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# A Workshop on Methods to Estimate Total and Natural Mortality Rates Using Mean Length Observations and Life History Parameters 



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# A Workshop on Methods to Estimate Total and Natural Mortality Rates Using Mean Length Observations and Life History Parameters 

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## INTRODUCTION

The Pacific Islands Fisheries Science Center (PIFSC) and the Southeast Fisheries Science Center (SEFSC) held a workshop on the topic of estimating total and natural mortality rates in datalimited stock assessment situations. The working group (WG) for this workshop consisted of Jon Brodziak, Dean Courtney, Joseph O’Malley and Benjamin Richards from the PIFSC and Todd Gedamke, Clay Porch, and John Walter from the SEFSC. The WG reviewed the survival estimation in non-equilibrium (SEINE) model which is based on the method of Gedamke and Hoenig (2006), and considered the application of this model for individual species. In particular, example applications of the SEINE model were developed for blacktip grouper, bluespine unicornfish, orangespine unicornfish, and blue shark. The WG also discussed and developed several extensions of the SEINE methodology. These extensions included: (i) multispecies extensions of the SEINE model; (ii) developing a random walk likelihood component for total mortality estimates; (iii) developing a simple Bayesian formulation of the SEINE model using a prior distribution for natural mortality under a two time-period application; (iv) developing an Rbased shell application to create input files and execute the SEINE model; and (v) developing a hierarchical Bayesian formulation of the SEINE model for three island areas. The WG also developed a simple Bayesian version of the Beverton-Holt (or single-period SEINE) model and considered a formulation of this model using mean weight instead of mean length observations. Other conceptual extensions of the SEINE model, including potential applications to multiple fleets or fishing gears, were discussed.

The WG also considered the estimation of natural mortality rates by using one or more predictive models. In this application, the candidate models used life-history parameters or fitted empirical relationships to estimate natural mortality rate. The WG also considered an approach to rescale the adult natural mortality rate to estimate juvenile natural mortality rates based on allometric scaling of body mass.

## SEINE MODEL

The survival estimation in non-equilibrium (SEINE) situations model was developed by Gedamke and Hoenig (2006). This model estimates total mortality ( $Z$ ) from mean length data and is a generalization of the equilibrium estimator of Beverton and Holt (1957). The method is appealing in data-limited situations in that it only requires: 1) Length at which animals become fully vulnerable to the gear $\left(L_{c}\right), 2$ ) von Bertalanffy growth $(K)$ and theoretical maximum length ( $L_{\text {inf }}$ ), and 3) the mean length of individuals above the $L_{c}$. The SEINE model has been incorporated into the NOAA Fisheries Toolbox. The WG used the ADMB code from the Toolbox version of the model as the basis for developing extensions that included an approach to incorporate a random walk for estimating a time series of total mortality rates, a two-period Bayesian version of the model, an R-Shell application to run the Toolbox model from within the R language interpreter, and a hierarchical Bayes extension of the SEINE model. The WG also considered three fishery applications of the Toolbox model to investigate its utility in different situations.

## APPLICATIONS OF THE SEINE MODEL

## Guam Reef Fish Using Creel Survey Data: Blacktip Grouper and Bluespine Unicornfish

The WG investigated the application of SEINE to estimate total mortality rates of reef fish from Guam using creel survey data. Total mortality of two species of Guam reef fish were estimated using the Toolbox version of SEINE. The first, blacktip grouper (Epinephelus fasciatus) was selected because of the large sample size of the 1982-2011 boat-based, creel survey/bottomfish gear type. The Akaike information criterion (AIC) values from the one-period SEINE gridsearch model only changed by 3.63 among all potential change years and the two-period model did not result in a better fit. Thus, there was no evidence of a temporal change in total mortality and the WG recommended estimating Z using the Beverton and Holt equilibrium estimator. The second species, bluespine unicornfish (Naso unicornus), was of interest because the 19852011 catch data originated from three different data sources. These were: (i) boat-based creel survey/snorkel spear, (ii) shore-based creel survey/snorkel spear, and (iii) shore-based creel survey/hook and line. Total mortality was estimated using one- and two-period SEINE models in the grid-search mode with runs for each data set. The boat-based/snorkel spear data oneperiod model AIC and negative log likelihood values, as well as residual plots, indicated a single change in mortality likely occurred sometime during 1999-2002. Prior to this time period $Z=$ 0.45 and afterwards $Z$ was reduced to 0.14 . In contrast, the shore-based/snorkel spear and shorebased/hook and line one-period models did not indicate any changes in total mortality. The shore-based/snorkel spear AIC values only changed by 2.53 among all potential change years and the shore-based/hook and line only changed by 1.93. Two-period models did not result in an improvement in fit in any of the data sets as indicated by AIC and unrealistic $Z$ estimates. Based on this, the WG recommend the Bayesian two-period approach for the boat-based snorkel spear and the Beverton and Holt equilibrium estimator for the shore-based snorkel spear and hook and line data sets.

## Guam Reef Fish Using Visual Census Survey Data: Orangespine Unicornfish and Blacktip Grouper

The WG investigated the application of SEINE to estimate total mortality rates of reef fish from Guam, using visual census survey data. Underwater visual census (UVC) data collected by the NOAA PIFSC Coral Reef Ecosystem Division (CRED) were used to estimate Z for two species of Guam reef fish using the GUI version of the SEINE model. These data were collected biennially from 2003 to 2010 using a combination of scuba diver belt transect and stationary point count methods. The orangespine unicornfish (Naso lituratus) and blacktip grouper (Epinephelus fasciatus) were chosen for this exercise based on large sample size, the existence of data on these species collected using other fishery dependent and fishery-independent methods, and potential management interest.

At present, the CRED UVC data set is a brief time series and, while the methodology has now been standardized, data collection methods have evolved over time. In 2007, the primary data collection method was changed from the belt transect to the stationary point count. Hence, the data should be treated only as an example of fishery-independent time series. Single-period
analyses can still be carried out and may be useful for estimating current natural or fishing mortality without the time-varying component. Primary strengths of these data are that information exists for the full suite of shallow-water ( $0-30 \mathrm{~m}$ ) coral reef fishes and has been collected around 52 islands, atolls, and reefs under jurisdiction of the United States in the tropical Pacific.

The UVC survey data for the two species were gathered using the CRED data dissemination tool (http://www.pifsc.noaa.gov/cred/index.php). The output data were in CSV format and were input to the R language for generating the input data for SEINE. Total mortality rates for both species were estimated for two-period SEINE models using the grid-search mode (Tables 1.1 and 1.2). For both species, the AIC values and negative log likelihood values, as well as residual plots, indicated that a change in mortality occurred around 2008. This finding is reasonable as it likely reflects the change in primary sampling methodology that occurred in 2007, rather than any fishery or environmentally induced change in mortality.

Table 1.1.--SEINE grid search results for orangespine unicornfish using UVC survey data from Guam with the best-fitting model in boldface.

| Naso lituratus |  |  |  |  |  |  |
| :--- | :---: | :--- | :---: | :---: | :---: | :--- |
| Case | AIC | -logLikelihood | Z1 | Z2 | Sigma | Change <br> Year 1 |
| 1 | 63.2437 | 27.6218 | 0.22139957 | 1.48409894 | 5.20778467 | 2003 |
| 2 | 59.4362 | 25.7181 | 0.34563686 | 1.56345420 | 4.21489987 | 2004 |
| 3 | 56.1950 | 24.0975 | 0.42934924 | 1.59046408 | 3.52035659 | 2005 |
| 4 | 48.0100 | 20.0050 | 0.45581510 | 1.68969251 | 2.23409670 | 2006 |
| 5 | 43.7807 | 17.8903 | 0.52742303 | 1.74997270 | 1.76628216 | 2007 |
| 6 | 39.3306 | 15.6653 | $\mathbf{0 . 5 8 5 0 7 3 9 7}$ | 1.94834698 | 1.37940371 | $\mathbf{2 0 0 8}$ |
| 7 | 55.0659 | 23.5329 | 0.74663007 | 2.06872509 | 3.30631202 | 2009 |
| 8 | 68.5288 | 30.2644 | 1.44616089 | 0.50003520 | 6.98506511 | 2010 |

Table 1.2.--SEINE grid search results for blacktip grouper using UVC survey data from Guam with the best-fitting model in boldface.

| Epinephelus fasciatus |  |  |  |  |  |  |
| :--- | :---: | :--- | :---: | :---: | :---: | :--- |
| Case | AIC | -logLikelihood | Z1 | Z2 | Sigma | Change <br> Year 1 |
| 1 | 63.4591 | 27.7296 | 1.16652505 | 1.12878094 | 5.27049375 | 2003 |
| 2 | 62.8786 | 27.4393 | 0.66014245 | 1.15580099 | 5.10322448 | 2004 |
| 3 | 61.8632 | 26.9316 | 0.60455808 | 1.19801982 | 4.82331326 | 2005 |
| 4 | 61.4689 | 26.7345 | 0.62753862 | 1.22604909 | 4.71881793 | 2006 |
| 5 | 60.8211 | 26.4105 | 0.64094038 | 1.26645755 | 4.55199598 | 2007 |
| 6 | 58.6534 | 25.3267 | 0.59820301 | 1.41873726 | 4.03553272 | 2008 |
| 7 | 56.8351 | $\mathbf{2 4 . 4 1 7 6}$ | $\mathbf{0 . 6 2 3 0 6 0 5 7}$ | 1.69772392 | 3.64779526 | $\mathbf{2 0 0 9}$ |
| 8 | 63.4601 | 27.7300 | 1.12918236 | 1.69771002 | 5.27077585 | 2010 |

In summary, it appears that the CRED UVC data can be used to estimate total mortality. If estimates of natural mortality can also be developed, then one can also use the UVC data to estimate fishing mortality for reef fish species that do not have any fishery-dependent catch or size composition data. For species for which fishery-dependent data does exist, the CRED UVC data can serve as an important comparison data set. As the more UVC survey data are collected, these data will be increasingly useful for assessing species in coral reef assemblages.

## Pelagic Shark Using Observer Data from the Hawaii Longline Fishery: Blue Shark

Blue shark Prionace glauca is the predominant shark species caught in the Hawaii-based pelagic longline fishery which targets swordfish Xiphias gladius in the shallow-set sector and bigeye tuna Thunnus obesus in the deep-set sector (Walsh et al., 2009). Blue shark catches in the Hawaii-based longline fishery have declined in response to the prohibition of shark finning in the year 2000 (Walsh et al., 2009). The SEINE Toolbox model was used to determine if total annual mortality of blue sharks in the deep-set, Hawaii-based pelagic longline fishery has also declined in response to the prohibition of shark finning.

Blue shark length data were queried from the Hawaii longline observer data base (LODS). Data were limited to the deep-set fishery because the shallow-set fishery was closed during the years 2000-2003 in response to management measures taken in 2000 and 2001 to protect sea turtles. The minimum cutoff length for computing mean length $\left(L_{c}\right)$ was selected based on an examination of total length frequency of male and female blue sharks in the Hawaii-based longline fishery from 1994 to 2010 (Fig. 2.1). The mode in female length was about 175 cm TL and the mode in male length was about 190 cm TL (Fig. 2.1). $L_{c}$ was set as the mode in male length ( 190 cm TL). Annual mean lengths and sample sizes were calculated for sharks greater
than $L_{c}\left(L_{c}=190 \mathrm{~cm} \mathrm{TL}\right)$ during the years 1994-2010 (Table 2.1) and input into the SEINE model.

The $L_{\text {inf }}\left(L_{\mathrm{inf}}=266 \mathrm{~cm}\right)$ and the $\mathrm{K}(\mathrm{K}=0.14)$ parameters for blue sharks in the North Pacific Ocean were obtained from Camhi et al., (2008) who cited Nakano (1994). $L_{\text {inf }}$ was reported as 289.7 cm for males and 243.3 cm for females. K was reported as 0.129 for males and 0.144 for females. Mean $L_{\text {inf }}$ and K for males and females were input into the SEINE model.

A single break in total mortality was assumed. A single run was conducted with one change year, an initial value of 2001, an initial value for sigma of 10, and an $L_{c}$ of 190 cm TL . A grid search was run from 1994 to 2010, with one change year, a step size of 1 year, and an $L_{c}$ of 190 cm TL. The best model was identified on the basis of AIC rules of thumb, i.e., using the differences in AIC values between the current model and the best-fitting model $\Delta$ AIC $=$ AIC $-\min$ (AIC). Burnham and Anderson (2002) suggest that there is weak evidence to rule out the next best model if $2<\Delta$ AIC $\leq 4$, there is definite evidence to rule out the next best model if $4<\Delta$ AIC $\leq 7$, and there is strong evidence if $7<\Delta$ AIC $\leq 10$, or very strong evidence if $10<\Delta$ AIC. Sensitivity to $L_{c}$ was examined by rerunning the SEINE grid search analysis over a range of $L_{c}$ values from 170 to 190 cm TL at 5 cm intervals. AIC rules of thumb were used to compare minimum AIC values among grid searches.

The change year estimated by the single run was 1999.26. Total mortality estimated before the change year $(\mathrm{Z} 1=0.55)$ was higher than total mortality estimated after the change year $(\mathrm{Z} 2=$ 0.27 ), Sigma $=14.4$, AIC $=146.8$, Likelihood $=69.4$.

Minimum AIC (AIC = 147.0) from the grid search occurred for a break in natural mortality during the year 1999. Based on AIC rules of thumb, there was not sufficient evidence to rule out the next best model $(\triangle \mathrm{AIC}=1.3)$ which had a break in natural mortality in 2000. In particular, there was definite evidence to rule out models with breaks in natural mortality in 1998 and 2001 ( $\Delta \mathrm{AIC}=4.5$ and $\Delta \mathrm{AIC}=6.1$, respectively), and there was either strong or very strong evidence to rule out the remaining models. (Table 2.2, Fig. 3).

The break year in natural mortality (1999) was not sensitive to the choice of Lc values from 170 to 190 cm TL at $5-\mathrm{cm}$ intervals (Table 2.3). Minimum AIC (AIC = 146.8) from the sensitivity analyses occurred for $L_{c}$ of 185 cm TL and a break year of 1999 (Table 2.3). Based on AIC rules of thumb, there was no evidence to rule out the next best model ( $L_{c}$ of 190 cm TL and a break year of 1999) $(\Delta \mathrm{AIC}=0.25)($ Table 2.3). However, there was very strong evidence to rule out models with $L_{c}<185 \mathrm{~cm}$ TL (Table 2.3).

The SEINE Toolbox model requires the assumption that input mean lengths greater than $L_{c}$ represent the length distribution of the population, i.e., there is no dome shape in the selectivity curve. Our assumption was that blue sharks greater than or equal to $L_{c}(190 \mathrm{~cm} \mathrm{TL})$ were fully selected in the deep-set Hawaii-based pelagic longline fishery, and that the selectivity was asymptotic. If the assumptions for the SEINE model are met, then the SEINE model results suggest that there was a break in blue shark total mortality about the same time as a prohibition in shark finning in the year 2000, and that total mortality of blue sharks decreased in the period
following the prohibition in shark finning in the waters fished by the deep-set, Hawaii-based pelagic longline fishery.

Total blue shark mortality estimated in the SEINE model $(Z 1=0.55)$ from 1994 to the change year (1999) was consistent with estimated annual fishing mortality of adult blue sharks in the North Pacific from an integrated MULTIFAN-CL stock assessment (Kleiber et al., 2009). Region 4 in Kleiber et al. (2009) extended from $180^{\circ} \mathrm{W}$ to $130^{\circ} \mathrm{W}$ and $0^{\circ}$ to $30^{\circ} \mathrm{N}$ and was assumed to have included waters fished by the deep-set, Hawaii-based pelagic longline fishery. Average annual adult fishing mortality in Region 4 during the years 1995 to 2002 was interpreted here from Figure 21 in Kleiber et al. (2009) as between $F=0.2$ and $F=0.25$. The integrated MULTIFAN-CL stock assessment model assumed an annual natural mortality for blue sharks in the North Pacific of $\mathrm{M}=0.2$ (Kleiber et al., 2009).

Sample sizes from the deep-set fishery for the SEINE model were very small in later years (Table 2.1). Observers measured sharks after they were caught and brought aboard fishing vessels. Prior to January 2006, the observer protocol called for as many intact sharks, tuna, swordfish, and billfish to be measured as possible, subject to time and safety constraints. As of February 2006, the observer protocol changed to measure every third fish brought aboard regardless of species (Walsh et al., 2009). Greater numbers of blue sharks are captured in the shallow-set fishery than the deep-set fishery (Walsh et al., 2009). Consequently, it may be worthwhile to repeat this analysis with data from the shallow-set fishery. A problem is that the shallow-set fishery was closed as a result of management measures during the years 2000 2003. Consequently, the SEINE model would need to be adapted to allow for missing years and/or blocks of years with constant mortality.

Table 2.1.--Mean length of blue shark catches $>L_{c}(190 \mathrm{~cm} T L)$ and sample size ( $n$ ) from the Hawaii-based pelagic longline fishery in the deep-set sector.

| Year | Sector | Mean Length (cm TL) | $n$ |
| :---: | :---: | :---: | :---: |
| 1994 | Deep | 204.4 | 156 |
| 1995 | Deep | 204.9 | 108 |
| 1996 | Deep | 207.6 | 200 |
| 1997 | Deep | 205.4 | 132 |
| 1998 | Deep | 204.7 | 124 |
| 1999 | Deep | 203.8 | 100 |
| 2000 | Deep | 205.7 | 177 |
| 2001 | Deep | 206.1 | 157 |
| 2002 | Deep | 211.0 | 64 |
| 2003 | Deep | 211.1 | 29 |
| 2004 | Deep | 212.8 | 23 |
| 2005 | Deep | 211.6 | 37 |
| 2006 | Deep | 213.1 | 14 |
| 2007 | Deep | 213.5 | 10 |
| 2008 | Deep | 195.0 | 1 |
| 2010 | Deep | 213.1 | 7 |

Table 2.2.--SEINE grid search results for blue shark from 1994 to 2010, using one change year, a step size of one year, and an $L_{c}$ value of 190 cm TL. Best-fitting model is listed in boldface.

| - Log |  |  |  |  |  |  | Change <br> Year |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Case | $\triangle$ AIC | AIC | Likelihood | Z1 | Z2 | Sigma |  |
| 1 | 15.00 | 162.03 | 77.02 | 0.59 | 0.46 | 22.45 | 1994 |
| 2 | 14.65 | 161.69 | 76.84 | 0.57 | 0.45 | 22.23 | 1995 |
| 3 | 13.33 | 160.37 | 76.18 | 0.57 | 0.43 | 21.38 | 1996 |
| 4 | 9.80 | 156.83 | 74.41 | 0.57 | 0.38 | 19.27 | 1997 |
| 5 | 4.46 | 151.49 | 71.75 | 0.57 | 0.33 | 16.47 | 1998 |
| 6 | 0 | 147.03 | 69.52 | 0.56 | 0.28 | 14.44 | 1999 |
| 7 | 1.28 | 148.31 | 70.16 | 0.54 | 0.24 | 15.00 | 2000 |
| 8 | 6.11 | 153.14 | 72.57 | 0.53 | 0.21 | 17.28 | 2001 |
| 9 | 10.45 | 157.48 | 74.74 | 0.53 | 0.18 | 19.64 | 2002 |
| 10 | 13.26 | 160.29 | 76.15 | 0.52 | 0.15 | 21.33 | 2003 |
| 11 | 15.54 | 162.58 | 77.29 | 0.52 | 0.14 | 22.82 | 2004 |
| 12 | 16.99 | 164.02 | 78.01 | 0.51 | 0.15 | 23.81 | 2005 |
| 13 | 17.56 | 164.59 | 78.29 | 0.51 | 0.15 | 24.21 | 2006 |
| 14 | 17.69 | 164.72 | 78.36 | 0.51 | 0.04 | 24.30 | 2007 |
| 15 | 17.69 | 164.72 | 78.36 | 0.51 | 0.00 | 24.30 | 2008 |
| 16 | 17.94 | 164.97 | 78.49 | 0.51 | 0.00 | 24.48 | 2009 |
| 17 | 18.13 | 165.16 | 78.58 | 0.51 | 0.50 | 24.62 | 2010 |

Table 2.3.--SEINE model results including $\triangle$ AIC, lowest AIC, and break year from the sensitivity analysis of based on rerunning the SEINE grid search analysis over a range of $L_{c}$ values from 170 to 190 cm TL in 5 -cm intervals. Best-fitting model is listed in boldface.

| $L_{c}$ | $\Delta$ AIC | AIC | Break Year |
| :---: | :---: | :---: | :---: |
| 170 | 15.12 | 161.9 | 1999 |
| 175 | 11.91 | 158.7 | 1999 |
| 180 | 10.78 | 157.6 | 2000 |
| 185 | 0 | 146.8 | 1999 |
| 190 | 0.25 | 147.0 | 1999 |



Figure 2.1.--Length frequency of male and female blue shark from the Hawaii-based pelagic longline fishery during the years 1994-2010. The shallow-set sector targets swordfish, Xiphias gladius, and the deep-set sector targets bigeye tuna, Thunnus obesus.


Figure 2.2.--Observed and predicted length (cm TL) of blue shark > $L_{c}(190 \mathrm{~cm} \mathrm{TL})$ from a single SEINE run with one change year, an initial value of 2001, and an initial value for sigma of 10. Change year estimated from the single run was 1999.


Figure 2.3.--AIC results of a grid search from 1994 to 2010, with one change year, a step size of one year, and an $L_{c}$ value of 190 cm TL.

## MULTISPECIES EXTENSION OF THE SEINE MODEL

Recent advances in methodology allow the history of total mortality rate experienced by a population to be estimated from a time series of periodic (e.g., annual) observations on mean length in the population (i.e., SEINE model; Gedamke and Hoenig, 2006). This nonequilibrium formulation is a modification of the Beverton and Holt $(1956,1957)$ mean length mortality estimator which assume mortality has been constant for at least the life span of the species under consideration.

During the first part of the workshop, the theoretical basis and mechanics of the models were discussed. The importance of data evaluation and the selection of the length at full vulnerability were stressed and case studies were examined to illustrate the point. Time series of mean lengths for a few Pacific species (blacktip grouper, blue shark, unicornfish) and for the redtail parrotfish (Sparisoma chrysopterum) in St. Croix were examined. Initially two different avenues were used to implement the model: (i) The GUI version in the NMFS toolbox (http://nft.nefsc.noaa.gov/SEINE.html) and (ii) case specific ADMB code developed by SEFSC staff. A few modifications and minor corrections to the original code used in the GUI were made including:

1) Generalization of the code used to calculate the number of estimated parameters.
2) AIC equations were changed to the $\mathrm{AIC}_{\mathrm{C}}$ value which includes a bias-correction for low sample sizes.
3) Modification of number of observation calculations to account for years in which no samples were present.

Additionally, a presentation and discussion of how the single species SEINE approach has been generalized (Todd Gedamke, John Hoenig, Clay Porch, unpublished manuscript) was held. This generalization allows data on several species that are caught together to be analyzed simultaneously on the theory that changes in fishing effort are likely to affect several species. Thus, the estimation of times when mortality rate changed for one species borrows strength from data on other species that are caught together. Information theory (e.g., AIC) can be used to select among various possible models concerning the degree of synchrony (if any) of mortality changes in a suite of species. The WG discussed ways to most efficiently modify and generalize the ADMB code which was developed for specific application to the Caribbean species.

## Theoretical Basis and Modification for Multispecies Estimation

The joint likelihood for $N$ species is simply the product of the likelihoods for all of the species. Let each species, indexed by $n$, have its own set of parameters $\Theta_{n}=\left\{Z_{i n}, d_{j n}\right\}$ where $Z_{i n}$ is the vector of period-specific total mortality rates for species $n$, and $d_{j n}$ is the vector of times at which mortality rate changes for species $n$, with $i=1,2, \ldots, I$, and $j=1,2, \ldots, I-1$. We can then envision a suite of models depending on the patterns of mortality across species.

## Single-species Model (SEINE model)

In this scenario, what happens to one species is not reflected in what happens in other species. For example, fishers may target certain species and avoid others so that changes in total mortality for one species are independent of what happens to another species. In this case, the likelihood for each species can be maximized independently because there are no parameters in common.

## Multispecies Model 1

In this scenario, changes in fishing effort affect all species in the complex being considered; however, the magnitudes of the changes in mortality rate are independent. Thus, all species have a common set of times at which mortality rate changed, i.e., $d_{j n}=d_{j n}$, for all periods $j$ and all pairs of species $n$ and $n$ '.

## Multispecies Model 2

Here, all species experience synchronous changes in mortality (i.e., changes occur at the same times, as in Multispecies Model 1) but, additionally, the proportional change in fishing mortality is the same for all species. To use this model, the total instantaneous mortality rate per year, $Z$, is broken down into its components fishing mortality, $F$, and natural mortality, $M$ :

$$
\begin{equation*}
Z=F+M \tag{1}
\end{equation*}
$$

Then, an increase in fishing effort would cause the fishing mortality to change by a factor $\delta$ to

$$
\begin{equation*}
Z=\delta \cdot F+M \tag{2}
\end{equation*}
$$

In Model 2, the factor $\delta$ for a given change point in time is assumed to be the same for all species in the complex. Everywhere in the model that a $Z$ parameter occurs, equation (2) is substituted. The values of $M$ are obtained external to the analysis of the mean length data. (In the appendix we show that the results are not very sensitive to errors in the specification of natural mortality.) Thus, the initial fishing mortality rate for each species is estimated and the common times of change and the common proportional changes are estimated.

## Number of Parameters

Under the single-species model, there are four parameters when we estimate two mortality rates, one change point, and one variance $\sigma^{2}$. For $N$ species, there are $4 N$ parameters. Addition of another change point and another mortality rate adds two parameters per species. Under multispecies model 1 , there are $2 N$ mortality rates, 1 change point and $N$ variances. Thus, there are $3 N+1$ parameters. For multispecies model 2, there are $N$ initial mortality rates, $N$ variances, $I$ 1 change points, and $I-1$ proportional changes in mortality rate for a total of $2(N+I-1)$ parameters (Table 3.1).

Table 3.1.--Number of parameters for three models when there are $N$ species being analyzed with $I$ time periods and $I-1$ change points.

| case | model |  |  |
| :---: | :---: | :---: | :---: |
|  | single-species model | multispecies m | multispecies model 2 |
| 1 change point and 2 periods | $4 N$ | $3 N+1$ | $2 N+2$ |
| For each additional species, add | 4 | 3 | 2 |
| For each additional change point, add | $2 N$ | $N+1$ | 2 |
| I - 1 change points and I periods | $2 I N$ | $I N+I+N+1$ | $2(N+I-1)$ |

## RANDOM WALK EXTENSION OF SEINE MODEL

A simple "random walk" structure was added to penalize deviations in the total mortality rate $Z$ from one time period $t$ to the next:

$$
\begin{gather*}
Z_{t+1}=Z_{t} \cdot e^{\delta_{t}}  \tag{3}\\
\delta_{t} \sim N\left(0, \sigma_{Z}^{2}\right) \tag{4}
\end{gather*}
$$

where $\delta_{\mathrm{t}}$ is a normally distributed random variable with mean 0 and standard deviation $\sigma_{\mathrm{z}}$. The subscript $t$ denotes a block of one or more years. The corresponding negative log-prior is added to the negative log-likelihood to create the penalized objective function (where $T$ is the total number of time blocks).

This negative log-prior is

$$
\begin{equation*}
-\log (P(\delta))=0.5\left(T \cdot \log (2 \pi)+T \cdot \log \left(\sigma_{Z}^{2}\right)+\sigma_{Z}^{-2} \sum_{t=1}^{T}\left(\log \left(Z_{t+1}\right)-\log \left(Z_{t}\right)\right)^{2}\right) \tag{5}
\end{equation*}
$$

Note that low values of $\sigma_{z}$ (say 0.01 ) tend to inhibit departures from constant $Z$, and very high values tend to allow a near-perfect fit to the data at the expense of having effectively too many parameters. To the extent that the penalty term can be thought of as 'data', the AIC criteria can be used to guide the most parsimonious choice for $\sigma_{z}$. In practice, the random walk structure may be more useful to identify periods when $Z$ may have changed or as a diagnostic tool to help identify outliers (mean length values that are implausible with reasonable variations in $Z$ ).

The random walk structure was applied to three examples (Fig. 4.1): Northwest Atlantic goosefish (Lophius americanus), Pacific Islands blacktip grouper (Epinephelus fasciatus) and Caribbean redtail parrotfish (Sparisoma chrysopterum). In the case of goosefish, the mean length observations were obtained from large samples collected since 1963 and there are consistent increasing and decreasing trends. The AIC criterion suggests that a small value of $\sigma_{z}(0.01)$ is much less appropriate than a larger value (0.5), thus implying that the observed trends in mean length are likely a result of real changes in the mortality rate. In contrast, the data for blacktip grouper fluctuated substantially from year to year with little long-term trend. Not surprisingly, the AIC criteria favor a lower value of $\sigma_{z}(0.01)$, implying that there is little evidence that $Z$ has changed through time and that the variation in mean lengths is attributable to other causes (low sample sizes and high sampling variability).

The example for redtail parrot fish demonstrates a case where the random walk is useful in a diagnostic sense, but the naïve use of AIC to guide the choice of $\sigma_{z}$ could be misleading. In this case, there is an apparent trend in mean lengths that results in a clear decreasing trend in $Z$ with time when the value of $\sigma_{z}$ is moderate to large ( 0.1 to 0.5 ). Nevertheless, the high year to year variability in mean lengths contributes to produce the lowest AIC when $\sigma_{z}$ is small (0.01). This apparent disconnect results because the random walk model in this specific example is allowing annual variations in $Z$. When instead the random walk was applied to two time blocks (before 1995, 1995-2010), then the AIC criteria supported a larger $\sigma_{z}$. In other words, the data do not provide evidence for annual changes in Z, but do provide evidence for a change in Z after 1994.




Figure 4.1.--Random walk estimates of total mortality rate $(Z)$ with three different values of $\sigma_{z}$ (green $=0.01$, brown $=0.1$, black $=0.5$ ) for each of three species.

## SIMPLE BAYES EXTENSION OF SEINE MODEL

The WG discussed the potential application of a Bayesian formulation of the SEINE model. Jon Brodziak developed some WinBUGS code for a two-period SEINE model with a fixed change point (Appendix 1) for a hypothetical application to some blacktip grouper mean length data collected from creel surveys in Guam. This example application showed how to set up priors for key SEINE model parameters in WinBUGS. The WG noted that the inclusion of prior distributions for growth parameters or other model parameters provided a useful way to characterize uncertainty in these quantities in the estimation of total mortality rate from changes in observed mean lengths. A nominal estimate of natural mortality rate of blacktip grouper was developed from Hoenig's (1983) predictive regression for fish. This estimate of $M=0.22$ was used as a mean for a prior with an assumed CV of $30 \%$ in the WinBUGS model. The M parameter was then included in the Bayesian formulation of the SEINE model. This made it possible to directly estimate the distribution of fishing mortality rate from the estimated posterior distribution of total mortality rate $(Z)$ as $F=Z-M$. The Bayesian formulation of SEINE was considered to be potentially useful by the WG and it was recommended that this initial version be generalized to select change points using goodness-of-fit criteria, perhaps using a more flexible programming language such as Python (http://www.python.org/).

## R-SHELL APPLICATION TO RUN THE SEINE MODEL

It became clear to the WG that the development of an R code to act as both a data evaluation tool and a "shell" to call the ADMB codes (including the random walk modification developed by Clay Porch and described elsewhere in this document) was to be a high priority. John Walter made substantial progress to this end and a beta version is in development which does (or will do) the following:

1) Creates annual histograms of length frequency data (Fig. 5.1) to evaluate and select the length at full vulnerability $\left(L_{c}\right)$.
2) Creates bubble plots of mean lengths (Fig. 5.2) of individuals above the $L_{c}$ from step 1.
3) Calls ADMB codes to do the following analyses:
a. A single-period SEINE, or Beverton-Holt equilibrium mean-length mortality estimate (written during workshop).
b. Multiple-years-of-change SEINE model (at the conclusion of the meeting a single year of change was completed) which includes a grid search over years of change generating a likelihood profile (Fig. 5.3) for comparison to (a) above and residual diagnostics (Fig. 5.4). At low sample sizes, or when little contrast is apparent, the model can be sensitive to the starting guess for year of change.
c. Sensitivity analysis to the selection $L_{c}$.
d. Implementation of random walk modification to the SEINE model. This includes options for time-blocking and a sensitivity analysis of the sigma penalty (described elsewhere).
e. In addition, an excel spreadsheet template was developed to visualize and evaluate results. Ideally, once completed this step will be included in the R code.

It was expected that this code would be heavily utilized in the Caribbean SEDAR meeting to be held in August 2011 where additional modifications were likely to occur. The WG also considered an illustrative example of the R-shell for running the SEINE model on redtail parrotfish from St. Croix. In this example, fitting a single-change SEINE model for redtail parrotfish (Table 5.1) resulted in an initial $Z$ estimated to be $\mathrm{Z} 1=1.59(\sigma=0.065)$ and a second $Z$ estimated to be $\mathrm{Z} 2=0.82(\sigma=0.104)$.

Table 5.1.--Results of fitting a single change SEINE model for redtail parrotfish.

| AIC | LLIKE | yinit1 | Z1 | Z2 | Sigma | ChangeYear1 | Z1_std | Z2_std | Sigma_std |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 117.758 | 53.7678 | 1996 | 1.58568 | 0.818875 | 37.5553 | 1996 | 0.065368 | 0.10345 | 5.5372 |



Histogram of $\mathrm{X}[[19 \mathrm{~L}]$







Figure 5.1.--Histogram of length frequencies by year for redtail parrotfish from St. Croix.


Figure 5.2.--Observed mean lengths for redtail parrotfish from St. Croix. Bubbles are proportional to sample size above $L_{c}=262 \mathrm{~mm}$. Solid blue line is a lowess fit.


Figure 5.3.--Testing null hypothesis of no change in $Z$ for redtail parrotfish. In this case, there is strong evidence to reject the null hypothesis of no change for years 1991-1999 as there is a reduction in AIC of 5 units or greater.


Figure 5.4.--Observed and fitted mean lengths for redtail parrotfish.

## HIERARCHICAL BAYES EXTENSION OF THE SEINE MODEL

The WG considered the idea of using hierarchical Bayes models for data-limited stockassessment situations. Hierarchical data are ubiquitous in fisheries applications where measurement occurs at different levels of aggregation, e.g., we collect measurements of individual fish which live in different island habitats. When this occurs, statistical analyses often assume that these island groups belong to entirely different populations or ignore the aggregate information entirely. Hierarchical Bayes models provide a means of pooling the information for the different island groups without assuming that they belong to precisely the same population. Jon Brodziak presented an example of a hierarchical Bayes production model that was developed for the Hawaii bottomfish stock assessment (Brodziak et al., 2011a). This model included a timevarying intrinsic growth rate where the time-variable fishing year was the hierarchy. The model was coded in the WinBUGS programming language. Jon used the WinBUGS code to describe the structure of a hierarchical Bayes model and how to include a hyperprior on a key model parameter. In this case, the hyperprior represented the aggregated ecosystem effect on timevarying production for the Hawaii bottomfish complex.

The WG also briefly considered an initial Bayesian formulation of the SEINE model that included a hierarchical prior on the total mortality rates for the two-period model. The hierarchical structure in this case was the two time periods, and the prior distribution for the total mortality rate for each time period was assigned a mean value based on a hyperprior assigned for the entire time horizon. Results of this hierarchical model were compared to the results of a simpler Bayesian model that assumed that the priors for total mortality rate in each period were equal. The comparison showed that including the hyperprior structure allowed for greater variability in the estimates of total mortality. This effect was based on the fact that the means of the prior distributions for the two time periods were allowed to differ with the hierarchical structuring. Overall, it was thought that the development of hierarchical Bayes extensions of the SEINE model would provide more flexibility in fitting models with stochasticity at multiple levels in space or time (e.g., Clark, 2005).


Figure 6.1.--Diagram of conceptual structure of a Hierarchical Bayes model for estimating total mortality of a fish population based on life history parameters and observed length distributions.

## MEAN WEIGHT EXTENSION OF BEVERTON-HOLT MODEL

The Beverton-Holt equilibrium estimator of total mortality based on observed mean length expresses total mortality as a function of von Bertalanffy growth parameters, observed mean length, and the critical length $L_{c}$ as

$$
\begin{equation*}
Z=\frac{K\left(L_{\mathrm{inf}}-\bar{L}\right)}{\bar{L}-L_{c}} \tag{6}
\end{equation*}
$$

If the mean weight at length of the population is based on the allometric equation $W=a \cdot L^{b}$, then the corresponding equilibrium estimator of total mortality based on observed mean weight ( $\bar{W}$ ) can be expressed as

$$
\begin{equation*}
\bar{W}=\frac{a \cdot\left(L_{\mathrm{inf}}\right)^{b} \int_{t_{c}}^{\infty} \exp (-Z t)\left(1-\exp \left(-K\left(t-t_{0}\right)\right)\right)^{b} d t}{\frac{1}{Z} \exp \left(-Z \cdot t_{c}\right)} \tag{7}
\end{equation*}
$$

where $t_{c}$ is the age corresponding to $L_{c}$. The value of Z corresponding the observed mean weight $\bar{W}$ can be solved for numerically using this equation; however, this was not pursued during the WG meeting.

## PREDICTIVE MODELS TO ESTIMATE NATURAL MORTALITY RATES

The WG considered the estimation of natural mortality rates based on life history parameters and empirical approaches (e.g., Brodziak et al., 2011b). Jon Brodziak described a number of methods to estimate natural mortality rate based on life history parameters with an example application to North Pacific swordfish. These methods included: Lorenzen (1996), Peterson and Wroblewski (1984), Jensen (1996), Chen and Watanabe (1989), Pauly (1980), Alverson and Carney (1975), and Hoenig (1983). It was noted that several of these estimators of M produced consistent estimates of $M$ for swordfish. An arithmetic average of the consistent estimators was used for swordfish in the stock assessment application. The WG discussed the merits of using multiple estimators to characterize M. The fact that several of the estimators used the same or similar life history parameters indicated that there was likely to be some correlation among the M estimates. The WG discussed assigning the estimators to categories based on the type of lifehistory parameters required and assuming a fixed proportion or weighting factor for each category. That is, if there were 4 categories of life-history parameters then the weighting factor for each category would be $1 / 4$ for the averaging of M estimates across categories. For example, one could assign all of the estimators that were only based on expected life span to a single category and all of the estimators that depended only on the von Bertalanffy K parameter to another category. This approach was not applied in the workshop, however.

Clay Porch made a presentation to the WG regarding the estimation of natural mortality rates at age based on the scaling of natural mortality rate with body mass in Lorenzen (1996). This approach has been successfully been applied to some stocks in the Southeast region.

John Walter made a presentation on the estimation of natural mortality rate for yellowedge grouper in the Southeast region. His presentation showed how multiple model-based estimates of natural mortality rate were developed to support a catch curve-based estimate based on data from a period of little or no fishing mortality for the stock. The information showed how the use of multiple predictors could help to support the estimate of $M$ used in a stock assessment.

## SUMMARY

The workshop provided a good opportunity for collaborative research on estimation of total mortality rate using the SEINE modeling approach when stock assessment data are limited but growth parameters and mean length data are available. The WG made progress on several fronts including three successful illustrative applications to mean length data from fishery-dependent creel surveys, fishery-independent visual census data, and fishery dependent observer data. Progress was also made on several types of extensions of the SEINE model, although further work would be needed to make these extensions available for direct stock-assessment application.

The multispecies extensions of the SEINE model was expected to improve the application of the approach to fisheries where multiple species are harvested with the same fishing gear. This extension allowed the model estimates to use multiple time series of mean-length data to resolve change points in total mortality rates.

The random walk extension of the SEINE model provided a useful framework to incorporate time-varying parameters. It was also thought that this extension could be used to help identify time periods when total mortality was changing and also to identify mean length observations that were outliers.

The simple Bayes extension of the SEINE model provided a means to explicitly incorporate uncertainty about model parameters through parameter priors. This extension can also provide direct probabilistic results for key parameters for risk analyses.

The R-Shell extension provided a flexible means to explore and visualize the input data and output model results of SEINE model runs. It was also expected that this extension would help to streamline the set of analyses needed to successfully use the SEINE model in a stock assessment workshop setting where multiple model configurations may need to be considered.

The hierarchical Bayes extension of the SEINE model provided an opportunity to include more realistic treatment of parameter uncertainty through the use of hyperpriors for different structural levels, which could include stochasticity for spatial or temporal effects.

Overall, the WG concluded that the workshop was a useful modeling exercise and that it would be beneficial to hold follow-up meetings to continue this work to improve the set of assessment tools available for data-limited situations.

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Appendix 1. WinBUGS cod to fit a two-period SEINE model with a fixed change point to hypothetical blacktip grouper data from creel surveys in waters off Guam.

```
####################################################################################
# Program GH_ZLEN2 implements the Gedamke-Hoenig mean length-based Z estimator with 2 periods
# and a fixed change period input by the user. Model is fit to hypothetical creel survey data for
# blacktip grouper from Guam
# Jon Brodziak, PIFSC, July 2011
#######################################################################################
model gh_zlen2
{
######################################################################################
# PRIOR DISTRIBUTIONS
##################################################################################
# Lognormal prior for VB growth parameter K
#(P1)#################################################################################
K_Prior_Precision <- 1.0/log(1.0+CV_K*CV_K)
K_Prior_Avg <- log(Target_K_Prior_Avg) - (0.5/K_Prior_Precision)
K ~ dlnorm(K_Prior_Avg,K_Prior_Precision)I(0.001,200.0)
# Lognormal prior for VB growth parameter LINF
#(P2)##################################################################################
LINF_Prior_Precision <- 1.0/log(1.0+CV_LINF*CV_LINF)
LINF_Prior_Avg <- log(Target_LINF_Prior_Avg) - (0.5/LINF_Prior_Precision)
LINF ~ dlnorm(LINF_Prior_Avg,LINF_Prior_Precision)I(0.01,100000.0)
# Normal prior for VB growth parameter TO
#(P3)################################################################################
TO_Std <- CV_TO*TO_Prior_Avg
T0_Prior_Precision <- 1.0/(T0_Std*TO_Std)
```

T0 ~ dnorm(TO_Prior_Avg,TO_Prior_Precision)
\# Lognormal prior for Z1
\#(P4)\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
Z1_Prior_Precision <-1.0/log(1.0+CV_Z1*CV_Z1)
Z1_Prior_Avg <- log(Target_Z1_Prior_Avg) - (0.5/Z1_Prior_Precision)
Z1 ~ dlnorm(Z1_Prior_Avg,Z1_Prior_Precision)I(0.001,200.0)
\# Lognormal prior for Z2
\#(P5)\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
Z2_Prior_Precision <- 1.0/log(1.0+CV_Z2*CV_Z2)
Z2_Prior_Avg <- log(Target_Z2_Prior_Avg) - (0.5/Z2_Prior_Precision)
Z2 ~ dlnorm(Z2_Prior_Avg,Z2_Prior_Precision)I(0.001,200.0)
\# Normal prior for observation error variance, tau2
\#(P6)\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
tau2 ~ dnorm(mean_tau2,precision_tau2)
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# SAMPLE LIKELIHOOD
\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
\# Observed mean length sample likelihood period 1

```
#(L1)##################################################################################
for (i in 1:changeyear) {
    predicted_mean_length[i] <- LINF - Z1*(LINF-LCRIT)/(Z1+K)
    sample_precision[i] <- n_length[i]/tau2
    mean_length[i] ~ dnorm(predicted_mean_length[i],sample_precision[i])
    residual[i] <- mean_length[i] - (LINF - Z1*(LINF-LCRIT)/(Z1+K))
    }
\# Observed mean length sample likelihood period 2
\#(L2)\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#\#
```

```
for (d in (changeyear+1):nsample) {
    predicted_mean_length[d] <- LINF - Z1*Z2*(LINF-LCRIT)*(Z1+K+(Z2-Z1)*exp(-
(Z2+K)*d))/((Z1+K)*(Z2+K)*(Z1+(Z2-Z1)*exp(-Z2*d)))
    sample_precision[d] <- n_length[d]/tau2
    mean_length[d] ~ dnorm(predicted_mean_length[d],sample_precision[d])
    residual[d] <- mean_length[d] - predicted_mean_length[d]
    }
# END OF CODE
########################################################################################
}
########################################################################################
# DATA
#########################################################################################
list(
LCRIT = 150.0,
nsample = 29,
changeyear = 15,
mean_length =
c(244.3181818,229.9795918,207.8571429,205.5944056,200.1724138,229.0701754,242.4421053,227.09
27835,241.5934066,225.6947368,235.4615385,230.4215686,233.5,235.4216216,241.208,238.2708333,
226.4011976,225.1594203,212.0285714,227.754902,224.3717949,215.7313433,231.9375,229.6111111,
223.8085106,220.5438596,222.0877193,222.578125,227.5783133,285),
n_length =
c(44,49,28,143,29,57,190,97,91,95,91,102,130,185,125,96,167,138,70,102,78,67,48,54,47,57,57,64,83),
mean_tau2 = 100.0,
precision_tau2 = 0.001,
Target_K_Prior_Avg = 0.26,
CV_K = 0.1,
Target_LINF_Prior_Avg = 414.0,
CV_LINF = 0.10,
```

TO_Prior_Avg= -0.054,
CV_TO $=0.10$,
Target_Z1_Prior_Avg = 0.5,
CV_Z1 $=0.3$,
Target_Z2_Prior_Avg = 0.5,
CV_Z2 $=0.3$
)
\# INIT1

list(
$K=0.26$,
LINF = 414.0,
T0 $=-0.054$,
$\mathrm{Z1}=0.5$,
Z2=0.5,
tau2 $=100$
)
\# End of WinBUGS code

Table A.1. Results of GH_ZLEN2 run for blacktip grouper in Guam. The node labeled "residual[k]" represents the observed minus predicted mean length in year k while the node labeled "tau2" is the observation error variance.

| node | mean | sd | MC error 2.5\% | 10.0\% | median | 90.0\% | 97.5\% | start | sample |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Z1 | 0.5026 | 0.07995 | 0.0039450 .363 | 0.404 | 0.4968 | 0.6068 | 0.679 | 10000 | 45000 |
| Z2 | 0.5612 | 0.0866 | 0.0042490 .4099 | 0.4548 | 0.555 | 0.6739 | 0.753 | 10000 | 45000 |
| residual[1] | 13.13 | 0.5971 | 0.00279311 .96 | 12.36 | 13.12 | 13.89 | 14.29 | 10000 | 45000 |
| residual[2] | -1.213 | 0.5971 | 0.002793-2.382 | -1.976 | -1.214 | -0.4457 | -0.04391 | 10000 | 45000 |
| residual[3] | -23.34 | 0.5971 | 0.002793-24.5 | -24.1 | -23.34 | -22.57 | -22.17 | 10000 | 45000 |
| residual[4] | -25.6 | 0.5971 | 0.002793-26.77 | -26.36 | -25.6 | -24.83 | -24.43 | 10000 | 45000 |
| residual[5] | -31.02 | 0.5971 | 0.002793-32.19 | -31.78 | -31.02 | -30.25 | -29.85 | 10000 | 45000 |
| residual[6] | -2.122 | 0.5971 | 0.002793-3.291 | -2.886 | -2.124 | -1.355 | -0.9533 | 10000 | 45000 |
| residual[7] | 11.25 | 0.5971 | 0.00279310 .08 | 10.49 | 11.25 | 12.02 | 12.42 | 10000 | 45000 |
| residual[8] | -4.099 | 0.5971 | 0.002793-5.269 | $-4.863$ | -4.101 | -3.332 | -2.931 | 10000 | 45000 |
| residual[9] | 10.4 | 0.5971 | 0.0027939 .232 | 9.638 | 10.4 | 11.17 | 11.57 | 10000 | 45000 |
| residual[10] | -5.497 | 0.5971 | 0.002793-6.667 | $-6.261$ | -5.499 | -4.731 | -4.329 | 10000 | 45000 |
| residual[11] | 4.269 | 0.5971 | 0.0027933 .1 | 3.506 | 4.268 | 5.036 | 5.438 | 10000 | 45000 |
| residual[12] | -0.7706 | 0.5971 | 0.002793-1.94 | $-1.534$ | -0.7724 | -0.0037 | 0.3981 | 10000 | 45000 |
| residual[13] | 2.308 | 0.5971 | 0.0027931 .139 | 1.544 | 2.306 | 3.075 | 3.476 | 10000 | 45000 |
| residual[14] | 4.229 | 0.5971 | 0.0027933 .06 | 3.466 | 4.228 | 4.996 | 5.398 | 10000 | 45000 |
| residual[15] | 10.02 | 0.5971 | 0.0027938 .847 | 9.252 | 10.01 | 10.78 | 11.18 | 10000 | 45000 |
| residual[16] | 12.9 | 0.6752 | 0.0030511 .58 | 12.04 | 12.9 | 13.77 | 14.23 | 10000 | 45000 |
| residual[17] | 1.034 | 0.6753 | 0.003059-0.2899 | 0.1694 | 1.032 | 1.899 | 2.358 | 10000 | 45000 |
| residual[18] | -0.2066 | 0.6753 | 0.003065-1.531 | -1.071 | -0.2087 | 0.6584 | 1.118 | 10000 | 45000 |

Table A.1. Continued.

| node | mean | sd | MC error $2.5 \%$ | $10.0 \%$ | median | $90.0 \%$ | $97.5 \%$ | start | sample |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| residual[19] | -13.34 | 0.6754 | 0.00307 | -14.66 | -14.2 | -13.34 | -12.47 | -12.01 | 10000 | 45000 |
| residual[20] | 2.39 | 0.6754 | 0.003074 | 1.065 | 1.525 | 2.388 | 3.255 | 3.715 | 10000 | 45000 |
| residual[21] | -0.9928 | 0.6754 | $0.003076-2.317$ | -1.858 | -0.9949 | -0.1276 | 0.3319 | 10000 | 45000 |  |
| residual[22] | -9.633 | 0.6754 | $0.003077-10.96$ | -10.5 | -9.635 | -8.768 | -8.308 | 10000 | 45000 |  |
| residual[23] | 6.573 | 0.6754 | 0.003078 | 5.249 | 5.708 | 6.571 | 7.439 | 7.898 | 10000 | 45000 |
| residual[24] | 4.247 | 0.6754 | 0.003079 | 2.922 | 3.382 | 4.245 | 5.112 | 5.572 | 10000 | 45000 |
| residual[25] | -1.556 | 0.6754 | $0.003079-2.88$ | -2.421 | -1.558 | -0.6902 | -0.231 | 10000 | 45000 |  |
| residual[26] | -4.82 | 0.6754 | $0.003079-6.145$ | -5.686 | -4.822 | -3.955 | -3.496 | 10000 | 45000 |  |
| residual[27] | -3.276 | 0.6754 | 0.00308 | -4.601 | -4.142 | -3.279 | -2.411 | -1.952 | 10000 | 45000 |
| residual[28] | -2.786 | 0.6754 | 0.00308 | -4.111 | -3.651 | -2.788 | -1.921 | -1.461 | 10000 | 45000 |

Figure A.1. Markov Chain Monte Carlo estimates of the posterior distributions of total mortality of blacktip grouper during period $1(\mathrm{Z} 1)$ and period $2(\mathrm{Z} 2)$.


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