An evaluation of the natural mortality rate used in the assessment of British Columbia Herring Stocks

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Abstract

The estimate of the natural mortality rate assumed in conducting assessments of population abundance of Pacific herring in British Columbia was reviewed and compared to empirical estimates derived from information on numbers of fish in the population based on spawn deposition surveys. Retrospective analyses of stock trajectories based on assuming a range of values of natural mortality were compared within and between stocks. Likelihood profiles indicated that natural mortality rate parameters were well determined in the catch-age analysis although the estimates remained more variable than might be anticipated from other biological information. There was no evidence that estimates of natural mortality obtained from either the empirical approach or from the catch-age analysis were unrealistic or flawed in any obvious manner. It was concluded that the current approach of estimating natural mortality annually as part of the assessment exercise was reasonable and should be continued but further effort is required to understand the interactions among model parameters such as vulnerability and natural mortality.

Résumé

On a tout d'abord examiné les estimations du taux de mortalité naturelle dont on se sert pour évaluer l'abondance des populations de hareng du Pacifique en Colombie-Britannique. Puis, on a comparé ces estimations aux estimations empiriques faites à partir de renseignements sur les quantités de poissons faisant partie des populations déterminées dans le cadre de relevés de la ponte. On a comparé des analyses rétrospectives des évolutions des stocks établies à partir d'une gamme de valeurs de la mortalité naturelle présumée, et ce, tant à l'intérieur d'un stock que d'un stock à un autre. Les profils de vraisemblance ont démontré que les paramètres du taux de mortalité naturelle étaient bien établis dans le cadre de l'analyse des prises selon l'âge. Cependant, les estimations restaient plus variables que ce qu'on aurait pu prévoir à partir d'autres renseignements biologiques. Rien n'indiquait que les estimations de la mortalité naturelle découlant de la méthode empirique ou de l'analyse des prises selon l'âge n'étaient pas réalistes ou comportaient des lacunes évidentes. On a conclu qu'il était raisonnable d'utiliser la méthode actuelle pour évaluer chaque année la mortalité naturelle dans le cadre de l'exercice d'évaluation et qu'on devrait continuer à l'utiliser. Toutefois, on a aussi conclu qu'il faudrait continuer de s'efforcer de comprendre les interactions entre les paramètres des modèles, par exemple la vulnérabilité et la mortalité naturelle.

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INTRODUCTION

The estimate of the natural mortality rate assumed in conducting assessments of population abundance is a critical parameter in determining the absolute level of the stock. In most assessments, an arbitrary value of natural mortality is assumed and the assessment conducted without good knowledge of the true mortality rate. Occasionally, it is possible to use catch curve analysis of the estimated numbers of fish at age in the population in combination with estimates of fishing effort to estimate the natural mortality rate. The natural mortality rate is also generally assumed to remain constant over time and age in most assessments. It is unlikely that many of the assumptions about the natural mortality rate are met for the majority of stock assessments. The objectives of this study were to investigate the estimates of natural mortality rate used in recent Pacific herring assessments with a view to evaluating the impact of variation in this parameter on our perception of the abundance and trends in stock abundance. The sensitivity of abundance estimates to variation in natural mortality also provides some insight into the significance of failures to meet some of the other assumptions about the natural mortality rate on abundance levels.

METHODS

Pacific herring stocks are assessed using two methods. The first, the escapement model relies on information on the abundance of eggs deposited on the spawning grounds to infer the abundance of fish which must have been present to account for the observed egg deposition (Schweigert and Stocker 1988). In this empirical approach no assumption about the natural mortality rate is required to determine current stock abundance but an apparent survival rate is estimated in forecasting future abundance. This apparent survival rate encapsulates the joint processes of partial recruitment and natural mortality to estimate future abundance. The second model, referred to as the age-structured model, is based on the error structure suggested by Fournier and Archibald (1982), and has been used to assess B.C. herring stocks since 1982. The age-structured model can estimate an average natural mortality rate over the course of the data series or an arbitrary fixed natural mortality rate may be assumed in the analysis. It models the two types of fishing gear used commonly in B.C. herring fisheries. Seine nets are assumed to be non-selective while gillnets are selective for larger, older fish. Herring fisheries have concentrated primarily on fish which are on, or migrating to the spawning grounds. Therefore, the relative availability of age-classes to non-selective gear should be equivalent to the partial recruitment of age-classes to the spawning stock. The age-structured model explicitly separates availability (partial recruitment) and gear selectivity. Seine and gillnet fisheries are temporally separate so catch and age-composition are partitioned into fishing periods, separating data for the different gears. Three fishing periods are modelled. The first period encompasses all catch prior to the spring roe herring fisheries. This includes reduction fishery catches prior to 1968 and the winter food and bait fisheries since

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1970. The second fishing period includes all seine roe herring catch and the third period includes all gillnet roe herring catch.

Briefly, the age-structured model estimates T_{ij}, the total number of fish in age class j at the beginning of season i, where season is equivalent to year, and λ_{ij} is the proportion of age j fish which are available to the fishery. Then N_{ij1}, the total number of age class j fish which are available at the start of period 1 in season i is given by

$$N_{ij1} = \lambda_{ij} T_{ij} \qquad\qquad\qquad 1.0$$

To model the fishing process a form of the catch equations which models fishing and natural mortality as continuous processes over time period r, is used:

$$C_{ijr} = \frac{F_{ijr}}{F_{ijr} + M_r}\left(1 - \exp\left(-F_{ijr} - M_r\right)\right) N_{ijr},$$

and, for $r < p$

$$N_{ijr+1} = N_{ijr} \exp\left(-F_{ijr} - M_r\right),$$

where

$\quad C_{ijr}$ is the catch of age class j in season i for period r,

$\quad F_{ijr}$ is the fishing mortality of age class j in season i for period r,

$\quad M_r$ is the natural mortality for period r,

$\quad N_{ijr}$ is the number of fish in age class j in season i for period r,

$\quad p$ is the number of fishing periods $(p=3)$,

$\quad n$ is the number of seasons $(n=47)$,

$\quad k$ is the number of age classes $(k=9)$.

$N_{i+1,j+1,1}$ is defined by equation 1.0 where for $j+1 < k$

$$T_{i+1,j+1} = N_{ijp} \exp\left(-F_{ijp} - M_p\right) + T_{ij}\left(1 - \lambda_{ij}\right) \exp\sum_r - M_r \qquad\qquad 1.1$$

In the model the last age class, k, accumulates all fish aged k and older, so for $j+1=k$ equation 1.1 is replaced by

$$T_{i+1,k} = N_{i,k-1,p} \exp\left(-F_{i,k-1,p} - M_p\right) + T_{i,k-1}\left(1 - \lambda_{i,k-1}\right)\exp\left(\sum_r - M_r\right)$$

$$+ N_{ikp} \exp\left(-F_{ikp} - M_p\right) + T_{ik}\left(1 - \lambda_{ik}\right)\exp\left(\sum_r - M_r\right).$$

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In recent assessments a natural mortality parameter, $M_{\bullet}$, is estimated for the time series of available data. Natural mortality for the three fishing periods is modelled as,

$$M_1 = 0.95M_{\bullet}$$

$$M_2 = M_3 = 0.025M_{\bullet}$$

The multipliers to natural mortality associated with each period correspond roughly with the proportion of the year encompassed by each fishing period and of the total mortality imposed on the stock by predation and other non-fishery factors. The longest period is the reduction or food fishery which runs from the beginning of the season, July 1 and continues until the beginning of the roe fishery in early March. The natural mortality rate may also be fixed at various levels in the age-structured model and the impacts on stock abundance and trends evaluated as we have done in this study.

It is also possible to calculate an apparent survival rate that will approximate the natural mortality rate for age-classes that are fully recruited to the mature stock from information on the spawn deposition and age composition data. The age-specific apparent natural mortality rate (M) was then estimated as:

$$M_{a,i} = \ln \frac{N_{a,i}}{S_{a-1,i,1}}$$

where N is number of fish in the pre-fishery biomass, a is age, i is season and S is the number of fish in the spawning escapement. The general assumption was that the numbers of fish-at-age in the samples from each source (test fishery, commercial fishery) and gear type (seine, gillnet) reflected the proportion in the commercial gillnet and seine fisheries, and for test-fishing samples, in the spawning escapement. Numbers of fish-at-age ($N_{a,g,s,i}$, where g is gear and s is the source) for the total sample weight ($W_{g,s,i}$, tonnes) were multiplied by the biomass of the total gillnet catch, seine catch or spawning escapement ($B_{g,s,i}$, tonnes) to estimate total number of fish-at-age ($T_{a,g,s,i}$) as follows:

$$T_{a,g,s,i} = \sum \frac{N_{a,g,s,i}}{W_{g,s,i}} \bullet B_{g,s,i}$$

For season i, the estimated number of fish-at-age was the sum of fish-at-age for all gear and source types. The average natural mortality rate over seasons was estimated as the annual mean weighted by the number of fish-at-age in season i.

Bayesian profile likelihoods were generated for the estimated natural mortality rate from the age-structured model. This is a feature of the AD Model Builder software (Otter Research Ltd. 1994), for determining the posterior probability distribution for the model parameters in a Bayesian context. Obtaining an exact estimate of the posterior

probability distribution requires evaluation of integrals over large dimensional spaces which is computationally intractable. An approximation to these integrals is provided in the form of the likelihood profiles.

RESULTS

The estimates of apparent natural mortality for the five major herring stocks determined from an analysis of the spawn assessment and total catch data are presented in Fig. 1-5 and summarized in Table 1 along with estimates of natural mortality determined by the age-structured model. While there is a considerable range in the estimates of M, the two partially independent estimates do not differ greatly from one another in each area. However, Fig. 1-5 suggest a slight increase in A_{ij} over time indicating a change in vulnerability or maturity of fish in recent years relative to the reduction fishery which would influence the natural mortality estimates from the age-structured assessment over the entire time series of data.

The result of conducting an age-structured assessment of each of the five major herring stocks assuming the apparent mortality rates as well as a range of values from 0.3 to 0.7 is presented in Figures 6 and 7. In the Queen Charlotte Islands the trends in stock biomass are consistent at all estimates of M (Figure 6). Biomass levels with M fixed at 0.6 or 0.7 appear to be unrealistically high for the early 1980s suggesting that the value of 0.47 estimated by the age-structured model, which is similar to the apparent M estimate of 0.44 is probably reasonable for this stock. Biomass trends for Prince Rupert are also similar at all estimates of natural mortality (Figure 6). Results with M fixed at 0.7 are probably too high but results for the model estimate of M (0.53) appear reasonable while the apparent estimate of M (M=0.25) may be too low. The model estimate of M for the Central Coast was 0.27 which is the lowest on the coast but similar to the apparent M estimate of 0.23 (Figure 6). Biomass trends assuming a natural mortality rate of 0.6 or 0.7 lead to unrealistically high values of stock abundance (Figure 6). An M value of 0.5 also appears high but lower values of 0.4 or less may be appropriate. The biomass trajectories for the Strait of Georgia are similar for all fixed values of M (Figure 7). The model estimate of M (M=0.59) is similar to the apparent M estimate of 0.69. While these estimates of natural mortality appear rather high for herring they result in estimates of levels of abundance similar to those observed historically during the reduction fishery when most of the stock was removed as catch and natural mortality had a relatively small influence on the estimate of total abundance. Finally, the estimate of natural mortality from the age-structured model for the west coast of Vancouver Island stock is 0.42 which is slightly lower than the apparent estimate of M of 0.54 (Figure 7). Biomass trajectories at all levels of M between 0.3 and 0.7 are similar although abundance levels at the fixed values of 0.6 and 0.7 appear to be unrealistically large.

While Figures 6 and 7 indicate that relatively small changes in the natural mortality rate can result in significant changes in our perception of the absolute level of stock abundance they provide limited guidance in determining an appropriate choice of M for stock assessment. To investigate the sensitivity of the age-structured model to

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changes in the natural mortality we examined the parameter space near the minimum. Estimates of the minimum objective function values from the model minimization at a range of natural mortality rates for the five assessment areas are presented in Figure 8. It appears from this figure that the parameter surface is quite flat suggesting that the natural mortality parameter may not be well determined with the available data and a range of M values could result in almost as good a fit to the data as the minimum estimate. While this makes determination of the appropriate value of M to use in the stock assessment in each area more difficult, it does indicate that the values of M estimated by the age-structured model are not unrealistic although they may appear to be too high or low in some areas relative to what has been assumed for other species with similar life histories.

It has been found in catch-age analysis that two model parameters, the natural mortality rate and the catchability or population scaling parameter are often highly correlated which makes the determination of their individual values quite difficult. The relationship between the estimate of the natural mortality rate and the spawn conversion factor relating the age-structure model estimate of spawning stock to the spawn index is presented in Figure 9 and indicates the frequently observed inverse relationship between M and q for all five stocks. The estimated q at the M resulting in the minimum function value does not occur near to the a priori expected level of unity for any of the stocks. The closest match is for the Central Coast that also was estimated to have the lowest natural mortality rate. This suggests that there may be a bias in the parameter estimates which needs to be examined further. A couple of possible reasons for this result are apparent. At intermediate natural mortality rates of about 0.45 the estimated q for the northern areas lies near or below unity consistent with the notion that the spawn index does not census all herring spawning beds and does not include adjustments for egg loss through predation and other factors. This also suggests that there may be some consistent difference in the quality and completeness of the spawn index information in the north relative to the south which may bias parameter the estimates.

Variations in the natural mortality rate may also be associated with changes or differences in the partial recruitment or maturity schedule in different stocks. Estimates of the availability at age or the partial recruitment vector for each stock are plotted in Figure 10. These data demonstrate a cline in maturity at age from south to north. Delayed maturity of herring in the northern areas would be consistent with estimates of lower natural mortality rates for these stocks although this pattern is not completely consistent across stocks. If delayed maturity is associated with slower growth of northern stocks the effect would be exacerbated in the past decade as herring have shown a marked decline in size at age. Attempts to estimate the natural mortality rate from these data would be all the more difficult.

Finally, Bayesian profile likelihoods were calculated for the natural mortality parameter using the age-structured model and are plotted in figures 11 and 12. These results suggest that the estimated natural mortality rates are quite well determined and ranges between 0.4 and 0.5 for three stocks while the Strait of Georgia has a distinctly higher value and the Central Coast a lower rate.

DISCUSSION

Several estimates of the instantaneous natural mortality rate are available for British Columbia herring. Tester (1955) estimated the age-specific mortality for the Strait of Georgia (0.45 to 0.79) and west coast of Vancouver Island (0.43 to 1.14) for ages 3^+ to 6^+ based on catch and age composition data. Taylor (1964) reported a natural mortality rate from catch curve analysis of 0.55 for ages 5^+ to 8^+ for Barkley Sound samples taken from unfished stocks. Schweigert and Hourston (1980) estimated the natural mortality at 0.36 from Barkley Sound catch and effort data during the period 1954 to 1967 for herring ages 2^+ to 4^+. These studies indicate a considerable range in the estimate of natural mortality that might be appropriate for use in catch-age analysis. A previous catch-age analysis also found a substantial range in estimates of the natural mortality rate for the major herring stocks within British Columbia (Haist 1991). The results from the current analysis indicate a similar range in estimates of natural mortality for B.C. herring stocks. The estimate of M at the minimum function value for each stock indicates a substantial range in M as well as a flat likelihood surface which conceivably indicates a poorly determined parameter estimate (Fig. 8). This result is contrary to the profile likelihoods in Figures 11 and 12 which suggest that M is quite well determined in each area. These contradictory results can be rationalized by recalling that the Bayesian posterior distribution is based on examining a likelihood function over all possible outcomes of M rather than the parameter surface for a single value of M. In addition, although the parameter surface for M at the minimum appears flat, the probability of obtaining as good a fit to the data as was obtained with the M at the minimum is unlikely given that a very small change in function value is statistically significant at the 5% level. Hence, one can conclude that M is well determined for each stock given the available data and current model structure.

A dilemma in conducting the catch-age analysis is whether to fix the estimate of natural mortality a priori or to attempt to estimate it as part of the data analysis exercise. Providing that the available data are consistent and unbiased estimators of the underlying structural relationships assumed within the catch-age model it should be possible to estimate the natural mortality rate with a reasonable degree of confidence. However, factors within the population dynamics can change dramatically over the course of a time series of data biasing many of the parameter estimates. For example, Pacific herring size at age has declined markedly over the past decade which could have implications for both maturity at age and natural mortality rate. These changes in population parameters over time could make it more difficult to estimate the natural mortality rate over the course of the time series and result in parameter estimates that appear to be biologically unrealistic.

The analyses conducted here to evaluate the variability in stock abundance estimates for B.C. herring stocks assuming a range of natural mortality rates indicates that abundance levels remain essentially unchanged for the reduction fishery period prior to 1970 when catch rates were very high for all stocks. However, abundance estimates are quite sensitive to changes in natural mortality in recent years where catch rates have been constrained. It is apparent that for most areas natural mortality rates higher than 0.6 are probably unrealistic as are those lower than 0.3. These results are

also consistent with the herring life history where few or no herring live to be older than 10 or 11 years of age implying an annual average M of about 0.5.

Determination of an accurate estimate of the natural mortality rate will continue to be a difficult challenge because of the year to year variability in the ocean environment and predator populations. As a result mortality rates will be unpredictable on a short term basis and consequently will introduce uncertainty into estimates of both current and forecast stock sizes. It appears that the best approach for Pacific herring will continue to be an attempt at annually estimating M within the framework of a catch-age model bounded by the historical reduction data. Provided that rates have not changed markedly in recent years, estimates of present stock size and forecasts of next year's spawning biomass and harvest surplus should be reasonably accurate.

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Table 1. Natural mortality rates estimated by the age-structured model and apparent M calculated from total catch and spawn deposition estimates of stock abundance.

	AS-Model	All Years Ages 3-11	Season>1973/74 Ages 3-11	Season>1978/79 Ages 3-11
Queen Charlotte Is.	0.47	0.30	0.46	0.44
Prince Rupert	0.53	0.21	0.28	0.25
Central	0.28	0.16	0.29	0.23
Georgia Strait	0.59	0.64	0.77	0.69
W.C. Vancouver Is.	0.42	0.51	0.48	0.54
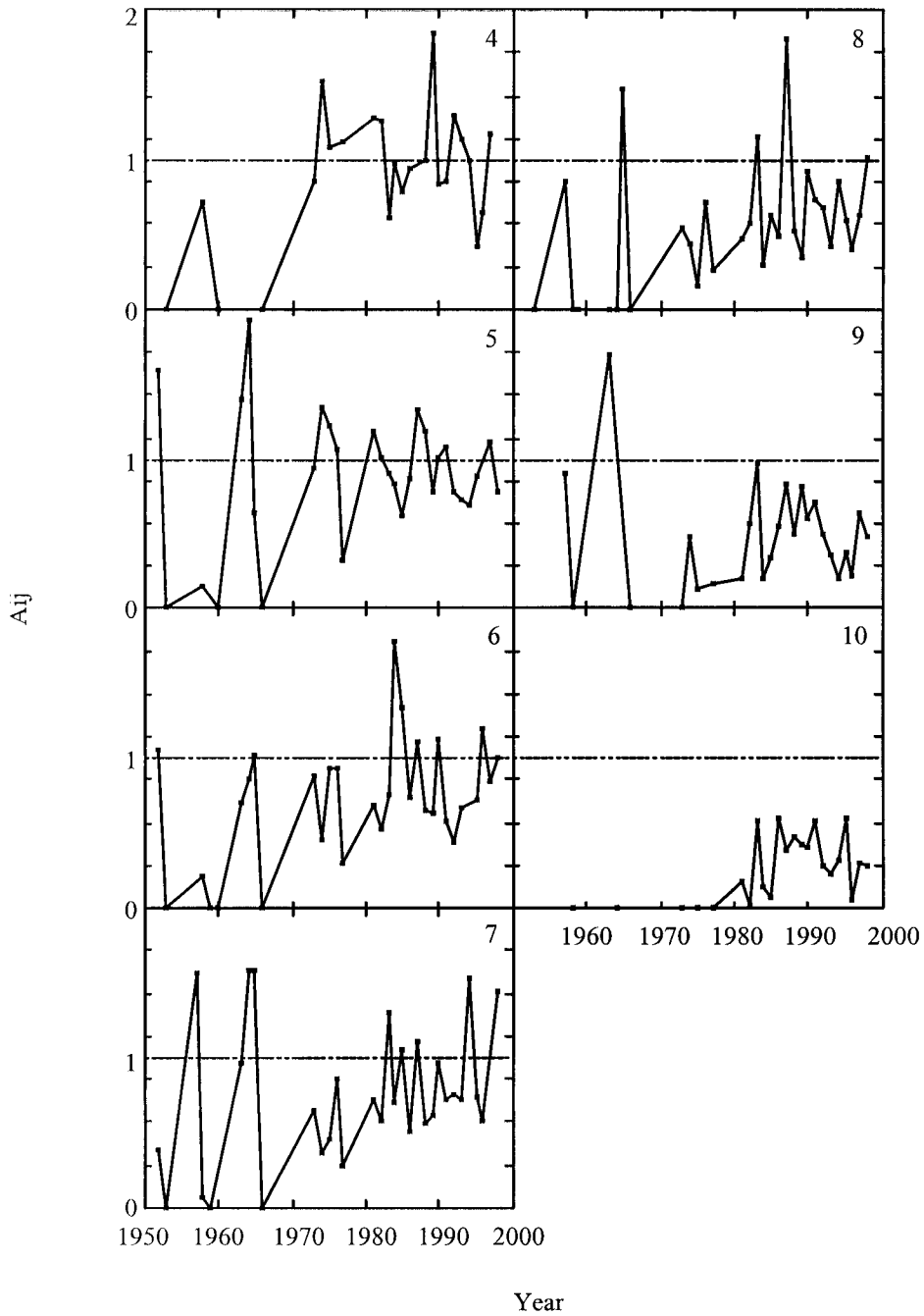
Fig. 1. Estimates of apparent survival rate (A_{ij}) for Queen Charlotte Islands herring. Dotted line is A=1. Age 4 refers to apparent survival from age 3 to age 4. No A_{ij} are calculated for the closure from 1968-72.
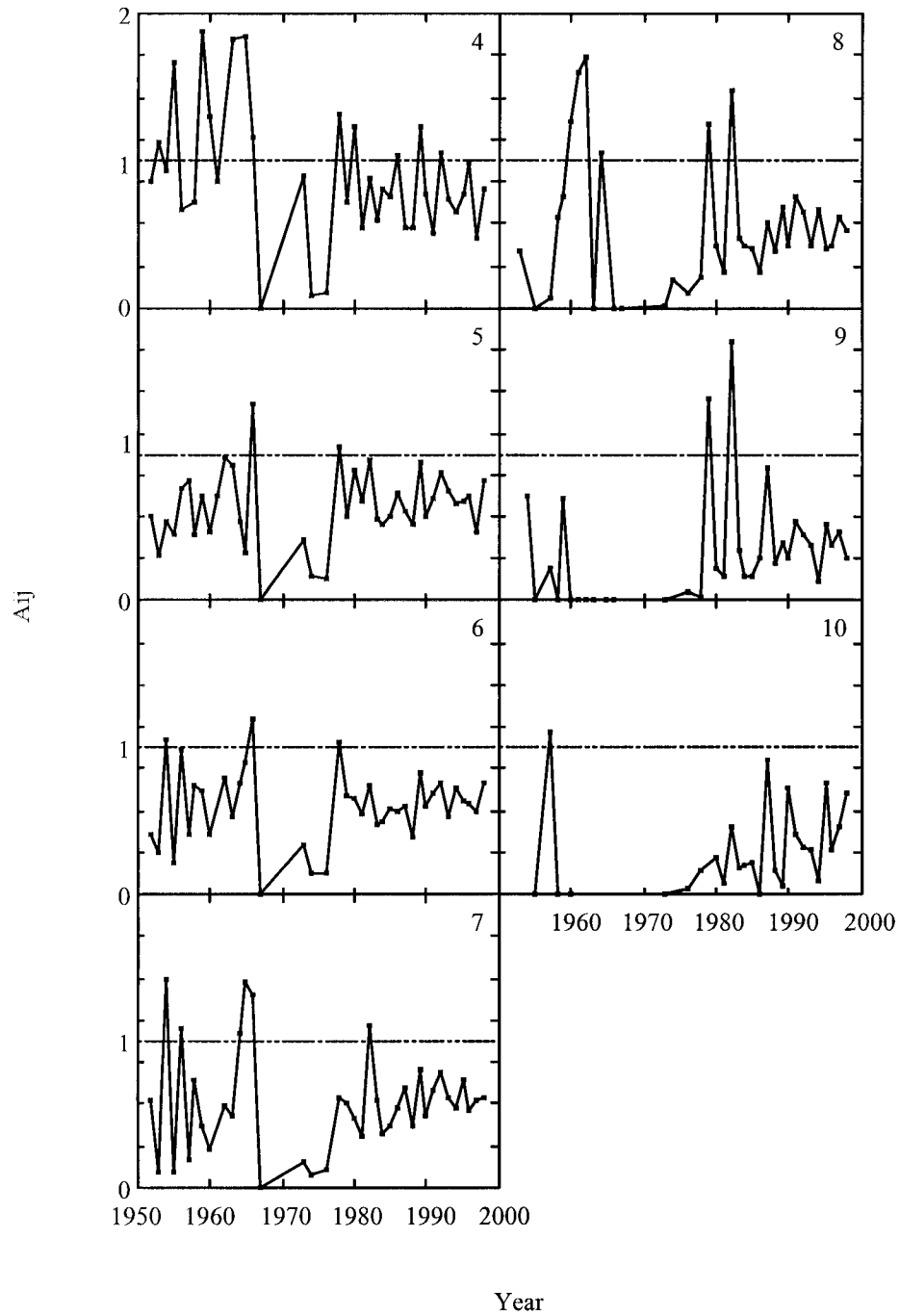
12
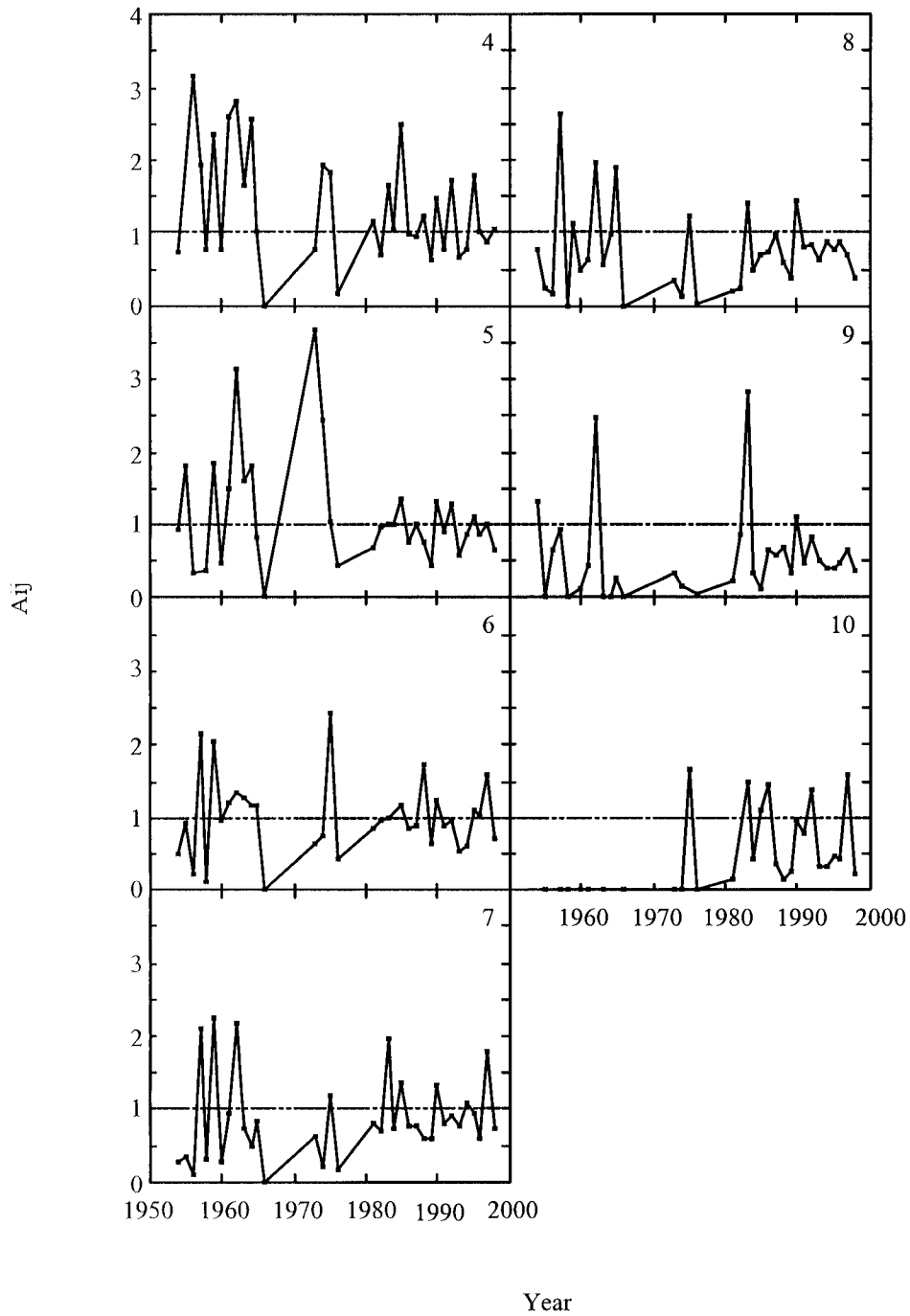
Fig. 2. Estimates of apparent survival rate (A_{ij}) for North Coast herring. Dotted line is A=1. Age 4 refers to apparent survival from age 3 to age 4. No A_{ij} are calculated for the closure from 1968-72.
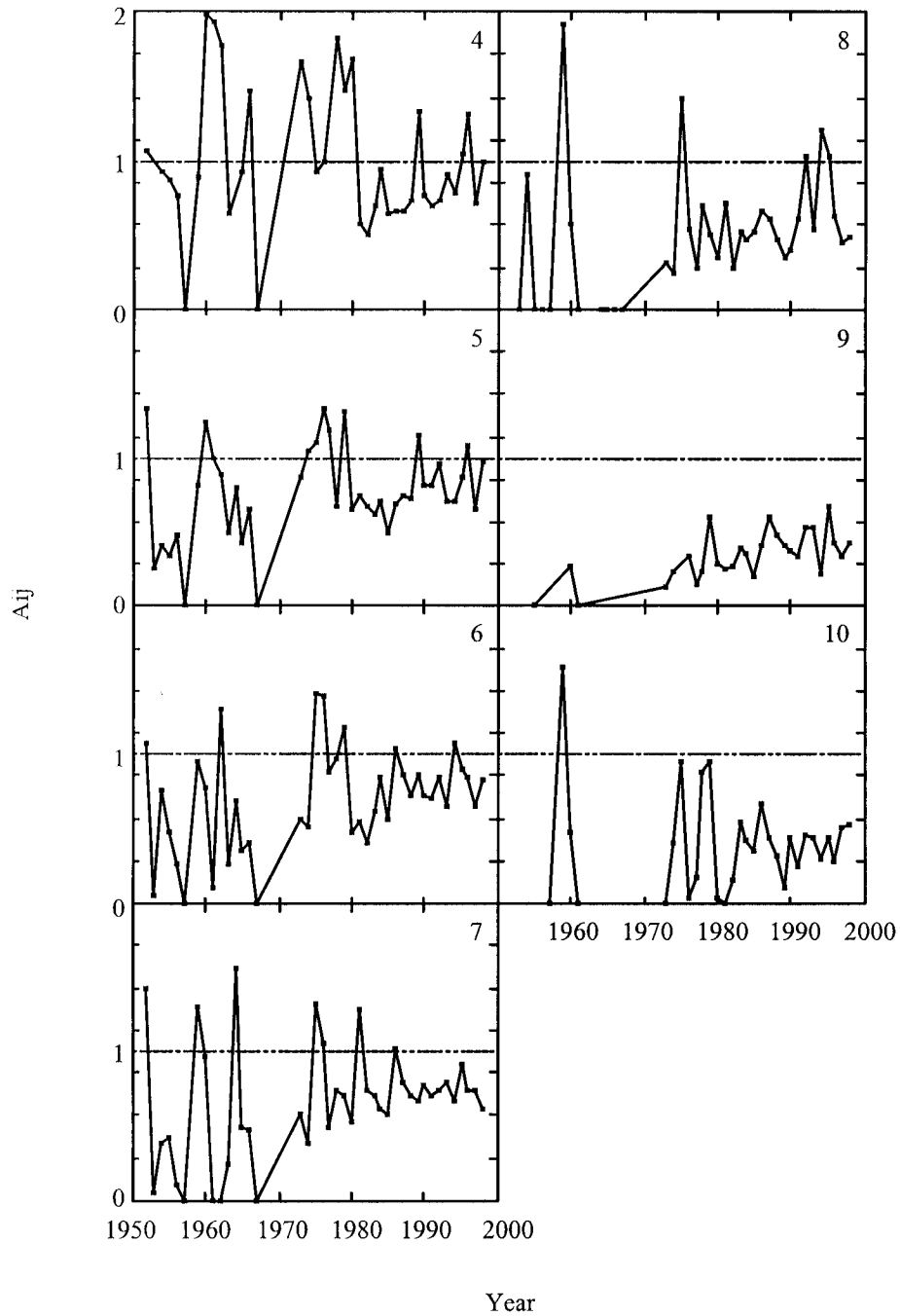
13
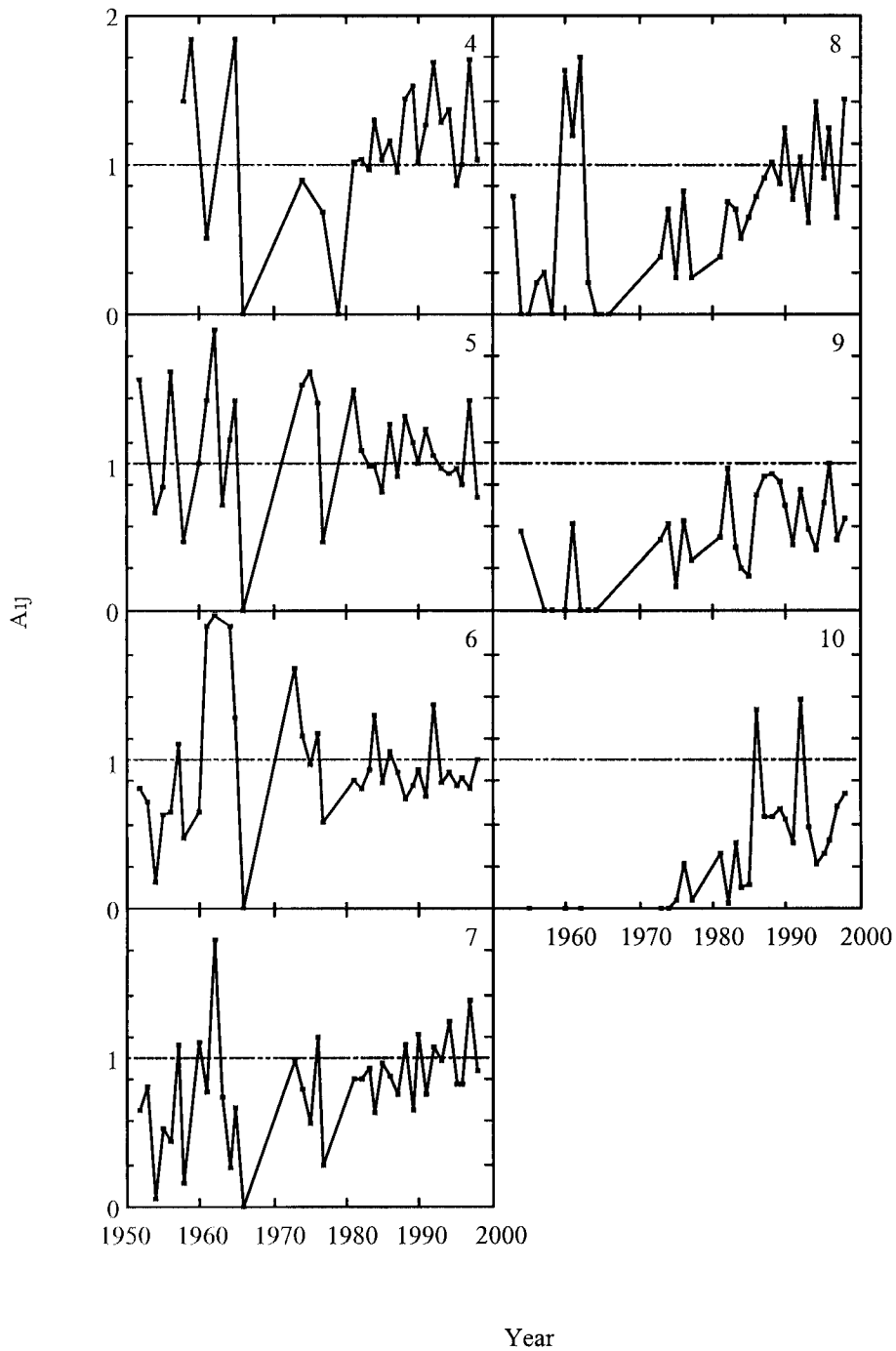
Fig. 3. Estimates of apparent survival rate (A_{ij}) for Central Coast herring. Dotted line is A=1. Age 4 refers to apparent survival from age 3 to age 4. No A_{ij} are calculated for the closure from 1968-72.

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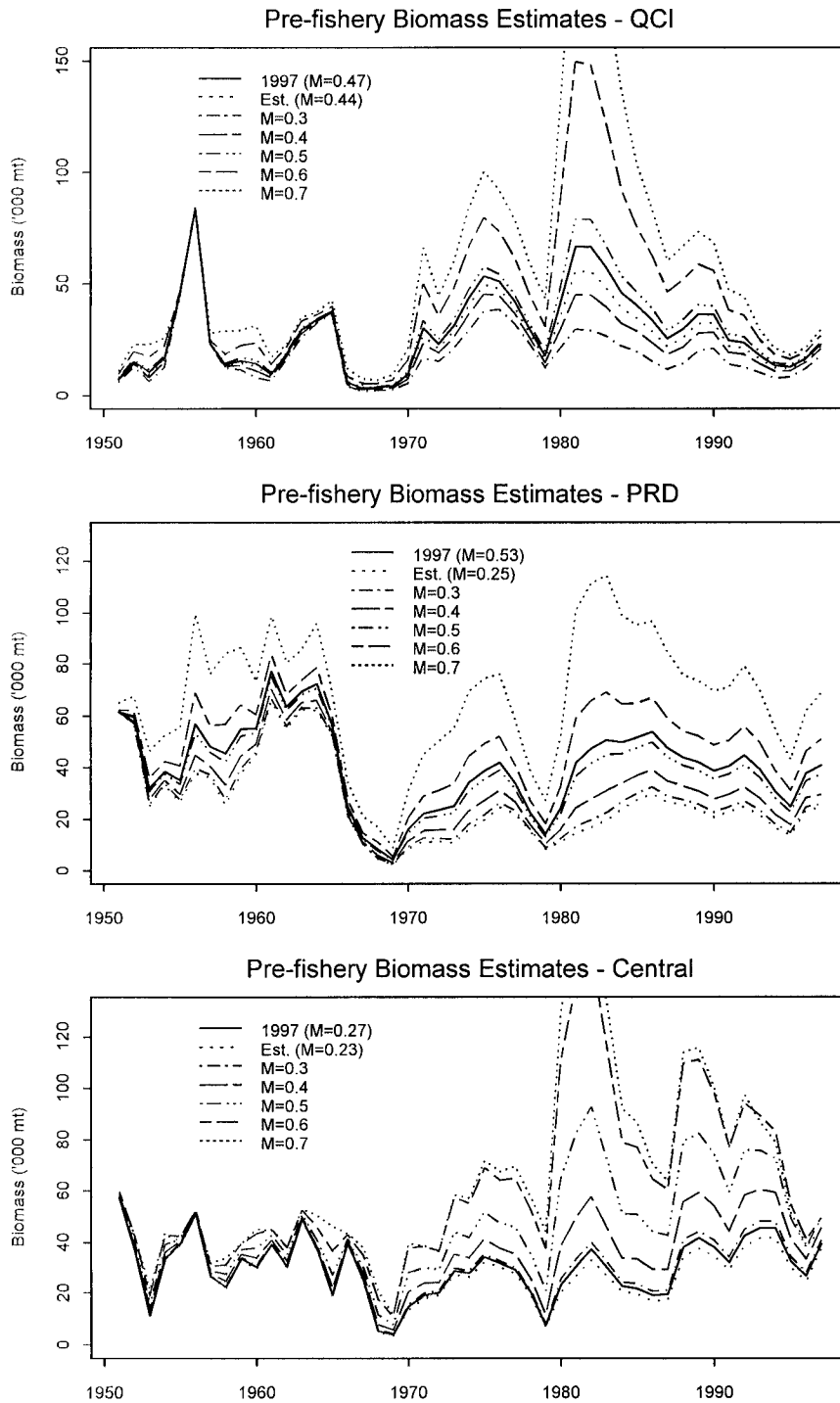Fig. 4. Estimates of apparent survival rate (A_{ij}) for Strait of Georgia herring. Dotted line is A=1. Age 4 refers to apparent survival from age 3 to age 4. No A_{ij} are calculated for the closure from 1968-72.

Fig. 5. Estimates of apparent survival rate (A_{ij}) for West Coast Vancouver Island herring. Dotted line is A=1. Age 4 refers to apparent survival from age 3 to age 4. No A_{ij} are calculated for the closure from 1968-72.

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Pre-fishery Biomass Estimates - QCI

Legend:
- 1997 (M=0.47)
- Est. (M=0.44)
- M=0.3
- M=0.4
- M=0.5
- M=0.6
- M=0.7

Pre-fishery Biomass Estimates - PRD

Legend:
- 1997 (M=0.53)
- Est. (M=0.25)
- M=0.3
- M=0.4
- M=0.5
- M=0.6
- M=0.7

Pre-fishery Biomass Estimates - Central

Legend:
- 1997 (M=0.27)
- Est. (M=0.23)
- M=0.3
- M=0.4
- M=0.5
- M=0.6
- M=0.7

Figure 6. Estimated pre-fishery biomass for northern B.C. herring stocks from 1950-97 assuming a range of natural mortality rates.

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Pre-fishery Biomass Estimates - GS

Pre-fishery Biomass Estimates - WCVI
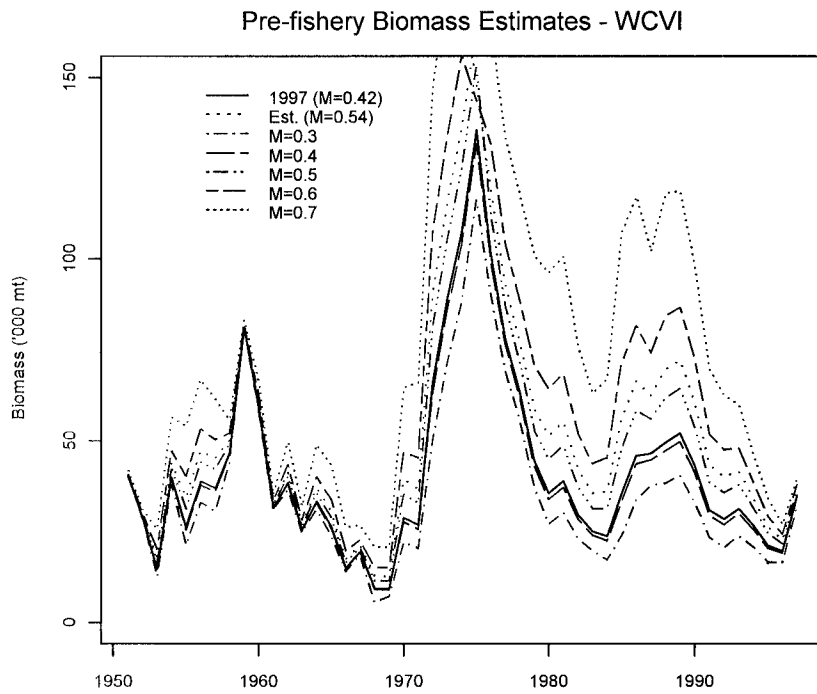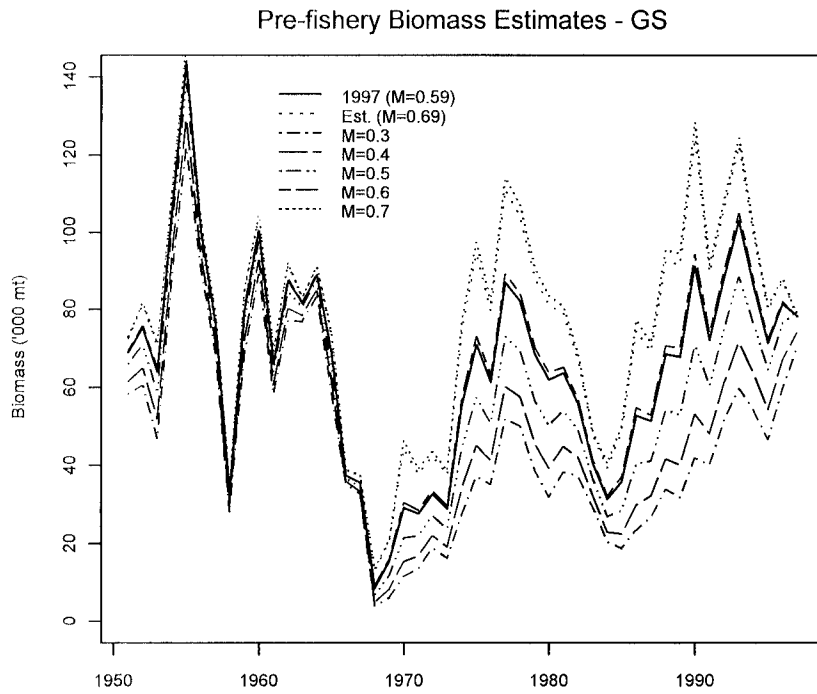
Figure 7. Estimated pre-fishery biomass for southern B.C. herring stocks from 1950-97 assuming a range of natural mortality rates.
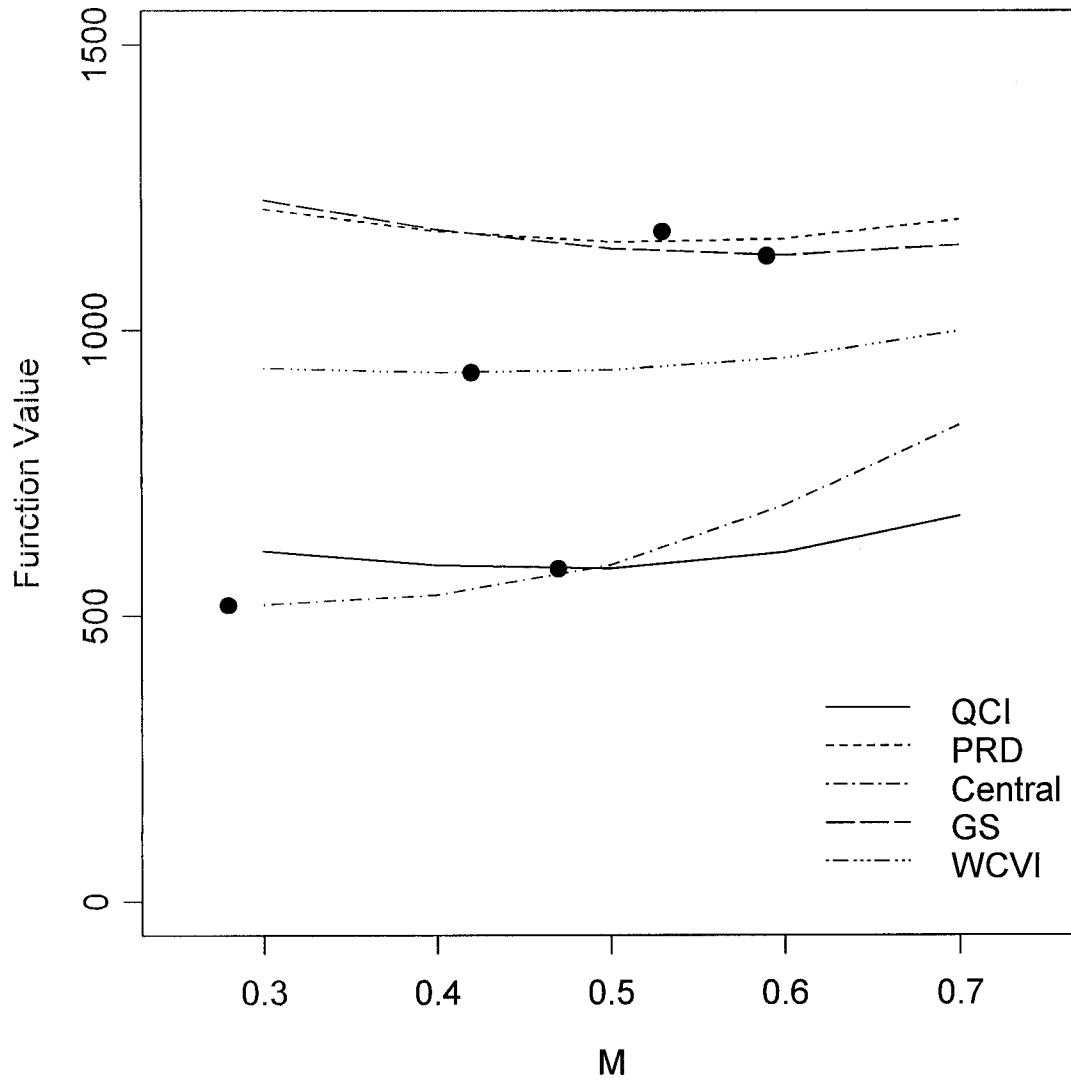
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M versus Minimum Function Value

Figure 8. Estimated minimum objective function values at a range of assumed natural mortality rates for the five B.C. herring stocks.
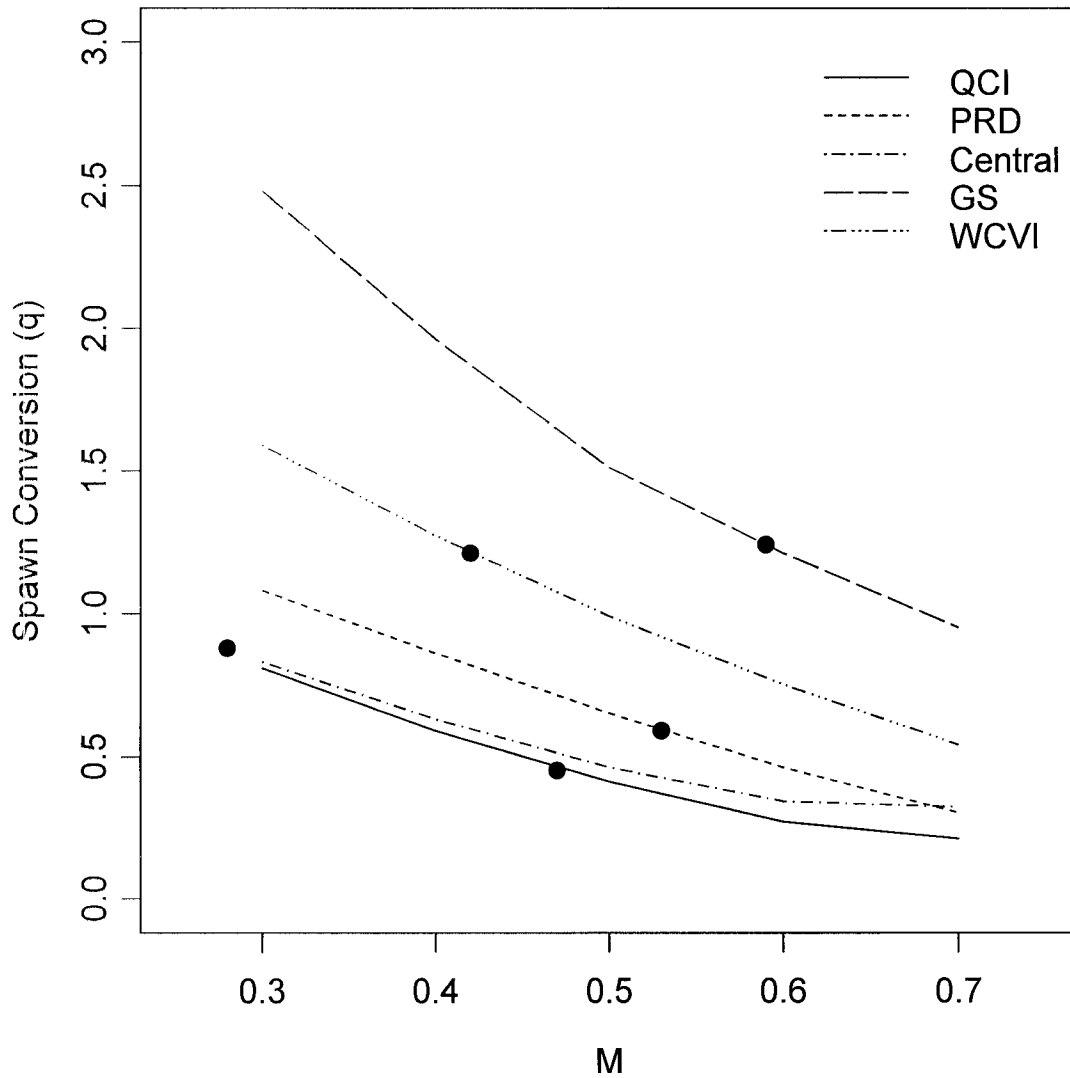
M versus Spawn Conversion (q)

Figure 9. Relationship between the estimated natural mortality rate and the spawn conversion parameter for the five B. C. herrings stocks.
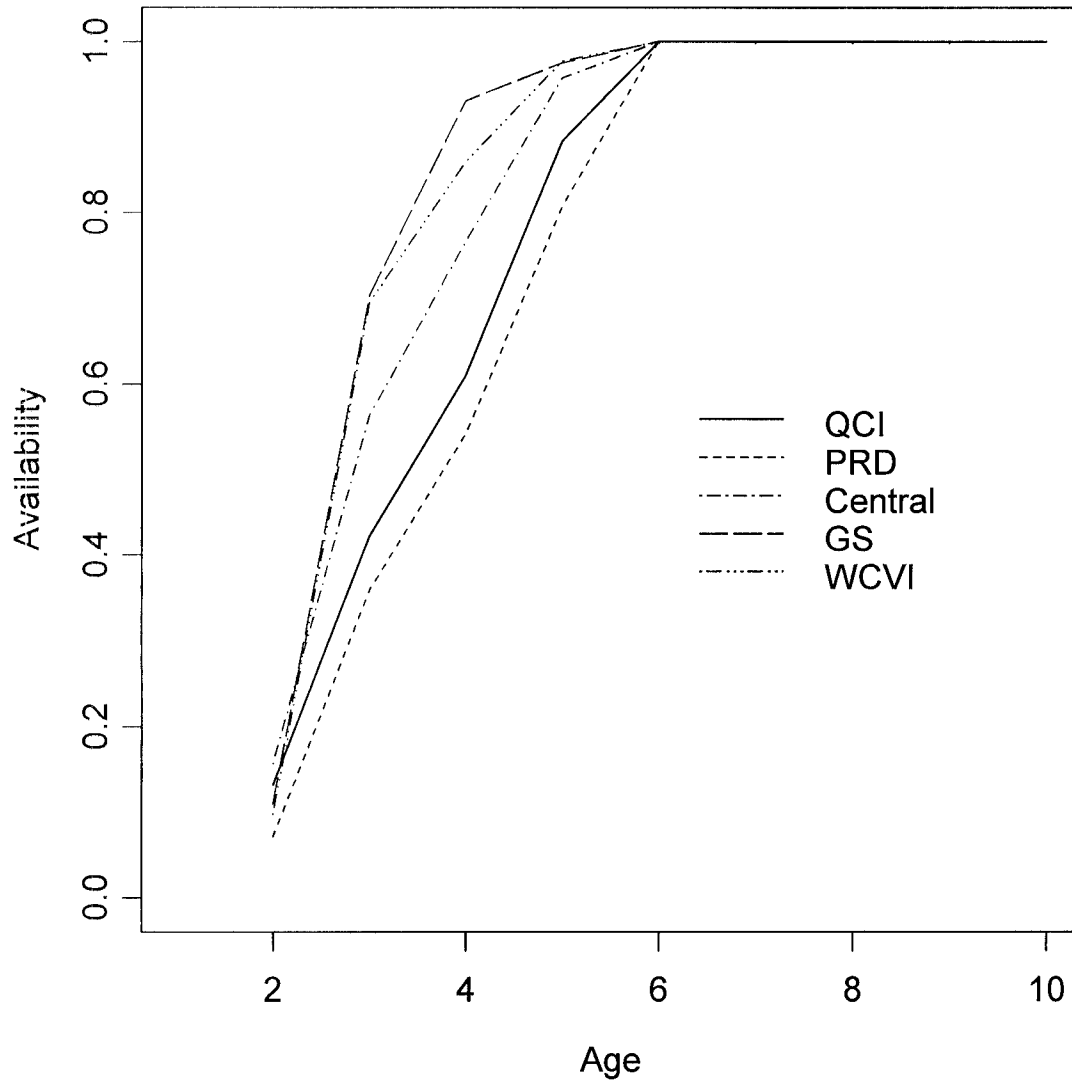
Availability at Age

Figure 10. Estimates of the average availability or partial recruitment vector for the five B.C. herring stocks from the age-structured analysis.

Queen Charlotte Islands

Prince Rupert District

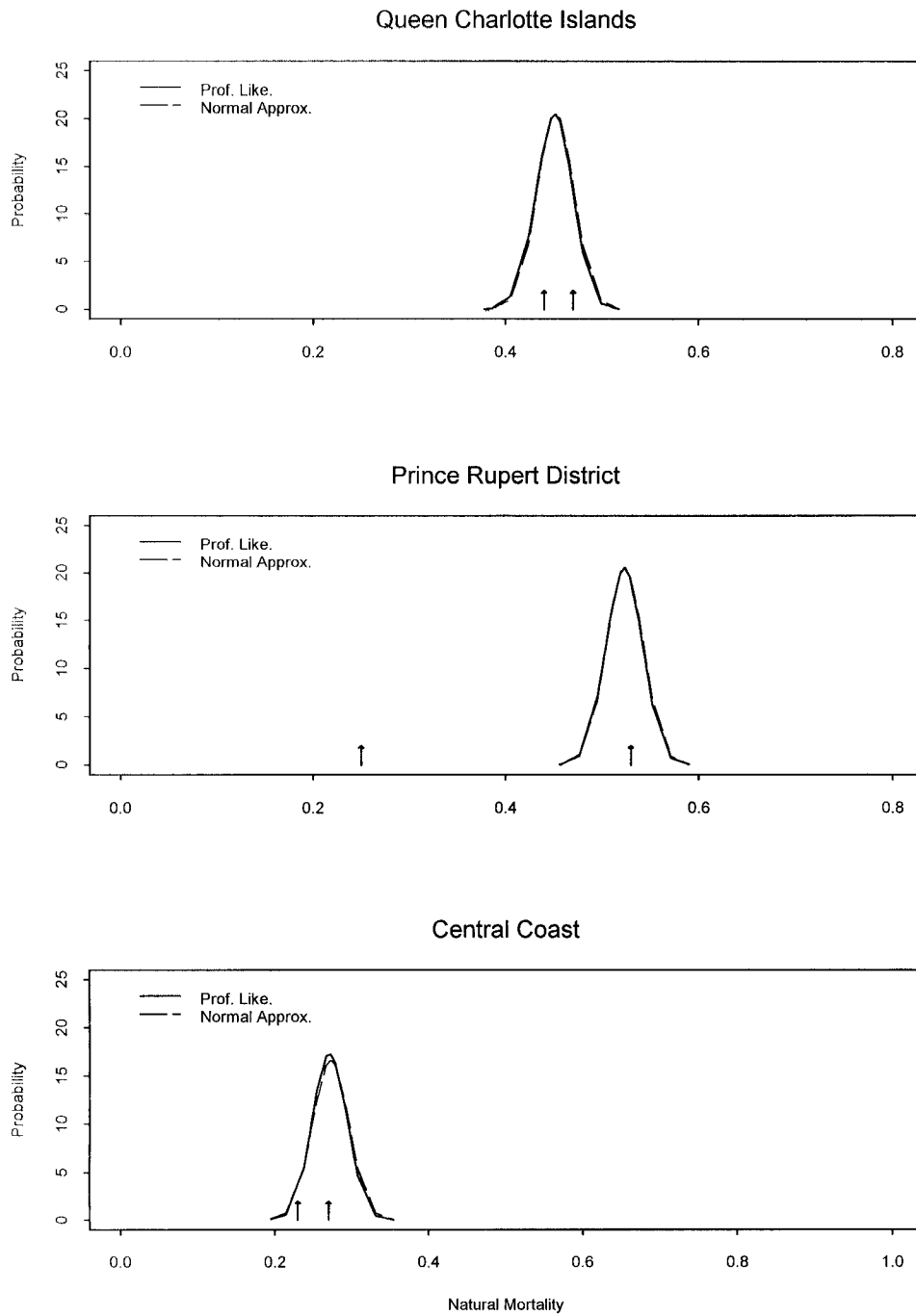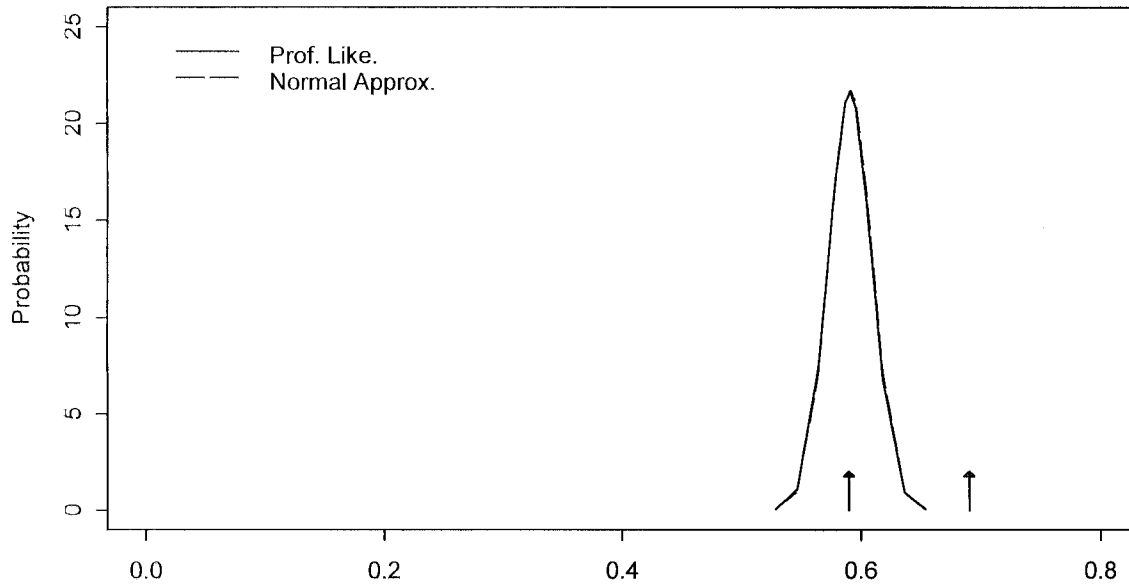## Central Coast

Natural Mortality

Figure 11. Estimated Bayesian profile likelihoods and normal approximations for the natural mortality rate parameter in the age-structured assessment model for the northern B.C. herring stocks. Arrows indicate the estimate of M at the minimum for the 1997 assessment and the apparent M value.

Strait of Georgia
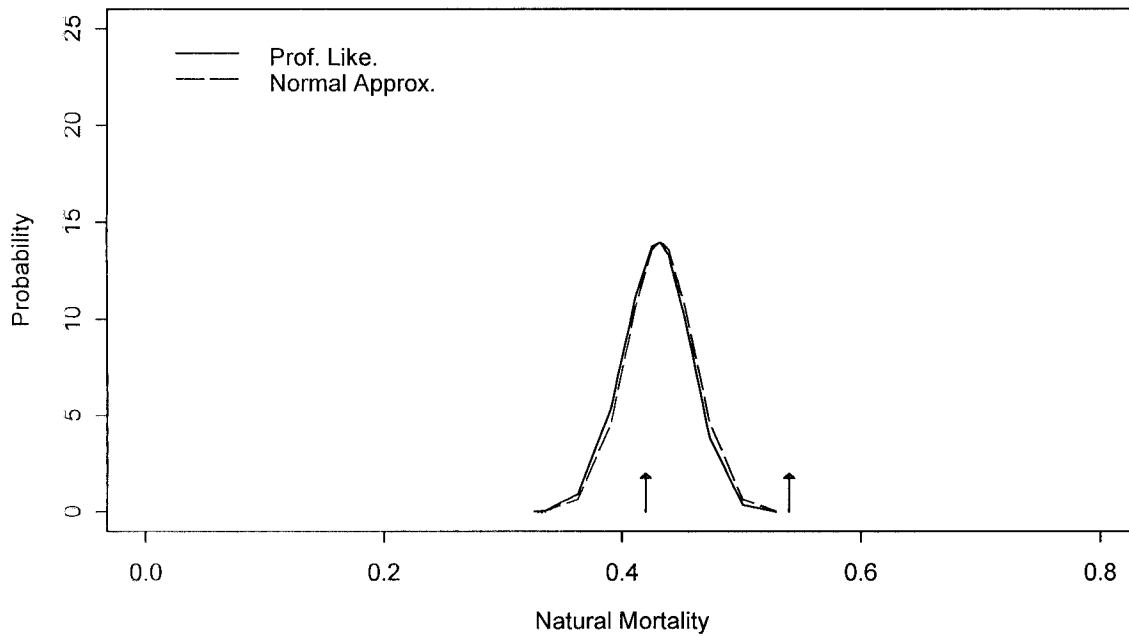

W.C. Vancouver Is.

Natural Mortality

Figure 12. Estimated Bayesian profile likelihoods and normal approximations for the natural mortality rate parameter in the age-structured assessment model for the sourthern B.C. herring stocks. Arrows indicate the estimate of M at the minimum for the 1997 assessment and the apparent M value.