Opportunities and Challenges for Marine Protected Areas in Fisheries Management

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ABSTRACT

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Marine protected areas (MPAs) are now recognized as effective tools for the conservation and long-term protection of marine resources. Their effectiveness from a traditional fisheries management perspective still remains equivocal. One of the argued research-related benefits of MPAs to management is that because the rate of fishing mortality inside of an MPA is controlled and often set at zero, it may be possible to precisely estimate the rate of natural mortality and better determine growth and maturity rates, parameters that are often pre-specified in a stock assessment. This thesis aims to assess the degree to which having an MPA increases the ability to directly estimate these parameters in a integrated stock assessment model frequently used for management, Stock Synthesis, how long it would take for these benefits to be reflected in improved estimates of management quantities (*e.g.* F_{MSY}), and the extent to which these improvements will be reduced or lost if there is spillover of adults from the MPA to the fished area. A two-area age- and length-structured simulation model is parameterized for generic fish with contrasting life-histories, a short-lived high-productive and a long-lived low-productive species. This model forms the basis for a Monte Carlo simulation which examines the benefits of data collected from MPAs on estimation performance for Stock Synthesis. Results indicate that the extent of improvement in estimation of growth and maturity parameters with data collected from MPAs is slight compared to directly estimating these parameters using fishery data. Estimation of natural mortality using data collected from MPAs does substantially improve estimation, but the extent of this improvement critically depends on model structure, data availability, and the degree of spillover from the MPA.

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Life-history parameters describe patterns in reproduction and longevity over the course of an organism's lifetime. In a fisheries management context, the magnitude of these parameters: natural mortality (M), growth and maturity are some determinants of the productivity of a stock, the basis on which many sustainable fisheries are managed (Hilborn and Walters 1992). There has been little success estimating these parameters, particularly natural mortality, within a population dynamics model framework, despite their importance for assessment and hence management recommendations. Consequently these parameters are often assumed fixed at pre-specified values when estimating the current state of a population. In doing so, the uncertainty associated with the final estimates of, for example, population size is not fully represented; which is inconsistent with the precautionary approach to fisheries management (FAO 1995).

In stock assessments, natural mortality has been among the most difficult parameters to estimate (Vetter 1998). The exact value of M has little effect on the estimated trend in abundance when fishing mortality (F) is much greater than natural mortality. In this case, the removal data typically provided to a stock assessment are not informative about natural mortality. Moreover, natural mortality is often highly confounded with other parameters (initial recruitment (R_0), catchability (q), and F) since they are all scaled to population size (Schnute and Richards 1995). While some studies have shown success estimating M (*e.g.* Fournier et al. 1998), more often it is thought that M can only be estimated precisely if catch age-composition data are available for the years prior to when the fishery started or if fishing effort is kept very low for some years (Beverton and Holt 1957), because the age-structure at this time can solely be attributed to natural mortality.

Growth and maturity are also important biological processes included in stock assessments. It is common to fix the values of the parameters which determine growth and maturity to values calculated from auxiliary analyses outside of the stock assessment, because the data required to estimate them are not typically included in a stock assessment. It is now possible to directly estimate the parameter κ of the von Bertalanffy curve (and other growth-related parameters) within an assessment through inclusion of conditional age-at-length (referred to as "age" hereafter) data (Punt et al. 2000, Methot 2005). However, this has only commonly been done on the U.S. west coast in very recent years for the small number of stocks for

which this information is available and no study has evaluated how well these parameters are estimated in a simulation framework.

Another long-standing challenge in fisheries management has centered on the effectiveness of Marine Protected Areas (MPAs[1]) in managing fisheries and optimizing yield compared to traditional fisheries management. As MPAs continue to be implemented, it is important to evaluate their effectiveness compared to traditional fisheries management techniques (Hilborn et al. 2004), but an equally important question is, what can fisheries management learn from data collected from MPAs once they have been implemented? Some authors (Sladek Nowlis and Roberts 1998, Punt and Methot 2004, Field et. al 2006) have suggested that MPAs provide an opportunity to better determine life-history parameters. Despite these suggestions, the magnitude of estimation improvement (compared to estimating these parameters using only data from a fishery) has yet to be explored quantitatively.

There are several reasons why one might expect to more reliably estimate life-history parameters if data from a MPA were available. For example, the rate of fishing mortality is known exactly ($F = 0$) within a MPA because no fishing of the targeted species is allowed inside of the protected area[2], and hence M and F are no longer confounded. Furthermore, the age-structure inside of an MPA should start to resemble that of an unfished population given enough time. Assuming negligible movement of fish between the MPA and the fished area, such data should be highly informative about M because the distribution of fish amongst age-classes can be attributed mostly to natural mortality. Estimates of growth and maturity are thought to be unreliable for heavily exploited populations (*i.e.* truncated age and length distributions) because insufficient data are available to adequately determine these parameters without information on the oldest and largest fish. The rebuilding of an overfished stock within a MPA should therefore be expected to provide data that are more informative about growth and maturity parameters.

MPAs may provide the data to better determine life-history parameters, but the ability to estimate them will largely depend on the assessment model's capability to account for spatial processes. Except for fish species with high site fidelity or negligible adult movement, we should expect an appreciable amount of

[1] Throughout this thesis, the term 'MPA' is defined as an area of the ocean completely protected from all extractive activities (*i.e.* all forms of fishing) except as necessary for monitoring and research, essentially a No take Marine Protected Area (NTMPA), but referred to as an MPA for simplicity.
[2] This, of course, will not be true if there is illegal fishing inside of the protected area or if the targeted species is caught as by-catch from other forms of fishing that are allowed inside of the protected area.

mixing or spillover (*e.g.* Abesamis and Russ 2005) between the protected and exploited components of the stock. Modern stock assessments have the ability to account for spatial processes, but there is rarely data that are informative about mixing-related parameters.[3] Lacking sufficient data to estimate a specific parameter leads to estimates which are confounded with those of other parameters. For instance, a stock assessment of an MPA might attempt to estimate the movement rate of adults in the MPA to the fishery, but this parameter may be highly confounded with natural mortality since trends in age-structure from surveys within the MPA could both be attributed to death due to natural causes of the oldest fish and spillover of the oldest fish to the fishery. Although MPAs may reduce uncertainty in estimates of key life-history parameters, the degree to which this expectation holds for realistic mixing rates remains unknown.

The aim of this thesis is to examine the hypothesis that having data from an MPA will lead to improved estimates of key life-history parameters for a simplified and then more realistic scenario. This hypothesis is framed within a Monte-Carlo simulation for a stock assessment model commonly used on the U.S. west coast, Stock Synthesis (SS) (Methot 2005). The extent to which having a MPA can improve estimates of life-history parameters for the case in which there is no spillover from the MPA, and hence the maximum expected improvement in estimation ability that a MPA can offer, is examined in Chapter 1. In addition, the ability to better estimate quantities important to management recommendations (*i.e.* the fishing mortality that achieves maximum sustainable yield, F_{MSY}) is also examined. Chapter 2 explores the extent to which these benefits are reduced or lost if there is spillover from the MPA to the fished area when spillover is either accounted for or ignored within a stock assessment. General conclusions are made and cases in which we might expect to see substantial improvement in estimation of life-history parameters and management quantities are identified in the final chapter.

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[3] Inclusion of tagging of data into stock assessments provides one possible way to estimate mixing-related parameters, but these data are rarely adequate. On the west coast of the U.S., tagging studies have been performed for sablefish (*Anoplopoma fimbria*) and several flatfish species, but the spatial resolution of tagging is typically very coarse and the subsequent fishery-effort distribution after initial release is poor. Consequently, no tagging data have ever been incorporated into any peer-reviewed stock assessment on the U.S. west coast (Ian Stewart NWFSC, personal communication).

CHAPTER 1

CAN MARINE PROTECTED AREAS IMPROVE ESTIMATES OF LIFE-HISTORY PARAMETERS?
ASSESSING THE MAXIMUM IMPROVEMENT IN ESTIMATION ABILITY

This chapter examines the hypothesis that having an MPA improves estimation ability given no movement of fish between the MPA and the fished areas. Although this scenario is unlikely to be true for most marine fishes, it provides a necessary starting point to understand the behavior of the SS model when given ideal data and hence the maximum improvement in estimation ability that data from an MPA may provide.

1.1 METHODS

1.1.1 *Monte Carlo Simulations*
Monte Carlo simulations have been used extensively in fisheries science to test the performance of stock assessment models (*e.g.* Yin and Sampson 2004). Monte Carlo simulation in the context of this thesis involves the following steps:

(1) define a model that represents the truth of the system (referred to as the operating model),

(2) generate data from the operating model that will be provided to the stock assessment,

(3) apply the stock assessment to the operating model,

(4) compare the estimates from the stock assessment with the true values from the operating model, and

(5) repeat steps (2)-(4) many times.

1.1.2 *Stock Synthesis*
Integrated (statistical catch-at-age) analysis has evolved over the past three decades to meet the growing demands of assessment of marine resources (as reviewed by Schnute et al. (2007)). Integrated analysis models fit the available data based on a linked set of sub-models. The core sub-model specifies the population dynamics of the assessed stock. This sub-model includes life history processes which lead to a time-series of projected population abundances. It is typically age- and length-structured, but spatial structure has been included in some integrated models (*e.g.* Fournier et al. 1998, Methot 2009). The observation sub-model is linked to the population dynamics sub-model and serves the purpose of creating expected values for the data available to the assessment. The last major component of an integrated model is the statistical sub-model which specifies the likelihood function for the data, along with any penalties (priors) imposed on the parameters.

The reauthorization of the Magnuson-Stevens Fishery Management and Conservation Act (2007) requires that annual catch limits (ACLs) be specified for all species that are "in the fishery" to ensure that overfishing does not take place for federally-managed fish species. This requirement has placed further demands on stock assessment scientists and on the need for the development of generalized integrated assessment models that have flexible population dynamic, observation and statistical sub-models. On the west coast of the United States, Stock Synthesis (SS) (Methot 2005) is the most common of these generalized models and is used for nearly every assessment of groundfish and coastal pelagic species. SS is the stock assessment model on which this thesis is based. By using this model, it is possible to address whether the presence of an MPA improves estimation of life-history parameters and management quantities within a state-of-the-art stock assessment method that is used frequently to provide the basis for management decisions, narrowing the gap (Holland 2002) between the types of models used to evaluate the benefits of MPAs and those which are used to provide scientific management advice.

1.1.3 *Operating Model*

The operating model (Appendix A) is a two-cell spatially-, age- and length- structured population dynamics model. The spatial structure is scaled so that cell 1 (referred to as the "MPA cell") represents 20% of the recruitment at unfished equilibrium ($0.2 R_0$) whereas cell 2 (referred to as the "fished cell") represents 80% of the recruitment at unfished equilibrium. A two-cell model was chosen for simplicity on the basis that if improvement in estimation is not observed for this simple of a model, then improvement in estimation performance will also not be observed in a more complicated and realistic, spatial structure such as a network of MPAs. 20% is often cited as the most appropriate size for an MPA because recruitment overfishing could be avoided by maintaining stocks at or above 20% of their unfished biomass (Goodyear 1993). Allocating 20% of a fishery to a MPA represents a substantial closure. If a much greater percentage were closed, the fishery could potentially extirpate the stock within it's boundaries since the fraction of total unfished population within the MPA could be close to that associated with maximum sustainable yield (B_{MSY}), which is the management target for groundfish stocks off the U.S. west coast. This implicitly assumes that the spawning biomass within the MPA is 'on the table' (Field et al. 2006) with respect to status determination of the stock. Current legislative obligations of stock status determination do not delineate whether the portion of the stock within the MPA should contribute to the overall estimate of exploitable biomass for the purposes

of status determination. It is assumed in this thesis that the spawning biomass within the MPA is 'on the table' with respect to status determination.

The stock is assumed to be at a non-stable equilibrium (Figure 1.1) in the first year of the operating model where the numbers-at-age in each cell depend on the pre-catch recruitment deviations (see Equation A.5). Catches prior to implementation of the MPA are relatively constant (although allowance is made for annual fluctuations in catch, Equation A6). The stock is fished down to 25% of the unfished spawning biomass (0.25 B_0, the overfished threshold for most groundfish stocks off the U.S. west coast) at a specified year by these catches. This is achieved for each realization in the simulation by first generating the deviations about the stock-recruitment relationship and the fluctuations in catch, and then numerically determining the value of R_0 that corresponds to the stock being depleted to 0.25 B_0 at a specified time.

After the MPA has been declared, the mean fishing mortality rate (bias-corrected log-normal error is added to this constant F as outlined in Equation A.6) is determined so that the spawning biomass rebuilds to 40% of the unfished spawning biomass (0.4 B_0 is the proxy for B_{MSY} for most west coast groundfish stocks) across both cells in a pre-specified amount of time. Allowing for exploitation during rebuilding is consistent with rebuilding strategies for west coast groundfish since the needs of the fishing community in addition to the status of the stock are considered when selecting fishing mortality targets for rebuilding stocks. In reality, future fishing mortality is never pre-specified at a mean value, but depends on the results of the stock assessment. The feedback process between assessments and target fishing mortality rates is not implemented here to avoid confounding the performance of the stock assessment method with the level of F (see Punt (2003) and Punt and Ralston (2007) for analyses which account for this feedback).

1.1.4 *Scenarios and parameterization*
The values for the parameters of the operating model are chosen to represent two generic fish with contrasting life-history strategies: a short-lived high-productive (SLHP) and a moderately long-lived low-productive (LLLP) species (Figure 1.2 and Table 1.1). On the U.S. west coast, these two fish can be thought of as a typical flatfish and a moderately long-lived rockfish respectively. The parameters for these two fish were determined by choosing a value of natural mortality (0.3yr^{-1} for SLHP and 0.15 yr^{-1} for LLLP) and then using the Beverton-Holt life history invariants (Beverton 1992) to determine the values for the other life history parameters. The "steepness" parameter (Mace and Doonan 1988) was arbitrarily chosen to be 0.9 and

0.6 based on values commonly assumed for stock assessments of flatfish and rockfish. These two contrasting life history strategies were chosen to examine the robustness of the results to assumptions about productivity.

Three of the scenarios (see Table 1.2 for the full list) examine the effects of implementing a MPA for a short, medium and long period (10, 20 and 30 years) to examine how long it would take to see improvement in estimation of life-history parameters and management quantities. Fishing mortality after the implementation of the MPA is selected for the SLHP species so that recovery to the target spawning biomass, $0.4B_0$[4], occurs 10 years after the stock is reduced to $0.25B_0$ (and would be declared overfished once below this threshold under the Fishery Management Plan for groundfish off the U.S. west coast) because a highly productive species should be able to rebuild within that amount of time. Recovery to $0.4B_0$ occurs 20 years after the overfished declaration for the LLLP species because even in the complete absence of exploitation, the LLLP species could not rebuild in ten years[5]. Figure 1.3 shows 100 projected spawning biomass and depletion (spawning biomass relative to B_0) trajectories when implementing the MPA for 30 years. Given the approach for setting B_0, the depletion trajectories for the entire stock always pass through the overfished threshold and then rebuild to the target depletion level. Depletion in the fished area remains relatively unchanged after recovery to the management target, but increases appreciably in the MPA.

Several variants of the operating and estimating models (Appendix B) are considered (Table 1.2) to examine the robustness of the results to the impact of assumptions about how density-dependence in recruitment operates, the presence of ageing error, whether survey-age data are available for the MPA, whether selectivity is asymptotic or dome-shaped, and whether life-history parameters are estimated or assumed known.

Two categories of scenarios (A and B in Table 1.2) examine the sensitivity of how density dependence may affect estimation ability. Equation A.2a assumes that density dependence operates at the cell level and that there is no dispersal of juveniles between the cells so that the number of fish recruiting to a cell only depends on the spawning biomass in that cell. In contrast, Equation A.2b assumes that density dependence is

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[4] The Pacific Fisheries Management Council changed the overfished threshold for flatfish from $0.25B_0$ to $0.125B_0$ in 2009 based on the presumed productivity of these stocks at low spawning stock sizes (Punt *et al*. 2008, Hilborn and Stokes 2010). This mandate has yet to be approved by the National Marine Fisheries Service. For comparability between the two species, both fish stocks are recovered to $0.4 B_0$.

[5] Section 304 of the Magnuson-Stevens Act imposes requirements on management of fish stocks that have been identified as overfished. This section dictates that "rebuilding the fishery shall be as short as possible and not exceed 10 years except where biology of the stock or other environmental conditions dictate otherwise." It is biologically impossible to rebuild most LLHP species on the U.S. west coast, to the target spawning biomass within 10 years even in the complete absence of fishing.

a function of the total population size (*i.e.* density dependence is post-dispersal) so that the number of fish recruiting (at age 0) to a cell depends not only on the spawning biomass in that cell, but also on the spawning biomass from the other cell. An intermediate case is that density dependence acts at the cell level, but all larvae then mix (*i.e.* density dependence is pre-dispersal). Although plausible, this case is not considered because equations A.2a and A.2b bound the strength of density dependence.

Scenario A5 examines the implications for selectivity being dome-shaped rather than asymptotic. Figure 1.4 shows the true dome-shaped curve used by the operating model. The values for the selectivity parameters were chosen so that the right-hand descending limb started at 10 cm less than the maximum length and selectivity at maximum length is 30% of the maximum selectivity. The ascending limbs remain consistent with those of the asymptotic pattern on which the remainder of the analyses are based. The estimation method also involves dome-shaped selectivity for this case (which implies the need to estimate additional parameters).

Scenario A7 examines the implications of obtaining no age-data from the MPA, but only length data, potentially for example, by means of an autonomous underwater vehicle (AUV). This is of particular interest for MPAs that provide the highest degree of protection from anthropogenic impacts and hence where lethal sampling for scientific purposes is not permitted. This type of sampling protocol also has potential future implications for survey data on the west coast because rockfish tend to aggregate in rocky areas that are often untrawlable to scientific surveys. However, the degree to which only having survey length data is informative about numbers-at-age has yet to be evaluated using Monte Carlo simulations. This scenario is implemented by generating survey lengths analogously to Equation A.18 and estimating separate survey catchability and selectivity parameters corresponding to when the MPA is declared. Sampling protocols and estimable parameters in the fished area do not change.

There is no movement of fish between the MPA and the fished area ($X_a^{c',c} = 1$ in Equation A.1) in this chapter.

1.1.5 *Assessment data*

Survey estimates of abundance, and length- and age-compositions from the survey and the fishery catches are available to the assessment beginning in year 20 for the SLHP species and year 40 for the LLLP species. The timing of data availability corresponds to the plus-group age for each of these species. When data are

available prior to these years, there is potentially still information in the age-composition data about the unfished population, and estimates of life history parameters, particularly natural mortality, are consequently more precise than that is typically observed in stock assessments (results not shown). This is also consistent with the data availability on the U.S. west coast for which there are only catch data for the first years of the assessed period.

A triennial survey is conducted with a total CV of 0.1. The CV in the MPA and the fished area (0.22 and 0.11) are chosen assuming that 20% of the survey hauls are conducted in the MPA and 80% in the fished area.

Fishery compositions are only available for the MPA prior to implementation of the protected area. Figure 1.5 shows a timeline of data availability and features of the operating model across time.

The numbers of length and age samples available to the assessments are assumed to be proportional to the fraction of animals in each cell prior to exploitation. Two hundred fish are proportionally sampled for length from the fishery resulting in 40 fish lengths from the MPA and 160 fish lengths from the fished area. Half of these fish are then sub-sampled for age, providing 20 and 80 ages for the MPA and fished area respectively. The same number of fish prior to implementation of the MPA is sampled from the fished area after implementation. The total triennial survey sample size is 300, resulting in 240 fish sampled for length from the fished area, 60 fish sampled for length from the MPA, 120 fish sub-sampled for age from the fishery, and 30 fish sub-sampled for age from the MPA. The baseline scenario does not include ageing error when generating the age data, although scenario A6 examines the sensitivity of the results to ageing error (CV = 0.2). The effects of assuming the correct aging error definition (scenario A6a) and no aging error (scenario A6b) when applying the stock assessment are examined. These two scenarios should bound the robustness of estimation performance to age-reading error. Scenario A9 examines the effect of halving the total sample sizes for both the fishery-dependent and -independent data, in addition to doubling the total survey CV.

1.1.6 *Stock Synthesis Estimating Model*
The SS assessment model (Appendix B) is based on an age- and length-structured population dynamics model. In structure, it is identical to the operating model except that the annual deviation from the mean recruitment is bias-adjusted (Methot and Taylor in prep) (Equation B.3). The data supplied to a stock

assessment are never perfectly informative about the true deviation about the stock-recruitment curve. Consequently, the standard deviation of estimated recruitment deviations will always be less than the standard deviation of the true process that generated the recruitment deviations (or the true total recruitment error, $\sqrt{\sigma_C^2 + \sigma_T^2}$, assumed in the operating model). Therefore, the best fit will occur by "shrinking" the estimated recruitment deviation towards 0 because each such deviation is penalized by the value of σ_R assumed in the stock assessment (Equation B.9). The bias-correction term in the estimating model, $-\sigma_R^2 / 2$ should then be multiplied by a factor to compensate for this shrinkage so that the estimated deviation remains mean unbiased. The annual bias adjustment is substantially less than 1 at the beginning and end of the time period considered in the assessment due to lack of data on the cohorts available at that time. The bias corrections are calculated using the r4ss package (Taylor et. al 2009). This involves two iterations of the stock assessment because the estimated bias adjustment depends on the asymptotic standard error of the estimated recruitment deviations (Equation B.3). The first iteration determines the asymptotic standard errors from an initial guess of the bias adjustment factor and the second iteration uses the correct bias adjustment in Equation B.3.

The estimated parameters for the baseline version of the SS stock assessment are: unfished recruitment, steepness, pre-catch recruitment deviations, main recruitment deviations, annual fishing mortality, survey catchability and three fishery and survey selectivity patterns (β_1, β_3 and β_5 described in Appendix A). The maximum likelihood estimates of these parameters are obtained by minimizing a single objective function (Appendix B). This function includes contributions from the fishery catches, the survey index of abundance, and the length- and age-compositions from the fishery catches and the survey. No priors (effectively penalized-likelihood in SS) are placed on any of the estimated parameters. SS also requires that parameter bounds be placed on estimated parameters. These bounds were chosen to constrain the parameters to biologically plausible values and were sufficiently large to not affect the results. The initial value for each parameter, θ_{Initial}, in each simulation is chosen randomly by jittering the parameter from its true value, θ_{True}:

$$\theta_{\text{Initial}} = \theta_{\text{True}} + 0.25\, Z\, \left(\theta_{\max} - \theta_{\min}\right) \tag{1.1}$$

where $Z \sim N(0,1)$ and $(\theta_{\min}, \theta_{\max})$ are the bounds on the parameter.

Punt and Methot (2004) examined the effects of implementing large scale MPAs on the performance of stock assessments. Using Monte Carlo simulations, they found that the impact of MPAs on stock assessments was substantial if data from the MPA and the fished area were aggregated into a single assessment. Such data aggregation violates the homogeneous stock assumption of a non-spatial stock assessment. However, the negative impact of a MPA on assessment ability is relatively slight if differences in population structure are accounted for by sub-dividing the stock assessment into smaller spatial units and applying the stock assessment method to each of those units. Similarly, spatial differences between the MPA and the fished area are accounted for in this chapter by conducting separate assessments for the MPA and the fished area. There are consequently four assessments for each trial; (a) an assessment of the MPA, (b) an assessment of the fished area, (c) a "subdivided" assessment which involves combining the results of the "MPA" and "fished" assessments together to obtain an assessment of the entire area, and (d) an "aggregated" assessment in which data aggregated over the MPA and fished area are analyzed as if they came from a homogeneous population. Nested within each scenario (Table 1.2), then, are 18 separate stock assessments, resulting in 24 stock assessment configurations when considering the subdivided assessment, that vary according to species, the area being assessed, and the length of data in the stock assessment:
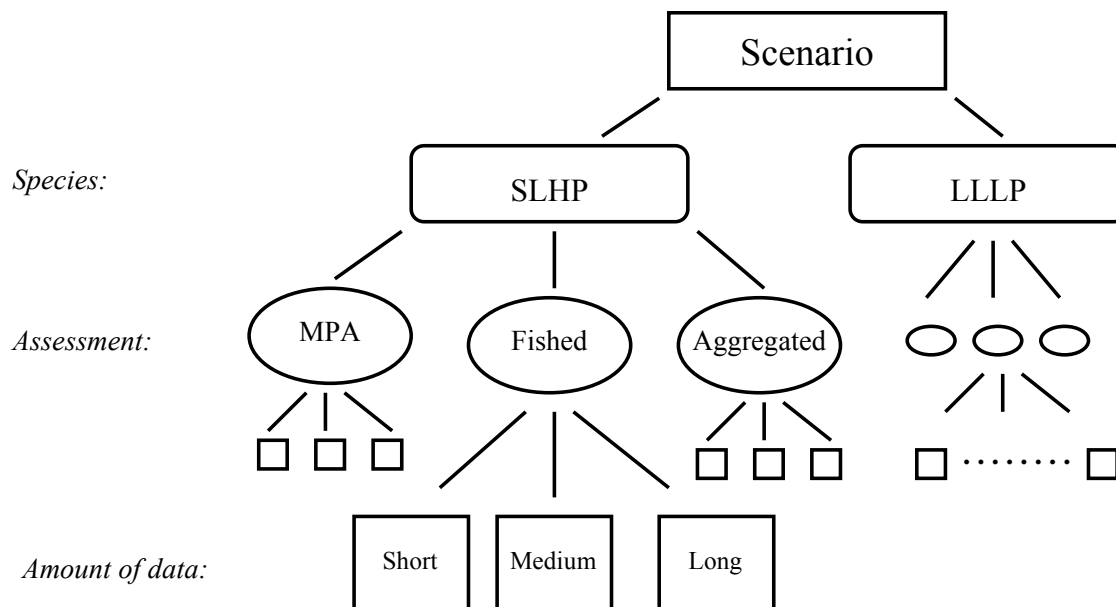
1.1.7 *Summary Statistics*

Each simulation involves generating 100 realizations of the exploitation history and subsequent rebuilding

with an MPA pattern as described above. Differences between the true and predicted spawning biomass,

depletion, and estimable parameters of the assessment model are compared to understand the behavior of the

assessment model. The percent of relative error (RE) statistic:

$$100 \times \frac{x^{est} - x^{true}}{x^{true}}$$

$$(1.2)$$

is used to measure these differences. This statistic provides an interpretable measure of bias. Differences

between true and predicted F_{MSY} and life-history parameters are also compared using the median absolute

error (MARE) statistic:

$$\text{median} \left| \frac{x^{est} - x^{true}}{x^{true}} \right|$$

$$(1.3)$$

to gauge the accuracy of the parameter estimates. This statistic cannot be decomposed into separate bias and

variance components such as the mean squared error statistic, but is less sensitive to outlying observations.

In general, any increasing function of distance, $x^{est} - x^{true}$, would serve to measure the performance of an

estimator (Casella and Berger 2002) and the MARE is a reasonable alternative when potential outlying

observations may be influential. The median relative error (MRE) is used to measure the bias of the

parameter estimates. It is assumed that a quantity is estimated with negligible bias when the MRE is between

-0.05 and +0.05.

1.2 RESULTS

1.2.1 *Baseline Results*

Prior to examining the scenarios in which the life-history parameters are estimated, it is instructive to

understand the behavior of the SS estimating model when these parameters are fixed at their true values

(scenarios A0 and B0). This section focuses on the no-dispersal density dependence scenario (scenario A0)

because the results for scenario B0 (density dependence in recruitment is post-dispersal) are essentially

identical to those for scenario A0 (results not shown). Figures 1.6 and 1.7 show time trajectories of relative

error for two management-related quantities: spawning biomass and fishing mortality. Figure 1.8 shows time

trajectories of relative error for the pre-catch and main recruitment deviations while Figure 1.9 shows boxplots of the estimates for steepness (*h*), a key parameter of management importance.

There are noticeable differences between the MPA, fished, aggregated and subdivided assessments in terms of relative error for spawning biomass (Figure 1.6). Specifically, the MPA and fished assessments are nearly median unbiased across all years, although there is a slight increases in relative error when the MPA is established. This error propagates forwards and backwards in time. The assessment for the MPA is much more variable than the assessment for the fished area because of the larger uncertainty associated with both the survey indices of abundance as well as the length and age compositions. The subdivided assessment is also nearly unbiased across all years. The results of the subdivided assessment can be compared to those of the aggregated assessment. Prior to implementation of the MPA, the relative errors for these two assessments are nearly indistinguishable, but the aggregated assessment tends towards underestimation of spawning biomass 10, 20 and 30 years after the MPA is implemented. The homogeneous stock assumption is violated for the aggregated assessment since it takes no account of the MPA, and hence fails to predict the increased productivity of the stock as a whole. This bias increases with years after MPA establishment. These results support those found by Punt and Methot (2004) and suggest that the potential negative impact of heterogeneous populations on a stock assessment is slight when account of this is taken by conducting separate assessments.

The relative errors for spawning biomass for the SLHP and LLLP species differ in three noteworthy ways. Specifically, both species show an increased variability in relative error during the early no-data period. This is hardly surprising because the assessment lacks survey and composition data during this period. However, the relative errors for the SLHP species are markedly more variable during this period compared to those for the LLLP species. This is likely because there is more information about the reconstructed population numbers-at-age in the first available LLLP age-composition due to the older age of this fish. This is somewhat surprising because the timing of the first available age composition corresponds to the plus-group age of the fish. Although the LLLP species lacks a longer series of data, the spawning biomass relative errors are not as large. The second feature is that the assessments of the MPA show an increase in relative error prior to and after implementation of the protected area. At this time, fewer data become available to this assessment since fishery length- and age-compositions are no longer available. This

effect is much more pronounced for the LLLP species, although the exact reasons for this are unclear. In contrast to the assessment for the LLLP species, the aggregated assessment performs much worse for the SLHP species after implementation of the MPA. The aggregated assessment is not aware of the spatial differences in sub-population trajectories and it is not surprising that the assessment of the SLHP species, due to its fast growth and high productivity, creates more spatial heterogeneity resulting in larger spawning biomass relative errors.

The assessments for the fished and MPA areas differ appreciably in terms of the relative error of fishing mortality (Figure 1.7). The median relative error for the fished area is close to zero at start of the assessed period and there is tendency for slight underestimation thereafter. In contrast, the median relative error for the MPA is positively biased at the start of the assessed period, after which there is a trend towards a median relative error of 0 for the SLHP species, but a substantially negative relative error for the LLLP species. This behavior is unexpected and cannot be easily explained. The relative error in fishing mortality for the aggregated assessment is not included in Figure 1.6 because fishing mortality cannot be summed across areas. One fish was removed from the MPA in the last year of the stock assessment so that SS could calculate F_{MSY}.[6] This is evident in the upper panel of Figure 1.7, where the relative error of fishing mortality is non-zero in the last year of each assessment.

Relative errors for the estimated recruitment deviations (Figure 1.8) show patterns over time that reflect how informative the age-composition data are about annual recruitment. There is no information about recruitment during the pre-catch period, and the estimated deviation from the spawner-recruit curve tends towards zero (or a percent relative error of -100). The estimated recruitment deviations become median unbiased as the model transitions into a data-rich period, and then tend again towards zero towards the end of the time series. The SLHP and LLLP species differ in how quickly this transition occurs, and information about the reconstructed cohorts extends much further back in time for the LLLP species.

Steepness is a notoriously difficult parameter to estimate. Conn et al. (2010) find that the true value of steepness and the exploitation history of a stock are the most important determinants of whether this parameter is estimated at its upper bound and the precision of the estimate. This is also evident here (Figure

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[6] SS uses fishing mortality in the last year of the assessment as a starting value for calculations of F_{MSY}. The algorithm searches for a multiplier of the ending year fishing mortality and there is consequently no basis to start the optimization search when $F = 0$ in the last year of the assessment. Therefore, "one fish" had to be removed in the last year of each assessment of the MPA for the estimate of this quantity to converge.

1.9). Steepness is more precisely estimated for the SLHP species and the median estimate is close to 1 (the true value is 0.9). Steepness for the LLLP species is estimated near 1 much less frequently and its estimates are more variable. The latter is expected because the true value of steepness for the LLLP species is 0.6. The estimate of steepness for the MPA for both species shifts towards its true value with increasing years of data. This is likely because the fishing down of the stock and subsequent rebuilding within the MPA (Figure 1.3) provides excellent contrast in productivity, which is usually more informative about this parameter (Magnusson and Hilborn 2007). The long data period in the aggregated assessment of the LLLP species provides the most unbiased estimate of steepness. This assessment has the most data, some contrast, and the effects of aggregating heterogeneous data consequently appear less severe for the LLLP species.

Figure 1.10 shows estimates of F_{MSY} for Scenario A0, while Table 1.3 summarizes the performance statistics (MARE and MRE) for this quantity across several scenarios. Scenarios A0 and B0 represent the best case scenario for estimation of F_{MSY} since M, and the growth and maturity parameters are all fixed at their true values. The estimates of F_{MSY} are much more variable for the SLHP species compared to the LLLP species. The median estimate in the MPA assessment gets closer to the true value with increasing years of data and the estimates become less variable with increasing years of data for the LLLP species. Estimates of F_{MSY} for the LLLP fished assessment are generally more precise and unbiased across all years compared to the MPA assessment. The MREs for F_{MSY}, particularly for the SLHP species, are more positively biased for scenario B0 than for scenario A0, which can be attributed to steepness being more positively biased for scenario B0. The increased precision (indicated by lower values for the MARE) with increasing years of data found in the LLLP assessment of the MPA in Scenario A0 is not evident for Scenario B0 (Table 1.3).

The results for scenarios A0 and B0 are encouraging in that the subdivided estimates of current spawning biomass are unbiased regardless of assumptions about density dependence in recruitment, but these results also indicate that the estimates of steepness (and hence quantities which depend on this parameter such as F_{MSY}) may be very poorly estimated.

1.2.2 *Estimation of life-history parameters*
This section shows results for the remaining scenarios identified in Table 1.2. Performance statistics for the estimated life-history parameters and F_{MSY} for each scenario are given in Tables 1.3 – 1.8.

Estimates of the von Bertalanffy growth coefficient, κ, are shown in Figure 1.11 for scenario A1 (as for scenario A0, except that growth is estimated; the results for scenario B1 are qualitatively identical to those for scenario A1). The mean sizes of fish at the young and old reference ages are also estimated when κ is estimated, in addition to the coefficient of variation around the lengths at those reference ages (results not shown). The data provided from the MPA do lead to improved estimates of κ, although the estimates are more biased and imprecise than those for the fished assessment. This parameter is estimated very well for both the fished and aggregated assessments (Table 1.4), which suggests that the effective sample size for the composition data, rather than the status of the population from which this sample comes from is much more important for estimating growth. Estimates of κ are much more precise for the LLLP species compared to the SLHP species. This is especially the case for the fished and aggregated assessments. As with scenarios A0 and B0, the aggregated assessment most frequently performs the best when estimating F_{MSY} for the LLLP species, but the MPA assessment is best for the SLHP species for scenario A1 (Table 1.3).

Figures 1.12 and 1.13 show the estimates of the length-at-maturity parameters for scenario A2 (as for scenario A0, except that maturity is estimated; results are again not shown for scenario B2 as these are qualitatively identical to those for scenario A2). The data provided by the MPA do not lead to more precise estimates of the intercept (Ω_2, length at 50% maturity), although the estimates of the slope Ω_1 of the length-at-maturity relationship shows a slight improvement over time in the MPA (Table 1.5). There is no discernable difference between the precision of the estimated intercept for the SLHP and LLLP species (Figure 1.12), but estimates of the slope for the LLLP species are more precise than those for the SLHP species. This is evident using data for both the MPA and fished area (Figure 1.13). The performance statistics for F_{MSY} for scenarios A2 and B2 are nearly identical to those for scenarios A0 and B0 (contrast Tables 1.3 and 1.6).

Estimates of M for scenario A3 are shown in Figure 1.14 (as for scenario A0, except that natural mortality is estimated; results are again not shown for scenario B3 as these are qualitatively identical to those for scenario A3). Performance statistics are given in Table 1.7. The MPA leads to more precise estimates of M over time, but the effect is much more marked for the SLHP species. However, the estimates of M for the SLHP species converge to a value that is slightly less than the true value (<5% bias). The estimates of natural mortality are generally more precise (have lower MAREs) for the LLLP species. Estimates of F_{MSY}

for scenario A3 are shown in Figure 1.15 and the associated performance statistics are given in Table 1.6. Estimates of F_{MSY} for the LLLP species from the MPA assessment become very precise with increasing years of data. This was also evident for scenario A0, although the estimates are much more variable when M is estimated. As was the case for scenario B0, the estimates of F_{MSY} are more positively biased when density dependence is post-dispersal (scenario B3) (Table 1.6).

Boxplots of the estimated F_{MSY} and M are not shown for the remaining scenarios, but performance statistics for M are given in Tables 1.7 and 1.8. These scenarios (Table 1.2) were designed to examine the sensitivity to changing aspects of scenarios A3 and B3 so the estimates of F_{MSY} should either remain unchanged or become more biased and less precise.

The growth parameters and the rate of natural mortality are both estimated in scenario A4. The same pattern in the variability of the estimated parameter with increasing time holds, but now the estimates of natural mortality are negatively biased (Table 1.7). The estimated growth coefficient is estimated with negligible bias (Table 1.4). To our knowledge, this is the first simulation study that has used an age- and length- structured stock assessment when estimating natural mortality and this analysis suggests that there is possible confounding between M and the growth parameters.

Scenario A.5 examines of the implications of dome-shaped selectivity. Estimates of M become negatively biased and the variability of the estimates of M from the MPA assessment do not decrease over time as appreciably (Table 1.7) in contrast to scenario A1. Thompson (1994) noted that selectivity and natural mortality were confounded because when selectivity does not fully target the oldest fish; the high frequency of older fish in the fishery and survey age composition can be fitted by increasing M. Estimates of M were negatively biased in this study, which can be attributed to SS overestimating the descending limb of the selectivity curve at the oldest ages (results not shown).

The effects of adding age-reading error (with a constant CV of 0.2) to the age composition data when the correct aging error definition is assumed are examined in scenario A6a. The results for scenarios A3 and A6a are nearly identical (compare Tables 1.7 and 1.8). However, a constant CV of 0.2 for ageing error is very large and the lack of impact on the ability to estimate M can be attributed to the stock assessment assuming the exact aging error definition that generated the data. In scenario A6b, age-composition data are generated assuming aging-error, but the stock assessment ignores this feature. Estimates of M become

substantially positively biased in the fished and aggregated assessments (Table 1.8), but the MPA shows the same pattern of increased precision over time for scenario A6b. Estimates of M in the short data period, however, are biased for both the SLHP and LLLP species.

Scenario A7 examines the impact of obtaining length, but no age, data from the MPA. The results for the SLHP species are the same for scenario A7 as for scenario A3. However, the estimates of M are now positively biased for the LLLP species and M is now estimated best using data from fished area (Table 1.8). However, the estimates of M are best using data from the MPA when there is a long time-series of data. Scenario A7 suggests that informative age composition data are potentially superfluous to estimation of a constant natural mortality when the exact F is known.

Scenario A8 considers the effect of obtaining no data at all from the MPA. This results in a dearth of survey composition data and estimates of abundance after implementation of the MPA. Without this information, estimates of M from the MPA are substantially negatively biased for the SLHP species and positively biased for the LLLP species (Table 1.8). There is no change in precision with increasing years of protection for the MPA assessment because there are no additional data to inform the stock assessment.

The effect of doubling the total survey CV and halving the length and age sample sizes is considered in scenario A9. This scenario still indicates that M is estimated better using data from the MPA primarily because the estimates of M in the fished and aggregated assessment become substantially more variable (Table 1.8). Estimates for all species and time periods become more biased when the data are less precise, but the estimates of M from the MPA continue to approach the true value with increasing years of protection.

1.3 DISCUSSION

Field et al. (2006) argue that MPAs may provide a source of older, larger fish which could improve biological studies on life-history. The main results presented here indicate that data from a MPA can potentially improve estimates of natural mortality, but it is unlikely that estimates of growth and maturity parameters will improve substantially because these parameters are already estimated reliably using data from fished populations.

Several scenarios examined the sensitivity of natural mortality estimation to assumptions about data availability. Not surprisingly, estimates of M are substantially biased when no data are collected from the

MPA. However, reliable estimates of M can still be obtained when only length data and an index of abundance are available from the MPA. This is very encouraging, particularly if lethal sampling for scientific purposes were to be prohibited from the MPA. It also suggests that new data collection techniques that only provide estimates of numbers and lengths can be incorporated into a stock assessment model without drastically affecting model performance in terms of estimates of $M,$ but estimates of current spawning biomass may be less precise (results not shown). The effects of having insufficient age-composition data also provide new insight into estimation performance of statistical catch-at-age models. It is usually perceived that age-composition data are essential to estimation of natural mortality. These results suggest that these data are not a necessity when the fishing mortality is known in addition to having an index of abundance. This, of course, would not likely be the case when attempting to estimate age-specific natural mortality.

These results differ somewhat from other studies (Thompson 1994, Schnute and Richards 1995, Wang 1999, Ianelli 2002, Magnusson and Hilborn 2007) that have attempted to estimate natural mortality within a stock assessment model. These studies showed that natural mortality was highly confounded with other parameters and estimates of $M,$ consequently, were unrealistic. The results presented here for the fished assessment of the LLLP species indicate that M can be estimated with reasonable accuracy and precision when selectivity is asymptotic. It should be recognized that there is a potential misconception that M cannot be estimated within a stock assessment. Progression of modern statistical catch-at-age models such as SS may now make estimation of this parameter more feasible (Lee et al. in review).

Parameters that were fixed in this study (*i.e.* σ_R), were at their true value and hence the model was specified correctly. Estimates of M can be erroneous when a model is not specified correctly, because the model attempts to adjust this parameter for the misspecification of other parameters (Lee et al. in review). A constant natural mortality that was independent of time, sex and age was only examined in this study. Thus, the success of estimating of M will likely depend on a variety of factors, including model specification and the structure of natural mortality that is modeled.

Estimates of management quantities such as spawning stock biomass and F_{MSY} were generally more precise for the LLLP species compared to the SLHP species. This was also noted by Haltuch et al. (2008) when comparing estimation performance for a shorter-lived species (Pacific whiting, *Merluccius productus*)

with that for a longer-lived rockfish species primarily because of higher annual recruitment variability in Pacific whiting. Variation in annual recruitment was the same for the SLHP and LLLP species in this study and yet, estimation of model parameters, and consequently management quantities was still much more precise for the LLLP species. This is likely because annual recruitment is a smaller fraction of the total biomass for a less productive species and thus the stock assessment is less affected by unusual recruitment events. In addition, faster turnover rates of a short-lived species mean that the population structure at any time does not carry as forward into the future compared to a long-lived species and so there is less data that is informative about past and present population structure.

This simulation study examined two forms of density-dependence in recruitment. Stock Synthesis assumes that there is no dispersal of fish between areas (Scenario A) and compensated for data that were generated under the post-dispersal scenario (Scenario B) by overestimating steepness. Although the estimates of life-history parameters were robust to assumptions about density dependence, those of F_{MSY} were sensitive to this assumption.

Overall, the main results presented in this chapter suggest that: i) the negative impact of heterogeneous populations on a stock assessment is slight when account of this is taken by conducting separate assessments of the MPA and fished area, ii) the data collected from an MPA can potentially lead to more precise estimates of natural mortality, but not growth and maturity related parameters, and iii) the differences in life-history characteristics affect the performance of stock assessment models and one might expect to obtain more precise results for longer-lived species with lower productivity. These results were obtained under a simplified data generating scenario in which there was no movement of between the MPA and the fished area.

FIGURES

Figure 1.1: Stable vs. non-stable population age distribution. R_0 represents the unfished recruitment and x is the maximum age, taken to be a plus-group.
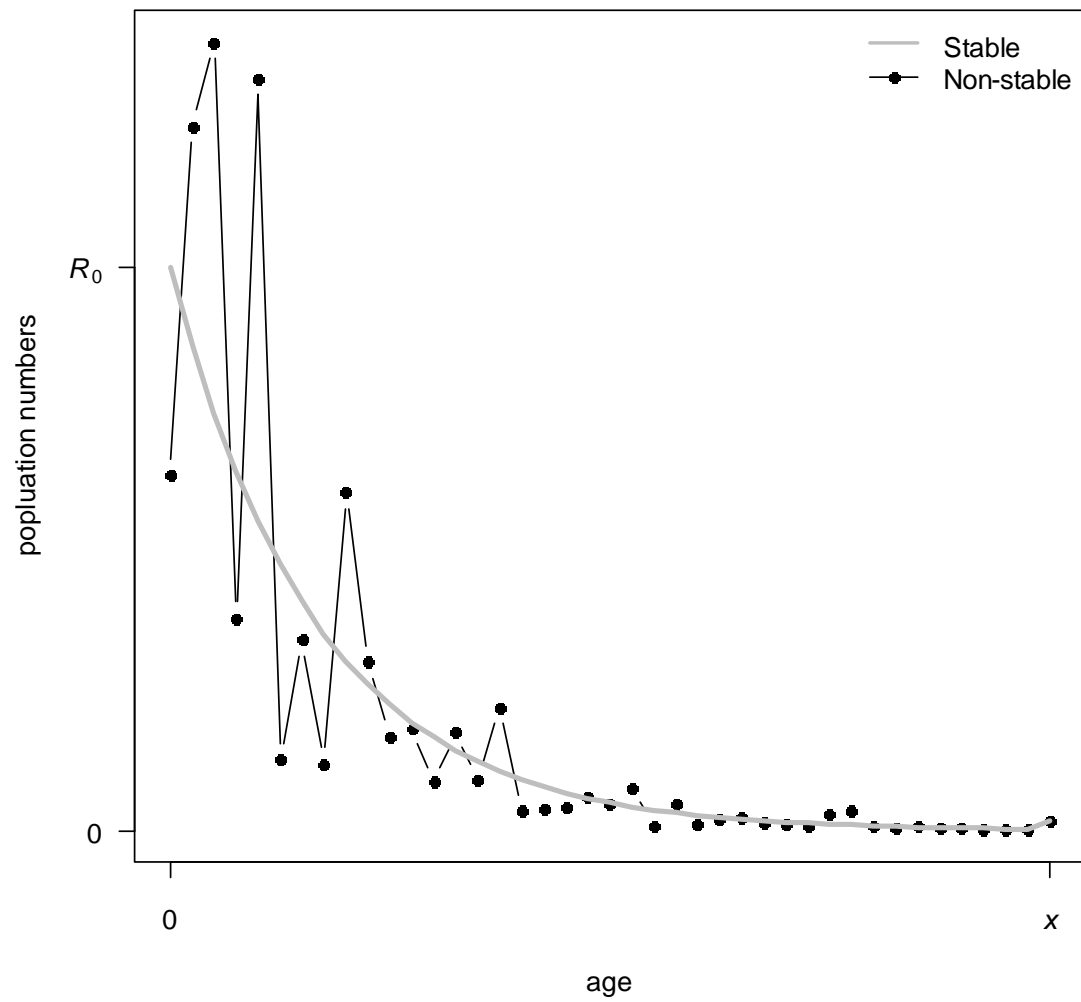
Figure 1.2: Biological- and exploitation-related functions for the LLLP and SLHP species. The solid line in the length v. selectivity panel indicates fishery selectivity and the dotted line indicates survey selectivity.
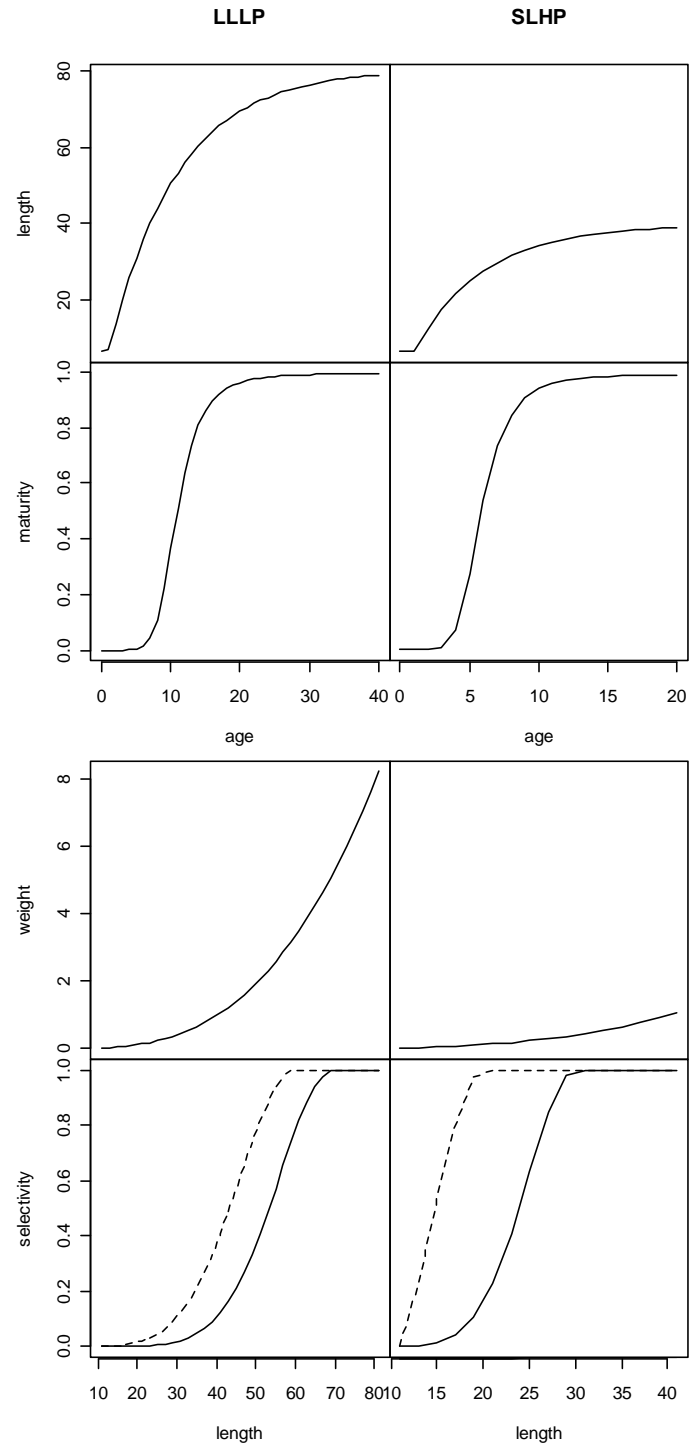
Figure 1.3: Illustration of the 100 simulated time-trajectories of spawning biomass and spawning biomass relative to B_0 (depletion) for the SLHP (upper panels) and LLLP (lower panels) species. For reference, the y-axis label, B_0, corresponds to the median total spawning biomass.
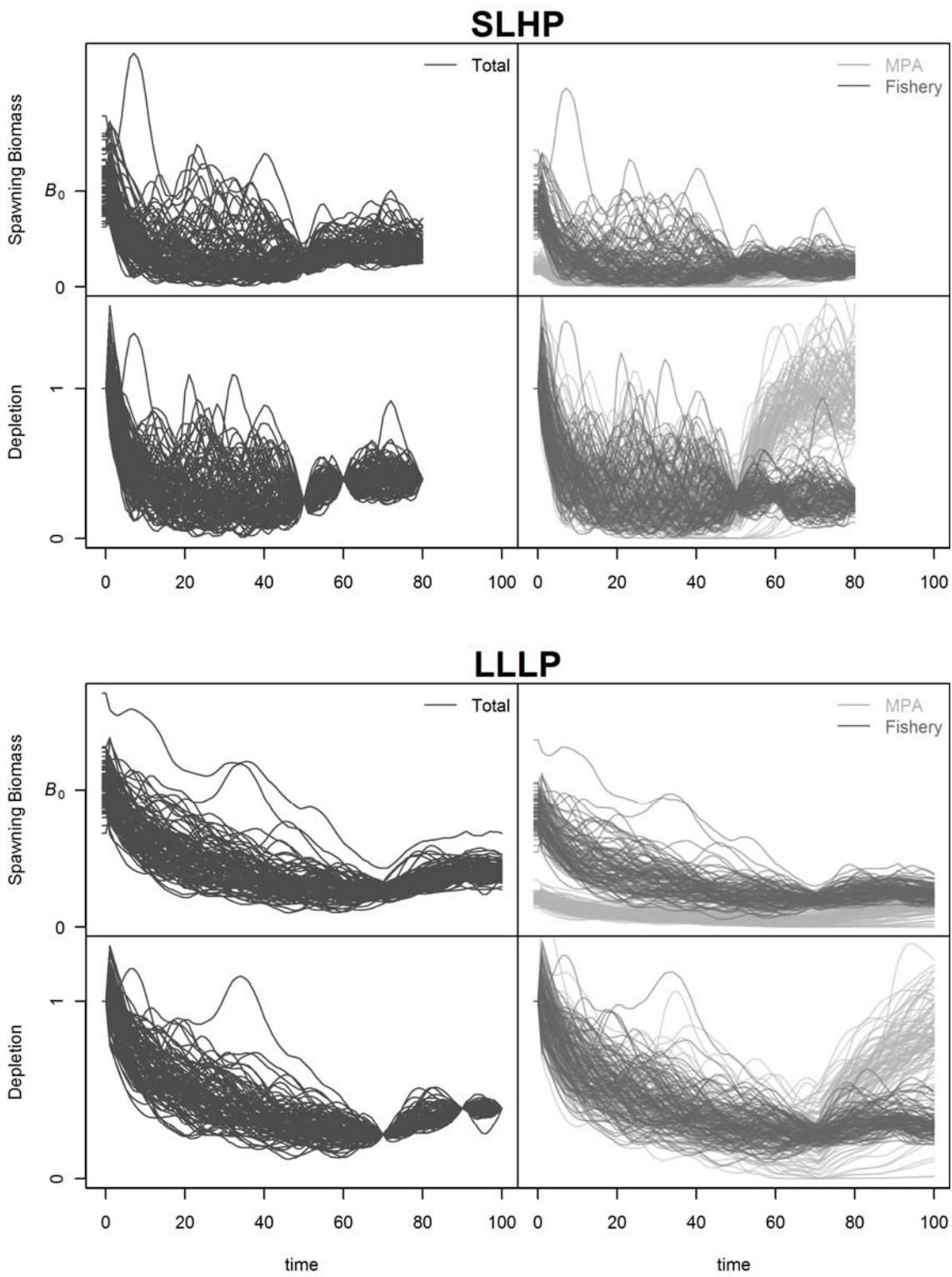
Figure 1.4: The dome-shaped selectivity patterns for scenario A.5.
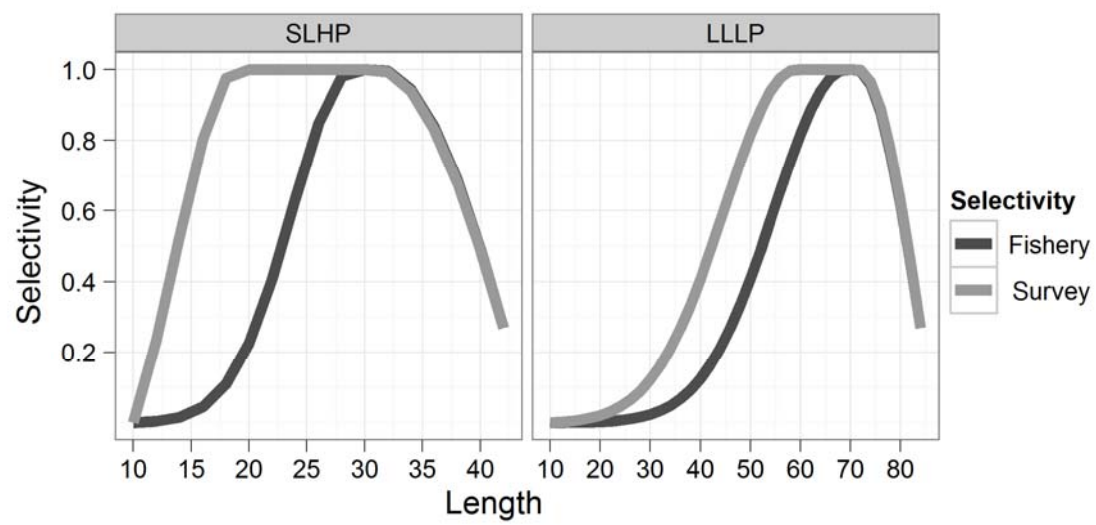
Figure 1.5: Schematic showing features of the data generated by the operating model and the status of the stock (across both the MPA and fished cells) at those times. Recruitment deviations are generated during the pre-catch period so that the population is not in equilibrium when catches commence. Year 0 is the first year for which catch data are available to the assessment, but no information on length and age, in addition to survey indices of abundance, are available until later in the assessment period. The length of the pre-catch period and the timing of data availability is scaled to the maximum age (x) of the fish. This then leads to the stock being declared overfished at different points in time for the SLHP and LLLP species, but the length of successive data years prior to and after the overfished declaration are the same. The "survey only" category indicates that a survey index of abundance is available, in addition to length and age composition from that survey. In the "both" category, survey data are available in addition to length and age composition data from the fishery.
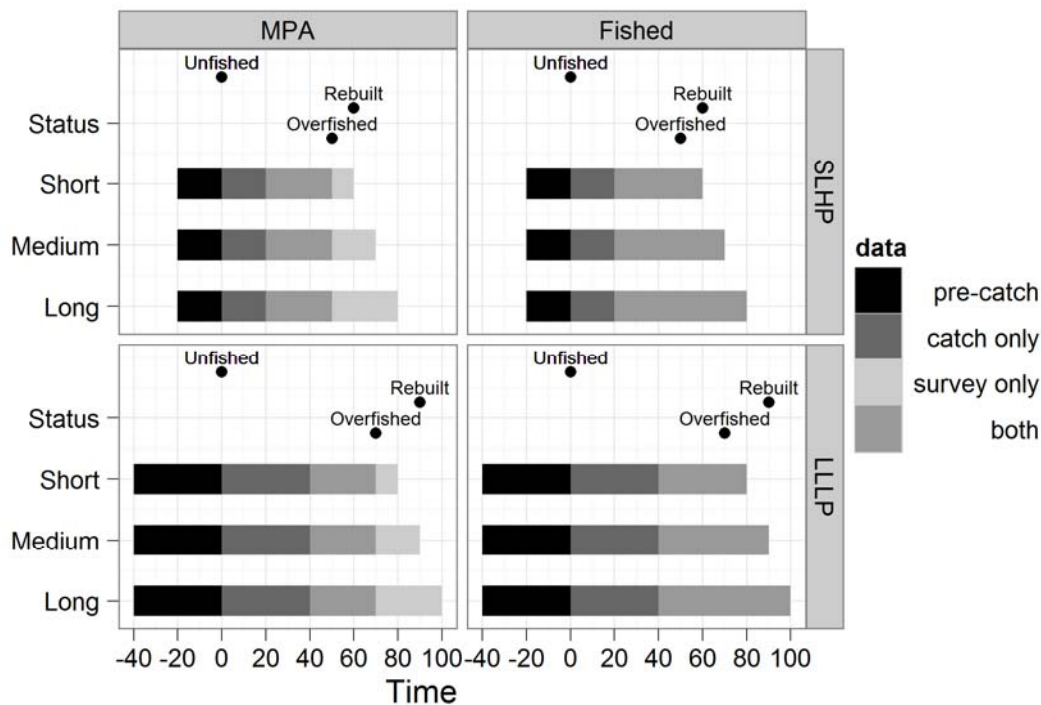
Figure 1.6: Median (dark line) and 90% simulation intervals (shaded gray) for the annual relative errors for spawning biomass for scenario A0. A dotted horizontal line is drawn at zero indicating no error. A dotted vertical line is drawn at the time corresponding to implementation of the MPA. The different shades of gray correspond to the assessment with short, medium and long lengths of data.
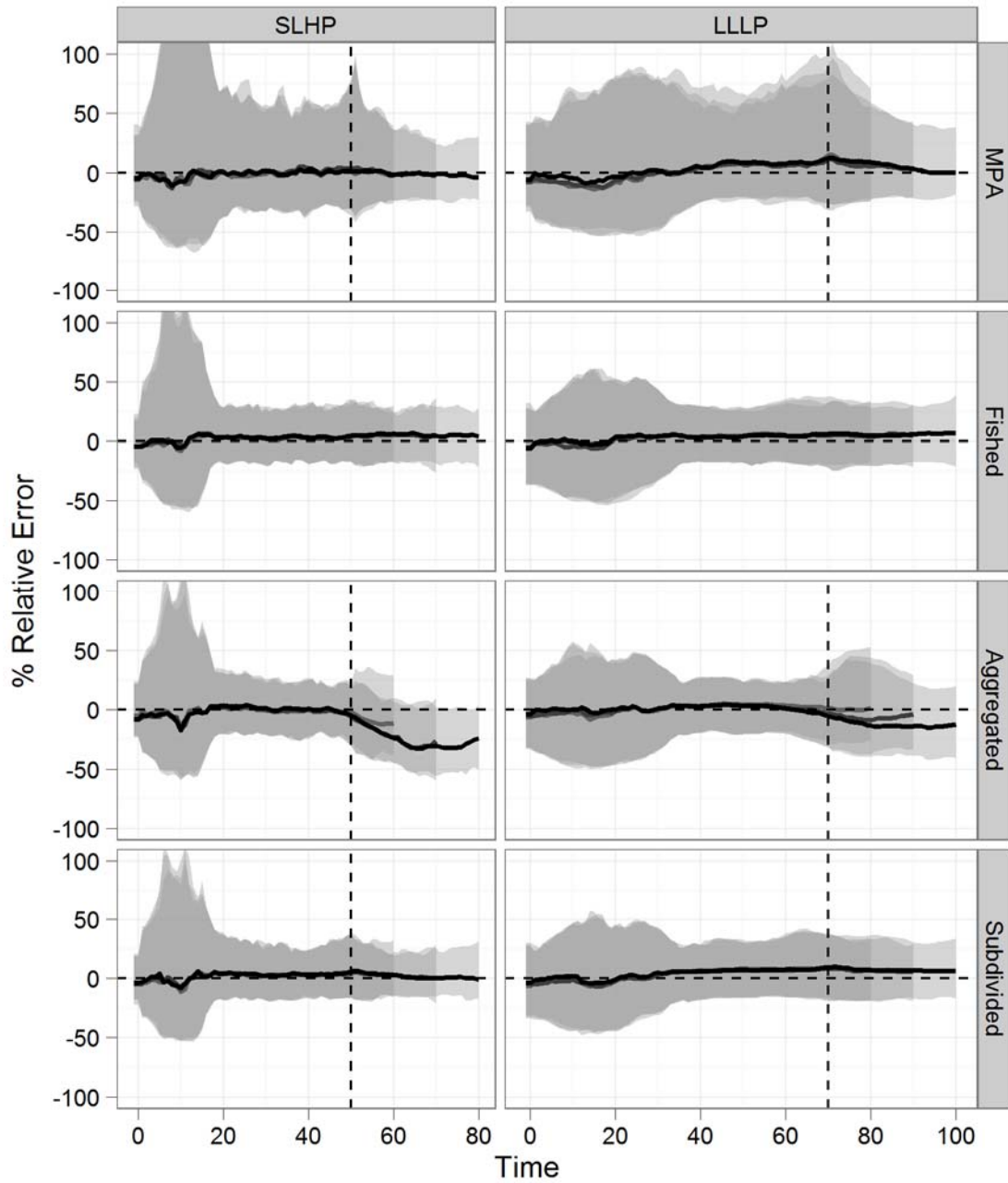
Figure 1.7: Median (dark line) and 90% simulation intervals (shaded gray) for the annual relative errors for fishing mortality for scenario A0. A dotted horizontal line is drawn at zero indicating no error. A dotted vertical line is drawn at the time corresponding to implementation of the MPA. The different shades of gray correspond to the assessment with short, medium and long lengths of data.
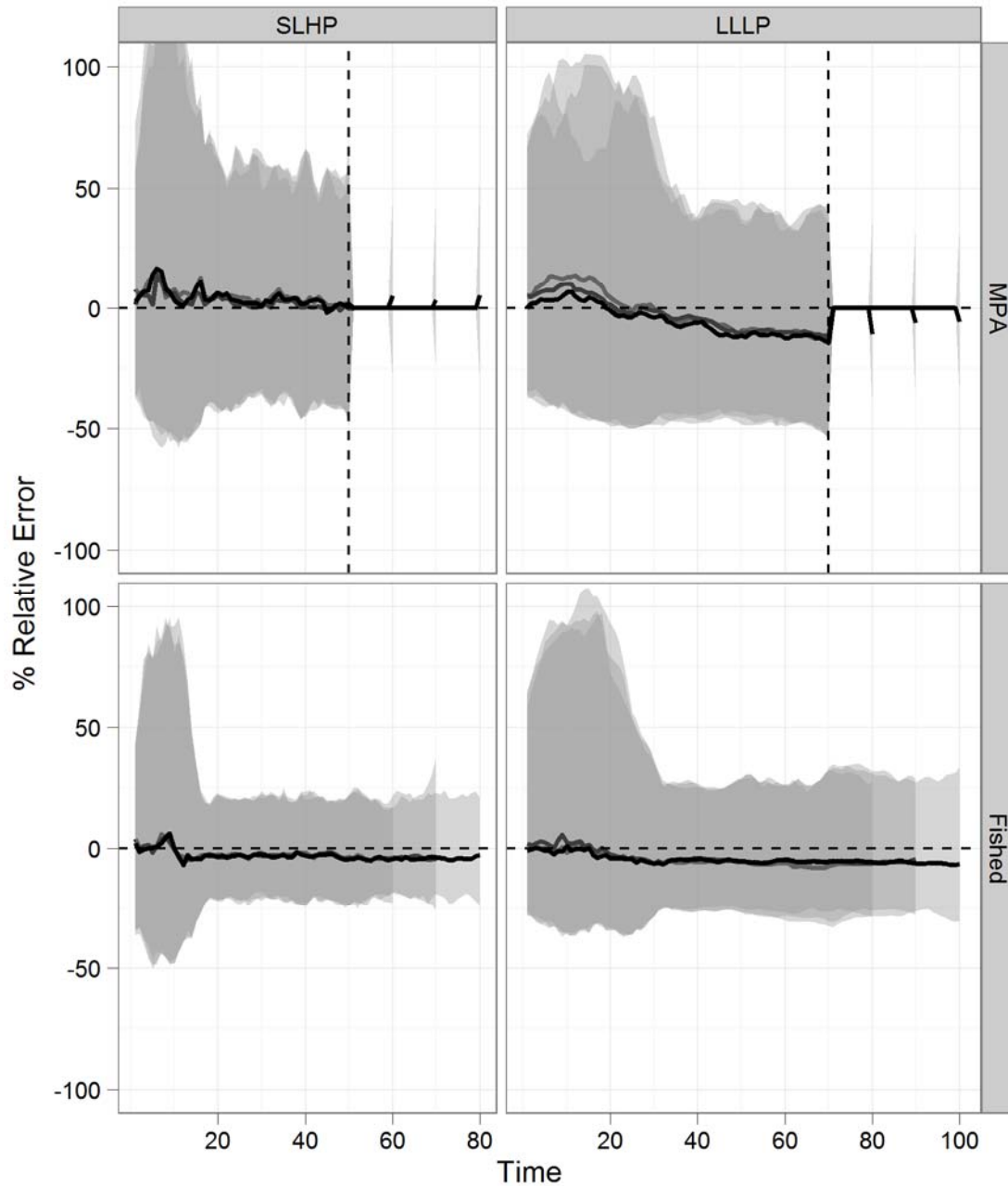
Figure 1.8: Median and 90% simulation intervals for the annual relative errors for recruitment deviations for scenario A0. A dotted horizontal line is drawn at zero indicating no error. A dotted vertical line is drawn at the time corresponding to implementation of the MPA. The different shades of gray correspond to the assessment with short, medium and long lengths of data.
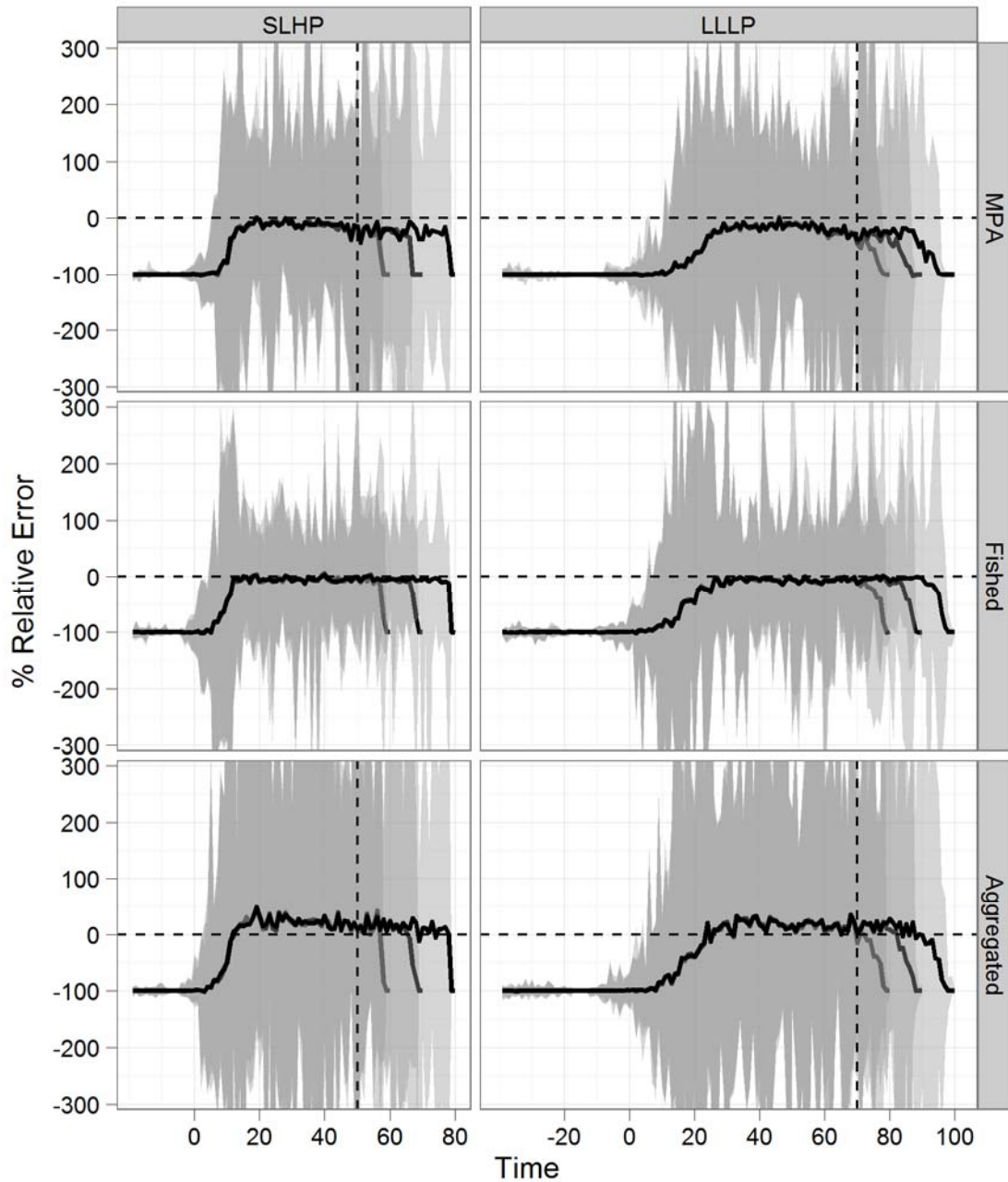
Figure 1.9: Boxplots of the estimated steepness parameter for scenario A0. A dotted horizontal line is drawn at the true value.
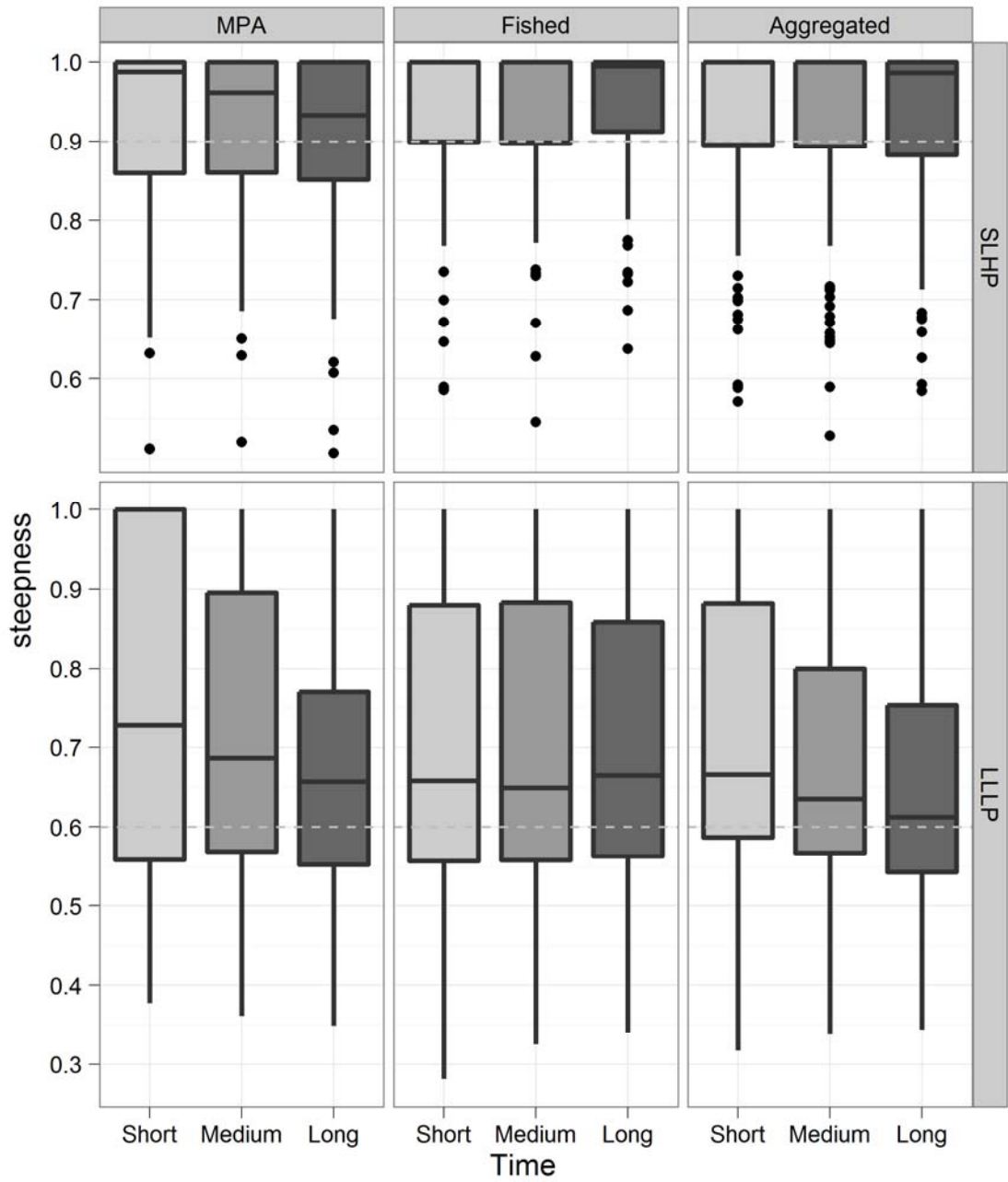
Figure 1.10: Boxplots of the estimated F_{MSY} for scenario A0. A dotted horizontal line is drawn at the true value.
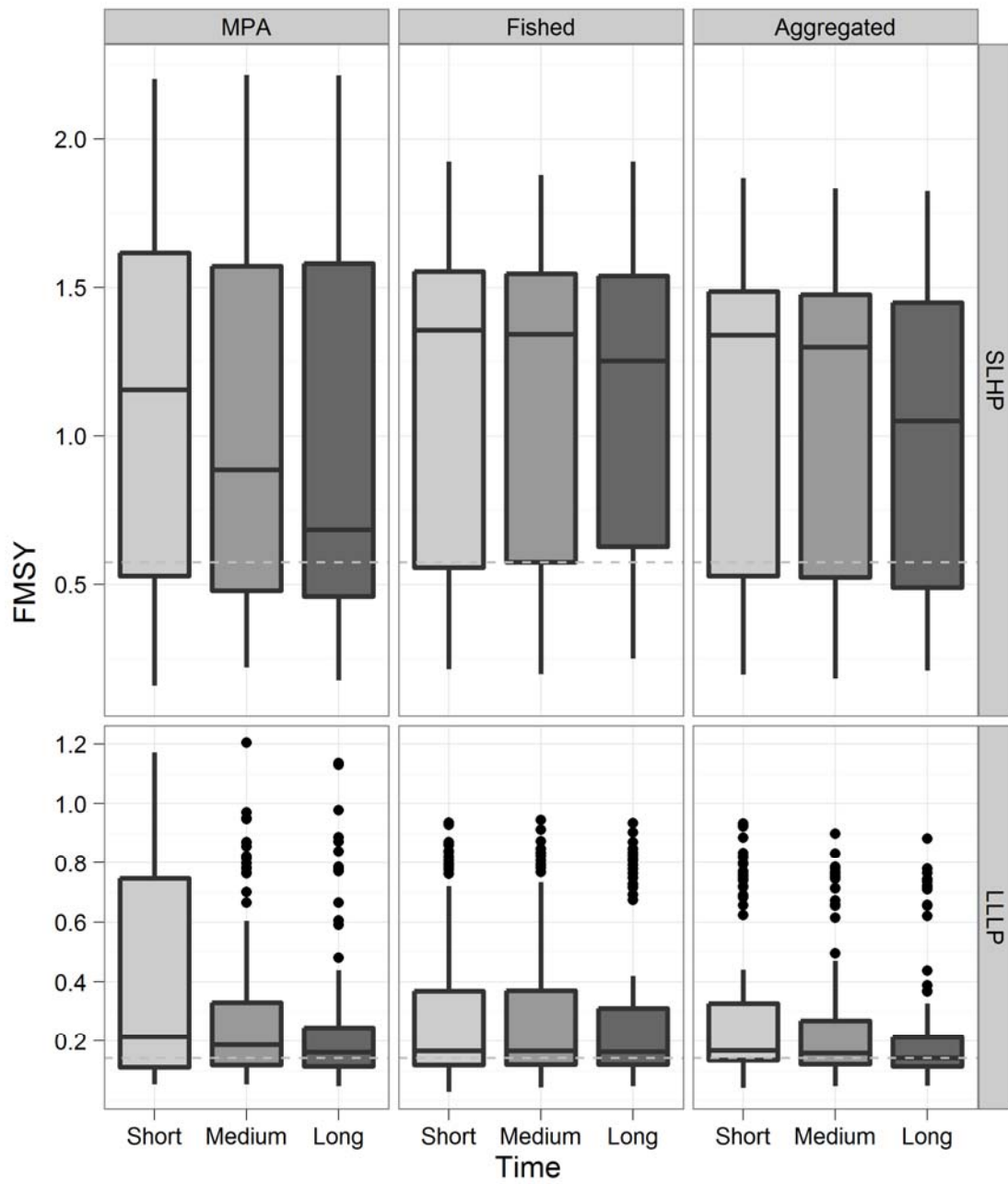
Figure 1.11: Boxplots of the estimated growth coefficient for scenario A1. A dotted horizontal line is drawn at the true value.
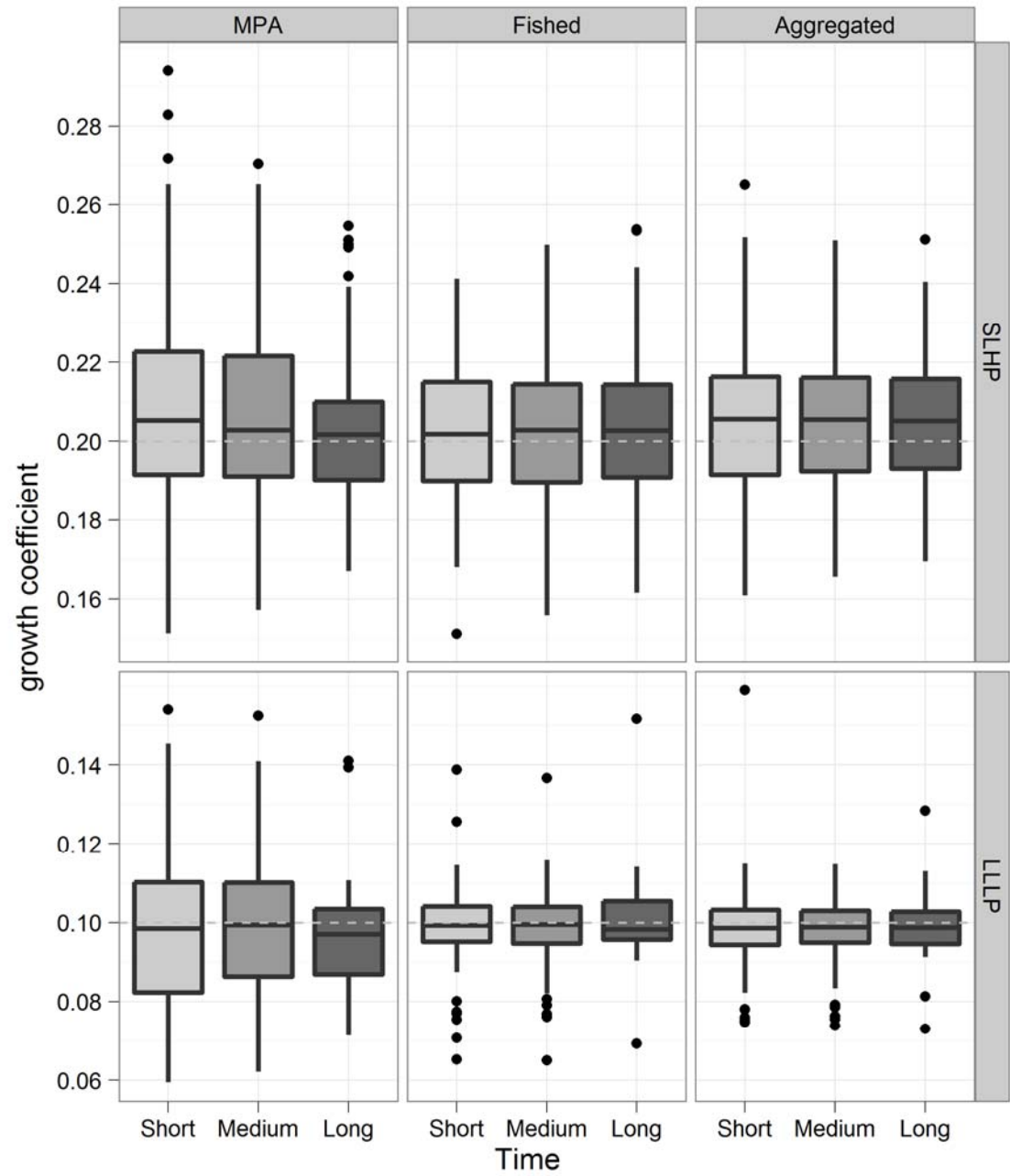
Figure 1.12: Boxplots of the estimated intercept (length at 50% maturity) of the length-at-maturity relationship for scenario A2. A dotted horizontal line is drawn at the true value.
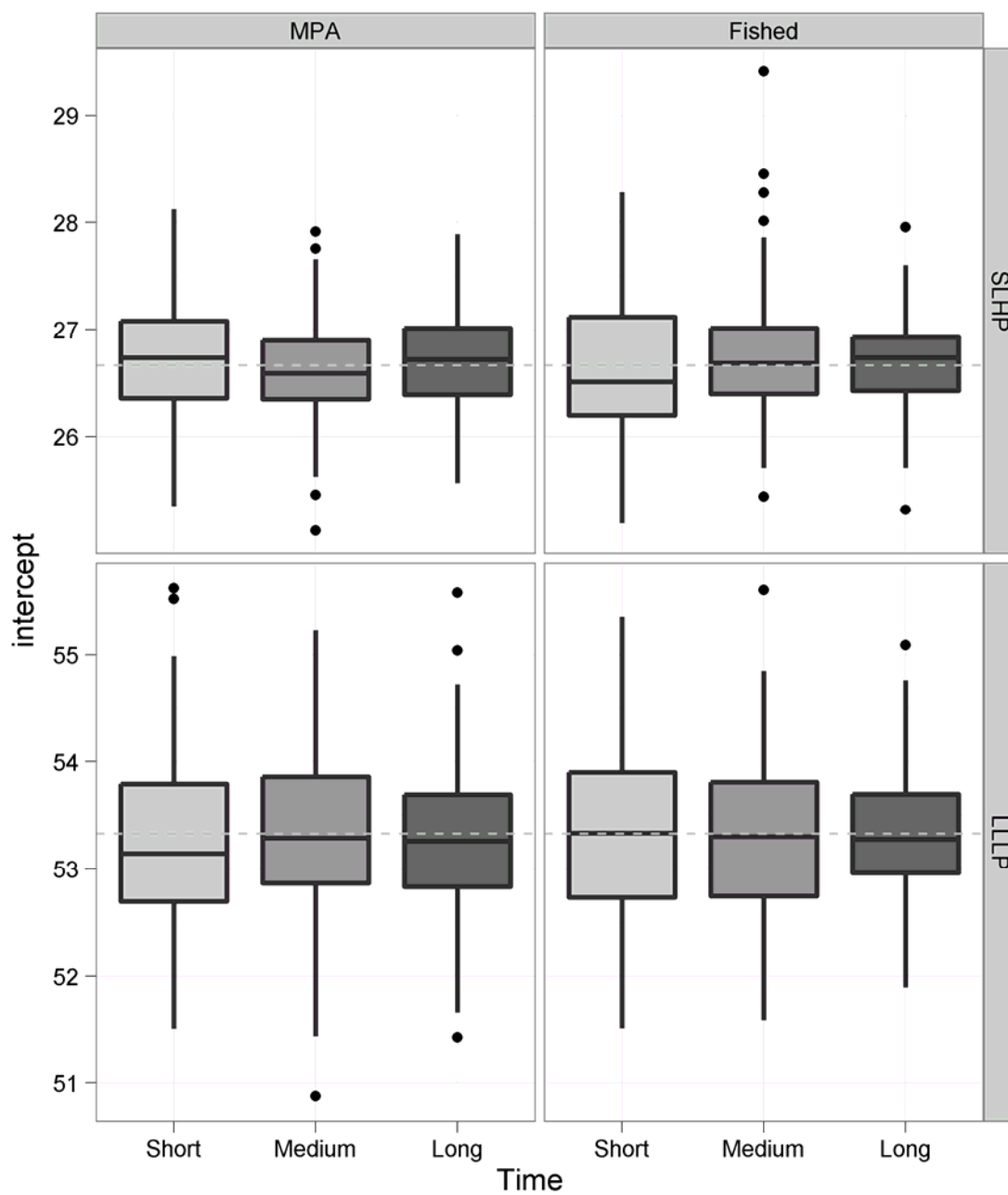
Figure 1.13: Boxplots of the estimated slope of the length-at-maturity relationship for scenario A2. A dotted horizontal line is drawn at the true value.
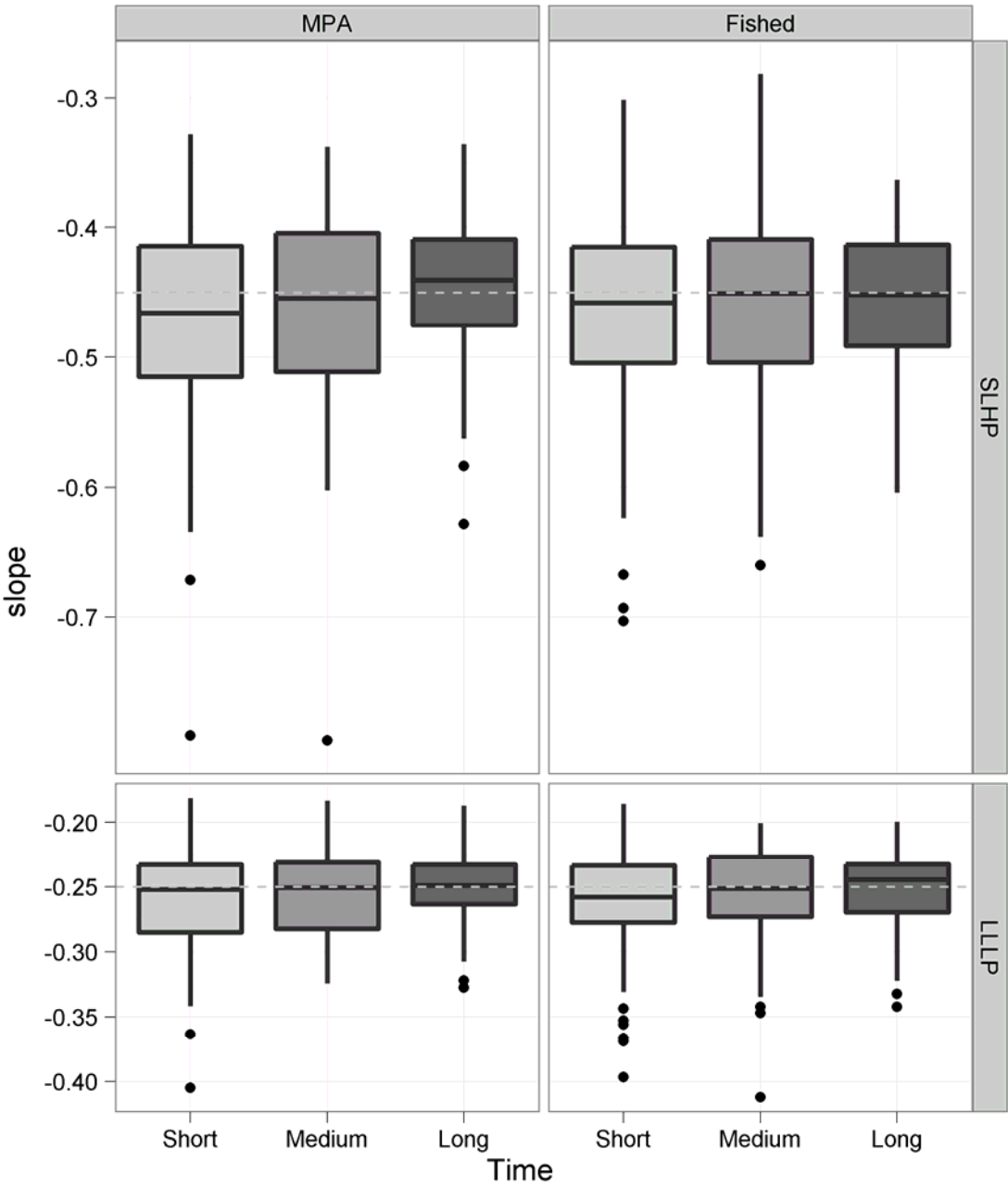
Figure 1.14: Boxplots of the estimated rate of natural mortality for scenario A3. A dotted horizontal line is drawn at the true value.
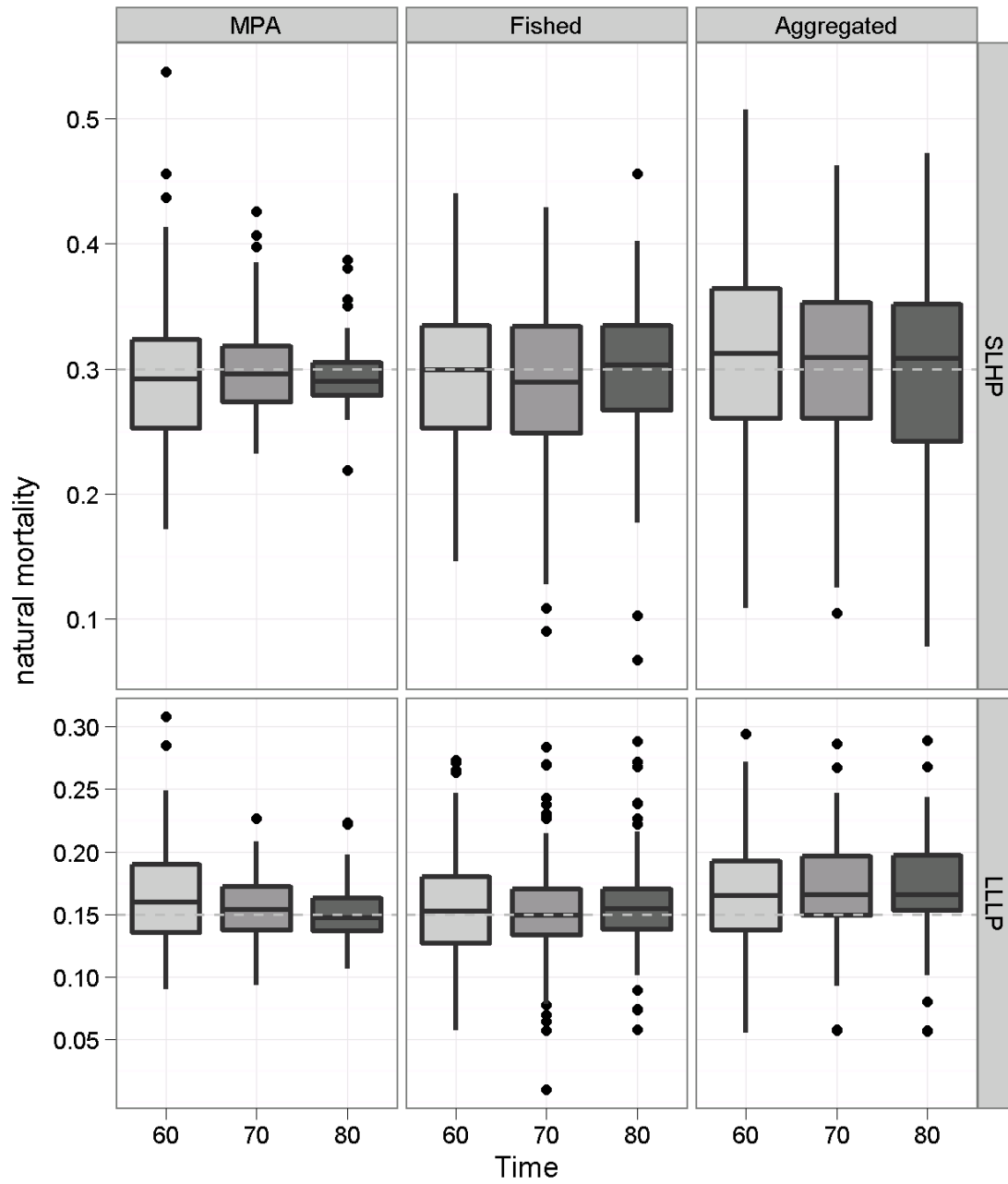
Figure 1.15: Boxplots of the estimated F_{MSY} for scenario A3. A dotted horizontal line is drawn at the true value. The y-axis is truncated because there are a few outlying observations ($F_{MSY} > 7$).
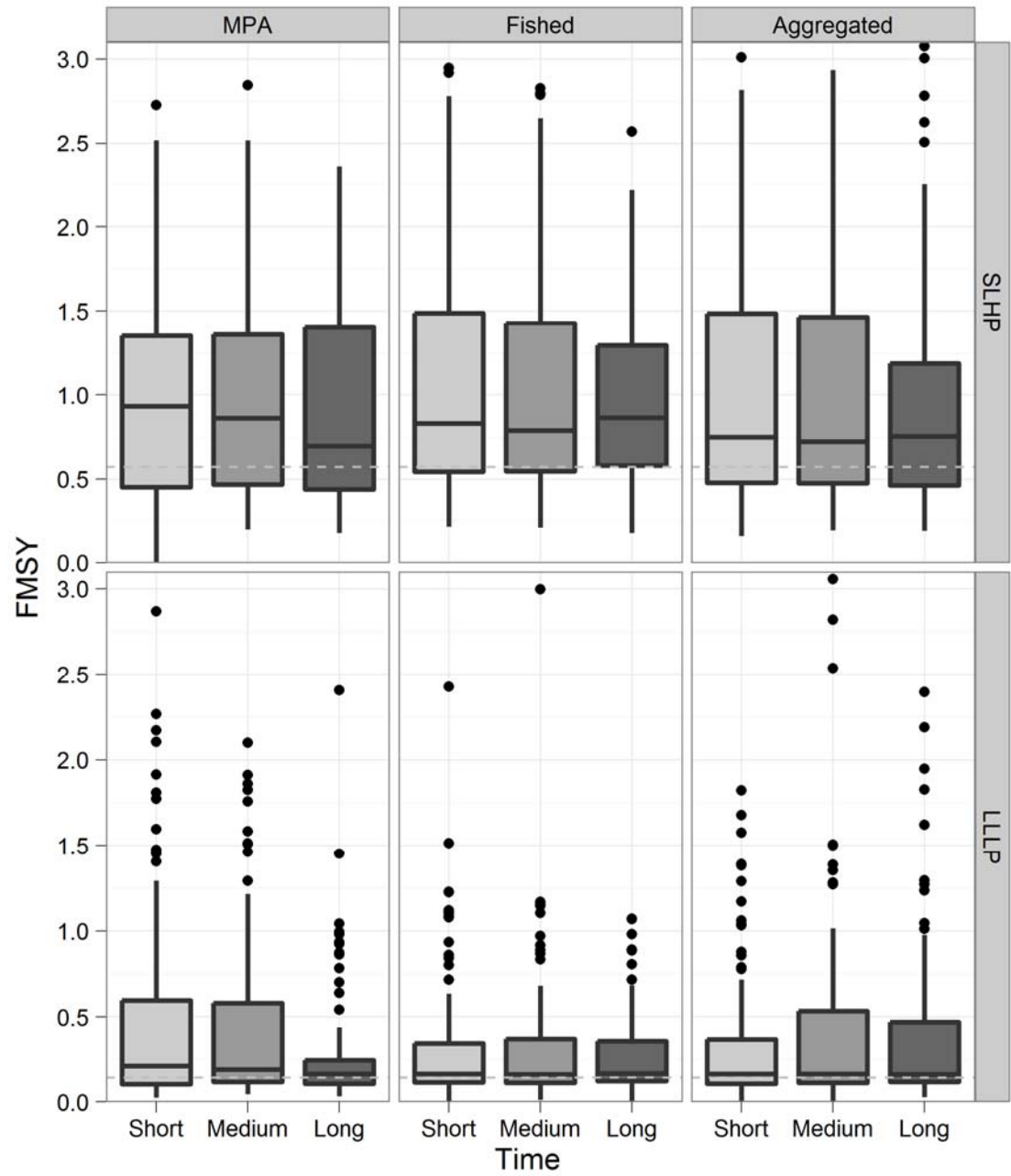
Tables

Table 1.1: The values for the baseline parameters of the operating model for the two life history strategies (assumed to be the same for the two sexes). The last column indicates whether the parameter concerned is estimated within the SS estimating model.

Parameter	Description	LLLP	SLHP	
M	Natural mortality (yr^{-1})	0.15	0.3	Estimated
x	Maximum age	40	20	Fixed
h	Steepness	0.6	0.9	Estimated
λ^c	Fraction of recruitment to each cell	(0.2,0.8)	(0.2,0.8)	Fixed
κ	Growth coefficient	0.1	0.2	Estimated
L_∞	Asymptotic size	80	40	Fixed
L_1	Mean length at reference age a_1	3	3	Estimated
L_2	Mean length at reference age a_2	78	38	Estimated
a_1	Reference age 1	1	1	Fixed
a_2	Reference age 2	35	16	Fixed
CV_1	Coefficient of variation for age a_1	0.1	0.1	Estimated
CV_2	Coefficient of variation for age a_2	0.1	0.1	Estimated
e_1	Allometric weight-at-length parameter	1.55×10^{-05}	1.55×10^{-05}	Fixed
e_2	Allometric weight-at-length parameter	3	3	Fixed
Ω_1	Maturity slope parameter	-0.25	-0.45	Estimated
Ω_2	Length at 50% maturity	53.33333	26.66667	Estimated
$\beta_{Fish,1}$	Fishery selectivity	70	30	Estimated
$\beta_{Fish,2}$	Fishery selectivity	3	3	Fixed
$\beta_{Fish,3}$	Fishery selectivity	6	4	Estimated
$\beta_{Fish,4}$	Fishery selectivity	6	6	Fixed
$\beta_{Fish,5}$	Fishery selectivity	-10	-10	Estimated
$\beta_{Fish,6}$	Fishery selectivity	-999	-999	Fixed
$B_{Surv,1}$	Survey selectivity	60	20	Estimated
$B_{Surv,1}$	Survey selectivity	3	3	Fixed
$B_{Surv,3}$	Survey selectivity	6	4	Estimated
$B_{Surv,4}$	Survey selectivity	6	6	Fixed
$B_{Surv,5}$	Survey selectivity	-10	-10	Estimated
$B_{Surv,6}$	Survey selectivity	-999	-999	Fixed
σ_C	Cell-specific recruitment variation	0.42	0.42	Fixed
σ_T	Common (across both cells) recruitment variation	0.42	0.42	Fixed
σ_q	Deviation from calculated fishing mortality	0.1	0.1	-
σ_B	Total (across both cells) survey biomass error	0.1	0.1	Fixed

Table 1.2: The scenarios considered in Chapter 1.

Scenario	S-R Relationship	Life-history parameters estimated	Additional specifications
A0	A.3a	-	-
A1	A.3a	Growth	-
A2	A.3a	Maturity	-
A3	A.3a	Natural mortality	-
B0	A.3b	-	-
B1	A.3b	Growth	-
B2	A.3b	Maturity	-
B3	A.3b	Natural mortality	-
A4	A.3a	Natural mortality and growth	-
A5	A.3a	Natural mortality	Dome-shaped selectivity
A6a	A.3a	Natural mortality	Aging error with correct aging error definition in the stock assessment
A6b	A.3a	Natural mortality	Aging error with incorrect aging error definition in the stock assessment
A7	A.3a	Natural mortality	AUV length data
A8	A.3a	Natural mortality	No survey
A9	A.3a	Natural mortality	Sample sizes halved and CVs of survey abundance doubled

Table 1.3: Median absolute relative errors for estimates of F_{MSY}. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	Fished	Aggregated
A0	SLHP	Short	**1.013** (+1.01)	1.36 (+1.36)	1.332 (+1.32)
		Medium	**0.591** (+0.55)	1.338 (+1.34)	1.301 (+1.3)
		Long	**0.52** (+0.19)	1.182 (+1.18)	1.131 (+1.13)
	LLLP	Short	0.575 (+0.5)	0.399 (+0.17)	**0.341** (+0.19)
		Medium	0.501 (+0.31)	0.331 (+0.16)	**0.289** (+0.15)
		Long	0.394 (+0.14)	0.32 (+0.15)	**0.255**
B0	SLHP	Short	1.459 (+1.46)	**1.335** (+1.34)	1.345 (+1.35)
		Medium	**1.215** (+1.22)	1.342 (+1.34)	1.331 (+1.33)
		Long	**1.154** (+1.15)	1.391 (+1.39)	1.246 (+1.25)
	LLLP	Short	1.079 (+1.08)	0.403 (+0.16)	**0.364** (+0.22)
		Medium	1.27 (+1.27)	**0.324** (+0.15)	0.279 (+0.18)
		Long	0.928 (+0.93)	0.337 (+0.24)	**0.231** (+0.06)
A1	SLHP	Short	**0.973** (+0.97)	1.193 (+1.19)	1.074 (+1.07)
		Medium	**0.572** (+0.48)	1.234 (+1.23)	1.116 (+1.17)
		Long	**0.532** (+0.24)	1.227 (+1.23)	1.071 (+0.1.07)
	LLLP	Short	0.557 (+0.39)	**0.327**	0.347 (+0.06)
		Medium	0.509 (+0.26)	0.319 (+0.12)	**0.293** (+0.14)
		Long	0.383 (+0.13)	0.331 (+0.16)	**0.209** (+0.07)
B1	SLHP	Short	1.327 (+1.33)	**1.207** (+1.21)	1.196 (+1.2)
		Medium	1.229 (+1.23)	1.227 (+1.23)	**1.244** (+1.24)
		Long	**1.089** (+1.09)	1.316 (+1.32)	1.152 (+1.15)
	LLLP	Short	1.295 (+1.3)	0.433 (+0.14)	**0.333** (+0.19)
		Medium	2.141 (+2.14)	0.338 (+0.14)	**0.299** (+0.16)
		Long	1.638 (+1.64)	0.34 (+0.22)	**0.252** (+0.07)

Table 1.4: Median absolute relative errors for estimates of the von Bertalanffy growth coefficient. This parameter was always estimated with negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*	*Aggregated*
A1	SLHP	Short	0.078	0.062	**0.057**
		Medium	0.059	0.063	**0.057**
		Long	**0.05**	0.056	0.057
	LLLP	Short	0.12	**0.044**	0.048
		Medium	0.12	**0.0469**	0.0474
		Long	0.085	0.049	**0.047**
B1	SLHP	Short	0.085	0.061	**0.055**
		Medium	0.069	0.063	**0.055**
		Long	0.059	0.06	**0.056**
	LLLP	Short	0.141	0.056	**0.054**
		Medium	0.096	0.048	**0.043**
		Long	0.088	0.051	**0.04**
A4	SLHP	Short	0.075	**0.058**	0.06
		Medium	0.068	0.061	**0.057**
		Long	0.054	0.062	**0.057**
	LLLP	Short	0.13	**0.044**	0.051
		Medium	0.116	**0.044**	0.05
		Long	0.0882	**0.0508**	0.0509

Table 1.5: Median absolute relative errors for estimates of maturity parameters (Equation A.15). The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*
A.2 (Ω_1)	SLHP	Short	0.115	**0.106**
		Medium	0.119	**0.103**
		Long	**0.083**	0.09
	LLLP	Short	0.109	**0.105**
		Medium	**0.09**	0.115
		Long	0.090	**0.076**
A.2 (Ω_2)	SLHP	Short	**0.015**	0.018
		Medium	**0.011**	0.012
		Long	0.011	**0.01**
	LLLP	Short	**0.010**	0.013
		Medium	0.009	0.009
		Long	**0.008**	0.01
B.2 (Ω_1)	SLHP	Short	0.111 (+0.06)	**0.11**
		Medium	0.096	**0.093**
		Long	**0.083**	0.087
	LLLP	Short	**0.098**	0.104
		Medium	0.1	**0.093**
		Long	0.088	**0.087**
B.2 (Ω_2)	SLHP	Short	0.018	**0.016**
		Medium	**0.013**	0.015
		Long	**0.013**	0.015
	LLLP	Short	**0.01**	0.011
		Medium	0.011	**0.009**
		Long	0.009	**0.008**

Table 1.6: Median absolute relative errors for estimates of F_{MSY}. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*	*Aggregated*
A2	SLHP	Short	**0.905** (+0.91)	1.307 (+1.31)	1.332 (+1.33)
		Medium	**0.576** (+0.56)	1.329 (+1.33)	1.225 (+1.22)
		Long	**0.522** (+0.2)	1.155 (+1.15)	0.974 (+0.97)
	LLLP	Short	0.579 (+0.49)	0.403 (+0.16)	**0.304** (+0.17)
		Medium	0.495 (+0.31)	0.314 (+0.16)	**0.304** (+0.12)
		Long	0.391 (+0.14)	0.32 (+0.14)	**0.274**
B2	SLHP	Short	**1.325** (+1.32)	1.36 (+1.36)	1.335 (+1.33)
		Medium	**1.226** (+1.23)	1.342 (+1.34)	1.31 (+1.31)
		Long	**1.141** (+1.14)	1.391 (+1.39)	1.259 (+1.26)
	LLLP	Short	1.071 (+1.32)	0.397 (+0.15)	**0.341** (+0.2)
		Medium	0.908 (+0.91)	**0.323** (+0.15)	0.333 (+0.15)
		Long	0.927 (+0.93)	0.338 (+0.24)	**0.251**
A3	SLHP	Short	0.713 (+0.63)	**0.552** (+0.45)	0.56 (+0.45)
		Medium	0.565 (+0.5)	**0.517** (+0.38)	0.547 (+0.49)
		Long	0.539 (+0.21)	0.543 (+0.51)	**0.516** (+0.3)
	LLLP	Short	0.6 (+0.46)	0.481 (+0.14)	**0.411** (+0.13)
		Medium	0.465 (+0.31)	0.439 (+0.11)	**0.361** (+0.11)
		Long	0.397 (+0.13)	0.413 (+0.15)	**0.324** (+0.09)
B3	SLHP	Short	0.81 (+0.77)	**0.602** (+0.58)	0.624 (+0.37)
		Medium	0.917 (+0.92)	**0.577** (+0.48)	0.608 (+0.48)
		Long	0.758 (+0.76)	0.657 (+0.66)	**0.533** (+0.5)
	LLLP	Short	1.098 (+1.1)	**0.49** (+0.2)	0.5 (+0.24)
		Medium	1.051 (+1.05)	**0.413** (+0.15)	0.436 (+0.16)
		Long	0.905 (+0.9)	0.407 (+0.21)	**0.353** (+0.05)

Table 1.7: Median absolute relative errors for estimates of natural mortality. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	Fished	Aggregated
A3	SLHP	Short	**0.127**	0.152	0.135
		Medium	**0.075**	0.132	0.14 (+0.06)
		Long	**0.052**	0.115	0.161
	LLLP	Short	**0.161** (+0.06)	0.168	0.181 (+0.1)
		Medium	**0.121**	0.129	0.149 (+0.12)
		Long	**0.089**	0.107	0.47 (+0.14)
B3	SLHP	Short	**0.108** (-0.07)	0.143	0.145
		Medium	**0.071**	0.135	0.145 (+0.06)
		Long	**0.046**	0.124	0.131 (+0.05)
	LLLP	Short	0.197 (+0.06)	0.21	**0.194** (+0.06)
		Medium	**0.104**	0.149	0.133 (+0.12)
		Long	**0.076**	0.123	0.146 (+0.14)
A4	SLHP	Short	0.131 (-0.08)	**0.116**	0.124
		Medium	**0.087** (-0.05)	0.118 (-0.06)	0.134
		Long	**0.064** (-0.05)	0.108	0.149
	LLLP	Short	0.216 (-0.08)	0.226 (-0.12)	**0.21**
		Medium	0.148 (-0.06)	**0.142** (-0.05)	0.174 (+0.08)
		Long	**0.127** (-0.07)	0.137 (-0.05)	0.162 (+0.14)
A5	SLHP	Short	0.17 (-0.15)	0.124 (-0.09)	**0.098**
		Medium	0.127 (-0.1)	**0.106** (-0.08)	0.132
		Long	**0.093** (-0.09)	0.119 (-0.07)	0.127
	LLLP	Short	0.19	0.184 (-0.1)	**0.159**
		Medium	**0.158** (-0.07)	0.167 (-0.07)	0.146
		Long	**0.125** (-0.08)	0.142 (-0.06)	0.145 (+0.07)

Table 1.8: Median absolute errors for estimates of natural mortality. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost rows describe the estimation, species and data length combination scenario. The bold value indicates the smallest MAE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*	*Aggregated*
A.6a	SLHP	Short	0.149 (-0.1)	**0.148**	0.15
		Medium	**0.077**	0.103	0.133 (+0.05)
		Long	**0.062**	0.113	0.135
	LLLP	Short	0.205	**0.19**	0.225 (+0.11)
		Medium	**0.106**	0.136	0.156 (+0.13)
		Long	**0.092**	0.115	0.157 (+0.15)
A.6b	SLHP	Short	**0.132** (+0.08)	0.234 (+0.22)	0.295 (+0.29)
		Medium	**0.066**	0.238 (+0.21)	0.269 (+0.26)
		Long	**0.054** (-0.05)	0.24 (+0.22)	0.269 (+0.23)
	LLLP	Short	**0.287** (+0.22)	0.423 (+0.42)	0.455 (+0.45)
		Medium	**0.116**	0.327 (+0.33)	0.294 (+0.29)
		Long	**0.091**	0.289 (+0.29)	0.256 (+0.26)
A.7	SLHP	Short	**0.107**	0.142	0.135 (+0.05)
		Medium	**0.063**	0.136	0.145 (+0.06)
		Long	**0.05**	0.118	0.145 (+0.05)
	LLLP	Short	0.23 (+0.17)	**0.168**	0.181 (+0.1)
		Medium	0.146 (+0.1)	**0.129**	0.149 (+0.12)
		Long	**0.094** (+0.05)	0.107	0.147 (+0.14)
A.8	SLHP	Short	0.31 (-0.23)	**0.142**	0.128
		Medium	0.322 (-0.26)	**0.125**	0.136 (+0.06)
		Long	0.321 (-0.24)	**0.126**	0.146 (+0.06)
	LLLP	Short	0.444 (+0.27)	**0.168**	0.181 (+0.1)
		Medium	0.44 (+0.2)	**0.129**	0.149 (+0.12)
		Long	0.419 (+0.07)	**0.107**	0.147 (+0.14)
A.9	SLHP	Short	**0.151** (-0.09)	0.2	0.163
		Medium	**0.107** (-0.06)	0.168	0.181
		Long	**0.088** (-0.05)	0.144	0.174 (+0.06)
	LLLP	Short	0.297 (+0.2)	**0.288** (+0.06)	0.292 (+0.11)
		Medium	**0.192** (+0.09)	0.23 (+0.05)	0.249 (+0.19)
		Long	**0.122**	0.243 (+0.1)	0.24 (+0.18)

CHAPTER 2

CAN MARINE PROTECTED AREAS IMPROVE ESTIMATES OF LIFE-HISTORY PARAMETERS?
ASSESSING THE ROLE OF SPATIAL DYNAMICS ON
STOCK ASSESSMENT MODEL PERFORMANCE

Chapter 1 examined the effects of applying subdivided and aggregated stock assessments to spatially

heterogeneous data for the case in which there is no movement of fish between an MPA and a fished area.

This chapter builds on the results presented in that chapter by adding movement between the two areas. In

addition, models with varying degrees of complexity: aggregated, subdivided, and two-areas are examined

for the case in which natural mortality is fixed at its true value and for the case when it is estimated.

Scenarios in which growth and maturity parameters are estimated are not examined in this chapter because it

is unlikely that data collected from MPAs will improve estimates of these parameters even in the best case

where there is no movement of fish between the MPA and fished area (Chapter 1).

2.1 METHODS

2.1.1 *Operating Model*
The operating model (Appendix A) is identical to that described in Chapter 1 section 1.1.3, except that the

probability of moving from a cell, $X_y^{c',c}$ (Equations A.16-A.17) is now a function of age. This formulation

for movement was selected to mimic that assumed by Stock Synthesis (SS), allowing for exact comparison of

the true and estimated movement parameters.

2.1.2 Scenarios and parameterizations
As with Chapter 1, two generic fish with contrasting life-history strategies: a short-lived high-productive

(SLHP) and a long-lived low-productive (LLLP) species (Figure 1.2 and Table 1.1) are modeled to examine

the robustness of the results to assumptions about productivity.

Movement of fish from the MPA to the fished area (and *vice versa*) is modeled under the assumption

that the probability of moving either increases or decreases with age (equation A.17). When the probability

of moving increases with age, the parameters in Equation A.17 (Table 2.1) are chosen so that the probability

of moving from the MPA to the fished area at a maximum reference age, a_4, is 0.05, 0.2 and 0.4,

corresponding to low, medium and high spillover (.l, .m, and .h in Table 2.2 and Figure 2.1)[7]. One scenario examines the sensitivity of the results to decreasing movement with age (.d in Table 2.2). The bulk of scenarios assume that there is a medium amount of spillover, although scenarios A3.l, A3.m and A3.h (Table 2.2) sequentially examine the effects of increasing spillover when estimating M in a stock assessment that ignores movement. Every combination of movement and species in Table 2.2 may not match realistic patterns of the two life-history strategies off the U.S. west coast (*i.e.* most long-lived LLLP species (*Sebastes sp*). are sedentary at maximum ages (Love et al. 2002)), but provide a general examination of all the scenarios.

The effects of implementing an MPA for a short, medium and long period (10, 20 and 30 years) are examined to determine how long it would take to see improvement in estimation of life-history parameters. Patterns in fishing mortality after implementation of the MPA and recovery to the target spawning biomass occurs within 10 years for the SLHP species and 20 years for the LLLP species (see section 1.1.4 for details).

Several variants of the operating and estimating models (Table 2.2) are considered to examine the robustness of the results to assumptions about how density-dependence in recruitment operates, the degree of spillover from the MPA to the fished area, whether natural mortality is estimated or assumed known, whether the stock assessment accounts for spatial dynamics, the presence of aging error, and whether survey-age data are available for the MPA. Two categories of scenarios (A and B in Table 2.2) examine the sensitivity of how density-dependence may affect estimation ability. Scenarios A and B correspond to no-dispersal and post-dispersal density dependence.

Scenarios A6.m and A7.m are designed to alleviate the negative impacts of not accounting for spillover when estimating natural mortality in a stock assessment that ignores movement. In such a scenario, SS should overestimate M in the MPA assessment because the model expects to observe older fish which are not present due to spillover into the fished area. Masking the true age-distribution by adding age-reading error or having no age-data at all could potentially stabilize the estimate of M by de-emphasizing age data that are otherwise uninformative to a stock assessment that does not account for movement of fish.

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[7] The probability of moving from the fished area to the MPA is always less than in the other direction because the probability of moving is scaled by λ^c (the fraction of total recruitment that recruits to a cell). This ensures that the net movement of fish between the two areas in equilibrium is zero because the fished area represents a greater proportion of the total biomass.

2.1.2 Additional considerations

As in Chapter 1, survey estimates of abundance, and length- and age-compositions from the survey and fishery catches are available to the stock assessment. The timing of data availability for the two species, the quantity of data, and the level of sampling error associated with each area are identical to those described in section 1.1.5.

The SS assessment model (Appendix B) for the stock assessment that ignores movement is also that which is described in section 1.1.6. Scenarios A0.m.sp and A1.m.sp examine the feasibility of using a two-area stock assessment model that estimates the movement rate of fish between areas when there are no tagging data to inform these parameters. Two fisheries and two surveys operate in the MPA and fished areas and hence this model has twice as many as exploitation and survey-related parameters to estimate compared to the aggregated assessment. In addition, λ^c (equation A.3) is now treated as a time-varying estimable parameter (equation B.10) in order to account for area-specific recruitment, η_y^c (equation A.3). Estimating λ_y^c requires specifying the standard deviation of the time series of random parameter deviates. This was chosen to be 0.10 and the sensitivity of the results was investigated when this standard deviation was set to 0.05 and 0.15. The parameters defining the probability of moving from a cell at reference ages a_3 and a_4 are not estimable within SS and are fixed at their true values.

The relative error (RE) statistic, median absolute relative error (MARE), and median relative error (MRE) (section 1.1.7) are again used to gauge the ability to estimate the management quantities (spawning biomass and fishing mortality) and the estimable parameters of the assessment model.

2.2 RESULTS

2.2.1 *Baseline Results*

Scenarios in which natural mortality is fixed at its true value are examined first to understand the behavior of the SS estimating model when there is movement between the MPA and the fished area. Three of these scenarios (A0.m, A0.d, A0.m.sp) assume that density-dependence acts at the cell level and larvae do not disperse. Scenario B0.m assumes that density dependence is post-dispersal. As with Chapter 1, estimates of management quantities for post-dispersal density-dependence (scenario B0.m) are qualitatively identical to those for pre-dispersal density-dependence (scenario A0.m) and are not shown.

Estimates of spawning biomass in the MPA and fished area are noticeably impacted when there is movement of fish between the MPA and fished areas (Scenario A0.m, upper panels Figure 2.2). These two assessments are nearly median unbiased prior to implementation of the MPA (although the LLLP species is slightly worse) and become increasingly positively biased with increasing years of MPA implementation. The patterns in the relative error of spawning biomass prior to implementation of the MPA can be attributed to patterns in the relative error of fishing morality (Figure 2.3) owing to the inverse relationship between these two quantities. After implementation of the protected area, the MPA assessment provides positively biased estimates of spawning biomass because the model does not account for a decrease in biomass due to spillover. The fished assessment also becomes positively biased once the MPA is implemented perhaps because of the presence of large old fish in the catch. The subdivided assessment, consequently, becomes increasingly positively biased over time. The aggregated assessment, however, performs very well for the LLLP species, but poorly once the MPA is implemented for the SLHP species owing to the fast-growing nature of this species (middle panels, Figure 2.2). The subdivided and aggregated assessments can be compared to the two-area assessment (scenario A0.m.sp, lower panel Figure 2.2). Performance is now slightly worse for the LLLP species, indicated by a positive median relative error in most assessment years, but substantially improved for the assessment of the SLHP species.

Performance statistics for estimated movement-related parameters for scenario A0.m.sp are listed in Table 2.3. The base parameter defining the fraction of recruitment to an area is estimated reliably, but the parameters controlling the movement of fish between areas are highly variable and biased. $m_3^{mpa,fish}$ and $m_3^{fish,mpa}$ always tends to be underestimated, although the effects of doing so should be negligible because the true values of these parameters are very close to zero (Table 2.1). $m_4^{mpa,fish}$ is always overestimated, implying that the model overestimates the rate of spillover, but $m_4^{mpa,fish}$ tends towards underestimation.

Patterns in the relative error of spawning biomass for scenario A0.m (Figure 2.2) only change slightly when the probability of moving decreases with age (scenario A0.d, results not shown). After implementation of the protected area, the MPA assessment is slightly more positively biased for scenario A0.d compared to scenario A0.m, suggesting that the effective number of animals that spill over from the MPA to the fished area is larger when the probability of moving decreases with age. The MPA is potentially less effective at

protecting a larger portion of the total biomass in this case because the probability of moving from the MPA to the fished area is largest for the most abundant age-classes. Declining movement with age in this scenario would be intermediate between the medium and high spillover scenarios (Table 2.1).

2.2.2 *Estimation of natural mortality*
This section shows results for the remaining scenarios in Table 2.2 and examines how estimates of natural mortality are affected at varying levels of movement between the MPA and the fished area. Performance statistics for the estimates of *M* are given in Tables 2.4 and 2.5.

Estimates of natural mortality for scenario A3.m are shown in Figure 2.4. Performance statistics are given in Table 2.4. Estimates of *M* from the MPA assessment become positively biased with increasing years of MPA implementation. The MPA assessment most frequently performs the best (as indicated by the smallest MARE) for the SLHP species, but the aggregated assessment outperforms the MPA and fished assessments for the LLLP species. The MPA assessment is always associated with the largest bias as indicated by the MRE. The results for scenario B3.m (Table 2.4) are similar to those for scenario A3.m. These results contrast with the situation in which there is no movement from the MPA (scenarios A3 and B3, Table 1.7). Estimates of *M* from the MPA in this case were nearly always unbiased and had smaller MAREs, particularly after implementing the MPA for 30 years (the long data scenario).

Scenarios A3.l, A3.m and A3.h sequentially examine the effects of low, medium and high spillover when estimating natural mortality. Estimates of *M* from the MPA assessment become, as expected, less precise and more biased as greater proportions of fish spill over into the fished area (Table 2.4). When this occurs, SS expects to observe older fish in the largest age-bins in the MPA, but these have spilled over into the fished area and the model compensates for this by increasing natural mortality. The aggregated assessment most frequently performs the best for the high spillover scenario (A3.h). This is always true for the LLLP species, regardless of the degree of spillover, but not for the SLHP species because higher diffusivity of fish acts to smooth sub-population differences between the MPA and fished areas because of the later species' rapid growth, the consequences of applying an aggregated assessment are less severe.

Estimation performance is worse for the aggregated assessment when the probability of moving decreases with age (scenario A3.d, Table 2.5). The MPA assessment always performs best for the SLHP

species and the fished assessment always performs best for the LLLP species when the probability of movement decreases with age. The estimates of M are always biased for scenario A3.d.

Adding age-reading error or having no age-data at all did not alleviate the positively-biased estimates of natural mortality (scenarios A6.m and A7.m in Table 2.5). Estimates of M for scenarios A6.m and A7.m are more biased and variable in the MPA assessment (compare the results for scenario A3.m in Table 2.4 with those for scenarios A6.m and A7.m in Table 2.5). Adding aging-reading error (scenario A6.m) results in slightly larger MAREs for the MPA assessment and the MAREs are sometimes twice as large when no age-data are available from the MPA (scenario A7.m).

Scenario A3.m.sp examines the potential of estimating natural mortality within a two-area model that also estimates the movement of fish between areas. Although the movement-related parameters are poorly estimated, estimates of M are now very precise (Table 2.5) and the MARE and MRE scores are comparable to those observed in Chapter 1 when there was no movement of fish between the MPA and the fished area (scenario A3, Table 1.7). The performance statistics for natural mortality in Table 2.5 can be compared to those for the aggregated assessment (for scenario A3.m in Table 2.4). The ability to estimate M is better using the two-area model, but at the expense of increased model complexity. The more precise and less biased estimates of M from the two-area model compared to those from the aggregated assessment underscore the importance of knowing that $F = 0$ when estimating natural mortality. The model was not sensitive to the assumed standard deviation of the time series of random parameter deviates (results not shown).

2.3 DISCUSSION

This chapter has examined the effects of different levels of movement on the performance of models with varying levels of complexity. Not accounting for the movement of fish between areas negatively impacted estimates of total spawning biomass for the SLHP species, but not the LLLP species. Accounting for movement of fish between areas, on the other hand, alleviated the negative impact for the SLHP species, but biased the estimates of spawning biomass for the LLLP species. Estimates of natural mortality were always biased when this parameter was estimated using data collected from the MPA, but a two-area model was able to estimate this parameter very reliably. The later result is very encouraging and suggests that the negative

impact of spillover on estimation performance of natural mortality can be alleviated by using an area-specific model in which movement is estimated.

The scenarios in this chapter that ignore movement can be compared to those in Chapter 1 in which the operating model also did not have this feature. Subdivided assessments were able to account for the spatial heterogeneity created by the MPA when there was no movement of fish between areas, but performed substantially worse when there was mixing of fish between areas. The benefits of having an MPA to estimate natural mortality were also reduced when there was mixing of fish between areas. Stock assessment models that do not account for movement, then, will need to be used carefully when estimating natural mortality from fish that have large degrees of spillover into the fished area.

Movement parameters in the two-area model were not estimated reliably except for that controlling the distribution of recruitment among areas. This is hardly surprising, because the only source of data included in the model that could potentially provide information about this process is the survey index of abundance. Several studies (Holland 2002, Pelletier and Mahévas 2005) have outlined how stock assessment models and data collection protocols will need to change to the meet the challenges that MPAs pose to stock assessments. Two scenarios in this chapter (scenarios A0.m.sp and A1.m.sp) have attempted to use a model that has been modified to meet the demands of MPAs and other spatial considerations in stock assessments. The results presented here echo the call of Holland (2002) and Pelletier and Mahévas (2005), and indicate that unless informative studies about movement, such as tagging studies, are conducted in areas with MPAs; the ability to estimate important parameters given to the effectiveness of the MPA (*i.e.* spillover) will be limited.

The approach of subdividing the stock into smaller spatial units or applying an aggregated assessment model to the entire stock rather than applying a spatially-structured model in which movement rates are estimated is likely to continue to be used in the short-term. This claim is supported by the 31 stocks assessed with SS on the U.S. west coast in which only one, Yelloweye rockfish (*Sebastes ruberrimus*) was assessed using an area-specific model[8] (Stewart et al. 2009). Scientists applying simpler models and attempting to estimate natural mortality using data collected from MPAs should, therefore, be cognizant of the potential biases, particular that spillover of adult fish will influence the outcome of the assessment. Although estimates of *M* from the MPA assessment had the lowest MAREs for the bulk of the SLHP scenarios in this

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[8] Although fish were not assumed to move among areas in this model

chapter, the estimates were biased and one would need to choose between a precise, but potentially wrong estimate of natural mortality calculated using data from an MPA or a more uncertain estimate from the fished and aggregated assessments.

FIGURES

Figure 2.1: The four movement scenarios for the SLHP and LLLP species.
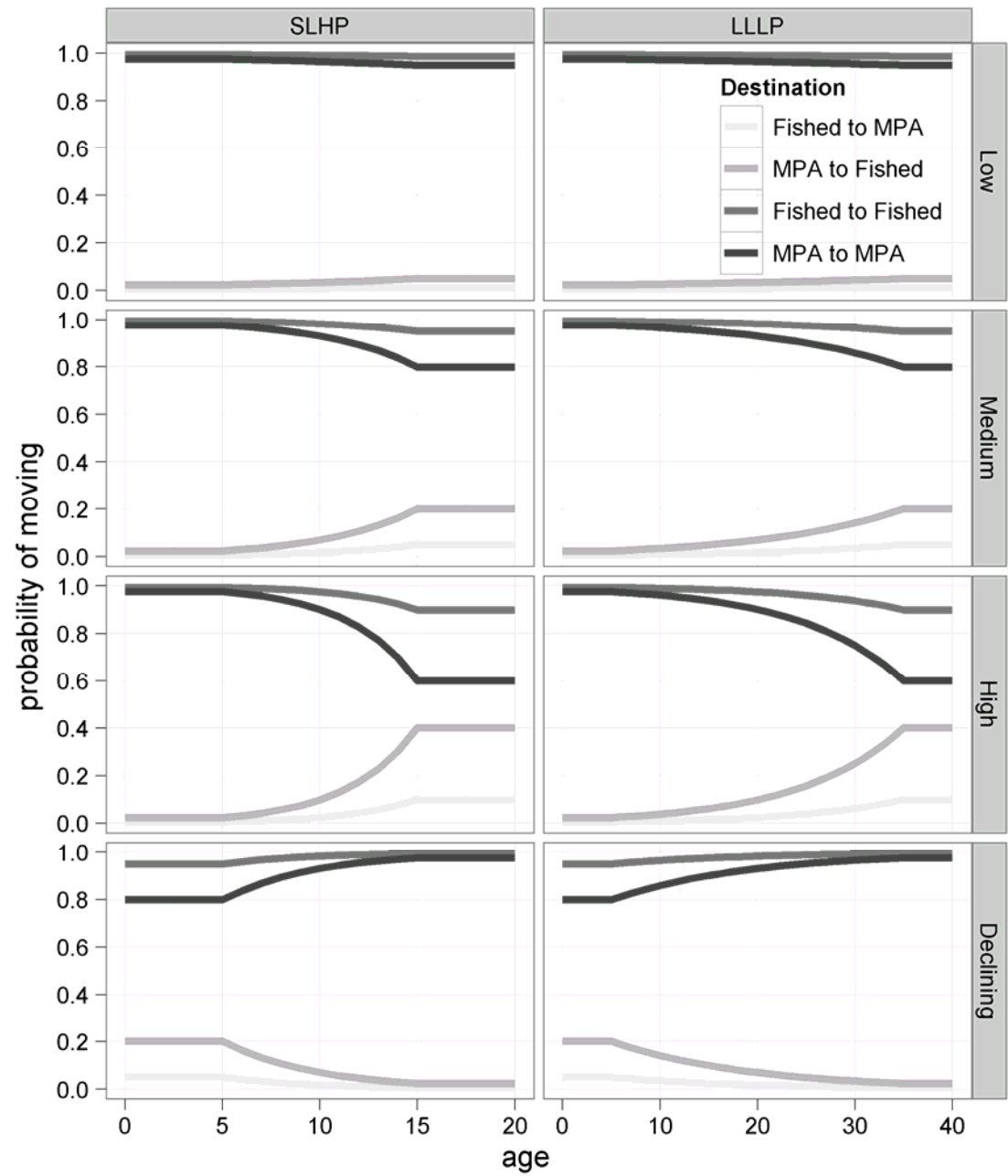
Figure 2.2: Median (dark line) and 90% simulation intervals (shaded gray) for the annual relative errors for spawning biomass for scenario A0.m. A dotted horizontal line is drawn at zero indicating no error. A dotted vertical line is drawn at the time corresponding to implementation of the MPA. The different shades of gray correspond to the assessment with short, medium and long lengths of data.
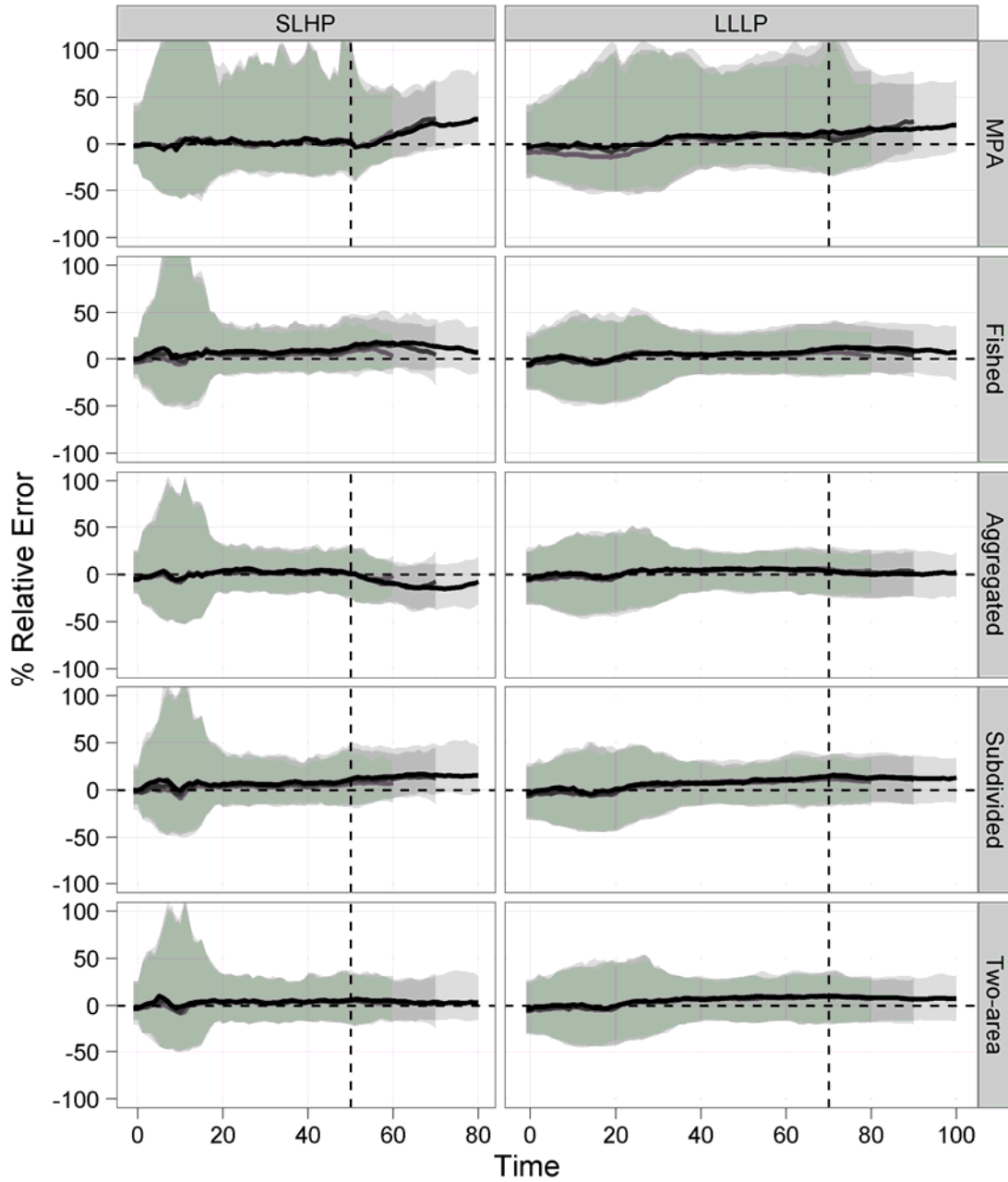
Figure 2.3: Median (dark line) and 90% simulation intervals (shaded gray) for the annual relative errors for fishing mortality for scenario A0.m. A dotted horizontal line is drawn at zero indicating no error. A dotted vertical line is drawn at the time corresponding to implementation of the MPA. The different shades of gray correspond to the assessment with short, medium and long lengths of data.
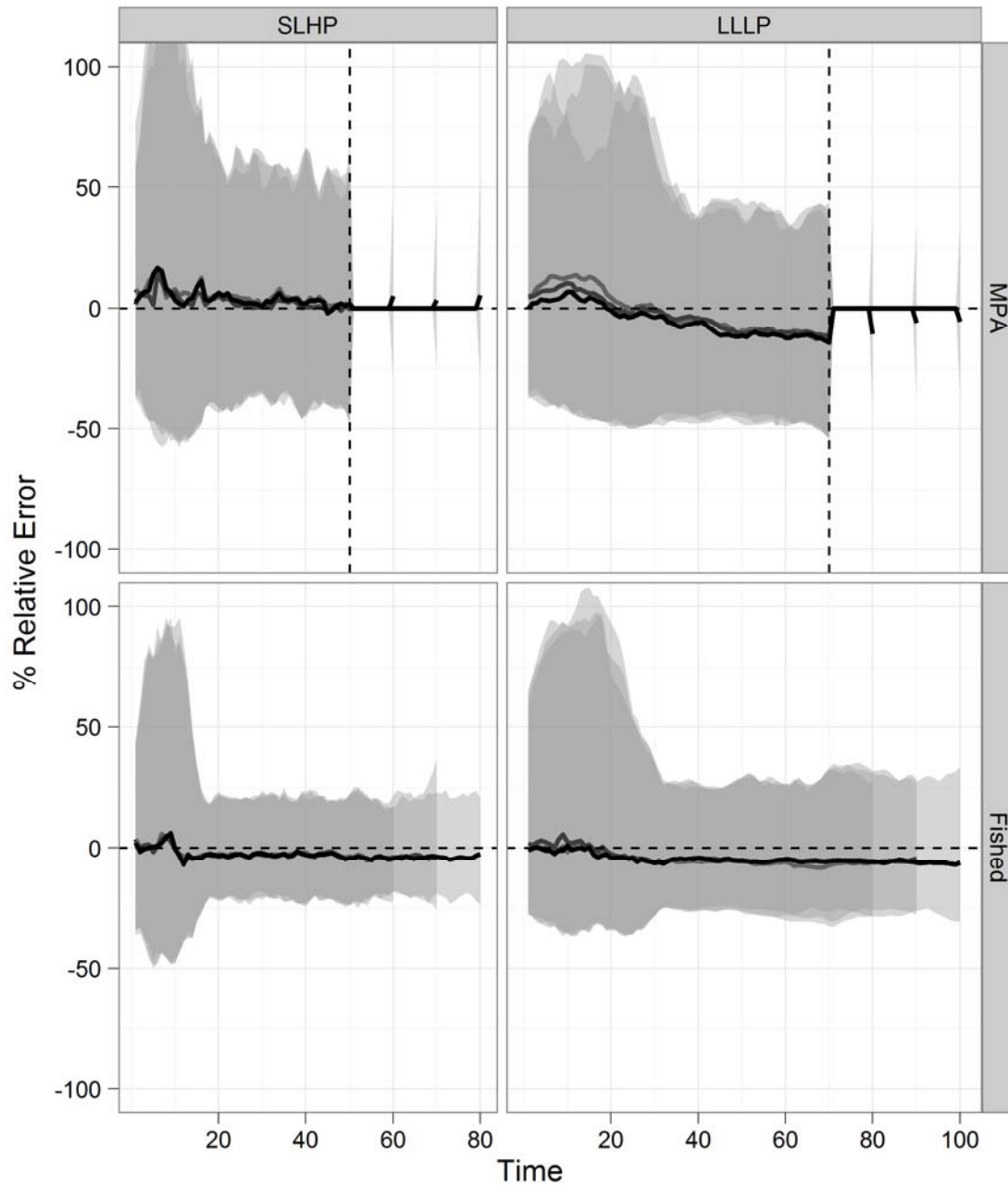
Figure 2.4: Boxplots of the estimated rate of natural mortality for scenario A1.m. A dotted horizontal line is drawn at the true value.
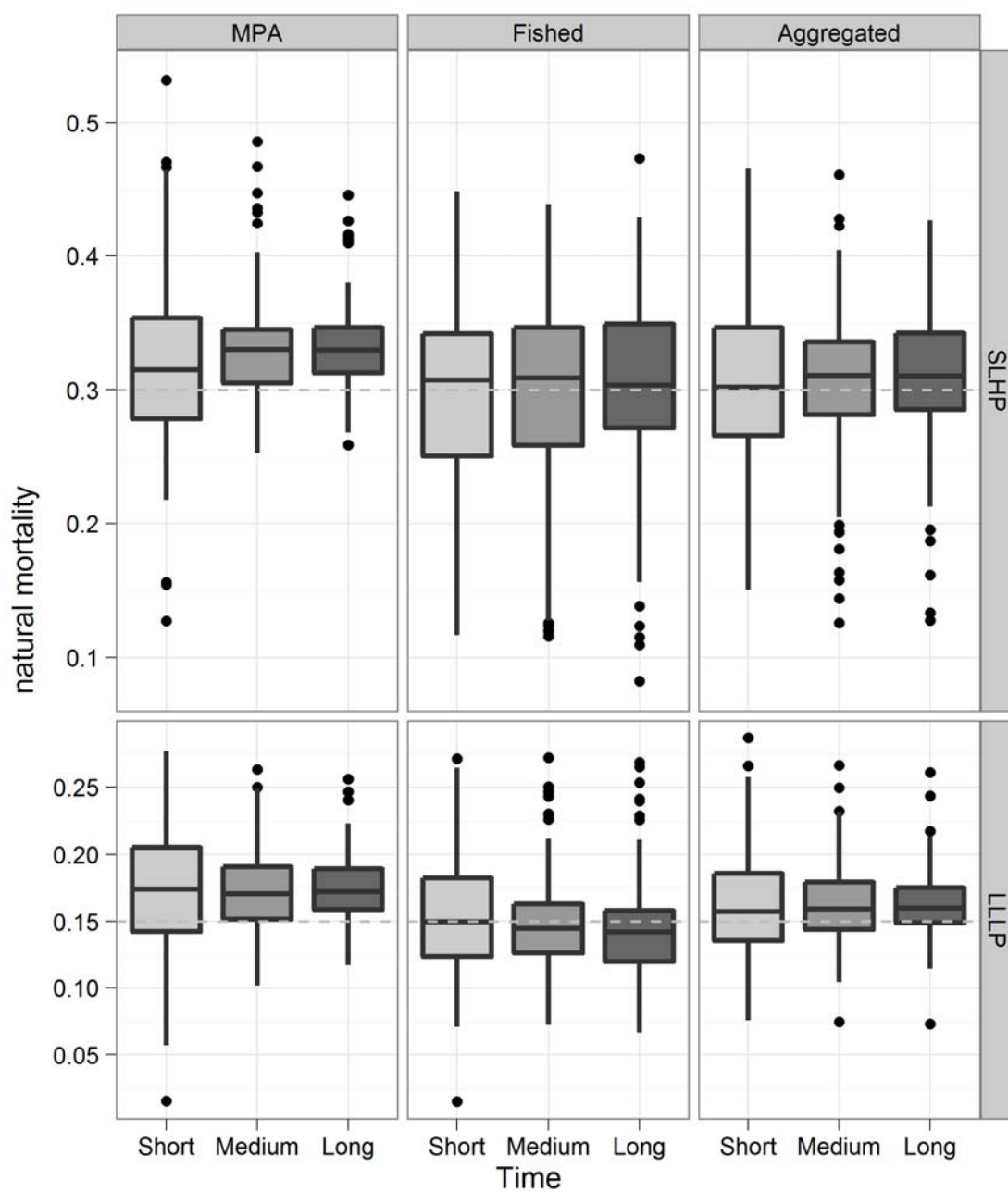
TABLES

Table 2.1: The values for the movement parameters of the operating model for the three movement scenarios. These movement parameters are the same for both the SLHP and LLLP species. x is the plus-group age of the species.

Parameter	Description	Low	Medium	High	**Declining**
a_3	Reference age	5	5	5	5
a_4	Reference age	x-5	x-5	x-5	x-5
$\exp(m_3^{c',c})$	probability in log-space of moving from cell c' to cell c for fish of age a_3	-3.47	-3.47	-3.47	-1.10
-	probability of moving from cell c' to cell c for fish of age a_3	0.03	0.03	0.03	0.25
$\exp(m_4^{c',c})$	probability in log-space of moving from cell c' to cell c for fish of age a_4	-2.71	-1.10	0	-3.47
-	probability of moving from cell c' to cell c for fish of age a_4	0.0625	0.25	0.5	0.03

Table 2.2: The scenarios considered in Chapter 2.

Scenario	S-R Relationship	Degree of spillover	Movement accounted for	Natural mortality estimated	Additional specifications
A0.m	A.3a	Medium	No	No	-
A0.d	A.3a	-	No	No	Probability of moving decreases with age
A0.m.sp	A.3a	Medium	Yes	No	-
B0.m	A.3b	Medium	No	No	-
A3.l	A.3a	Low	No	Yes	-
A3.m	A.3a	Medium	No	Yes	-
A3.d	A.3a	-	No	Yes	Probability of moving decreases with age
A3.m. sp	A.3a	Medium	Yes	Yes	-
B3.m	A.3b	Medium	No	Yes	-
A3.h	A.3a	High	No	Yes	-
A6.m	A.3a	Medium	No	Yes	Aging error with correct aging error definition in the stock assessment
A7.m	A.3a	Medium	No	Yes	AUV length data

Table 2.3: Median absolute relative errors for estimates for movement-related quantities (in real-space). The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the parameter, species and data length combination for each set of results.

				Two-area
A0.m.sp	λ_c	SLHP	Short	0.115
			Medium	0.114
			Long	0.105
		LLLP	Short	0.184 (+0.05)
			Medium	0.182 (+0.05)
			Long	0.172
	$m_3^{mpa,fish}$	SLHP	Short	0.898 (-0.9)
			Medium	0.861 (-0.84)
			Long	0.832 (-0.82)
		LLLP	Short	0.898 (-0.9)
			Medium	0.898 (-0.9)
			Long	0.898 (-0.9)
	$m_4^{mpa,fish}$	SLHP	Short	1.04 (+1.01)
			Medium	0.941 (+0.62)
			Long	0.702 (+0.61)
		LLLP	Short	0.988 (+0.21)
			Medium	0.944 (+0.58)
			Long	0.793 (+0.48)
	$m_3^{fish,mpa}$	SLHP	Short	0.659 (-0.16)
			Medium	0.72 (-0.35)
			Long	0.688 (-0.18)
		LLLP	Short	0.792 (-0.71)
			Medium	0.702 (-0.63)
			Long	0.668 (-0.57)
	$m_4^{fish,mpa}$	SLHP	Short	0.951
			Medium	0.951 (-0.27)
			Long	0.951 (-0.25)
		LLLP	Short	0.951 (-0.21)
			Medium	0.951 (-0.33)
			Long	0.951

Table 2.4: Median absolute relative errors for estimates of natural mortality. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*	*Aggregated*
A3.l	SLHP	Short	**0.122**	0.139	0.14
		Medium	**0.073** (+0.05)	0.13	0.134 (+0.06)
		Long	**0.057** (+0.05)	0.13	0.121 (+0.06)
	LLLP	Short	0.212 (+0.07)	0.165	**0.16** (+0.05)
		Medium	0.12 (+0.07)	0.122	**0.107** (+0.07)
		Long	**0.094** (+0.06)	0.128	0.107 (+0.09)
A3.m	SLHP	Short	**0.121** (+0.05)	0.142	0.138
		Medium	0.1069 (+0.1)	0.155	**0.1066**
		Long	**0.101** (+0.1)	0.124	0.108
	LLLP	Short	0.244 (+0.16)	0.186	**0.175** (+0.05)
		Medium	0.147 (+0.14)	0.137	**0.109** (+0.06)
		Long	0.149 (+0.15)	0.153 (-0.05)	**0.103** (+0.07)
B3.m	SLHP	Short	**0.113**	0.144	0.135
		Medium	**0.112** (+0.11)	0.141	0.123 (+0.05)
		Long	**0.11** (+0.11)	0.119	0.121
	LLLP	Short	0.193 (+0.13)	0.173	**0.17** (+0.05)
		Medium	0.143 (+0.14)	0.128	**0.101** (+0.05)
		Long	0.168 (+0.16)	0.144	**0.1** (+0.07)
A3.h	SLHP	Short	**0.122**	0.138	0.134
		Medium	0.119 (+0.12)	0.133	**0.11**
		Long	0.149 (+0.15)	0.136	**0.117**
	LLLP	Short	0.242 (+0.16)	0.191	**0.186**
		Medium	0.172 (+0.16)	0.117 (-0.06)	**0.109** (+0.05)
		Long	0.195 (+0.2)	0.168 (-0.06)	**0.084** (+0.05)

Table 2.5: Median absolute relative errors for estimates of natural mortality. The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the scenario, species and data length combination for each set of results. The bolded value indicates the smallest MARE when comparing the MPA, fished and aggregated assessments.

			MPA	*Fished*	*Aggregated*
A3.d	SLHP	Short	**0.126** (+0.06)	0.137	0.191
		Medium	**0.106** (+0.1)	0.153	0.157
		Long	**0.106** (+0.11)	0.149	0.168 (+0.05)
	LLLP	Short	0.185 (+0.17)	**0.176** (-0.05)	0.19 (+0.05)
		Medium	0.146 (+0.13)	**0.126** (-0.05)	0.138 (+0.07)
		Long	0.145 (+0.14)	**0.121** (-0.05)	0.131 (+0.08)
A6.m	SLHP	Short	0.137	**0.135**	0.141
		Medium	**0.109** (+0.1)	0.13	0.121 (+006)
		Long	**0.108** (+0.11)	0.134	0.128
	LLLP	Short	0.234 (+0.15)	0.21	**0.184** (+0.09)
		Medium	0.164 (+0.15)	0.133	**0.126** (+0.09)
		Long	0.177 (+0.17)	0.143 (-0.05)	**0.103** (+0.08)
A7.m	SLHP	Short	**0.124** (+0.05)	0.139	0.138
		Medium	0.132 (+0.13)	0.142	**0.11** (+0.06)
		Long	0.139 (+0.14)	0.109	**0.108** (+0.06)
	LLLP	Short	0.359 (+0.23)	0.185	**0.175** (+0.06)
		Medium	0.229 (+0.22)	0.137	**0.107** (+0.06)
		Long	0.24 (+0.22)	0.153 (-0.05)	**0.103** (+0.07)

Table 2.6: Median absolute relative errors for estimates of natural mortality and movement-related parameters (in real-space). The median relative error is given parenthesis. Blank entries denote negligible bias. The leftmost columns describe the parameter, species and data length combination for each set of results.

				Two-area
A3.m.sp	M	SLHP	Short	0.098
			Medium	0.067
			Long	0.058
		LLLP	Short	0.192
			Medium	0.092
			Long	0.088
	λ_c	SLHP	Short	0.138
			Medium	0.117
			Long	0.12 (+0.05)
		LLLP	Short	0.173
			Medium	0.207 (+0.1)
			Long	0.189
	$m_3^{mpa,fish}$	SLHP	Short	0.898 (-0.9)
			Medium	0.898 (-0.88)
			Long	0.848 (-0.83)
		LLLP	Short	0.898 (-0.9)
			Medium	0.898 (-0.9)
			Long	0.898 (-0.9)
	$m_4^{mpa,fish}$	SLHP	Short	0.988 (+0.84)
			Medium	0.92 (+0.74)
			Long	0.686 (+0.55)
		LLLP	Short	0.988 (+0.9)
			Medium	0.972 (+0.56)
			Long	0.866 (+0.58)
	$m_3^{fish,mpa}$	SLHP	Short	0.648 (-0.27)
			Medium	0.736 (-0.23)
			Long	0.66 (-0.28)
		LLLP	Short	0.716 (-0.62)
			Medium	0.738 (-0.69)
			Long	0.669 (-0.6)
	$m_4^{fish,mpa}$	SLHP	Short	0.951 (+0.15)
			Medium	0.951 (-0.28)
			Long	0.951 (-0.25)
		LLLP	Short	0.951 (+0.34)
			Medium	0.951 (-0.13)
			Long	0.951 (+0.28)

CONCLUSIONS

This thesis has shown that data collected from MPAs can potentially improve estimates of natural mortality, but it is unlikely that estimates of growth and maturity parameters will improve substantially because these parameters are already estimated reliably using data from fished populations. The cases in which natural mortality can be reliably estimated will be highly contextual and depend on a variety of factors including: model structure, data quality, data availability, and extent of movement between the MPA and the fished area.

The claims presented in this thesis need to be evaluated in light of: (1) the two life-history characteristics (SLHP vs. LLLP) that are consistent with actual observations of juvenile/adult movement patterns, and (2) the data availability that will determine the complexity of the model of the species being assessed.

Reef dwelling fish, such as the LLLP *Sebastes sp.* modeled tend to be site attached and sedentary with increasing age. Jorgensen et al. (2006) showed with radio-acoustic positioning telemetry data that blue rockfish (*Sebastes mystinus*) have high site fidelity and remarkably small home ranges ($\approx 9000 \ m^2$). Core areas within this home range ($\approx 1300 \ m^2$) accounted for 83% of the activity. This species is found mostly in California from Point Conception to the Oregon border and represents one of the target species for the network of MPAs that has been put in place in California. Together, this suggests that the methods and results presented in Chapter 1 of this thesis are likely to be applicable for such a species. This is highly encouraging, particular for blue rockfish, in which M was fixed at pre-specified constant in the most recent stock assessment (Key et al. 2008).

MPAs are most effective when there is limited movement within a home range (Kramer and Chapman 1999). It is more common, however, for fish to have ontogenetic shifts in distribution, spawning migrations or density-dependent movement (Botsford et al. 2009 and references therein). Chapter 2 of this thesis showed that estimating natural mortality using data collected from MPAs in such cases may be problematic if movement of animals is ignored. This negative effect was alleviated using a two-area model, although the movement-related parameters, particularly spillover, were poorly estimated. The complexity of the two-area model increases with the number of years and number of areas, and so such a model would only be applicable for data-rich stocks. Petrale sole (*Eopsetta jordani*) is one potential candidate species, particularly

because this stock was recently declared overfished by the Pacific Fishery Management Council and has identified the use of closed-areas as a future research need (Haltuch and Hicks 2009).

This thesis has modeled an MPA as one large contiguous area adjacent to a fishery. Future studies will need to extend the results presented in this thesis to MPAs that are designed as a network, such as those on the California coast of the United States, rather than a single area. One approach could involve aggregating data from the fine-scale network of MPAs into a single assessment. This will be extremely challenging owing to: changing habitat characteristics which affect the distribution of fish inside and outside of the protected area, indices of abundance that are either missing or sparse that would need to be aggregated into a model with annual time-steps, varying fleet dynamics in areas that ultimately form the network of MPAs and other exogenous factors that will undermine the feasibility of aggregating fine-scale data into a single assessment. The results presented here, nonetheless, are a valuable starting point for studies that attempt to estimate life-history parameters from data collected from MPAs.

It was assumed in this thesis that life-history parameters were time-invariant and more specifically that the implementation of the MPA did not result in a shift in life-history characteristics. As the biomass within an MPA approaches its carrying capacity, compensatory density-dependent processes that decrease growth, increase natural mortality and reduce reproductive success could occur (Lizaso 2000, Field et al. 2006 and references therein) and thus estimates of these parameters within an MPA may not reflect those in the surrounding fishery. Having recognized this, the potential to gain insight into plausible ranges of these parameters, particularly natural mortality, may still be very valuable. An estimate of M for the fish inside of an MPA, for example, could potentially be used to derive a prior distribution (Punt and Hilborn 1997) for this parameter in the stock assessment for the fished area. Given the difficulty in estimating M for many stock assessments, such information would be highly valuable even if only a plausible range of values was available.

Monte Carlo simulations were used in this thesis to address the hypothesis that having an MPA will lead to improved estimates of key life-history parameters. Simulation techniques in which the "truth" is known are necessary, but not sufficient, to address this hypothesis since such a technique is a drastic simplification of underlying ecological processes and data collection protocols that result in the data included in a real stock assessment. We would expect that life-history parameters change over time due to: variable

environmental and habitat conditions, changing species compositions that affect predator-prey interactions and density-dependent mechanisms, all of which are never constant (Caswell 1983). Furthermore, data are collected with error, and more often than not a model will assume the incorrect error that resulted in the observed data. Realized estimates of life-history parameters will be more uncertain than is suggested here and further empirical studies will be needed to validate the results presented in this thesis using data collected from MPAs or closed areas in light of the sensitivities that may affect estimation performance.

The majority of the literature on MPAs from traditional fisheries management perspectives has focused on the merits and flaws of using MPAs as effective management tools when confronted with the paucity of information that determines the effectiveness of MPAs (*e.g* spillover or larval dispersal).   While in the future it will still be important to address these questions, we are now at time where MPAs have been implemented because of these merits, but also without regard to these flaws. It is argued here, then, that a more relevant question is, what can fisheries management learn from data collected from MPAs now that they have been implemented?   This thesis has shown that in some cases, it may be possible to better determine the rate of natural mortality with data collected from MPAs.

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APPENDIX A: OPERATING MODEL

Basic population Dynamics

The model keeps track of the numbers-at-age by sex, g, and assessment cell, c. The population is projected

using an annual time step, with catch removed continuously throughout the year. The number of fish of age a

and sex g at the start of year $y+1$ in assessment cell c, $N^c_{y+1,a,g}$, is given by:

$$
N^c_{y+1,a,g} = \begin{cases}
N^c_{y+1,0} & \text{if } a = 0 \\[2ex]
\sum_{c'} X^{c',c}_a N^{c'}_{y,a-1,g} e^{-Z^{c'}_{y,a-1,g}} & \text{if } 0 < a < x \\[2ex]
\sum_{c'} X^{c',c}_a \left(N^{c'}_{y,x-1,g} e^{-Z^{c'}_{y,x-1,g}} + N^{c'}_{y,x,g} e^{-Z^{c'}_{y,x,g}} \right) & \text{if } a = x
\end{cases}
\qquad (A.1)
$$

where $X^{c',c}_a$ is the fraction of fish that move from cell c' to cell c of age a, $Z^c_{y,a,g}$ is the total mortality rate:

$$
Z^c_{y,a,g} = M + F^c_y \sum_{l=1}^{A_l} \phi_{a,g,l} S_l
\qquad (A.2)
$$

M is the instantaneous rate of natural mortality (assumed to be independent of age, time, sex and length), F^c_y

is the instantaneous fishing mortality rate on fully-selected animals in cell c, l is a length bin, A_l is the

maximum number of length bins, $\varphi_{a,g,l}$ is the proportion of fish of sex g and age a which are in length bin l,

S_l is the selectivity of a fish in length bin l, and x is the maximum age (taken to be a plus-group).

Recruitment

The number of 0-year-olds at the start of each year in cell c, $N^c_{y+1,0}$, is related to the spawning biomass by

means of a Beverton-Holt stock-recruitment relationship taking one of two forms:

$$
N^c_{y+1,0,g} = \begin{cases}
\lambda^c R^T_0 \dfrac{4hB^c_y}{B^c_0(1-h)+B^c_y(5h-1)} e^{\varepsilon_y - \sigma^2_T/2} e^{\eta^c_y - \sigma^2_C/2} & (A.3a) \\[3ex]
\lambda^c R^T_0 \dfrac{4hB^T_y}{B^T_0(1-h)+B^T_y(5h-1)} e^{\varepsilon_y - \sigma^2_T/2} e^{\eta^c_y - \sigma^2_C/2} & (A.3b)
\end{cases}
$$

where λ^c is the fraction of the total recruitment that recruits to cell c, R_0^T is the total unfished recruitment, h is the steepness of the stock-recruitment relationship, B_y^c is the spawning biomass at the start of year y in cell c:

$$B_y^c = \sum_{a=1}^{x} N_{y,a,\text{fem}} f_a \tag{A.4}$$

f_a is the average spawning biomass for a female of age a, B_0^c is the spawning biomass in cell c at pre-exploitation equilibrium, B_0^T is the total (summed over both cells) spawning biomass at pre-exploitation equilibrium, σ_T^2 is the variation in recruitment that is common across cells, $\varepsilon_y \sim N(0, \sigma_T^2)$, and σ_C^2 is the variation in recruitment that is cell-specific, $\eta_y^c \sim N(0, \sigma_C^2)$.

The numbers-at-age for sex g in assessment cell c in the initial year of the simulation correspond to an unfished population at a non-stable age distribution. This is achieved by initializing a virgin age-structure by:

$$N_{0,a,g}^c = \begin{cases} 0.5 \lambda^c R_0^T e^{-aM} & \text{if } a \neq x \\ 0.5 \lambda^c R_0^T \sum_{i=x}^{3x} e^{-iM} & \text{if } a = x \end{cases} \tag{A.5}$$

and projecting the model forward using equations (A.1) and (A.3) for x years with $F_y^c = 0$. This perturbs the unfished population from a deterministic equilibrium and reflects the impact of fluctuations in recruitment.

Exploitation Rate and Catch

The fully-selected exploitation rate in cell c during year y, F_y^c, is given by:

$$F_y^c = \chi_y^c \tilde{F}_y^c e^{\tau_y^c - \sigma_q^2/2} \tag{A.6}$$

where χ_y^c is 1 if cell c is open to fishing during year y and 0 otherwise, $\tilde{F}_y^c$ is the fully-selected fishing

mortality in cells open to fishing during year y, τ_y^c is cell specific variation in fishing mortality,

$\tau_y^c \sim N(0,\sigma_q^2)$.

The catch in numbers, C_y^c from cell c during year y is computed as:

$$C_y^c = \sum_g \sum_{a=0}^x \sum_{l=1}^{A_l} C_{y,a,g,l}^c \; ; \; C_{y,a,g,l}^c = \frac{F_y^c \varphi_{a,g,l} S_l}{Z_{y,a,g}^c} N_{y,a,g}^c (1-e^{-Z_{y,a,g}^c}) \tag{A.7}$$

Under this formulation, the fully-selected fishing mortality for year y does not have an analytical solution

given the numbers-at-age at the start of year y and the total catch in numbers during year y, and Equation A.7

must therefore be solved for numerically to find $\tilde{F}_y^c$.

Body weight
Body weight-at-length is modeled using an allometric relationship based on the mid-point of each length bin:

$$w_{l,g} = e_1 (L_l)^{e_2} \tag{A.8}$$

where e_1, e_2 are the parameters of the relationship between length and weight.

Length-at-age
The mean size-at-age, $L_{a,g}$, is modeled as:

$$L_{a,g} = L_{a-1,g} + (L_{a-1,g} - L_{\infty,g})(e^{-\kappa} - 1) \tag{A.9}$$

where $L_{\infty,g}$ is the asymptotic size for a fish of sex g:

$$L_{\infty,g} = L_{1,g} + \frac{L_{2,g} - L_{1,g}}{1 - e^{-\kappa_g (a_2 - a_1)}} \tag{A.10}$$

κ_g is growth coefficient for sex g, a_1, a_2 are reference ages, and $L_{1,g}, L_{2,g}$ are the mean sizes of animals of sex g at ages a_1 and a_2 respectively. The mean size of a fish of sex g and age a in the middle of the year is given by:

$$\tilde{L}_{a,g} = L_{a,g}e^{-0.5\kappa} + L_{\infty,g}(1-e^{-\kappa})$$
(A.11)

The coefficient of variation of length-at-age changes linearly with size-at-age between ages a_1 and a_2. The standard deviation $\sigma_{a,g}$ of length-at-age is given by:

$$\sigma_{a,g} = \begin{cases} \tilde{L}_{a,g}(CV_1) & \text{if } a < a_1 \\ \tilde{L}_{a,g}\left(CV_1 + \dfrac{(\tilde{L}_{a,g} - L_{1,g})}{(L_{2,g} - L_{1,g})}(CV_2 - CV_1)\right) & \text{if } a_1 < a < a_2 \\ \tilde{L}_{a,g}(CV_2) & \text{if } a > a_2 \end{cases}$$
(A.12)

where CV_1 is the coefficient of variation of length-at-age for a fish of age a_1, and CV_2 is the coefficient of variation of length-at-age for a fish of age a_2.

The numbers-at-age for sex g are distrusted across the defined length bins according to a normal distribution. The proportion of fish of age a and sex g in length bin l at the beginning of year y is calculated as:

$$\varphi_{a,g,l} = \begin{cases} \Phi\left(\dfrac{L'_{min} - \tilde{L}_{a,g}}{\sigma_{a,g}}\right) & \text{if } l = 1 \\ \Phi\left(\dfrac{L'_{l+1} - \tilde{L}_{a,g}}{\sigma_{a,g}}\right) - \Phi\left(\dfrac{L'_{l} - \tilde{L}_{a,g}}{\sigma_{a,g}}\right) & \text{if } 1 < l < A_l \\ 1 - \Phi\left(\dfrac{L'_{max} - \tilde{L}_{a,g}}{\sigma_{a,g}}\right) & \text{if } l > A_l \end{cases}$$
(A.13)

where Φ is the standard normal cdf, L_l' is the lower limit of length bin l, L_{min}' is the lower limit of the smallest length bin, and L_{max}' is the lower limit of the largest length bin.

Selectivity

Domed-shaped selectivity is modeled using the SS double-normal selectivity function. This function is composed of three sections: an ascending curve for small fish (asc_l), a flat-top at which selectivity equals 1.0, and a descending curve for large fish (dsc_l). The three sections have two intersections. The sections are joined using steep logistic functions j_{1l} and j_{2l},

$$sel_l = asc_l(1 - j_{1l}) + j_{1l}\left(1 - j_{2l} + dsc_l j_{2l}\right) \tag{A.14a}$$

where:

$$asc_l = 1 - (1 - \beta_5)\left(\frac{1 - e^{-\frac{(L_l - \beta_1)^2}{\beta_3}}}{1 - e^{-\frac{(L_{min} - \beta_1)^2}{\beta_3}}}\right) \tag{A.14b}$$

$$dsc_l = 1 - e^{-\frac{(L_l - \beta_2)^2}{\beta_4}} \tag{A.14c}$$

$$j_{1l} = \left(1 + e^{-20\frac{L_l - \beta_1}{1 + |L_l - \beta_1|}}\right)^{-1} \tag{A.14d}$$

$$j_{2l} = \left(1 + e^{-20\frac{L_l - \beta_2}{1 + |L_l - \beta_2|}}\right)^{-1}$$

$$\tag{A.14e}$$

l is the index for the length bin ($1 \le l \le A_l$), L_{min} is the midpoint of the smallest length bin, L_{max} is the midpoint of the largest length bin, β_1 is the smallest size at which selectivity=1.0, β_2 is the largest size at which selectivity=1.0, β_3 determines the slope of the ascending section, β_4 determines the slope of the descending section, and β_5 is the selectivity at L_{min}. The quantities β_3 and β_4 are exponential transforms,

$\beta = e^{\beta^*}$, of associated estimated parameters to remain positive, and the quantity β_5 is a logistic transform,

$\beta = \left(1 + e^{-\beta^*}\right)^{-1}$, of the estimated quantity to keep the value between 0 and 1. The quantity β_2 is

transformed from a parameter, β_2^*, which determines the end of the peak selectivity section as an offset β_1,

according to the function

$$\beta_1 + L_{width} + \frac{0.99 L_{max} - \beta_1 - L_{width}}{1 + e^{-\beta_2^*}} \tag{A.14f}$$

where L_{width} is the width of each of the length bins in the population.

Fecundity

Fecundity-at-age for a female depends on maturity-at-age, weight-at-length, and eggs-per-kg body mass, according to the equation:

$$f_{fem,a} = \sum_{l=1}^{A_l} \varphi_{a,fem,l} \left(1 + e^{\Omega_1 (L_l - \Omega_2)}\right)^{-1} w_l \tag{A.15}$$

where Ω_1, Ω_2 are the parameters controlling the relationship between maturity and age and that between weight and fecundity.

Movement

Space is accounted for by modeling two areas, a fished and a protected area. The fraction of fish of age a in

cell c' that move to cell c ($X_a^{c',c}$) is calculated by assuming that movement either increases or decreases

linearly (in log-space) with age:

$$X_a^{c',c} = \begin{cases} \dfrac{(1 - \lambda^c) e^{x_a^{c',c}}}{1 + e^{x_a^{c',c}}} & \text{if } c' = c'' \\[4mm] \dfrac{\lambda^c e^{x_a^{c',c}}}{1 + e^{x_a^{c',c}}} & \text{otherwise} \end{cases} \tag{A.16}$$

$$x_a^{c',c} = \begin{cases} m_3^{c',c} & \text{if } a <= a_3 \\ m_3^{c',c} + (a - a_3)\left(\dfrac{m_4^{c',c} - m_3^{c',c}}{a_4 - a_3}\right) & \text{if } a_3 < a < a_4 \\ m_4^{c',c} & \text{if } a >= a_4 \end{cases} \qquad (A.17)$$

where λ^c is the fraction of the total recruitment that recruits to cell c, $m_3^{c',c}$ and $m_4^{c',c}$ are the probability (in log-space) of moving from cell c' to c for fish of age a_3 and a_4. This formulation for movement was selected to mimic that assumed by SS.

Generating Data

The data available for assessment purposes are catch, survey indices of relative abundance, and survey and fishery length and age composition data. The fishery catch (in numbers) in cell c *is* generated without error using equation (A.7). The fishery length composition data for cell c are generated by sampling n_y^c fish multinomially with probabilities for length bin l given by:

$$p_{y,g,l}^c = \frac{\displaystyle\sum_a C_{y,a,g,l}^c}{\displaystyle\sum_a \sum_g C_{y,a,g,l}^c} \qquad (A.18)$$

The fishery age composition data by sex are assumed to be a multinomial sub-sample (of size $n_y^c / 2$) of the fish measured for length conditional on age:

$$p_{y,i,g,l}^c = \frac{\displaystyle\sum_a \Omega_{ia} C_{y,a,g,l}^c}{\displaystyle\sum_{a'} C_{y,a',g,l}^c} \qquad (A.19)$$

where Ω_{ia} is an age-reading error matrix describing the probability of a fish age a being assigned to age bin i:

$$\Omega_{ia} = \begin{cases} \Phi\left(\dfrac{\tilde{a}_i - \mu_a}{\sigma_a}\right) & \text{if } i = 1 \\[2mm] \Phi\left(\dfrac{\tilde{a}_{i+1} - \mu_a}{\sigma_a}\right) - \Phi\left(\dfrac{\tilde{a}_i - \mu_a}{\sigma_a}\right) & \text{if } 1 < i < A_i \\[2mm] 1 - \Phi\left(\dfrac{\tilde{a}_i - \mu_a}{\sigma_a}\right) & \text{if } i = A_i \end{cases} \tag{A.20}$$

and Φ is the standard normal cumulative density function, $\tilde{a}_i$ is the lower limit of age bin i, μ_a is the mean age assigned to fish of "true" age a, and σ_a is the standard deviation of aging error for fish of "true" age a. The bulk of the scenarios assume that ageing error is negligible, although scenario A.6 examines the impact of adding error on ability to estimate natural mortality.

The survey estimates of abundance, $N_y^{c,obs}$, for year y and cell c are assumed to be lognormally distributed about a survey-selected value:

$$N_y^c = \tilde{N}_y^c e^{\gamma_y^c - \sigma_B^2/2} \quad \gamma_y^c \sim N(0, \sigma_B^2) \tag{A.21}$$

where σ_B is a cell-specific coefficient of variation of N_y^c, $\tilde{N}_y^c$ is the survey-selected numbers for cell c and year y, calculated from the fish available to a survey:

$$\tilde{N}_{y,a,g,l}^c = \varphi_{a,g,l} S_l^s \left(N_{y,a,g}^c e^{-0.5(M + F_y^c \varphi_{a,g,l} S_l)} \right) \tag{A.22}$$

where $S_l^{\prime s}$ is the survey-selectivity function. The survey length- and age-composition data for cell c are generated analogously to equations (A.18) and (A.19), except that the data are generated using the survey-selected numbers, $\tilde{N}_{y,a,g,l}^c$,.

The number of fish that are mature-at-length (needed for estimating fecundity) is generated by sub-sampling 15 (or half of the total survey age-composition from the MPA) fish from the survey length composition data and then generating a Bernoulli random variable with probability given by $(1 + e^{\Omega_1(L_l - \Omega_2)})^{-1}$. Proportional sampling was not conducted here (*i.e.* more fish sampled in the fished area), because sampling for maturity is rarely conducted by on-board observers.

APPENDIX B: STOCK ASSESSMENT METHOD

Population Dynamics Model

The dynamics of the population calculated in the SS sub-model are similar to those outlined in Appendix A.

The recruitment in year $y+1$ and cell c for fish of sex g is calculated as

$$N^c_{y+1,0,g} = 0.5\bar{R}_y e^{\varepsilon^c_{y+1}}$$

<div align="right">(B.1)</div>

where $\varepsilon_y \sim N(0,\sigma_r^2)$. $\bar{R}_y$ is the expected mean recruitment in year y, calculated as

$$\bar{R}_y = R_y e^{-b_y 0.5\sigma_r^2}$$

<div align="right">(B.2)</div>

where R_y is the level of recruitment calculated using Equation A.3, b_y is the bias adjustment for year y which

is linearly interpolated using the r4ss package (Taylor et. al 2009) using the equation

$$b_y = 1 - \frac{SE(\hat{\varepsilon}_y)}{\sigma_r^2}$$

<div align="right">(B.3)</div>

where $SE(\hat{\varepsilon}_y)$ is the asymptotic standard error of the estimated recruitment deviation in year y (see Methot

and Taylor (In prep) for details).

Parameter Estimation

The parameters estimated in the assessment model are: unfished recruitment, steepness, pre-catch recruitment

deviations, main recruitment deviations, annual fishing mortality, survey catchability, selectivity parameters

(β_1, β_3 and β_5) for the fishery and survey, and natural mortality, growth-related parameters, and maturity

parameters depending upon the specifications of the simulation scenario. The values for these parameters

(except maturity) are determined by maximizing an objective function that includes contributions from a) the

survey index, b) the catch data and c) the length-frequency and age-frequency data from the surveys and the

fishery. The length-frequency and age-frequency variances are computed from effective sample sizes which

are set equal to the sample sizes used when generating the data. The maturity parameters are fit externally to

the stock using logistic regression.

The survey indices are assumed to be lognormally distributed about the corresponding model quantity. The contribution of the survey indices to the objective function is:

$$L_1 = \sum_y \frac{\left(\log(N_y^{c,obs}) - \log(\hat{N}_y^c)\right)^2}{2\sigma_B^2}$$

(B.4)

where N_y^c is the "observed abundance" generated by the operating model, and $\hat{N}_y^c$ is the model estimate of abundance in cell c and year y:

$$\hat{N}_y^c = q^c \sum_g \sum_{a=0}^{x} \sum_{l=1}^{A_l} \varphi_{a,g,l} S_l^s \left(N_{y,a,g}^c e^{-0.5(M + F_y^c \varphi_{a,g,l} S_l)} \right)$$

(B.5)

where q^c is the median unbiased catchability coefficient for the abundance in cell c, calculated as:

$$q^c = \exp\left[\sum_y \frac{\log(N_y^{c,obs}/\hat{N}_y^c)}{\sigma_B^2} / \sum_y \frac{1}{\sigma_B^2} \right]$$

(B.6)

The contribution of the catch data to the likelihood, L_2, is calculated similarly to equation B.4 where the observed and model estimated survey indices are replaced by those corresponding to the catch. The value of q^c is set equal to 1 to reflect the assumption that the catches are unbiased.

The length composition data from the fishery are assumed to be multinomially distributed. The contribution of the fishery length composition data to the objective function is:

$$L_3 = \sum_y \sum_g n_{y,g}^c \sum_{l=1}^{A_l} p_{y,g,l}^c \log(p_{y,g,l}^c / \hat{p}_{y,g,l}^c)$$

(B.7)

where $n_{y,g}^c$ is the number of fish of sex g for which length measurements were available during year y,

$\hat{p}_{y,g,l}^c$ is the model estimate of the proportion of fish of sex g in length bin l during year y calculated analogously to equation (A.18). The contribution of the survey length composition data to the objective function, L_4, is calculated analogously to equation (B.7) except the model-estimates are calculated using the survey selected numbers $\hat{\tilde{N}}_{y,a,g,l}^c$.

The age data from the fishery are also assumed to be multinomially distributed. The contribution of these data to the objective function is:

$$L_5 = \sum_y \sum_g (n_{y,g}^c / 2) \sum_{i=1}^{A_i} p_{y,i,g,l}^c \log(p_{y,i,g,l}^c / \hat{p}_{y,i,g,l}^c) \tag{B.8}$$

where $\hat{p}_{y,i,g,l}^c$ is the model-estimate of the proportion of fish of sex g in length bin l which are aged to be age i during year y, calculated similarly to equation (A.19).

The contribution of the recruitment deviations to the objective function is given by:

$$L_7 = \frac{1}{2\sigma_r^2} \sum_y \varepsilon_y^2 + n_r \log(\sigma_r) \tag{B.9}$$

where n_r is the number of years for which recruitment deviations is estimated.

When λ^c is allowed to vary over time, it is modeled as an exponential offset from a base parameter:

$$\lambda_y^c = \lambda^c e^{\gamma_y} \tag{B.10}$$

where γ_y is an exponential deviation of λ^c, $\gamma_y \sim N(0, \sigma_\lambda)$ and σ_λ is the assumed standard deviation of the random time series of parameter deviates. The contribution to the objective function for the deviations in these parameters is then:

$$L_8 = \frac{1}{2\sigma_\lambda} \sum_y \gamma_y^2 \tag{B.11}$$

The total negative log-likelihood to be minimized is then:

$$L = -\sum_i L_i \tag{B.12}$$