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Herring multi-stock analysis: Integration of tagging data and evaluation of alternative dynamics

Analyse de divers stocks de hareng: Intégration des données de marquage et évaluation de diverses dynamiques

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Abstract

The work presented in this document extends the multi-stock functionality of the HCAM model through inclusion of a tag-recapture module, and investigates alternative hypotheses about the natural mortality process and its impact on stock dynamics. The primary objective of the work is to investigate alternative stock dynamics assumptions in support of a future herring MSE project.

The assumption that natural mortality is related (inversely) to stock abundance fits the herring data as well as modelling natural mortality as a random walk process, though with considerably fewer parameters estimated. General patterns in the natural mortality trends are similar between the two parameterizations. In terms of developing operating models for a future MSE project, the density-dependent natural mortality assumption is more satisfactory because natural mortality rates are driven by internal stock dynamics rather than by external and unknown factors. Some difficulty was encountered in finding formulations for the stock-recruitment and density-dependent natural mortality that did not generate implausible estimates of B_0, but a Ricker stock-recruitment relationship produced reasonable results when other restricting assumptions were included in the model formulation.

The estimates of spawning site fidelity obtained from the integrated HCAM analysis are quite high, at the stock assessment region level. Spawning region fidelity estimates were 89% for QCI, 98% for PRD, 96% for CC, 98% for SoG, and for WCVI. Dispersal rate estimates were highest between regions that are geographically close.

Résumé

Les travaux présentés dans le présent document élargissent la fonctionnalité visant l'analyse de plusieurs stocks du modèle d'évaluation HCAM grâce à l'inclusion d'un module de marquage, et ils examinent d'autres hypothèses concernant la mortalité naturelle du hareng et son effet sur les dynamiques des stocks. L'objectif premier de ces travaux vise à analyser d'autres hypothèses sur les dynamiques des stocks en appui à un projet futur d'évaluation de la stratégie de gestion (ESG) du hareng.

L'hypothèse voulant que la mortalité naturelle soit (inversement) liée à l'abondance du stock correspond aux données sur le hareng de même que la mortalité naturelle modélisée selon la méthode de marche aléatoire, même si beaucoup moins de paramètres ont été estimés. Les schémas généraux des tendances liées à la mortalité naturelle sont semblables entre les deux paramétrages. Quant à l'élaboration de modèles d'exploitation d'un projet futur d'ESG, l'hypothèse de la mortalité naturelle dépendante de la densité obtient des résultats plus satisfaisants parce que le taux de mortalité naturelle est infléchi par les dynamiques internes des stocks plutôt que par des facteurs externes inconnus. On a éprouvé une certaine difficulté à trouver les formulations de modèle pour la mortalité naturelle liée au recrutement des stocks et dépendantes de la densité qui ne produisaient pas des estimations peu vraisemblables de B_0, mais un modèle de stock-recrutement de Ricker a produit des résultats raisonnables lorsque d'autres hypothèses restrictives étaient intégrées à la formulation de modèle.

Les estimations de la fidélité à la frayère obtenues au moyen de l'analyse intégrée du modèle HCAM sont très élevées, à l'échelle régionale de l'évaluation du stock. Les estimations de la fidélité à la région de frai s'établissaient à 89 % pour les îles de la Reine-Charlotte, à 98 % pour le district de Prince Rupert, à 96 % pour la côte centrale, à 98 % pour le détroit de Georgie et pour la côte ouest de l'île de Vancouver. Les estimations sur le taux de dispersion étaient plus élevées entre les régions rapprochées géographiquement.

1 Introduction

The herring catch-at-age model (HCAM) currently used for stock assessments was developed as a generic model that could be used to reconstruct multiple stocks simultaneously (Haist and Schweigert, 2006), although annual stock assessments analyze data from each of the 5 major stock assessment regions separately (eg. Schweigert et al. 2008). One of the advantages of reconstructing all herring stock simultaneously is that tagging data can be incorporated in the analysis to estimate movement among the stocks, and to inform total mortality estimates. Additionally, meta-analytic approaches can be used so that parameter estimates are informed by the joint information in the data from all stocks. This paper focuses on incorporating tagging data in the multi-stock herring model and on investigating a density-dependent natural mortality relationship for the five major herring stocks.

Three major B.C. herring tagging programs have been conducted to estimate inter-annual spawning site fidelity: belly tagging, 1936-1967; external anchor tagging, 1979-1992; and CWT tagging, 1999-2006. Numerous studies have analyzed different components of these data, with considerable variability in the estimated spawning site fidelity at the stock assessment region level (Flostrand et al. 2009, Ware and Schweigert 2002, Hay et al. 2001, Schweigert and Schwarz 1993, Hourston 1982). In general, estimated fidelity rates are lower for analyses using the external anchor tagging data, which may result from higher error rates in reported tag recovery location (fishery of recapture) for that study. Unlike the other tagging programs, data collected in conjunction with the CWT program is comprehensive and includes estimates of the amount of herring scanned for tags for each of the potential recovery fisheries. Additionally, studies were conducted to estimate initial acute mortality associated with tagging and tag detection rates in fish plants (Flostrand and Schweigert 2007). Data used in these analyses are restricted to the CWT tag releases and recoveries.

Incorporating tagging analysis within the stock assessment model should have superior performance relative to approaches that analyze tag release-recapture data separately (eg. Hampton and Fournier 2001). This approach explicitly accounts for differences in the size of populations tagged, differences in the proportion of the populations (and catch) sampled for tags, and differences in the size-selectivity of tag and recapture fishing gear.

Time-varying natural mortality (M) assumptions have been included in B.C. herring models in various forms. Haist et al. (1993) explored density-dependent natural mortality and found that, for the 5 major herring stocks, the density-dependent assumption significantly improved model fits relative to an assumption of time-invariant M. Fu et al. (2004) estimated annual variability in natural mortality, and Haist and Schweigert (2006) modeled natural mortality as a random-walk process (Gudmundsson 1994). The random-walk parameterization of M has been used in recent herring stock assessments (eg Schweigert et al. 2008). This approach is somewhat unsatisfactory as it does not ascribe changes in natural mortality to either internal stock dynamics or external environmental factors.

The primary objective of the analyses presented here is to provide a basis for future management strategy evaluations (MSE) for B.C. herring. A MSE requires operating models, assumed to reflect reality, that encompass a broad range of plausible scenarios describing stock dynamics and interactions among stocks (see Stokes et al. 1999, and papers therein). The work presented here should provide a starting basis for developing operating models that encompass a range of uncertainty about herring stock dynamics and interactions amongst the stocks.

2 Model Description

The starting version of the age-structured model is identical to that used for the 2008 stock assessment (Schweigert et al. 2008), and used again with minor revision for the 2009 stock assessment. A number of minor changes were made to the model code (HCAMv2) so that the multi-stock functionality worked correctly. The full model structure, as used for these analyses, is described in Appendix 1. Major modifications to the code are described below.

2.1 Density-dependent natural mortality and stock-recruitment functions

For the density-dependent natural mortality relationship, natural mortality (*M*) is parameterized as a non-linear function of beginning of year biomass (Appendix 1). The age-classes that are vulnerable to the density-dependent natural mortality are user specified: for these analyses we investigate age-classes 2 and older and age-classes 3 and older being affected by the density-dependent natural mortality.

Early runs that explored the density-dependent *M* parameterization assumed a Beverton-Holt (BH) stock recruitment relationship and generated results that were problematic. For some stocks, estimates of B_0 were low and the stock was estimated to be above B_0 for most of the historical period. In general, fisheries models that assume a BH stock recruitment relationship assume that *M* is time-invariant. In that case, spawners per recruit in the unfished state increases as spawning biomass increases from 0 to B_0 and then decreases continuously as spawning biomass increases above B_0. This generates a single stable stock-recruitment equilibrium point at B_0. The Ricker (R) stock-recruitment relationship behaves the same. However, when natural mortality is parameterized as a function of stock biomass there may no longer be a stable stock-recruitment equilibrium point. In that case, density-dependent natural mortality increases spawners per recruit (in the unfished state) as biomass increases and this can outweigh the stock-recruitment effect of reduced spawners per recruit as spawning biomass increases above B_0. B_0 is still an equilibrium point but it is no longer stable because there can be a point above B_0 where spawners per recruit increases as biomass increases.

To deal with the instability caused by the interaction of density-dependent *M* and the standard stock-recruitment functions (ie. BH and R), a modified form of the Beverton-Holt (ABH) relationship was modelled. The ABH stock-recruitment relationship incorporates a term that adjusts for the changes in spawning per recruit resulting from the density-dependent *M* parameterization (see Appendix 1 for equations) .

2.2 Tagging data

A new component was added to the HCAM model to incorporate tagging data into the model fits. Tag release groups, defined by the region and year of tag releases, are tracked from 1999 to 2006, the period when tag detector equipment was used in fish plants to scan catches for tags.

Tagged fish follow the same dynamics as the untagged populations, except that all tagged fish are assumed available to the fisheries (see Appendix 1 for equations). The predicted age-composition for the SN roe fishery is assumed to correspond to the age-composition of tagged fish. Following tagging, tagged fish are lost due to tagging-induced mortality and loss of tags. Then they are vulnerable to the SN and GN roe fisheries in the year and region of release. Movement is assumed to occur instantaneously at the beginning of the year.

Predicted tag recoveries are a function of the tagged fish in the region, the age-specific fishing mortality rates, the proportion of the catch scanned for tags, and the tag detector efficiency. A Poisson distribution is assumed for tag recoveries, and the model is fitted separately for the GN and SN fishery recoveries.

Movement is assumed to be a Markov process, that is, independent of previous movements. Movement parameters, reflecting the probability that a fish moves from one region to another, are time-invariant. Untagged fish are assumed to move the same as tagged fish, and this is also parameterized to occur instantaneously at the beginning of the year.

2.3 Summary statistics

A number of statistics are presented to summarize characteristics of individual model runs and facilitate comparisons among them. Two pertain to normalized residuals for model fits to data observations. These are: the standard deviation of normalized residuals (SDNR), and the median absolute normalized residual (MAR). The normalized residuals should conform to a standard normal curve if the statistical assumptions about the data are correct. Expected values are 1 for SDNR and 0.67 for MAR.

Average annual natural mortality rates are calculated to provide a simple statistic to compare among alternative model runs:

$$1-\left(\left(\sum_{y}-\exp\left(-M_{y}\right)\right)\Big/ nyr\right),$$

where M_y is the instantaneous natural mortality in year *y* (averaged over all age-classes) and *nyr* is the number of years. The total objective function value is termed *OBFval*, and depletion is the ratio of 2008 spawning stock biomass to B_0.

3 Data

The main data sources fitted in the HCAM model are: spawn survey biomass estimates, age-composition data from three fisheries (winter, seine roe, and gillnet roe), and total catch estimates from the three fisheries. Auxiliary data includes annual mean weight-at-age and annual geometric mean weight-at-age (used in fitting the gillnet selectivity functions). The data is the same as that used for the 2008 stock assessment model (Schweigert et al. 2008), except for minor changes that are described below. All model runs were conducted analyzing data for the five major herring stocks (Figure 1) simultaneously.

The CWT tag release and recapture data, used in model formulations that include the tagging and movement structure, is essentially the same as that analysed by Flostrand et al. (2009), though that study summarized release and recovery data by statistical area and this study

summarizes the data by stock assessment region. Tagging occurred close to the spawning grounds, and tagged fish were released annually from 1999 to 2004. There were multiple release years for all stock assessment regions except for the QCI and WCVI stock, for which there was a single release (Table 1). Tags were recaptured using CWT metal detectors in fish plants, ensuring 100% accuracy in the reported fishery tag recaptures occurred in. Additionally, the quantity and proportion of the total landings that were scanned for tags is known with minimal error (Table 2 and Table 3).

Tag returns that occurred during the fisheries immediately after the tagging events (within days or weeks) were not fitted in the analysis, rather only recoveries that occurred after 1 year-at-liberty or greater were used. Tag recovery data is fitted in the model based on tag release group (year and stock region of tagging), recovery fishery (seine or gillnet fishery and stock region), and years-at-liberty. A high proportion of tags were captured in the same region as where they were released (Table 4).

4 Results

4.1 Verification of multi-stock code & model changes

The data files used for this analysis are identical to those used for the 2008 stock assessment. The initial step of this analysis was to ensure that the multi-stock version of the HCAM code produced identical results to those from the 2008 stock assessment. The model was run using the same options as used for the 2008 assessment, but analyzing the data for all 5 stocks simultaneously. The multi-stock version of the HCAM code replicated the 2008 assessment - objective function values and all parameter values were identical to those from the 2008 assessment (Table 5).

A few minor modifications of the model data and model structure were made in order to address some specific concerns about estimation and model performance. These were conducted in a step-wise incremental fashion so that their impact on key model parameters could be tracked. The following list summarizes these changes:

Run Name	Run description
2008Assess	Same formulation as the 2008 stock assessment
2008Assess-a	3 age-composition samples removed
2008Assess-b	*InitF* parameter included in 1942 population initialization
2008Assess-c	Include age-composition data for 2000-2008 where no commercial seine fishery
2008Assess-d (Base case)	Change standard deviation of fit to total catch data

The first change was to remove age-composition samples that resulted in normalized residuals that were more extreme than 10. The reason for this was a concern that large outliers could unduly influence the model fits, and potentially result in local minima solutions. Examples of local minima had been found with previous versions of the HCAM model, though this problem appears to be resolved with the version used for the 2008 stock assessment. Three age-composition samples were removed from the analysis because they resulted in residuals more extreme than $\pm$ 10 (SoG 1972 SN fishery; SoG 2007 Winter fishery; WCVI 1974 SN fishery).

The impact of this change on model parameter estimates was negligible (Table 5). The age-composition SDNR statistic decreased slightly, though the MAR statistic was not affected.

In an attempt to resolve implausible estimates of B_0 when estimating density-dependent natural mortality, an alternative form for the population initialization was evaluated. For the 2008 stock assessment version of HCAM, the populations are initialized at near-equilibrium conditions in 1942. That is, age-classes 3 and older are at their unfished equilibrium level while the number of age 2 fish is estimated as a free parameter. For the period 1943 – 1950, a constant level of fishing mortality is assumed (*initF*) and annual recruitment deviations are estimated. The alternative form for initializing the populations assumed that the *initF* level of fishing mortality was operating through the pre-history of the fisheries. This is perhaps a more realistic assumption, given there is a long exploitation history for the fisheries. The impact of this change on the model fit and parameter estimates was minimal (Table 5). Although this change did not resolve the issues when estimating density-dependent natural mortality, the alternative form of the population initialization was maintained in all runs.

HCAM is structured to fit age-composition data only where there is associated catch data. Thus, for years where there is age-composition data from pre-fishery charter sampling but no associated seine roe fishery catch the samples are not included in the model fits. In particular, there have been few fisheries in QCI in recent years, so little age-composition data is being fit for the recent period. The additional information from the unused age-composition samples contains information that is particularly useful when estimating time-varying natural mortality rates. The model code was modified so that where there are pre-fishery charter age samples but no commercial seine catch, a nominal catch (10 Kg) is assigned to the fishery thus resulting in the age-composition samples being fit. Initially all additional age-composition samples were included in the fit (Table 6), however the total objective function value increased substantially and resulted in some extremely large residuals, suggesting some of the samples were problematic. Rather than investigate each individual age-composition, the pragmatic solution was to include only the pre-fishery charter age-composition samples for years 2000 and onward (Table 6). This provides greater estimation stability at the end of the time series which is potentially more unstable because of cohorts that have not fully transited the age structure, while avoiding lack-of-fit issues with some of the earlier samples.

When the additional 2000-onward age-composition samples were included in the model fits, model parameters were not greatly affected (Table 5). The model fit to the spawn data was slightly degraded, indicating some conflict between the additional age-composition samples and the spawn survey data. Estimates of B_0 were virtually identical to those from the previous run, and estimates of depletion changed only slightly for the QCI and PRD stocks.

The final change made to the HCAM model in generating a *base* case for these analyses, was a reduction in the assumed variance in the fit to catch data. The standard deviation of the catch residuals had been set at 0.0707 for the 2008 stock assessment runs, though actual fits to the catch observations were much tighter than the specified level (Table 5). When fitting to tagging data (see below), the fitted catch estimates can be substantially different than the catch observations to allow better fits to the tag recovery data. This type of result is unrealistic because the tag recovery data is unlikely to be informative about catch levels. Specifying a lower standard deviation for the catch residuals (0.005 for these analyses) ensures a tight fit between observed and fitted catch values, even when tagging data is fitted in the analysis. The impact of this change on model parameter estimates was minimal. This version of the HCAM model is termed the *Base* model parameterization. It has the same structure as that used for the 2008 stock assessment, with the exception of changes noted above.

4.2 Estimating density-dependent natural mortality

A large number of runs that explored alternative ways to parameterize density-dependent natural mortality and the stock-recruitment relationship were conducted. Many solutions were found that were implausible, that is, solutions where the B_0 estimate was low and the population was estimated to be above B_0 for most of the historical period. In general, this problem was not encountered for all stocks and the CC stock was particularly susceptible. The model runs described below demonstrate this problem and provide some potential solutions in terms of model parameterization. A summary of the alternative model parameterizations is provided in Table 7.

The first two runs have the same structure as the *Base* model, with the exception that natural mortality is not modelled as a random walk, rather as a density-dependent process. The standard form of the BH stock recruitment relationship is fitted, and steepness parameters estimated for each stock. A density-dependent natural mortality rate parameter (*Mdd*) is estimated for each stock. The two runs differ in which age-classes are subject to the density-dependent *M* (either age 2 and older – *ddM-1*, or age 3 and older – *ddM-2*). For comparison, a model run like the *Base* model but without the natural mortality random walk (ie. constant natural mortality, *Base-ConstM*) is also presented.

Comparing the constant *M* run (*Base-ConstM*) with the *Base* run shows that inclusion of the natural mortality random walk improves the model fit substantially (*OBFval* of 2762.1 versus 2471.9, Table 8), decreasing the objective function value by 290 log-likelihood units. However, this improvement is attained with 290 additional model parameters. The average natural mortality rate is relatively similar between the constant *M* and random-walk *M* runs, though somewhat lower for the PRD, CC, and WCVI stocks and somewhat higher for the QCI and SoG stocks under the constant *M* model (Table 8). The first two model runs with the density-dependent natural mortality parameterization improve the model fit by 209 and 292 log-likelihood units, for *Mdd-BH1-5h* and *Mdd-BH2-5h,* respectively, with only 5 additional parameters (Table 8). As with the random-walk *M* run, average natural mortality rates are similar to those from the constant *M* runs. Clearly, the density-dependent *M* parameterization captures a substantial amount of the apparent trend in natural mortality rates, and does so with substantially fewer parameters than the random-walk *M* parameterization.

A major problem with these two density-dependent *M* runs is that they result in implausible stock reconstructions for some stocks, with biomass estimates above B_0 for many years (Table 8, Figure 2). This is a particular issue for the CC stock, and to a lesser extent for the PRD and QCI stocks. High values for the *Mdd* parameter or low values for *steepness* appear to be associated with the problem.

For the next sequence of runs, the model was parameterized with a common *steepness* parameter and a common *Mdd* parameter (all stocks share the same *steepness* and *Mdd* parameter). These runs were conducted with three alternative forms for the stock recruitment relationship (BH, R, and ABH) and the two options for the age-classes effected by the density-dependent natural mortality (*ddM-1* and *ddM-2*).

Common *steepness* and *Mdd* parameters do not resolve the problem that many biomass estimates are above B_0 for the BH stock-recruitment function, but for the ABH and R stock-

recruitment functions the problem is mostly eliminated. Although model fits for the ABH and R parameterizations are generally not as good as for the BH parameterization (*OBFval,* Table 8), they result in more stable and credible stock reconstructions. In general, the runs using the ABH stock-recruitment function result in higher estimates of B_0 .

Relative stock biomass trends $\left(B_y / B_0\right)$ from the four credible density-dependent *M* models are similar, although the *Mdd-R2* run generally has larger fluctuations in relative biomass and the *Mdd-ABH1* run generally has smaller fluctuations in relative biomass (Figure 3). Depletion estimates are similar among the runs for all stocks except PRD (Figure 3,Table 8). While the form of the density-dependent natural mortality function tends to be similar among the alternative stock-recruitment formulations, the range in natural mortality rate estimates is highest for the *Mdd-ABH1* runs and lowest for the *Mdd-R1* runs (Figure 4). The stock-recruitment relationships (Figure 5) are very different for the ABH functions and the R functions, with the ABH functions showing much higher compensation in recruitment as biomass decreases from B_0 .

Comparison of the natural mortality time series from the *Base* run and two of the density-dependent runs shows they generally have similar trends, but the density-dependent runs show much larger inter-annual variability (Figure 6).

Another comparison among the constant *M*, random-walk *M*, and density-dependent *M* runs is the total annual mortality resulting from natural (ie. non-fishing) sources. Annual natural mortality, in tonnes, is calculated from the catch equations. The constant *M* run has the highest variability in total annual natural mortality (Figure 7), because it fluctuates in conjunction with stock abundance. The density-dependent natural mortality runs have the lowest variability in total natural mortality because of the inverse relationship between stock abundance and natural mortality rates. Variability in total annual mortality for the random-walk natural mortality run is generally intermediate between the others (Figure 7).

Although the overall model fits for the density-dependent natural mortality runs are almost as good as those for the *Base* run which parameterizes natural mortality as a random walk process, this result does not hold for all stock assessment regions. Table 9 presents negative log-likelihood components (total, spawn, and age-composition) for the individual stock assessment regions and a subset of the model runs. For three of the areas, QCI, CC, and WCVI model fits for the density-dependent *M* parameterization are as good as those for the random walk *M* parameterization. For the other two regions, PRD and GS, better model fits are obtained with the random-walk parameterization.

Parameter correlations for a sub-set of model parameters (*M*, steepness, Mdd, B_0 , and q_{early}) are shown in Table 10 for the Mdd-R2 model run. The highest correlations are between the *M* and B_0 parameters, ranging from -0.64 to -0.89. The remainder of the parameter correlations are low or moderate.

4.3 Incorporating tagging data

A number of runs were conducted that included the tagging data in the model fits. This included variants of the *Base* model structure as well as variants including a density-dependent natural mortality parameterization (Table 7).

4.3.1 Base case model variants

For the first run using the base model structure (*BaseT-minMove*), movement parameters are only estimated between regions where tagged fish had been recovered. Hence, there are two region pairs where there were no recovery opportunities (ie. no fisheries) and an additional 7 region pairs where there were recovery opportunities but no tagged fish were recovered. This parameterization added 13 tag survival/tag loss parameters and 11 movement parameters to the model fit (Table 11).

The addition of tag data in the *BaseT-minMove* model fit resulted in an improved fit to the spawn data and only a slight degradation in the fits to the age-composition and total catch data (see likelihood components, SDNRs and MARs in Table 11). Estimates of the tag survival/tag loss parameters were quite variable among the tag release groups, ranging from 0.025 for the SoG_2003 releases to 0.217 for the PRD_2002 releases (Table 12). For both the SoG and PRD regions there are multiple tag release groups, and the estimates of the tag survival parameters are less extreme than for the other release groups. The model imposes a certain coherence among the multiple tag release groups (they share total mortality estimates for some years), so the variation in tag survival estimates are likely quite well determined. All tag release groups in the CC have relatively high tag survival estimates, and it is possible that there is an underlying bias among these estimates.

Movement estimates suggest a high degree of spawning site fidelity (at the stock region level), with 90% to 99% of the fish returning to their previous spawning region on an annual basis (Table 13). The highest level of movement was estimated from the WCVI to the SoG region, with 9% moving annually. For the WCVI, there is a single tag release group (2004) and WCVI tag recovery opportunity only after 1 year-at-liberty, making this estimate more uncertain than others. It is interesting to note that the 2005 WCVI fisheries (both seine and gillnet) occurred in Area 25 and recaptured fish that were tagged in Areas 23, 24, 25, and 26 (Table 16), suggesting high movement rates among the WCVI areas.

Fits to the tagging data, as measured by the SDNR and MAR statistics, indicate reasonable agreement with the statistical model assumption of a Poisson distribution and independent and identically-distributed observations. The standardized residuals have a slightly leptokurtic distribution (MAR less than expected value of 0.67 and SDNR greater than the expected value of 1.0), but do not indicate over-dispersion of the residuals (Table 11).

For the next run, movement parameters were estimated for all region pairs even where there were no tag recoveries (*BaseT*). It is possible that there is information in other data fitted in the analyses that can inform fish movement rates. Comparison of estimated movement parameters for the *BaseT-minMove* and *BaseT* model runs is provided in Table 13 and Table 14. While most of the movement parameters did not change significantly when estimating movement among all region pairs, movement from QCI to PRD was estimated at 5.9%, movement from CC to QCI was estimated at 2.7%, and movement from QCI to WCVI was estimated at 2.0%, even though there were no associated tag recoveries. It appears that improved fits to the age-composition data are informing those movement estimates (Table 11). Most tag survival parameters did not change significantly from the values estimated for the *BaseT-minMove* run , with the exception of the QCI 1999 tagging where the survival parameter decreased from 0.091 to 0.072 (Table 12).

All additional model runs that incorporate tagging data use the formulation where movement parameters are estimated among all region pairs.

The efficiency of the tag detection machines at recovering tagged fish should not affect model parameter estimates other than the tag survival parameters so long as the efficiencies remain constant over time. A model run was conducted where the tag recovery efficiency parameter was fixed at 70% (*BaseT-0.7E*). The only model parameters that changed were the tag survival parameters which increased inversely to the assumed efficiency (Table 11, Table 12).

Although model fits to the tagging data are very good based on the SDNR and MAR statistics, the quality of the fits are variable among the tag release groups. To generate a visually simple graphic to display the model fits, observed and predicted tag recoveries were summed across regions by fishery and year for each tag release group. For example, the observed and predicted 2002 recoveries from the 2001 PRD tag releases were summed across all 2002 seine fisheries and across all 2002 gillnet fisheries. Because little movement is estimated, the majority of the observed and predicted recoveries are in the release region.

Observed and predicted tag recoveries, summarized as described above, are shown in Figure 10. For all CC tag release groups, the model fits are extremely good for both the SN and GN fisheries. The PRD tag release groups show a persistent pattern: fits for the SN fishery recoveries are quite good but fits for the GN fishery show a tendency for negative residuals for 1 year-at-liberty recoveries and positive residuals for 2 and greater years-at-liberty recoveries. Model fits for the 2000 SoG tag releases are quite good while fits for other SoG releases are not as good. For those, there is a tendency for positive residuals for the SN fisheries and negative residuals for the GN fisheries.

4.3.2 6-area model

For the PRD, the tag release groups are readily separated into Area 3/4 and Area 5 tag releases. Additionally, recovery data is readily separated by Area because all GN fisheries occurred in Area 3/4 and all SN fisheries in Area 5. A summary of the raw tag recovery data by Area of release and fishery of recovery suggests that fish tagged in Area 3/4 are more likely to be recaptured in Area 3/4 fisheries and likewise for Area 5 (Table 17). Some of the lack-of-fit seen in the PRD tag recovery fits may result from not accounting for spawning site fidelity at the Area level. To investigate this idea, separate Area 3/4 and Area 5 data files were generated (spawn, age-composition, total catch, tag release-recovery) and a 6-area model fitted to the coastwide data (*BaseT-6Area*).

Estimated movement parameters for the 6-area model (*BaseT-6Area*) suggest reasonably high spawning site fidelity for the two PRD areas, with annual fidelity rates estimated at 91% for Area 3/4 and 93% for Area 5 (Table 15). Most of the movement out of each Area is to the other PRD area. The remaining movement parameter values are similar to those from the *BaseT* model run, with the exception of movement away from QCI which increases slightly.

Model fits to the tagging data is somewhat improved for the *BaseT-6Area* run relative to the *BaseT* run. Components of the log-likelihood function cannot be directly compared because the data observations are different, but the tag residual summary statistics are directly comparable. The tag residual SDNR decreases from 1.83 to 1.42 and the MAR decrease from 0.37 to 0.33 for the *BaseT-6Area* model run relative to the *BaseT* run (Table 11). Comparison of the observed versus predicted tag recoveries, calculated as described above, shows very good fits

for the Area 5 tag release groups but fits for the Area 3/4 tag release groups are still somewhat problematic (Figure 11 and 12).

4.3.3 Estimating 2 q's

Herring stock assessments generally assume that the proportionality constant between spawn survey estimates of spawning biomass and actual spawning biomass (q_{late}) is 1 for the period where surveys have been conducted using dive survey methods (1988 – 2008), though a q_{early} parameter is estimated for the early period . Given not all spawning events are surveyed and there can be considerable egg predation prior to surveys, the assumption that q_{late} is 1 can potentially result in biased model estimates of spawning abundance. The inclusion of tag release-recapture data in the HCAM model should provide some information on total mortality (*Z*), which may inform estimates of q_{late} .

To investigate the effect of including tagging data in the HCAM model on estimates of q_{late} , variants of the *Base* and *BaseT* models where both *q* parameters were estimated were run. For three of the stocks (CC, SoG, and WCVI) model estimates of *Z* were relatively insensitive to inclusion of the tagging data and to estimation of the q_{late} parameter (Figure 8). For the QCI stock, inclusion of tagging data tended to increase estimates of *Z* and estimation of the q_{late} parameter tended to decrease estimates of *Z* for the most recent years. Because of limited tag recovery opportunities in QCI fisheries, the tagging data is likely not very informative about *Z* for this stock. For the PRD stock, inclusion of tagging data had a relatively strong effect reducing estimates of *Z* for the years where the tagging data was informative (Figure 8). *Z* estimates were relatively insensitive to estimation of the q_{late} parameter.

Estimates of spawning stock biomass were generally more sensitive than *Z* estimates to inclusion of tagging data and estimation of q_{late} (Figure 9). For two of the stocks, PRD and SoG, similar spawning stock biomass trajectories were obtained for the *Base*, *BaseT* and *BaseT-2q* model runs with much higher biomass trajectories for the *Base-2q* runs. For the QCI stock, spawning stock biomass estimates are sensitive to including the q_{late} parameter, but relatively insensitive to inclusion of the tagging data. Spawning stock biomass trajectories for the WCVI stock are insensitive to inclusion of either the tagging data or the q_{late} parameter (Figure 9).

Analytical estimates of the c.v. of the q_{late} parameter estimates also suggest that the tagging data provides some information about this parameter (Table 18). For the three stocks where there are multiple tag release groups and multiple tag recovery opportunities (PRD, CC, and SoG), the c.v.s of the q_{late} parameter are significantly reduced for the model run that includes the tagging data (*BaseT-2q*).

4.3.4 Density-dependent natural mortality variant

The final model runs examined included both the tagging data and the density-dependent natural mortality assumption. For these runs, the Ricker form of the stock-recruitment relationship was used, as it had produced more credible stock-recruitment relationships for the runs reported previously. Both variants for parameterizing the density-dependent relationship

(applied to age-classes 2 and older and applied to age-classes 3 and older, *MddT-R1* and *MddT-R2*) were run.

As for the *Base* model structure, inclusion of tagging data in these density-dependent natural mortality runs improved the fits to both spawn and age-composition data (Tables 8 and 11). Model parameter estimates were generally not strongly affected, though estimates of B_0 changed in both positive and negative directions. Depletion estimates were not strongly affected, with the exception of the PRD stock where depletion estimates decreased with the inclusion of the tagging data (Tables 8 and 11). For the CC stock, the proportion of years where stock biomass was estimated to be above B_0 was relatively high (0.46) for the *MddT-R2* run, though estimates were acceptable for the *MddT-R1* run (0.20).

A MCMC simulation was conducted for the *MddT-R1* run to estimate marginal posterior distributions of some key model parameters and to ascertain if there would be potential convergence problems. Of the alternative models evaluated, this one has characteristics that would be useful to explore within the context of a herring MSE. A MCMC chain of 5 million was run and the output thinned to sample of 2000 to represent the joint posterior distribution.

The resulting marginal posterior samples from the MCMC chain indicate lack of convergence, at least from some quantities of management interest (B_0 and depletion, Fig. 13). Clearly a longer MCMC chain is required to ensure the posterior samples capture the true uncertainty in key parameter values. However, the marginal posterior distributions from this chain should be at least somewhat informative about parameter uncertainty.

Marginal posterior distributions show relatively high levels of uncertainty in B_0 and depletion estimates, while stock fidelity estimates (annual proportion remaining in the region) are relatively certain (Table 19). Autocorrelation in recruitment deviations is relatively low for all stocks, except for WCVI (Table 19). Correlation in recruitment deviations between stocks tends to be high, in particular for stocks with close geographical proximity. The between stock correlation in recruitment deviations should be considered when developing operating models for a herring MSE.

5 Discussion

The work presented in this document extends the multi-stock functionality of the HCAM model through inclusion of a tag-recapture module, and investigates alternative hypotheses about the natural mortality process and its impact on stock dynamics. The primary objective of the work is to investigate alternative stock dynamics assumptions in support of a future herring MSE project.

The assumption that natural mortality is related (inversely) to stock abundance significantly improves the model fit to the herring data, relative to the assumption of a constant natural mortality rate. Haist et al. (1993) investigated density-dependent natural mortality for the 5 B.C. herring stocks and reached a similar conclusion. Their work was extended to include harvest simulations, and they concluded that population responses to exploitation were more extreme under the assumption of density-dependent natural mortality and would require more stringent harvest control rules. The model structure used by Haist et al. (1993) did not assume a stock-recruitment relationship, so they did not encounter the issues in estimating B_0 that we faced.

The assumption of time-varying natural mortality, modelled as a random walk process, fits the herring data as well as the density-dependent natural mortality assumption, though with considerably more parameters estimated. The general patterns in the natural mortality trends are similar between the two parameterizations. In terms of developing operating models for a future MSE project, the density-dependent natural mortality assumption is more satisfactory because natural mortality rates are driven by internal stock dynamics rather than by external and unknown factors. Age-specific natural mortality was explored in some early runs and found to significantly improve model fits, but results are not presented here. Implications of age-specific natural mortality may warrant consideration in future MSE work.

There was some difficulty in finding formulations for the stock-recruitment and density-dependent natural mortality functions that did not generate implausible estimates of B_0. The Ricker form for the stock-recruitment relationship produced reasonable results - for all stocks B_0 estimates were higher than the historical estimates of spawning stock biomass for most years. Although estimates of steepness are high for the Ricker stock-recruit parameterization, relative to expectations based on meta-analyses, it is a natural consequence of the density-dependant natural mortality parameterization. That is, given higher natural mortality rates at lower stock abundance fewer fish survive to be vulnerable to the fisheries, so the model compensates by maintaining high levels of recruitment.

Estimates of tag survival rates, representing both tag loss and acute tagging-induced mortality, were quite low, ranging from 2.4% to 18.8% for the different tag release groups under the base case model formulation. These values were higher, 3.5% to 26.8%, when a tag detection efficiency of 0.7 was assumed. Holding trials to estimate tag loss and tagging-induced mortality, conducted in conjunction with the CWT tagging program, estimated tag loss rates ranging from 0 to 6% among independent trials (Linnea Flostrand, DFO, pers. comm.). Because of high mortality rates for the control groups of herring (ie. not tagged), estimates of tagging-induced mortality are not easy to estimate from the holding trial study. Over four trials ranging from 23 to 90 days duration, total mortalities of tagged fish and control fish were 22.5% and 18.5%, respectively, with mortalities continuing to increase for both groups throughout the course of the study. Tag survival estimates obtained from the analyses reported here suggest a higher level of tagging-induced mortality than would be inferred by the field study.

The assumption that all tags scanned for tags are detected (ie. a tag detection efficiency of 1), does not affect HCAM model parameter estimates, with the exception of the tag survival rate parameters. This, of course, is only true if the tag detection efficiencies are constant among all recovery fisheries. Tag detection efficiencies were estimated at the three plants used to recover tags by seeding the sampled catch. For two of the plants, recovery rates were high (75% and 84% for GN catch, 79% and 90% for SN catch), while for the third plant recovery rates were much lower (34% for GN catch and 63% for SN catch). Given this variability among plants inter-fishery differences in tag detection efficiency may introduce error in these analyses.

The estimates of spawning site fidelity obtained from the integrated HCAM analysis are quite high, at the stock assessment region level. This is particularly true for regions where there were multiple releases and multiple recapture opportunities, with fidelity estimates of 96% for the CC and 98% for PRD and SoG. Fidelity estimates are lower, 89% for QCI and 91% for WCVI, for regions with limited tag releases and recovery opportunities. Dispersal rate estimates were highest between regions that are geographically close, a result that is consistent with analyses of the B.C. herring tagging data based on “isolation by distance” models (Flostrand et al. 2009, Ware et al. 2000).

Previous analyses of the herring tagging data have varied in the analytical approach taken and in the data sets used in the analyses. Analyses by Hourston (1982), Ware et al. (2000), Hay et al. (2001) did not standardize tag recoveries by harvest rates, tag reporting rates, etc., but rather assumed that rates would be generally similar among stock assessment regions. The range in stock fidelity estimates for these studies were similar: 77% to 94 % for the Hourston (1982) study based on belly tags; 75% to 96% for the Ware et al. (2000) study based on belly tags and anchor tags; and 78% to 96% for the Hay et al. (2001) study based on belly tags and anchor tags. For the Ware et al. (2000) study, the estimated average fidelity rate was 95% for the belly tags and 78% for the anchor tags. Based on these data, Ware et al. (2000) and Ware and Schweigert (2001) hypothesize a density-dependent dispersal relationship, however, there is a clear confounding between the tagging methods and average stock abundance during the tagging periods. That is, during the belly tagging period stock abundances were relatively low (high *F*s) and during the anchor tagging period stocks abundance was relatively high (low *F*s).

Schweigert and Schwarz (1993) analyzed the northern B.C. belly tagging data set using a migration rate model that required minimal assumptions about the tag recapture process, but did require external estimates of relative population sizes. They estimated spawning region fidelity rates >95% for the PRD and CC stocks, results that are consistent with estimates obtained for this study.

Ware and Schweigert (2001, 2002) postulate a metapopulation structure for B.C. herring whereby density-dependent dispersal rates stabilize the spatial distribution of spawners within the metapopulation and increase the persistence of less productive local populations. A large year-class in one of the local populations sets up a dispersal wave that radiates through the metapopulation until it is depleted by natural and fishing mortality. Density-dependent dispersion is potentially an important mechanism for regulating population abundance because it will tend to stabilize populations, whereas the density-dependent natural mortality explored in this study will tend to de-stabilize population abundance.

Density-dependent dispersion, as suggested by Ware and Schweigert (2001, 2002), was not investigated here because the tag release data used in these analyses were restricted to the recent CWT tag releases and estimation of annual migration rate parameters would have decreased the information in these data about total mortality (*Z*) rates. However, in the context of a MSE and developing operating models that account for a broad range of plausible stock dynamics, a herring metapopulation structure should be considered. The updated version of the HCAM model, which includes between-region movement, could readily be modified to investigate metapopulation dynamics.

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Table 1. Region, year, and number of tags released by tag release group.

ID	Region	Year	Number of tags
1	QCI	1999	6175
2	PRD	2001	88196
3	PRD	2002	74661
4	PRD	2003	111500
5	CC	2002	49195
6	CC	2003	79920
7	CC	2004	159892
8	SoG	1999	43268
9	SoG	2000	245694
10	SoG	2001	60558
11	SoG	2002	83528
12	SoG	2003	89247
13	WCVI	2004	131811

Table 2. Amount (tonnes) of herring scanned for tags by fishery and year.

Year	Seine Fisheries					Gillnet Fisheries				
Year	QCI	PRD	CC	SOG	WCVI	QCI	PRD	CC	SOG	WCVI
2000	136	152	1713	1677	246	0	208	242	1249	57
2001	0	72	2202	2038	0	0	206	179	2151	0
2002	99	207	949	3304	171	0	897	69	2722	41
2003	0	192	1123	2467	961	0	344	62	1854	40
2004	0	132	1181	1446	1612	0	441	0	1210	84
2005	0	347	1072	1936	1262	0	499	0	2058	274
2006	0	246	607	3020	0	0	264	0	1934	0

Table 3. Proportions of total catch scanned for tags by fishery and year. – denotes years with no fishery.

Year	Seine Fisheries					Gillnet Fisheries				
Year	QCI	PRD	CC	SOG	WCVI	QCI	PRD	CC	SOG	WCVI
2000	0.077	0.116	0.266	0.260	0.266	-	0.069	0.261	0.164	0.081
2001	-	0.071	0.392	0.280	-	-	0.108	0.346	0.280	-
2002	0.140	0.100	0.328	0.355	0.395	-	0.369	0.173	0.341	0.106
2003	-	0.132	0.488	0.231	0.374	-	0.134	0.215	0.231	0.042
2004	-	0.069	0.395	0.206	0.418	-	0.201	-	0.232	0.142
2005	-	0.198	0.284	0.244	0.374	-	0.243	-	0.230	0.306
2006	-	0.257	0.198	0.324	-	-	0.159	-	0.266	-

Table 4. Number of tag recoveries by release group, years at liberty and recovery fishery.

Release				Recovery Fishery								
ID	Region	Year	Years at liberty	QCI Sn	PRD Sn	PRD Gn	CC Sn	CC Gn	SoG Sn	SoG Gn	WCVI Sn	WCVI Gn
1	QCI	1999	1	4	0	0	0	1	0	0	0	0
1	QCI	1999	2	0	0	0	0	0	0	0	0	0
1	QCI	1999	3	1	0	0	0	0	0	0	0	0
1	QCI	1999	4	0	0	0	0	0	0	0	0	0
1	QCI	1999	5	0	0	0	0	0	0	0	0	0
1	QCI	1999	6	0	0	0	0	0	0	0	0	0
1	QCI	1999	7	0	0	0	0	0	0	0	0	0
2	PRD	2001	1	0	48	109	1	0	0	0	0	0
2	PRD	2001	2	0	31	73	9	1	0	0	0	0
2	PRD	2001	3	0	13	94	3	0	0	0	0	0
2	PRD	2001	4	0	26	53	0	0	0	0	0	0
2	PRD	2001	5	0	2	19	0	0	0	0	0	0
3	PRD	2002	1	0	60	82	10	0	0	0	0	0
3	PRD	2002	2	0	30	147	6	0	0	0	1	0
3	PRD	2002	3	0	38	126	1	0	0	1	0	0
3	PRD	2002	4	0	12	43	2	0	0	0	0	0
4	PRD	2003	1	0	82	19	9	0	0	0	0	0
4	PRD	2003	2	0	174	24	5	0	0	1	2	0
4	PRD	2003	3	0	62	13	7	0	0	1	0	0
5	CC	2002	1	0	0	0	238	7	0	3	0	0
5	CC	2002	2	0	2	1	155	0	1	2	0	0
5	CC	2002	3	0	0	0	54	0	1	0	0	0
5	CC	2002	4	0	1	0	8	0	0	0	0	0
6	CC	2003	1	0	1	0	435	0	1	2	0	0
6	CC	2003	2	0	2	0	170	0	0	1	1	0
6	CC	2003	3	0	3	0	33	0	2	2	0	0
7	CC	2004	1	0	8	1	977	0	6	2	1	0
7	CC	2004	2	0	1	2	233	0	5	0	0	0
8	SoG	1999	1	0	0	0	0	0	75	45	2	0
8	SoG	1999	2	0	0	0	0	0	32	67	0	0
8	SoG	1999	3	0	0	0	0	0	14	52	0	1
8	SoG	1999	4	0	0	0	0	0	2	9	1	0
8	SoG	1999	5	0	0	0	0	0	1	3	0	0
8	SoG	1999	7	0	0	0	0	0	0	1	0	0
8	SoG	1999	6	0	0	0	0	0	0	0	0	0
9	SoG	2000	1	0	0	0	1	0	137	199	0	0
9	SoG	2000	2	0	0	0	0	0	98	199	0	0
9	SoG	2000	3	0	0	0	0	0	23	66	5	0
9	SoG	2000	4	0	0	0	1	0	6	27	0	0
9	SoG	2000	5	0	0	0	0	0	0	6	0	0
9	SoG	2000	6	0	0	0	0	0	0	3	0	0
10	SoG	2001	1	0	0	0	2	0	123	74	0	0
10	SoG	2001	2	0	0	0	0	0	26	38	0	0
10	SoG	2001	3	0	0	0	1	0	8	25	0	0
10	SoG	2001	4	0	0	0	1	0	8	17	0	0
10	SoG	2001	5	0	0	0	0	0	2	7	0	0
11	SoG	2002	1	0	0	0	0	0	69	39	2	0
11	SoG	2002	2	0	0	0	0	0	22	34	2	0
11	SoG	2002	3	0	0	0	1	0	3	32	1	0
11	SoG	2002	4	0	0	0	0	0	6	11	0	0
12	SoG	2003	1	0	0	0	0	0	26	8	5	0
12	SoG	2003	2	0	0	0	1	0	10	17	0	0
12	SoG	2003	3	0	0	0	0	0	13	17	0	0
13	WCVI	2004	1	0	1	0	0	0	3	6	185	39
13	WCVI	2004	2	0	0	0	0	0	4	7	0	0

Table 5. Summary statistics and parameter estimates for the initial runs of the multi-stock HCAM model conducted to develop a base case model. Values presented are: components of the negative log-likelihood function and total objective function value (OBFval); the number of parameters estimated (NPAR); MAR and SDNR statistics for components of the likelihood; and estimated and derived parameter values (B_0), average natural mortality (avM), steepness, q_{early} and q_{late} , and depletion).

		2008Assess	*2008Assess -a*	*2008Assses -b*	*2008Assess -c*	*2008Asess -d (base)*
OBFval	Total	2540.6	2399.1	2398.4	2462.4	2471.9
	NPAR	1143	1143	1143	1156	1156
Likelihoods	spawn	-79.3	-79.3	-79.2	-72.7	-68.5
	age-comp	2411.9	2270.2	2269.7	2323.3	2336.9
	catch	9.2	9.2	9.2	9.3	0.0
	Priors	198.8	199.1	198.6	202.6	203.5
MARs	spawn	0.26	0.26	0.26	0.27	0.27
	age-comp	0.65	0.65	0.65	0.65	0.65
	tot catch	0.04	0.04	0.04	0.04	0.00
SDNRs	spawn	0.43	0.43	0.43	0.43	0.44
	age-comp	1.45	1.29	1.29	1.29	1.29
	tot catch	0.20	0.20	0.20	0.19	0.01
B0	QCI	29	29	29	29	29
	PRD	68	68	68	68	69
	CC	58	58	58	58	58
	SoG	178	176	178	178	178
	WCVI	61	61	61	62	62
av M	QCI	0.45	0.45	0.45	0.45	0.45
	PRD	0.35	0.35	0.35	0.35	0.35
	CC	0.40	0.40	0.40	0.40	0.41
	SoG	0.42	0.42	0.42	0.42	0.42
	WCVI	0.48	0.49	0.49	0.48	0.48
Steepness	QCI	0.76	0.76	0.76	0.74	0.74
	PRD	0.67	0.67	0.67	0.67	0.67
	CC	0.86	0.86	0.86	0.86	0.86
	SoG	0.71	0.71	0.70	0.70	0.70
	WCVI	0.72	0.71	0.71	0.69	0.68
q- early	QCI	0.27	0.27	0.27	0.27	0.26
	PRD	0.51	0.51	0.51	0.51	0.51
	CC	0.28	0.28	0.28	0.27	0.27
	SoG	1.03	1.01	1.01	1.01	1.00
	WCVI	0.64	0.63	0.63	0.64	0.63
q-late	QCI	1	1	1	1	1
	PRD	1	1	1	1	1
	CC	1	1	1	1	1
	SoG	1	1	1	1	1
	WCVI	1	1	1	1	1
B>B0	QCI	0.28	0.28	0.27	0.37	0.27
	PRD	0.10	0.10	0.09	0.12	0.09
	CC	0.03	0.03	0.00	0.13	0.01
	SoG	0.01	0.01	0.00	0.00	0.00
	WCVI	0.04	0.04	0.03	0.18	0.03
Depletion	QCI	0.17	0.17	0.17	0.15	0.15
	PRD	0.25	0.25	0.26	0.27	0.27
	CC	0.11	0.11	0.11	0.11	0.11
	SoG	0.19	0.17	0.17	0.17	0.17
	WCVI	0.04	0.04	0.04	0.04	0.04

Table 6. Age-composition samples (pre-fishery charter) with no associated catch.

Pre-2000		2000 onward	
Region	Year	Region	Year
QCI	1995	QCI	2001
QCI	1996	QCI	2003
QCI	1997	QCI	2004
PRD	1983	QCI	2005
PRD	1996	QCI	2006
PRD	1997	QCI	2007
PRD	1998	QCI	2008
CC	1980	PRD	2007
SoG	1979	CC	2008
SoG	1990	WCVI	2001
		WCVI	2006
		WCVI	2007
		WCVI	2008

Table 7. Summary of differences in HCAM model structure for alternative models explored. M parameterizations include: random walk (R-walk); constant M (ConstM); density-dependent M applied to all age-classes (ddM-1); density-dependent M applied to age-classes 3 and older. SR parameterizations include: Beverton-Holt (BH); an alternative form of Beverton-Holt (ABH); and Ricker (R). Movement options include: movement parameters only estimated between regions with tag recoveries (minMove); or movement estimated among all regions (allMove).

	Form of parameterization			Number of parameters			Tag detection efficiency
Name of model run	M	SR	Movement	Mdd	steep	*q* (per stock)	
Exploring density-dependent M							
Base	R-walk	BH	-	-	5	1	-
Base-ConstM	ConstM	BH	-	-	5	1	-
Base-2q	R-walk	BH	-	-	5	2	-
Mdd-BH1-5h	ddM-1	BH	-	5	5	1	-
Mdd-BH2-5h	ddM-2	BH	-	5	5	1	-
Mdd-BH1	ddM-1	BH	-	1	1	1	-
Mdd-BH2	ddM-2	BH	-	1	1	1	-
Mdd-ABH1	ddM-1	ABH	-	1	1	1	-
Mdd-ABH2	ddM-2	ABH	-	1	1	1	-
MDD-R1	ddM-1	R	-	1	1	1	-
MDD-R2	ddM-2	R	-	1	1	1	-
Exploring tag model							
BaseT-minMove	R-walk	BH	minMove	-	5	1	1
BaseT	R-walk	BH	allMove	-	5	1	1
BaseT-0.7Eff	R-walk	BH	allMove	-	5	1	0.7
BaseT-2q	R-walk	BH	allMove	-	5	2	1
BaseT-6Area	R-walk	BH	allMove	-	6	1	1
MddT-R2	ddM-1	R	allMove	1		1	1

Table 8. Summary statistics and parameter estimates for the density-dependent natural mortality runs of the multi-stock HCAM model. Values are: negative log-likelihood components and total objective function value (OBFval); the number of parameters estimated (NPAR); MAR and SDNR statistics for components of the likelihood; and estimated and derived parameter values (B0), average natural mortality (avM), steepness, q_{early} and q_{late}, and depletion). Model runs are described in Table 7. [1]-values for the 5 stocks.

		Base	Base-ConstM	Base-2q	Mdd-BH1-5h	Mdd-BH2-5h	Mdd-BH1	Mdd-BH2	Mdd-ABH1	Mdd-ABH2	Mdd-R1	Mdd-R2
OBFval	total	2471.9	2762.1	2393.3	2553.2	2470.1	2558.6	2481.4	2515.8	2548.8	2580.1	2531.3
	NPAR	1156	866	1156	871	871	863	863	863	863	863	863
Likelihoods	spawn	-68.5	60.4	-102.6	-58.2	-81.0	-59.0	-81.1	-60.7	-59.1	-49.5	-64.6
	age-comp	2336.9	2537.7	2310.2	2438.2	2435.0	2437.6	2434.5	2435.9	2468.4	2448.2	2457.1
	catch	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.1	0.0	0.0	0.0
	Priors	203.5	164.0	185.7	173.2	116.1	180.0	127.9	140.6	139.5	181.3	138.7
MARs	spawn	0.27	0.33	0.26	0.28	0.25	0.27	0.24	0.29	0.29	0.29	0.27
	age-comp	0.65	0.66	0.65	0.65	0.65	0.65	0.65	0.65	0.65	0.66	0.65
	tot catch	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	tags	0.00	0	0	0	0	0	0	0	0	0	0
SDNRs	spawn	0.44	0.53	0.41	0.45	0.43	0.45	0.43	0.44	0.44	0.45	0.44
	age-comp	1.29	1.35	1.28	1.34	1.34	1.34	1.33	1.34	1.35	1.33	1.34
	tot catch	0.01	0.02	0.01	0.01	0.01	0.01	0.01	0.02	0.01	0.01	0.01
B0	QCI	29	54	50	25	18	26	33	49	42	43	40
	PRD	69	76	101	161	13	203	8	96	72	65	41
	CC	58	75	72	2	8	5	8	61	53	51	38
	SoG	178	184	225	436	320	561	705	234	225	198	183
	WCVI	62	91	66	68	42	72	59	108	86	72	65
av M	QCI	0.45	0.50	0.52	0.48	0.48	0.48	0.47	0.46	0.45	0.48	0.46
	PRD	0.35	0.32	0.47	0.32	0.38	0.32	0.40	0.35	0.34	0.34	0.36
	CC	0.41	0.36	0.49	0.39	0.44	0.40	0.44	0.41	0.40	0.40	0.40
	SoG	0.42	0.48	0.53	0.49	0.48	0.49	0.46	0.50	0.48	0.50	0.49
	WCVI	0.48	0.45	0.50	0.47	0.47	0.47	0.46	0.46	0.44	0.47	0.46
Steepness	QCI	0.74	0.51	0.75	1.00	0.79						
	PRD	0.67	0.77	0.58	0.98	0.55						
	CC	0.86	0.79	0.85	0.38	0.83	0.97	0.88	-	-	1.30	0.99
	SoG	0.70	0.68	0.61	0.93	0.86						
	WCVI	0.68	0.58	0.69	1.00	0.81						
Mdd					0.87, 0.78, 0.57, 0.71, 0.89[1]	0.79, 1.75, 1.88, 0.74, 0.94[1]	0.91	1.19	1.99	1.46	1.04	1.24
q- early	QCI	0.26	0.15	0.17	0.34	0.37	0.34	0.37	0.39	0.37	0.31	0.35
	PRD	0.51	0.54	0.31	0.53	0.56	0.53	0.58	0.49	0.48	0.50	0.49
	CC	0.27	0.30	0.19	0.35	0.40	0.35	0.37	0.31	0.31	0.31	0.32
	SoG	1.00	0.73	0.66	0.69	0.69	0.69	0.69	0.65	0.68	0.64	0.64
	WCVI	0.63	0.56	0.57	0.75	0.81	0.74	0.81	0.84	0.82	0.74	0.80
q-late	QCI	1	1	0.25	1	1	1	1	1	1	1	1
	PRD	1	1	0.32	1	1	1	1	1	1	1	1
	CC	1	1	0.44	1	1	1	1	1	1	1	1
	SoG	1	1	0.44	1	1	1	1	1	1	1	1
	WCVI	1	1	0.76	1	1	1	1	1	1	1	1
B>B0	QCI	0.27	0.18	0.18	0.33	0.51	0.33	0.30	0.04	0.15	0.10	0.21
	PRD	0.09	0.06	0.04	0.00	0.88	0.00	0.91	0.00	0.07	0.09	0.30
	CC	0.01	0.00	0.01	0.94	0.90	0.88	0.88	0.03	0.24	0.13	0.45
	SoG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	WCVI	0.03	0.09	0.03	0.10	0.40	0.06	0.15	0.01	0.04	0.06	0.13
Depletion	QCI	0.15	0.21	0.34	0.17	0.22	0.16	0.12	0.10	0.12	0.10	0.10
	PRD	0.27	0.38	0.47	0.16	1.28	0.13	2.06	0.22	0.29	0.32	0.43
	CC	0.11	0.18	0.18	1.66	0.47	0.66	0.45	0.10	0.12	0.12	0.13
	SoG	0.17	0.20	0.24	0.08	0.10	0.06	0.05	0.13	0.14	0.14	0.15
	WCVI	0.04	0.07	0.04	0.05	0.05	0.05	0.03	0.02	0.03	0.04	0.03

Table 9. Change in negative log-likelihood from constant natural mortality run (Base_ConstM) to runs with time-variant natural mortality by stock and likelihood component.

		Difference in negative ln-likelihood from Base_Const M run			
Stock	Likelihood component	Base	Mdd-_BH1-5h	Mdd-_ABH1	Mdd-_R2
QCI	Total	-82.0	-75.2	-81.6	-73.2
	Spawn	-33.2	-28.3	-24.6	-27.4
	Age-comp	-48.8	-47.0	-57.0	-45.7
PRD	Total	-76.6	-26.3	-4.9	-9.8
	Spawn	1.8	-7.6	-0.7	-1.2
	Age-comp	-78.4	-18.7	-4.2	-8.6
CC	Total	-61.0	-73.4	-60.3	-55.0
	Spawn	-34.6	-47.8	-36.6	-36.9
	Age-comp	-26.4	-25.6	-23.7	-18.1
SoG	Total	-41.2	-4.3	-11.9	-2.7
	Spawn	-10.3	-5.4	-7.4	-6.8
	Age-comp	-30.9	1.1	-4.5	4.1
WCVI	Total	-68.8	-65.1	-64.2	-64.8
	Spawn	-52.6	-52.5	-51.8	-52.7
	Age-comp	-16.2	-12.6	-12.4	-12.2

Table 10. Parameter correlations for run Mdd_R2. Correlations more extreme than ±0.5 are highlighted.

		M					steep	Ln_B0					M_dd	q				
		QCI	PRD	CC	SoG	WCVI	All	QCI	PRD	CC	SoG	WCVI	ALL	QCI	PRD	CC	SoG	WCVI
M	QCI	1																
	PRD	0.03	1															
	CC	0.10	0.08	1														
	SoG	0.14	0.06	0.08	1													
	WCVI	0.37	0.05	0.10	0.12	1												
steep	All	-0.38	-0.26	-0.30	-0.26	-0.36	1											
Ln_B0	QCI	-0.69	-0.03	-0.05	-0.06	-0.14	0.18	1										
	PRD	0.04	-0.72	-0.06	-0.03	0.01	0.18	0.00	1									
	CC	0.02	-0.07	-0.64	-0.04	0.00	0.19	0.00	0.06	1								
	SoG	-0.01	-0.04	-0.04	-0.89	-0.02	0.14	0.01	0.04	0.04	1							
	WCVI	-0.16	-0.03	-0.05	-0.06	-0.72	0.19	0.06	0.00	0.01	0.01	1						
M_dd	ALL	-0.67	-0.01	-0.10	-0.17	-0.54	0.44	0.24	-0.09	-0.07	-0.01	0.22	1					
q	QCI	0.03	0.00	-0.02	-0.04	-0.11	0.10	-0.66	-0.02	-0.01	0.00	0.05	0.21	1				
	PRD	-0.03	-0.39	-0.02	-0.02	-0.03	0.08	0.02	-0.31	0.01	0.01	0.02	0.04	0.01	1			
	CC	-0.12	-0.01	-0.27	-0.04	-0.10	0.10	0.04	-0.01	-0.50	0.00	0.04	0.17	0.04	0.01	1		
	SoG	0.03	-0.03	-0.03	-0.21	0.02	0.08	-0.01	0.03	0.03	-0.17	0.00	-0.06	-0.01	0.01	-0.01	1	
	WCVI	-0.09	-0.02	-0.03	-0.03	-0.05	0.10	0.04	0.00	0.00	0.01	-0.55	0.13	0.03	0.01	0.02	0.00	1

Table 11. Summary statistics and parameter estimates for the runs of the multi-stock HCAM model that include tagging data. Values are: negative log-likelihood components and total objective function value (OBFval); the number of parameters estimated (NPAR); MAR and SDNR statistics for components of the likelihood; and estimated and derived parameter values (B0), average natural mortality (avM), steepness, q_{early} and q_{late}, and depletion). Model runs are described in Table 7. [1] -values for the 2 PRD stocks.

		Base	BaseT-minMove	BaseT	BaseT-0.7Eff	BaseT-2q	BaseT-6Area	MddT-R1	MddT-R2
OBFval	total	2471.9	-19685.1	-19709.6	-19709.6	-19738.8	-19412.9	-19621.2	-19676.8
	NPAR	1156	1180	1189	1189	1189	1364	896	896
Likelihoods	spawn	-68.5	-71.3	-71.4	-71.4	-92.9	-38.7	-58.4	-79.2
	age-comp	2336.9	2341.5	2314.2	2314.2	2310.0	2311.0	2405.6	2405.2
	catch	0.0	0.8	0.8	0.8	0.8	0.4	0.8	0.8
	tags	-	-22178.3	-22180.2	-22180.2	-22172.8	-21979.5	-22186.0	-22178.3
	Priors	203.5	222.2	226.9	226.9	216.2	294.0	216.8	174.6
MARs	spawn	0.27	0.27	0.27	0.27	0.27	0.30	0.27	0.25
	age-comp	0.65	0.64	0.64	0.64	0.64	0.63	0.65	0.65
	tot catch	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	tags	-	0.41	0.41	0.41	0.42	0.34	0.41	0.41
SDNRs	spawn	0.44	0.44	0.44	0.44	0.42	0.47	0.45	0.43
	age-comp	1.29	1.29	1.28	1.28	1.27	1.22	1.31	1.31
	tot catch	0.01	0.06	0.06	0.06	0.06	0.04	0.06	0.06
	tags	-	1.72	1.68	1.68	1.69	1.16	1.68	1.68
B0	QCI	29	31	33	33	46	43	51	41
	PRD	69	57	44	44	46	31, 8[1]	55	32
	CC	58	53	55	55	63	57	47	36
	SoG	178	140	141	141	155	141	160	149
	WCVI	62	77	69	69	70	68	79	60
av M	QCI	0.45	0.44	0.43	0.43	0.50	0.38	0.46	0.46
	PRD	0.35	0.30	0.31	0.31	0.30	0.38, 0.43[1]	0.30	0.31
	CC	0.41	0.43	0.42	0.42	0.48	0.42	0.41	0.40
	SoG	0.42	0.43	0.43	0.43	0.47	0.43	0.50	0.49
	WCVI	0.48	0.43	0.46	0.46	0.49	0.46	0.44	0.44
Steepness	QCI	0.74	0.74	0.76	0.76	0.76	0.79		
	PRD	0.67	0.66	0.71	0.71	0.71	0.78, 0.80[1]		
	CC	0.86	0.85	0.86	0.86	0.86	0.86	1.30	1.00
	SoG	0.70	0.72	0.72	0.72	0.68	0.72		
	WCVI	0.68	0.72	0.71	0.71	0.72	0.71		
Mdd								1.08	1.32
q- early	QCI	0.26	0.26	0.26	0.26	0.18	0.24	0.27	0.32
	PRD	0.51	0.63	0.62	0.62	0.63	0.46, 0.28[1]	0.75	0.74
	CC	0.27	0.27	0.26	0.26	0.21	0.26	0.33	0.34
	SoG	1.00	1.16	1.15	1.15	0.99	1.15	0.79	0.75
	WCVI	0.63	0.64	0.63	0.63	0.57	0.63	0.69	0.77
q-late	QCI	1	1	1	1	0.33	1	1	1
	PRD	1	1	1	1	1.11	1, 1[1]	1	1
	CC	1	1	1	1	0.59	1	1	1
	SoG	1	1	1	1	0.71	1	1	1
	WCVI	1	1	1	1	0.75	1	1	1
B>B0	QCI	0.27	0.25	0.22	0.22	0.16	0.18	0.12	0.22
	PRD	0.09	0.10	0.13	0.13	0.12	0.16, 0.63[1]	0.12	0.33
	CC	0.01	0.03	0.03	0.03	0.03	0.03	0.18	0.46
	SoG	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
	WCVI	0.03	0.01	0.01	0.01	0.01	0.03	0.06	0.16
Depletion	QCI	0.15	0.14	0.13	0.13	0.29	0.10	0.09	0.09
	PRD	0.27	0.21	0.27	0.27	0.24	0.38, 0.43[1]	0.20	0.31
	CC	0.11	0.12	0.12	0.12	0.16	0.11	0.12	0.13
	SoG	0.17	0.23	0.22	0.22	0.25	0.22	0.16	0.19
	WCVI	0.04	0.03	0.03	0.03	0.04	0.03	0.05	0.04

Table 12. Estimates of tag survival (tag loss and tag-induced mortalities) by tag release group for model runs *BaseT-minM*, *BaseT*, *BaseT-0.7E*, and *BaseT-2q*.

		Tags	Estimated survival			
Region	Year	Released	*BaseT-minM*	*BaseT*	*BaseT-0.7E*	*BaseT-2q*
QCI	1999	6175	0.091	0.070	0.100	0.116
PRD	2001	88196	0.088	0.088	0.125	0.088
PRD	2002	74661	0.168	0.166	0.237	0.168
PRD	2003	111500	0.086	0.084	0.121	0.085
CC	2002	49195	0.165	0.166	0.237	0.242
CC	2003	79920	0.150	0.153	0.218	0.228
CC	2004	159892	0.183	0.188	0.268	0.275
SoG	1999	43268	0.137	0.137	0.196	0.166
SoG	2000	245694	0.054	0.054	0.077	0.065
SoG	2001	60558	0.092	0.093	0.132	0.111
SoG	2002	83528	0.057	0.057	0.082	0.069
SoG	2003	89247	0.024	0.024	0.035	0.029
WCVI	2004	131811	0.031	0.032	0.046	0.038

Table 13. Movement estimates (proportion moving each year) from model run *BaseT-minMove* (parameters not estimated for cells w/o recoveries). Green highlighted: no recovery opportunity. Yellow highlighted: no recoveries, but recovery opportunity.

	To:				
From:	QCI	PRD	CC	SoG	WCVI
QCI	0.977		0.023		
PRD		0.982	0.016	0.001	0.001
CC		0.009	0.985	0.006	0.000
SoG			0.002	0.986	0.012
WCVI		0.020		0.084	0.896

Table 14. Movement estimates (proportion moving each year) from model run *BaseT* (parameters estimated for all cells). Green highlighted: no recovery opportunity. Yellow highlighted: no recoveries, but recovery opportunity.

	To:				
From:	QCI	PRD	CC	SoG	WCVI
QCI	0.892	0.059	0.029	0.000	0.020
PRD	0.004	0.978	0.016	0.001	0.001
CC	0.022	0.007	0.964	0.006	0.000
SoG	0.000	0.000	0.002	0.985	0.013
WCVI	0.000	0.008	0.000	0.082	0.910

Table 15. Movement estimates (proportion moving each year) from model run *BaseT-6Area*. Green highlighted: no recovery opportunity. Yellow highlighted: no recoveries, but recovery opportunity.

	To:					
From:	QCI	Area 3/4	Area 5	CC	SoG	WCVI
QCI	0.810	0.048	0.095	0.029	0.000	0.017
Area 3/4	0.001	0.913	0.080	0.005	0.000	0.001
Area 5	0.000	0.055	0.929	0.015	0.000	0.001
CC	0.029	0.001	0.008	0.956	0.006	0.000
SoG	0.000	0.000	0.000	0.002	0.985	0.013
WCVI	0.000	0.000	0.001	0.000	0.082	0.917

Table 16. Summary of WCVI tag release and recovery information by statistical area.

2004 Tag releases		2005 Area 25 Tag recoveries	
Area	Number	GN	SN
23	33,608	5	17
24	32,421	11	56
25	38,601	3	4
26	27,181	20	108

Table 17. Summary of PRD tag releases and recoveries from those releases, by Area of release and fishery of recovery

Release		Recovery	
Area	Year	Area 3/4 GN	Area 5 SN
3/4	2001	309	30
3/4	2002	359	15
3/4	2003	14	6
5	2001	39	90
5	2002	39	125
5	2003	42	312

Table 18. Estimates of the q_{late} parameter and their c.v.s for the *Base-2q* model run and the *BaseT-2q* model run which incorporates the tagging data.

	Base-2q		*BaseT-2q*	
Stock	q_{late}	c.v.	q_{late}	c.v
QCI	0.252	0.228	0.328	0.199
PRD	0.315	0.169	1.109	0.078
CC	0.444	0.220	0.593	0.159
SoG	0.439	0.135	0.712	0.097
WCVI	0.761	0.176	0.746	0.154

Table 19. Percentiles of the marginal posterior distribution for some estimated and derived parameter of the HCAM model. Results are from the MddT-R2 model MCMC.

		Percentiles of marginal posterior distribution				
Parameter	Stock(s)	2.5	25	50	75	97.5
B0	QCI	47	49	51	52	56
	PRD	43	45	46	48	57
	CC	41	44	46	47	51
	SoG	138	144	149	160	176
	WCVI	71	75	78	81	88
av M	QCI	0.44	0.46	0.47	0.48	0.49
	PRD	0.28	0.28	0.29	0.29	0.31
	CC	0.38	0.39	0.40	0.41	0.42
	SoG	0.47	0.49	0.49	0.50	0.51
	WCVI	0.42	0.43	0.44	0.44	0.45
Steepness		1.18	1.20	1.23	1.27	1.35
Mdd		1.00	1.03	1.05	1.07	1.10
Depletion	QCI	0.07	0.08	0.09	0.10	0.12
	PRD	0.16	0.19	0.22	0.24	0.30
	CC	0.09	0.11	0.12	0.14	0.17
	SoG	0.12	0.15	0.17	0.19	0.23
	WCVI	0.04	0.05	0.05	0.05	0.07
Recruitment autocorrelation	QCI	0.02	0.06	0.07	0.10	0.13
	PRD	0.19	0.23	0.26	0.29	0.33
	CC	-0.06	-0.02	0.00	0.02	0.05
	SoG	-0.05	0.02	0.05	0.08	0.12
	WCVI	0.36	0.40	0.42	0.44	0.48
Recruitment correlation	QCI-PRD	0.20	0.22	0.24	0.26	0.30
	QCI-CC	0.45	0.49	0.51	0.53	0.56
	QCI-SoG	0.24	0.29	0.32	0.34	0.38
	QCI-WCVI	0.36	0.40	0.42	0.44	0.48
	PRD-CC	0.19	0.24	0.26	0.27	0.31
	PRD-SoG	0.24	0.29	0.31	0.34	0.38
	PRD-WCVI	-0.03	0.02	0.05	0.07	0.11
	CC-SoG	0.43	0.47	0.49	0.51	0.55
	CC-WCVI	0.48	0.51	0.53	0.55	0.58
	SoG-WCVI	0.37	0.42	0.44	0.46	0.50
Stock fidelity	QCI	0.87	0.88	0.89	0.89	0.90
	PRD	0.97	0.97	0.98	0.98	0.98
	CC	0.96	0.97	0.97	0.98	0.99
	SoG	0.98	0.98	0.98	0.99	0.99
	WCVI	0.88	0.89	0.90	0.90	0.91

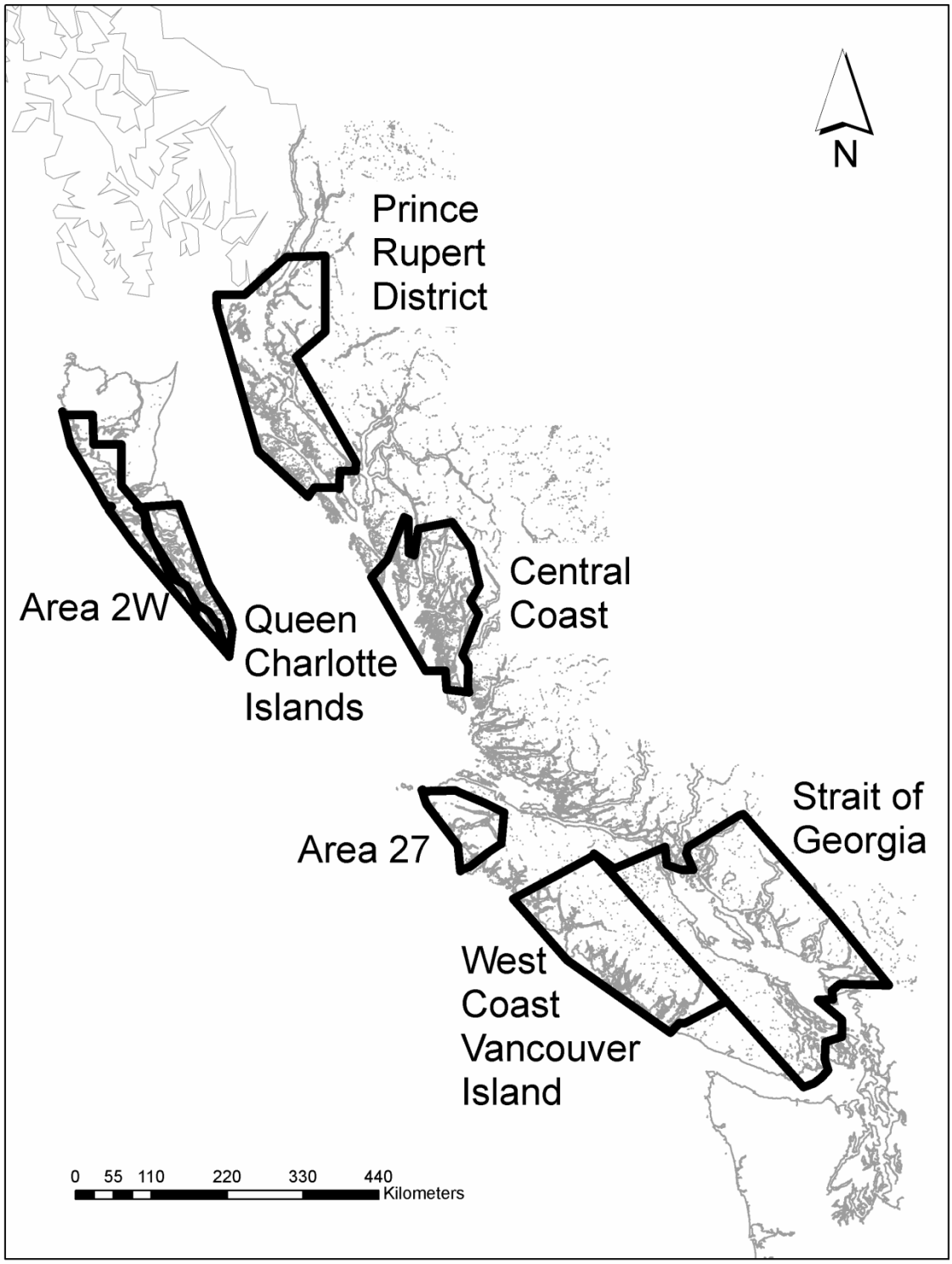

Figure 1. The five major British Columbia herring stock assessment regions: Prince Rupert District (PRD), Queen Charlotte Islands (QCI), Central Coast (CC), west coast Vancouver Island (WCVI), the Strait of Georgia (SoG).

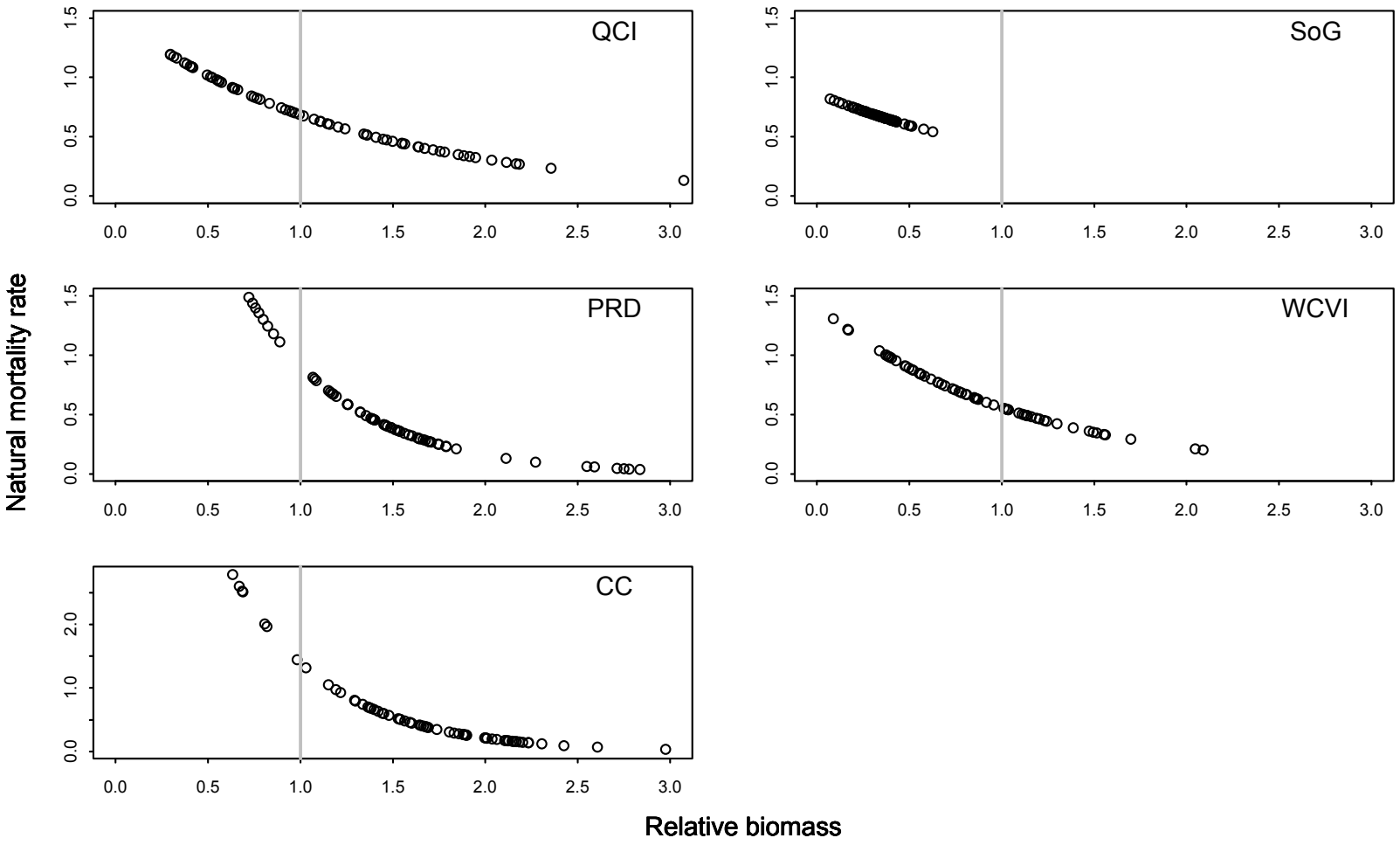

Figure 2. Annual estimates of the natural mortality rate versus biomass relative to the unfished level, for the 5 herring stocks. Results are from the *Mdd-BH1-5h* model run. The vertical line is drawn at B_0.

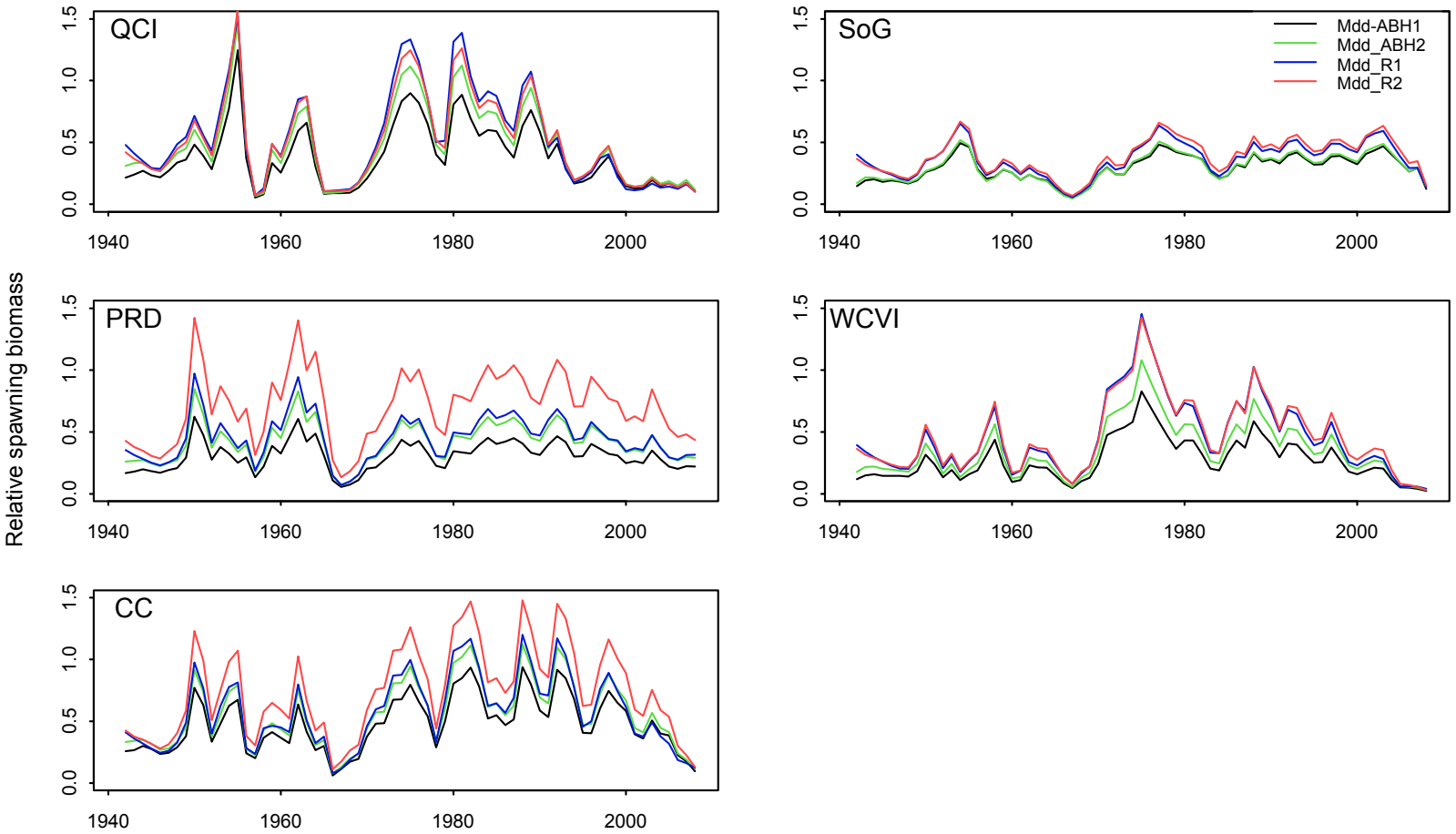

Figure 3. Relative spawning stock biomass (relative to B_0) estimates from 4 alternative density-dependent natural mortality runs for the 5 herring stock assessment regions.

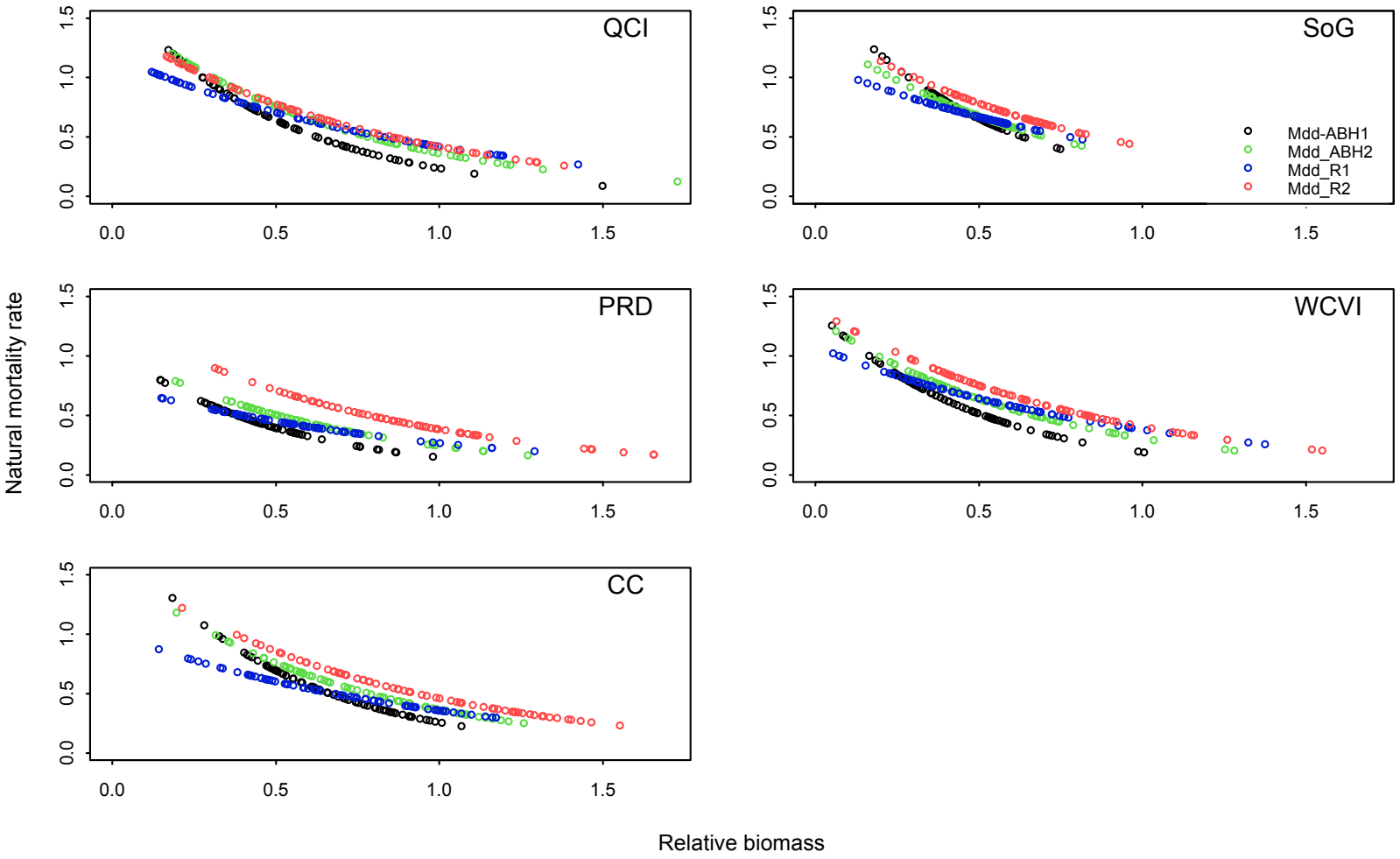

Figure 4. Estimates of natural mortality rates versus relative biomass (relative to B_0) from 4 alternative density-dependent natural mortality runs for the 5 herring stock assessment regions.

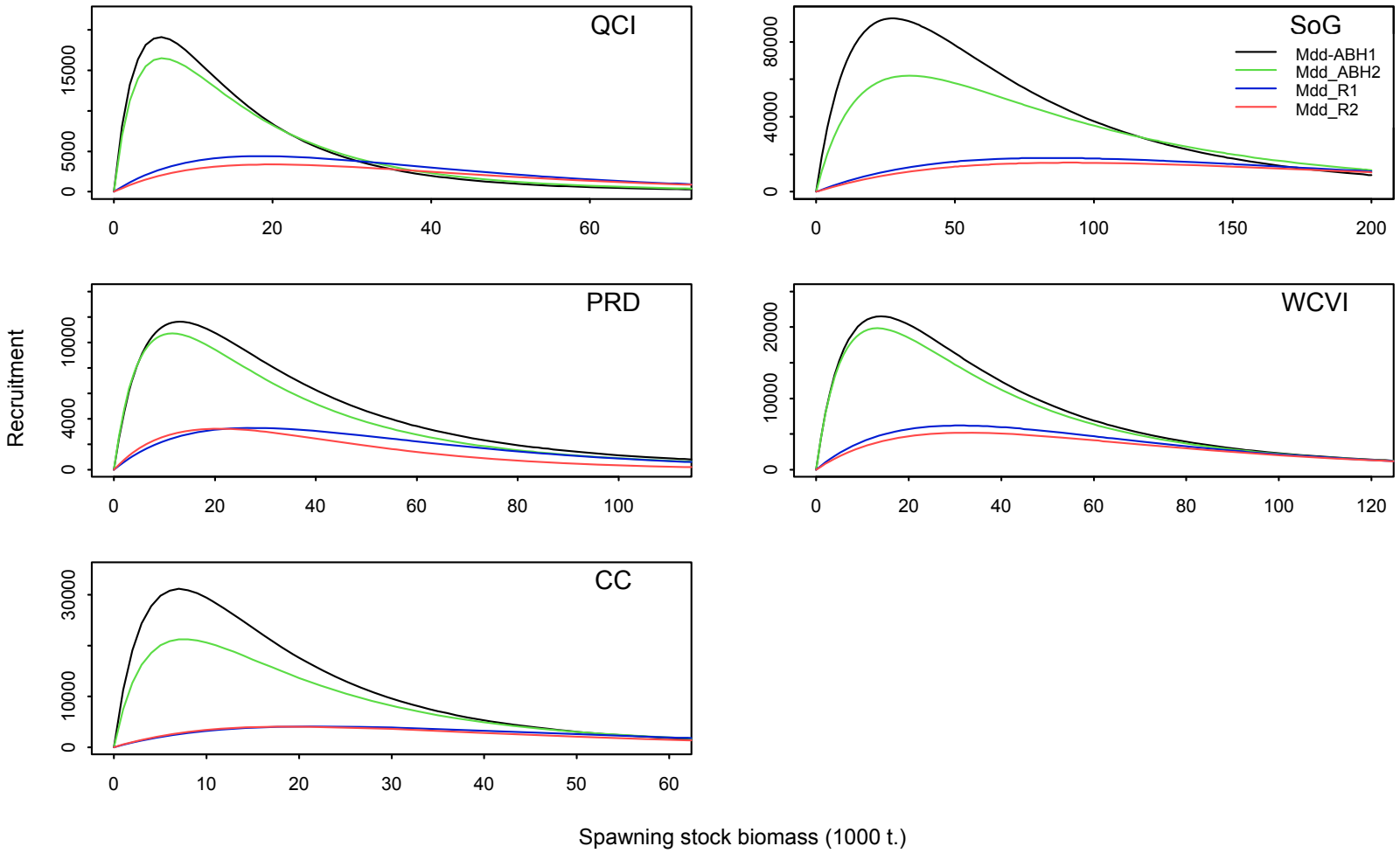

Figure 5. Stock-recruitment relationship estimates from 4 alternative density-dependent natural mortality runs for the 5 herring stock assessment regions. The ABH lines are based on the assumption that beginning year biomass is proportional to spawning stock biomass, which is not the case.

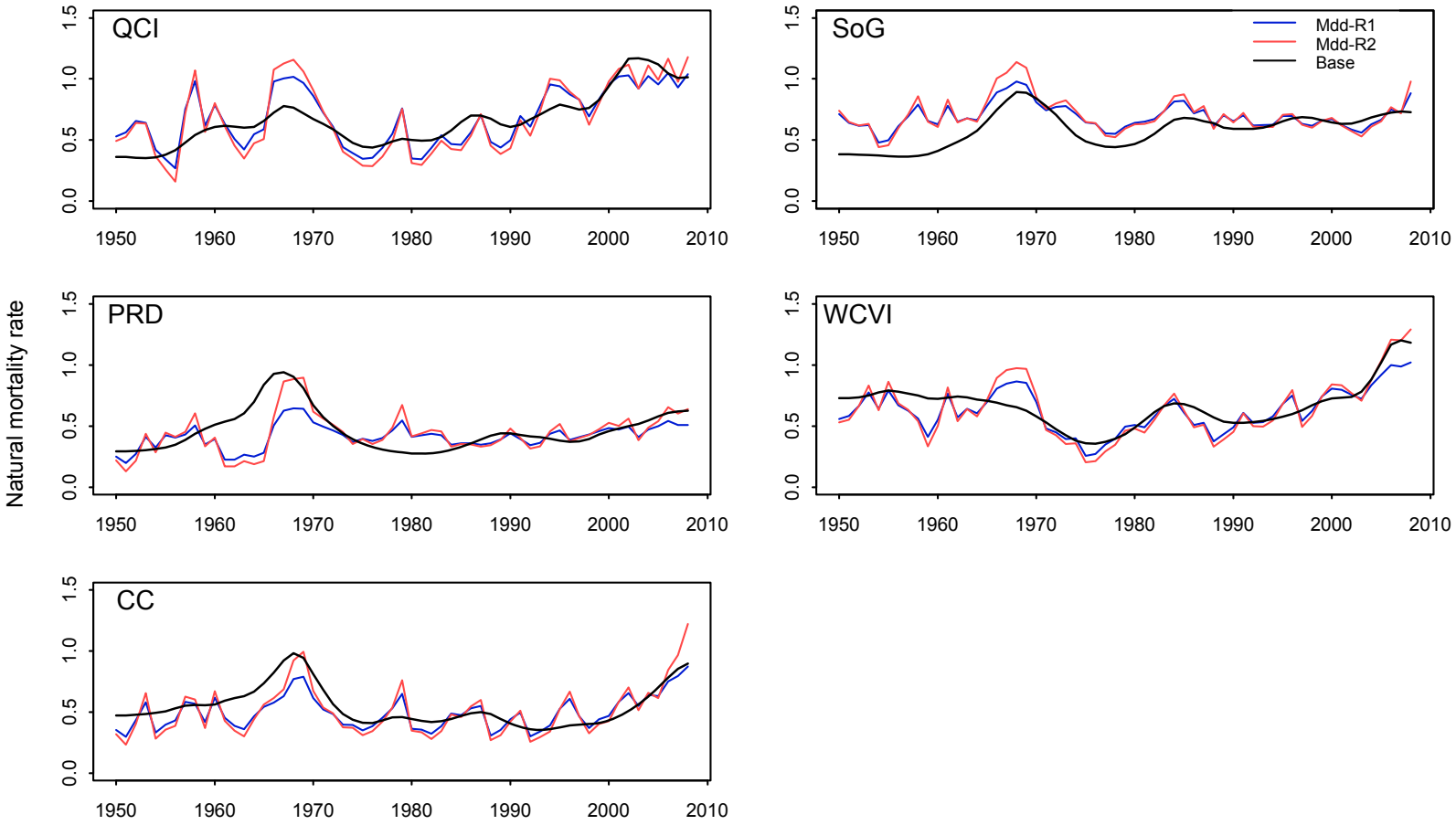

Figure 6. Comparison of natural mortality rate estimates from 2 alternative formulations of density-dependent natural mortality (*Mdd-R1* and *Mdd-R2*) and the *Base* model run for the 5 herring stock assessment regions.

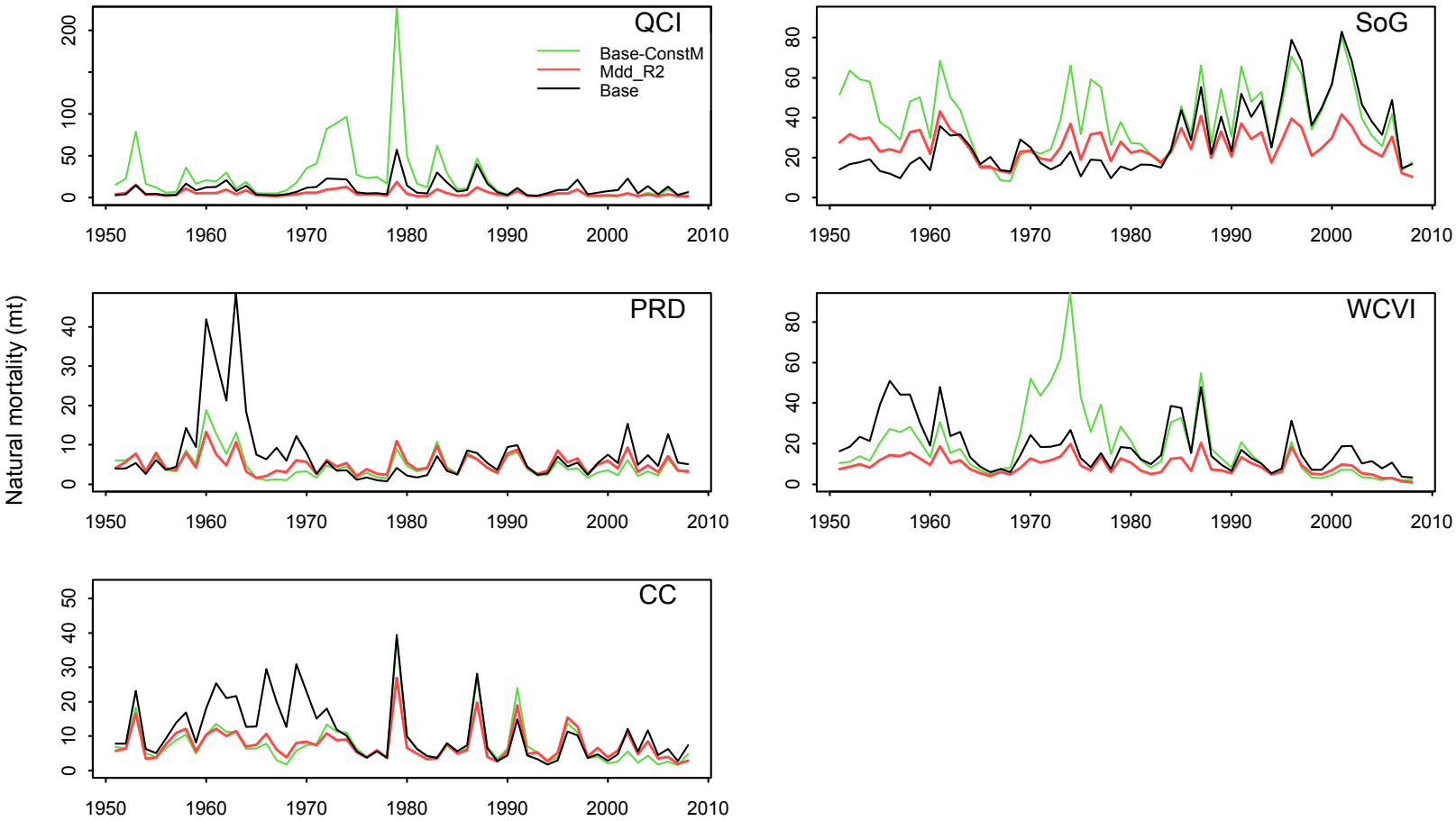

Figure 7. Comparison of natural mortality estimates (in metric tonnes) from the *Base* model run, the Base model run with constant mortality (*Base-ConstM*) and a density-dependent natural mortality model run (*Mdd-R2*) for the 5 herring stock assessment regions.

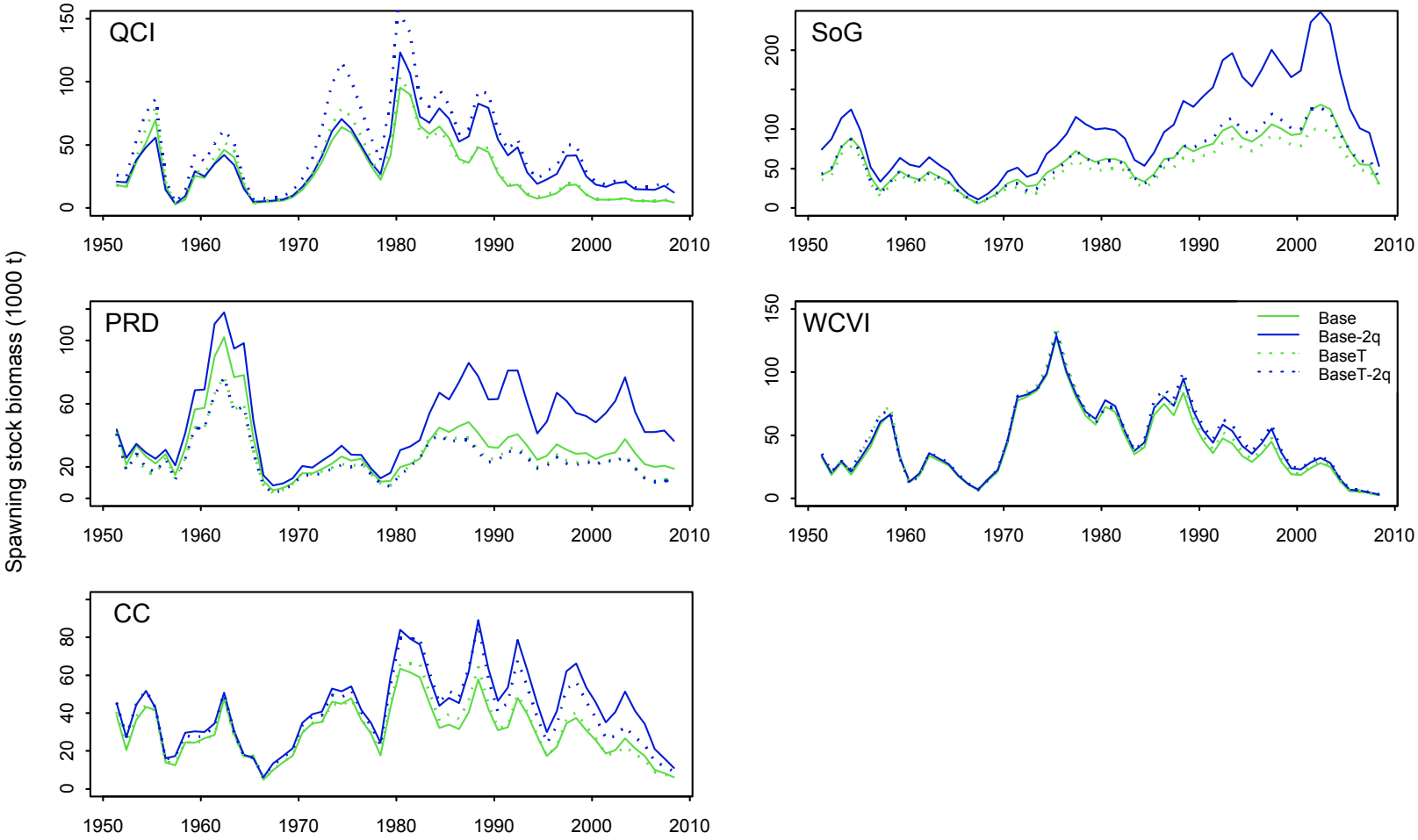

Figure 8. Spawning stock biomass estimates (1000 t) for model runs with (*BaseT* and *BaseT- 2q*) and without (*Base* and *Base-2q*) tagging data and with and without a second, post 1988 spawn conversion *q* parameter for the 5 BC herring stocks.

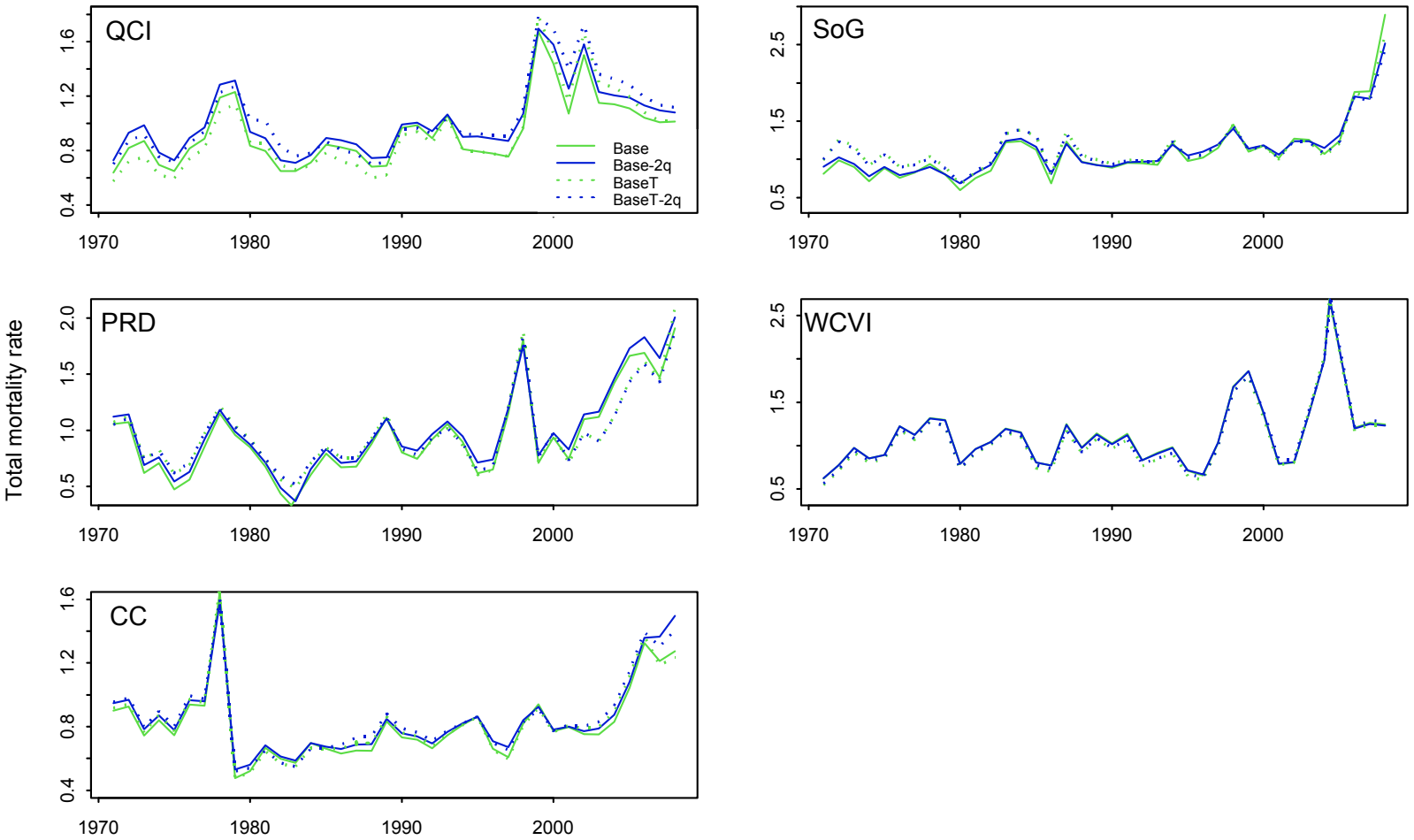

Figure 9. Total mortality rate estimates for model runs with (*BaseT* and *BaseT- 2q*) and without (*Base* and *Base-2q*) tagging data and with and without a second, post 1988 spawn conversion *q* parameter for the 5 BC herring stocks.

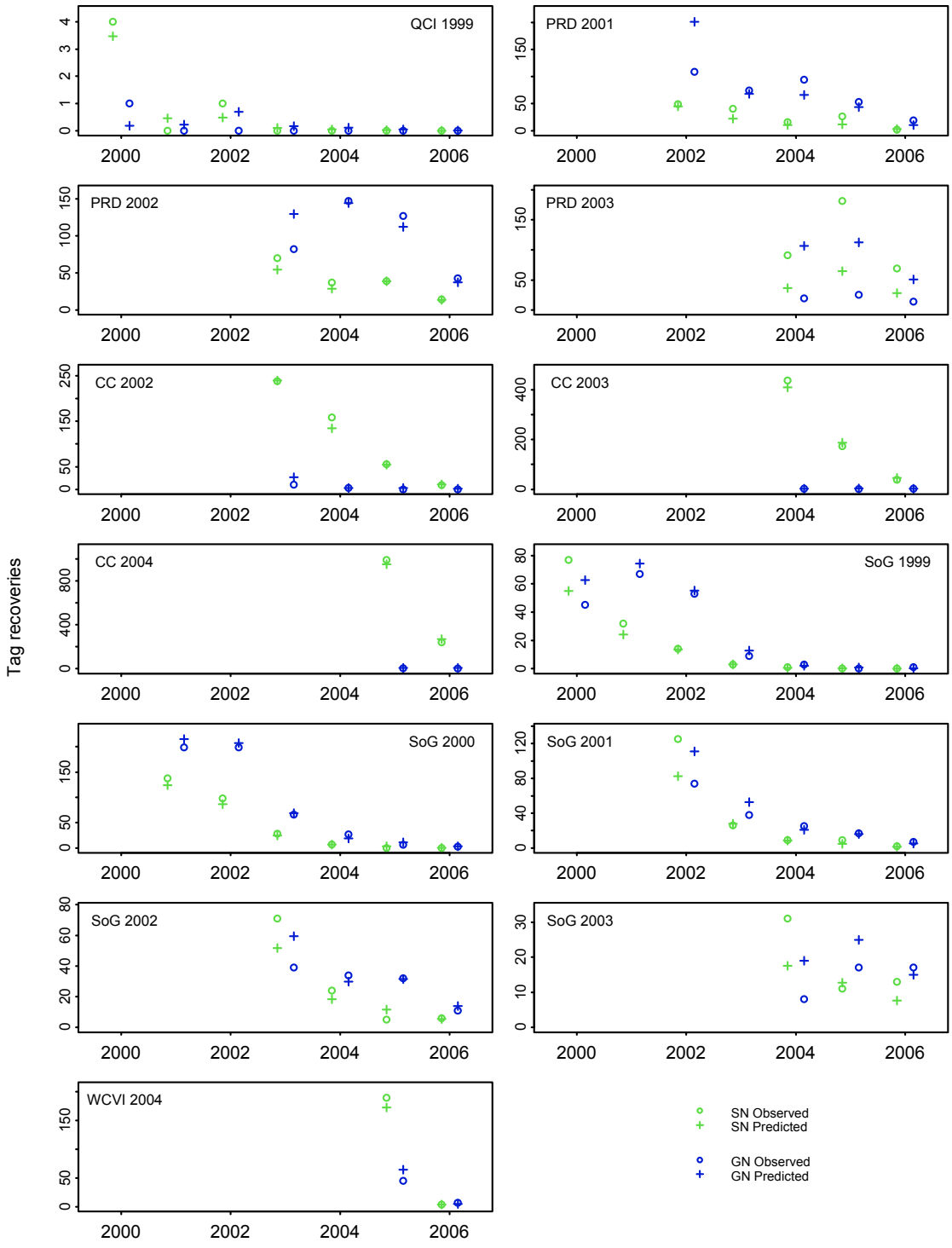

Figure 10. Predicted and observed tag recoveries by tag release group and fishery (SN and GN) and year of recovery for the *BaseT* model run.

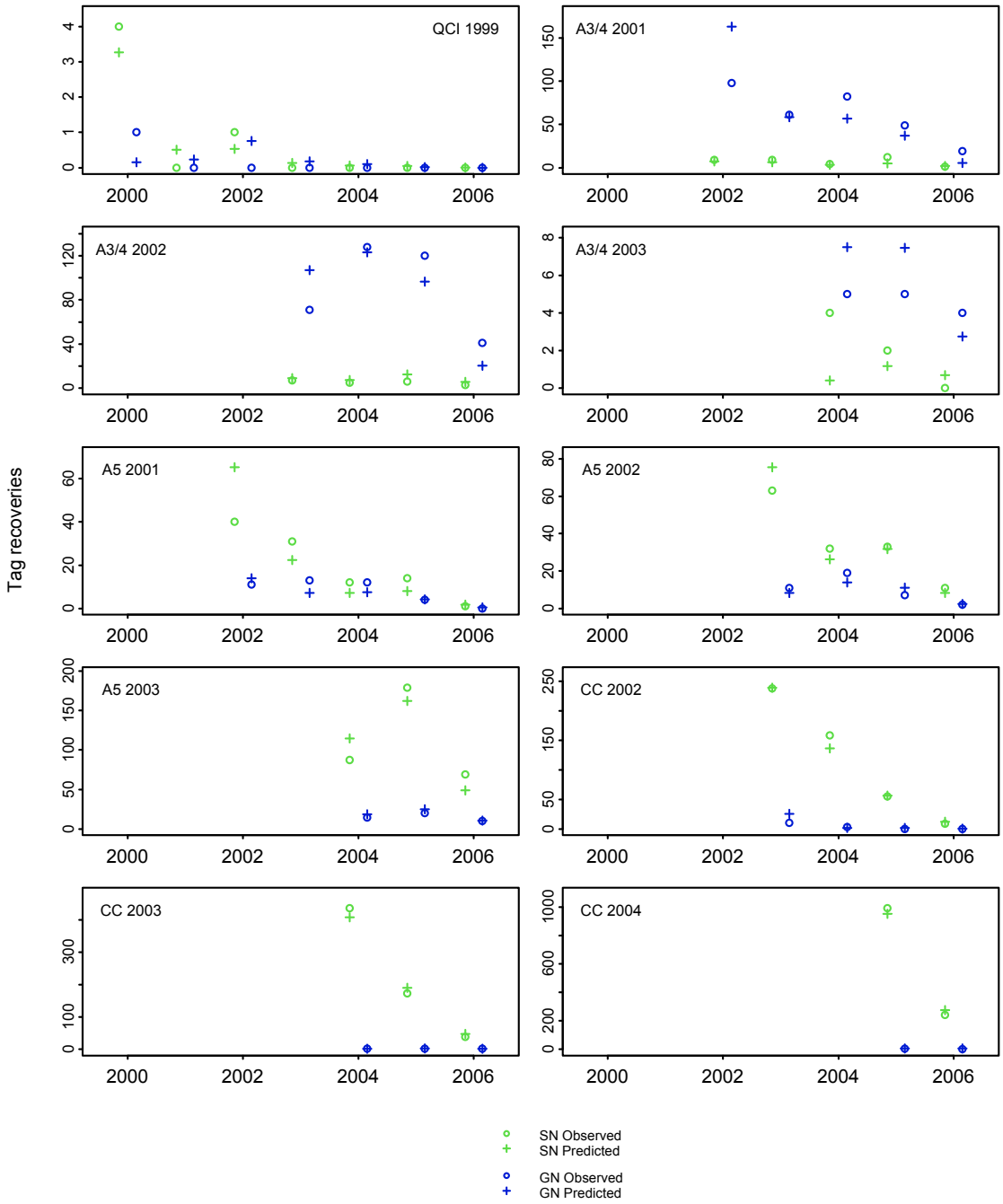

Figure 11. Predicted and observed tag recoveries by tag release group and fishery (SN and GN) and year of recovery for the *BaseT-6area* model run.

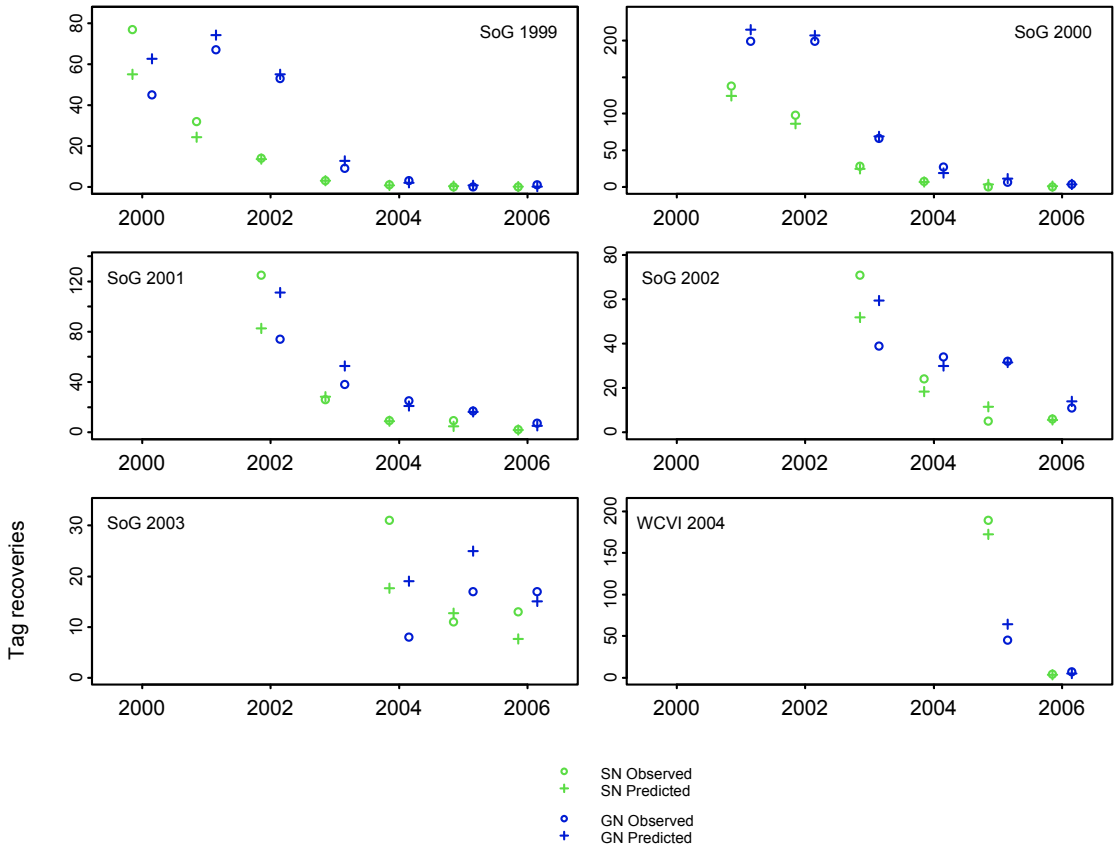

Figure 12. Predicted and observed tag recoveries by tag release group and fishery (SN and GN) and year of recovery for the *BaseT-6area* model run.

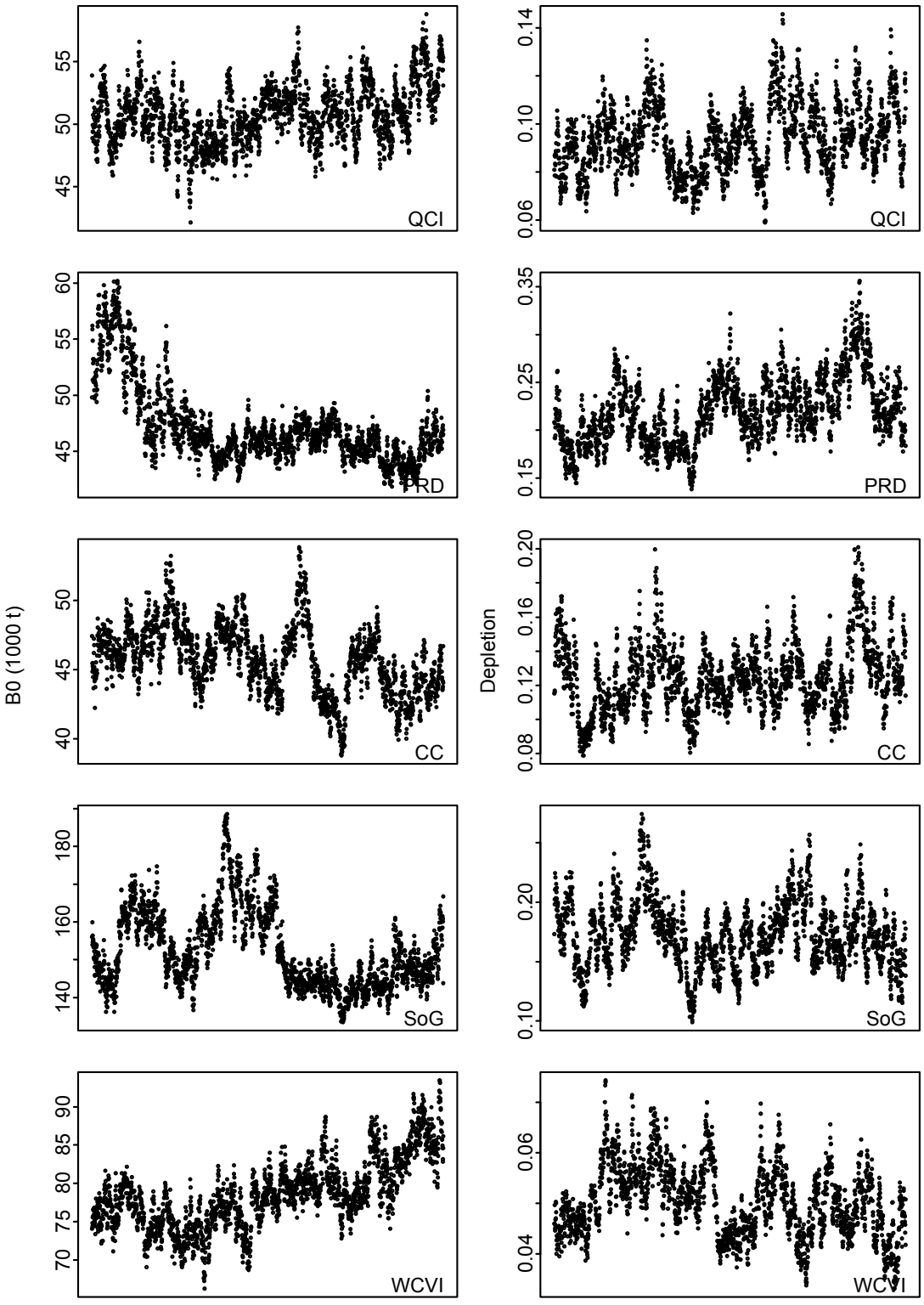

Figure 13. Trace plots of B_0 (1000 t) and stock depletion from the *MddT-R1* model MCMC. The MCMC chain was 5 million, which was thinned to a sample of 2000.

Appendix I – Description of the generic herring catch-age model (HCAM).

The version of the herring catch-age model described here partitions the populations by region, year, fishing period, and age. Only options that are used in the current analyses are described.

The following table describes model parameters:

Parameter	Description
Derived parameters	
$N^r_{i,j}$	The number of fish of age *j* at the beginning of year *i* in region *r*
$A^r_{i,p,j}$	The number of fish of age *j* at the beginning of period *p* of year *i* that are available to the fishery in region *r*
B^r_i	The spawning stock biomass in year *i* in region *r*
$F^r_{i,p,j}$	The instantaneous fishing mortality for fish of age *j* during fishing period *p* and year *i* in region *r*
$M^r_{i,p,j}$	The instantaneous natural mortality for fish of age *j* during fishing period *p* and year *i* in region *r*
$M^r_{i,\bullet,j}$	The total natural mortality for fish of age *j* during year *i* in region *r*
$M^r_{0,\bullet,j}$	The total natural mortality for fish of age *j* in region *r* in the virgin state
R^r_i	The recruitment in year *i* in region *r*
R^r_0	The average recruitment in region *r* in the virgin state
λ^r_j	Proportion of fish at age *j* available to the fisheries in region *r*
$s^r_{i,p,j}$	Selectivity at age *j* for fishing period *p* in year *i* in region *r*
α^r, β^r	Parameters of the stock-recruitment relationship for region *r*
${}^dB^r_i, {}^dB^r_0$	Stock biomass in region *r* that is vulnerable to density-dependent natural mortality in year *i* and in the virgin state.
S^r_i, S^r_0	Spawning biomass per recruit in region *r* in the virgin state and as a result of the density-dependent natural morality in year *i*
$N^r_{0,j}$	The number of fish of age *j* in region *r* in the virgin state.
$m_{s,r}$	The annual proportion of fish in region *s* that move to region *r*
${}^TT^r_{i,j,p}$	The number of tagged fish from tag group *T* of age *j* in period *p* and year *i* in region *r*
$\hat{C}^r_{i,p,j}$	Fitted catch at age *j* (numbers) during fishing period *p* and year *i* in region *r*
$\hat{p}^r_{i,p,j}$	Fitted proportion at age *j* during fishing period *p* and year *i* in region *r*
${}^T\hat{D}^r_{i,p}$	Fitted number of tag recoveries from tag group *T* during fishing period *p* and year *i* in region *r*
Indices	
i, i_l, i_h	Indexes year: i_l and i_h are the first and last years, respectively
j, j_l, j_h, j_k	Indexes age-class: j_l and j_h are the first and last age-classes, respectively, and j_k is the first age-class that experiences density-dependent natural mortality
p, p_h	Indexes fishing period: p_h is the final fishing period

Observations	
$\tilde{C}_{i,p}^{r}$	Catch in mass or numbers during fishing period *p* and year *i* in region *r*
$\tilde{p}_{i,p,j}^{r}$	The proportion of fish at age *j* in the catch of fishing period *p* and year *i* in region *r*
$\tilde{S}_{i,p}^{r}$	The number of fish aged for fishing period *p* and year *i* in region *r*
${}^{T}X$	The number of fish tagged in tag group *T*
${}^{T}\tilde{D}_{i,p}^{r}$	The number of tags recovered from tag group *T* during fishing period *p* and year *i* in region *r*
$\tilde{I}_{i}^{r}$	Spawn index in year *i* in region *r*
$c_{i,p}^{r}$	The proportion of the catch (in weight) sampled for tags
Fixed quantities	
λ_j	The proportion of age class *j* that is available to the fisheries: $\lambda_2 = 0.25, \lambda_3 = 0.90, \lambda_{j\geq 4} = 1.0.$
σ_R^2	The assumed variance of the stock-recruitment deviations. Fixed at 0.8.
u	The efficiency of tag detection machines. Fixed at 1 for most runs.
${}^{S}w_{i,j}^{r}$	Mean spawning weight of fish at age *j* in year *i* in region *r*
${}^{C}w_{i,j}^{r}$	Mean weight of fish in the catch at age *j* in year *i* in region *r*
${}^{G}w_{i,j}^{r}$	Geometric mean weight of fish at age *j* in year *i* in the gillnet catch in region *r*

The following table describes parameters that are estimated through the minimization:

Parameter	Description
R_0^r	Average recruitment at unfished equilibrium in region *r*
${}^{R}d_i^r$	Recruitment deviations for region *r*
h^r	Stock-recruitment steepness for region *r*
ψ^r	Natural mortality parameter for region *r*
${}^{M}d_i^r$	Annual deviations for natural mortality for region *r*
$\gamma_{p,1}^r, \gamma_{p,2}^r$	Selectivity ogive parameters for fishery *p* in region *r*
χ^r	Density-dependent natural mortality parameter for region *r*
$f_{i,p}^r$	Fully-selected fishing mortality rates for fishery *p* in year *i* in region *r*
q_{early}, q_{late}	Spawn index proportionality constants for periods 1 and 2
κ^r	The pre-history average fishing mortality rate in region *r*
${}^{T}\eta$	Survival of tags after tag loss and tagging induced mortality
$\omega_{s,r}$	The proportion of fish moving from region *s* to region *r*. Defined where $s \neq r$

The model description follows.

Fishing and population dynamics:

The following equations describe the population and fishing dynamics:

$$A^r_{i,1,j} = \lambda_j N^r_{i,j} \qquad j_l \le j \le j_h$$

$$A^r_{i,p+1,j} = \exp\left(-M^r_{i,p,j} - F^r_{i,p,j}\right) A^r_{i,p,j} \qquad 1 \le p \le p_h$$

$$N^r_{i+1,j+1} = m_{s,r} \sum_s \left(A^s_{i,p_h+1,j} + \left(1-\lambda_j\right) \exp\left(-M^s_{i,\bullet,j}\right) N^s_{i,j} \right) \qquad j_l \le j < \left(j_h - 1\right)$$

$$N^r_{i+1,j+1} = m_{s,r} \sum_s \begin{pmatrix} A^s_{i,p_h+1,j} + \left(1-\lambda_j\right) \exp\left(-M^s_{i,\bullet,j}\right) N^s_{i,j} + \\ A^s_{i,p_h+1,j_h} + \left(1-\lambda_{j_h}\right) \exp\left(-M^s_{i,\bullet,j_h}\right) N^s_{i,j_h} \end{pmatrix} \qquad j = j_h - 1$$

$$N^r_{i,j_l} = R^r_i$$

$$B^r_i = \sum_j {}^S w^r_{i,j} A^r_{i,p_h+1,j}$$

Note that when tagging data is not fitted and movement not estimated, the movement parameters $\left(m_{s,r}\right)$ are fixed at one for the diagonal and zero for all non diagonal elements. The availability parameters, λ_j, are fixed at 0.25 for age-class 2, 0.90 for age-class 3, and 1.0 for all older age-classes.

Catch equations:

The instantaneous (Baranov) catch equations are used for the current analyses:

$$\hat{C}^r_{i,p,j} = \frac{F^r_{i,p,j}}{F^r_{i,p,j} + M^r_{i,p,j}} \left(1 - \exp(-F^r_{i,p,j} - M^r_{i,p,j}\right) A^r_{i,p,j}$$

where $F^r_{i,p,j} = s^r_{i,p,j} f^r_{i,p}$. The fully selected fishing mortality rates, $f^r_{i,p}$, are estimated as free parameters.

For the period 1 and period 2 fisheries (SN), age-dependent selectivity is modeled with a logistic function:

$$s^r_{i,p,j} = \left(1 + \exp\left(-\gamma^r_{p,2}\left(j - \gamma^r_{p,1}\right)\right)\right)^{-1}$$

For the period 3 fishery (GN), age-dependent selectivity is modeled as a logistic function of the geometric mean weight-at-age:

$$s^r_{i,p,j} = \left(1 + \exp\left(-\gamma^r_{p,2w}\left({}^G w^r_{i,j} - \gamma^r_{p,1}\right)\right)\right)^{-1}$$

Natural Mortality:

Natural mortality is apportioned across the fishing periods based on the specified mortality fractions $\left(t_p\right)$ for each period:

$$M^r_{i,p,j} = t_p M^r_{i,\bullet,j} \qquad \text{where } 0 \le t_p \le 1 \text{ and } \sum_p t_p = 1$$

For the current analysis $t_1 = 0.9$ and $t_2 = t_3 = 0.05$.

A number of options are evaluated for the parameterization of natural mortality. The annual instantaneous natural mortality rates can be constant, vary annually with a time-series component or be density-dependent.

M estimated as free parameters:

$$M^r_{0,\bullet,j} = M^r_{i,\bullet,j} = \psi^r .$$

The parameterization of natural mortality as a random walk is:

$$\begin{aligned} M^r_{i_l,\bullet,j} &= \psi^r \\ M^r_{i,\bullet,j} &= \exp\left({}^M d^r_i\right) M^r_{i-1,\bullet,j} \qquad i_l > i \le i_h \\ M^r_{0,\bullet,j} &= \sum_i M^r_{i,\bullet,j} \Big/ \left(i_h - i_l + 1\right) \end{aligned}$$

The parameterization of density-dependent M is:

$$\begin{aligned} M^r_{0,\bullet,j} &= M^r_{i,\bullet,j} = \psi^r \qquad j < j_k \\ M^r_{i,\bullet,j} &= \psi^r \exp\left(\chi^r \left(1 - \frac{{}^d B^r_i}{{}^d B^r_0}\right)\right) \qquad j \ge j_k \end{aligned}$$

where

$${}^d B^r_i = \sum_{j=j_k}^{j=j_h} w^r_{i,j} N^r_{i,j} \quad \text{and} \quad {}^d B^r_0 = \sum_{j=j_k}^{j=j_h} w^r_{0,j} N^r_{0,j}$$

Stock-recruitment relationship:

A number of stock-recruitment options are investigated. The model is parameterized in terms of B_0 and steepness, the fraction of virgin recruitment obtained when spawning biomass is 20% of B_0. The relationship between R_0 and B_0 is:

$$R_0^r = B_0^r \left(\sum_{j=j_l}^{j \le j_h} \left(\lambda_j {}^S w_{0,j}^r N_{0,j}^r \right) \right)^{-1}$$

where

$$N_{0,j}^r = \exp\left(-\sum_{k=j_l}^{k \le j} M_{0,\bullet,k}^r \right) \qquad \text{for } j < j_h$$

$$N_{0,j_h}^r = \exp\left(-\sum_{k=j_l}^{k=j_h} M_{0,\bullet,k}^r \right) \left(1 - \exp\left(-M_{0,\bullet,j_h}^r \right) \right)^{-1}$$

The Beverton-Holt stock recruitment relationship is:

$$R_{i+j_l}^r = \frac{\alpha^r B_i^r}{\beta^r + B_i^r} \exp\left({}^R d_i^r - 0.5\sigma_R^2 \right),$$

where α and β are defined in terms of B_0 and steepness (h),

$$\alpha^r = R_0^r \frac{\left(4h^r\right)}{\left(5h^r - 1\right)} \quad \text{and} \quad \beta^r = B_0^r \frac{\left(1 - h^r\right)}{\left(5h^r - 1\right)}.$$

The Ricker stock recruitment relationship is:

$$R_{i+j_l}^r = B_i^r \exp\left(\alpha^r - \beta^r B_i^r \right) \exp\left({}^R d_i^r - 0.5\sigma_R^2 \right),$$

where α and β are defined in terms of B_0 and steepness (h),

$$\alpha^r = \ln\left(\frac{R_0^r}{B_0^r} \right) + \beta^r B_0^r \quad \text{and} \quad \beta^r = \frac{\ln\left(5h^r\right)}{0.8 B_0^r}.$$

A modified form of the Beverton-Holt relationship (ABH), that adjusts for the reduced spawning potential per recruit relative to that in the virgin state a result of higher natural mortality rates at lower biomass when density-dependent natural mortality is modeled, is:

$$R_{i+j_l}^r = \frac{S_0^r}{S_i^r} \frac{\alpha^r B_i^r}{\beta^r + B_i^r} \exp\left({}^R d_i^r - 0.5\sigma_R^2 \right),$$

where

$$S_0^r = B_0^r \Big/ R_0^r$$

$$S_i^r = \sum_{j=j_l}^{j<j_h} \left(\lambda_j {}^S w_{i_l,j}^r \exp\left(-\sum_{k=j_l}^{k\le j} M_{i,\bullet,k} \right) \right) + \lambda_{j_h} {}^S w_{i,j_h}^r \exp\left(\sum_{k=j_l}^{k=j_h} -M_{i,\bullet,k} \right) \left(1 - \exp\left(-M_{i,\bullet,j_h}\right)\right)^{-1}.$$

For the ABH stock recruit relationship the α and β parameters are defined in terms of B_0 and steepness as for the normal Beverton-Hold relationship, but the meaning of the steepness parameter is changed. The steepness parameter is still bounded between 0.2 and 1.0, but the effective steepness can be greater than 1.

Population Initialization:

The populations are initialized in 1942, but catch data are not fitted in the model until 1951. The initialization assumes a population at equilibrium (either with fishing or without) in 1942, though the first age-class is estimated with a free parameter.

The initial (1942) population is given by:

$$\begin{aligned}
N_{i_l,j_l}^r &= R_{i_l}^r \\
N_{i_l,j_l+1}^r &= R_0^r \left(\lambda_j \exp\left(-Z_{j_l}^r\right) + \left(1-\lambda_{j_l}\right) \exp\left(-M_{0,j_l}^r\right) \right) \\
N_{i_l,j+1}^r &= N_{i_l,j}^r \left(\lambda_j \exp\left(-Z_j^r\right) + \left(1-\lambda_j\right) \exp\left(-M_{0,j}^r\right) \right) \qquad j_{l+1} < j < j_h \\
N_{i_l,j_h}^r &= N_{i_l,j_h-1}^r \left(1 - \exp\left(\lambda_j \exp\left(-Z_j^r\right) + \left(1-\lambda_j\right) \exp\left(-M_{0,j}^r\right)\right)\right)^{-1}
\end{aligned}$$

where $Z_j^r = M_{0,j}^r$ under the assumption of no fishing prior to the first year of the analysis, and $Z_j^r = M_{0,j}^r + \kappa^r$ under the assumption of a constant level of fishing (κ) prior to the first year of the analysis.

For years between 1942 and 1951, the pre-history fishing mortality values assumed for the initialization (κ) apply and the following equations define the stock dynamics:

$$\begin{aligned}
N_{i,j_l}^r &= R_i^r \\
N_{i+1,j+1}^r &= N_{i,j}^r \left(\lambda_j \exp\left(-Z_j^r\right) + \left(1-\lambda_j\right) \exp\left(-M_{0,j}^r\right) \right) \qquad j_{l+1} < j < j_h \\
N_{i+1,j_h}^r &= N_{i,j_h-1}^r \left(\lambda_{j_h-1} \exp\left(-Z_{j_h-1}^r\right) + \left(1-\lambda_{j_h-1}\right) \exp\left(-M_{0,j_h-1}^r\right) \right) + \\
&\qquad N_{i,j_h}^r \left(\lambda_{j_h} \exp\left(-Z_{j_h}^r\right) + \left(1-\lambda_{j_h}\right) \exp\left(-M_{0,j_h}^r\right) \right)
\end{aligned}$$

Note that when density-dependent natural mortality is estimated, the quantities $M_{0,\bullet,j}^r$ in the equations above are replaced with $M_{i,\bullet,j}^r$.

Spawn index proportionality constants:

Spawn index proportionality constants are defined for two periods, 1951–1987, and 1988–2008 $\left(q_{early} \text{ and } q_{late}, \text{respectively}\right)$. Both indices can either be fixed or estimated. When not fixed, analytical solutions of the parameter estimates are calculated.

Tagged fish:

Tagged fish follow the same dynamics as the untagged populations, except that all tagged fish are assumed available to the fisheries. The age-composition of tagged fish is that predicted for the SN roe fishery in the year of tagging. Following tagging there is a loss of tagged fish due to tagging-induced mortality and loss of tags, and then the tagged fish are vulnerable to the SN and GN roe fisheries in the region of release. The number of tagged fish after the SN and GN fisheries in the year of tagging is given by:

$$ {}^{T}T^{r}_{i,p_{h+1},j} = {}^{T}\eta\ \hat{p}^{r}_{i,2,j}\ {}^{T}X\ \exp\left(\sum_{p=2}^{p=3}\left(-F^{r}_{i,p,j} - M^{r}_{i,p,j}\right)\right) $$

where *i* is the year of tagging and *r* is the region of release for tag group *T*. The tagged fish dynamics, and predicted tag recovery is given by:

$$ {}^{T}T^{r}_{i+1,1,j+1} = \sum_{s} m_{s,r}\ {}^{T}T^{r}_{i,p_{h+1},j} $$

$$ {}^{T}T^{r}_{i,p+1,j} = {}^{T}T^{r}_{i,p,j}\exp\left(-F^{r}_{i,p,j} - M^{r}_{i,p,j}\right) \qquad 1 \le p \le p_h $$

$$ {}^{T}\hat{D}^{r}_{i,p} = c^{r}_{i,p}\,u\sum_{j}\left(\frac{F^{r}_{i,p,j}}{F^{r}_{i,p,j} + M^{r}_{i,p,j}}\left(1-\exp\left(-F^{r}_{i,p,j} - M^{r}_{i,p,j}\right)\right){}^{T}T^{r}_{i,p,j}\right) \qquad 2 \le p \le 3 $$

Movement:

Movement parameters, representing annual dispersal probabilities, are estimated for all region pairs, and the probability of region fidelity is the proportion which don't disperse. That is:

$$ m_{s,r} = \omega_{s,r} \qquad s \ne r $$

$$ m_{s,s} = 1 - \sum_{r:r\ne s}\omega_{s,r} $$

Note that for some runs, if there were no fish tagged in region *s* recovered in region *r* the corresponding $\omega_{s,r}$ parameters are fixed at 0. Also, for runs where movement is not estimated the elements of the symmetrical matrix *m* are fixed at 0 except for the diagonal elements which are fixed at 1.

Likelihoods:

Age composition data:

The multinomial distribution is assumed for fitting to age composition data. The negative log likelihood given the multinomial error assumption is:

$$-\log(L) = \sum_r \sum_i \sum_p \sum_j \tilde{S}''^r_{i,p} \ln\left(\hat{p}^r_{i,p,j}\right) - \tilde{S}'_{i,p} \ln\left(\tilde{p}^r_{i,p,j}\right).$$

Note that the second term of this equation is a constant.

We include the option of allowing additional error in the fits to the age composition data to allow for process error. For the multinomial likelihood, the overall variance of a data set is proportional to its sample size. When process error is assumed, the quantities $S'_{i,p}$ are given by:

$$\tilde{S}''^r_{i,p} = \frac{1}{1/\tilde{S}^r_{i,p} + 1/S_{process\_error}}.$$

Spawn index data:

Lognormal distributions are assumed for the spawn index data. The negative log likelihood is given by (ignoring the constant):

$$-\ln(L) = \frac{\sum_r \sum_i \ln\left(\tilde{I}^r_i \Big/ q^r_i B^r_i\right)^2}{2\ \sigma^2_i}.$$

Catch data:

Lognormal distributions are assumed for the catch data. The negative log likelihood for the catch data is given by (ignoring constants):

$$-\ln(L) = \frac{\sum_r \sum_i \ln\left(\tilde{C}_{i,p} \Big/ \hat{C}_{i,p}\right)^2}{2\sigma^2_C},$$

where $\hat{C}^r_{i,p} = \sum_j {}^C w^r_{i,p,j} \hat{C}^r_{i,p,j}$.

Tagging data:

The Poisson distribution is assumed for the tag recovery data. The negative log likelihood for the catch data is given by (ignoring constants):

$$-\ln(L) = -\sum_T \sum_r \sum_i \sum_p \left({}^T\tilde{D}^r_{i,p} \ln\left({}^T\hat{D}^r_{i,p}\right) - {}^T\hat{D}^r_{i,p}\right).$$

Priors:

HCAM is implemented for Bayesian estimation and thus require specification of priors for all "free" model parameters. These priors contribute to the objective function in the Bayesian integration.

Recruitment residuals $\left(d_i^R\right)$*:*

Stock-recruitment residuals are assumed to be normally distributed with mean 0 and variance σ_R^2. The prior contribution to the objective function is:

$$\sum_r \sum_{i=il+1}^{i_h} \left(\frac{\left({}^R d_i^r\right)^2}{2\sigma_R^2} \right).$$

Stock-recruitment steepness $\left(h\right)$*:*

The stock-recruitment steepness parameter is assumed lognormal distributed with mode 0.67 and standard deviation 0.17. Additionally, for the Beverton-Holt and modified Beverton-Holt stock-recruitment functions the steepness parameter is bounded on the interval 0.2-1.0, making this an improper prior. Note that for the modified Beverton-Holt stock-recruitment relationship the effective steepness differs from the value of the steepness parameter. The prior contribution to the objective function is:

$$\sum_r \frac{\ln\left(h^r / 0.67\right)^2}{2\left(0.17\right)^2}.$$

Natural mortality deviations $\left(d_i^M\right)$*:*

The parameters representing natural mortality deviations are assumed normal distributed with mean 0 and standard deviation of 0.1. The prior contribution to the objective function is:

$$\sum_r \sum_i \frac{\left({}^M d_i^r\right)^2}{2\left(0.1\right)^2}.$$

Average natural mortality rate:

The mean natural mortality rate, $\left(\bar{M}^r = \sum_{i,j} M^r_{i,\bullet,j} \Big/ \left(\left(i_h - i_l + 1\right)\left(j_h - j_l + 1\right)\right) \right)$, is assumed normally distributed with mean 0.45 and standard deviation 0.2. The prior contribution to the objective function is:

$$\sum_r \frac{\left(\bar{M}^r - 0.45\right)^2}{2\left(0.2\right)^2}.$$

Pre-history fishing mortality:

The pre-history fishing mortality rate is assumed lognormal distributed with mode of 0.3166 and standard deviation of 0.6633. The prior contribution to the objective function is:

$$\sum_r \frac{\ln\left(\kappa^r / 0.3166\right)^2}{2\left(0.6633\right)^2}$$

Remaining parameters:

The remaining estimated parameters, $R_0^r,\ \gamma_{p,k}^r,\ f_{i,p}^r, q_{early}^r, q_{late}^r, \lambda^r, {}^T\eta, \omega_{s,r},$ are assumed to be uniformly distributed, so the prior contribution to the objective function is constant.

The total objective function value (*OBFval*) is the sum of the negative log-likelihood components plus the sum of the prior components.

Residuals:

HCAM calculates normalized residuals which express the residual on a standard normal scale.

Let O be an observation and F the corresponding fit. Normalized residuals for the normal, the multinomial, and the Poisson distributions are defined as:

$$\left(O - F\right) \Big/ st.dev.\left(O\right)''.$$

For the lognormal error distribution, the normalized residual is:

$$\ln\left(O/F\right) \Big/ st.dev.\left(O\right).$$

For the normal and lognormal distributions the $st.dev.\left(O\right)$ are their input assumed values. For the multinomial distribution

$$st.dev.\left(O\right) = \sqrt{\left(1-F\right)F \Big/ N}$$

and for Poisson distribution $st.dev.\left(O\right) = \sqrt{F}$.