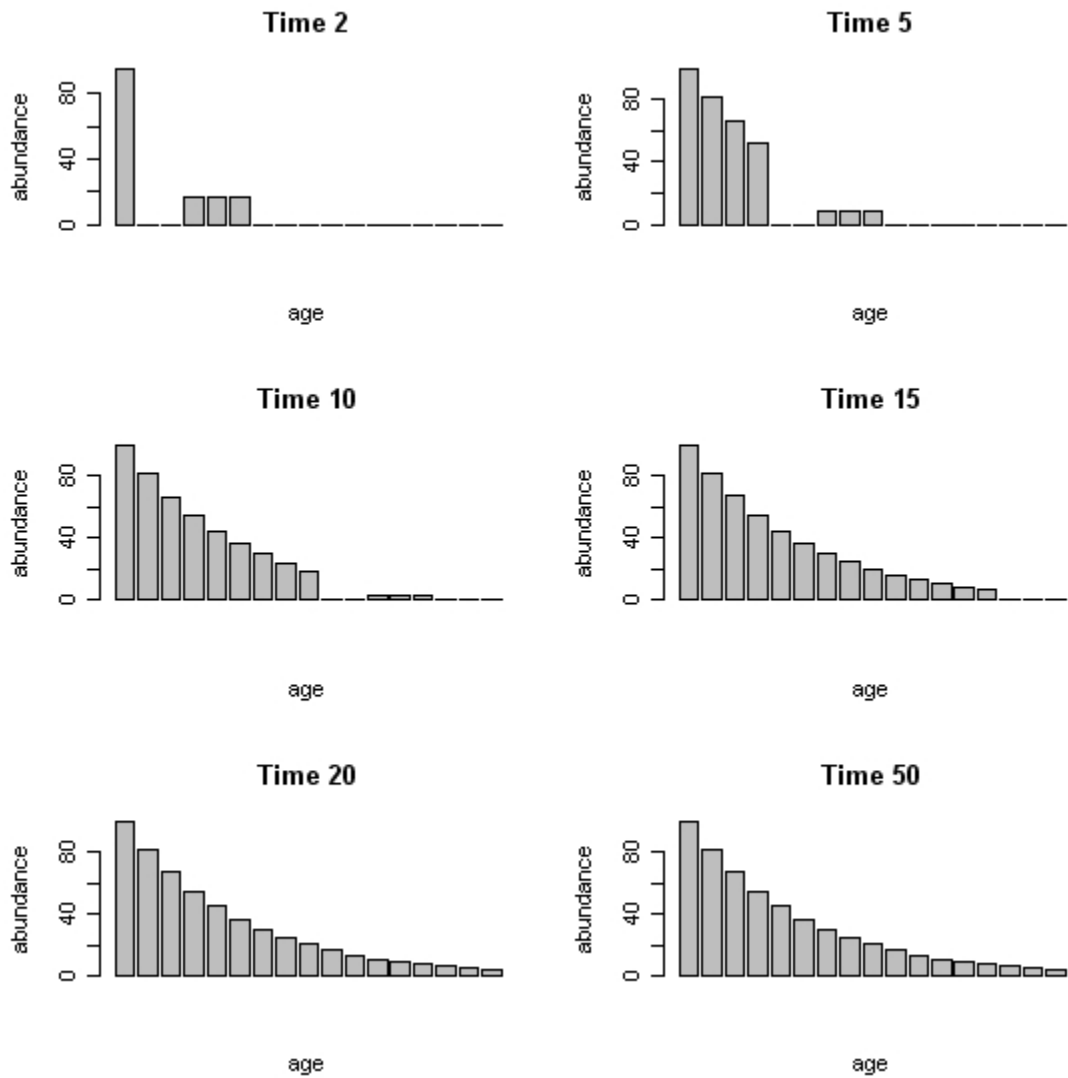


Figure 1. The age distribution of blue shark in our simulated population.

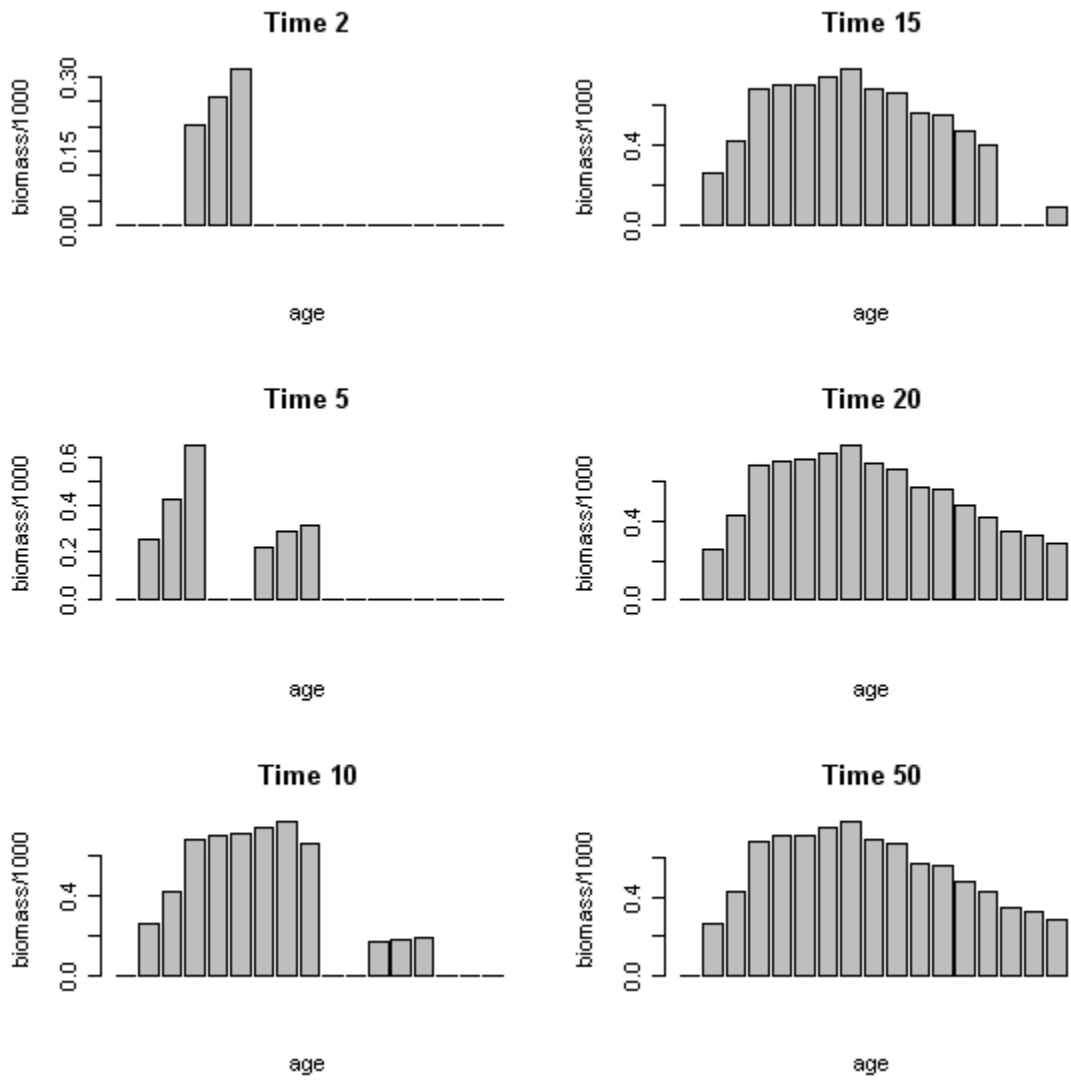


Figure 2. The distribution of biomass at age in our population simulation.

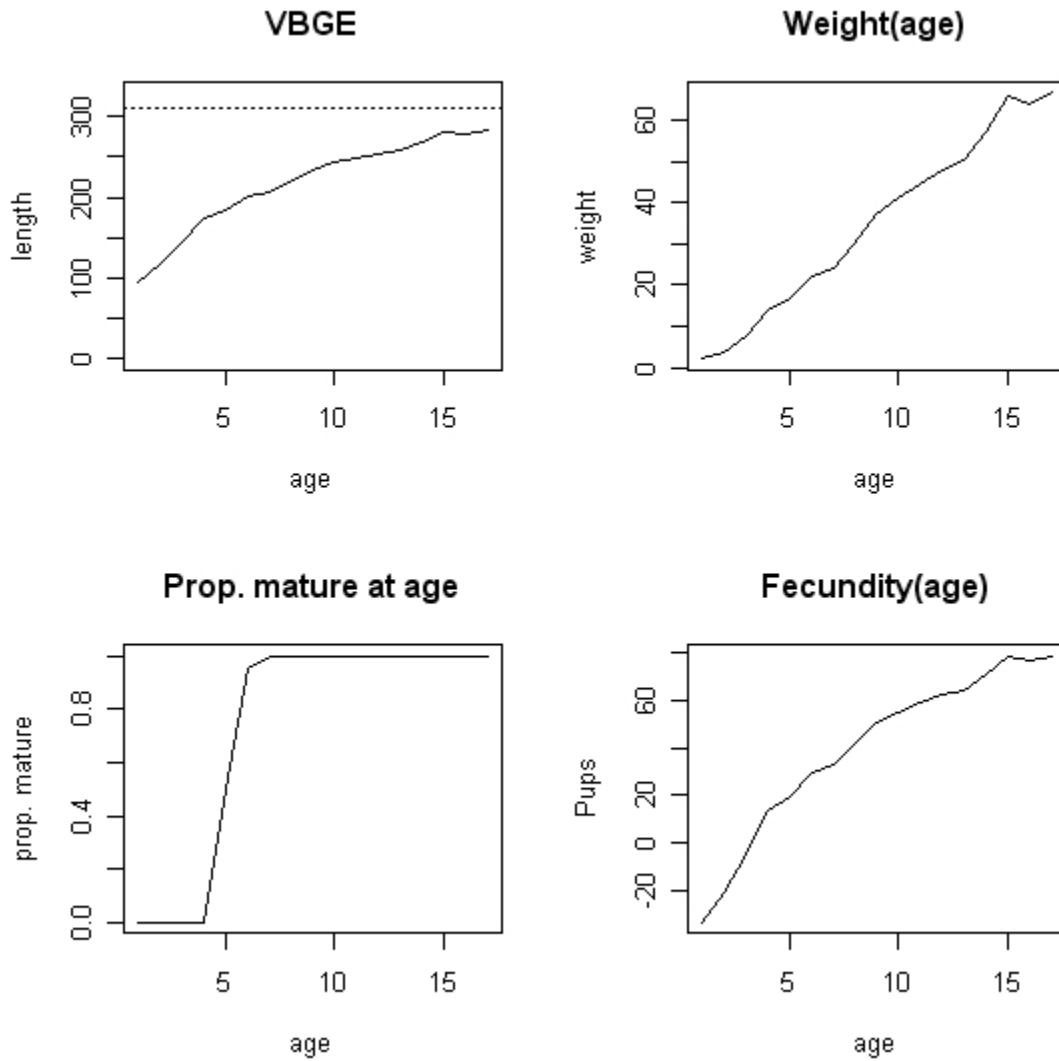


Figure 3. The length at age, weight at age, fecundity at weight, and proportion mature at age relationships in our pseudo-population.

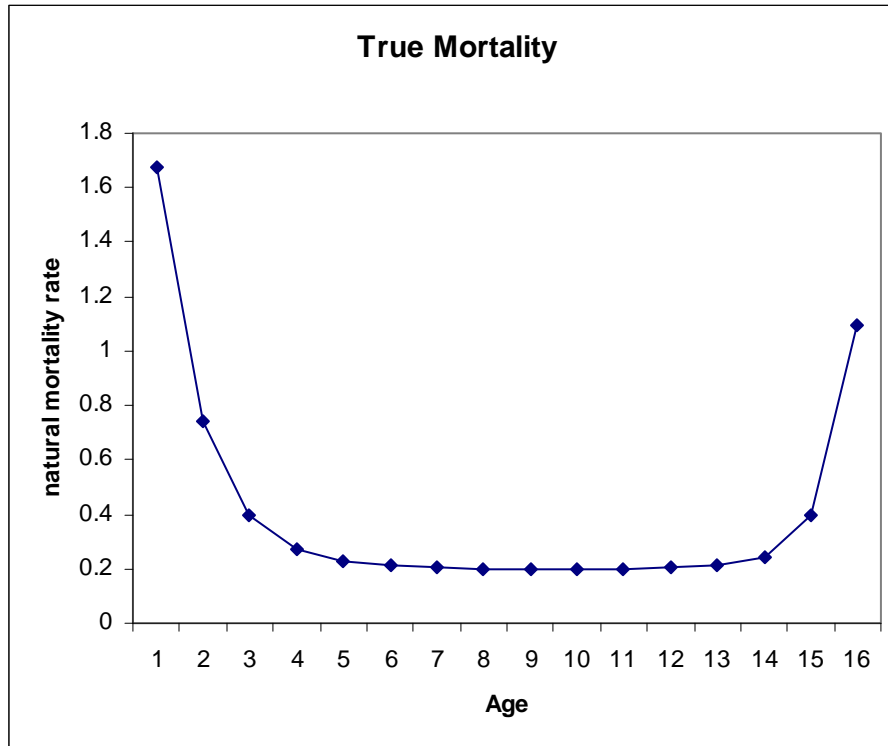


Figure 4. The true mean mortality at each age in our simulated population.

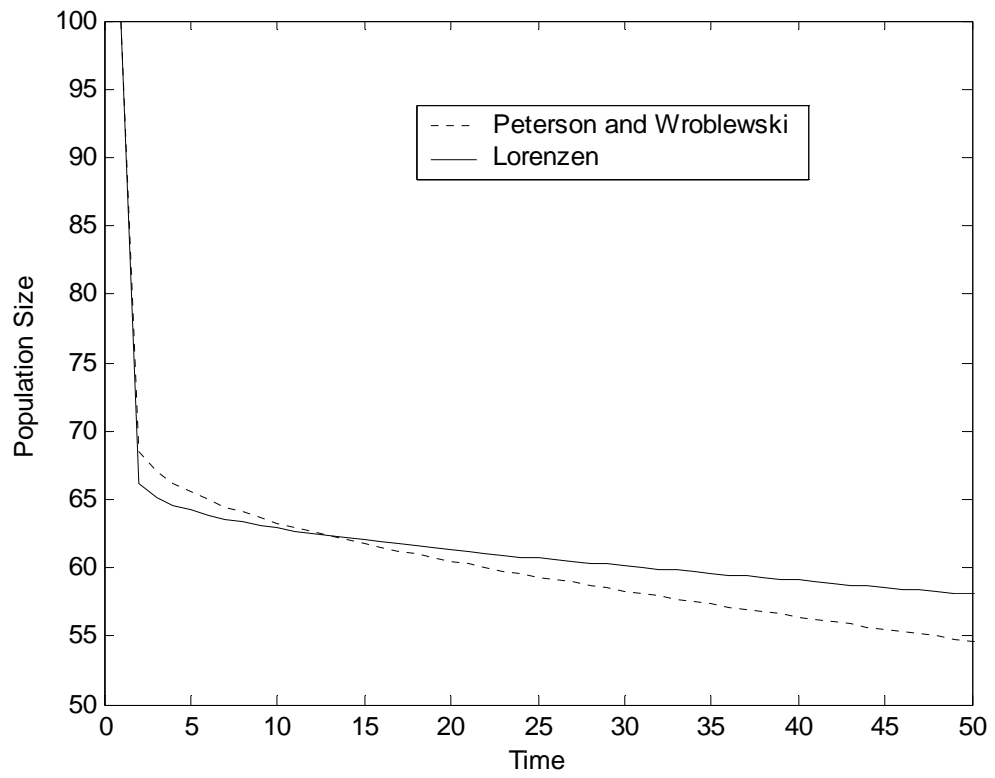


Figure 5. Population Size as a function of time for both mortality models.

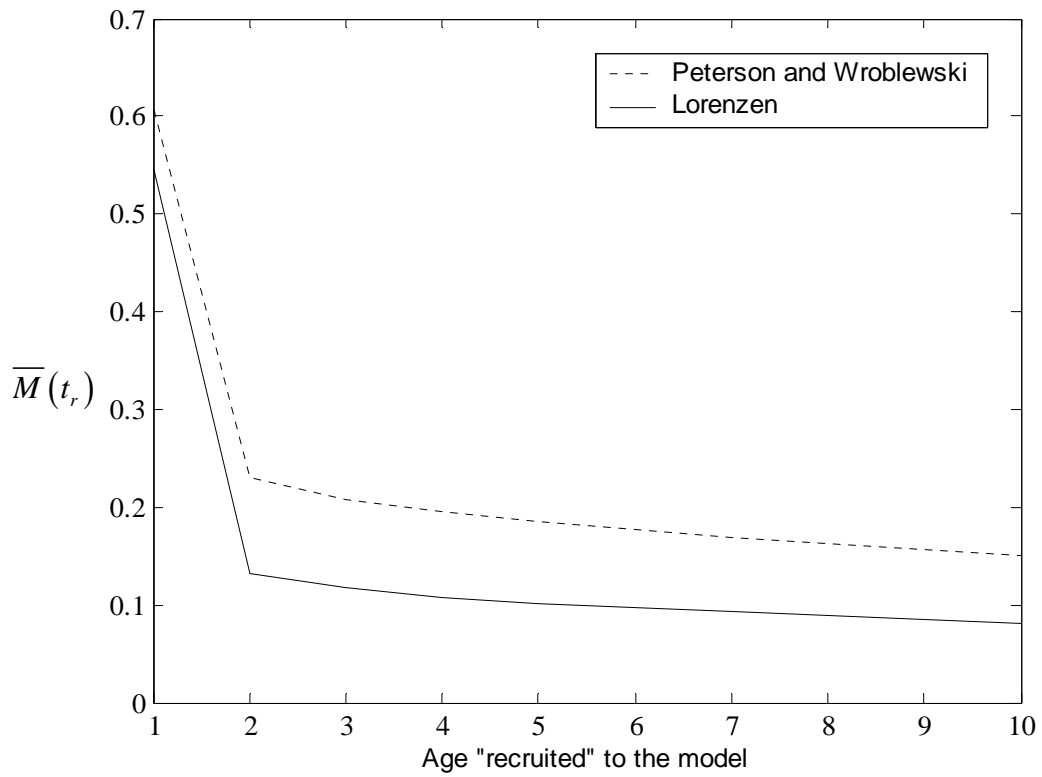


Figure 6. Comparing average mortality estimates, both with different ages of recruitment to the model, and different mortality models. When fish recruit to the model at age two, we see a dramatic change in the average mortality estimate—approximately 0.2 and 0.1 compared to 0.6 and 0.54 when the fish immediately recruit to the model.

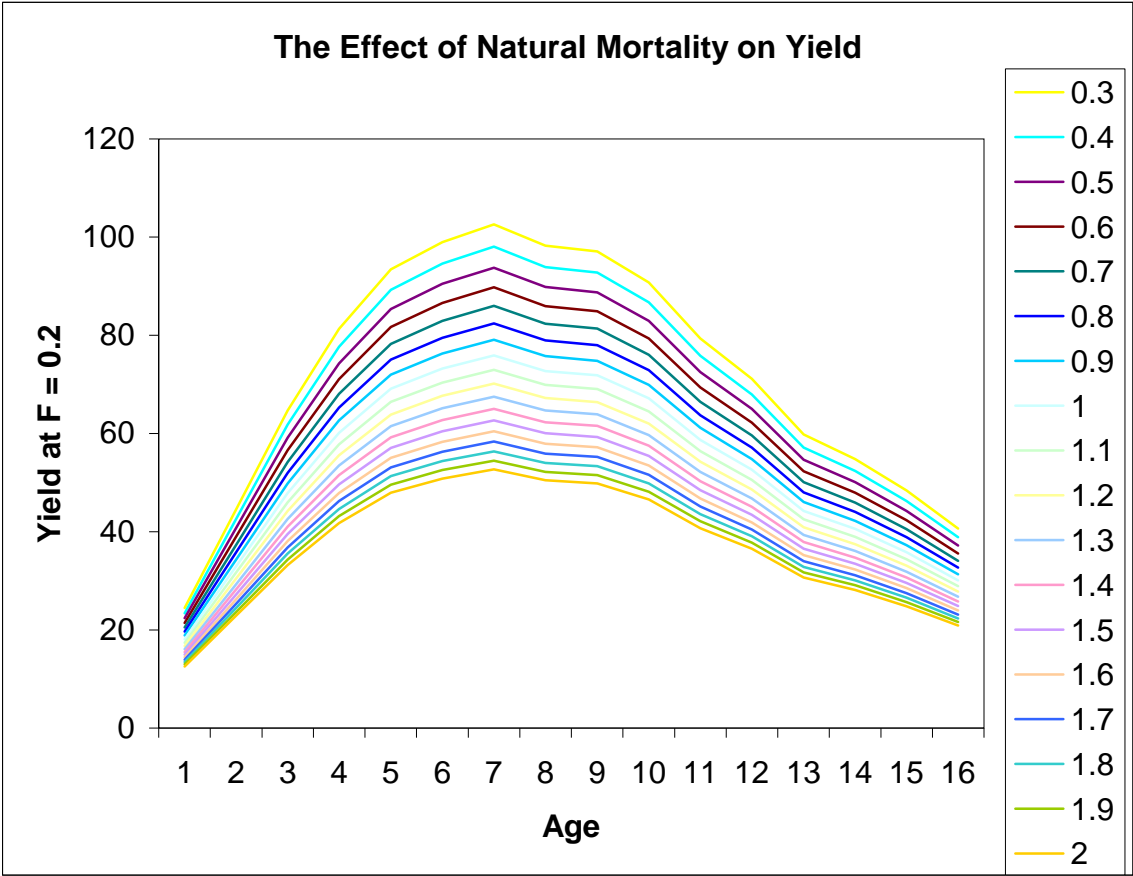


Figure 7. This graph illustrates the difference mortality can make on setting yield.

Table 1. Life history traits related to natural mortality rate as published in the literature

| Traits | Species | Source |
|--|----------------------|--------------------------------|
| t_{\max} , k , L_{∞} , metabolic rate, reproduction | various | (Beverton and Holt 1959) |
| t_{\max} , k , L_{∞} | Clupeids, Engraulids | (Beverton 1963) |
| W_{∞} | general | (Ursin 1967) |
| t_{\max} , k , $t_{\max.biomass}$ | general | (Alverson and Carney 1975) |
| growth rate | Larval fish | (Ware 1975) |
| L_{∞} , gonad size, condition factor | Gadoids | (Jones and Johnston 1977) |
| t_{\max} | general | (Blinov 1977) |
| GSI, ASM, t_{\max} , L_{∞} | general | (Gunderson 1980) |
| W_{∞} , k , L_{∞} , water temperature | 175 stocks | (Pauly 1980) |
| energy cost of reproduction | general | (Myers and Doyle 1983) |
| t_{\max} | various | (Hoenig 1983) |
| weight | various | (Peterson and Wroblewski 1984) |
| k , L_{∞} | various | (Roff 1986) |

Table 2. The results of applying eight mortality models to simulated data.

| Age | Weight | Constant | | Weight-based | | | Age-based | |
|-----|--------|-----------|-----------|--------------------|-------------------------|----------|-----------|-------------------|
| | | Hoening's | Jensen | Rickter and Efanov | Peterson and Wroblewski | Lorenzen | McGurk | Chen and Watanabe |
| 1 | 1.90 | M=0.27725 | M = 0.33 | M = 0.32 | 0.16 | 0.25 | 0.41 | 0.43 |
| 2 | 4.23 | | M = 0.195 | | 0.13 | 0.20 | 0.31 | 0.34 |
| 3 | 7.47 | | | | 0.12 | 0.17 | 0.25 | 0.28 |
| 4 | 11.48 | | | | 0.10 | 0.15 | 0.21 | 0.25 |
| 5 | 16.04 | | | | 0.10 | 0.13 | 0.19 | 0.22 |
| 6 | 20.96 | | | | 0.09 | 0.12 | 0.17 | 0.20 |
| 7 | 26.07 | | | | 0.08 | 0.12 | 0.16 | 0.19 |
| 8 | 31.22 | | | | 0.08 | 0.11 | 0.15 | 0.18 |
| 9 | 36.28 | | | | 0.08 | 0.11 | 0.14 | 0.17 |
| 10 | 41.17 | | | | 0.08 | 0.10 | 0.13 | 0.17 |
| 11 | 45.83 | | | | 0.07 | 0.10 | 0.13 | 0.18 |
| 12 | 50.20 | | | | 0.07 | 0.10 | 0.12 | 0.20 |
| 13 | 54.27 | | | | 0.07 | 0.09 | 0.12 | 0.22 |
| 14 | 58.03 | | | | 0.07 | 0.09 | 0.12 | 0.24 |
| 15 | 61.48 | | | | 0.07 | 0.09 | 0.11 | 0.25 |
| 16 | 64.62 | | | | 0.07 | 0.09 | 0.11 | 0.26 |

Table 3. A summary of the estimates of natural mortality. The last two rows of the last two columns contain estimates for M with respect to a range of body weights: 5.84 kg to 0.15 kg respectively.

| | Model | Parameters | Estimates for M |
|------------------------------------|---|--|--|
| Jensen (1996) | $\frac{M}{k} = 1.5$ | $k = 0.0683$ | 0.1025 |
| | $M = \frac{1.65}{x_m}$ | $x_m = 4 \text{ to } 6 \text{ years}$ | 0.4125 to 0.275 |
| Peterson and Wroblewski 1984 | $M_w = 1.29 \text{ year}^{-1} W^{-0.25}$ | $W = 2.6935 \times 10^{-5} (FL^{2.857})$ | 0.22 for 5.84kg to 0.55 for 0.15kg |
| Lorenzen (1996a, 2000) | $M_w = 3.00 \text{ year}^{-1} W^{-0.288}$ | $W = 2.6935 \times 10^{-5} (FL^{2.857})$ | 0.24 for 5.84kg to 0.71 for 0.15kg |

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